Developments in Primatology: Progress and Prospects
Series Editor: Louise Barrett

Laura K. Marsh
Colin A. Chapman *Editors*

Primates in Fragments

Complexity and Resilience

Springer

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Editors

Primates in Fragments

Complexity and Resilience

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To JMF, because you keep
on believing in me.
Laura K. Marsh

To all of those individuals who
have dedicated their time and energy to
conservation.
Colin A. Chapman

Foreword

Modern attention to habitat fragmentation and its implications for conservation and science really grew from the theory of island biogeography after it emerged in the late 1960s when many of today's senior scientists were schoolchildren. I vividly recall seeing a copy of MacArthur and Wilson's 1867 book when it arrived for the first time in the Amazon where I was doing my dissertation field work. It ignited a burst of research and by early in the subsequent decade, application of island biogeography to actual island faunas quickly raised implications for the island analogs of forest fragments.

Initially the question that was sweeping in scale, namely, what was better for conservation a single (S) large (L) reserve or (O) several (S) small (S) ones of equal total area (the famous SLOSS debate). While studies on animals with extensive home ranges certainly implied that large areas were important, the debate raged as only one can in the absence of direct data. It led my Brazilian colleagues and me to initiate the forest fragments project in the late 1970s in collaboration with Brazil's National Institute for Amazon Research (Instituto Nacional de Pesquisas da Amazonia; INPA) north of Manaus. An ongoing project in its 34th year, it has shed lots of insights on the important and complex consequences of fragmentation.

In retrospect it is interesting how little appreciated fragmentation was as a major factor in the way humans affect nature, even though fragmentation is close to ubiquitous as the handmaiden to habitat destruction. Surely scientists and naturalists observed some of the effects without necessarily attributing them to fragmentation, but I think it is fair to say that virtually nobody detected the seriousness of its impact is on biodiversity.

Primates, along with birds and woody plants, were and are an obvious group to study to illuminate the consequences of fragmentation. Thinking back on the Manaus project, at a coarse level some of the results were predictable from what is known of diet and home ranges. From that perspective howler monkeys and saki monkeys should (and did) do very well even in 10 ha fragments, while spider monkeys with their 600 ha home ranges found even 100 ha fragments untenable. But those were the simple results; whereas, the biology of the actual animals themselves was affected in more complex ways.

Now, of course, much more is known, both in particular and in general, about habitat fragmentation and primate biology, and this volume makes a significant contribution by assembling professionals from throughout the tropics. Indeed it is notable that this is the second such volume. The first appeared in 2003 also edited by Laura Marsh. Together they are testament to the complexity and richness of the subject of primates and habitat fragmentation and most intriguingly, to how this science has grown and changed over the last three to four decades.

The studies in this volume span the continents where primates are found, and it is clear that the topic is rich and complex. Beyond fragment size, factors of importance include the degree of isolation from other primate populations, the cause of the fragmentation, the type of the intervening habitat (the "matrix") within which the fragments occur (and their spatial configuration), and of course, the other human stresses (like hunting) which are often involved. Disease is an important factor both in terms of wildlife diseases spilling over into human populations, as well as in human diseases and parasites affecting the isolated primate populations. The summary chapter makes the richness and the complexity of the topic of this volume quite clear.

It is encouraging to see the growing understanding of the art and science of restoration of connectivity between fragments in landscapes. While such efforts may seem like just individual efforts here and there (such as in golden lion tamarin habitat in the Atlantic Forests of Brazil), they should be seen as just the first halting—although very important—steps of a much more extensive ecosystem restoration to come. Indeed, it is my fervent hope that this volume will be succeeded by a third one, in which ecosystem restoration research and action are central.

An era characterized by a wave of restoration across the face of the planet is essential for the future of primates and biodiversity and, for that matter, the management of the planet as the living planet that it is. That will be no simple task—no matter of simply standing back and just letting nature recover. Grand and important as restoration at scale is, it will in the end consist of a tremendous amount of detail based on the kind of growing understanding of the complexities of "fragmentation ecology and biology" of the sort these volumes so superbly examine and illustrate. A thriving science of primates and habitat fragmentation is essential to restoration and sustainable development in the tropical forest regions of the world.

Washington, DC, USA

Dr. Thomas Lovejoy
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Economics, and the Environment

Preface

Ten years ago when I put together the first *Primates in Fragments* book, I had great hope for the business of damaged habitats. Even as I was initially gathering the chapters for this second volume—calling in the experts and seeking new authors—I was sure the story we would tell would be one of promise: that somehow our combined efforts over the last decade had made a difference to the lives of primates around the world. Don't get me wrong, in many ways I believe we did have an impact: one of awareness, if nothing else, that Fragmentation Science is its own discipline and that primates that experience these landscapes have a different skill set than those that live in continuous habitat.

The first volume, subtitled "Ecology and Conservation," was meant to show promise and movement in the field. This volume, "Complexity and Resilience," is meant to show our maturity in the field. We know there are issues that primates and the people who live with them face. We know there are challenges to conservation and the study of these animals. We also know both primates and people are managing in many cases in very bleak circumstances. Every decade brings a new host of stories about primates in fragments that we are eager to tell, as many species' very existence depends upon us paying attention to them, even in the worst of habitats.

Compared to the first *Primates in Fragments*, where we had 51 authors from 10 countries and 4 sections with 21 chapters, we have 104 authors from 23 countries and 7 sections with 34 chapters in this volume. In the first volume, there was only one chapter on genetics, seven on population dynamics, seven on behavioral ecology, and five on conservation and management. In this volume we branch out. We had far more genetics chapters than we could include, but settled on six that discuss not only advances in genetic work on primates in disturbed habitats, but also diseases and parasites. New to this volume are the Long-Term and Regional Studies and Endemic, Endangered, and Nocturnal sections. The latter is of particular relevance since it is likely in the next decade, we will see more and more chapters on endangered primates in fragmented landscapes. Several things have become clear in the last 10 years: more people are studying primates in damaged habitats, more people acknowledge fragmentation as distinct science, and more people have a concern for them.

No collected work is ever perfect, and we certainly have some holes. For one, we do not have any chapters on apes this time, and in the section on long-term studies some obvious sites are missing. But unlike the introductory nature of the first volume, we go deeper in this volume into topics like climate change, disease, and survivability. This time, it starts and ends with conservation because without a collective focus on habitat loss in general and how best to mitigate it, our forest-dwelling primate species are doomed.

I am grateful that the first *Primates in Fragments* has had over 500 citations for all of the chapters combined, has been used by universities and classes as a text book, and has been a go-to reference for students all over the world. And I am even more grateful that the first volume will be available electronically with this one, so that even more people can get a good, inexpensive resource that can be made available in even the remotest campuses.

When I was 18, I was standing in a rainforest before I ever knew what one was. In high school in southern California, our biology texts had a final chapter in them called "Environment." It in part had two paragraphs and one photo on each of the major biomes—including rainforest—and a paragraph about conservation. We never got to that chapter. I always wanted to read the texts that started with environment as a cohesive unit, or that started with conservation. Now we have two excellent volumes where students can be informed about the current tropical landscape. It is my hope to everyone reading about forest fragments for the first time that you understand what you are getting into before you are standing in one.

I have to thank all of the contributing authors and especially my co-editor Colin A. Chapman without whom we would not have this finished book. He very consistently and enthusiastically nudged me to keep going on it and helped mightily with the editing of individual chapters.

We are also two of the first in the new generation of authors and editors of primate books to put our money where we say our conscience lies: both Colin and I will donate all of our personal proceeds from the sale of this book to the International Primatological Society's Conservation Fund. We challenge other authors in our field to do the same.

Santa Fe, NM, USA Laura K. Marsh

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Section I
Introduction

Chapter 1
Because Conservation Counts: Primates and Fragmentation

Laura K. Marsh

Introduction

Books about wild primates are plagued with opening paragraphs about rates of deforestation. There are new estimates of forest loss popping up all of the time, making the "real" determination of forest coverage difficult to effectively interpret. However, it is increasingly clear that these rates mean a variety of things pending the definitions used. When primatologists speak of fragmentation, we typically mean forest within the tropical dry to humid biome and the resultant fragmentation–matrix combinations that dominate tropical landscapes. Seemingly simple enough, but Lund (2008) found more than 800 different definitions for forests and wooded areas in use around the world, with some countries adopting several definitions for the same patch of land. Thus, instead of beginning with the various predictions of loss, a closer look at what remains is worthwhile.

Closed Forests

Closed forest is not synonymous with continuous forest (c.f., Marsh et al., this volume, Chap. 34). The United Nations Environment Programme/Food and Agriculture Organization (UNEP/FAO) defined closed canopy forest (all forests, not just tropical) as forest that has at least 40 % of its canopy interlocking (UNEP 2001). According to their report as of 1995, 21 % of land in the world contained closed forests with 81 % found in 15 countries, 12 of those tropical, with Russia, Canada, and Brazil containing 49 % of all closed forests. In 2006, the UNEP used this definition for forests: 10 % of canopy interlocking with a 0.5 ha minimum land cover, and

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a minimum tree height of 5 m (FAO 2006)—a definition that clearly includes fragments. However, for any country reporting per the Kyoto Protocol (starting in 2005), there is a sliding scale for values: 0.01–1.0 ha for minimum area, 2–5 m for minimum tree height, and 10–30 % for minimum crown cover. Whereas the FAO maintains true "closed forest" as 40 % crown cover, forest with 10–40 % is considered either open or closed, depending on the connectivity. In general, the UNEP/FAO does not take into account agroecosystems or mono-cropped forests, which can be important to primates living within or in proximity to these systems (Marsh 2003a).

The percentage of forests that are actively being protected varies greatly by country, and even report. Only 9 % of all global closed forests have been accorded some sort of protection (FAO 2001). Venezuela is the highest with 62 % of its forests under federal protection. Other countries with comparatively higher amounts of protected forests are: Bolivia (29 %), Colombia (25 %), Indonesia (20 %), Brazil (17 %), and India (12 %). At the lower end of the scale is the Democratic Republic of Congo with 9 % and the USA at 7 %. Although not tropical, the USA is far worse at protecting forest resources than many countries in the tropics (FAO 2001). Almost more important than simple percentages of forest protected is the human pressures on the environment. For instance, India has 12 % of its forests under protection, but has 2,697 people per hectare nationwide versus the DR Congo with only 9 % of its closed forests protects and only 160 people/ha (FAO 2001). These numbers have of course increased in the last decade, but are staggering regardless.

In general, the world's closed forests have survived because: (1) particular areas are economically not worth exploiting as they lack sufficient quality or quantity of commercially valuable species, (2) particular areas are located in remote or inaccessible areas, (3) particular areas have been protected as national parks and sanctuaries, (4) the forest is valued over below-ground resources, and/or (5) there is a local community willing to protect the area for heritage rights, religious reasons, ecotourism, or by law. All of these vary depending on the cultures and governments in power. All habitats are negotiable in terms of use for profit or development, and their fate rests on politics. Furthermore, studies are now showing that even these fundamental reasons for forests to remain standing are increasingly under threat (Evans et al. 2012).

The rapid destruction of tropical forests imperils global biodiversity more than any other contemporary phenomenon. Laurance et al. (2012) reviewed 60 protected areas throughout the tropics to determine their functionality in terms of "ecosystem health" and their ability to maintain the biodiversity they were set up to preserve. They concluded that about half were meeting the needs of the species within their boundaries, but that the other half were "experiencing an erosion of biodiversity that is often alarmingly widespread taxonomically and functionally." The primary culprits are familiar to those working in fragmented forest regions: habitat disruption, hunting, and forest product exploitation. These were the strongest predictors of declining reserve health. Changes inside reserves strongly mirrored effects taking place in the surrounding matrix, so much so, the authors suggested that the fates of the protected forests were intimately tied to the surrounding habitat. The best way to prevent further loss of species within protected areas is to develop effective buffer zones, something that has been proposed repeatedly since the 1980s (c.f., Marsh

2003b). Understanding what forest remains, whether closed, open, fragmented, continuous, or protected, helps us determine how to improve conservation such that cumulative effects do not continue to undermine our efforts.

Cumulative Effects

Those who work in tropical fragmented ecosystems can easily cite the ever-expanding litany of disturbances that impact not only the remaining primate habitat but also humans within the matrix. Effects like logging, non-timber forest product harvesting, fires, hunting (for subsistence), bushmeat (for market sales), roads, oil exploration and extraction, land tenure disputes, poverty, war, hydroelectric dams, pet and trophy trade (e.g., freshwater fish, butterflies, and orchids, especially), poaching for medicinal use (plant and animal), "pest" extermination (e.g., crop raiders), firewood gathering, charcoal, tourism, small- and large-scale mining, agriculture, and ranching all amplify each other. Rarely does one impact occur without a ripple of multiple disturbances.

An example of both cumulative deforestation effects and the success or failure of protected areas within a complex agroecological matrix is a new study that quantifies across South America's biodiversity hot spots' indirect impacts on deforestation from coca cultivation for the global cocaine market. Davalos et al. (2011) studied coca cultivation regions in the southern Colombian Andes, Choco, and Amazon between 2002 and 2007. The authors conducted landscape-level analyses of forest conversion and revealed that forest with proximity to newly developed coca plots, and thus a greater proportion of an area planted with coca, increased the probability of forest loss. The principal reason was the rural population's additional use of forest products in the remaining non-protected forest: "Neither eradication nor coca cultivation predicted deforestation rates across municipalities. Instead, the presence of new coca cultivation was an indicator of municipalities, where the increasing population led to higher deforestation rates." Conversely, the authors showed that designating protected areas successfully reduced forest conversion of those plots in coca-growing regions. They concluded, like in all regions throughout the tropics where poverty demands are higher than forest protection, that the manner in which a rural population is developed makes all of the difference. They maintained that conservation in Colombia's vast forest frontier, which overlaps with its coca frontier, requires a mix of protected areas and strategic rural development on the front-end to succeed (Davalos et al. 2011). In terms of primate conservation, some of our efforts are best used toward understanding the cumulative drivers to deforestation and working at a management level with the people on a landscape scale, rather than only on understanding the remaining forest.

While illegal drug growers in Colombia are respecting protected areas, indigenous people living within critically endangered primate habitat in Madagascar, a country where 90 % of its forest has been lost, are not. In another case of "hidden" effects, bushmeat hunting is on the rise in Madagascar—even in regions where the lemurs were respected under tribal consumption taboos or "fadys" (Jenkins et al. 2011).

Jenkins et al. (2011) suggest that hunting of protected species in eastern Madagascar is “increasing due to rapid social change as appetites for meat increases and traditional taboos protecting the species, especially lemurs, become less powerful.” The authors observed that young men in particular have more available cash and leisure time due to the transition from subsistence farming to panning for gold. As a result, they spend more time than ever before in bars eating fried meat snacks with their drinks. Lemur hunting appears to have increased to supply this new market even among those who cite their knowledge of fadys on *Indri*, for instance. According to the authors, “The power of the taboo is declining under pressures of globalization and human mobility.” Cumulative insults like these can amass over time into what is now being described as creeping environmental changes.

Creeping Environmental Changes

There are a growing number of researchers working in the field of creeping environmental changes, in particular with regard to global diplomacy (http://www.disasterdiplomacy.org/cep.html), which in turn impacts environmental conservation. Glantz (1994, 1999) and Kelman (2006) defined creeping environmental changes as incremental changes in conditions which accumulate to create a major catastrophe or crisis, that are apparent only after a threshold has been crossed. Such as changes that significantly impact all spatial scales, frequently crossing borders, making them useful cases for disaster diplomacy. These are human interactions with the natural environment that have a slow onset, advance incrementally, and eventually pass a threshold that quickly leads to changes in the environment, and then ultimately, to society. The ones most familiar to primatologists are tropical deforestation, biodiversity loss, and climate change, but others include acid rain, stratospheric ozone depletion, desertification, mangrove destruction, soil erosion, water pollution, overfishing, coral bleaching, and more localized impacts, such as groundwater contamination by leaky landfills (FAO 2012). All of these began as something simple to manage and were correctable in the small scale, but can expand to be encompassing and cumulative if left unattended.

Socioeconomic drivers are some of the most insidious underlying reasons for habitat degradation (FAO 2012). Critical socioeconomic factors outlined by the United Nations Intergovernmental Forum on Forests include (1) poverty, (2) lack of secure land tenure patterns, (3) inadequate recognition within national laws, and jurisdiction of the rights and needs of forest-dependent indigenous and local communities, (4) inadequate cross-sectoral policies, (5) undervaluation of forest products and ecosystem services, (6) lack of participation, (7) lack of good governance, (8) absence of a supportive economic climate that facilitates sustainable forest management, (9) illegal trade, (10) lack of capacity, (11) lack of an enabling environment at both national and international levels, and (12) national policies that distort markets and encourage the conversion of forest land to other uses (IFF 2000). Understanding the baselines that have layered creeping and compounding environmental issues may help us to better plan for the future of primates living in fragments.

Early intervention on any one of the environmental issues would avoid expensive local and global environmental and social costs in the long run. In regions where deforestation has taken costly tolls on a government, say from excessive flooding of downhill towns (e.g., Catemaco, Mexico hill deforestation for tobacco, pers. obs.), it might be possible to convince policymakers and stakeholders to work toward front-end interventions with the goal of not saving habitat, but of saving the local economy from having to backtrack to correct outcomes if these changes are left unmanaged. Action is not likely to be taken unless scientists can make a clear connection between a particular change and an important consequence of this change (FAO 2012). The challenge then for primatologists working in disturbed habitats is to collaborate with country professionals and officials to mitigate and identify potential future changes and underlying socioeconomic issues before they impact primates and the people living with them.

Global Carbon

We discuss in the final chapter climate change as a landscape-level impact to primates. But what about global carbon specifically as it relates to primate conservation? Tropical deforestation is finally getting more attention with respect to global carbon emissions; however, results are conflicting (Drake et al. 2003; Harris et al. 2012). Baccini et al. (2012) determined that deforestation contributed up to 6–17 % of carbon dioxide emissions, and that 229 billion tons of carbon are currently stored in standing rainforest. These authors found that forests in the Americas stored about 51 %, Africa 28 %, and Asia 20 % and that net emissions from deforestation from 2000 through 2010 amounted to 1.14 billion tons of carbon per year, suggesting that deforestation accounted for roughly 13 % of greenhouse gas emissions between 2008 and 2010 alone.

Remaining forest, whether closed or open, fragmented or continuous, is starting to be valued as carbon repositories, and the subsequent deforestation of these resources counts toward total carbon emissions, particularly under the post-Kyoto U.N. directed Reduced Emissions from Deforestation and Degradation (REDD or REDD +) framework (Lu and Liu 2012). Payments to landowners for not deforesting their land so that it is maintained as carbon storage “sinks”, are swiftly becoming the most lucrative tool available for tropical forest conservation purposes (FAO 2012). Creating an economic incentive for retaining standing forests regardless of size has been in discussion for decades among conservation biologists, with better tech for determining actual on-the-ground carbon values of tropical forests and ever-pressing policies to mitigate global climate change, the time may be ripe for adding on biodiversity needs, including those of primates to the REDD dispersements. However, it is still too early to know if these payouts will translate to real on-the-ground change in forest use by local communities (Griscom et al. 2009; Lund et al. 2009; Virgilio et al. 2010), particularly with respect to use of the fauna, including primates (Kapos et al. 2008).

In many cases, governments have excellent laws to combat environmental crimes "on the books," but very little to show for them in terms of on-the-ground enforcement. Environmental crime is a top priority, not only because of the deforestation itself, but also as a means for controlling the rate of fragmentation and global climate gas emissions (Nellemann 2012). It has long been a challenge for conservation biologists and primate scientists to enforce or to seek enforcement of wildlife protection laws in any given country. However, a newly established International Consortium on Combating Wildlife Crime (ICCWC), chaired by the CITES Secretariat comprising INTERPOL, the United Nations Office on Drugs and Crime (UNODC), the World Bank, and the World Customs Organization (WCO), has been created that "provides the entire enforcement chain—customs, police, and justice—a substantial new commitment to the sharing and coordination of a comprehensive international effort to help combat wildlife crime, including illegal logging" (Nellemann 2012). The success of this organization will rely heavily on constant and determined commitment from governments, society, and the private sector—which includes on-the-ground national and international researchers, students, and locals.

Compounding Conservation

The accumulation of effects on any given remaining habitat is cause for great alarm for those working with primates in fragments. If we can compound impacts, then certainly conservation can be cumulative as well. We all long for the days when the cry of "sustainable use" felt like it was enough, and that it was the right track for maintaining forests and the wildlife within them. And while there are cases where sustainable use practices do make a difference, it is this combined front that must be addressed, starting with how we perceive our world. We desperately need to know the impacts of human actions on the primates we study. Once, we believed that the behaviors of source country people were fixed, and that as cultural outsiders we should not tamper with their ways except to provide education through workshops or by other means aimed at the children or degradation perpetrators (e.g., hunters). But with smart phones in the hands of even the most rural villagers the world over—the connection to cultural ideas is merging. And while it is important for every culture to retain their core values in whatever manner that is significant to them, there is a shift toward global environmental acculturation that is as important to primate conservation as it is to global diplomacy.

We called for human behavioral changes in the last Primates in Fragments volume (Marsh 2003a), and now, so have many experts around the world: "Behavioural change is at the core of many environmental problems. Behavioural transformations support more effective systems of governance and help build human capacities for change. Such changes are also vital in addressing many other issues, from the depletion of water resources by overconsumption, to the mitigation of climate change by modifying mobility patterns and life-styles" (FAO 2012). The support of behavioral change is not new per se, and it has been part and parcel of environmental and health policies for decades. Yet, Lucas et al. (2008), Crompton and Kasser (2009), and others believe that previous efforts to encourage sustainable behavior were not sufficient. The much desired sustainability transition is less likely, or more difficult, without a substantial transformation in modern lifestyles, from the rich industrialized countries to the rapidly developing megacities in the South (FAO 2012). Imagine a world where we all—scientists, politicians, rural and urban dwellers—have the same goals for the environment on behalf of the global community. It is the pursuit of resilience, the capacity to deal with the interplay of gradual or rapid change on a daily basis, that will result in our comprehensive perspectives to reinvent policies and governance to foster stewardship of our future, as humans in collaboration with the biosphere (FAO 2012). It is this kind of goal we should strive for in our work, particularly with primates in fragmented habitat regions.

Something I am fond of saying is: "Business professionals and politicians got their MBAs and JDs because they hated science. We got our Ph.D.s in science because we hated business and politics." The communication gap is something that is no longer unknown to international agencies working toward environmental stewardship. We need to establish one of the most basic bridges—the one between science and everybody else. UNEP (2012) says, "The task of strengthening or rebuilding bridges between science and policy requires a new look at the way science is organized and how the science-society-policy interface can be improved." Primate scientists, particularly those working in fragmented habitats, should become even stronger leaders in the integration of scientific information for accessibility by those who determine conservation status and the public.

And Finally…

We outline many paths forward in our final chapter, but I would like to offer a few, if simplistic, conservation "truisms" we must understand as a place we are starting from, and as a path forward to change in the future. These are detailed in Marsh (2007).

- Conservation has little to do with the species or ecosystems we are trying to protect. It has everything to do with people. Considering people is critical for every project involving primates in fragments.
- Conservation at its very base is controlled by money such as multinationals, poverty, and debt. Species are endangered because humans exploit their habitats for human needs, often in a cash ecenomy.
- Conservation outcomes are determined by those in power, such as governments, politicians, and landowners, and conservation policies can always be reversed.
- Conservation is not a universal ideology. Many cultures do not embrace conservation concepts the way scientists do or vice versa.
- Global conservation is not a priority for those with low- or poverty-level incomes.
- You are excluded from vital information as a researcher if you are not a member of that culture.

- All cultures are driven to create the highest quality of life for themselves that they can. This may include hunting and eating the species you study. Since the cornerstone of every culture is food, we must understand how best to achieve conservation goals that satisfy everyone in the long term. And that may mean coming up with new ideas, not supporting old "sustainable" ones.
- It's all fragments. It's all conservation. It's all we have.

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Chapter 2
Assessing Habitat Fragmentation Effects on Primates: The Importance of Evaluating Questions at the Correct Scale

Víctor Arroyo-Rodríguez, Eddaly Cuesta-del Moral, Salvador Mandujano, Colin A. Chapman, Rafael Reyna-Hurtado, and Lenore Fahrig

Abstract Forest-dwelling mammals such as primates could be particularly vulnerable to habitat fragmentation; however, the definition and quantification of fragmentation have varied considerably among studies. This has resulted in contradictions and thus results are difficult to interpret and compare. To encourage a consistent and more precise use of the term "habitat fragmentation," we reviewed 100 fragmentation studies on primates to quantify how fragmentation effects are assessed. We advocate that habitat fragmentation is a landscape-scale process that involves both loss and the breaking apart of habitat. Hence, independently analyzing both effects is necessary to assess the effects of the breaking apart of habitat while controlling for habitat loss (fragmentation per se). This needs to be done through landscape-scale studies (that is, using landscapes as the independent unit of observation); however, fragmentation studies on primates are typically at the single fragment scale, often with a single continuous forest used for comparison. We suggest that primate responses at the fragment scale can vary dramatically in landscapes with different habitat amounts

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and configurations. In this review we provide clear and consistent terminology to help future studies to accurately assess the effects of fragmentation on primates and to help to form a body of literature where comparisons among studies are possible?

Introduction

Habitat loss represents a significant threat to biodiversity and many ecological processes (Andrén 1994; Bender et al. 1998; Fahrig 1999, 2003). In contrast, habitat fragmentation per se, or the breaking apart of habitat while controlling for habitat area (sensu Fahrig 1999, 2003), has highly variable effects, which are sometimes positive and sometimes negative, depending on the species and the way in which fragmentation is measured (Henle et al. 2004; Ewers and Didham 2006; Fahrig 1999, 2003). The number of fragmentation studies has dramatically increased in past decades (Fig. 2.1); however, the term habitat fragmentation has been used in variable ways. This has resulted in contradictions and results that are difficult to interpret (Fahrig 2003; Lindenmayer and Fischer 2007).

Forest-dwelling mammals, such as primates, may be particularly vulnerable to habitat fragmentation (Chapman and Peres 2001; Arroyo-Rodríguez and Dias 2009). Despite the number of primate fragmentation studies (Fig. 2.1), the ways of conceptualizing and measuring fragmentation effects have been highly variable (Arroyo-Rodríguez and Mandujano 2009). This has led to conflicting conclusions from different studies about fragmentation effects on the same primate species (Arroyo-Rodríguez and Dias 2009). To encourage a consistent and more precise use of the term "habitat fragmentation," we first present what we view to be a useful description of what habitat fragmentation is and how it should be measured. Second, we present results from a search of the SCOPUS (©Elsevier, The Netherlands) database on 9 June 2010 for original papers containing "primate," plus "habitat fragmentation," "forest fragmentation," or "landscape fragmentation" in the title,

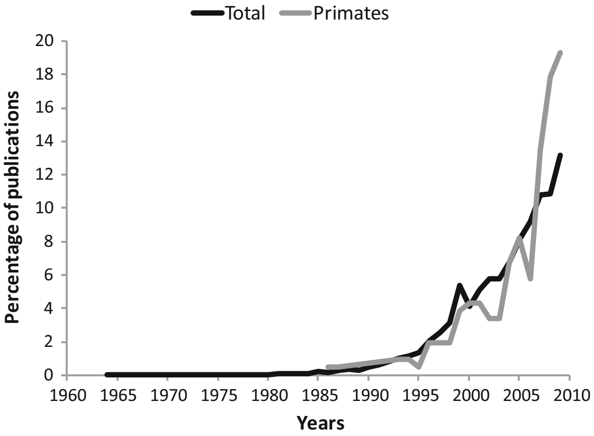

Fig. 2.1 Percentage of publications found in the SCOPUS database up to the end of 2009 containing "habitat fragmentation," "forest fragmentation," or "landscape fragmentation" in the title, abstract, and/or keywords (*black line*: total $n = 8{,}584$ papers). The same search was then conducted with the additional term "primate" (*grey line*: primates $n = 227$ papers)

abstract, and/or keywords. This search revealed a total of 227 papers. We randomly selected 100 of these papers and identified the ways in which habitat fragmentation effects are being assessed.

Evaluating and Measuring Habitat Fragmentation

Habitat may be broadly defined as "the range of environments suitable for a given species" (Hall et al. 1997). For primates this generally refers to broad vegetation types, such as tropical rain forest and tropical dry forest (Arroyo-Rodríguez and Mandujano 2009). Because native vegetation is important for many species, numerous researchers have equated "habitat" with native vegetation (Fischer and Lindenmayer 2007; Arroyo-Rodríguez and Mandujano 2009).

Habitat fragmentation is a landscape-scale process in which continuous habitat is broken apart into smaller pieces (fragments) scattered within a matrix of non-habitat. This implies the loss of habitat and its subdivision (fragmentation) into a variable number of fragments (Fahrig 1999; McGarigal and Cushman 2002; Fahrig 2003). However, habitat loss can occur without the subdivision of habitat (Fig. 2.2), and therefore, we advocate that it will be valuable for researchers to consider analyzing the independent effects of habitat loss and fragmentation to determine whether it is the overall loss of habitat or the separation of habitat into smaller pieces (hereafter termed "habitat fragmentation per se"; sensu Fahrig 1999, 2003) that actually causes negative effects on primates. This can only be done through landscape-scale studies, that is, by using landscapes as the independent units of observation (McGarigal and Cushman 2002; Fahrig 2003; Arroyo-Rodríguez and Mandujano 2009). By using fragments as the unit of analysis (hereafter named "fragment-scale studies"), researchers cannot differentiate between the effects of the habitat loss and the breaking apart of habitat, as both processes can result in smaller and more isolated fragments (Fahrig 2003; Fig. 2.2).

Most fragmentation measures (e.g., mean fragment isolation, total amount of edge, number of fragments) are strongly related in a nonlinear manner to the amount of habitat within a landscape, in such a way that below a certain threshold of habitat area, small changes in the extent of the habitat lead to big changes in these measures (Neel et al. 2004). For this reason, it is often difficult to determine the separate effects of habitat loss and fragmentation. For instance, studies with plants (Arroyo-Rodríguez et al. 2009) and animals (Andrén 1994; Pardini et al. 2010) suggest that species diversity in a fragment of a given size may vary in landscapes with different habitat amount. Actually, the effects of fragmentation per se are thought to be relatively more important below certain thresholds of habitat amount remaining in the landscape (Andrén 1994; Fahrig 1997, 1998; With and King 2001). Below this threshold of habitat amount, the probability of persistence of populations drops significantly. Given the crucial management implications that these thresholds have for primate conservation, we urgently need to analyze the response of primates under different scenarios of habitat loss and fragmentation. This cannot be done through fragment-scale studies; it requires studies at the landscape scale.

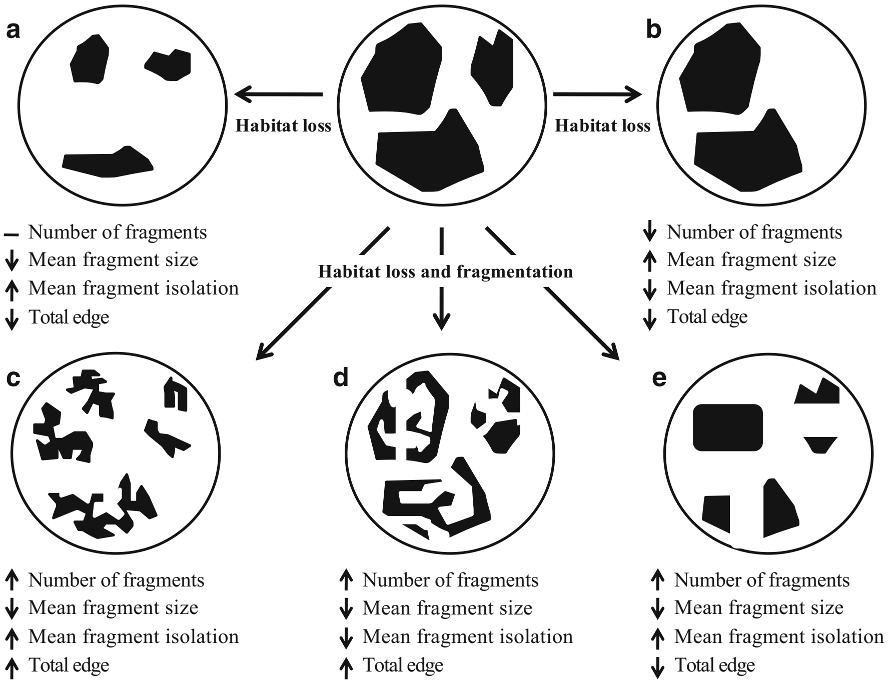

Fig. 2.2 Some (not all) of the effects of habitat loss on landscape spatial pattern. Habitat loss alone (A and B) can result in higher or lower mean fragment size and either higher or lower mean fragment isolation. The increase of the number of fragments with habitat loss and habitat fragmentation (C, D, and E) can lead to contrasting landscape spatial patterns (for instance, higher or lower mean fragment isolation and total habitat edge), but in all cases mean fragment size decreases. Other potential changes in landscape spatial pattern expected from habitat loss and fragmentation can be found in Fahrig (1999, 2003)

Additionally, the relationship between fragmentation and habitat configuration is very intricate (Fahrig 2003). The fragmentation process results in the reduction in habitat amount, increase in the number of habitat fragments, and decrease in sizes of habitat fragments (Fig. 2.2). However, other spatial attributes, such as total habitat edge and mean fragment isolation, can either increase or decrease with fragmentation (Fig. 2.2). Although the number of measures of fragmentation is huge (>40 measures: e.g., number of fragments, fragment density, total edge, edge density, landscape shape index, largest patch index; see McGarigal et al. 2002), researchers commonly measure only one effect (fragment size is the most frequent), whereas others assess two or three effects, but not more (Fahrig 2003), and rarely recognize the interrelationships among measures of fragmentation. As stated by Fahrig (2003, p. 492): “this leads to ambiguous conclusions regarding the effects of habitat configuration on biodiversity … and … makes results difficult to interpret.” Also, as each aspect of fragmentation could potentially affect primates in different ways (Arroyo-Rodríguez and Dias 2009; Arroyo-Rodríguez and Mandujano 2009), using one or few of these effects results in biased assessments of the general effects of habitat fragmentation on primates. For example, both abiotic conditions, such as temperature, humidity, and wind speed, and biotic conditions, such as population density, and species richness, can be altered near habitat edges: the so-called edge effects (Saunders et al. 1991). Edge effects can lead to vegetation changes, particularly in smaller and more irregularly shaped fragments (Laurance et al. 2000; Hill and Curran 2003; Arroyo-Rodríguez and Mandujano 2006), which can affect the abundance of the most frequently eaten food plant species for primates, reducing the quantity and quality of food sources available to them (Arroyo-Rodríguez and Mandujano 2006; Tutin 1999). Although these vegetation changes can significantly impact primates (population distribution: Arroyo-Rodríguez et al. 2007; population density: Worman and Chapman 2006; feeding behavior: Dunn et al. 2009), studies reporting edge and/or vegetation effects as synonymous of "fragmentation effects" are misusing the term "fragmentation," as total forest edge is strongly related to the amount of remaining forest in the landscape (Fahrig 2003). Furthermore, all of these processes have only been evaluated at the fragment scale, and it is unclear (i.e., not tested) whether they can be extrapolated to the landscape scale (McGarigal and McComb 1995).

Assessing Habitat Fragmentation Effects on Primates

Database

The 100 reviewed papers were published in 24 journals, but 84 % of these papers were found in 11 journals, almost half (47 %) in *American Journal of Primatology*, *International Journal of Primatology*, and *Primates* (Fig. 2.3a). These studies were conducted in 22 countries, but 89 % were from 11 countries, with Mexico, Brazil, and Madagascar being the best represented (Fig. 2.3b). They include 85 species from 35 genera, with 9 species (11 %) in ≥ 5 papers, *Alouatta palliata* being the most studied (Fig. 2.3c). In contrast, 44 species (52 %) were studied in only one paper. Primate genera followed a similar pattern: few (11 genera, 29 %) appeared in ≥5 papers, with *Alouatta* being the most studied, appearing in 38 papers (Fig. 2.3d). In contrast, 19 genera (50 %) were present in ≤2 papers, with *Galago*, *Lagothrix*, *Lemur*, *Leontopithecus*, *Lophocebus*, *Nomascus*, and *Nycticebus* studied in only one paper each.

Goals in Fragmentation Studies with Primates

Despite the fact that we limited our literature search to original papers containing the word "fragmentation" in the title, the abstract, and/or keywords of the paper, we found that approximately one-third (34 papers) of the 100 reviewed papers did not aim to explicitly or implicitly assess the effects of habitat fragmentation on primates.

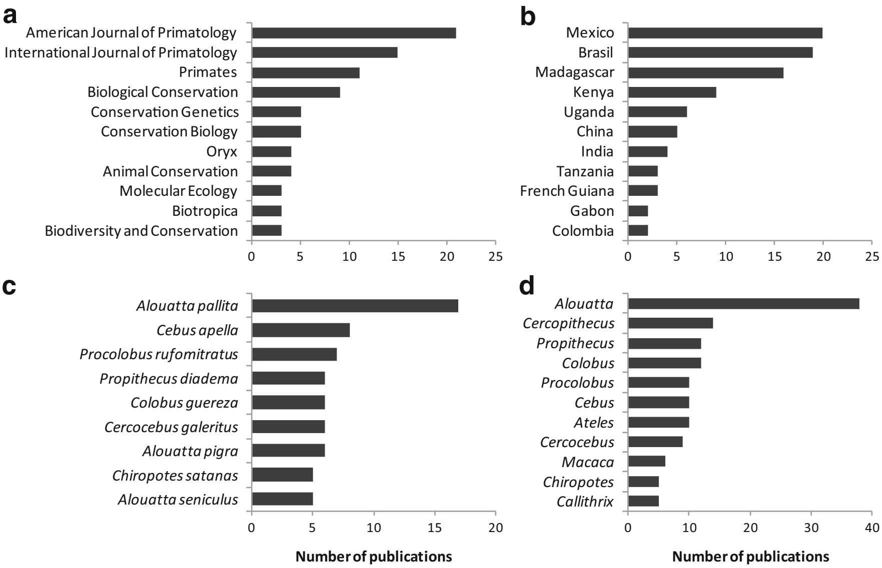

Fig. 2.3 Best represented journals (**a**), study countries (**b**), study species (**c**), and genera (**d**) in a review of 100 randomly selected papers from a SCOPUS search of papers containing the word "primate" and "habitat fragmentation," "forest fragmentation," or "landscape fragmentation" in the title, abstract, and/or keywords. The search resulted in a total of 227 papers from 1986 to 9 June 2010

Although most of these studies (28 of 34 papers) were performed in fragmented landscapes, their objectives were highly variable, from "investigating the effects of anthropogenic habitat degradation on group size, ranging, fecundity, and parasite dynamics" (Mbora et al. 2009) to "assessing habitat use of the monkeys in a series of succession habitats following clear-cutting" (Li 2004). In other words, they were not actually aimed at studying fragmentation effects directly. Hereafter, we focus our analyses and discussion on the remaining 66 papers which aimed to explicitly or implicitly evaluate the effects of habitat fragmentation on primates.

Experimental Designs

Three of the 66 studies (4 %) analyzed groups or populations in different geographical localities, without specifying the habitat configuration of the landscapes (for example, forest cover in the landscape, number of fragments, fragment size, fragment isolation, total forest edge) in which monkeys were studied (Morin et al. 1993; Bergl et al. 2008; Parker et al. 2008). However, the remaining 63 papers specified the habitat configuration of the landscapes in which monkeys were studied, and used forest fragments, islands, and/or continuous forests as the units of observation,

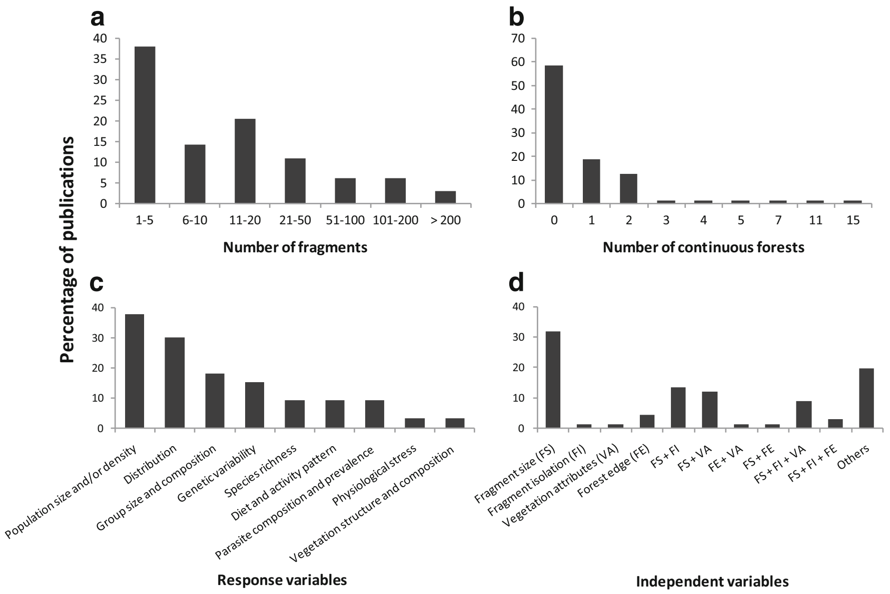

Fig. 2.4 Number of fragments (**a**) and continuous forests (**b**), response variables (**c**), and factors (**d**) measured in a review of 66 papers which aimed to assess the effects of habitat fragmentation on primates. The percentage of papers per category is indicated; however, as three studies analyzed primates in different geographical localities without specifying the habitat configuration of the landscapes in which monkeys were studied, the percentages in cases (**a**) and (**b**) are based on 63 papers (not 66)

that is, all were fragment-scale studies (Fig. 2.4a, b). From these studies, 13 (21 %) only described the study fragment(s)/island(s)/continuous forest(s), and did not give information on the habitat configuration surrounding the study sites, that is, they did not specify the habitat configuration of the landscape in which the study sites were imbedded (Lehman et al. 2006; Rangel-Negrín et al. 2009). Most of the studies that specified the habitat configuration of the landscape in which the sites were imbedded (50 papers) were performed in only one landscape (48 papers, 96 %; for example, Chapman et al. 2007; Silva and Ferrari 2009); one paper investigated two landscapes (Pope 1998); and another analyzed three landscapes (Arroyo-Rodríguez et al. 2008).

The average (± SD) number of study fragments/islands in fragment-scale studies (63 papers) was 48.8 ± 190 (median = 6 fragments), ranging from one fragment (5 papers; for instance, González-Solís et al. 2001; Lehman et al. 2006) to 1,502 fragments (Zhang et al. 2010; Fig. 2.4a). Thirty-six (57 %) papers focused their study on forest fragments/islands, whereas 27 papers (43 %) compared forest fragments with 1 (12 papers; for example, Chapman et al. 2007; Dausmann et al. 2008) to 15 (Michalski and Peres 2005) continuous forests (Fig. 2.4b).

Response Variables and Factors Assessed

The response variables were highly variable (Fig. 2.4c), including population size and/or density (Wahungu et al. 2005), distribution (Arroyo-Rodríguez et al. 2008), group size and composition (Umapathy and Kumar 2000), genetic variability (Mbora and McPeek 2010), species richness (Harcourt and Doherty 2005), diet and activity pattern (Dunn et al. 2009), parasite composition and prevalence (Gillespie and Chapman 2008), physiological stress (Martínez-Mota et al. 2007), and vegetation structure and composition (Stevenson and Aldana 2008). Some papers assessed more than one of these response variables. For example, Michalski and Peres (2005) examined the species richness and distribution of primate and carnivore assemblages in a Brazilian fragmented forest. Onderdonk and Chapman (2001) assessed variation in species richness, population size, and group composition and structure in Uganda.

The factors measured (predictor variables) were also highly diverse, but the most common were fragment size (47 papers, 71 %; for example, Harcourt and Doherty 2005), fragment isolation (18 papers, 27 %; Estrada and Coates-Estrada 1996), vegetation attributes (16 papers, 24 %; Asensio et al. 2007), and forest edge (5 papers, 8 %; Lehman et al. 2006) (Fig. 2.4d). Twenty-six papers (39 %) measured only one of these effects, with fragment size the most frequent (Fig. 2.4d). Nineteen papers (29 %) included two factors: fragment size and isolation (Estrada et al. 1999), fragment size and vegetation attributes (Singh et al. 2002), fragment size and forest edge (Quemere et al. 2010), or forest edge and vegetation attributes (Mbora and Meikle 2004). Finally, eight papers (12 %) included three factors: fragment size, fragment isolation, and vegetation attributes (Cristóbal-Azkarate et al. 2005) or fragment size, fragment isolation, and forest edge (Arroyo-Rodríguez et al. 2008; Fig. 2.4d).

Conceptual and Methodological Problems

The conceptual and methodological problems in papers aimed to evaluate the effects of habitat fragmentation on primates are that the studies (1) lack consideration of landscape context, (2) are conducted only at the fragment scale, (3) use small sample sizes, and (4) consider only one or a few measures of habitat fragmentation.

Lack of Consideration of Landscape Context

To fully assess habitat fragmentation effects on primates it is necessary to quantify (e.g., using a geographical information system) the habitat configuration in the landscape(s), but as stated above, there is a lack of this type of information in 25 % of the studies we reviewed. Studies in fragmented landscapes should consider that what happens at the fragment scale may vary in landscapes with different habitat configurations and that it can be affected by processes that interact at various spatial and temporal scales (Andrén 1994; Fahrig 2003; Arroyo-Rodríguez et al. 2008, 2009). Information on the habitat configuration in the landscape, such as forest cover, connectivity, number of fragments, fragment size, and/or total forest edge surrounding the study sites, is necessary to assess processes operating at the landscape scale (neighboring effects, source–sink dynamics, landscape supplementation, landscape complementation: Dunning et al. 1992; metapopulation dynamics: Hanski 1999). For example, the neighboring effect predicts that species abundance in a particular fragment should be more strongly affected by characteristics of contiguous fragments than by those of more distant parts of the landscape. Source–sink dynamics also predicts that there can be individual movements from relatively productive fragments (sources) to less productive fragments (sinks) (Pulliam 1988). Thus, to understand which factors explain primates' responses to the characteristics imposed by particular forest remnants, and to test the effect of habitat loss and/or fragmentation on primates, it is necessary to describe the landscape spatial context surrounding the sites.

Conducting Studies Only at the Fragment Scale

All reviewed papers were at the fragment scale (i.e., they used fragments, islands, and/or continuous forests as the units of observation), and hence, they cannot evaluate the effects of the breaking apart of habitat while controlling for habitat area (Fahrig 2003). Although 27 out of 63 papers (47 %) analyzed ≥5 fragments, and related (e.g., using regression analyses) the effects of fragment characteristics, such as size, isolation, and habitat quality, to different attributes of primate populations, the effects of habitat loss and fragmentation are confounded in these kinds of studies (Fahrig 1999, 2003; Arroyo-Rodríguez and Mandujano 2009). Papers comparing primates inhabiting continuous forests and forest fragments/islands (47 %, see above) also have several weaknesses (Fahrig 2003). For example, as fragmentation is a landscape-scale process, the sample size for comparisons in such studies is in reality only two: one continuous landscape and one fragmented landscape. Furthermore, as stated in Fahrig (2003), this categorization of fragmentation is strictly qualitative (that is, each landscape can be in only one of the two states, continuous or fragmented, and it is not possible to analyze the relationship between the degree of habitat fragmentation and the magnitude of the species responses).

Using a Small Sample Size

Using larger sample sizes allows the researcher to achieve narrower inferential error bars, and more precise estimates of true population values, and hence, a larger sample size leads to increased precision in estimates of population properties

(Cumming et al. 2007). Of the 63 papers that used fragments, islands, and/or continuous forests as the unit of observation, a third (20 papers, 32 %) analyzed ≤4 study sites, and from these papers 5 (8 %) used only 1 fragment/island. As argued by Arroyo-Rodríguez and Mandujano (2009), with such a study design researchers can investigate the population(s) within 1 or few fragments/islands, but it is not possible to attribute these results to habitat fragmentation. These studies cannot establish the relationship between the spatial attributes (e.g., fragment size, isolation, and total edge) of the study sites and the response variable(s), nor can they identify which spatial attributes have the biggest influence on primates. To do so, there are different statistical approaches, such as multiple regression analysis, and path analysis, which need larger sample sizes (see below).

Similarly, we found that most studies analyzed islands, fragments, and/or continuous forests in only one landscape, and therefore, the sample size at the landscape level is only one (Fahrig 2003). With such a study design researchers cannot quantify the relationship between the degree of habitat fragmentation and the magnitude of the species responses. They also cannot assess the effect of fragmentation per se (that is, controlling for the effect of habitat loss) on primates, and cannot determine the threshold values of habitat amount below which the probability of persistence of populations drops significantly (Fahrig 2003; Arroyo-Rodríguez and Mandujano 2009).

Considering Only One or Few Measures of Habitat Fragmentation

Our review indicates that fragmentation studies on primates have only included four measures of fragmentation (Fig. 2.4d): fragment size, fragment isolation, vegetation attributes, and forest edge. Most of the papers measured only one of these effects (fragment size is the most frequent), and very few include two or more effects (see above). Surprisingly, none of the papers we reviewed evaluated the effects of the number of fragments remaining in the landscape on primates. This is perhaps one of the most obvious changes in habitat configuration caused by fragmentation, but we know virtually nothing about its effects on primates. Thus, further studies including a larger number of fragmentation measures will improve our understanding of the effects of habitat configuration on primates.

Each of these spatial attributes can have different effects on primates (Arroyo-Rodríguez and Dias 2009), and these effects depend on the habitat amount remaining in the landscape. For example, recent investigations analyzing tree species richness in three fragmented landscapes at Los Tuxtlas, Mexico, have demonstrated that species–area relationships may differ in landscapes with different forest cover (Arroyo-Rodríguez et al. 2009). These findings could have important implication for frugivorous–folivorous species such as primates, which can be affected by plant species richness availability in the home fragments (Estrada and Coates-Estrada 1996; Cristóbal-Azkarate et al. 2005). Actually, Arroyo-Rodríguez et al. (2008)

demonstrated that the spatial attributes affecting the probability of fragment occupancy by howler monkeys (*Alouatta palliata*) in Los Tuxtlas differed among landscapes with different forest cover. Thus, although many studies have demonstrated fragment size effects, fragment isolation effects, edge effects, and/or vegetation effects on primates, they are probably highly site dependent (see conflicting results among studies of these measures in Arroyo-Rodríguez and Dias (2009)), and do not allow assessment of the effects of fragmentation per se on primates. While extremely logistically difficult, studies comparing the effects of these spatial attributes in landscapes with different forest cover are necessary to have a better understanding of their impacts on primates.

Problems Related to the Interpretation of the Results in Primate Literature

Currently it is difficult to interpret the findings of many investigations in the primate literature. For example, we found that all the papers reviewed assessed habitat fragmentation without controlling for the effect of habitat loss, but most of them (49 out of 66, 74 %) suggested that observed patterns were a result of fragmentation, while they may not be, and 35 papers (53 %) even concluded that fragmentation was the cause of the observed pattern(s). For example, Gómez-Posada et al. (2009) assessed the density and population status of *Alouatta seniculus* in an isolated bamboo forest fragment in La Tebaida, Colombia, and concluded that their results demonstrate the tolerance of this species to fragmentation. Asensio et al. (2007) investigated the foraging habits of *A. palliata* in three forest fragments in Los Tuxtlas, Mexico, and concluded that monkeys cope well with the restrictions imposed by habitat fragmentation. Similarly, but comparing population density and species diversity between one large peninsula and nine small islands in French Guiana, Granjon et al. (1996) concluded that the results illustrated short-term effects of fragmentation at the community level for forest-dwelling mammals. All these conclusions are difficult to evaluate because, while fragmentation is a landscape-scale process, all these studies were conducted at the fragment scale. In particular, it is not possible to tell whether the observed effects are due to the overall loss of forest in the area, or something about the pattern of forest that remains following forest removal (for example, its degree of fragmentation per se), or some other human impact, such as hunting, that is correlated with forest loss. We suggest that the discussions in fragmentation studies should be limited to the spatial and temporal scales of analysis. If a study assesses monkeys in a number of fragments and finds that, for instance, the density and/or species richness of monkeys is positively associated with fragment area (Harcourt and Doherty 2005; Mbora and McPeek 2009), researchers should conclude just this, and not attribute the observed pattern to fragmentation, as it is highly probable that the results are difficult to extrapolate to the landscape scale (McGarigal and McComb 1995).

Conclusions and Recommendation for Future Research

Despite the growing number of publications evaluating primates in fragmented landscapes, we found that approximately 25 % of them do not describe the habitat configuration in the landscapes in which the monkeys were studied. We advocate that assessing habitat fragmentation effects requires adopting a landscape perspective, which includes quantifying the habitat configuration (forest cover, connectivity, number of fragments, fragment size, total forest edge, etc.) in the landscape(s). We also found that all primate studies are at the fragment scale, and thus, no study has evaluated the impact of habitat fragmentation controlling the effect of habitat loss, that is, they do not assess the effects of habitat fragmentation per se on primates.

To accurately quantify the relationship between the degree of habitat fragmentation and the magnitude of the species responses, researchers need to assess primate responses in a range of landscapes with different levels of habitat loss and fragmentation. By increasing the sample size (number of landscapes) researchers not only can assess the effect of fragmentation per se, but may also be able to assess the threshold values of habitat amount below which the probability of persistence of wild populations drops significantly. With such a study design, researchers can also study the effect of important synergies, such as the effect of post-fragmentation anthropogenic activities (logging and hunting) in parallel with the effect of fragmentation (see Ewers and Didham 2006; Arroyo-Rodríguez and Mandujano 2009). Although it is probable that, as demonstrated by Fahrig (1999, 2003) and Arroyo-Rodríguez and Días (2009), habitat loss has larger consistent negative effects on primates than habitat fragmentation per se, this hypothesis needs to be more thoroughly tested through landscape-scale studies.

This being said, it is important to acknowledge that primate researchers face a particular difficulty in assessing the effects of fragmentation per se. Given the spatial scale that is relevant for primate research, it will often be difficult or impossible to sample a sufficient number of landscapes with a wide enough range of value of habitat amount and fragmentation to conduct powerful statistical tests. Such constraints should be explicitly recognized by researchers and, in particular, extreme caution should be taken when interpreting the effect of landscape features on primates, whenever the analysis is only based on one landscape.

We highlight the importance of measuring and testing the effects of a larger number of fragmentation metrics, including the number of fragments remaining in the landscapes. The impact this landscape metric has on primates has not been tested, despite the fact that fragmentation consistently results in an increase in the number of forest fragments in the landscape.

In general, studies at the fragment scale should limit their conclusions to this scale, avoiding speculations about the impact of landscape-scale processes. This is particularly important in studies that test the effects of spatial characteristics, such as fragment size and isolation, of the study site(s) on primates, but not of the habitat configuration surrounding the study sites. These studies cannot test the impact of processes operating at the landscape scale.

To perform reliable and accurate landscape-scale studies we recommend investigating as many landscapes as possible, which is why we suggest considering smaller landscapes (e.g., 500–1,000 ha), adequately separated to impede the exchange of individuals among them and increase its independency (Arroyo-Rodríguez and Mandujano 2009). However, different biological attributes (e.g., distribution, population size, group composition, diet) are likely affected by different spatial scales (Theobald and Hobbs 2002), and therefore, researchers should evaluate questions at the correct scale.

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Section II
Long-Term and Regional Studies Summary

Laura K. Marsh

One of the issues that has become clear in the study of primates in fragments is that over time conditions change, not only for the species in a particular locale, but also regionally. Thus, we have discovered that the value of long-term studies has deepened our understanding of cascading effects and habitat alteration on primates across biomes. Probably the most famous of all long-term studies in an ever-increasingly fragmented site is Gombe, where Jane Goodall got her start and continues to work to this day. Started in 1965, the Gombe Stream Research Center makes an effort to catalog the long-term status of not only the primates in the region, but the human social conditions. Like Goodall's site, the other two "Leakey Angels": the late Dian Fossey and Birute Galdikas sites in Rwanda and Borneo respectively, both are comparable to Gombe in that they have become increasingly isolated and fragmented, and the apes there are increasingly endangered. Even so, all of these sites have provided important and often surprising information on the animals studied there precisely because they have been researched over the long-term. We have found that long-term work begun even as much as 10-years ago is vastly more informative in fragmented habitats that the often one-off projects of a year or less, unless they are at a site established for long-term studies and can be considered cumulative.

The first experiment in fragmentation was the Biological Dynamics of Forest Fragments Project (BDFFP) outside of Manaus, Brazil (Boyle et al., Chap. 5). The BDFFP was established in 1979 by working with a local cattle concession to leave specified sized plots of forest standing, such that the study area would consist of a variety of isolated, connected, and continuous plots ranging from 1 to 10,000 ha (Lovejoy et al. 1986). Numerous important findings have been reported based on studies at this site, including the Laurance et al. (2000) report on the disappearance of big trees, ones that well could be in the 100–1,000 year old range and will never be replaced, at a rate three times faster than those in continuous forest. Currently, the BDFFP matrix consists of varying degrees of isolation of the fragments, in many cases connected with tall secondary regrowth that is more than 20 years old. The authors present findings for three decades of primate study on the six species that reside in the area: red howler (*Alouatta macconnelli*), black spider (*Ateles paniscus*), brown capuchin (*Sapajus apella*), northern bearded saki (*Chiropotes satanas chiropotes*), golden-faced saki (*Pithecia chrysocephala*), and golden-handed tamarin (*Saguinus midas*). The studies include, among others, changes in group size, patch use, activity budgets, and diet of the primates still living within the project boundaries.

Cristobal-Azkarate and Dunn (Chap. 6) discuss a long-term study started in 1984 in Los Tuxtlas, Mexico—the northernmost limit of tropical rainforest in the Americas. It is home to two species of primates: Mexican howler monkey (*Alouatta palliata mexicana*) and the Mexican spider monkey (*Ateles geoffroyi vellerosus*). Early fragmentation studies discovered the effects on the local primate population, and subsequent generations of researchers have contributed to that body of knowledge. The authors report results on migration, metapopulation, and island biogeography, diet, activity, parasitology, and ecological interactions.

In a study of red colobus (*Procolobus rufomitratus*) and black-and-white colobus (*Colobus guereza*) over 15-years in forest fragments outside of Kibale National Park, Uganda, Chapman et al. (Chap. 7) documented a rapid decline in populations as a result of tree removal. They found that parasites were transferred at a higher rate between primates, humans, and livestock, compared to the same species in continuous forest within national park boundaries. Without long-term monitoring at a site like this, it would be impossible to know the status of the primates outside of the park. In this case, authors discuss the future chances for survival outside of the national park system, which appears to be bleak.

Region-wide analyses are popping up throughout the literature as well. Early rainforest inhabitant's forest use has been debated for decades. For instance, original hypotheses suggested that the ancient Mayans caused their own civilization collapse due to rapid deforestation of their lands (McNeil et al. 2010); however, authors now refute the causality of deforestation and its conversion to agriculture with the demise of the people. With increased data sets and more evidence, thoughts on wide-scale total deforestation may not be the case after all, as the media and popular lore would have us believe. Instead, it appears that the ancient Maya, dispite occasional episodes of mismanagement of resources, have survived more than a hundred generations without wide-scale destruction of lands, and in places like southern Mexico, Honduras, and Belize, are managing the forest sustainably to this day (Fedick 2010; McNeil et al. 2010). Rodriguez-Luna et al. (Chap. 4) point out that while Olmec and Mayan civilizations have lived in Central America since 1500 BC, true alteration of landscapes came with the Spanish conquest of 1500 AD. The authors point out that since then, 80 % of Mesoamerica has been converted from natural habitat/forest into human dominated landscapes. And as a result, the primates that remain are part of a relic population that is continuously encroached upon even today.

In Indonesia, the island of Java has suffered at the hands of humans since the first millennium AD (Chap. 3). Today, the island is covered in isolated patches of only about 10 % of its original habitat and it is within those fragments that Nijman surveyed for remaining primates. Using current and historical data, he found that most of the species remaining in Java exist primarily in forest plots between 50 and 400 km^2. In Java at least, the close relationship between size of forest remaining and species presence might explain not only the current distribution of species, but the historic absence of others, such as siamang and orangutan.

As the science of fragmentation matures, more and more field studies will pull together the collective information they have gathered over the years so that we can continue to learn from a wider swath. Just as nothing humans do is static, the adaptations of primates to their ever-changing habitats is something we all can learn from in the long-term.

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Chapter 3
One Hundred Years of Solitude: Effects of Long-Term Forest Fragmentation on the Primate Community of Java, Indonesia

Vincent Nijman

Abstract Unlike many other tropical regions where large-scale habitat loss and habitat fragmentation is a recent phenomenon, deforestation on the island of Java, Indonesia, dates back to the first millennium AD. Today forest remains as numerous isolated patches, covering less than 10 % of the island. This makes it an excellent area to study the effect of forest fragmentation in long-lived animals, such as primates. I surveyed 31 forest fragments, ranging from 1 to 1,300 km^2, to assess the primate community composition. Fragments held between one and five species. Excluding the dry easternmost part of the island, there was a significant relationship between species number and fragments size, with a z-value (slope) of 0.20. A nestedness analysis showed the composition of the different fragments to be highly ordered, with smaller fragments comprising subsets of larger ones. True rainforest species, such as the Javan gibbon (*Hylobates moloch*), are the first species to disappear after isolation. Based on these analyses the minimum fragment size for an area to harbour the entire Javan primate community is between 50 and 400 km^2. The close relationship between fragment size, primate number, and rainforest dependence may explain the historic extinction of species, such as the siamang *Symphalangus syndactylus* and the orang-utan *Pongo* spp., from Java. With forest disappearing rapidly throughout Southeast Asia the patterns observed on Java allow us one potential view into the future for other regions if forest loss and fragmentation continue along their current trajectory.

> It was the last that remained of a past whose annihilation had not taken place because it was still in a process of annihilation, consuming itself from within, ending at every moment but never ending its ending.
>
> Gabriel García Márquez, One Hundred Years of Solitude, Harper Perennial, 1998

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Introduction

Due to its dynamic geological past (Holloway and Hall 1998), relatively stable climates (Gathorne-Hardy et al. 2002), and associated rapid speciation processes (Whitmore 1987), the Southeast Asian islands [Malaysia, Indonesia, and the Philippines, known as zoogeographically as Sundaland] are among the richest islands in the world in terms of biodiversity (Myers et al. 2000). A large number of the islands of Sundaland are merely highpoints of an immense shallow continental shelf. During Pleistocene glacial periods the shelf was exposed periodically as dry land allowing species to move through (parts of) the area (Beaufort 1926; Heaney 1985). Given its complex zoogeography (Heaney 1984; Meijaard 2003a, b) the area makes an excellent subject for studying the interrelationships of species richness, island area, and isolation (Harcourt 1999; Harrison et al. 2006; Heaney 1984, 1985; MacArthur and Wilson 1967; Meijaard 2003a, b; Nijman and Nekaris 2010; Nijman and Meijaard 2008; Wallace 1876; Wilcox 1980).

Small areas, be it islands, forest fragments, or sections of larger areas ('samples'), are expected to harbour less species than large areas. There have been many attempts to fit equations to such species–area relationships. The most widely model in use to date is a power-function model, usually expressed as a double-logarithmic transformation, $\log S = z \log A + \log k$, where S represents the number of species, A is the (island) area, and k and z are fitted parameters that describe intercept (the extrapolated fitted line intercepts the species number axis, that is, when area 'is zero' reflects the overall species richness of the study area) and slope (increase in species number as the area increases; Huggett 2004; MacArthur and Wilson 1967; Preston 1960). As a rule of thumb, for islands the values of the exponent z normally ranges from 0.24 to 0.34 (land-bridge islands tend to have smaller values than oceanic islands) and those for mainland samples fall within the range of 0.12–0.17.

Increasingly species–area relationships are used to assess the impacts of forest fragmentation in a biodiversity conservation context (Brooks et al. 1999a, b; Cowlishaw 1999; Kuussaari et al. 2009; van Balen 1999; Wilcox 1980). By comparing small forest fragments with larger ones, and under the assumption that the smaller one once harboured the same species community as the larger one at present, one can estimate extinction rates due to fragmentation (Brook et al. 2003; Diamond et al. 1987). Including a large number of fragments in the comparison allows one to assess minimal fragment sizes for individual species to persist, as well as which species or types of species are most affected by forest fragmentation. Instead of just considering species number in fragmentation studies, it may be worthwhile to consider the community compositions in the different fragments.

Nestedness is a measure of order in an ecological system, referring to the order in which the number of species is related to, for instance, area or degree of isolation. The more a system is 'nested' the more it is organised (Atmar and Patterson 1993). The concept has been frequently applied to questions concerning habitat fragmentation (Michalski and Peres 2005; van Balen 1999). Nestedness analysis gives a good picture of which species are most resilient to fragmentation and which are not, and which fragments 'behave' idiosyncratic in terms of the primate community it has retained after isolation.

Difficulty with these assessments is that the theory behind species–area relationship is based on the explicit assumption of equilibrium (Loreau 2000) and indeed a nestedness analysis becomes less meaningful if species compositions change (rapidly) over time. When fragmentation is a recent event, fragments may contain more, especially long-lived, species than predicted by the species–area relationship, simply because equilibrium has not been reached (Cowlishaw 1999). Even in the absence of any change, over time more species will become extinct. A further problem with assessing the effects of habitat fragmentation in tropical regions is the often recent nature of habitat loss; many not yet reflect the final situation.

The island of Java in Indonesia, situated just south of the equator, is an excellent area to study the effects of long-term forest fragmentation. Densely populated, large-scale deforestation and concomitant forest fragmentation started >1,000 years ago (Whitten et al. 1996) and today little forest remains. Large-scale pattern of deforestation is properly documented, especially for the last 120 years or so. Here I report on the effects of long-term forest fragmentation on Java's primate community.

Study Area and Its Primate Community

History of Forest Fragmentation on Java

The island of Java, Indonesia's political and industrial centre, is one of the most densely populated areas in the world. The very fertile soils which lend themselves to terracing for irrigated rice sustain about 121 million inhabitants, at an average population density of 914 people km^2 (data from 2000: BPS 2004); this is a striking difference to other locations where the effects of fragmentation on primates have been studied (e.g., Amazon; 2 people km^2: Chapman and Peres 2001). Java is largely deforested and most of the remaining 10 % forest cover (parts of) the numerous volcanoes on the island. Forest has been replaced by a mosaic of cities and villages, agricultural land, cash-crop plantations (e.g., coffee *Coffea* sp., tea *Camellia sinensis*), and forest plantations (e.g., teak *Tectona grandis*, Sumatran pine *Pinus merkusii*, rubber *Hevea brasiliensis*). Unlike many other tropical regions Java has a long history of cultivation and large-scale deforestation, which had already started in the first millennium AD (possible introduction of teak forest in the second to fifth century, introduction of irrigated rice field system in the eighth to tenth century) (Geertz 1963; Smiet 1990). Deforestation accelerated from the 1830s onwards when the Dutch colonial government imposed the so-called cultuurstelsel which lasted until 1870. To support this agro-economic system, farmers were forced to grow export crops on communal grounds, which were often forest (Whitten et al. 1996). By the end of the nineteenth century the natural forest was severely fragmented, and at the beginning of the last century the remaining forest, especially in the western provinces of Banten, West and Central Java, showed a fragmentation pattern very similar to that seen today.

While the people of Java have a long history of deforestation and intense agriculture, hunting, and in particular hunting of primates, has been, and is, less of an issue. The major religions that have been adopted by the people of Java (Geertz 1960; Ricklefs 2001) either revere primates or consider them unfit for consumption. Some 2,000 years ago two-way contact was established between Java's small coastal kingdoms and India. This ultimately resulted in the arrival of Buddhism and Hinduism to Java, with the former peaking in the seventh and eighth century AD and the latter in the fourteenth and fifteenth century AD (Geertz 1960). While both Buddhist and Hindu kingdoms cleared forest and developed the area for agriculture (Whitten et al. 1996), present-day Buddhist and Hindu attitudes towards primates suggest that hunting of primates may have been less of an issue than in other parts of the tropics. While attitudes towards primates may have changed considerably with the arrival of Islam to the island in the sixteenth century AD (in terms of human consumption, primates are considered *haram*—forbidden—under Islamic tenets), its effect in terms of hunting levels may have remained similar. At present over 90 % of the people on Java consider themselves Muslim, with small Hindu communities scattered around the island and Christian and Buddhist minorities living mainly in urbanised areas. Despite hunting not being a significant issue in studying the effects of forest fragmentation on primate communities in Java, capturing for the pet trade is. Despite legal protection, all species of Javan primates are offered for sale in animal markets, this probably having its greatest effect on Javan gibbons *Hylobates moloch* and Javan slow lorises *Nycticebus javanicus* (Nijman 2004; Thorn et al. 2009).

Java's Primate Community

The distribution pattern of primates on Java is determined by the severe degree of forest fragmentation, as well as by the climate (primarily rainfall, having its effect on forest type). The climate of Java differs greatly over the length of the island. In the central Javan mountains there is up to 9,000 mm of rain annually and not a single month with <200 mm, while in the easternmost corner annual rainfall is typically <1,000 mm annually and there is a pronounced dry season. In general the eastern part and the north coast have a marked dry season, whereas the western half does not. In Java rainforest only occurs in areas where the length of the dry season is short and hence can be mostly found in western Java and the slopes of the higher mountains in eastern Java (van Steenis and Schippers-Lammertse 1965).

The extant primate community of Java comprises five species. Three are endemic to the island, i.e., Javan gibbon found east to 109°49′E (Nijman 2006), the grizzled langur *Presbytis comata* found east to 111°19E (Nijman 1997), and the Javan slow loris found east to 112°51′E (Thorn et al. 2009). The ebony langur *Trachypithecus auratus*, also occurs on the smaller islands of Bali and Lombok to the east of Java (Nijman 2000); and, the long-tailed macaque *Macaca fascicularis*, has a wider distribution including much of Southeast Asia (Nijman and Meijaard

2008). This sequence also reflects the species' dependence on rainforest, with the Javan gibbon being confined to it, and the long-tailed macaque additionally occurring in drier forest types, including mangrove forests.

Methods

Data Acquisition

Between 1994 and 2005 I surveyed 31 forest areas on Java for a total of ~350 days in the forest. While most national parks and larger nature reserves were included in the surveys over 80 % of the survey effort was outside the established protected area network. Small forest fragments may have visited for 1 or 2 days, often more, however, most large forest areas (>150 km^2) were visited typically for some 2 weeks (median 13 days, range 3 days to 6 months). A forest area was considered a fragment if it was isolated from other natural forest areas by >1 km of non-forest land (this included tree plantations) and was judged to be isolated for at least 30 years. The latter was assessed using forestry maps presented by van Steenis and Schippers-Lammerste (1965) [forest cover ~1963], Anonymous [1938], and Hoogerwerf and Rengers Hora Siccama (1938) [forest cover early 1930s] and Koorders (1912) [forest cover ~1891]. Often forest fragments were very isolated with gaps of non-forested land of >10 km and were indeed isolated from other fragments for >100 years.

For each forest fragment I established which of the five species were present. For the nocturnal slow loris I largely relied on data from the literature, through correspondence with other primatologists, and less so on personal observations: in all likelihood this will have led to an under-recording of this species' presence but the pattern that emerged from the surveys is similar to that when using museum specimen data (Thorn et al. 2009).

The gibbons and the langurs are confined to forest (as is the slow loris), but the long-tailed macaque often can be found at the edge of the forest or outside forest areas. When recorded in close vicinity of the forest fragment it was included as being present, and if it was recorded a >0.5 km distance, it was not.

Analysis

The relationship between species-richness and fragment size was calculated using log-transformed data. The analysis was run for the entire dataset and, given that a number of species are confined to rainforest, to a subset of fragments that exclude the areas east of Mt Lawu [111°19E]. The resultant z-values were assessed to see if the fragments act as 'islands' or as 'samples'.

Atmar and Patterson (1993) introduced ‘temperature’ as a measure of nestedness. The calculation of ‘temperature’ is based on the number of unexpected occupied sites in the species–fragment matrix as well as unexpected unoccupied sites (gaps) and outliers. In studies of fragmentation, the temperature expresses the order in which species’ extinctions have occurred (in real island studies it reflects the order of colonisation). The ‘colder’ the system is, the more fixed the order of extinction is (in each fragment species 1 goes extinct first, then species 2, and so on) whereas in warmer systems, extinctions have taken place in a more random order. Temperatures range from 0°, indicating an absolutely fixed extinction pattern, to 100° indicating a total random pattern of extinction.

I used the nestedness temperature calculator (Atmar and Patterson 1995) to calculate the coolest matrix possible (i.e., the matrix with the highest degree of nestedness); significance of the model was tested by running 100 Monte Carlo simulations on the same programme.

Results

Species–Area Curves

When considering all 31 fragments, there is no significant relationship between area and species-richness. The relationship has a *z*-value of 0.108, with a mere 24 % of the variation in species-richness being explained by the area size. Focussing on fragments in the western three-quarters of the island only (21 fragments), there is a significant relationship between log*S* and log*A* with a *z*-value of 0.205, explaining 60 % of the variation (Fig. 3.1). Note that the *z*-value is what we typically find for real islands as opposed to samples. Hence, for primates the fragments act as islands and are truly isolated from one another.

Nestedness

Of the 31 fragments, six had all six primate species present, i.e., from west to east, Ujung Kulon [750 km^2], Halimun [400 km^2], Salak [50 km^2], Gede Pangrango [150 km^2], Telaga Warna [5 km^2], and Dieng [255 km^2]. These are represented by Dieng in the upper row of Fig. 3.2. The fill was 44.6 %. There was a very high degree of nestedness, expressing itself as a low system temperature of 7.95°. With an average temperature of 46.27° ± 8.99°, the Monte Carlo-derived probability that the matrix was randomly generated was extremely low [$T < 7.95° = 1.04\ \mathrm{e}^{-05}$].

As can be seen (Fig. 3.2), the first species to drop out are the Javan slow loris and the Javan gibbon, with the slow loris recorded in 6 of the 31 fragments and the gibbon in 7. The most resilient species appear to be the ebony langur and the long-tailed macaque, with the latter showing the most idiosyncratic pattern. The most

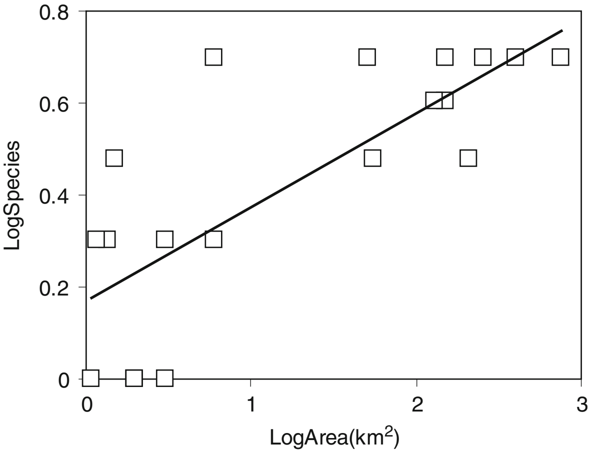
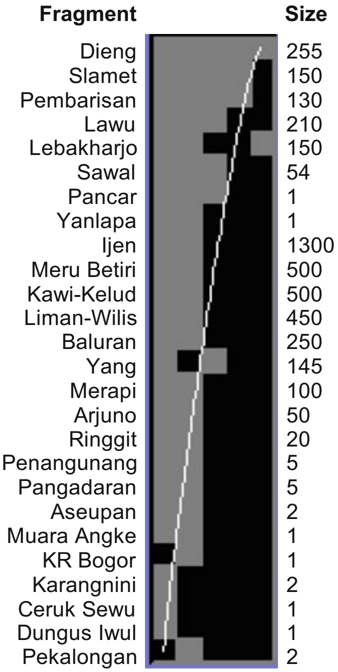


Fig. 3.1 Relationship between the number of primate species and forest areas size in Java, Indonesia, following a double-logarithmic function ($\log S = 0.205 \log A + 0.168$, $R^2 = 0.600$, with A being size of the forest area in km^2 and S being primate species-richness). Included are 21 isolated forests east to Mt. Lawu, excluding forest areas in the drier eastern part of the island



Fragment	Size
Dieng	255
Slamet	150
Pembarisan	130
Lawu	210
Lebakharjo	150
Sawal	54
Pancar	1
Yanlapa	1
Ijen	1300
Meru Betiri	500
Kawi-Kelud	500
Liman-Wilis	450
Baluran	250
Yang	145
Merapi	100
Arjuno	50
Ringgit	20
Penangunang	5
Pangadaran	5
Aseupan	2
Muara Angke	1
KR Bogor	1
Karangnini	2
Ceruk Sewu	1
Dungus Iwul	1
Pekalongan	2

Fig. 3.2 Nestedness of primate communities of 31 forest fragments on Java. Fragments (*rows*) with similar primate communities are listed from large to small, with the species order (*columns*) being ebony langur, long-tailed macaque, grizzled langur, Javan gibbon, and Javan slow loris. Note that in addition to Dieng, listed at the top, there are five other fragments that have all five species present, viz., Ujung Kulon [750 km^2], Halimun [400 km^2], Gede Pangrango [150 km^2], Salak [50 km^2], and Telaga Warna [5 km^2]

idiosyncratic fragment in terms of primate community was Lebakharjo in East Java. This coastal lowland forest harbours ebony langurs, long-tailed macaques, and Javan slow loris, but lacks Javan gibbons and grizzled langurs. It seems that the area is too far east for the latter two species to exist as it is situated up to 100 km east of their easternmost (historical) records.

Large areas with a relatively impoverished primate community, such as Ijen [1,300 km^2], Meru Beteri [500 km^2], and Kawi-Kelud [500 km^2], are all situated in the drier easternmost part of the island, which accounts for the absence of rainforest primates. On the other end of the spectrum, Telaga Warna, which is on 5 km^2, harbours all five species. Situated close to the forest Mt Gede Pangrango it may in fact be less isolated than the other forest fragments included in the analysis.

Discussion

Effects of Fragmentation on Primate Communities

I here show that the primate community in 31 fragments on Java shows a clear pattern, with smaller fragments containing a subset of larger ones. When focussing on the fragments situated in the wetter parts of the island—hence those that can potentially harbour all species of primate, including those that are dependent on rainforest—the size of a fragment is a good predictor for species number. The slope of the regression equation is steep, suggesting that (1) the fragments indeed isolate primate communities with only very limited or no emigration between them, and (2) the fragments have been isolated for long times with (multiple) extinctions having occurred in the smaller fragments.

In highly nested matrices, such as seen in this study, all islands and species contribute rather uniformly to the system temperature of the matrix, regardless of the matrix's temperature. This suggests similar biogeographical histories for these fragments. The single 'outlier' Lebakharjo may result from habitat heterogeneity, or signify a different biogeographical history. Idiosyncratic species (here, albeit only to a minor degree, the long-tailed macaque) might variously recolonise some fragments after they became locally extinct on them or may be affected by competitive exclusion. Recolonisation seems consistent with the species ecology but to what extent long-tailed macaques are affected by competitors remains largely unknown.

The data from the regression and nestedness analysis suggests that for an area to harbour the entire Javan primate community it needs to be some 50–400 km^2 in size. Below this species drop out. The single exception is the small forest fragment of Telaga Warna that probably until recently was not effectively isolated from nearby larger fragments. While Javan slow loris, Javan gibbon, and grizzled langur generally need areas >50 km^2, ebony langurs and long-tailed macaques can persist in significantly smaller areas. Note that these values are probably mostly valid for the wetter part of Java only, and extinction patterns in the drier parts of Java may have followed a slightly different pattern.

Extinction Following Fragmentation

An analysis of the primate communities on 25 islands >500 km^2 in the Sunda Region shows a very strong relationship between the size of the island and number of primate species (Nijman and Meijaard 2008; Nijman, unpubl. data). It also shows that for its size Java has a relatively low number of primate species. Remains of three species of primate currently not found on Java, i.e., pig-tailed macaque *M. nemestrina*, siamang *Symphalangus syndactylus*, and orang-utan *Pongo* sp. dated to ~120 ka, are known from Punung [08°08′S, 111°01′E] on the south coast of East Java (Westaway et al. 2007). At present this part of Java has a prolonged dry season and the nearest rainforest is found >30 km away on the slopes of Mt Lawu. These rainforest primates probably disappeared from Java during the last glacial maximum when drier conditions and increased seasonality reduced the amount of available rainforest (van den Bergh et al. 2001) but one or more species may have persisted much longer in the wetter parts of Java. Further deforestation and resultant fragmentation, exacerbated by the capturing of primates for the pet trade, have led all but the long-tailed macaque to be considered globally threatened.

If data from present-day forest fragments can teach us anything about primates in the past we can infer the minimum sizes of fragments to sustain larger communities. Extrapolating from the regression equations, to sustain a community with two or three additional species (as was the situation in the past) fragments would have to have been some 3,500–13,000 km^2 in size. Judging from forest maps presented by Koorders (1912) fragments of these sizes must have been very rare even over 120 years ago, especially in the wetter western part of the island where species such as pig-tailed macaque, siamang, and orang-utan could have persisted.

Lessons from Java

While large-scale anthropogenic deforestation on Java dates back hundreds if not thousands of years, one may expect that the primate community has reached the so-called relaxation phase (i.e., the number of species is in equilibrium with the available habitat). Following Brooks et al. (1997) the number of species in the remaining forest can be predicted by $S_{n2} = S_{o2}\ (F_n/F_o)^z$ where S_{o2} is the number of expected species for an area (here the island of Java) as derived from a species area curve (based on 23–36 primate species on 116 islands in Sundaland: Nijman and Meijaard 2008), S_{n2} is the number of predicted species on the basis of the remaining forest (the number of species we expect to find at present if indeed the number of species is in equilibrium with the available habitat), F_o is the original and F_n is the remaining forest area (136,920 and 12,912 km^2, respectively: MacKinnon et al. 1982; van Balen 1999), and z is the slope of the regression line (0.13–0.16: Nijman and Meijaard 2008). Filling in the equations it turns out that on the basis of present forest cover Java should have three to four primate species (i.e., one or two less than at present).

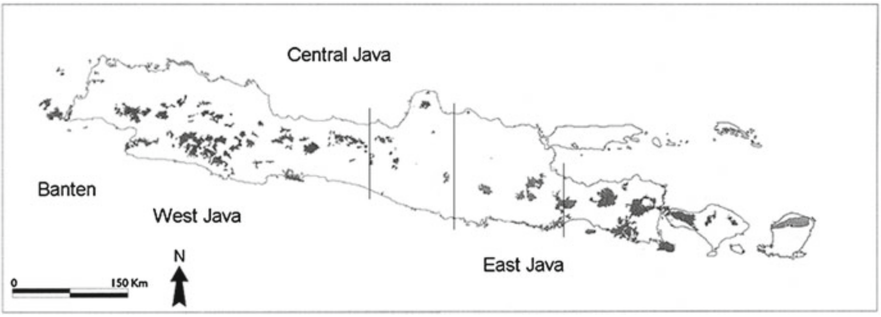


Fig. 3.3 Mid 1980s forest cover on Java, and the islands of Bali and Lombok to the east of Java (after RePPProT 1990), showing the severe degree of forest fragmentation. The *three vertical lines* indicate the geographical boundary of (from west to east) Javan gibbon *Hylobates moloch*, grizzled langur *Presbytis comata*, and Javan slow loris *Nycticebus javanica*; the ebony langur *Trachypithecus auratus* is restricted to the islands of Java, Bali, and Lombok, whereas the long-tailed macaque *Macaca fascicularis* can be found on all three islands, as well as islands to the north, west, and east

The results are only partially dependent on the choice of parameters, i.e., the steeper slope [0.16] gives rise to the higher number of primate species [four as opposed to three], but not on the exact estimation of the amount of remaining forest (note that in the equation it is the ratio that is of relevance, thus replacing all the remaining forest in the equation with lowland forest only, under the correct assumption that some primate species are attitudinally restricted, and do not change the results). These findings are comparable to that which has been found for primate communities in African forest, with typical ‘extinction debts’ of 30 % (i.e., an excess of between four and eight primates in individual fragments) (Cowlishaw 1999). The sobering lesson is that while in Cowlishaw’s dataset the extinction debt was present some 50 years after deforestation commenced, the data from Java suggest that these extinction debts can last for centuries (cf. Vellend et al. 2006).

One major caveat in using species–area curves and nestedness analysis to explain present-day primate community composition and past extinctions is that they are based on the implicit assumption that the primates are evenly distributed over the available forest area, both in the present and in the past. For Java this is not the case (see Fig. 3.3), with more species occurring in the west than in the east. Hence loss or preservation of forest areas in the wetter parts will have a disproportional effect on the number of species that (theoretically) can persist in the remaining forest. Likewise, fragmentation per se has its effect on the composition and number of the remaining species, and we can use this knowledge to guide habitat and species conservation as it allows maximising results with the limited resources available.

In conclusion, despite centuries of deforestation resulting in a close relationship between forest fragment size and primate species number and composition, it appears that, on the basis of habitat availability alone, Java may expect to lose one or two more species, in addition to the three it has lost already since Pleistocene times. The history of deforestation and forest fragmentation on Java is currently repeated in other parts of Asia (Sodhi et al. 2004, 2010), and hence, we can expect primate extinctions similar as observed in Java to occur elsewhere.

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Chapter 4
A Region-Wide Review of Mesoamerican Primates: Prioritizing for Conservation

Ernesto Rodríguez-Luna, Aralisa Shedden, and Brenda Solórzano-García

Historical Perspective of Mesoamerica

Mesoamerica can be defined in at least three dimensions: biogeographical, cultural, and political (Coates 2003; Hall et al. 2003; Wallace 2003). For this reason, there are numerous and mixed visions of the same region. And from this variety of visions, people understand, occupy, and transform territories (that we describe as a complex matrix of processes that occur on different scales). One level of analysis of this territorial transformation is from a species and habitat perspective: the present Mesoamerican landscape is a mosaic of natural and transformed areas, and, according to Rackham (1998) all natural areas have a history, usually involving hundreds or thousands of years of interaction with people who have lived and worked in them. This history with the land is an essential part of conservation.

A contemporary and conservationist vision, as Conservation International (2007) proposed, established that this region extends from central Mexico to the Panama Canal, encompassing different types of natural ecosystems throughout Guatemala, Belize, El Salvador, Honduras, Nicaragua, and Costa Rica (Fig. 4.1). With less than one half percent of the landmass on Earth, Mesoamerica possesses between 7 and 10 % of all known forms of life and 17 % of all terrestrial species; this region is among the most biologically diverse on the planet (CEPF 2004). This notable biodiversity can be explained through the establishment of a bridge that united both continental masses, in which two biotas independently evolved (Jackson and D'Croz 2003). The creation of the Central American isthmus, about three million years ago, allowed plant and animal movements from south to north and vice versa (Webb 2003), and in these successive migrations, we can distinguish the flows of human and nonhuman primates (Callithricidae and Cebidae as part of the southern regions).

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Fig. 4.1 Mesoamerica and Mesoamerican primates. (1) Mexico, (2) Belize, (3) Guatemala, (4) El Salvador, (5) Honduras, (6) Nicaragua, (7) Costa Rica, (8) Panama. Illustrations copyright 2003 Stephen D. Nash/IUCN/SSC Primate Specialist Group. Used with permission. *Alouatta pigra* illustrated by Marco Antonio Pineda Maldonado/Banco de Imágenes CONABIO

We can assume that incessant human population growth and landscape transformations are accompanied by the proportional decrease of species and their habitat. From this perspective, the fate of many Mesoamerican species ultimately will depend on their capacity to persist in perturbed and fragmented landscapes or isolated natural reserves.

Mesoamerica possesses one of the richest concentrations of species and ecosystem diversity in the world; however, its political, social, and economic aspects are extremely unfortunate. This region's biological diversity has its counterpart in its cultural diversity: Mesoamerica is inhabited by 32 different ethnic and indigenous groups, represented by a population of over nine million, and in this context, almost 50 % of the total 45 million habitants in this region live below the poverty line (FAO 2005). In rural areas, 70 % percent of the population is considered poor (CEPF 2004). Poverty is a major factor in maintaining threats to all habitats in this region, and much of the population lacks access to basic health care, education, and even safe water (Miller et al. 2001).

Evidence of human presence in the Central American isthmus dates from 11,000 years ago (Garcia-Montiel 2002). With the first Olmec civilizations in 1500 BC and with the subsequent Mayan settlements, human influences began to determine forest structures and compositions (Coe et al. 2006). However, we can recognize that the alteration of the Mesoamerican natural landscape intensified since the Spanish conquest (1500 AC). From this moment on, a new structure of territoriality is established, and with it, a new form of appropriation and transformation of natural resources (Cooke 2003; Hall et al. 2003; Heckadon-Moreno 2003; Herlihy 2003;

Rodríguez-Luna et al. 1996). In the present day, globalization of market forces, agricultural industrialization, migration, public policy, and cultural changes are driving the transformation of diverse, traditional, smallholder agroecosystems into agroindustrial systems dependent on chemical inputs and mechanization (Angelsen and Kaimowitz 2001; Harvey et al. 2007).

Mesoamerica's biodiversity is under continuous threat from the variety of factors, which include a deforestation rate of approximately 1 % per year from 2000 to 2005 (FAO 2005), a human population growth rate of over 2 % per year (Miller et al. 2001), and the reliance of the majority of the human population on biological resources taken directly from the wild (Miller et al. 2001; Sarkar et al. 2009). Since approximately 80 % of the region's original ecosystems has been converted to agriculture, more than 300 of the region's endemic species of flora and fauna are threatened, including at least 107 that are critically endangered (CI 2007). With continuing habitat loss and fragmentation of remaining forests, pressure on the region's biodiversity will intensify (Harvey et al. 2007).

And in the case of primates, it translates into extensive loss of habitat (Estrada et al. 2006).

This evident anthropogenic fragmentation process has become a main issue in ecological research, and constitutes a departure point for species and habitat conservation strategies. Even though investigation on habitat fragmentation and its effects on species have increased there are a number of theoretical and methodological issues that must be resolved to fully understand the phenomenon, starting with the definitions of habitat and fragmentation (Franklin et al. 2002). Despite many decades of research there is a lack of essential information regarding the conservation status of habitats and populations in Mesoamerica (Estrada et al. 2006). Therefore, we consider it necessary to fully review primate conservation studies that have been conducted in recent years (2003–2010).

Mesoamerican Primates

Currently, several taxonomic arrangements have been proposed for Mesoamerican primates (Groves 2001; Rylands et al. 1995, 2000), but for this review we used the species considered by the World Conservation Union (IUCN) Primate Specialist Group (Rylands et al. 2006) which recognizes eight species and 21 taxa of primates in Mesoamerica. In Table 4.1, we list 20 of these taxa, their distribution, and their conservation status according to the IUCN Red List. It is important to clarify that we are not including the Colombian black spider monkey (*Ateles fusciceps rufiventris*) in this analyses, since its distribution is outside of our Mesoamerican delimitations.

When examining the conservation status of the 20 taxa, we can assume that all Mesoamerican primates are under some degree of threat from a number of direct and indirect factors, and the tendency is that this set of threats will constantly and severely affect their populations and habitat in the coming decades. This situation is

Table 4.1 Taxonomy and conservation status for Mesoamerican primates, according to the IUCN Red List (IUCN 2011)

Species	Subspecies	Red list	Distribution
Alouatta palliata (*LC*)	*A. palliata aequatorialis*	VU	Panama
	A. palliata coibensis	VU	Panama
	A. palliata trabeata	CR	Panama
	A. palliata mexicana	CR	Mexico
	A. palliata palliata	LC	Costa Rica, Guatemala, Honduras, Nicaragua
Alouatta pigra (*EN*)		EN	Belize, Mexico, Guatemala
Ateles geoffroyi (*EN*)	*A. geoffroyi azuerensis*	CR	Panama
	A. geoffroyi frontatus	VU	Costa Rica, Nicaragua
	A. geoffroyi geoffroyi	CR	Costa Rica, Nicaragua
	A. geoffroyi grisescens	DD	Panama
	A. geoffroyi ornatus	EN	Costa Rica, Nicaragua, Panama
	A. geoffroyi vellerosus	CR	México, Belize, El Salvador, Guatemala, Honduras
	A. geoffroyi yucatanensis	EN	Belize, Mexico, Guatemala
Cebus capucinus (*LC*)	*C. capucinus capucinus*	LC	Panama
	C. capucinus imitator	LC	Costa Rica, Nicaragua, Panama
	C. capucinus limitaneus	LC	Honduras, Nicaragua
Saimiri oerstedii (*VU*)	*S. oerstedii oerstedii*	EN	Costa Rica, Panama
	S. oerstedii citrinellus	EN	Costa Rica
Saguinus geoffroyi (*LC*)		LC	Panama
Aotus zonalis (*DD*)		DD	Panama

CR critically endangered, *EN* endangered, *VU* vulnerable, *LC* least concern, *DD* data deficiency

clearly exemplified when comparing the data on degree of threat published by Rodríguez-Luna et al. (1996) in which 23 taxa were acknowledged: three critically endangered (CR), four endangered (EN), six vulnerable (VU), nine least concern (LC), and one data deficient (DD), as compared to the IUCN's 20 recognized taxa: five CR, five EN, three VU, five LC, and two DD.

Published Studies

To identify the approach and the trends developed in primate research, we reviewed the published studies on primates in fragments in Mesoamerica from 2003 to June 2010, using the bibliographic database for primatology *PrimateLit* as main reference. We complemented our search by including the *Neotropical Primates* journal, since it has not been cited by *PrimateLit* since 2006. Nevertheless, we are aware of the limitations implicated with this method and these data should be considered as a representative sample of existing publications. To quantify the publications, we classified the studies by country, species, study site, and category where the categories consisted of: (1) Demography (including distribution), (2) Ecology (including parasitism), (3) Physiology, (4) Behavior studies (including diet), (5) Conservation, and (6) Genetics. With this assessment we identified information deficiencies for the planning of effective conservation actions towards Mesoamerican primates at a country and species/subspecies level. We also examined each study's inclusion of social, economic, and political factors.

Results

During the past seven and a half years, 143 of the 528 publications for Mesoamerican primates have been oriented towards primates in fragments. The majority of the publications have been from studies in Mexico (59 %), Costa Rica (13 %), and Panama (11 %). In the remaining countries, research has been minimal: Nicaragua (7 %), Belize (6 %), while Guatemala, Honduras, and El Salvador have had only two publications each (2 %, 1 % and, 1 % respectively).

The most studied species are *Alouatta palliata*, *A. pigra*, and *Ateles geoffroyi* with 93 % of the publications. The remaining 7 % is distributed among the other four species (Table 4.2). Of all taxa, only *A. palliata* and *A. pigra* have publications related to fragments in all of the countries that comprise their distribution range. On a country level, we noted that investigation efforts were concentrated on few localities, while large areas where primate species are distributed have remained unexplored.

The different categories that have been studied for each Mesoamerican primate are shown in Fig. 4.2. We can observe that some issues or aspects have been more developed than others. For example, studies on demography, ecology, and behavior

Table 4.2 Publications about primates in fragments for each Mesoamerican species from 2003 to 2010

	Alouatta palliata	*Alouatta pigra*	*Ateles geoffroyi*	*Cebus capucinus*	*Saimiri oerstedii*	*Saguinus geoffroyi*	*Aotus zonalis*	Total
Mexico	55	27	17	–	–	–	–	99
Belize	–	7	0	–	–	–	–	7
Guatemala	0	3	1	–	–	–	–	4
El Salvador	–	–	2	–	–	–	–	2
Honduras	2	–	0	0	–	–	–	2
Nicaragua	8	–	0	0	–	–	–	8
Costa Rica	4	–	5	4	2	–	–	15
Panama	4	–	4	2	0	0	2	12
Total	73	37	29	6	2	0	2	

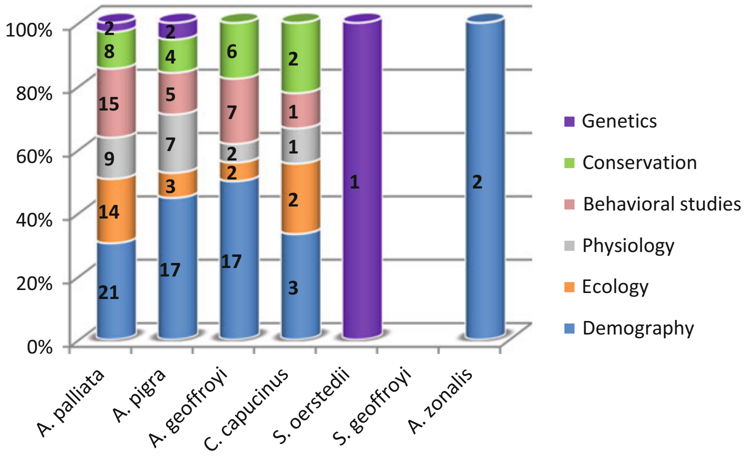

Fig. 4.2 Categories of Mesoamerican primates in fragments publications 2003–2010, where the numbers/category represent the number of publications reviewed

are predominant, while questions on genetics and physiology are barely addressed. Another notable aspect is that within each research topic a certain number of studies tend to be reiterative.

The higher prevalence of studies on certain categories and species could be explained by two main reasons: (1) The existence of personal research lines established years ago focused on one topic, one species, and developed in one locality, and (2) the opportunities that a country offers for studying different species at different locations, such as access to the site, security, and funding. A high percentage of these studies throughout Mesoamerica have been conducted by foreign researchers which contrasts with Mexico, where research is primarily conducted by national institutions and researchers.

Discussion

The majority of publications on Mesoamerican primates in fragments, between 2003 and 2010, are distributed between Mexico and Costa Rica and have mainly focused on *Alouatta palliata* and *Ateles geoffroyi*. These results are similar to those found in previous reviews (Estrada et al. 2006; Rodríguez-Luna et al. 1996). Mexico is the country where the largest number of studies on primates in fragments has been conducted; however, Mexico possesses only three of the seven primate species and four of the 20 taxa in this region.

Since most of the available habitat for primates in Mesoamerica is fragmented, and as transformation rates are particularly high, the conservation of the remaining primate populations is critical for species permanence. Thus, their study becomes even more relevant, especially developing projects that focus on population viability, the differential effects of habitat fragmentation on a species/population/individuals, and the analysis of factors and processes that determine landscape transformation, using approaches such as historical ecology (Lunt and Spooner 2005) and landscape ecology (Turner 2005).

Based on the reviewed categories, we can assume that there are important information voids that prevent us from having an accurate assessment of the conservation status of the primates in the region; particularly, severely understudied species like *Saimiri*, *Aotus,* and *Ateles* subspecies. In order to determine the degree of threat that these species are facing, the IUCN Red List methodology requires specific data that includes: total population size, population decline rates, and total number of mature individuals (IUCN 2011). Even though the IUCN has assigned a conservation status for all of the Mesoamerican primates, according to our review, the studies over the last few years for this region have not been designed to fill the needed requirements. As such, there is insufficient information for all taxa (even well-studied ones, such as howlers and spiders monkeys in Mexico), which does not allow us to sustain a classification with certainty.

One of the main concerns, regarding viability in fragmented habitats, has been the loss of genetic diversity and the subsequent problems caused by inbreeding (Bicca Marques 2003; Charpentier et al. 2007; Pope 1992). Yet there is very little information about this topic for Mesoamerican primates in general, as it only has been addressed for three of the seven species (*Alouatta palliata*, *Alouatta pigra,* and *Saimiri oerstedii*).

Conclusions

Although primatological research in Mesoamerica has continued and has provided valuable information, most of these efforts have originated from personal and isolated interests, which do not necessarily obey the need for specific data required for evaluating and determining the taxa's conservation status. Another issue that must be considered when developing research is data homogeneity. Since, as some authors have pointed out (Arroyo-Rodríguez and Mandujano 2009), a large number of studies are not comparable, as they have been developed with different methods and orientations. Under the term of "studies with primates in fragments" there is a diverse assemblage of research approaches that range from simple demographic data collection to more complex theories.

Consequently, we have incomplete records for most species and habitats, making the establishment of a regional framework for primatological research necessary in order to fulfill this aim. Thus, primate research in Mesoamerica should be oriented towards obtaining key data that allows conservation strategies to be performed. We suggest when planning a particular research topic researchers should consider what has been published and how we can enrich this information. Studies that provide basic data such as: demography, habitat, real distribution, and genetics, should be a priority for institutions that grant funding. We should also aim to provide a comprehensive analysis of the situation in which our research and results are immersed.

As we mentioned before, there is a huge information void for Central America and in order to generate the necessary data for effective primate conservation, both institutions and universities need to promote primate studies. In this sense, primates may be seen as umbrella species and by studying them researchers can provide data on habitats important for other species.

Within the matrix of human communities, transformed land, and natural ecosystems, we find primate populations in habitat relicts which are being continuously reduced, perturbed, and isolated. The future of primate populations and species is being conditioned by the historical course of political, economic, and social processes that exists in this region, and it is evident that all conservation actions developed to maintain biodiversity (including primates) cannot be considered separately from Mesoamerica's overall problems.

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Chapter 5
Primates of the Biological Dynamics of Forest Fragments Project: A History

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Abstract The Biological Dynamics of Forest Fragments Project (BDFFP), located approximately 80 km north of Manaus, Brazil, is the longest-running study of forest fragmentation in the world. The BDFFP was created in 1979 and the first primate census occurred in 1980. Six primate species inhabit the study area: red howler

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L.K. Marsh and C.A. Chapman (eds.), *Primates in Fragments: Complexity and Resilience*, Developments in Primatology: Progress and Prospects,
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(*Alouatta macconnelli*), black spider (*Ateles paniscus*), brown capuchin (*Sapajus apella*), northern bearded saki (*Chiropotes satanas chiropotes*), golden-faced saki (*Pithecia chrysocephala*), and golden-handed tamarin (*Saguinus midas*). The distribution of these six species throughout the forest fragments has varied during the past three decades with some species (i.e., howler monkeys) being more prevalent than others (i.e., spider monkeys), particularly in the smaller fragments. Researchers did not find primates in some of the 1-ha forest fragments prior to 2007. Here we present a history of primate research at the BDFFP, including findings from three decades of primate censuses and behavioral and ecological studies of several species in the forest fragments, the surrounding matrix, and the continuous forest. These primate studies have provided information on seed dispersal in forest fragments, parasite infections, use of the matrix, and changes in group size, activity budget, and diet of groups in the forest fragments. Many of the once-cleared pastures surrounded by continuous primary forest are now dominated by various stages of secondary growth. Unfortunately, deforestation continues in many areas of the continuous forest north of Manaus. We discuss the implications of these land-cover changes on the primate community and suggest avenues for future primate research at the BDFFP.

Introduction

The Biological Dynamics of Forest Fragments Project (BDFFP), located 80 km north of Manaus, Brazil (Fig. 5.1), began in 1979. The project, originally called the Minimum Critical Size of Ecosystems Project (Lovejoy et al. 1986), is a joint international collaboration between the Brazilian Instituto Nacional de Pesquisas da Amazônia (INPA) and the U.S. Smithsonian Tropical Research Institute (STRI). The study area was formed when areas of forest were cleared for large cattle ranches; however, according to Brazilian law half of each land parcel had to remain as forest (Bierregaard Jr and Gascon 2001). Researchers delineated boundaries of the forest fragments, and censuses occurred prior to and after fragmentation of the forest in order to quantify changes in plants, animals, and local climate (Bierregaard Jr and Gascon 2001).

The BDFFP study area consists of forest fragments that range in size from 1 to 100 ha and have variable isolation distances to the continuous forest. Many BDFFP studies have grouped the fragments into three size classes (1, 10, and 100 ha), although actual sizes vary (e.g., 1-ha fragments range from 1.1 to 2.8 ha). Isolation of the forest fragments occurred both with and without fire leading to differences in plant composition in the matrix (Williamson and Mesquita 2001). Subsequent re-isolation of the fragments at different time intervals (Bierregaard Jr and Stouffer 1997) has resulted in a matrix that varies from clear-cut to tall secondary-growth forest that is more than 20 years old (Boyle and Smith 2010b). Laurance et al. (2011) provide a review of 20 major findings from BDFFP research.

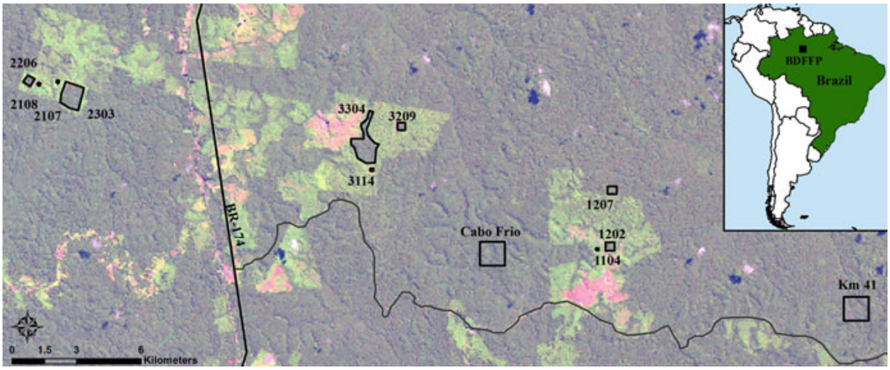

Fig. 5.1 Biological Dynamics of Forest Fragments Project (BDFFP) located in Brazil. Map prepared using Landsat 5 imagery from 2006. Forest fragments surveyed for primates are indicated by the dark polygons. *Gray areas* surrounding the fragments represent the matrix. Two areas used frequently as continuous forest sites (Cabo Frio and Km 41) are indicated by *hollow polygons*. The BR-174 highway runs north–south through the study area

As of 2013, primate research at the site has resulted in 11 doctoral dissertations, master theses, and undergraduate monographs, and more than 25 peer-reviewed publications (Table 5.1). These studies document three decades of research and provide a wealth of data on the BDFFP primate community, including: interspecific differences in response to fragmentation, detailed behavioral and dietary analyses, fragmentation effects on parasite loads and seed dispersal, and assessments of available dietary resources in the study area. Here we present a review of these findings and suggestions for future research.

Overall Patterns: 1979–2010

Primate censuses were conducted prior to and following the isolation of many of the BDFFP fragments (Lovejoy et al. 1986; Rylands and Keuroghlian 1988), and censuses have continued sporadically following the initial studies in the 1980s (Boyle and Smith 2010b; Gilbert 2003; Gilbert and Setz 2001). In addition, other researchers have focused on a subset of the forest fragments (Lenz 2013; Santamaría Gómez 2004; Schwarzkopf and Rylands 1989; Setz 1993, 1994).

Six species of New World monkeys inhabit the continuous forest of the BDFFP: red howler (*Alouatta macconnelli*) (Fig. 5.2), black spider (*Ateles paniscus*), brown capuchin (*Sapajus apella*), northern bearded saki (*Chiropotes satanas chiropotes*), golden-faced saki (*Pithecia chrysocephala*, sensu Marsh in press), and golden-handed tamarin (*Saguinus midas*). Ecological and behavioral

Table 5.1 Primate studies at the Biological Dynamics of Forest Fragments Project (BDFFP)

		Location of data collection			Type of data collected								
Species studied	Dates	Forest fragments	Continuous forest	Matrix	Primate census	Activity budget	Diet	Home range	Seed dispersal	Parasites	Predation	Resource availability	Citations
All[a]													
	1980–1984[b]	x	x		x								Rylands and Keuroghlian (1988)
	1985	x			x								Schwarzkopf and Rylands (1989)
	1983–2001[b]	x	x		x								Gilbert and Setz (2001); Gilbert (2003)
	2003, 2005–2006	x	x		x							x	Boyle (2008a, b); Boyle and Smith (2010b)
	2007, 2008, 2009–2010	x	x	x	x							x	Lenz (2013); Johnson and Stouffer (unpublished data)
Alouatta													
	1984–1985	x				x	x						Neves (1985); Neves and Rylands (1991)
	1991–1993; 1995	x	x			x	x			x		x	Gilbert (1994a, b, 1997)
	1996–1998	x	x						x				Andresen (2000, 2002, 2003); Andresen and Levey (2004)
	1998		x			x	x	x	x				Santamaría Gómez (1999); Santamaría and Rylands (2003)
	2001–2003	x	x			x	x	x	x			x	Santamaría Gómez (2004)

Chiropotes										
1980, 1981	x	x		x	x					Ayres (1981)
1987–1988		x		x	x					Frazão (1991, 1992)
2003, 2005–2006	x	x	x	x	x	x			x	Boyle (2008a); Boyle et al. (2009a, b, 2012, 2013); Boyle and Smith (2010a)
2010		x						x		Lenz and dos Reis (2011)
Pithecia										
1986–1991	x			x	x				x	Setz (1993, 1994); Setz and Gaspar (1997); Setz et al. (1999)
2000	x							x		Gilbert (2000)
Sapajus										
1985–1987		x		x	x	x	x			Spironello (1991, 1999, 2001)

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[a] Censuses conducted for the six primate species in the study area: *Alouatta macconnelli*, *Ateles paniscus*, *Chiropotes satanas chiropotes*, *Pithecia chrysocephala*, *Saguinus midas*, and *Sapajus apella*

[b] Dates include syntheses of past censuses

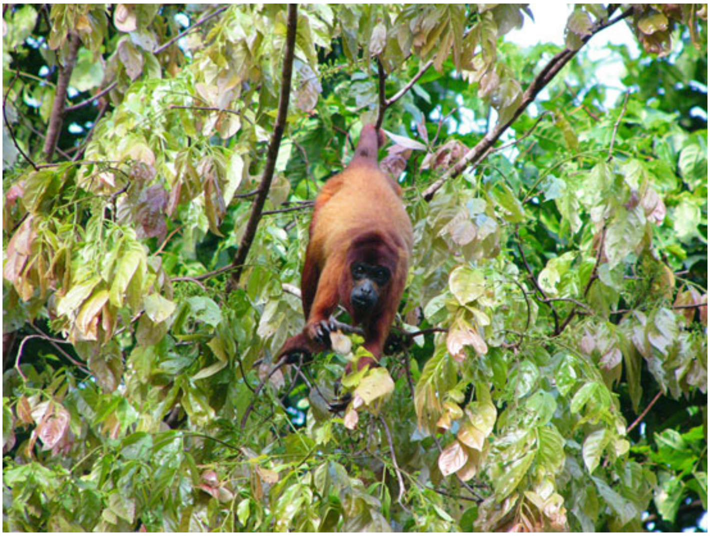

Fig. 5.2 *Alouatta macconnelli* one of the most common of the BDFFP residents in Dimona Camp north of Manaus. Photo by Sarah Boyle

studies have been conducted on *Alouatta* (Andresen 2000, 2002; Gilbert 1994a, b, 1997; Neves 1985; Neves and Rylands 1991; Santamaría Gómez 2004), *Chiropotes* (Ayres 1981; Boyle 2008a; Boyle and Smith 2010a; Boyle et al. 2009, 2012, 2013), and *Pithecia* (Setz 1993, 1994; Setz et al. 1999; Setz and Gaspar 1997) in some of the BDFPP fragments with additional research on *Alouatta* (Andresen 2000, 2002; Santamaría Gómez 1999; Santamaría and Rylands 2003), *Sapajus* (Spironello 1991, 1999, 2001), and *Chiropotes* (Boyle 2008a; Boyle and Smith 2010a; Boyle et al. 2009, 2012, 2013; Frazão 1991, 1992) in the continuous forest. Recent work has also focused on edge effects, niche partitioning, and primate use of the secondary growth matrix (Lenz 2013). To date there has been no published behavioral research on *Ateles* or *Saguinus*, and no studies of *Sapajus* in the forest fragments.

The six primate species have never been uniformly distributed across the fragment size classes, and during the past three decades the presence of each species in the fragments has been dynamic (Table 5.2). Primate species richness has been consistently lower in the smaller fragments than the larger fragments and continuous forest (Boyle and Smith 2010b; Gilbert 2003). However, there has been a strong correlation between the size of the forest fragment and its distance to the nearest forested area (forest fragment or continuous forest), so species presence may be due to fragment size, its proximity to other forested areas, or a combination of the two variables (Boyle and Smith 2010b).

Table 5.2 Primates in the BDFFP fragments

Reserve	Size class	1980–1981	1983–1984	1985–1986	1987–1990	1991–1992	1992–1993	1995–1997	2000–2001	2001–2003	2005–2006	2007–2010
1104	1	–	–	–	–	_Alouatta_	_Alouatta_	_Alouatta_ _Chiropotes_ _Saguinus_	_Alouatta_ _Chiropotes_	_Alouatta_* _Sapajus_* _Saguinus_*	_Alouatta_*	_Alouatta_ _Chiropotes_* _Saguinus_*
2107	1	–	–	–	–	0	0	0	0	_Alouatta_ _Chiropotes_	_Alouatta_*	_Alouatta_*
2108	1	–	–	–	–	0	0	0	0	0	0	_Saguinus_*
3114	1	–	–	–	–	0	0	0	0	0	0	_Saguinus_*
1202	10	_Alouatta_ _Chiropotes_* _Saguinus_	_Alouatta_	_Alouatta_ _Saguinus_* _Pithecia_*	–	_Alouatta_ _Saguinus_ _Pithecia_	_Aloutta_ _Saguinus_ _Pithecia_	_Alouatta_ _Saguinus_ _Pithecia_ _Chiropotes_* _Ateles_	_Alouatta_ _Saguinus_ _Pithecia_ _Chiropotes_ _Ateles_	_Alouatta_ _Chiropotes_ _Saguinus_ _Pithecia_*	_Alouatta_ _Saguinus_* _Pithecia_* _Chiropotes_ _Ateles_*	_Alouatta_ _Chiropotes_ _Saguinus_*
1207[a,b]	10	–	_Alouatta_ _Saguinus_*	_Alouatta_ _Saguinus_	–	–	–	_Alouatta_* _Saguinus_	–	–	–	_Alouatta_* _Saguinus_* _Sapajus_* _Chiropotes_*
2206	10	–	_Alouatta_ _Saguinus_	_Alouatta_ _Pithecia_	–	_Alouatta_ _Saguinus_ _Pithecia_ _Chiropotes_*	_Alouatta_ _Saguinus_	_Alouatta_	_Alouatta_ _Saguinus_ _Pithecia_	_Alouatta_ _Saguinus_ _Chiropotes_	_Alouatta_ _Saguinus_ _Pithecia_* _Chiropotes_	_Alouatta_* _Saguinus_* _Chiropotes_* _Sapajus_* _Ateles_*
3209	10	–	_Alouatta_ _Saguinus_	_Alouatta_ _Saguinus_	–	_Alouatta_ _Pithecia_	_Alouatta_	_Alouatta_	_Alouatta_	_Alouatta_	_Alouatta_* _Saguinus_* _Pithecia_* _Sapajus_*	_Alouatta_* _Saguinus_* _Sapajus_*

(continued)

Table 5.2 (continued)

Reserve	Size class	1980–1981	1983–1984	1985–1986	1987–1990	1991–1992	1992–1993	1995–1997	2000–2001	2001–2003	2005–2006	2007–2010
No ID[b]	10	–	–	*Alouatta* *Saguinus** *Pithecia*	*Alouatta* *Saguinus** *Pithecia**	–	–	–	–	–	–	–
2303	100	–	–	–	–	*Alouatta* *Saguinus* *Pithecia*	*Alouatta* *Saguinus* *Pithecia*	*Alouatta* *Pithecia*	*Alouatta* *Saguinus* *Pithecia* *Chiropotes*	*Alouatta* *Saguinus* *Chiropotes* *Sapajus*	*Alouatta* *Saguinus* *Pithecia** *Chiropotes** *Sapajus**	*Alouatta* *Saguinus** *Pithecia** *Chiropotes** *Sapajus** *Ateles**
3304	100	–	*Alouatta* *Saguinus* *Pithecia* *Sapajus**	–	–	*Alouatta* *Saguinus* *Pithecia*	*Alouatta* *Saguinus* *Pithecia* *Sapajus*	*Alouatta* *Saguinus* *Pithecia* *Sapajus*	*Alouatta* *Saguinus* *Pithecia* *Chiropotes*	*Alouatta* *Saguinus* *Pithecia* *Sapajus*	*Alouatta* *Saguinus** *Pithecia** *Chiropotes** *Sapajus**	*Alouatta* *Saguinus** *Pithecia** *Chiropotes** *Sapajus** *Ateles**

Dash (–) indicates that data were not collected at that time period. Asterisk (*) indicates that the species was not consistently present in the fragment. Data were compiled from Ayres (1981), Rylands and Keuroghlian (1988), Setz (1993), Gilbert and Setz (2001), Gilbert (2003), Santamaría Gómez (2004), Boyle and Smith (2010b), Lenz (2013), and Johnson and Stouffer (unpublished data)

[a] Not maintained as a forest fragment

[b] Used for some studies, but not part of regular censuses

Upon isolation of the fragments, *Alouatta* was the most common primate species (Lovejoy et al. 1986; Rylands and Keuroghlian 1988), a pattern that has continued for three decades (Table 5.2) and is likely the result of their highly flexible diet (Gilbert 2003; Rylands and Keuroghlian 1988). *Ateles*, *Sapajus*, and *Chiropotes* have been the least common species in the fragments due to the habitat requirements of highly frugivorous species; indeed the degree of frugivory was the primary characteristic predicting a primate species' vulnerability in the BDFFP fragments (Boyle and Smith 2010b).

Although sampling effort has not been equally distributed across the three decades of research, there appears to be an increase in the number of species using the fragments through time. Recent recolonizations of the forest fragments have occurred by *Ateles*, *Sapajus*, and *Chiropotes*, with *Chiropotes* consistently present in two of the 10-ha fragments for periods of several years. It is thought that these fragment recolonizations are principally related to an increase of secondary growth in the matrix (Boyle and Smith 2010b) that allows for arboreal travel. All six species have been noted traveling arboreally through the tall secondary-growth matrix at one time or another (Boyle 2008a; Gilbert and Setz 2001; Lenz 2013), and researchers have witnessed *Alouatta* (Santamaría Gómez 2004), *Sapajus* (Rylands and Keuroghlian 1988) and *Saguinus* (Boyle 2008a; Gilbert 1994b, 2003; Rylands and Keuroghlian 1988) crossing the matrix terrestrially. In terms of population density differences between secondary and undisturbed primary forest, *Sapajus* and *Saguinus* were more common in secondary forests, *Alouatta*, *Ateles*, and *Chiropotes* were more common in undisturbed primary forest, and *Pithecia* was rare in both habitats but appeared to be evenly distributed across them (Lenz 2013).

Prior to 2003, primates had been spotted in only one 1-ha fragment (no. 1104), but *Alouatta* and *Chiropotes* were first documented in a second 1-ha fragment (no. 2107) in 2003 (Boyle and Smith 2010b). Although the single *Chiropotes* from 2003 disappeared from no. 2107 and was never spotted again in the fragment, *Alouatta* has continued to use this fragment intermittently (Boyle and Smith 2010b; Lenz 2013). *Alouatta* rarely traveled out of the 10-ha and 100-ha fragments (Boyle 2008a; Gilbert 1994b) though they are now leaving the 10-ha fragments more frequently (Lenz 2013). There are only two fragments (nos. 2108 and 3114), both of which are 1-ha fragments, where primates had never been observed prior to 2007. *Saguinus* was spotted once during six visits in 2007 to both 1-ha fragments (Johnson and Stouffer, unpublished data), and *Sapajus* and *Saguinus* have recently been seen in the secondary growth 100–300 m from the borders of both fragments (Lenz 2013).

Home Range Reduction: Behavioral and Ecological Comparisons

All six primate species in the BDFFP area have home ranges that are larger than the 10-ha and 1-ha BDFFP fragments. The largest home range recorded to date has been 852 ha for *Sapajus* (Spironello 2001), but *Sapajus* has never been consistently present in the BDFFP fragments. On the other hand, *Chiropotes* also used a large home range (559 ha) but was consistently found in two 10-ha fragments (nos. 1202 and 2206) in 2003–2006 (Boyle et al. 2009). In the case of *Alouatta*, which had a home range of 21 ha in the continuous forest (Santamaría and Rylands 2003), there have been two *Alouatta* groups living in a 10-ha fragment (no. 1202, actual size is 13 ha) since 1985 (Boyle 2008a; Neves and Rylands 1991; Santamaría Gómez 2004). These studies suggest a high degree of home range size flexibility in *Chiropotes* and *Alouatta*. In the 1980s, three groups of *Saguinus* had overlapping home ranges in a 100-ha fragment (no. 3304), while in 100-ha areas of continuous forest the monkeys had exclusive home ranges (Lovejoy et al. 1986). Although home range reduction has led to the same patterns across all of the behavioral studies to date (e.g., an increase in the amount of time spent resting in the smaller forest fragments), other patterns have been species-specific (e.g., smaller group sizes of *Chiropotes*, but not *Alouatta*, in forest fragments).

Group Size and Density

Chiropotes, which has groups of up to 35 individuals at the BDFFP, lived in groups of three to four individuals in 10-ha fragments nos. 1202 and 2206 (Boyle and Smith 2010a). *Alouatta* (Gilbert 1994b; Santamaría Gómez 2004; Santamaría and Rylands 2003) and *Pithecia* (Setz 1993; Setz and Gaspar 1997), which do not typically have large group sizes, did not experience such reductions in the fragments. All sightings of *Ateles* in a 10-ha fragment (no. 1202) (Boyle 2008a; Gilbert 2003) and 100-ha fragment (no. 2303) (Lenz 2013) have been of single individuals that were not permanent residents of the fragments.

Although the smaller forest fragments have had fewer primate species than larger fragments and continuous forest, densities of individual species have been greatest in the forest fragments. This pattern was present for all primate species present in the forest fragments in the 1980s (Rylands and Keuroghlian 1988), as well as during subsequent species-specific studies (Table 5.3). While at first it may seem that increased densities are the result of groups being “trapped” in the fragments, it is possible that reduced interspecific competition due to the decrease in primate species richness allows the species that can utilize the fragments to do so at higher densities than are normally found in the nearby continuous forest.

Living at greater densities can lead to greater parasite loads, as was found for *Alouatta* (Gilbert 1994b, 1997). Gilbert (1997) also noted specific actions by *Alouatta* that were thought to be parasite-avoidance behavior: defecation in areas where there was little underlying vegetation and use of specific defecation sites in both the continuous forest and the forest fragments. Research on *Alouatta* seed dispersal found that, in addition to specific defecation sites, the monkeys also use some random sites (Santamaría Gómez 2004).

Table 5.3 Primate behavioral and ecological comparisons: Forest fragments versus continuous forest

						Activity budget					
Species	Size class	Reserve	Behavioral data collection months	Group size	Density (ind./ha)	% Resting	% Feeding	% Moving	% Other	List of food species?	Citations
Alouatta											
	1	1104	01/2002–01/2003	5–6	2.4	70.9	15.7	11.0	2.4	Yes	Santamaría Gómez (2004)
	10	1202	09/1984–01/1985	8	1.0	67	22	11	–	Yes	Neves and Rylands (1991)
	10	1202	01/2002–01/2003	5–6	1.0	65.9	21.5	10.7	1.9	Yes	Santamaría Gómez (2004)
	Continuous	Km 41	07/1998–12/1998	7	0.3	67.5	22.2	8.8	1.5	Yes	Santamaría and Rylands (2003)
	10	1202	10/1991–06/1993	12	1.2	61.9	23.8	14.3	–	Yes	Gilbert (1994a)
	10	2206	10/1991–06/1993	5	0.5	67.9	17.9	14.2	–	Yes	Gilbert (1994a)
	10	3209	10/1991–06/1993	7	0.7	63.2	21.0	15.8	–	Yes	Gilbert (1994a)
	100	2303	10/1991–06/1993	6, 6, 7[a]	0.2	56.5	28.3	13.0	2.2	Yes	Gilbert (1994a)
	100	3304	10/1991–06/1993	4, 6, 8[a]	0.2	62.5	20.8	12.5	4.2	Yes	Gilbert (1994a)
	Continuous	Km 41	10/1991–06/1993	5, 5, 6, 7[a]	0.2	54.4	26.0	17.4	2.2	Yes	Gilbert (1994a)
Chiropotes											
	1	2107	08/2003	1	0.6	67.2	25.0	7.8	0.0	No	Boyle and Smith (2010a)
	10	1202	07/2003 01/2005–04/2006	3–4	0.3	51.7	30.7	16.5	1.1	Yes	Boyle and Smith (2010a); Boyle et al. (2012)
	10	2206	07/2003, 01/2005–04/2006	4	0.4	49.2	28.1	20.5	2.1	Yes	Boyle and Smith (2010a); Boyle et al. (2012)

(continued)

Table 5.3 (continued)

Species	Size class	Reserve	Behavioral data collection months	Group size	Density (ind./ha)	Activity budget % Resting	 % Feeding	 % Moving	 % Other	List of food species?	Citations
	100	2303	07/2003, 01/2005–04/2006	8–12	0.1	35.4	27.6	33.1	4.0	Yes	Boyle and Smith (2010a); Boyle et al. (2012)
	100	3304	07/2003, 01/2005–04/2006	13–14	0.1	55.9	8.9	27.7	7.4	Yes	Boyle and Smith (2010a); Boyle et al. (2012)
	Continuous	Km 41	07/2003, 01/2005–04/2006	17–33	0.04	26.3	31.1	37.9	4.6	Yes	Boyle and Smith (2010a); Boyle et al. (2012)
	Continuous	Cabo Frio	07/2003, 01/2005–04/2006	14–35	0.07	40.3	23.2	30.9	5.6	Yes	Boyle and Smith (2010a); Boyle et al. (2012)
Pithecia											
	10		02/1985–01/1991	6–7	0.7	31[b]	24.8[b]	42.6[b]	1.2[b]	Yes	Setz (1993)

[a] Multiple groups

[b] Average of dry- and wet season data

Activity Budget, Diet, and Use of Space

Santamaría Gómez (2004) found that *Alouatta* rested more and fed less in a 1-ha fragment (no. 1104) than in a 10-ha fragment (no. 1202) and, although more plant species were consumed in the larger fragment, a greater richness and diversity of flowers were consumed in the smaller fragment. She also found that *Alouatta* increased its consumption of flowers during periods of fruit scarcity. The amount of fruit and number of fruiting species consumed were similar between the two groups, though the monkeys in the larger fragment visited more fruiting trees (Santamaría Gómez 2004).

Chiropotes spent more time resting and less time traveling in the smaller fragments (Boyle and Smith 2010a). There were no differences in the amount of time spent feeding, but there was very little overlap in dietary species among the six groups of *Chiropotes*. Bearded sakis in the 10-ha fragments consumed plant species that were ignored by those in the larger forested areas (Boyle et al. 2012). In the smaller fragments, *Chiropotes* also traveled shorter daily distances, revisited feeding trees more often throughout the day, and used the forest in a more uniform manner suggesting that the monkeys were maximizing the amount of forest available (Boyle et al. 2009). *Pithecia* spent more time foraging and traveling in the dry season, but traveled greater distances and had a more diverse diet in the rainy season (Setz 1993).

In the undisturbed primary forest surrounding the ranches, Lenz (2013) found positive edge effects in *Alouatta*, *Chiropotes*, *Saguinus*, and *Sapajus*, neutral edge effects in *Pithecia*, and negative edge effects in *Ateles*. This study also found that body size was the only trait that predicted primate presence in secondary-growth forests and that there were differences in microhabitat use by the primate species in mature forests, but that these differences tend to break down in secondary forests (Lenz 2013).

Seed Dispersal

Andresen (2002) found that 64 % of *Alouatta* fecal samples collected at a continuous forest site (Km 41) during a 25-month period contained the seeds of a total of 137 plant species and that the number of seeds present varied seasonally and annually. The rates of dung removal and seed burial were greater and the rates of seed predation were lower in the continuous forest than in 1-ha and 10-ha fragments (Andresen 2003). Santamaría Gómez (2004) found 146 species, including seeds less than 3 mm in length, in 342 fecal samples from five *Alouatta* groups (continuous forest: 3 groups; fragments: 2 groups). She concluded that *Alouatta* play important roles as seed dispersers in the continuous forest and in forest fragments, although after approximately 1 year seedling survival was greater in the continuous forest and in the 10-ha fragment (no. 1202) than in the 1-ha fragment (no. 1104). While dispersal distances were also greater in the 10-ha fragment than in the 1-ha fragment, seeds were usually dispersed beyond the parental tree's crown in both fragment sizes. Since this *Alouatta* group occasionally moved between the 1-ha fragment and the continuous forest, some of the seeds consumed in the continuous forest were dispersed in the forest fragment. Such findings highlight the importance of having a matrix that seed dispersers can transverse. Furthermore, seeds from unripe and ripe fruit that were dropped by *Chiropotes* during feeding bouts germinated in ex situ germination trials; these seeds represented 26 plant species (Barnett et al. 2012). These results indicate that even primates that are often considered seed predators (i.e., *Chiropotes*) may also assist with primary seed dispersal.

Predation

Although predation pressures have not been quantified in the continuous forest and the BDFFP fragments, predation does exist. In the mid-1980s, Keuroghlian (pers. comm.) witnessed a predation attempt by two tayras (*Eira barbara*) on a group of *Sapajus* in a 100-ha fragment (no. 3304). Gilbert (2000) noted a successful predation attempt by a crested eagle (*Morphnus guianensis*) on a juvenile *Pithecia* in a 100-ha fragment (no. 2303), and an unknown species of eagle attacked an adult *Alouatta* in a 1-ha fragment (no. 1104) (Santamaría Gómez 2004). Lenz and dos Reis (2011) documented a successful predation attack on a juvenile female *Chiropotes* by a harpy eagle (*Harpia harpyja*) in continuous forest, and they discuss two previous harpy eagle predation attempts in continuous forest with unknown outcomes, one attempt on *Alouatta* and another on *Chiropotes*, while noting separate observations of harpy eagles with carcasses of both *Alouatta* and *Chiropotes*. Lenz also recorded a harpy eagle in a 100-ha fragment (no. 2303) and has a probable record in a 10-ha fragment (no. 1202), illustrating that the largest avian predator at the site at least occasionally visits forest fragments (Lenz and dos Reis 2011).

Primate Conservation

We have documented the presence of all six primate species in the BDFFP area, but unfortunately there has been a recent increase in deforestation, hunting, fires, and development near the BDFFP reserves and along the BR-174 highway that runs through the BDFFP study area (Laurance and Luizão 2007). These activities threaten the conservation of the primates living in the BDFFP sites and surrounding forested areas, especially those species (e.g., *Ateles*) that are most vulnerable to habitat fragmentation and hunting pressure.

The presence of secondary growth in the matrix, at least enough to form corridors, may be key to encourage the movement of primates throughout the landscape. Such corridors may be critical for species that do not cross open areas terrestrially.

Furthermore, the presence of primates in the smaller 10-ha and 1-ha forest fragments, even if only temporarily, suggests that these fragments provide resources for the monkeys. Increasing the permeability of the matrix may also significantly increase primate dispersal and help to speed forest regeneration via seed dispersal by the primates.

Conclusions and Future Directions

Research at the BDFFP has provided great insight into the use/avoidance of forest fragments by a community of six primate species. Ten major findings include: (1) Species do not respond to forest fragmentation in the same manner; (2) Larger fragments have greater primate species richness than the small fragments (yet the larger BDFFP fragments are also less isolated); (3) Several species will cross a young secondary growth matrix, but all six species use the tall secondary growth matrix (to differing degrees); (4) Frugivores are less likely to be in the forest fragments, but some frugivores are regular inhabitants of 10-ha fragments; (5) Primates that live in the fragments live at greater densities in the smaller fragments than in the continuous forest; (6) *Alouatta* groups in fragments have higher endoparasite loads; (7) *Alouatta* and *Chiropotes* exhibit different activity budgets in forest fragments than they do in continuous forest, with the main difference being an increase in resting; (8) Monkeys play important roles as seed dispersers in all forest areas, but seedling survival is greatest in the continuous forest; (9) Fragmentation has not alleviated the predation pressure that primates face in continuous forest, as predation does occur in the forest fragments; and (10) The human population surrounding the BDFFP, along with the associated negative anthropogenic impacts on the flora and fauna, poses a growing conservation threat due to increased hunting and habitat loss.

Although much has been learned about the primates of the BDFFP, more studies are necessary. First, there is a need for regular, methodological primate censuses in the forest fragments, the matrix, and the continuous forest. Primate censuses occurred throughout almost all of the forest fragments in the 1980s, 1990s, and 2000s, but there have been gaps in the data where data are either present for only a few forest fragments or are solely based on opportunistic primate sightings. In addition to the primate censuses, long-term phenological studies are necessary in order to evaluate changes in food availability.

Second, there is still little known about the behavior and ecology of many of the species living in the study area. For example, species that are rarely present in the forest fragments (e.g., *Ateles*) and those that spend much of their time in the regenerating matrix (e.g., *Saguinus*) have not been studied. Since many of the species travel in and out of the forest fragments, future studies of the monkeys' use of the landscape (e.g., use of the matrix) would provide important information regarding the overall primate community dynamics at BDFFP. Lenz (2013) conducted primate and plant censuses in the secondary-growth matrix, but there is a need for future studies that address the interactions between individual species and the regenerating matrix at a finer resolution. For example, we suggest a systematic examination of how the riparian corridors (*igarapes*) in the matrix are used by the six primate species.

Third, the increased human presence (and the resulting changes in the landscape) in Amazônia means that it is crucial for *all* future primate research to assess the impact of increased human activities on primate behavior, ecology, and conservation.

Finally, BDFFP researchers should compare their data with research from other areas of the world in order to better determine which primate responses to forest fragmentation and regeneration are site-specific and which are universal.

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Chapter 6
Lessons from Los Tuxtlas: 30 Years of Research into Primates in Fragments

Jurgi Cristóbal-Azkarate and Jacob C. Dunn

Abstract The region of Los Tuxtlas in the state of Veracruz, southeast Mexico, represents the northernmost limit of tropical rainforest in the Americas and is home to populations of two primate species, the Mexican howler monkey (*Alouatta palliata mexicana*) and the Mexican spider monkey (*Ateles geoffroyi vellerosus*). Los Tuxtlas, like many other regions throughout the tropics, has suffered from extensive habitat loss and fragmentation. It was in this region that the alarm was first raised over the threat that forest fragmentation may signify for primates, and where primatologists first began studying how this phenomenon affects wild primate populations. These early efforts have been continued by subsequent generations of primatologists, making Los Tuxtlas one of the most important regions in the world in terms of research into primates in fragments. In this chapter we will analyze the history and development of the studies of primates in fragments in Los Tuxtlas and summarize the main lessons and recommendations that have resulted from these studies. Finally, we will outline the most important gaps in our knowledge in the study of primates in fragments in the region and make some suggestions for future directions for research.

Los Tuxtlas Biosphere Reserve

The region of Los Tuxtlas in the southeast of Veracruz, Mexico (18°37′–18°35′N, 95°08′–95°05′W), is formed from a mountainous mass of volcanic rock elevated above the plains of the Gulf of Mexico (Fig. 6.1). The region represents the northernmost limit of tropical rainforest in the Americas and was decreed a Biosphere

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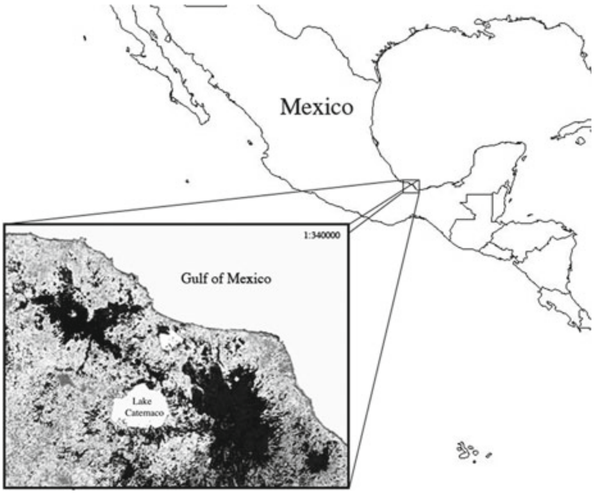

Fig. 6.1 Location of the Los Tuxtlas Biosphere Reserve, Veracruz, Mexico. *Black* areas represent mature forest and old secondary forest, *dark grey* areas young secondary forest, and *light grey* areas pasture and agricultural fields. Ocean and lakes are presented in *white*

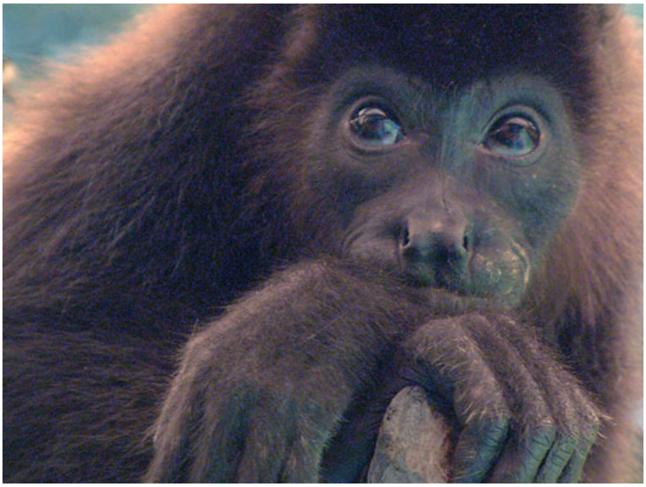

Fig. 6.2 The Mexican howler monkey *Alouatta palliata mexicana*. Photo by Jurgi Cristóbal-Azkarate

Reserve in 1998 owing to its biological and cultural importance (Laborde 2004). The reserve covers 155,122 ha and is home to populations of two primate species, the Mexican howler monkey (*Alouatta palliata mexicana*) (Fig. 6.2) and the Mexican spider monkey (*Ateles geoffroyi vellerosus*) (Fig. 6.3). Los Tuxtlas is now considered the northernmost limit in the distribution of both of these taxa. Although there are reports that *A. g. vellerosus* was previously distributed even further north (Estrada

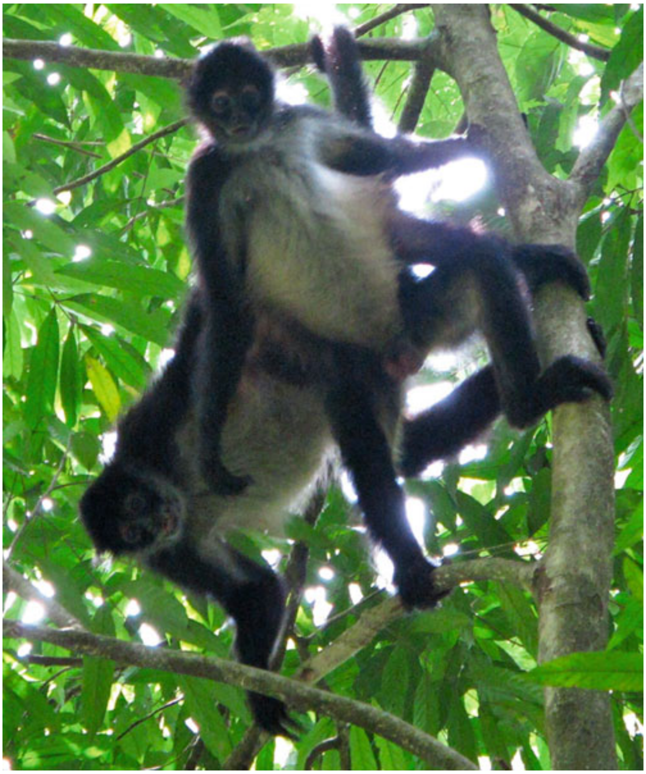

Fig. 6.3 Mexican spider monkey (*Ateles geoffroyi vellerosus*) males. Photo by Jurgi Cristóbal-Azkarate

and Coates-Estrada 1984), this subspecies is now considered to be locally extinct in the north of Los Tuxtlas. The climate is generally warm and humid, with a mean annual temperature of 21 °C and rainfall between 3,000 and 4,600 mm (Soto 2004). The original dominant vegetation at altitudes below 700 m asl was tropical rainforest. However, Los Tuxtlas, like many other regions throughout the tropics, has suffered from extensive habitat loss, transformation, and fragmentation, principally as a result of cattle farming. By 1996, approximately 75 % of the original habitat had been lost, 20 % remained in the form of isolated fragments of vegetation, and only 5 % remained as continuous rainforest (Estrada and Coates-Estrada 1996). Today, at least 88 % of the original forest cover is thought to have been lost (Guevara-Sada et al. 2004) and the little remaining forest is surrounded by a matrix of cattle pastures and croplands (Castillo-Campos and Laborde 2004). Both subspecies of primates found in Los Tuxtlas are currently listed as Critically Endangered by the International Union for the Conservation of Nature, principally as a result of widespread habitat loss and fragmentation throughout their natural range (Cuarón et al. 2008).

Studies of Primates in Fragments in Los Tuxtlas

The threat that habitat loss and fragmentation represented for the conservation of primates did not go unnoticed by Alejandro Estrada and Rosamond Coates of the Biological Field Station "Los Tuxtlas" of the National Autonomous University of Mexico (UNAM), and in 1984 they published an article entitled, "Some observations on the present distribution and conservation of *Alouatta* and *Ateles* in Southern Mexico" in the *American Journal of Primatology* (Estrada and Coates-Estrada 1984). In this article the authors described how the extensive deforestation in southeast Mexico, including Los Tuxtlas, was forcing populations of howler monkeys and spider monkeys to live in forest fragments. It was in this publication that the alarm was first raised over the threat that forest fragmentation may signify for primates (Estrada and Coates-Estrada 1984). This was followed by an article by Rodríguez Luna et al. in 1987 in which the authors attempted to explain the effect of habitat fragmentation on *Alouatta* and *Ateles* populations in the southern range of Los Tuxtlas and by another paper by Estrada and Coates-Estrada in 1988 in which the authors estimated that only about 200 *Ateles* individuals and about 1,200 *Alouatta* individuals remained in the forest fragments of Los Tuxtlas.

Despite such early alarm calls, it was not until 1994, in an article about nonflying mammals (Estrada et al. 1994), that the results of quantitative studies on the effects of forest fragmentation on primates and other mammals in Los Tuxtlas began to be published. This was followed by more specific studies of primates in fragments in 1995 (Estrada and Coates-Estrada) and 1996 (Estrada and Coates-Estrada). These have been followed by many publications from which lessons about the effects of fragmentation on primates in Los Tuxtlas have been learned. For example, in a revision (on the 1st of October 2010) of the PrimateLit database (http://primatelit.library.wisc.edu), 155 citations were found using the keywords "Los Tuxtlas." Of these, 75 (48 %) were abstracts from congresses and symposiums, 20 (13 %) were books or book chapters, and 60 (39 %) were publications in scientific journals of which 26 (17 % of total) were publications in international journals indexed by the ISI Web of Knowledge. When adding the search term *fragment** (in order to search with wildcard truncation for "fragments," "fragmented," "fragmentation," etc.) 63 citations were found: 34 (54 %) were abstracts from congresses and symposiums, 5 (8 %) were books or book chapters, and 24 (38 %) were publications in scientific journals of which 8 (13 % of total) were publications in international journals indexed by the ISI Web of Knowledge. There is a clear bias towards studies of howler monkeys, with only two abstracts from congresses and symposiums, one book chapter, and seven papers in scientific journals (one published in a journal indexed in the ISI Web of Knowledge) published about spider monkeys. In this review we will summarize the main lessons and recommendations that have resulted from these studies and will also include several other publications that are known to us, but that were not found by this search engine.

Lessons Learned

Migration

One of the first observations of the effects of forest fragmentation on the primates of Los Tuxtlas was the limitation that this process may have on their movement and dispersal (Estrada and Coates-Estrada 1984, 1996). Both howler monkeys and spider monkeys are highly arboreal and almost all of their activity is carried out in trees in the wild. Mandujano et al. (2004) observed that howler monkeys rarely travel between fragments more than 100 m apart, thus more isolated fragments receive fewer individuals through migration. Cristóbal-Azkarate et al. (2004) arrived at the same conclusion when analyzing the frequency of injuries in male howler monkeys, which has previously been related to group takeovers by solitary males. Supporting the idea that forest fragmentation disrupts the typical bisexual migratory processes in howler monkeys, Cristóbal-Azkarate et al. (2005) found practically no solitary females (1 compared to 16 solitary males) in a census of 333 individuals. Further, Arroyo-Rodríguez et al. (2008a), in a long-term study regarding the demographic evolution of a howler monkey group in Los Tuxtlas, found that three males and a female born into a study group did not migrate and two of them (a male and a female) reproduced within their natal group. What's more, those dispersal events that did occur were between the study group and the immediately adjacent group. Overall, these events could result in a loss of genetic variability for howler monkey groups, a situation that has been observed in other primate populations inhabiting highly fragmented habitats (Goossens et al. 2006; Pope 1996), and a reduction in the probability of persistence on a regional level due to the imbalance between the extinction rate and colonization rate of local populations is likely (Ovaskainen and Hanski 2004). The increase in the density of solitary males (males that have abandoned their natal groups and are solitary for a period before joining other groups or founding new groups of their own) is related to an increase in levels of testosterone in group males, and cortisol in group females (Cristóbal-Azkarate et al. 2006, 2007) which, amongst other effects, increases energy requirements and vulnerability to diseases. These effects become even more relevant when we consider that forest fragmentation, as we will see later in this chapter, also limits the amount of food resources available to primates.

Metapopulations and Island Biogeography

Forest fragments can act as "islands," isolating populations in an area of suitable habitat, surrounded by an expanse of unsuitable habitat. Estrada and Coates-Estrada (1996) found that more isolated fragments contained fewer howler monkeys and Arroyo-Rodríguez et al. (2008b) found that the probability of howler monkeys inhabiting fragments was negatively related to isolation distance in one of the landscapes considered in their study. On the other hand, in this same study no relationship was found between isolation distance and the distribution of howler monkeys in another two landscapes studied. Cristóbal-Azkarate et al. (2005) also found no relationship between isolation distance and the distribution or number of howler monkeys in fragments. Arroyo-Rodríguez and Mandujano (2009) consider that the lack of consistency in these results could be due to the way in which the isolation of fragments has typically been measured in studies. This is, in part, because other elements that are present in the anthropogenic matrix, such as isolated trees and live fences (i.e., strands of barbed wire held up by a line of trees) are generally not considered part of the useful habitat. Such elements can be important for primates not only as they facilitate the movement of individuals between fragments (Asensio et al. 2009; Estrada and Coates-Estrada 1996; Mandujano et al. 2004), but also because they themselves can be an important source of food resources (Asensio et al. 2009). This highlights the need to consider not only fragments, but also the entire surrounding habitat when evaluating the viability of primate populations in fragments.

Studies carried out in Los Tuxtlas have corroborated other maxims of Metapopulation Theory and Island Biogegraphy Theory, such as: when more fragments are occupied by primates, the total number of primates in the landscape is greater (Arroyo-Rodríguez et al. 2008b), when fragment size is greater, the number of primates in the fragment is greater (Cristóbal-Azkarate et al. 2005; Estrada and Coates-Estrada 1996) and so is the probability that the fragments will be occupied by primates (Arroyo-Rodríguez et al. 2008b; Cristóbal-Azkarate et al. 2005). Furthermore, according to a Population Viability Analysis (PVA) carried out by Mandujano and Escobedo-Morales (2008) in Los Tuxtlas, the probability of extinction of a population of howler monkeys depends exponentially upon the size of the fragments they inhabit.

The studies carried out in Los Tuxtlas have analyzed the reason why fragment size appears to be the most important variable explaining the distribution, size, and viability of populations of howler monkeys. As demonstrated by Cristóbal-Azkarate and Arroyo-Rodríguez (2007), the home range of howler monkeys is larger in bigger fragments. Furthermore, population density is lower in bigger fragments (Cristóbal-Azkarate et al. 2005; Estrada and Coates-Estrada 1996), all of which reduces the availability of resources for howler monkeys in smaller fragments. In this sense, Estrada and Coates-Estrada (1996) showed spider monkeys are more susceptible to habitat loss than howler monkeys, which they related to their more frugivorous diet.

Diet and Activity

Studies in Los Tuxtlas have extended beyond population surveys. More recently, several studies have focused on the behaviour and ecology of primate groups. Most of these studies focus on the effects of forest fragmentation on the primate diet. For example, Rodríguez-Luna et al. (2003) report an increase in the consumption of leaves, as well as in feeding time and travelling time, associated with an increase in the population density of a group of howler monkeys living on an island in Los

Tuxtlas. Asensio et al. (2007a) also found that the same group of howler monkeys spent more time consuming leaves, feeding, and travelling than another group living in a larger forest fragment at a lower population density. However, Juan et al. (2000) found no real differences in diet and activity pattern between three groups with different home range areas. Cristóbal-Azkarate and Arroyo-Rodríguez (2007) found a similar pattern in a meta-analysis of 20 groups of howler monkeys in Los Tuxtlas. This may be related to the fact that a smaller home range does not necessarily contain fewer resources than a bigger one (Gillespie and Chapman 2001). In this sense, studies in Los Tuxtlas have found that variables, such as the diversity of plant species in a fragment (Cristóbal-Azkarate et al. 2005; Estrada and Coates-Estrada 1996), and the availability of big trees (diameter at breast height > 60 cm) (Arroyo-Rodríguez et al. 2007) are related to the presence and abundance of primates in fragments. Another important variable not considered by these studies is the availability of fruit, which, as in the case of big trees, is greater and generally more constant in bigger fragments (Arroyo-Rodríguez and Mandujano 2006; Dunn 2009). Dunn et al. (2009) analyzed the effect of the availability of big trees and fruit on the diet and activity of howler monkeys and found that a greater availability of such resources resulted in more time being spent consuming both of these resources, which had important effects on diet and activity. When consuming more fruit and from bigger trees, howler monkeys needed to visit fewer food sources in order to meet their daily requirements. As a consequence, they travelled less, rested more, and spent less time feeding. Dunn et al. (2013) also found that this increase in feeding effort associated with less time consuming fruit (more leaves) and with feeding from smaller trees was related to greater levels of stress as measured by faecal glucocorticoid levels. Moreover, the authors observed that the increased levels of stress were particularly significant for females, which may help explain the low proportion of immatures to females found in howler monkeys groups living at high population densities in forest fragments in Los Tuxtlas (Cristóbal-Azkarate et al. 2005).

Parasitology

Several studies in Los Tuxtlas, have attempted to analyze the effects of forest fragmentation on parasite loads in primates. For example, high population densities of howler monkeys in forest fragments in Los Tuxtlas have been related to increases in gastrointestinal parasite loads (Aguilar-Cucurachi et al. 2007), and the prevalence of these parasites (i.e., the proportion of parasitized individuals) has also been found to be higher in howler monkeys inhabiting forest fragments than those inhabiting continuous forest (Trejo-Macías et al. 2007). In both studies, these phenomena were suggested to be a consequence of the increased population density of howler monkeys in fragments, which favours the transmission of parasites. However, Cristóbal-Azkarate et al. (2010) found that parasite prevalence was not affected by fragment size and parasite species richness was lower in smaller fragments. Finally, Valdespino et al. (2010) studied the relationship between different forest fragment characteristics (including host density and fragment size) and parasite loads in howler monkeys and did not find a general pattern. However, supporting the previous studies, they found that although parasite richness was lower, prevalence and density were both higher than values reported for howler monkeys in conserved forests.

Ecological Interactions

The final area of primatological research in Los Tuxtlas has been related to the ecological interactions between primates and other animal species. For example, the presence of dung beetles has been shown to be closely related to the presence of howler monkey dung in forest fragments (Estrada et al. 1999), while howler monkey dung has also been shown to be an important source of *Ficus perforata* seeds and even structural material for nest building in canopy ants in forest fragments (Martínez-Mota et al. 2004). Further, Asensio et al. (2007b) suggest that reduced home range area in forest fragments may result in more frequent interactions and increased tolerance between sympatric howler monkeys and coatis (*Nasua narica*) in Los Tuxtlas.

Recommendations from the Literature

The studies of primates carried out in Los Tuxtlas have not only investigated the way in which primates are affected by the fragmentation of their habitat, but have also formulated a series of recommendations regarding the ways in which the negative consequences of this process may begin to be mitigated. The first of such recommendations was to increase the connectivity of the landscape, both to promote the movement of individuals between subpopulations (Cristóbal-Azkarate et al. 2004, 2005; Estrada and Coates-Estrada 1996; Mandujano et al. 2004) and to increase the accessibility of fragments not occupied by primates, and in this way increase the amount of habitat available to them (Cristóbal-Azkarate and Arroyo-Rodríguez 2007; Cristóbal-Azkarate et al. 2005; Estrada and Coates-Estrada 1996).

In this sense, the numerous live fences that delimit the fields and plantations in the matrices of Los Tuxtlas may play a key role in the conservation of primates (Asensio et al. 2009). In order that the live fences found in Los Tuxtlas may play such a role, it is necessary that they are widened and enriched with different tree species, as this process can reduce the vulnerability of primates to predation, hunting, and other potential risks that could be greater in this kind of habitat. A solution that would meet both the interests of howler monkeys and farmers would be to persuade farmers to plant species along the fences that can be used by livestock as tree fodder as well as by howler monkeys as food. Fruit species such as *Leucaena leoucocephala* and *Brosimum alicastrum* have been shown to help maintain livestock productivity during the dry season when there is pasture shortage in the tropics (Gillespie et al. 2004; Suttie 2007) and these species are also eaten by howler monkeys in Los Tuxtlas (Cristóbal-Azkarate and Arroyo-Rodríguez 2007). However, the first measure that should be taken is an educational program with the people living in the vicinity of primate groups as to the importance of protecting endangered primates because, as demonstrated by Asensio et al. (2009), the protection offered by the landowners at any particular site may determine the tendency of primates to use elements outside of their home fragments.

Finally, although there is a general perception that agricultural activities are the principal threat to primate biodiversity in the tropics, some agricultural practices may actually favour the persistence of primate populations in human modified habitats. For example, in Los Tuxtlas both howler and spider monkeys have been reported to subsist in cacao plantations; coffee plantations; mango, citrus, and banana plantations; and in old live fences (Estrada et al. 2006). Therefore, although they are clearly no substitute for original habitat, agroecosystems may play an important role in the long-term preservation of primates in Los Tuxtlas and must be considered in landscape level approaches to conservation (Estrada et al. 2012).

Another recommendation has been to focus particular attention on protecting larger fragments, as well as increasing the size of small and medium-sized fragments (Arroyo-Rodríguez and Mandujano 2006; Arroyo-Rodríguez et al. 2008b; Cristóbal-Azkarate and Arroyo-Rodríguez 2007; Cristóbal-Azkarate et al. 2005; Dunn et al. 2009; Estrada and Coates-Estrada 1996; Mandujano and Escobedo-Morales 2008). As suggested by (Cristóbal-Azkarate and Arroyo-Rodríguez 2007), this should be done by first planting secondary and non-secondary light-demanding species consumed by primates, like *Cecropia obtusifolia* and *Ficus* spp. respectively, which could create the condition for the establishment and growth of primary species.

Finally, several studies have demonstrated the importance of big trees, both for howler monkeys (Arroyo-Rodríguez and Mandujano 2006; Arroyo-Rodríguez et al. 2007; Dunn et al. 2009) and spider monkeys (González-Zamora and Mandujano 2003; González-Zamora et al. 2009), which is why their protection is highly recommended as, despite the fact that the logging of trees is prohibited in the region, selective logging is still common both for the use of wood by the local community and for increasing the amount of land available for cattle-farming.

Future directions

Despite nearly 30 years of studying primates in Los Tuxtlas, there are an extremely limited number of publications focused on *A. geoffroyi* in fragmented landscapes. The little data that is available remains in the form of theses or grey literature in university libraries. Thus we have learned very little about how forest fragmentation affects the biology of Mexican spider monkeys other than that they appear to be more vulnerable to habitat loss than howler monkeys (Estrada and Coates-Estrada 1996) and that they depend on large trees, and consequently mature forests (González-Zamora and Mandujano 2003; González-Zamora et al. 2009). This situation is likely owing to several intrinsic attributes of this species, which make the study of this primate difficult in the wild (González-Zamora et al. 2009). Consequently, there is an urgent need for studies of Mexican spider monkeys in forest fragments.

On the other hand, the only long-term study of demographic evolution of primates in Los Tuxtlas is that by Arroyo-Rodríguez et al. (2008a) with a single group of howler monkeys. A shorter study, with fewer groups (ten groups of howler monkeys over 2 years), was carried out by Mandujano et al. (2004). However, these studies are not sufficient to tell us whether the populations of howler monkeys in Los Tuxtlas are stable, growing, or reducing. Further, they do not tell us anything about the key characteristics of fragments which are important for the persistence of primates, as we may have found the same relationships between, for example, fragment size and population size, if all of the populations were either increasing or decreasing.

What we do know is that the populations of howler monkeys in the forest fragments of Los Tuxtlas are not growing at the same rate as the population of howler monkeys introduced to an island (Agaltepec) of 8.4 ha in the same region. After initial release onto the island in 1988, this population grew from 9 to 57 individuals in just 10 years (Rodríguez-Luna et al. 2003) and in 2002 the population was estimated to be 95 individuals (Rodríguez-Luna, personal communication). The reason for this explosion in population size is probably related to the characteristics that make this population unique. We may consider that the vegetation on the island may have some particular characteristic that resulted in a superabundance of food resources. However, existing evidence suggests that this is not the case, as individuals were found to consume large quantities of leaves and items such as lianas, considered to be of secondary choice to howler monkeys (Asensio et al. 2007a, b; Rodríguez-Luna et al. 2003), and have developed strategies to minimize feeding competition, including fission–fusion feeding behaviour (Dias and Rodríguez-Luna 2005, 2006). Another reason could be the fact that their habitat is an island and that they are protected from predators. However, in Los Tuxtlas arboreal predators, such as the harpy eagle (*Harpia harpyja*), puma (*Puma concolor*), or jaguar (*Pantera onca*) are no longer present which is why it seems unlikely that this is the cause (Asensio et al. 2009). A further possibility could be that mortalities associated with migration events between fragments are common in the fragments of Los Tuxtlas, but do not occur on the island. There is evidence of predatory attacks on howler monkeys that have come to the ground to move between fragments by coyotes (*Canis latrans*) and tayras (*Eira barbara*) (Camargo and Ferrari 2007; Pozo-Montuy and Serio-Silva 2007). Finally, the fact that they live on an island may be isolating this population from infectious agents. Supporting this idea is the frequent observation of howler monkeys in forest fragments in Los Tuxtlas being parasitized by botfly larvae (up to five larvae at any one time) (Cristóbal-Azkarate et al. 2005), which have been related the death of immature individuals (Arroyo-Rodríguez et al. 2008a). However, on Agaltapec Island this parasite has only been observed sporadically in the population and never with more than two nodules at any one time (Cristóbal-Azkarate, unpublished data).

The study of the dispersal processes of both *Alouatta* and *Ateles* in fragmented landscapes is urgently needed in Los Tuxtlas. Such studies should analyze various aspects of the biology of the migrating individuals, from the distances and routes used to the diet, activity patterns, and social interactions with conspecific group members. We also consider it important to analyze the effects of infectious diseases and how fragmentation can affect parasite–host ecology. It is necessary to develop reliable diagnostic tools for the state of health of individuals. In this sense, we have already mentioned that levels of physiological stress have been related to fragmentation, particularly with the reduction in the consumption of fruit and big trees (Dunn 2009), but it would be useful to relate stress levels with other demographic parameters, such as reproductive success, fecundity, and survival, as has been done with other species of primates (e.g. Pride 2005). No genetic studies of primates in the fragments of Los Tuxtlas are available and analyses of the genetic variation within and between these isolated populations are urgently required to enable us to understand the population genetics of these critically endangered species.

Finally, it is important to mention that although there is still much to be learned about how forest fragmentation affects primates in Los Tuxtlas, it is true that we currently have a great deal of knowledge with which to implement effective conservation strategies. Despite the fact that more than a decade has passed since the region was declared a Biosphere Reserve, to our knowledge there is not a single project directed directly towards the conservation of primates in the region. Given our knowledge of not only the study species in question but also the local political, economic, and cultural conditions, we, the biologists working in the Los Tuxtlas region, are in a special position to direct our knowledge and efforts towards the development and initiation of projects that secure the future conservation of the howler monkeys and spider monkeys of Los Tuxtlas. It is time we started doing so.

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Chapter 7
Going, Going, Gone: A 15-Year History of the Decline of Primates in Forest Fragments near Kibale National Park, Uganda

Colin A. Chapman, Ria Ghai, Aerin Jacob, Sam Mugume Koojo, Rafael Reyna-Hurtado, Jessica M. Rothman, Dennis Twinomugisha, Michael D. Wasserman, and Tony L. Goldberg

Abstract Given accelerating trends of deforestation and human population growth, immediate and innovative solutions to conserve biodiversity are sorely needed. Between 1995 and 2010, we regularly monitored the population size and structure of colobus monkey populations in the forest fragments outside of Kibale National

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Park, Uganda. Through this monitoring we assessed the monkeys' gastrointestinal parasites and fecal cortisol levels. Over 15 years, we documented a rapid decline in the number of fragments that supported primates, largely as a result of tree removal. Fecal cortisol levels of primates found in the fragments were consistently higher than in populations found in the continuous forest of the national park. The fragment populations also harbored gastrointestinal parasites rarely found in the main forest and exchanged bacteria with nearby people and livestock at high rates, suggesting that fragmentation facilitates disease transmission. Fragments supported the fuelwood needs of an average of 32 people living immediately adjacent to the fragment, and partially supported families up to three farms away (~400 m, representing 576 people). Intensive fuelwood harvesting occurred when neighboring households engaged in brewing beer (an average of 9.6 % of the households), distilling gin (8.8 %), or producing charcoal (14.5 %). Our data suggest that the future of small and unprotected forest fragments is bleak; a scenario that is unfortunately typical outside protected areas in many tropical regions.

Introduction

Tropical habitats around the world are experiencing increasing stress; the majority of which results from direct (e.g., deforestation) or indirect (e.g., climate change) human activities. This increased stress is largely due to human population growth: our species has grown by 3.7 billion people in the last 50 years (Potts 2007) and is expected to reach between eight and ten billion people in the next 50 years (United Nations 2009). The majority of this growth will occur in tropical countries (Potts 2007) and will substantially increase the demands for environmental products and services (Houghton 1994). For example, the net loss in global forest area between 2000 and 2005 was ~7.3 million ha per year (~200 km^2 of forest per day, (FAO 2005)). This does not consider the vast areas being selectively logged or the forests degraded by fire. For example, during the 1997/1998 El Niño, seven million ha of forest burned in Brazil and Indonesia alone (Chapman and Peres 2001). Even when the physical structure of the forest remains intact, subsistence and commercial hunting can have a profound impact on forest animal populations. For example, it is estimated that 3.8 million primates are eaten annually in the Brazilian Amazon (Chapman and Peres 2001).

In the face of these threats, parks and protected areas have become the main tools of most national strategies to conserve biodiversity and ecosystem processes (Bruner et al. 2001). Tropical forest parks are thought to be particularly important in protecting biodiversity since they contain over half of the world's known species (Wilson 1992). However, these statistics invoke the question: What about the remaining half of the world's biodiversity? Such questioning has led a number of researchers to examine the conservation value of disturbed lands (Brown and Lugo 1994), the potential of restoration (Chapman and Chapman 1999; Lamb et al. 2005), and, given their increasing frequency of occurrence, the conservation significance of

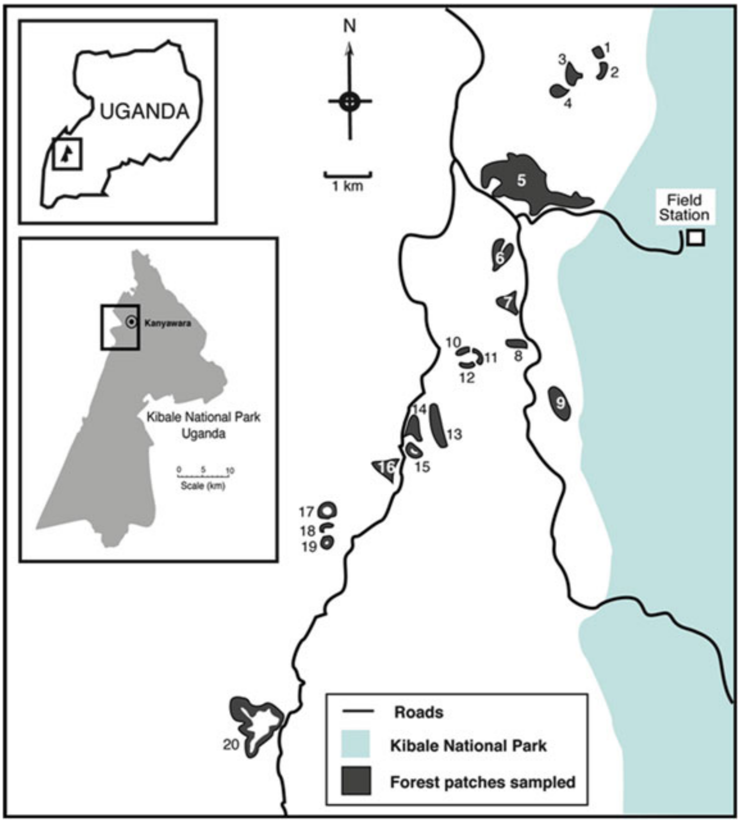

Fig. 7.1 Twenty forest patches surveyed outside of Kibale National Park, Uganda, starting in 1995 (*note*: this does not represent all forest patches in the region). *1*=Kiko #3; *2*=Kiko #4; *3*=Kiko #2; *4*=Kiko #1; *5*=Kasisi; *6*=Rusenyi; *7*=Kyaibombo; *8*=Durama; *9*=C. K.'s Durama; *10*=Rutoma #1; *11*=Rutoma #4; *12*=Rutoma #3; *13*=Rutoma #2; *14*=Nkuruba—fish pond; *15*=Nkuruba—lake; *16*=Ruihamba; *17*=Lake Nyanswiga; *18*=Dry Lake; *19*=Lake Nyaherya; *20*=Lake Mwamba. In 2010 only Lake Nyaherya, Ruihamba, Lake Nkuruba, and CK Durama still supported colobus monkeys

forest fragments (Chapman et al. 2007; Harcourt and Doherty 2005; Hartter and Southworth 2009; Marsh 2003). However, when conservation strategies rely on unprotected forest fragments to conserve biodiversity, a number of assumptions are inherent and the validity of these assumptions is largely unknown. Two of the most critical assumptions are (1) that the fragments will maintain their value to conserve biodiversity over time and (2) that the animal populations within the fragments will be healthy.

A principal objective of our research program over the last 15 years has been to test whether these assumptions are valid. We conducted our investigations in a series of community-owned forest fragments adjacent to Kibale National Park, Uganda (Fig. 7.1). We focused our research on two species of colobus monkeys: red colobus

(*Procolobus rufomitratus*) and black-and-white colobus (*Colobus guereza*). These species were chosen because the red colobus is endangered, neither species moves among forest fragments, and noninvasive methods can be used to monitor their physiological status and health (Chapman et al. 2005), making these species a valuable study system.

Forest Fragments Near Kibale National Park, Uganda

Kibale National Park (hereafter Kibale) can itself be considered a large fragment as it is 795 km^2 surrounded by agriculture, grazing land, and tea plantations. It is a mid-altitude, moist evergreen forest in central-western Uganda, Africa (0 13′–0 41′N and 30 19′–30 32′E), in the foothills of the Ruwenzori Mountains (Struhsaker 1997; Chapman and Lambert 2000). Kibale was designated a Forest Reserve in 1932 and became a National Park in 1993 (Fig. 7.2). Most of the area inside the boundary was protected to at least some degree after becoming a forest reserve (Chapman and Lambert 2000), but forested areas outside the boundary were not.

Historically the Kibale region was noted for its extensive forest and abundant big game (Naughton-Treves 1999). Historians describe western Uganda's forests as sparsely populated before the twentieth century (Osmaston 1959). The Game Department archives of 1934 state: "*The Toro district is the most difficult of the control areas and will be hard work for many years to come. There are some thirty to forty herds of elephant totaling fully 2000 animals, the majority of which live in close proximity to settlements and cultivation. This is only made possible owing to the appalling nature of the country and the density and height of the grass*" p. 319 (Naughton-Treves 1999). However, this situation soon changed and by early 1959 the area had been converted to a series of community-owned forest fragments immersed in a matrix of agricultural lands (as substantiated by early aerial photographs). These fragments tended to persist in areas unfavorable for agriculture, such as wet valley bottoms and steep hillsides; today they contain remnant populations of four of the nine diurnal primate species found in the park (Onderdonk and Chapman 2000).

We would like to stress that much of the previous work on primates living in fragmented habitats involves fragments protected from human use (Laurance and Bierregaard 1997; Tutin et al. 1997). In reality, most fragments are not protected; they are on land managed by private citizens who depend on them for resources. People around Kibale use these forest fragments for activities ranging from forest product extraction (e.g., timber, charcoal, medicinal plants) to slash-and-burn agriculture. In the Kibale region, previous studies have shown that fragments supported the fuelwood needs of an average of 32 people who lived immediately adjacent to the fragment, and partially supported families up to three farms away (~400 m), representing 576 people. Fuelwood harvesting was most intensive when neighboring households were engaged in brewing beer (an average of 9.6 % of the households), distilling gin (8.8 %), or producing charcoal (14.5 %; Naughton et al. 2006).

Fig. 7.2 A typical forest fragment surrounding a crater lake neighboring Kibale National Park, Uganda

While domestic consumers use the most plant species for fuelwood (>50), their consumption is potentially sustainable because they generally harvest fast-growing species from fallows on their own land or their neighbors' land. In contrast, commercial charcoal producers prefer old-growth hardwood species and are responsible for the greatest loss of natural forest. They access forests by finding landholders who, either willingly or through coercion, allow trees on their lands to be cleared. The impact of charcoal production is exacerbated by a license system in Uganda that undervalues natural forests and rewards rapid harvesting across large areas (Naughton et al. 2006).

The Fate of Fragments and Primate Populations

In 1995 we censused 20 forest fragments near Kibale that had been isolated for at least 36 years (Onderdonk and Chapman 2000). In each fragment we determined the presence or absence of all diurnal primate species, and estimated the population size of black-and-white colobus (since 1995) and red colobus (since 2000). We measured the fragment area, distance to the nearest fragment, distance to Kibale, and counted the number of food trees. We recensused the same fragments in 2000 (Chapman et al. 2007), 2003, and 2010. From 1995–2010 there was a drastic decline in the number of fragments occupied and in population size for both colobines (Fig. 7.3).

In 2000 and 2003 we measured all the trees (>10 cm DBH) in each fragment including all red colobus food trees to examine changes in the food available to each population. All fragments showed evidence of forest clearing; however, the extent of clearing was extremely variable (Chapman et al. 2006b). The average size of the fragments containing red colobus in 2000 was 4.4 ha (range 1.2–6.4, $n = 8$). In 2000 there were on average 99 trees/ha in each fragment (range 27–259 trees/ha), while in 2003 there were 86 trees/ha (range 30–230 trees/ha). The basal area of trees in the fragments averaged 9002 m^2 in 2000 (range 1981–39,012 m^2) and 5293 m^2 in 2003 (range 1772–28,397 m^2). The cumulative basal area of red colobus food trees was 915 m^2 in 2000 (range 317–2,430 m^2) and 535 m^2 in 2003 (42–2387 m^2). Thus, although forest change was highly variable between fragments, on average the basal area of food trees declined by 29.5 % over the 3 years. In 2000, exotic species, primarily *Eucalyptus grandis*, constituted 16 % of the food tree basal area, while in 2003 this value had risen to 28 % (Chapman et al. 2006b, 2007).

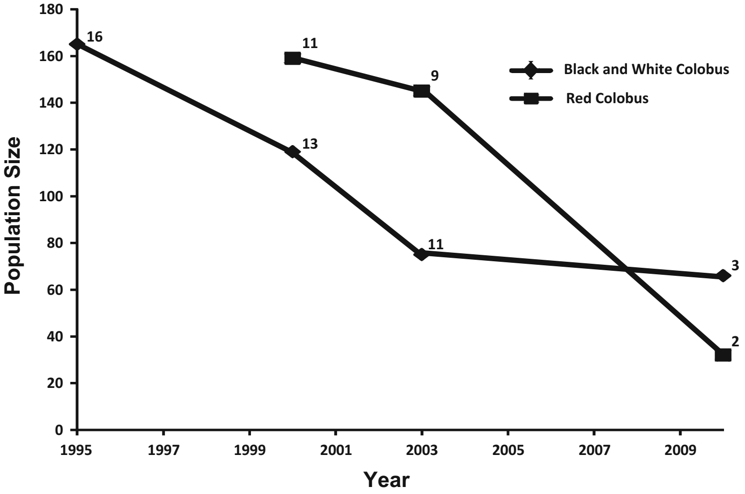

Fig. 7.3 The population size of *red* (*squares*) and *black*-and-*white* (*diamonds*) colobus in a series of forest fragments adjacent to Kibale National Park, Uganda. The number above each point is the number of fragments that the species were found at that time

The changes in the forest fragments had dramatic consequences on the resident primate populations. Black-and-white colobus populations declined by 60 % between 1995 and 2010, while red colobus populations declined by 83 % between 2000 and 2010 (Fig. 7.3). Over the 15 years many of the initial fragments were largely cleared and resident primate populations were no longer present. In fact by 2010, 92 % of the colobus monkeys were found in only two fragments, and 65 % of all the monkeys were found in one specific fragment—Lake Nkuruba. This site is unique because in 1991 a small-scale ecotourism operation, established by C. Chapman, L. Chapman, and M. Steenbeek, maintained the forest and improved the local communities' welfare. After a short period of external input, the ecotourism operation was turned over to the local community that it is still protecting this forest fragment.

Health of the Primates in the Fragments

The Kibale EcoHealth Project (http://svmweb.vetmed.wisc.edu/KibaleEcoHealth/) was founded in 2004 by Tony Goldberg as an ecological study of animal and human health in the Kibale region. The project is an attempt to evaluate the "ecohealth paradigm" using scientific rigor. Ecohealth refers to the idea that human and animal health are inherently connected to each other and to the physical environment (Goldberg et al. 2012). Thus, improving the health of any component of the animal health, human health, and environment triangle will improve the health of the other two.

Some of our initial studies focused on gastrointestinal parasites. We documented that elevated parasite infections were associated with logging or an increase in the proportion of forest edge (Chapman et al. 2006a, 2010; Gillespie et al. 2005). When we turned to studying forest fragments, we discovered that indices of animal health were affected in a number of ways. We were particularly interested in whether food availability and parasite infections synergistically affected red colobus abundance and if these animals showed physiological signs of stress. We monitored gastrointestinal parasites, evaluated faecal cortisol levels (an indicator of physiological stress), and determined changes in food availability in eight fragments between 2000 and 2003. During this time, the red colobus populations in fragments declined by 21 %. The change in red colobus population size was correlated both with food availability and a number of indices of parasite infections. In addition, the stress levels of groups inhabiting the fragments were approximately 3.5 times greater than those living within Kibale. In fact, red colobus from Kibale seldom had cortisol values as high as the lowest values of those in fragments (Chapman et al. 2006b).

Our interest in the ecohealth concept led us to focus on possible human–primate disease transmission. Microscopic evaluation of gastrointestinal helminths is inadequate for understanding cross-species transmission because many helminths are host specific, yet morphologically indistinguishable at the species level. This was clearly illustrated by elegant studies of nodular worms, *Oesophagostomum bifurcum*, in West Africa: Traditional parasitological analyses suggested a transmission link between humans and nonhuman primates, but subsequent molecular analyses demonstrated that the parasites infecting nonhuman primates were entirely distinct from those infecting humans (Gasser et al. 2006, 2009). We therefore turned to the common gastrointestinal bacterium *Escherichia coli*, which inhabits the gastrointestinal tracts of all vertebrates, but is highly variable genetically and clinically (Donnenberg 2002). Using this system we documented that people living near forest fragments harbored *E. coli* bacteria approximately 75% more similar to bacteria from primates living in these fragments than to bacteria from primates living within Kibale (Goldberg et al. 2008b). Furthermore, genetic similarity between bacteria from human, livestock, and primates increased by approximately threefold as anthropogenic disturbance within fragments increased from moderate to high (Goldberg et al. 2008b).

While *E. coli* is typically not pathogenic, other microbes can cause significant clinical effects (Bonnell et al. 2010; Garcia 1999). For example, we found the pathogenic gastrointestinal protozoans *Giardia duodenalis* and *Cryptosporidium parvum* in red colobus living in fragments (Salzer et al. 2007). In the case of *G. duodenalis*, molecular analyses indicated two genotypes: one (assemblage B IV) appears to move from people to red colobus, while the other (assemblage E) appears to move from livestock to red colobus (Johnston et al. 2010). Of perhaps even greater concern for public health, we have subsequently identified novel pathogens in this system (Goldberg et al. 2008a; Goldberg et al. 2009). We found evidence of a previously uncharacterized *Orthopoxvirus* in Kibale red colobus; this pathogen is similar but distinct from cowpox, vaccinia, and monkeypox viruses (Goldberg et al. 2008a). With further investigations, we found three novel simian retroviruses in these red colobus (Goldberg et al. 2009), related to viruses in West Africa that are known to be zoonotic (Wolfe et al. 2004; Wolfe et al. 2005). This last finding is particularly troublesome since primates in the forest fragments near Kibale have regular antagonistic interactions with people that can result in people receiving bites and scratches (Goldberg et al. 2006; Skorupa 1988). As a result, this setting appears to be ideal for novel zoonotic transmissions to occur.

Discussion

Our results paint a grim picture of the conservation value of the fragmented landscape near Kibale National Park, Uganda. As a result of resource extraction, most fragments did not last more than the 15 years of the study. Furthermore, the primates in these fragments were generally unhealthy and physiologically stressed. Because most fragmented landscapes are not in protected areas, but are locally owned and used by the communities for extractive purposes, our results are generally representative of other landscapes with similar human density and demographic trends (Jacob et al. 2008). However, for other primate species that can use the matrix more effectively or are not forest dependent our findings may not prove general. The fragmented landscape near Kibale is therefore of little conservation value for tropical forests and forest-dependent species, such as colobus monkeys. However, these findings raise five interesting questions.

First, while the fragmented landscape near Kibale appears to be of limited conservation value, it raises the question of when conservation effort should be applied to such habitats. In the case of the Kibale region, there is no evidence that the fragments support wildlife that is not present within the national park. Therefore, it seems reasonable to suggest that conservationists should concentrate their efforts to sustaining the protected area, rather than the surrounding fragments. In the case that endemic species are present within fragments, an argument can be made to protect these fragments. A similar argument could be made if particular fragments have the additional value of facilitating movement corridors. Our study demonstrates the problems associated with protecting small areas of habitat, especially with regard to the declining health and fitness of its inhabitants. However, given the threat of infectious disease, isolated fragmented populations may hold value as safeguards against future epidemics that could occur in larger populations. In the Kibale situation translocations of the red colobus is not an option because there are no known suitable habitat nearby to translocate the animals to. Similarly, it is not possible to manage this region as a metapopulation because it is habitat clearing that causes single populations in the metapopulations to go extinct, thus, there is no habitat remaining to recolonize.

Second, our study raises the question of what minimum fragment size will permit the long-term health and survival of primates in forest fragments. This question has been of interest since the conservation value of fragments was first considered (Lande 1995; Soule 1987). Our data can be used to evaluate this question over 15 years. This is insufficient to address any genetic issues; however, a large and relatively stable population continued to exist in the one fragment where the canopy trees were not cut: Lake Nkuruba. The persistence of this population suggests that the most essential short-term issue for survival of colobus populations is simply to maintain the forest as intact as possible.

A third question that arises from our study is what primate species are most resilient to living in fragmented landscapes. During the last census in 2010, we asked local agriculturalists if they had seen primates in the study fragments. Many reported that while colobus were no longer present, red-tailed monkeys (*Cercopithecus ascanius*) frequently visited the fragment. Unlike colobus, red-tails travel among fragments and can forage and persist successfully in the agricultural matrix outside of the fragments. Similarly, Pozo-Montuy et al. (2011) reports that howler monkeys (*Alouatta palliata*) in Southern Mexico are capable of using very modified landscapes that have very small fragments and few native trees. They survive by travelling among trees and shrubs (even travelling along barbed-wire fences) and using exotic trees as food sources.

Fourth, our research leads to the question of what conditions create unhealthy primates. In the fragments outside Kibale, poor nutrition is associated with increased stress levels, which are both related to elevated gastrointestinal parasite infections (Chapman et al. 2006b). Similarly, we have demonstrated that contact with humans and livestock can lead to the acquisition of benign and pathogenic parasites by red colobus (Goldberg et al. 2008b; Johnston et al. 2010). Future studies should examine how other human-induced or mediated factors may lead to elevated stress and disease in fragments (e.g., hunting, shared water sources, selective harvesting of food trees).

Lastly, to successfully protect community-owned fragments we need to know what leads community members to degrade forest fragments and what can be done to prevent such activities. This is stepping out of the classical framework of biological research, but such interdisciplinary research is needed to conserve fragmented landscapes where socioeconomic conditions create demands for forest products and new arable land.

To conclude, our study documented a dramatic rate of fragment clearing and colobus decline in 15 years. The primates in this group of fragments were physiologically stressed and had high disease levels, some of which were clearly transmitted among humans, livestock, and primates. We expect that all colobus will disappear from these fragments within the next few years; the only exception is the fragment at Lake Nkuruba that is protected by a small-scale ecotourism operation. The persistence of the forest and primates at this site highlights the potential role that community-based conservation projects can play in protecting forests and wildlife. If current or future researchers find themselves in the situation that we happened upon 15 years ago, they need to think carefully about the appropriate action to take. Reversing the trends of clearing forest and declining primate populations, such as the ones we documented, requires a major conservation effort on a scale and nature that is rarely feasible. Specifically, halting fragment clearing requires the cooperation of local people. To do this, alternative sources of income must be found (e.g., ecotourism), fuelwood supplies from elsewhere must be made available (e.g., a large scale woodlot project, or solar stoves could be provided), and a great deal of effort must be placed on education and outreach. In reality, it is unlikely that a project of this magnitude could be initiated unless the fragments contained species of very special value. Sadly, we believe that this is the reality of biodiversity conservation outside of protected areas in many tropical areas of the world. Thus, if the situation in fragments is well illustrated by the title “Going, Going, Gone” and this pattern is general, the question needs to be asked, should conservationists just place their efforts into protected areas? While the logical extension of our study would suggest that the answer to this question is yes, we have hope that in some locations and at some future time the situations will be different, so that conservation of such community-owned fragments will become a profitable conservation strategy. As we conduct more research into community needs and restoration methods, this may become a reality.

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Section III
Landscape, Metapopulations, and the Matrix Summary

Laura K. Marsh

It is important to not only consider scale in the evaluation of landscapes for the overall metapopulation picture (c.f., Chap. 2), but to understand within a region where the primates do occupy, can occupy, or do not occupy remnants. For a regional understanding it is important to ask how primates use the matrix surrounding fragments, how they respond to the fragmentation they are subjected to, and where in the landscape they are the most vulnerable. Primate survivability in human-dominated landscapes does not appear to have any global trait-based preconditions, as there are no reliable significant associations between size of smallest fragment and any one biological trait (Gibbons and Harcourt 2009; Onderdonk and Chapman 2000). One of the over-arching reasons for this is that fragments by their nature are in a chaotic matrix, and have far too many confounding variables for any singular answers on how a primate species or populations may manage. And, as the authors in this section point out, there are multiple variations on a theme for primates within a larger disturbed landscape for their persistence, at least in the present, if not over time.

Williams-Guillén et al. (Chap. 8) investigated the fragmented forests of southern Nicaragua, a highly disturbed habitat containing some of Central America's last remaining tropical dry forest. Three species are found in that area: *Alouatta palliata*, *Cebus capucinus*, and *Ateles geoffroyi*. And while not surprisingly, the howlers fared the best both in protected and unprotected fragments, all of them appeared to be less threatened in the more fragmented, unprotected forests than in the region that was supposed to be under protection in the wildlife refuge. The endangered spider monkeys were even inexplicably more abundant in the highly fragmented area outside of the refuge. As we discovered in the last section, Chapman et al. (Chap. 7) found the opposite to be true: that primates living outside of protected status were far less abundant and had a higher incidence of disease than those within the national park. The point is clear: no region or situation is the same, and no matter if the primates are the same—site to site and country to country may tell different stories. Thus, while making generalizations are important, they currently ellude our field.

Ferrari et al. (Chap. 9) found that in Sergipe, Brazil, *Callicebus barbarabrownae* and *Callicebus coimbrai* in Caatinga, a xeric scrub forest that is part of the Atlantic

Forest, seem to be maintaining respective viable metapopulations despite the fragility of the ecosystem. But as the lesson goes for many sites, suggest the authors, their long-term persistence will depend on newly granted wildlife refuges and landowner stewardship.

Country-wide surveys are rare and important, particularly in regions with high human populations as Aggimarangsee (Chap. 11) points out for Thailand. When populations are not only isolated but remain in heavily human-dominated landscapes, such as macaques in Buddhist temples, regular monitoring is useful so that population trends can be discovered. For instance, while the metapopulation of *Macaca fascicularis* remains of Least Concern, there was still an instance of a population being extirpated from one of the original surveyed sites. Likewise, fewer *M. assamensis* and *M. arctiodes* were noted over time, and a new population was observed of introduced, and what may become invasive, zoo population of *Cercopithecus aethiops*. It cannot be stressed enough that when the opportunity arises for country-wide surveys it must be taken as these data are critical for understanding the scope and changes of the metapopulations over time.

Additionally, when populations are small and endemic, it is clear that surveys must be conducted regularly to determine their status, demonstrates Ceballos-Mago and Chivers in Chap. 13. The Margarita capuchin (*Sapajus apella margaritae*) was surveyed in the forest fragments in the mountains of its native home of the Isla de Margarita, Venezuela. It was discovered that within the fragment regions, the capuchins preferred evergreen forest, but were also occupying dry forest patches. In addition to the ever-encroaching human population, a primary concern is for hybridization with introduced *Sapajus apella* from the mainland. Connectivity for these remnant populations is key.

Carretero-Pinzón (Chap. 12) found for primates isolated in forest fragments in the Colombian Llanos that using fencerows as part of the landscape matrix was one means of populations staying connected, but this was not the most efficient method. *Alouatta seniculus*, *Sapajus apella*, *Callicebus ornatus*, *Saimiri sciureus albigena* and *Aotus brumbacki* were present in the fragments. Even though the fragments were within a matrix of palm oil plantations, petrol extraction, and human villages (with agriculture, cattle, hunting) in general the small to medium-sized fragments had higher population densities than reported in other studies for the same species, and the extra-large fragments held similar densities of *Alouatta*, *Callicebus*, and *Sapajus* as continuous forest.

Silva and Bicca-Marques (Chap. 10) conducted a test of fragmentation theories, including island biogeography, metapopulation, and landscape ecology to determine if fragment size, distance to nearest patch, and distance to mainland are good predictors of the presence of *Alouatta guariba clamitans* in Southern Brazil. In a highly mixed matrix of ranching, farming, and eucalyptus forestry, none of the predicted models explained presence or absence of howlers. The authors concluded that the best fit for howlers in this context is the non-equilibrium metapopulation model. Work such as this is not simply an exercise in science; it helps us to understand that different species in different situations throughout the tropics have a multitude—from random to defined—means of surviving in fragments.

As primatologists and practitioners within complex, fragmented habitats we all are aware that whether data in our particular site expresses it or not, that there is likely a global threshold under which our species simply cannot remain (Harcourt et al. 2001; Harcourt and Doherty 2005; Marshall et al. 2009). For some authors, that number is less than 1 km^2 (Harcourt and Doherty 2005). We work locally and often that means at a very small scale. And as our field continues to mature, both on the ground and in the literature, we will continue to see conflicting data: one site says their primates are in abundance and thrive in very small fragments, another says they are all but doomed.

But, as the authors in this section demonstrate, we persist to explain all of the parts of the whole. And although fragmentation is creating more "parts" for us to explore, none of the discoveries are wasted. Harcourt and Doherty (2005) point out that there are a disproportionate number of studies on primates in fragments in Central and South America as compared to the rest of the world: four times as many studies in Latin America than the next closest region (Asia). We all must be aware of this and work toward increasing our knowledge base, in all sizes of fragments, for all of the less studied regions where primates reside.

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Chapter 8
Primate Populations in Fragmented Tropical Dry Forest Landscapes in Southwestern Nicaragua

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Abstract The lack of information on how primates respond to habitat fragmentation across a variety of ecosystems and regions hampers conservation efforts in the fragmented landscapes where populations are most threatened. We investigated the status of primates in the highly fragmented forests of southwestern Nicaragua, a region containing some of Central America's few remaining patches of tropical dry forest. We surveyed primates in two areas, the Chococente Wildlife Refuge comprising the country's largest remaining fragments of tropical dry forest, and an area of Rivas just north of the Costa Rican border, where tropical dry forest exists in much smaller, more isolated patches without formal protection. Of the three species found in Nicaragua, howler monkeys (*Alouatta palliata*) were least affected by fragmentation remaining relatively abundant in both areas. However, capuchins (*Cebus capucinus*) and spider monkeys (*Ateles geoffroyi*) were far less abundant and have suffered local extinctions both inside and outside of protected areas. Interestingly, our data suggest that all three species are currently least threatened in the human-dominated landscape on the Rivas Isthmus, the more fragmented study region where

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forests receive no official protection. In spite of extensive fragmentation, southwestern Nicaragua's remaining tropical dry forests may maintain a functioning metapopulation of primates, including populations of the endangered spider monkey. However, reasons why the endangered spider monkey is more common in the more fragmented region are unclear. Our results demonstrate both the surprising ability of primates to survive in highly modified landscapes, and the critical importance of coordinating conservation efforts with private landowners, local communities, and other stakeholders. Planning for primate conservation in such anthropogenic landscapes must consider historical factors and larger spatial context. In Nicaragua, the local NGO Paso Pacífico has adopted the spider monkey as a flagship species, and is working extensively with landowners and local communities to conserve this species and the forest fragments in which it lives.

Introduction

Challenges to Primate Conservation in Southwestern Nicaragua

The widespread transformation of once-intact closed canopy tropical forest into fragments embedded in a matrix of anthropogenic land uses poses one of the greatest challenges of conservation in the twenty-first century. As forest-adapted mammals whose life histories make their populations particularly vulnerable in the face of hunting pressure, primates are expected to suffer particularly severe declines as tropical landscapes become increasingly fragmented. Although the effects of fragmentation on primates have been investigated in depth at a few sites (within Central America, investigations at Los Tuxtlas have provided the most multidimensional picture of fragmentation effects on primate populations; see Cristobal-Azkarate and Dunn, this volume), our lack of knowledge of how primates cope with fragmentation in a variety of contexts hampers current conservation efforts. Responses to fragmentation are likely to be highly idiosyncratic, reflecting both local land-use history and species-specific responses to forest transformation.

In Nicaragua, the rapid conversion of tropical dry forests to agricultural areas presents both a conservation challenge, as well as an opportunity to investigate the ways in which fragmentation, matrix quality, and social aspects of land use interact to affect primate populations. As Central America's largest and least developed country, Nicaragua retains much of its original forest cover, particularly in the eastern half of the country (Fig. 8.1a). However, rapid changes in forest cover threaten its biodiversity, particularly in the country's densely populated Pacific coast, where highly endangered tropical dry forest has undergone particularly extensive fragmentation and loss (Fig. 8.1b). Nicaragua is losing approximately 3 % of its forest area every year (FAO 2009). In southwestern Nicaragua, subsequent land cover includes a mix of pasture, small-scale agriculture and traditional agroforestry systems, and large-scale plantations of nonnative hardwood trees. The interplay between fragmented areas and anthropogenic matrix is further complicated by the conflicting interests of diverse stakeholders, from wealthy foreign investors to impoverished rural communities.

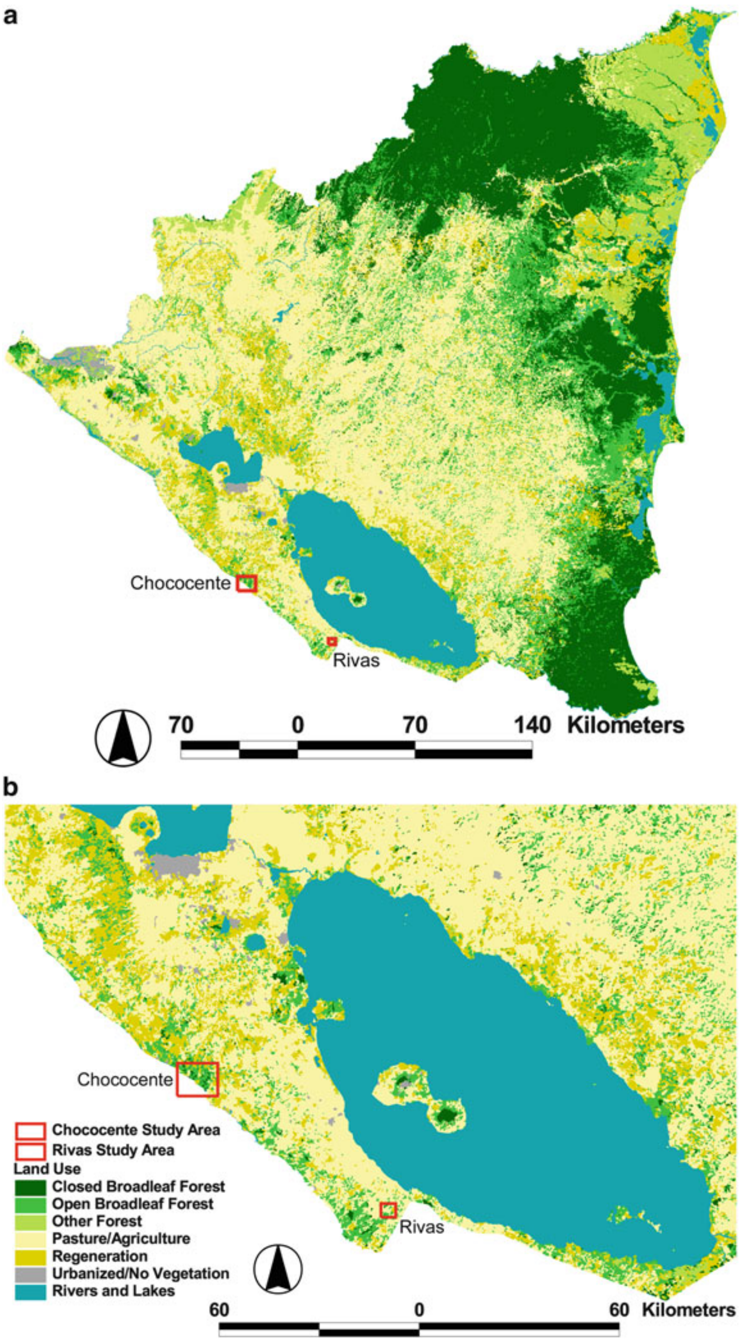

Fig. 8.1 Land cover and study area locations of (**a**) Nicaragua and (**b**) the southwestern area of the country, where our study areas are located. Note the highly fragmented nature of forested areas in our study region; data on land coverage (from a publically available coverage from the Nicaraguan government) were derived from satellite images taken in the late 1990s, meaning that forests have been subject to further conversion and fragmentation

Since the Nicaraguan government does not own the land comprising most of the country's protected areas, land tenure and management is inconstant. These fluctuating influences on local and landscape-level land use have differential effects on the country's three primate species. To understand the conservation status and potential for primates in Nicaragua—and throughout the tropics—it is key that we understand how primates are negotiating these new landscapes (Hagell et al. 2011).

Efforts to conserve Nicaragua's primates are hampered not only by a poor understanding of how fragmentation affects primates but also by a lack of even basic information on the status and distribution of the country's primate populations: there is only one country-wide survey of Nicaraguan primates (Crockett et al. 1997), and long-term studies of primates in the country have been limited to a mere handful of sites. As the first steps towards understanding the effects of fragmentation on Nicaraguan primates, we undertook surveys of primates at two sites in southwestern Nicaragua, where forests are under the greatest pressure due to habitat conversion.

In this chapter, we briefly review current knowledge on primates in Nicaragua to provide the context for our surveys; we present the results of primate surveys in one of the largest forested reserves on Nicaragua's Pacific coast, contrasted with surveys in one of the region's most highly fragmented areas. We discuss our results in the context of species-specific responses to forest transformation, local histories of land use and tenure, and the knowledge and next steps necessary to conserve primate populations in a region where multiple conservation challenges intersect to form multiple challenges to biodiversity conservation in a rapidly changing world.

Primates in Fragmented and Pristine Forests of Nicaragua

Nicaragua is home to three primate species, whose behavioral and ecological adaptations make them differentially sensitive to anthropogenic disturbance and forest change. Currently, Geoffroy's black-handed spider monkey (*Ateles geoffroyi*) is considered Endangered, while the mantled howler monkey (*Alouatta palliata*) and white-faced capuchin (*Cebus capucinus*) are Least Concern (IUCN 2010). Crockett et al. (1997) provided the only published country-wide assessment of primate distribution in which they found howler monkeys at most sites visited, with spider and capuchin monkeys limited to more remote sites. Since then, several investigators have described the behavior, ecology, and genetics of howlers on Ometepe Island in Lake Nicaragua (e.g., Bezanson et al. 2008; Garber et al. 1999; Garber and Jelinek 2006; Winkler et al. 2004). McCann et al. (2003) and Williams-Guillén et al. (2006b) studied howlers in a cloud forest reserve and surrounding coffee plantations of Mombacho Volcano in western Nicaragua. Despite the vast expanse of forested areas in Nicaragua's eastern region, the only published information on its primates comes from a wider survey of large mammals in the Bosawás Biosphere Reserve in northeastern Nicaragua (Williams-Guillén et al. 2006a).

All available data on Nicaragua's primates suggest mantled howler monkeys suffer the fewest negative consequences of forest fragmentation; indeed, the published accounts of howlers in Nicaragua focus on populations in fragmented (Ometepe) and matrix (Mombacho) habitats. In western Nicaragua, howlers use both small forest patches as well as shade coffee plantations for foraging and travel (Garber et al. 1999; Williams-Guillén et al. 2006b), and hunters throughout consider their meat unpalatable (KWG, personal observation). Nevertheless, howlers have low genetic diversity compared to sympatric primates (Ruíz-García et al. 2007), and howlers in Ometepe have reduced microsatellite allele diversity (Winkler et al. 2004). Reduced genetic diversity could make howlers susceptible to stochastic events and population decline as gene flow and reproductive success is further impacted by the loss of forest habitat (Mandujano and Escobedo-Moráles 2008).

Capuchins are opportunistic foragers capable of exploiting human encroachment and can respond quickly to forest restoration (Sorensen and Fedigan 2000). In anthropogenic landscapes in Nicaragua, they may suffer the greatest threat from hunting—for their meat, to reduce crop raiding, and for the market in illegal pets (Nietschmann 1972; SH, personal observation). Published reports have documented capuchins in both western (McCann et al. 2003) and northern (Williams-Guillén et al. 2006a) Nicaragua; in both cases they are less abundant than howlers.

Multiple studies suggest spider monkey populations are less likely to persist outside of landscapes with connected forests and effective protection from human predation (Estrada et al. 1994, 2004; Pruetz and Leasor 2002; Sorensen and Fedigan 2000). Spider monkeys require large fragments of native forests that can support their frugivorous diets (González-Zamora et al. 2009) and large home ranges (Spehar et al. 2010; Wallace 2008), coupled with a relatively low reproductive rate, which may make them more sensitive to habitat disturbance than the other species in Central America (Zaldívar et al. 2004). The few published studies on Nicaragua's primates have not documented any appreciable numbers of spider monkeys on Nicaragua's heavily populated Pacific region. Although some distributions suggest that spider monkeys are not found in northern Nicaragua (e.g., Collins and Dubach 2000). Williams-Guillén et al. (2006a) observed them several times near the Río Coco; however, even in the remote and near-pristine forests of Bosawás, spider monkeys are subject to intense hunting pressure and have become rare near indigenous settlements.

Research Questions

We set out to evaluate the status of primate populations at a wider variety of sites in western Nicaragua where remaining forested areas have undergone extensive fragmentation and are embedded in a matrix composed primarily of pasture and other deforested land-use types (Fig. 8.1b). Do primate populations persist in these highly fragmented areas, and if so, what factors are associated with their presence? We began with surveys in Chococente Wildlife Refuge, which includes the largest remaining fragments of tropical dry forest in Nicaragua. Based on reports of primates persisting in highly fragmented tropical dry forest near the border with Costa

Rica, we surveyed primates in the region south of Rivas, Nicaragua. Given the patterns described above, we expected that howlers would be more common than capuchins and spider monkeys, and that the larger, protected forest fragments of Chococente would house a more substantial primate population. This research has formed the basis of subsequent studies on the effects of fragmentation on the genetic structure of *Ateles geoffroyi* in the area (Hagell 2010; Hagell et al. 2011); we continue to follow up this work with ongoing monitoring of primates in forest fragments throughout the Rivas area (KWG, unpublished data).

Methods

Study Areas

The Rio Escalante-Chococente Wildlife Refuge (11°32′N, 86°12′W; also known as Chacocente) is one of the largest forested areas on Nicaragua's Pacific coast (Fig. 8.1b), encompassing approximately 4,800 ha of deciduous upland and semi-perennial riparian forests (Sabogal 1992; Fig. 8.2a). Two large watersheds border the southern and northern edge of the reserve where wildlife congregates during the dry season. Patches of nonforested areas are also scattered throughout the reserve due to clearing for agriculture and cattle pasture (Otterstrom 2004; Otterstrom et al. 2006). Forest areas are heavily used for resource extraction (Castro-Marín et al. 2005; Cordón et al. 2006; Wallace 2008). In spite of forest disturbance, Chococente is a conservation priority because it maintains Nicaragua's largest stands of high-quality dry forest (Sabogal 1992), presents the highest bird diversity along Nicaragua's Pacific slope (Gillespie and Walter 2001), and is a major nesting site for Olive Ridley and Pacific Leatherback turtles (Hope 2002). At the time of our study, two groups of foreign investors owned approximately 70 % of the reserve, including the majority of the forested areas. The remaining land was distributed among ~70 subsistence-farming households grouped in small communities throughout the inland portion of the reserve (Otterstrom 2004). In 2001, a Nicaraguan biology student conducted a limited survey for primates, during which he sighted howlers, capuchins, and a small number of spider monkeys in Chococente.

Our study area on the southern extent of the Rivas Isthmus comprises a mosaic of privately owned forest fragments and agricultural areas, located at approximately −85.66′W, 11.17′N, just north of the Costa Rican border (Fig. 8.2b). On the Nicaraguan side of the border, some larger patches of open-canopy dry forest persist (Fig. 8.1b); larger fragments of closed-canopy forest can still be found on the Costa Rican side of the border. Forest vegetation is primarily seasonally dry deciduous forest with perennial riparian areas. Properties in the area are either small, locally owned farms (20–150 ha) focused on subsistence agriculture and maintaining small forest fragments (usually on slopes or along watercourses), or one of three large (>500 ha) properties with affluent owners who use the properties as tropical hardwood plantations but also maintain large fragments of native

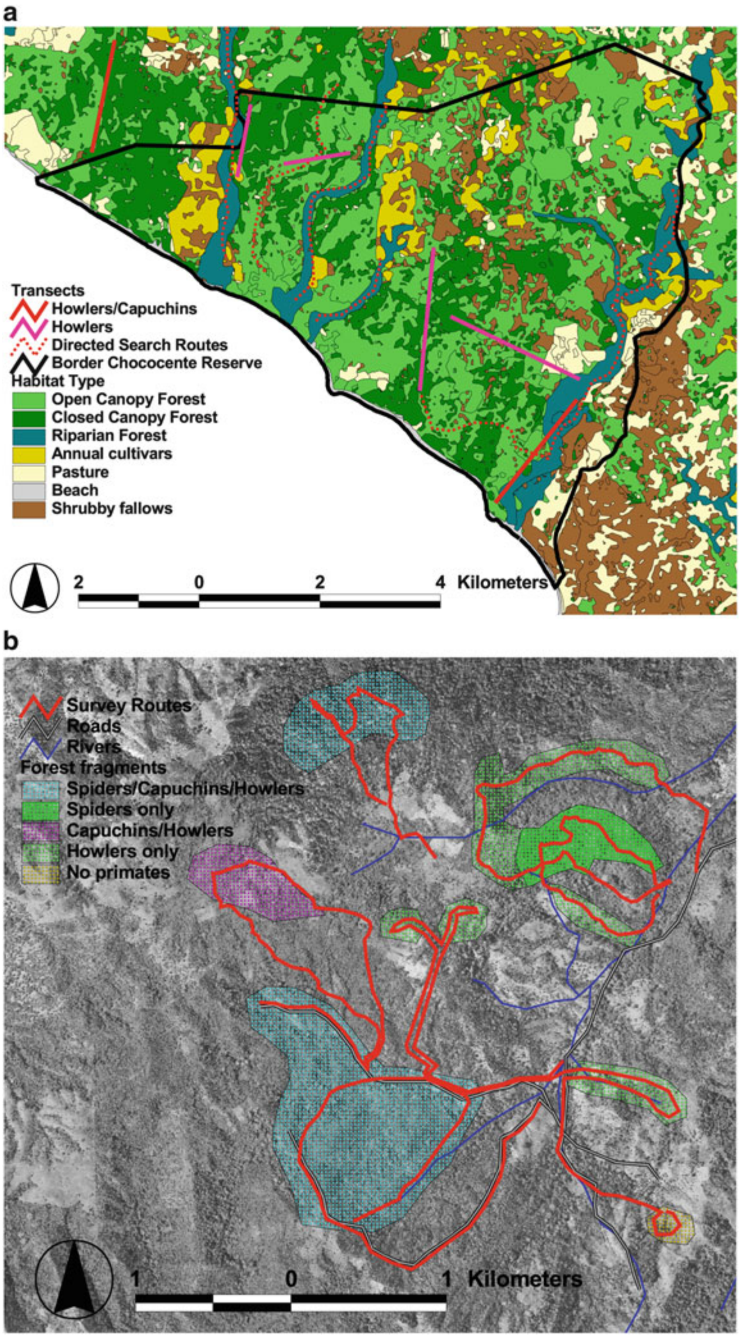

Fig. 8.2 (**a**) Land cover, transect locations, and directed search locations in Chococente wildlife reserve; (**b**) Survey routes and approximate extent of forest fragments in our survey on the Rivas Isthmus. The land cover map of Chococente was commissioned by the landowners. No land cover maps of appropriate resolution are available for the Rivas study area, and we therefore imposed fragment areas and routes over a georeferenced aerial photograph

forest. Anecdotal evidence and first-hand observations indicate that spider monkeys are frequently hunted in the area's privately held forests for their meat and for the widespread domestic and international pet trade.

Survey Methods

In Chococente, we used line transect sampling along with opportunistic directed searches in areas where we expected to find primates based on habitat type or prior reports. We established seven straight-line transects with lengths of 1.25–2.5 km (Fig. 8.2a). Placement of transects minimized passage through nonforested areas, with four transects oriented on a roughly north–south axis and sampling riparian and closed canopy forest, and three transects oriented on a roughly east–west axis and sampling more diverse habitats. Transects were divided into western and eastern sectors. Within each sector, transects were visited on a rotating basis by two teams of local investigators; each team visited one transect per day. Weather permitting, each transect was visited approximately eight times per month in August–December 2005 and February–June 2006. When primates were sighted, location on the transect and perpendicular distance to the center of the primate group were measured. Observers also recorded information on group size, age/sex composition, and trees used for feeding, resting, or locomotion. Primates other than howlers were very rarely observed, thus we also conducted directed searches in forested areas and areas where spider and capuchin monkeys had previously been reported. Directed searches were conducted at the height of the dry season (March 2006) along watercourses and dry river beds (Fig. 8.1b): because many of the trees in tropical dry forest shed their leaves, primates are known to congregate in riparian forests during the dry season (Fedigan and Jack 2001). Whenever primates were encountered, the location was recorded with a GPS unit, and the group size and composition were determined.

Due to the need to repeatedly cross property lines, the highly fragmented landscape and the more mountainous terrain, transect surveys were not tenable in the Rivas isthmus. We therefore conducted directed searches for primates as a means to systematically survey for species across properties and environments. Additionally, such directed searches can be more successful than line-transect surveys in documenting the presence of low-density species such as spider monkeys (e.g., Pruetz and Leasor 2002). We first used information from topographic maps, vegetation cover GIS layers, and aerial photographs to identify the probable locations of remaining forest fragments. Existence and the approximate extent of fragments were then ground trothed by using informal interviews with property owners to identify the forest fragments most likely to harbor primates. Under our guidance, a team of local data collectors conducted directed searches along existing roads and trails in each forest fragment twice a month May–July 2007. During the searches, our team recorded data regarding all primates encountered, including the number of individuals and age-sex class when possible.

Data Analysis

Line transect data from Chococente were analyzed using the program DISTANCE 5.0 (Thomas et al. 2010). Sightings for all transects were combined to determine species-specific effective strip width, individual density per hectare, and total population size for the study area. Observations more than 50 m perpendicular from the transect were censored, since it is improbable that primates could be seen this far off the line, such distances more likely represent recorder error. When sufficient data points were collected, we used DISTANCE 5.0 to estimate primate densities in Chococente. To determine if species were sighted more often than expected with respect to vegetation type, we used a chi-square goodness-of-fit test to compare the actual number of sightings by each factor with expected number as calculated based on the proportion of transect distance walked in each season or based on the contributions of each forest type to the proportion of transect length in each habitat. In the Rivas study area, where primates were for the most part limited to clearly delineated forest fragments, we calculated the minimum density of each primate species encountered in each fragment by dividing the largest number of animals sighted at once by fragment area. At both study areas, encounter rates were calculated as the total number of individuals observed per km transect or search route.

Results

Rio Escalante-Chococente Wildlife Refuge

Between August 2005 and June 2006, we encountered 1,963 individual primates 168 times over 667 km of transect walks; howlers comprised over 96 % of encounters ($N=162$) for an encounter rate of 2.8 individuals/km along transects. We estimated the effective strip width (ESW) to be 32.7 m. Based on these calculations, the density of howlers is estimated to be 0.43 individuals/ha. Given a study area of approximately 4,800 ha, an estimated 2,066 howlers are estimated to live in and around Chococente reserve. In contrast, capuchins were encountered only six times during line transect walks, for an encounter rate of 0.12 individuals/km. All but one of the capuchin sightings took place on the southeastern transect, which included a large amount of riparian forest. The capuchin groups sighted ranged in size from 3 to 19 individuals. Because capuchins would flee immediately upon sighting human observers, it was difficult to obtain complete group counts, and our counts most certainly underestimate capuchin group sizes at Chococente. In March of 2006, we covered 23 km of roads, trails, and streambeds as part of directed searches for primates. During this time, a total of 192 howlers and 5 capuchin monkeys were observed during 24 encounters with primate groups, primarily along the Río Escalente. During this period, howlers in particular congregated in huge numbers in riparian habitats, with at least 116 individuals sighted in one morning during a ~3 km walk along the banks of the Río Escalente. Mean group compositions for both howlers and capuchins are shown in Table 8.1.

Table 8.1 Total groups encountered, encounter rates (total individuals per km), and group compositions (mean ± SD with range in parentheses) of primates encountered during line transect surveys and directed searches in Chococente Wildlife Refuge, Nicaragua, and during directed searches in forest fragments in the southern region of the Rivas Isthmus, Nicaragua

			Encounter	Group composition				
Species	Location	Groups sighted	Rate (Inds/km)	Total	Males	Females	Juveniles	Infants
Alouatta palliata	Chococente[a]	183	3.02	11.4 ± 6.5 (1–40)	2.0 ± 1.2 (0–9)	5.8 ± 1.6 (0–20)	2.0 ± 1.6 (0–8)	1.6 ± 1.4 (0–8)
	Rivas[b]	12	6.27	8.0 ± 5.2 (1–16)	1.8 ± 1.1 (0–4)	5.6 ± 4.2 (0–12)	0.2 ± 0.6 (0–2)	0.3 ± 0.5 (0–1)
Cebus capucinus	Chococente[a]	9	0.12	9.6 ± 7.2 (1–19)	2.1 ± 1.2 (1–4)	4.7 ± 3.6 (0–10)	1.9 ± 1.8 (0–5)	0.9 ± 1.0 (0–2)
	Rivas[b]	5	3.40	10.4 ± 7.6 (2–19)	2.4 ± 1.3 (1–4)	6.4 ± 4.7 (1–12)	0.2 ± 0.4 (0–1)	1.4 ± 3.1 (0–7)
Ateles geoffroyi	Rivas[b]	5	2.09	6.4 ± 2.9 (2–9)	1.8 ± 0.8 (1–3)	4.2 ± 2.2 (1–6)	–	0.4 ± 0.5 (0–1)

[a] Data for transect walks and directed searches combined

[b] Encounter rates calculated based on total km surveyed in forest fragments only

Eleven sample points in transects were riparian forest, 59 % were upland dry forest, and 30 % were classified as secondary forest. Primates were encountered significantly more often than expected in riparian habitat, and less often than expected in secondary forest ($\chi^2 = 13.00$, $p = 0.005$) emphasizing the importance of the riparian areas for Chococente's primate populations. In spite of scattered reports by reliable community members, and our own directed searches, spider monkeys were never observed. Although the nonresident investors who owned the majority of the land comprising Chococente had made multiple attempts to exclude livestock, we observed extensive cattle grazing and trampling in all transects, both in more remote areas of dry forest and in the riparian forests which comprise favorable primate habitat in Chococente.

Rivas Isthmus

Between May and July 2007, we conducted 36 directed searches along six survey routes across the Rivas Isthmus study area (six searches per route, covering ~300 ha of forest fragments); a total of 28.5 km of trails were covered in the survey, with 15.3 km in forest fragments. We encountered a total of 180 primates 22 times. Unlike in Chococente, we encountered capuchins and spider monkeys relatively frequently—howlers accounted for a modest 55 % of encounters. We found howlers in nearly all forest fragments (as well as along roads and strips of riparian forest not included in our survey routes), capuchins in three fragments, and spider monkeys in the three largest forest fragments (Fig. 8.2b).

Not surprisingly, howlers were the most frequently encountered and abundant primate species encountered in the study area; unlike in Chococente, juveniles and infants were rarely observed (Table 8.1). We encountered five groups each of spider monkeys and capuchins, all with males and females. Capuchins were encountered only in the relatively large and well-connected forest fragments. However, relatively large groups were observed; all capuchins were observed in bisexual groups, frequently with immatures (Table 8.1). As at Chococente, when encountered, the majority of group members fled, with males remaining to threaten observers. Spider monkeys were also observed frequently, usually in the largest forest fragments (Fig. 8.2b); lack of observations of spider monkeys in the larger riparian forest fragment in the northeastern part of the study area may reflect limited survey effort, since they had been observed in that area in 2006 (SH, personal observation). Subgroup size ranged from 2 to 9 individuals; immatures were rarely observed (Table 8.1).

While it is possible that there are 180 individual primates in these forest fragments, it is far more likely that some sightings represent repeated encounters with the same groups. Because the majority of the matrix surrounding the fragments comprises pasture or agriculture lacking arboreal pathways, we assume that primates were unlikely to travel between fragments and be sighted along other survey routes. We therefore consider the maximum group count of each species along each route representative of the fragments' minimum populations. Using these criteria, we observed a minimum of 63 howlers, 34 capuchins, and 30 spider monkeys. With an estimated 300 ha of forest fragments in the study area, these numbers suggest a minimum density of 0.21 individuals/ha for howlers, 0.11/ha for capuchins, and 0.10/ha for spider monkeys within the forest fragments.

Discussion

Our results conform to our expectations—howlers were the most abundant primates in both of our fragmented tropical dry forest sites, with group sizes and compositions well within the ranges described by researchers at other sites. However, we were initially surprised to find that the more fragmented, less protected Rivas Isthmus study area retains a more diverse primate population. Although differences in methodology mean that data are not directly comparable, all evidence suggests that primates are more abundant in the Rivas forest fragments than in Chococente. The only suggestion of greater population health in Chococente versus Rivas comes from the relatively low numbers of immatures observed in the latter region, particularly for howlers. Although we had no comparable information on spider monkeys in Chococente, those found in Rivas also included few infants and no juveniles. The low ratio of immatures to females could indicate reduced reproductive output by females (potentially as a result of energetic stress or social instability in groups) and/or increased mortality of juveniles (older juveniles emigrate from natal groups, but movement through a hostile matrix may hamper this process). Nevertheless, primates demonstrated higher diversity and evenness in the more fragmented Rivas region. More recent monitoring focused on the largest and least disturbed forest fragments in the Rivas area reveals juvenile-to-adult ratios of all three primate species that are more consistent with the results from Chococente, suggesting that at least *within* forest fragments female reproductive output is similar to that seen within the larger continuous forest to the north (KWG, unpublished data).

When assessing landscapes for their potential in primate conservation in the absence of location-specific data, the seemingly obvious conclusion to draw is that the regions retaining the largest, least fragmented forests will be those with the greatest conservation value. Although our data set is limited, it highlights both the degree to which fragmented landscapes can vary in their value as conservation areas for primates and the need for further research elucidating the best predictors of primate persistence in such areas. What accounts for the differential survival of primates in these two ecologically similar areas, located only 70 km apart? At this time our responses to this question are speculative; nevertheless, we believe we can point to several ecological, historical, and economic factors which could underlie the observed differences—and whose changing status could impact the future survival of the few primate populations that do remain in southwestern Nicaragua. One important factor is proximity to larger, less disturbed forests: despite Chococente's larger size, it is further away from the large expanses of undisturbed forests that remain in eastern Nicaragua and to the south in Costa Rica. To the extent that primates are able to move through the pasture-dominated anthropogenic matrix surrounding both Chococente and the Rivas forest fragments, more immigrants may arrive in the Rivas area. However, recent investigations reveal that the spider monkey populations in the Rivas isthmus show significant heterozygote deficiency at multiple microsatellite loci, suggesting little in-migration from source populations (Hagell 2010).

Differences in land-use history are less well established but could also influence the patterns observed. Increased population urbanization and export-oriented agriculture are associated with increased deforestation in the humid tropics (DeFries et al. 2010). Land in both study areas was distributed to cooperatives of campesino agriculturalists in the 1980s during the Sandinista revolution. Beginning in the late 1990s, western Nicaragua has experienced unprecedented changes in land tenure as an increasingly urbanizing population has sold cooperative land holdings, often to expatriate investors with diverse development goals encompassing everything from low-impact eco-tourism to wholesale land transformation with the establishment of cattle herds, hardwood plantations, and luxury housing developments. While both Chococente and Rivas have been impacted by these trends, they have been at work longer in the Chococente region. The information we have available do not allow us to directly attribute differences in primate populations to changes in forest management and exploitation related to land tenure; however, they do demonstrate that concentrating ownership of forested lands in the hands of a few individuals—even those whose stated goals are biodiversity conservation—does not automatically result in increased wildlife protection in Nicaragua's fragmented tropical dry forests.

The Rivas forest fragments and their resident spider monkeys are in a precarious situation: comparison maps of current forest extent with even recently generated maps indicate that deforestation has continued in the area (SH, unpublished data), threatening the long-term persistence of spider monkeys and other native forest-dependent wildlife. The rate of development and forest conversion is increasing rapidly with foreign investment: since we began work in this area in 2005, more than 3,000 ha of land—including large patches of forest—have been purchased for conversion to nonnative teak plantations. Other development includes expanded infrastructure (roads, water, and electricity) and wind power for tourism and the growing resident population, all of which impact forests and forest wildlife. We thus are facing a critical moment in primate conservation: monkey populations appear healthy enough to maintain or grow numbers in the future, but if deforestation in the area continues at the current rate, these populations will surely be lost.

Conclusion

We found that the highly fragmented tropical dry forests of southwestern Nicaragua can retain surprisingly large primate populations, and that fragment size itself did not explain which areas had the most diverse or abundant primate communities.

Significantly, endangered spider monkeys were repeatedly encountered in several small forest fragments on the Rivas Isthmus, suggesting that this area is vital for the conservation and future recovery of this species in southwestern Nicaragua. The presence of spider monkeys in the Rivas Isthmus is serving as a focal point for conservation activities in southwestern Nicaragua.

In partnership with the conservation NGO Paso Pacífico, our current conservation efforts in this region include environmental education, establishment of new protected areas, and support of sustainable agriculture. Paso Pacífico's environmental education program has engaged with over 100 school children in the Rivas Isthmus, with lessons have focused on primate life history and respect for primates and other wildlife. In 2008, Paso Pacífico expanded its environmental education program through its "Binoculars For Slingshots" program, providing school children with binoculars and training in exchange for the slingshots that local children use to harass primates and other arboreal wildlife. We continue working with landowners in the study area who are willing to establish forest patches as private protected areas. Paso Pacífico supports landowners with an interest in conservation by assisting them with applications to establish private reserves and in conducting baseline biodiversity studies. One important forest patch is currently on the market for sale and we are working to identify a conservation-minded buyer.

Forest fragments in isolation are not enough for wildlife survival; rather, the quality of the matrix of anthropogenic habitat surrounding the forest fragments plays an equally critical role in biodiversity conservation in fragmented landscapes (Perfecto and Vandermeer, 2008). Land-use patterns in the area are diverse, including pasture, small-scale agricultural production, traditional agroforestry systems, and large-scale hardwood cultivation. The effects of these varied land-use types on wildlife remain largely unknown. The survival of Nicaragua's primates depends critically on further investigation of how primates cope with fragmentation and how both fragments and matrix can be managed in an integrative manner to meet multiple social, ecological, and economic goals.

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Chapter 9
Living on the Edge: Habitat Fragmentation at the Interface of the Semiarid Zone in the Brazilian Northeast

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Abstract The Brazilian Northeast is dominated by the Caatinga, a xeric scrub forest characterized by "semiarid" climatic conditions, with annual precipitation often below 600 mm, and an unpredictable rainy season. North of 13ºS, the Atlantic Forest forms a narrow coastal strip, of only a few dozen kilometers in width, with a relatively humid climate. Both biomes have been subjected to intense anthropogenic habitat fragmentation over the past few decades, although this process has different implications for each ecoregion. In Sergipe, the geographic ranges of two titi species, *Callicebus barbarabrownae* and *Callicebus coimbrai*, appear to correlate with the Caatinga and Atlantic Forest, respectively. Titis are relatively rare in the Caatinga, in terms of both the number of populations and their density. In the lower Rio São Francisco basin, 41.2 % of Atlantic Forest fragments ($n=17$) had titi populations, whereas only 28.1 % of Caatinga sites ($n=32$) had titis. In the ecotone between the two (the Agreste), however, no populations were found ($n=21$), suggesting a lacuna in their distribution. Population surveys at sites representative of the distribution of the two titi species indicate that the density of *C. coimbrai* may be two to four times higher than that of *C. barbarabrownae*. Overall, the data appear to indicate that while the survival of titi populations in the Caatinga may be dependent on factors such as fragment size and the presence of groundwater, the survival of the populations of the Atlantic Forest may be more closely related to more random factors such as the history of colonization.

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Northeastern Brazil: Dwindling Forests and Hardy Monkeys

The Brazilian Atlantic Forest stretches along the whole of the country's eastern seaboard, from Rio Grande do Sul in the extreme south, to Rio Grande do Norte, at the easternmost tip of the South American continent. While this biologically rich biome extends inland for hundreds of kilometers in its main southern portion, between Paraná and southern Bahia, it dwindles to a narrow coastal strip a few dozen kilometers in width in its northern extreme (north of approximately 13°S), where it forms a relatively lush coastal margin to the Caatinga, the vast xeric scrublands of the Northeast, that stretch westwards almost as far as the eastern limit of the Amazonian Hylea (Fig. 9.1).

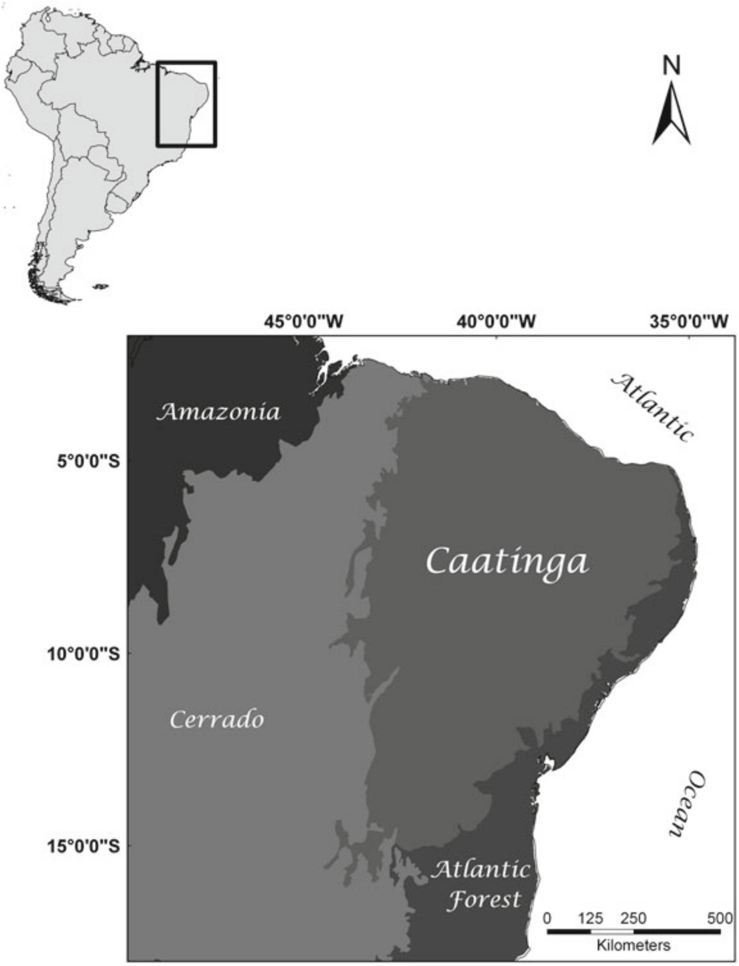


Fig. 9.1 Distribution of the terrestrial biomes in northeastern Brazil

The Brazilian Northeast was one of the first regions of the country to be colonized in the sixteenth century, and has a long history of deforestation, primarily for the cultivation of sugar cane (Atlantic Forest) and extensive cattle ranching (Caatinga). In the twentieth century, new crops, such as citrus fruit, were introduced, and the recent establishment of irrigation projects fed by the São Francisco River has created new agricultural frontiers in the Caatinga, which has put increasing pressure on the region's natural habitats.

As annual precipitation at most sites in the Caatinga is between 250 and 500 mm, it is generally classified as a semiarid zone, according to the criteria of Meigs (1953). Precipitation is not only low overall, by tropical standards, but also highly unpredictable, and prolonged periods of drought are common. While much of this zone is relatively inhospitable to most platyrrhine monkeys, there are extensive tracts of arboreal habitat (scrub forest), and even enclaves of humid forest associated with topographic features, known locally as "brejos de altitude."

Despite the potential hardships, these habitats are occupied by some of the more adaptable platyrrhine species, in particular the common marmoset (*Callithrix jacchus*) and the bearded capuchin, *Cebus libidinosus* (Fig. 9.2). The ability of the common marmoset to occupy relatively inhospitable environments is based on the species' morphological specializations for the systematic exploitation of plant exudates as a food source (Ferrari 1993), whereas recent studies of *C. libidinosus* have revealed that it uses tools such as stone anvils to gain access to otherwise inaccessible resources, such as the fleshy endocarp of hard-cased palm seeds (Ferreira et al. 2010).

A third species, the red-handed howler (*Alouatta belzebul*), is the only platyrrhine that ranges across three biomes, i.e., the Caatinga, Atlantic Forest, and Amazonian Hylea. However, in the Caatinga, the species has an extremely patchy distribution (Fig. 9.2), being limited basically to the "brejo de altitude" enclaves of more humid forest. Like capuchins and marmosets, howlers are relatively well adapted to marginal and highly seasonal environments, in this case, due to their adaptations for folivory (Di Fiore and Campbell 2011).

Four other platyrrhine species are also found in the Caatinga, although on a more limited scale (Fig. 9.2). A second howler species—*Alouatta caraya*—ranges into the southern Caatinga from the neighboring Cerrado savannas further south. Little is known of the ecology of this species in the Caatinga, but in the Cerrado, it is typically an inhabitant of the gallery forests, and presumably, occupies similar habitats in the Caatinga. The geographic distribution of the second marmoset species—*Callithrix penicillata*—is roughly similar to that of *A. caraya*, and it occupies an ecological niche very similar to that of *C. jacchus*.

The two other species present a more complex picture, not least because the ranges of both are limited to the right bank of the São Francisco River, which isolates the southeastern corner of the Caatinga from the rest of the biome (Fig. 9.2). The yellow-breasted capuchin, *Cebus xanthosternos*, is found primarily in the Atlantic Forest of southern Bahia, but a small number of isolated populations appear to exist further west, in the Caatinga, although little information is available on their status.

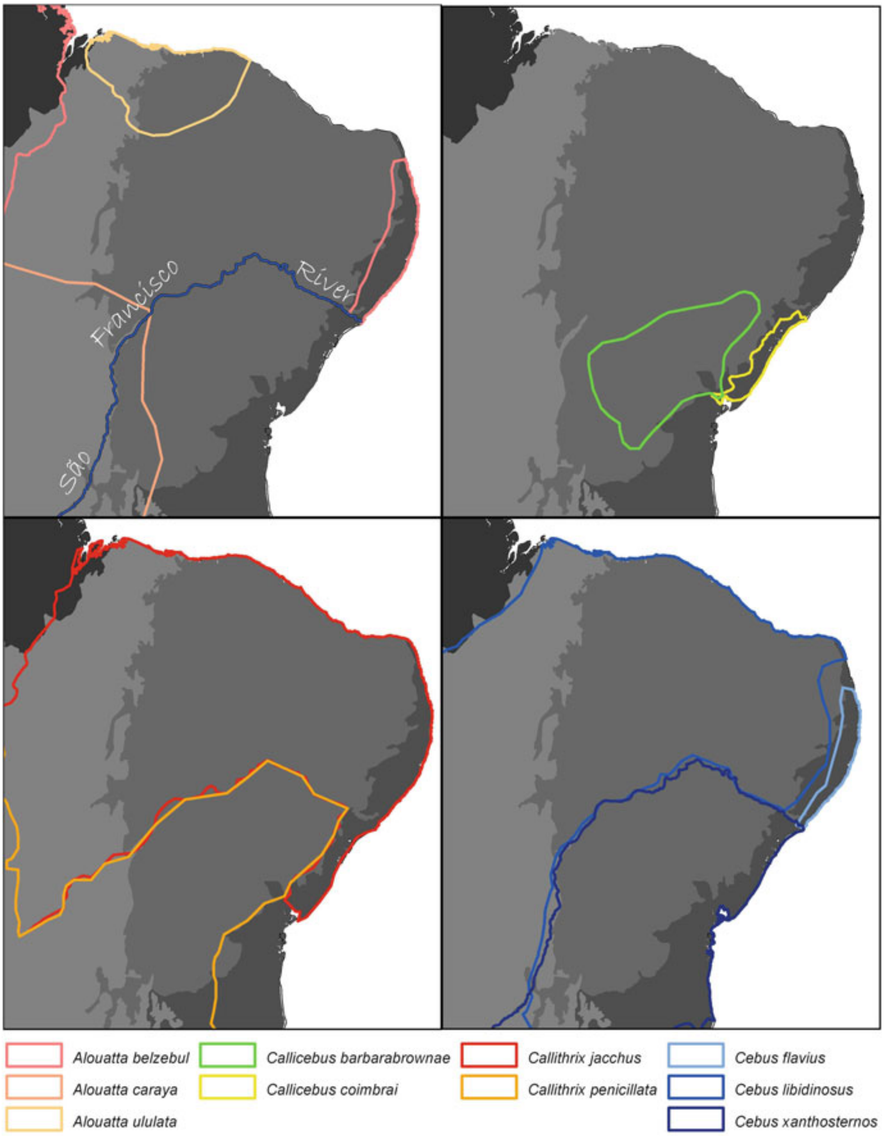


Fig. 9.2 Geographic distribution of the four platyrrhine genera that occur in the semiarid Brazilian Caatinga biome

Last, but not least, Barbara Brown's titi—*C. barbarabrownae*—is possibly the only platyrrhine species found exclusively in the Caatinga (Fig. 9.2). Unlike marmosets, capuchins, and howlers, titis are not regarded as dietary or habitat specialists, although some recent evidence does indicate that they may be relatively tolerant of the effects of habitat fragmentation (Arroyo-Rodrígues and Dias 2010; Bicca-Marques and Heymann 2013). The closely related species *Callicebus nigritus* and *Callicebus personatus* can be found in the Cerrado further south, although they are more typically observed in the Atlantic Forest. *Callicebus barbarabrownae* appears to be more widespread than *Cebus xanthosternos* in the Caatinga, but even so, it has a very patchy distribution, and appears to be relatively rare at most of the sites where it does occur.

That titis should be found in the Caatinga at all is unexpected, given the absence of the genus from the vast savannas of central Brazil (see below), although the Amazonian *Callicebus donacophilus* does range south into the relatively arid Chaco scrublands of northern Paraguay. An additional feature of the occurrence of *C. barbarabrownae* in the Caatinga is the apparent ecological juxtaposition with species that occur in the Atlantic Forest, i.e., *C. coimbrai*, to the north, and *Callicebus melanochir*, to the south. This supports an implicit understanding that the species are ecologically distinct, based on possible behavioral, zoogeographic, and even physiological or morphological adaptations to the respective environments in which they occur (Printes et al. 2013).

The reality of this situation is far from clear, however, and there is precious little evidence on which to interpret the ecological and zoogeographic relationships of these species. Worse still, the ongoing anthropogenic fragmentation of habitats within the region has all but obscured natural distribution patterns, making the task of understanding the ecological differences among species all the more difficult. Despite this situation, the analysis of the available data on the occurrence of titis in the Brazilian Northeast may provide important insights not only into the ecological differences among species, but also their potential for survival over the long term. In this context, the *Projeto Guigó* (Titi Project) has conducted a number of surveys and more detailed ecological studies in the Brazilian state of Sergipe over the past 5 years, which provide the data for the overview presented here.

Zoogeography of the Titis

Callicebus is the only platyrrhine genus that has a fully disjunct geographic distribution on a regional level. While most species are endemic to the Amazon and Orinoco basins, a completely separate group of five species—the *personatus* species group (cf., Kobayashi 1995)—is found in eastern Brazil, primarily in the Atlantic Forest between the São Francisco and Paraná–Parnaíba rivers (Fig. 9.3). This separation is further reinforced by the fact that the Amazonian group is absent from the southeastern Amazon basin, east of the Tocantins River.

The current distribution of the genus may be accounted for by the more ample distribution of forest ecosystems during the warmer and more humid periods of the Plio-Pleistocene, when the forests of the Amazon basin would have been contiguous with those of eastern Brazil (Ab'Saber 2003). This would have permitted the formation of continuous populations over a wide area, which would have subsequently been interrupted by the natural fragmentation of habitats, on a continental scale.

Fig. 9.3 Geographic distribution of the genus *Callicebus* (based on Hirsch et al. 2002). The *personatus* group is shown in *dark gray*, the Amazonian groups in *light gray*

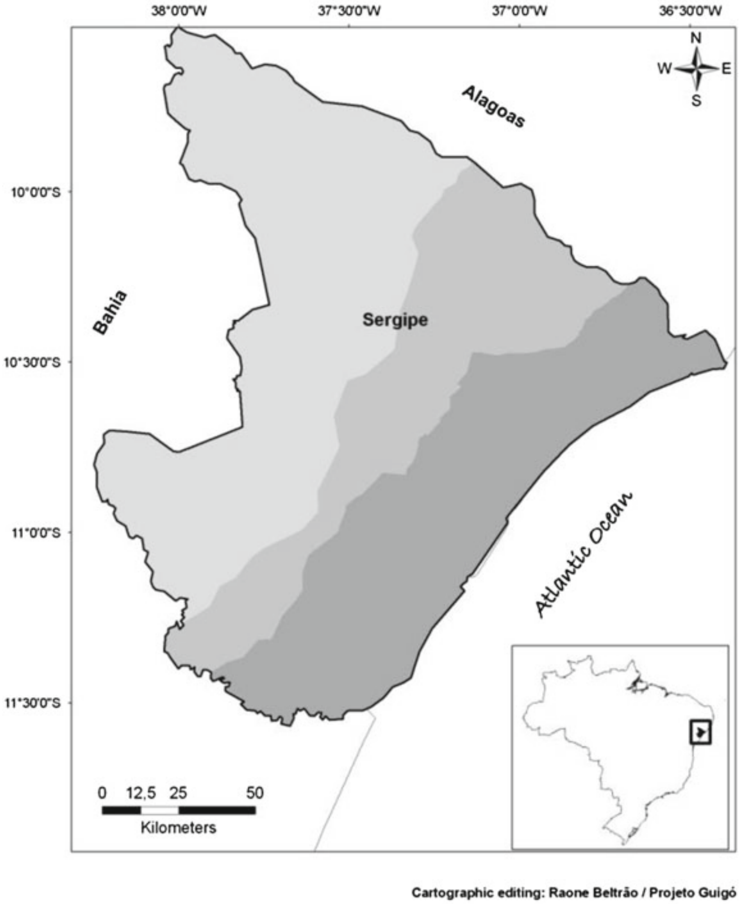
While the present-day range of the genus can be understood in the context of these long-term ecological changes, it is somewhat enigmatic for two reasons. One is the fact that howlers, capuchins, and marmosets are widespread in the savannas of central Brazil, at least where suitable habitat is available. The second reason is that titis of the *personatus* group occur in both the Cerrado and the Caatinga adjacent to the Atlantic Forest in eastern Brazil. In other words, the absence of titis from central Brazil may not be the result of an absolute inability to occupy savanna-type habitats, but rather, specific ecological and zoogeographic factors, in particular, the role of the São Francisco and Paraná–Parnaíba rivers as barriers to the dispersion of the species of the *personatus* group (Fig. 9.3).

While these rivers do not form a continuous barrier, they do restrict the potential dispersion of the group to a relatively narrow corridor between the headwaters of the São Francisco and Parnaíba rivers in eastern Minas Gerais. While there is no obvious physical barrier to dispersal within this area, one potentially limiting factor may be competition with pencil-tufted marmosets (*C. penicillata*) for limited habitat and resources. While the nature of the ecological relationship between marmosets and titis is unclear, Ferrari et al. (2003) found an inverse relationship between the abundance of *Callicebus moloch* and the silvery marmoset *Mico argentatus* in a fragmented landscape in central Amazonia, and there is some evidence of a similar situation within the present study area.

Titis in the Brazilian State of Sergipe

At just over 20,000 square kilometers, Sergipe is the smallest Brazilian state. It lies on the right bank of the lower São Francisco River, and thus at the easternmost extreme of the distribution of the genus *Callicebus*. Extending some 150 km inland from the Atlantic Ocean, the state encompasses the transition from the coastal strip of humid Atlantic Forest to the Caatinga, passing through an upland ecotonal region known locally as the "Agreste" (Fig. 9.4).

The occurrence of titis in Sergipe was unknown to science until Kobayashi and Langguth (1999) described *C. coimbrai* from specimens collected at a site in Pacatuba, in the eastern extreme of the state. Originally recorded from only three Atlantic Forest sites, the species was almost immediately allocated to the critically



Cartographic editing: Raone Beltrão / Projeto Guigó

Fig. 9.4 Distribution of the three principal morphophysiological domains (per Ab'Saber 2003) in the Brazilian state of Sergipe. *Dark gray*=Atlantic Forest; *medium gray*=Agreste; *light gray*=Caatinga

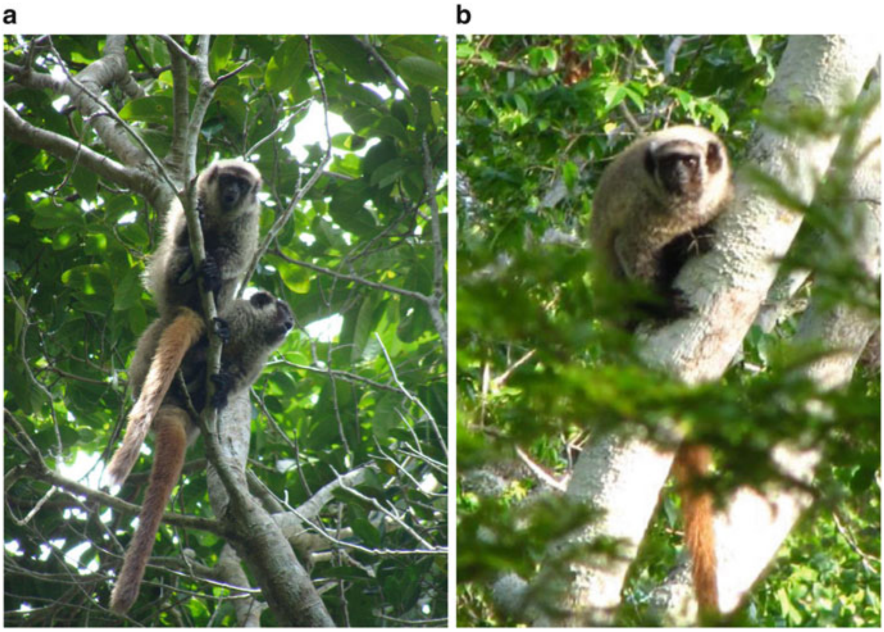


Fig. 9.5 Titi monkeys from (**a**) the Fazenda Trapsa in the Atlantic Forest of southern Sergipe (photograph: J.P. Souza-Alves), and (**b**) Lamarão in northern Bahia, the type locality of *C. barbarabrownae* (photograph: A. Estrela)

endangered category by the IUCN (2000), but subsequent surveys have revealed that titis occur throughout most of the state of Sergipe, and that *C. coimbrai* may range as far south as Salvador, in the neighboring state of Bahia. This contributed to the allocation of the species to the endangered category in the subsequent evaluation (Veiga et al. 2008).

Given the known occurrence of *C. barbarabrownae* in the Caatinga and the apparent preference of *C. coimbrai* for the Atlantic Forest, the implicit assumption that the two species are ecologically specialized for survival in these respective biomes has influenced the interpretation of their zoogeographic relationships. In particular, published distribution maps have invariably shown the limits of their ranges correlating with those of the two biomes, although the evidence supporting such an interpretation is, at best, scant. In fact, the subtle variation in the external morphology of the two species makes reliable visual identification of the taxa almost impossible under typical field conditions (Fig. 9.5). Printes (2007) recorded considerable variation in the coloration of the pelage in *C. barbarabrownae*, which further impedes reliable identification. Given this problem, species identification has more often than not been influenced by the implicit assumption of habitat specialization, with the location of the sighting having priority over physical traits.

Despite these problems for the identification of the species, and the interpretation of the ecological relationships between them, recent surveys along the lower São

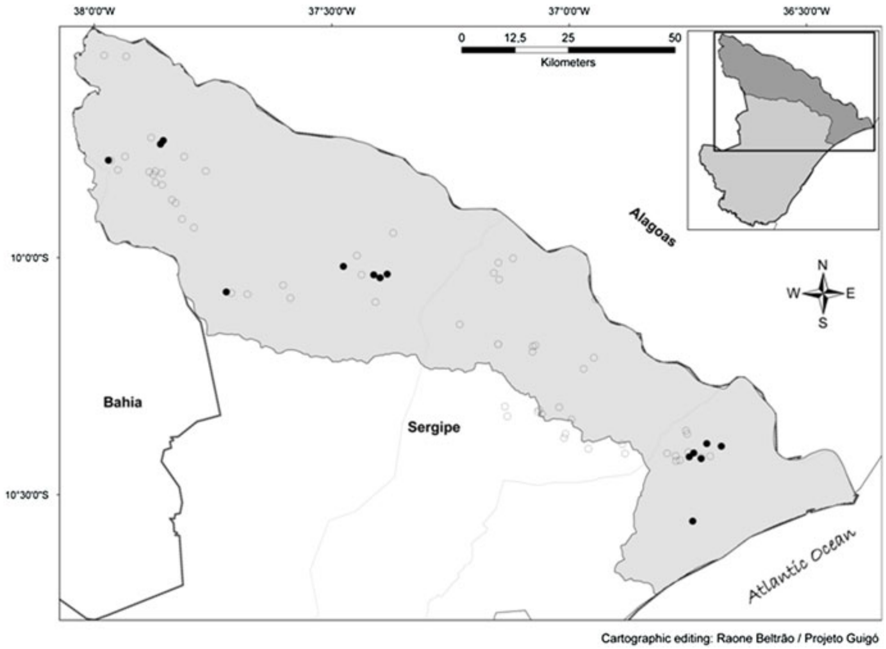


Fig. 9.6 Distribution of titis at sites surveyed within the São Francisco drainage basin in Sergipe. *Open circles* = titis absent; *black circles* = titis present

Francisco basin (Beltrão-Mendes 2010; Santos Junior 2010) have revealed an intriguing distribution pattern (Fig. 9.6), with a lacuna corresponding almost exactly to the region of the Agreste (Fig. 9.4). Rather than a gradual intergradation between the two species, then, as seen further south between *C. jacchus* and *C. penicillata* (Alonso et al. 1987), this evidence suggests an allopatric distribution, which would tend to support the habitat specialization hypothesis.

However, there are a number of important considerations here, not least the enigma of the absence of these monkeys from this ecotonal area. As such areas normally combine elements of the adjacent biomes (Shmida and Wilson 1985), they are typically more, rather than less diverse, so, a priori, the presence of both titi species might be expected within the Agreste, if not in sympatry, necessarily. It is also still unclear whether this lacuna is a localized phenomenon, i.e., restricted to the São Francisco basin, or whether it is typical of the limit between the ranges of the two species. Ongoing surveys are targeting this area specifically with the aim of providing more definitive evidence on this unique distribution pattern.

Perhaps an even more intriguing question here is whether the phenomenon is natural or a relatively recent development, provoked by anthropogenic changes in the local landscape. As the absence of titis from the Agreste is difficult to account for on the basis of ecological factors alone, it seems possible that the current scenario may be related to patterns of habitat fragmentation within the area. With rich soils and a relatively amenable climate, the Agreste is a valued agricultural zone, which is mostly occupied by smallholders, rather than the larger properties more typical of the Caatinga and Atlantic Forest. This implies a possible difference in the pattern of habitat fragmentation, in particular the formation of smaller fragments, which may have contributed to the local extinction of titi populations. However, while such an explanation seems plausible, it remains unclear why the populations should have been eliminated so completely, given that titis are able to survive in relatively tiny fragments—of less than 5 ha—in both the Caatinga and the Atlantic Forest.

Habitat Fragmentation and Biome Differences

As for most of northeastern Brazil, Sergipe has suffered extensive deforestation and, while estimates vary, the loss of the original forest cover is around 90 % in both the Caatinga and the Atlantic Forest (Santos 2009; Santos Junior 2010). The remaining habitat is distributed in isolated fragments, the vast majority of which are of relatively small size of typically less than 100 ha. As titis generally occupy home ranges of 20–40 ha in continuous forest (Bicca-Marques and Heymann 2013), fragments of this size might be expected to have a population of a few dozen monkeys, at most.

While there is an overall tendency for larger fragments to be occupied by titis, fragment size is not a good predictor of occupancy, and titis have been observed in fragments smaller than 5 ha in both the Atlantic Forest and the Caatinga. In some cases, only a single animal was sighted, suggesting the temporary occupation of the habitat by a dispersing animal, but some of these smaller fragments are clearly occupied by family groups. The apparent absence of titis from many of the larger fragments suggests the influence of a complex of factors, which may include the history of occupation, fragmentation patterns, hunting pressure, interspecific competition, and predation pressure, as well as the composition of the anthropogenic matrix.

Most of these variables are difficult to evaluate systematically, although there is some evidence of variation among different sites. For example, Beltrão-Mendes et al. (2011) found that *C. xanthosternos*—both a potential competitor and predator of *Callicebus* (Sampaio and Ferrari 2005)—occurs at only a small handful of sites in Sergipe, and was sympatric with *C. coimbrai* at only three of these sites. Souza-Alves (2010) noted that members of the *C. coimbrai* study group at the Fazenda Trapsa in southern Sergipe would invariably react to the approach of capuchins with typical predator avoidance behaviors. While there is no direct evidence of predation, it seems possible that habitat fragmentation may exacerbate the pressure. Guedes et al. (2010) recorded *C. jacchus* in the diet of *Puma concolor* at the Fazenda Trapsa, but it is unclear whether this is symptomatic of increased predation pressure.

Data on demographic parameters are available from only two sites—Fazenda Trapsa (Atlantic Forest) and Fazenda São Pedro (Caatinga)—but nevertheless provide potential insights into the differences between biomes. At the Fazenda Trapsa, the population density of *C. coimbrai* was considerably higher in smaller fragments (Table 9.1). This supports the idea that this species is relatively tolerant of habitat fragmentation. Surprisingly, common marmosets—among the most ecologically

Table 9.1 Estimated abundance of *Callicebus* and *Callithrix jacchus* at two sites in Sergipe, representing the Atlantic Forest (Fazenda Trapsa: Chagas and Ferrari 2011) and the Caatinga (Fazenda São Pedro: Freitas 2010)

	Estimated density, ind./km^2 (sighting rate, per 10 km walked) of:	
Site/fragment size (ha)	*Callicebus*	*Callithrix*
Fazenda Trapsa		
118	10.2 (1.1)	(0.1)[a]
107	10.3 (2.8)	(1.3)
62	16.2 (3.7)	(0.4)
61	18.0 (2.4)	(0.3)
Fazenda São Pedro		
115	4.3 (0.2)	169.7 (4.5)

[a] Number of sightings insufficient for a reliable estimate of density

flexible platyrrhines—were rare at this site. The data from the Fazenda São Pedro reveal an exactly opposite pattern, however (Table 9.1), with a more typical marmoset density and a much-reduced abundance of titis (in this case, *C. barbarabrownae*). At this site, titis are not only rare overall, but are also restricted to the better-preserved portion of the fragment, whereas the marmosets are found throughout the available forest habitat (Freitas 2010).

The data suggest not only that there is a degree of competition between these two monkeys, but also that the marmosets may be relatively better adapted to Caatinga habitats. This would be consistent with both the geographic distribution of *C. jacchus* and its morphological specializations for a gummivorous diet, which underpin the ecological success of the species in marginal habitats (Ferrari 1993). These differences might also contribute to the lower occurrence rates of *Callicebus* in the Caatinga of Sergipe—28.1 % of the 32 fragments surveyed by Santos Junior (2010), as against 41.2 % in the Atlantic Forest ($n = 17$)—and, by extension, the absence of the genus from central Brazil.

Unfortunately, no detailed ecological data are available on titis in the Caatinga, although Souza-Alves (2010) and Fontes (2011) have now monitored a group of *C. coimbrai* at the Fazenda Trapsa for more than 1 year. Despite occupying a relatively small fragment of less than 20 ha, this group was able to maintain a relatively frugivorous diet throughout the year (61.2 % of feeding records), complemented primarily with young leaves, and, to a lesser extent, seeds. The most surprising finding from this study is the predominance of resources provided by lianas, rather than trees, in the group's diet. Overall, lianas provided 70.7 % of the records of feeding on fruits and seeds, and were prominent throughout most of the study period.

As the density of lianas tends to be higher in more disturbed habitats (Morellato et al. 2000), this characteristic may be an important factor in the ability of the titis to tolerate habitat fragmentation in this region. However, it remains unclear to what extent this is a typical pattern, given that the data refer to a single group inhabiting a relatively small fragment. For example, Heiduck (1997) noted that the closely related *C. melanochir* simply fed on the most available resources at any given time, and this may have been the case at the Fazenda Trapsa. If lianas are a key factor in the ability of the titis to survive in the region's forests, it will be necessary to design a new approach to the evaluation of habitat quality for the management of titi populations (cf., Beltrão-Mendes 2010).

Titis: A Special Case of Metapopulation Dynamics

Dispersal from the natal group is a key dynamic in the demography of any social species, and is especially systematic in the titis. All titi species are strictly monogamous, and the structure of social groups is maintained by the obligatory dispersal of maturing offspring. Successful dispersion depends on a series of factors, such as the availability of potential reproductive partners and territories, which are rarely abundant, even in continuous, pristine habitat. The risks of dispersal are multiplied in the fragmented landscape, where the dispersing animals may often be obliged to migrate between isolated patches in order to have any chance of achieving reproductive status.

It seems likely that the frequency of migration between habitats will be inversely related to fragment size, given that opportunities for dispersal will tend to decrease with decreasing population size. In the most extreme scenario, where the fragment is inhabited by a single group, dispersal from the fragment will be obligatory under most circumstances. No empirical data are available on dispersal or survival, but a number of cases of dispersal through the anthropogenic matrix have been reported, and it seems likely that this life phase is characterized by relatively high mortality rates in comparison with populations in continuous forest. While dispersal rates are likely determined by fragment size, it seems likely that the probability of successful migration will be inversely related to the distance between fragments.

In addition to the intrinsic risks of movement through the man-made matrix, the probability of successful dispersal—i.e., the establishment of a breeding pair—would likely be very low under most circumstances, and dependent on multiple migrations between fragments (Fig. 9.7). Even when a dispersing animal is able to find a potential breeding partner (i.e., a solitary adult), there is a 50 % chance that it will be of the same sex, and therefore, ineligible. Overall, then, successful dispersal from the natal group in the fragmented landscape of the region can be characterized as a "lottery" type of process.

This scenario suggests that the occupation of the smallest fragments will be discontinuous over the long term, so that a distinct and shifting subset of fragments will be occupied by breeding groups at any given moment, depending on the outcome of the combined lottery of the outcome of births, mortality, and migrations. In other words, while groups will disappear from some fragments during a given period (one case has been observed in *C. coimbrai*), they will be established in others during the same period, but the overall result will be the occupancy of a relatively small proportion of fragments at any one moment. In this context, the primary aim of any metapopulation management program should be assurance of dispersal among fragments, and the maintenance of higher overall occupancy rates. Ideally, this would involve the

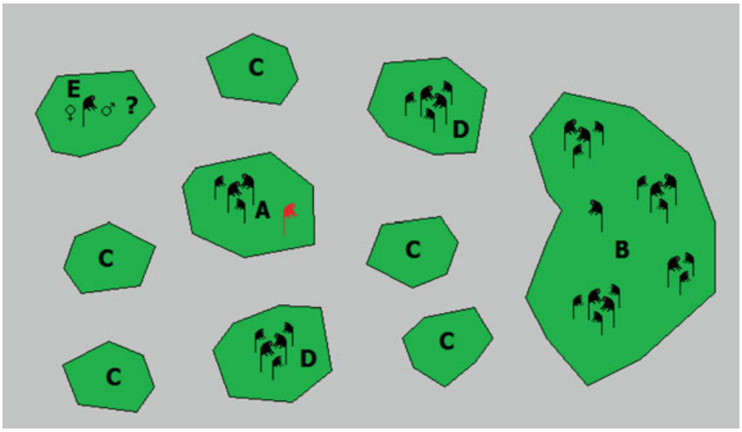


Fig. 9.7 Schematic landscape faced by a maturing titi monkey (*red* animal in fragment A) in the Atlantic forest of Sergipe. While larger fragments (B) offer the best opportunities for dispersal, they are relatively rare and require long migrations through the anthropogenic matrix (*gray*). While smaller fragments are more common, most are unoccupied (C), some have resident groups (D), and only a few present viable dispersal opportunities (E), depending on the gender of the animals

systematic monitoring of maturing individuals, which would be translocated to appropriate fragments prior to emigration, and the management of existing groups.

Long-Term Perspectives

Virtually nothing was known of the primates of Sergipe prior to the discovery of *C. coimbrai* in 1999, and its forest ecosystems were almost as poorly understood. More than a decade later, our knowledge of the region and its fauna and flora has advanced considerably, revealing unexpected diversity, and provides cautious optimism for the future. Despite the extensive deforestation suffered by the region and the delicate balance of the remaining habitat, the intrinsic resilience of the surviving primate populations suggests that they will be able to persist, at least over the short term. Ultimately, however, their survival may depend on the effective management of both populations and habitats, primarily to ensure the minimization of stochastic effects on habitat quality, population levels and genetic variability.

The Sergipe state government has provided one important initial step in this process, by creating the 800-ha Mata do Junco Wildlife Refuge specifically to protect the local population of *C. coimbrai* (Sergipe 2007). It remains to be seen whether this first, crucial measure will evolve into a wider, and more effective network of protected areas and populations. Given the current distribution of fragments and land ownership, one vital component of this process will be the creation and integration of privately owned reserves, in order to guarantee the protection of the maximum possible area of forest cover.

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Chapter 10
Do Patch Size and Interpatch Distance Influence the Distribution of Brown Howler Monkeys (*Alouatta guariba clamitans*) in a Fragmented Landscape in South Brazil?

Felipe Ennes Silva and Julio Cesar Bicca-Marques

Abstract The theories of island biogeography, metapopulation, and landscape ecology have been applied to study the influence of habitat loss, patch size, spatial isolation, and dispersal ability on species survival in fragmented landscapes. Here we test whether forest fragment size, distance to the nearest patch, and distance to the nearest potential mainland are good predictors of the presence of brown howler monkeys (*Alouatta guariba clamitans*) in fragments immersed in a matrix dominated by ranching, farming, and eucalyptus forestry in south Brazil. We also infer to which model of metapopulation (classical, mainland–island/source–sink, patchy, and nonequilibrium) the set of howler monkey populations best fit. From March 2003 to July 2005, we conducted censuses on 63 forest fragments and sighted brown howlers in 28 (occupancy index = 44 %). Fragment size (0.5–992 ha), distance to the nearest potential mainland (61–13,460 m), and distance to the nearest fragment (47–13,460 m) did not predict the presence of howler monkeys in these forest remnants. We conclude that the absence of brown howlers in many forest patches and the lack of relationship between their presence and fragment size and interpatch distances suggest that the set of populations in the study region best fits a nonequilibrium metapopulation model.

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Introduction

The expansion of the agricultural frontier, forestry industry, and urbanization were major drivers of habitat loss and fragmentation in the last decades (Bierregaard et al. 1992; Laurence et al. 2002), threatening biodiversity (Bierregaard et al. 1992; Michalski and Peres 2005; Simberloff and Abele 1976). The effects of habitat loss and fragmentation on species survival have been studied based on the theories of island biogeography, metapopulations, and landscape ecology (Arroyo-Rodríguez and Mandujano 2009).

According to the island biogeography, the ability of a species to disperse and colonize a patch ("island") is inversely related to its distance to the "mainland," a variable that affects the spatial distribution of its populations (MacArthur and Wilson 1967). The ability to cross the interpatch matrix is another factor that influences population spacing (Doak and Mills 1994; Margules et al. 1982). In this regard, metapopulation theory assumes that the processes of dispersal and immigration connect isolated populations into a network—the metapopulation. The colonization of unoccupied habitat patches and the extinction of discrete populations within a metapopulation are respectively equivalent to the processes of birth and death in the dynamics of a traditional population. Therefore, the persistence of a metapopulation depends on the balance between the rates of extinction and (re) colonization (Elmhagen and Angerbjörn 2001). There are at least four types of metapopulations: (1) "classical," (2) patchy, (3) mainland–island/source–sink, and (4) nonequilibrium (Harrison 1991). The "classical" model considers that all subpopulations are equally likely to go extinct and that recolonization ensures metapopulation persistence, whereas a patchy metapopulation is found when a high migration rate creates a virtually panmictic network of populations (Harrison and Hasting 1996). If differences in patch size influence species persistence, the metapopulation is likely to fit a mainland–island model. But, if quality affects individual movement among habitat patches, the metapopulation dynamics may take on a source–sink structure. In this scenario, patches presenting positive population growth rates are classified as sources, whereas those with negative growth are sinks. In addition to the processes of natality and mortality, these growth rates reflect the role immigration may play in preventing extinction or the disappearance of a subpopulation caused by the emigration of all its members rather than by their death (Elmhagen and Angerbjörn 2001). A rate of subpopulation extinction that exceeds the rate of patch recolonization characterizes a nonequilibrium metapopulation, which tends to shrink and disappear over time (Harrison and Hasting 1996). Dispersal and patch (re)colonization are particularly influenced by the landscape a patch is immersed in, including the presence of corridors and the pattern of land use in the matrix (Arroyo-Rodríguez and Mandujano 2009; Estrada and Coates-Estrada 1996; Marsh et al. 2003).

While some species do not adapt and disappear, others cope relatively well with habitat fragmentation and degradation (Bicca-Marques 2003; Marsh et al. 2003; Michalski and Peres 2005; Wijesinghe and Brooke 2005). Primates have been particularly impaired by habitat loss, a threat that has a stronger effect on forest living species than those found on the savanna (Cowlishaw and Dunbar 2000; Johns and Skorupa 1987). The best known New World monkey genus, *Alouatta*, represents a good model for studying the effects of habitat fragmentation and landscape attributes on species survival. Howler monkeys present the largest primate distribution in the Neotropics (Crockett and Eisenberg 1987; Neville et al. 1988), where they inhabit a wide range of forest habitats due to their eclectic folivorous–frugivorous diet (Bicca-Marques 2003; see also Bicca-Marques et al. 2009; Estrada et al. 1999; Estrada and Coates-Estrada 1996; Horwich 1998). However, their long-term survival in isolated forest fragments is hindered by higher levels of predation, hunting, parasitism, and inbreeding depression (Bicca-Marques 2003; Bicca-Marques and Freitas 2010; Chiarello and Galetti 1994; Fortes and Bicca-Marques 2008).

Therefore, a key element for making appropriate conservation decisions is the identification of the environmental variables that allow or impede howler monkey persistence in fragmented habitats (Arroyo-Rodríguez and Mandujano 2009). Different studies have shown that fragment size, number of tree species used as primary food sources, and distance from human settlements have a positive effect on howler presence, whereas distance to the nearest patch or to a potential source area has a negative effect (Arroyo-Rodríguez and Dias 2010; Arroyo-Rodríguez and Mandujano 2003; Arroyo-Rodríguez et al. 2008; Chiarello and Melo 2001; Estrada and Coates-Estrada 1996; Mandujano et al. 2005; Ribeiro and Bicca-Marques 2005).

In this study we test whether forest fragment size, distance to the nearest patch, and distance to the nearest potential mainland are good predictors of the presence of brown howler monkeys (*Alouatta guariba clamitans*) in a fragmented landscape in south Brazil. We also infer to which model of metapopulation the set of populations best fit. If it fits a patchy metapopulation we predict that most habitat patches are inhabited. If there are occupied and unoccupied patches and fragment size and distance to a potential mainland (or source area) are good predictors of howler presence, it fits a mainland–island metapopulation, but if fragment size and distance to the nearest patch predict howler presence, it best fits a "classical" model. On the other hand, if there are uninhabited patches and neither fragment size nor distance to the nearest patch nor distance to the nearest potential mainland predict howler occurrence, it fits a nonequilibrium model.

Methods

The study was conducted in the municipality of Barra do Ribeiro (30°12′38″–30°26′11″S, 51°08′08″–51°29′42″W), State of Rio Grande do Sul, Brazil. Current vegetation is characterized by fragments of Atlantic Forest within a matrix composed of cattle ranching, irrigated rice, subsistence farming, and eucalyptus forestry. Although we concur with Arroyo-Rodríguez and Mandujano (2009) that differences in land management influence primate dispersal among forest fragments and may better represent patch isolation than simple analyses of interpatch distances, we have no quantitative data on the spatial distribution of the major economic activities in the matrix surrounding fragments and, therefore, focus our analysis on patch size and interpatch distances. There is only one officially protected reserve in Barra do Ribeiro—the Reserva Particular do Patrimônio Natural Capão Grande, a small 9-ha private forested area.

Data on the occurrence of brown howler monkeys on 63 forest fragments were collected from March 2003 to July 2005. A fragment was defined as any cluster ≥0.5 ha of native tree species that was isolated from the nearest fragment by at least 30 m, irrespective of its shape. Censuses were often conducted by two researchers walking together preexisting trails, whenever available. Only sightings were recorded as evidence of the presence of howler monkeys in the fragments as suggested by NRC (1981) and Rodríguez-Toledo et al. (2003). The geographic coordinates of each fragment was recorded with a GPS and plotted in LandSat TM7 satellite images for calculating their surface area (ha) and the distances to the nearest fragment and to the nearest potential mainland (the largest forest fragments in the landscape, >200 ha, that may also function as source areas). These variables were compared between occupied and unoccupied patches by the Mann–Whitney test. A simple logistic regression was run in the software BioEstat 5.0 (Ayres et al. 2007) to test whether fragment size, distance from a fragment to the nearest potential mainland and to the nearest fragment were good predictors of the pattern of presence–absence of howler monkey subpopulations in the forest remnants.

Results

Howler monkeys were recorded in 28 of the 63 forest fragments; an occupancy index of 44 %. Forest remnants ranged from 0.5 to 992 ha (median = 6.6 ha, N = 63), and inhabited (0.5–216 ha, median = 7.5 ha, n = 28) and unoccupied (1–992 ha, median = 5.1 ha, n = 35) fragments were similar in size ($Z(U) = 1.107$, $p = 0.269$). Distance from a fragment to the nearest potential mainland ranged from 61 to 13,460 m (median = 785 m, N = 60). Fragments inhabited by howlers were farther from a potential mainland (70–4,121 m, median = 1,409.5 m, n = 26) than unoccupied ones (61–13,460 m, median = 553.5 m, n = 34; $Z(U) = 2.312$, $p = 0.021$). The distance between nearest fragments ranged from 47 to 13,460 m (median = 120 m, N = 63). The nearest fragment of an inhabited forest was also farther (50–1,275 m, median = 138 m, n = 28) than that of an unoccupied forest (47–13,460 m, median = 94 m, n = 35; $Z(U) = 2.428$, $p = 0.015$). Despite these differences, analyses including all 63 fragments found that no variable was a good predictor of the pattern of presence–absence of howler monkeys (fragment size: $Z = –0.421$, $p = 0.674$; distance to the potential mainland: $Z = 0.859$, $p = 0.391$; distance between nearest fragments: $Z = –0.739$, $p = 0.460$).

Because no monkey sightings, dung, carcasses, or skeletons were obtained in 24 fragments east of roads BR-116 and RS-709 (Fig. 10.1), we reanalyzed the data excluding these fragments. This analysis similarly indicated that no variable

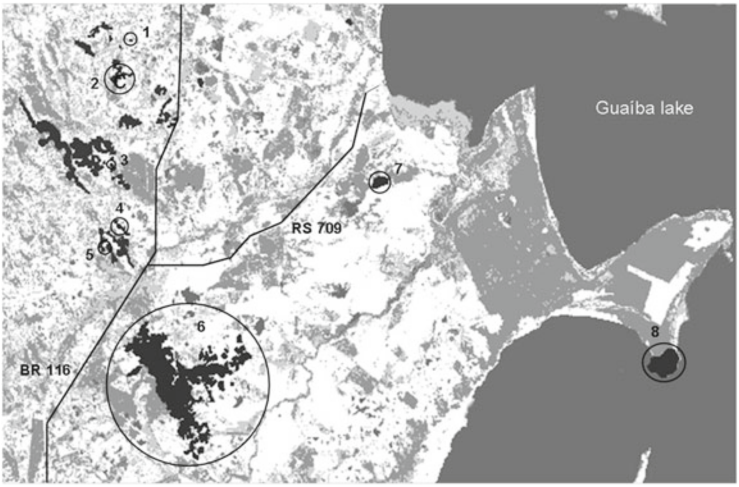

Fig. 10.1 Map of the study region showing the distribution of forest fragments (fragments outside *circles* were inhabited by howler monkeys, while *circled* and *numbered* [1–8] isolated fragments or clusters of fragments were unoccupied)

predicted the presence of howler monkeys in these forest remnants (fragment size: $Z=1.543$, $p=0.123$; distance to the potential mainland: $Z=1.050$, $p=0.294$; distance between nearest fragments: $Z=1.082$, $p=0.279$).

Therefore, this scenario suggests that the distribution of brown howler monkey populations in the study region best fits a nonequilibrium metapopulation model. There are many unoccupied forest patches and fragment size and interpatch distances (either to the nearest potential mainland or fragment) do not predict howler monkey presence.

Discussion

This study confirms that brown howlers can survive in small habitat patches (Fortes 2008; Fortes and Bicca-Marques 2008; Ribeiro and Bicca-Marques 2005). However, the high proportion of forest fragments that were unoccupied and the lack of relationship between interpatch distances and monkey presence suggest that as in other howler species (Estrada and Coates-Estrada 1996; Oklander et al. 2010), patch isolation hampers *A. guariba clamitans* dispersal. As a consequence, isolated populations are likely to only rarely (or not at all) exchange genes, ultimately compromising population long-term survival. Therefore, the individual behavioral flexibility that characterizes howlers and allows them to cope with habitat impoverishment (Bicca-Marques 2003; Bicca-Marques et al. 2009; Cristóbal-Azcarate and Arroyo-Rodríguez 2007) is likely to be surpassed by the negative effects of a putative increase in predation, hunting, parasitism, and inbreeding depression under these circumstances (Bicca-Marques 2003; Bicca-Marques and Freitas 2010; Chiarello and Galetti 1994; Fortes and Bicca-Marques 2008). A 2008–2009 outbreak of sylvatic yellow fever in the fragmented landscape of the State of Rio Grande do Sul, Brazil (Bicca-Marques 2009; Bicca-Marques and Freitas 2010) resulted in many howler monkey populations going extinct (Freitas and Bicca-Marques 2011), illustrating this increasing danger. The dispersal mechanism of the yellow fever virus among fragments is unknown. The limited dispersal ability of howler monkeys (Mandujano and Estrada 2005), their high susceptibility to the disease (Vasconcelos 2003), and the morbidity of sick individuals (F.E. Silva, pers. obs.) make them highly unlikely candidates to spread the disease among fragments. The role played by the dispersal of mosquito vectors, other infected animals, and, most probably, infected people (40–65 % of which are asymptomatic; Vasconcelos 2003) remains to be investigated (Bicca-Marques and Freitas 2010). Hence, the combination of the aforementioned factors tends to lead to higher rates of mortality than natality and, as a consequence, of population extinction rather than recolonization.

These trends also provide a possible explanation for the apparently long-term absence of howler monkeys east of the roads BR-116 and RS-709 (elders report to never have seen howler monkeys in this area). This hypothesis is compatible with the existence of an Mbya-guarani Indian reserve in the region. Mbya-guarani hunters (Ladeira 2003) may have extirpated howler monkeys near their settlements before the promulgation of the federal law that prohibits wildlife hunting and trapping in Brazil ("Lei de Proteção à Fauna," Law # 5197, 3 January 1967). Supporting this hypothesis is the observation that Indians are reported to have been seen in modern times trying to illegally sell infant brown howler monkeys along roadsides in other parts of the species distribution in the State of Rio Grande do Sul.

The long-term fate of the remaining subpopulations may be extinction, since the spatial distribution and limitations to dispersal support classifying them as a nonequilibrium metapopulation (microsatellite DNA analyses could be used to assess the level of gene exchange among them; see Oklander et al. 2010). Because time and space constrains witnessing events of extinction and (re)colonization in mammals with long generation times and low reproductive rates (Elmhagen and Angerbjörn 2001), short-term studies on species occurrence across a range of landscapes and habitat patches, such as ours, are critical for understanding species response to varying degrees of habitat quality and fragmentation (Andrén 1994) and providing insight into the best metapopulation model to fit a set of subpopulations. The observation that there is no difference in size between occupied and unoccupied fragments and the unexpected longer distances between inhabited fragments and the nearest potential mainland or fragment is also compatible with a nonequilibrium metapopulation. Our scenario contradicts the pattern observed for *Alouatta palliata* by Mandujano et al. (2005) in a similar landscape in México. In this *A. palliata* system the likelihood of finding howlers increases in fragments >20 ha and closer (<200 m) to other forests.

Therefore, we conclude that the long-term persistence of viable populations of brown howler monkeys in the forest remnants of Barra do Ribeiro is dependent upon a management program aiming at increasing habitat connectivity and gene exchange between isolated populations. To reach the goal of converting the set of remaining howler populations to a metapopulation structure, it is mandatory to promote the establishment of corridors. Because howler dispersal may occur via stepping stones (Glander 1992), the simple establishment of live fences, small orchards, or isolated trees in the matrix decreases interpatch distances and may be sufficient for improving individual movement among patches (Arroyo-Rodríguez and Mandujano 2009; Bicca-Marques and Calegaro-Marques 1994; Estrada and Coates-Estrada 1996; Marsh et al. 2003). In this sense, the controversial activity of eucalyptus forestry in the study region may serve to facilitate dispersal. Furthermore, depending on the plant species composition of these elements of the landscape, howlers may use them for many purposes, such as shelters, resting areas, and feeding patches (Arroyo-Rodríguez and Mandujano 2009; Bicca-Marques and Calegaro-Marques 1994; Mandujano et al. 2005). Considering that cattle ranching is the major economic activity in this region, convincing land owners to prevent cattle from wandering into forest fragments where they browse seedlings and saplings and compromise forest regeneration is another necessary measure for allowing the long-term survival of howler monkeys (Marsh 2007). Enforcing environmental laws and supporting the creation of reserves are also important conservation measures.

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Chapter 11
Status Monitoring of Isolated Populations of Macaques and Other Nonhuman Primates in Thailand

Nantiya Aggimarangsee

Abstract Macaques and other nonhuman primates in Thailand play important roles both in the ecosystem and as mythological figures in Thai society. Most live safely in the country's protected areas such as national parks, wildlife sanctuaries, and Buddhist temples; however, these populations are isolated. The first survey to confirm the status of 52 isolated populations of primates in Thailand was conducted in 1989–1991 and it assessed population size, age–sex composition, habitat availability, resource provisioning by humans, and the attitude of local people. Of the 52 sites, 21 sites were completely isolated from other populations of the same species. A resurvey of some of these populations was conducted after 20 years in 2009–2010. Twenty-three out of the 25 visited sites had *Macaca fascicularis*, only one site had *Macaca assamensis* with two *Macaca arctoides* individuals, and one newly discovered site had the introduced green monkey (*Cercopithecus aethiops*) that was released from a zoo. At one site, *M. fascicularis* was extirpated, while 12 sites experienced an increase in the number of populations.

Introduction

It has been widely documented that habitat fragmentation impacts wildlife populations, including nonhuman primates (hereafter primates). Thailand, similar to other developing countries, has been facing the problem of habitat fragmentation. To examine the effects of fragmentation, surveys of 52 isolated populations of primates were conducted in 1989 (Aggimarangsee 1992) and a resurvey of 25 these fragments was carried out 20 years later.

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Thailand is home to five species of macaques: assamese (*Macaca assamensis*), stump-tailed (*Macaca arctoides*), long-tailed (*Macaca fascicularis*), rhesus (*Macaca mulatta*) and pig-tailed (*Macaca nemestrina*); four species of langurs: dusky langur (*Trachypithecus obscurus*), Phayrei's langur (*Trachypithecus phayrei*), banded langur (*Presbytis femoralis)*, silvered langur (*Presbytis cristata*); four species of gibbons: white-handed gibbon (*Hylobates lar*), Pileatus gibbon (*Hylobates pileatus*), black-handed gibbon (*Hylobates agilis*), and siamang (*Hylobates syndactylus*); and two species of loris (*Nycticebus coucang* and *Nycticebus bengalensis*) (Lekagul and McNeely 1988; Rowe 1996).

There are two sects of Buddhism in Thailand, the "Mahanigai" sect and the "Thammayut" sect. Most of the monks in Thailand belong to the less conservative Mahanigai sect, which has many temples in rural and forested areas (Aggimarangsee 1992). Thai culture is strongly influenced by Buddhism, "the religion of nature" (Laohavanich 1989). There are "Wan Phra" (Buddhist monk days) every week when Buddhists visit temples to make offerings of food and money to the monks. The monks will also give excess food to pilgrims, villagers, students, and animals (Aggimarangsee 1992).

In rural areas of Thailand, temples and monasteries are the center of religious activities in Buddhist societies; they are often the center of community activities as well. Temples are usually located on or near hills, and many have forested areas to give the idea of single and continuous existence with nature (Aggimarangsee 1992). In general, Thai people regard these forests with fear and reverence as they believe that there are "Rhuka Thevada" (tree spirits) and "Chao Pho" (male spirits) that protect the forest and animals from being disturbed (Buri 1989; Kriengkraipetch 1989; Vichit-Vadakan 1989). Animals living in the temples are legally protected by category 6 section 41 of the Wildlife Conservation and Protection Act, 1992. Socially, Buddhist temples are regarded as a "khet apai than" (forgiveness areas) within which humans and animals are protected; however, once outside the temple's ground this protection is no longer guaranteed (Aggimarangsee 1992; Brockelman 1989).

I assessed the degree of human–primate interaction, as well as resource provisioning by humans, health, attitude, and habitat quality, at 36 visited temple sites in Thailand (Aggimarangsee 1992).

Methods

In 1988, there were only 12 sites known to have macaques living in association with people in the country. To verify the presence of primates, I sent questionnaires to the head abbots of each sect of each province in Thailand. Out of a total of 166 questionnaires I mailed out, I received 41 replies (35 %), 18 of which indicated the presence of primates. A total of 68 possible sites were established from information gathered from various sources, such as colleagues and visitors of the former Wildlife Research Center (Mahidol University), monks, villagers, and tourists. Of these 68 sites, 53 sites were visited, 42 of these were inhabited by primates where two sites had captive monkeys and eight had both free-ranging and captive monkeys (Aggimarangsee 1992). Twenty years after the first survey, I conducted the survey once more and visited 25 selected sites and age–sex compositions were obtained from 14 of these locations.

Results

All of the 25 revisited sites had *M. fascicularis*, one site had *M. assamensis* with two *M. arctoides* individuals. There was a newly discovered site where vervet monkeys (*Cercopithecus aethiops*) were introduced 20 years ago from an open zoo near Bangkok. A small group of long-tailed macaques at Wat Khao Tham Kunchorn is extirpated due to hunting about 16 years ago. Macaque populations have dramatically increased in several locations (Table 11.1) and the degree of human–primate interaction has changed (Table 11.2). In some populations there were many obese individuals, while other several low ranking individuals were thin (Health Category 2; Table 11.2).

Wat Tham Pla, Chiang Rai Province—This Buddhist temple is located at the base of a limestone hill in Mae Sai District. The hill is surrounded by villages, schools, orchards, and pineapple fields. A stream flows out of a cave and the water is kept as a big pond. People regularly visit the temple to gain merit by releasing fish, turtles, snails, and other aquatics, also to give food to the fish and macaques. There are at least four groups of assamese macaques (*M. assamensis*) that regularly visit the temple for food given to them by local pilgrims and foreign tourists. I observed 36 macaques in 1989, 56 individuals in 1991 and about 130–163 individuals in 2008–2009. There was no long-term study on the behavior of assamese macaques in Thailand until Komkhich Kaewpanus from Chiang Mai University studied the seasonal variation of the macaques' behavior during 2008–2009, and found that the macaques relied 61.7 % on provisioned food and 38.3 % on natural food (Kaewpanus 2010).

Wat Khao Noh, Nakhon Sawan Province—This Buddhist temple covers an area of 68 ha, and is located at a base of an isolated limestone hill. The hill is covered with shrub forest and some large trees. The hawkers in the area use crocodile dolls and sticks to keep the macaques away from their food stalls. The former abbot was a revered monk and as a result many pilgrims and tourists regularly visited this temple. I observed only 179 *M. fascicularis* at this temple in 1991 and in 2009 I estimated there to be approximately 700 individuals. I could not count the age–sex composition of the macaques in 2009 because they were very aggressive.

Wat Kriengkrai Klang, Nakhon Sawan Province—This old Buddhist temple was founded in the Ayutthaya era about 400 years ago. It is located by the Nakhon Sawan River (Aggimarangsee 1992). After my first survey, several new buildings were erected with donation money due to the highly venerated former abbot of the temple; several tall dipterocarp trees were conserved. The temple is surrounded by rice fields and villages. I counted 195 *M. fascicularis* in February, 1991 and 430 individuals were counted in October, 2009.

Table 11.1 Primate population size in isolated fragments in Thailand at 25 visited sites during 1989–2010

Sites	Estimated location	Area (ha.)	Size class	Sp.	Date observed	Total (idv.)	Pop. change
1. Wat Tham Pla	N 20° 19′	17.6; 90*	L	as	14–16 Sep 1989	56	++
	E 99° 51′				10 Sep 2009	129	
2. Wat Khao Noh	N 15° 57′	68*	L	fa	22 Feb 1991	179	++++
	E 99° 52′				28 Feb 2009	ca. 700	
3. Wat Kriengkrai Klang	N 15° 44′	NA	NA	fa	22 Feb 1991	195	++
	E 100° 11′				17 Oct 2009	430	
4. San Prakarn Lopburi	N 14° 47′	0.3	S	fa	1 Jul 1989	104	++++++
	E 100° 27′				1–2 Mar 2009	619	
5. Wat Kai	N 14° 30′	NA	NA	fa	NA	NA	NA
	E 100° 31′				26 May 2010	222	
6. Wat Hansang	N 14° 30′	NA	NA	fa	NA	NA	NA
	E 100° 31′				26 May 2010	184	
7. Wat Tham Sala	N 13° 48′	3.2	S	fa	15–19 Dec 1990	59	+++
	E 100° 06′				24 May 2009	167	
8. Wat Ratch Singkhorn	N 13° 34′	8; 125*	L	fa	1 Dec 1990	137	+
	E 99° 46′				5 Jul 2009	292	
9. Tham Chomphon	N 13° 38′	15*	M	fa	1 Dec 1990	216	++
	E 99° 35′				5 Jul 2009	358	
10. Wat Khao Chong Pran	N 13° 44′	11*	M	fa	20 Dec 1990	20	NA
	E 99° 46′				4 Jul 2009	NA	
11. Wat Khao Tham Kunchorn	N 13° 29′	12*	M	fa	20 Dec 1990	9	Extirpated
	E 99° 42′				4 Jul 2010	0	
12. Wat Ngern Rung Sawang (Tham Nam)	N 13° 43′	NA	NA	fa	20 Dec 1990	26	NA
	E 99° 45′				5 Jul 2009	NA	
13. Khao Suan Luang	N 13° 35′	25*	M	fa	24 Dec 1990	63	Stable
	E 99° 49′				5 Jul 2009	51	

14. Wat Huai Ta-khaeng	N 13° 35′	5*	S	fa	20 Dec 1990	28	+++
	E 99° 45′				5 Jul 2009	89	
15. Tham Khao Bin	N 13° 36′	NA	NA	fa	NA	NA	NA
	E 99° 40′				5 Jul 2009	6	
16. Wat Nong Hoi	N 13° 36′	NA	NA	fa	NA	NA	NA
	E 99° 45′				5 Jul 2009	31	
17. Wat Khao Yoi	N 13° 14′	NA	NA	fa	NA	NA	NA
	E 99° 49′				7 Jul 2009	176	
18. Wat Khao Takhrao	N 13° 13′	12.5; 7*	M	fa	11 Feb 1991	17	++++
	E 99° 56′				7 Jul 2009	67	
19. Khao Wang	N 13° 08′	23*	M	fa	9 Feb 1991	121	+
	E 99° 58′				7 Jul 2009	162	
20. Khao Sammuk	N 13° 18′	125*	L	fa	16 Nov 1990	126	+++
	E 100° 54′				16 Oct 2009	374	
21. Wat Tham Sua	N 08° 07′	32*	M	fa	19 Sep 1990	23	+++++++++++
	E 98° 55′				28 Jul 2010	266	
22. Wat Suwan Khuha	N 08° 25′	17.5*	M	fa	NA	NA	NA
	E 98° 28′				27 Jul 2010	78	
23. Wat Khuha Sawan	N 07° 37′	55*	L	fa	20 Sep 1990	51	++
	E 100° 05′				29 Jul 2010	119	
24. Khao Tangkuan and Khao Noi	N 07° 12′	20* and 13*	M	fa	9 Apr 1989	66	++++
	E 100° 35′				29 Jul 2010	262	
25. Mineburi	NA	NA	NA	ae	NA	NA	NA
					23 May 2009	8	

Area (*) = area size (ha) of hill at that site

Size class = size of fragments: *S* = small (<10 ha), *M* = medium (11–50 ha), *L* = large (51–200 ha)

Species (Sp.): *as* = *Macaca assamensis*, *fa* = *Macaca fascicularis*, *ae* = *Chlorocebus aethiops*, NA = not applicable

Table 11.2 Human and nonhuman primate interaction at 25 visited sites in Thailand

Sites	Area (ha)	Total (ind.)	Provision[a]	Health[b]	Attitude[c]	Habitat[d]
1. Wat Tham Pla	17.6; 90*	56	2	1	2	2
		129	**2**	**2**	**2**	**1**
2. Wat Khao Noh	68*	179	1	1	2	2
		ca. 700	**1**	**0**		**1**
3. Wat Kriengkrai Klang	NA	195	1	1	2	2
		430	**2**	**1**	**2**	**1**
4. San Prakarn Lopburi	0.3	104	2	1	1	0
		619	**2**	**2**	**2**	**0**
5. Wat Kai	NA	NA	NA	NA	NA	NA
		222	**2**	**2**	**2**	**0**
6. Wat Hansang	NA	NA	NA	NA	NA	NA
		184	**2**	**1**	**2**	**0**
7. Wat Tham Sala	3.2	59	1	0	2	0
		167	**2**	**2**	**2**	**0**
8. Wat Ratch Singkhorn	8; 125*	137	2	1	1	2
		292	**2**	**1**	**2**	**1**
9. Tham Chomphon	15*	216	1	1	2	2
		358	**2**	**1**	**2**	**1**
10. Wat Khao Chong Pran	11*	20	0	1	1	2
		NA	**0**	**NA**	**0**	**2**
11. Wat Khao Tham Kunchorn	12*	9	0	1	1	2
		0	**NA**	**NA**	**0**	**1**
12. Wat Ngern Rung Sawang (Tham Nam)	NA	26	0	1	1	2
		NA	**1**	**NA**	**1**	**2**
13. Khao Suan Luang	25*	63	1	1	1	2
		51	**1**	**1**	**2**	**2**
14. Wat Huai Takhaeng	5*	28	1	1	2	2
		89	**2**	**1**	**2**	**2**
15. Tham Khao Bin	NA	NA	NA	NA	NA	NA
		6	**0**	**1**	**1**	**1**
16. Wat Nong Hoi	NA	NA	NA	NA	NA	NA
		31	**2**	**1**	**2**	**1**
17. Wat Khao Yoi	NA	NA	NA	NA	NA	NA
		176	**2**	**2**	**2**	**1**
18. Wat Khao Takhrao	12.5; 7*	17	1	1	1	2
		67	**2**	**1**	**2**	**1**
19. Khao Wang	23*	121	2	2	2	2
		162	**2**	**2**	**2**	**2**
20. Khao Sam Muk	125*	126	2	2	1	2
		374	**2**	**2**	**2**	**2**
21. Wat Tham Sua	32*	23	0	1	1	2
		266	**1**	**1**	**2**	**2**
22. Wat Suwan Khuha	17.5*	NA	NA	NA	NA	NA
		78	**2**	**1**	**2**	**2**
23. Wat Khuha Sawan	55*	51	1	1	2	2
		119	**2**	**1**	**2**	**2**

(continued)

Table 11.2 (continued)

Sites	Area (ha)	Total (ind.)	Provision[a]	Health[b]	Attitude[c]	Habitat[d]
24. Khao Tangkuan and Khao Noi	20* and 13*	66 **262**	1 **2**	1 **1**	1 **2**	2 **2**
25. Mineburi	NA	NA **8**	NA **1**	NA **1**	NA **1**	NA **2**

Normal letters represent the survey in 1989–1991 while bold letters represent the survey in 2009–2010

"*" represents the area of hill in that location whereas the one without * means the temple's area

[a] 0 = occasionally provisioned; 1 = semi-provisioned; 2 = fully provisioned

[b] 0 = undernourished; 1 = healthy; 2 = several obese individuals, with or without hair loss, with some skinny individuals

[c] 0 = intolerant; 1 = indifferent; 2 = tolerant

[d] 0 = no viable natural habitat left; 1 = some natural habitat left; 2 = adequate natural habitat left

Sarn Pra Karn (Pra Karn Shrine), Lopburi Province—Pra Karn Shrine is a Hindu and Buddhist shrine (0.3 ha). I counted 104 *M. fascicularis* in and around the shrine in July 1989 and 619 individuals around the shrine and in town in March 2009. The macaques in this location were considered a nuisance and they often attacked visitors. There were many obese macaques; however, many individuals that were likely low ranking were thin and exhibited hair loss. The Lopburi Business Association gives a monkey buffet party annually with fruits and sweets. Though provisioned, the macaques did not receive full protection and there were reports of the monkeys being hit by cars and caught. The Lopburi Zoo, which belonged to the Royal Thai Military, regularly examined the monkeys' health.

Wat Kai, Phra Nakhon Si Ayutthaya Province—This Buddhist temple is located in Bang Pahan District. To promote the temple, big models of a fighting cock and *M. fascicularis* are placed at the temple's entrance by the Highway. The current abbot and the municipality try to conserve the macaques by feeding them large amounts of food and have built a park with a playground, waterfall, and pond. I did not visit this temple during my first survey; however, 222 individuals were counted in May 2009.

Wat Hansang, Phra Nakhon Si Ayutthaya Province—This Buddhist temple is located by a river and about 10 km from Wat Kai. Long-tailed macaques are living in a patch of dipterocarp forest within the temple's ground. I did not visit this temple during my first survey, but I counted 184 individuals in May 2009. The present abbot encourages people to feed the macaques to gain merit and promote the temple.

Wat Tham Sala, Nakhon Pathom Province—Pilgrims and visitors regularly visit this temple to pay respects to the highly respected and long deceased former abbot of the temple, whose body rests within the temple. During his lifetime, the abbot protected and conserved the free-ranging *M. fascicularis* that inhabited the temple. Villages, a school, streams, and paddy fields surround the temple. As a response to macaque invasions of the monks and villager's living compounds, the municipality built a big cage to keep the macaques away from humans. However, this action was not successful. I counted 59 individuals in December 1990 and 167 individuals in May 2009.

Wat Ratcha Singkorn (Khao Ngu), Ratchaburi Province—This Buddhist temple is located at the base of a huge limestone hill named "Khao Ngu" (Snake Hill).

Fig. 11.1 Hawkers and tourists at Tham Chomphon, Ratchaburi Province

There are several hawkers selling monkey food, such as bananas and peanuts, to visitors. The macaques raid villagers and hawkers' houses around the temple. I counted 137 *M. fascicularis* in December 1990 and 437 individuals in July 2009.

Tham Chomphon, Ratchaburi Province—"Tham Chomphon" (General Cave) is located in Chom Beung District and is one of the popular tourist sites in this province. There are a number of hawkers selling food for monkeys (Fig. 11.1). I counted 216 long-tailed macaques in December 1990 and 358 individuals in July 2009.

Wat Khao Chong Pran, Ratchaburi Province—This Burmese-Buddhist temple is located at the foot of the Khao Chong Pran (11 ha). Many visitors regularly visit this temple from late afternoon into the evening to see bats that fly from the Chong Pran cave. Guano is collected and sold for fertilizer. There were about 20 *M. fascicularis* counted in December 1990. I had not seen the macaques during my last visit in 2009, though the abbot reported that they were fine.

Wat Tham Kunchorn, Ratchaburi Province—This temple (Elephant Cave Temple; named after its shape) is located at the foot of the Khao Kunchorn. I counted nine individuals of *M. fascicularis* at this temple in 1990 but they were killed by poachers about 10 years ago. There are presently no macaques at this location.

Wat Ngern Rung Sawang (Wat Tham Nam), Ratchaburi Province—"Wat Tham Nam" (Water Cave Temple) is located at the base of Tham Nam. I counted 26 long-tailed macaques in December 1990, but was unable to sight the macaques in July 2009 due to heavy rain.

Khao Suan Luang, Ratchaburi Province—There is a nun monastery located at the Suan Luang limestone hill. I counted 64 *M. fascicularis* in December 1990 and 51 individuals in July 2009. It was reported that in 1990 a group of men came to hunt the macaques, probably to sell the meat. There is a Buddhist temple named Wat Khao Kaew located on the other side of the hill. The monks at this temple do not give food to the macaques because they have learned the human–monkey conflict.

Wat Huai Takaeng, Ratchaburi Province—This small Buddhist temple is located by a small limestone hill named Khao Takaeng. About 50 *M. fascicularis* from this temple were caught and released at Sai Yok Temple in Kanchanaburi Province in 1990 (Aggimarangsee 1992). I counted 28 long-tailed macaques in December 1990 and 89 individuals in July 2009.

Tham Khao Bin, Ratchaburi Province—At this site there are several stalls selling local and handicraft products. The macaques here are shy and have not yet created any problems for humans. I counted only six *M. fascicularis,* of which three were adult males, two adult females and an infant of unknown sex in July 2009.

Wat Nong Hoi, Ratchaburi Province—This large Buddhist temple is located on top of the "Khao Raeng" (Vulture Hill). There are several buildings, statues of Lord Buddha, Photisatava, and many other gods and spirits. The temple provides free vegetarian food and accommodation for people who want to practice meditation. Crocodile dolls are seen all over the temple to keep the macaques away. I did not visit this temple during my first survey, but counted 31 *M. fascicularis* in July 2009.

Wat Khao Yoi, Phetchaburi Province—This Buddhist temple is located at Tha Yang District not far from the highway leading to the south of Thailand. There is an old reclining Lord Buddha image in the cave that brings a good number of people to visit this site. There is also a big pond where the macaques play and swim. I did not visit this site during the first survey, but counted 176 *M. fascicularis* in July 2009.

Wat Khao Takhrao, Phetchaburi Province—This Buddhist temple is located on an isolated limestone hill. When I made my first visit in February 1991, the temple was small and surrounded by villages, a prawn farm, and patches of mangrove forest. In 2009, I was surprised to see an increased number of buildings, cable cars, and visitors. I counted 17 *M. fascicularis* in February 1991 and 67 individuals in July 2009.

Khao Wang (Phra Nakhon Khiri Palace), Phetchaburi Province—Khao Wang is a limestone hill at the edge of the city. It is a major tourist attraction drawing several thousand tourists on weekends and festive days. On top of the hill is King Mongkut's Phra Nakhon Khiri Palace that dates back to 1869. I counted 73 *M. fascicularis* in August 1989, approximately 120 individuals in February 1991, and 162 individuals in July 2009.

Khao Sam Muk, Chonburi Province—This is a rocky hill located east of the Gulf of Thailand. The monkeys are protected by the stall-keepers who venerate the "Chao Mae Sam Muk," a female spirit who loved monkeys and committed suicide there about 300 years ago. I counted 126 *M. fascicularis* in November 1990 and 374 individuals in 2009.

Wat Tham Sua, Krabi Province—This is a Buddhist temple located at a limestone hill with a big cave named "Tham Sua" (Tiger Cave). Due to the development of famous islands and beaches, this province has become a popular tourist spot. The present abbot of this temple is revered and famous for his talisman, the tiger. The temple has changed dramatically in the last 20 years. Previously, there were only a few small "guti" or monk residences, but now there are large buildings, statues of the Lord Buddha, Pothisatava, Kanesh, dragons, and tigers (both living and statues). I counted 23 *M. fascicularis* in September 1990, but the population dramatically increased to 266 individuals in July 2010.

Wat Suwan Khuha, Phang-Nga Province—This Buddhist temple is located by a medium sized "Khao Tham" (Cave Hill) and is a tourist attraction due to the presence of many caves, with one of the caves bearing inscriptions of King Rama V and King Rama IX on its walls. In September 1990, villagers reported that there were about 20 macaques living there, but that they rarely came down due to hunting pressure. In July 2010, stall-keepers reported about 300 individuals from three groups of macaques living here; however, I counted 78 individuals from one group during my brief visit in July 2010.

Wat Khuha Sawan, Phatthalung Province—This old Buddhist temple was founded in 657 AD beside a limestone hill "Khao Tham Khuha Sung." There were 56 *M. fascicularis* counted in 1989, 51 individuals in February 1991 and I counted 119 *M. fascicularis* in July 2010. The late former abbot was very interested in conservation. He informed me in 1989 that eight monkeys were shot by poachers and their skins peeled off so the bodies could be pass off as langurs, and later sold for food (Aggimarangsee 1992).

Khao Tang Kuan and Khao Noi, Songkhla Province—These are two adjacent hills located near Samila beach that are regularly visited by local and foreign tourists as a side attraction to the beach. The municipality has covered the cable tracks in the area to prevent macaque injuries and a cross over net was installed for monkeys to safely cross the road. I counted a troop of 63 *M. fascicularis* in April 1989 and 262 individuals in July 2010.

Mineburi Community, Bangkok—A group of green or vervet monkeys (*C. aethiops*) was released from the Safari World, a private zoo and amusement park located in Mineburi about 16 years ago. The monkeys have adapted well to the new environment that comprises rice fields, shrubs, a riverine forest, villages, orchards, housing estates and golf courses. These monkeys receive food from villagers, staff and tourists at golf courses.

Discussion

In the past 20 years Thailand has developed considerably and rural areas have become connected with roads, which has increased access and donations to rural temples. I have met several abbots, monks, and pilgrims that encouraged people to feed monkeys to gain merit, receive donations, and promote the temples.

Malaivijitnond et al. (2005) conducted an extensive survey to assess the distribution and population of various species of primates in Thailand, though many locations are located in the government protected areas and age–sex composition was not included. They found an increase in the number of primates at most of the sites they visited when compared to Aggimarangsee (1992). The need to verify these findings motivated the current study as most of the populations assessed to date have increased (Table 11.1); however, an overall evaluation cannot yet be made since only approximately a quarter of the proposed sites have been surveyed. The population of *M. fascicularis* at Wat Khao Tham Khunchorn that was estimated to be nine individuals in 1990 was extirpated due to hunting and an overall negative attitude of humans toward the monkeys (Aggimarangsee 1992). I believe that if they had been fully protected by the monks and villagers, this population would have persisted. These data suggest that population size is not a major factor leading to local fragment extinction, rather is it the threat from humans (see also Rodriguez-Luna et al. 2003)

When the economy is good, people tend to spend more. This is especially true for the Thai people who like to donate money to temples because of their belief that this will better their next life. However, the world financial crisis has impacted Thailand's economy, consequently reducing the number of foreign and local tourists, and thus reducing the food given to primates at temples. I am convinced by the data gathered, especially at Wat Khao Tham Khunchorn where the monkey population was extirpated, and at Wat Than Sua where monkey numbers have increased, that human attitude impacts the probability of primate survival. However, one must ask how long humans will tolerate the large number of primates roaming around, stealing, and fighting with people.

Finally, disease transmission between humans and nonhuman primates should be a concern. I came across some *M. assamensis* individuals with tumors and individuals that were half paralyzed that later died. An important country-wide issue is that no one takes the responsibility to diagnose the animals that have died. Jones-Engel et al.'s collaborative project regarding disease transmission between these species in Asia and Thailand signals the need for research in this area (Jones-Engel et al. 2007; Jones-Engel et al. 2008).

Recommendations

Based on the findings of this study I would make the following recommendations with respect to fragmentation and primate conservation:

(1) As is indicated by the changes documented here: population size, age–sex composition, attitude of humans, hunting pressure, human and primate health, and wildlife trade should be monitored regularly and systematically to obtain rigid data for the population assessment.
(2) To reduce controversy among primate taxonomists and to confirm species identification, research on primate genetics is needed.
(3) The transfer of knowledge between the government, local authorities, monks, pilgrims, villagers, students, and tourists on how to conserve primate habitat and deal with primate disease is vital. Therefore, training and workshops should be continuously provided to the relevant authorities.

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Chapter 12
An Eight-Year Life History of a Primate Community in the Colombian Llanos

Xyomara Carretero-Pinzón

Abstract Forest areas in Colombian Llanos are highly degraded due to the expansion of palm oil crops, petrol extraction, and other human interferences, making primate species in Colombia more susceptible to population reduction and local extinction. An eight-year study of primate density monitoring was conducted in five forest fragments of different sizes in San Martín, Colombian Llanos. *Alouatta seniculus*, *Sapajus apella*, *Callicebus ornatus*, *Saimiri sciureus albigena*, and *Aotus brumbacki* were present in the fragments. Direct visual contacts were made in small (1–10 ha) and medium (10–100 ha) fragments. Primate density in an extra-large fragment (1,050 ha) was calculated using line transect method. Results showed that population density for *A. seniculus* ranged from 0.81 to 78.57 ind/km^2, *S. apella*, 0.95–52.98 ind/km^2, *C. ornatus*, 1.07–54.76 ind/km^2, *S. s. albigena*, 3.85–170.24 ind/km^2, and *A. brumbacki,* 3.26–13.10 ind/km^2. Most species reported in small and medium fragments have a higher population density than those reported in other studies, except for *A. seniculus,* which fell in a normal range. Densities in the extra-large fragment for *Alouatta*, *Callicebus,* and *Sapajus* are similar to that reported in continuous forest, while densities for *Saimiri* was lower than that reported for continuous forest. Variations that affected population density among fragments are due to differences in-group composition per species, vegetation, and size of the fragment. All primate species present in this region use fencerows as part of the landscape matrix to cross among fragments. Increasing the connectivity between fragments is necessary in this region to improve sustainability of this primate community.

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Introduction

Colombian Llanos or the Orinoco is an area composed of different ecosystems including flooded and unflooded savannas, tropical rainforest, and gallery forest. This study is focused on the western Orinoco basin in Meta, Colombia which has been colonized since the sixteenth century. However, Stevenson and Aldana (2008) suggest that several factors provide evidence that this area was a continuous tropical forest before human disturbance: (1) Abandoned pastures in this area rapidly convert into forest succession suggesting that ecological conditions are favorable to support continuous forests, (2) Climate and geographical position close to the Andes is similar to that found at Tinigua National Park which is a continuous tropical forest (>2,500 mm with a 2–3 month dry period) as defined by Holdridge (1967), (3) Soils correspond to depositional zones that are relatively rich in nutrients and can sustain continuous forest in flooded and terra firme soils, and (4) Cultivated oil palms in San Martin have a biomass similar to that of a humid forest.

San Martin has historically been a livestock town due to its natural savannas. These natural savannas have been converted to pastures over the years leaving fragments of different sizes, especially around watercourses. In recent years, palm oil plantations and extractive activities, such as petrol extraction, have increased the fragmentation process. This is especially true of palm oil crops since the Meta Department is the main producer of palm oil in Colombia (Fedepalma 2010).

Fragmentation produces changes in environmental conditions, composition, and abundance of animals and plant species (Saunders et al. 1991; Stevenson and Aldana 2008) including habitat reduction, isolation, distance between fragments, fragment size, changes in quantity and quality of food, and forest structure all affects primate species densities (Hobbs and Yates 2003; Marsh 2003; Saunders et al. 1991; Stevenson and Aldana 2008). Fragmentation and habitat loss are the main threats to Colombian primates (Defler 2004). Therefore, persistence in small fragments of some species of primates depends on their skill to use the matrix surrounding forest fragments.

Primate density has been studied in tropical rainforest throughout the world (Carvalho 2003; Chapman et al. 2004; Crockett 1996; Crockett and Eisenberg 1987; Defler 1981; Dvoskin et al. 2004; Estrada and Coates-Estrada 1996; Freese 1976; Mbora and Meikle 2004; Plumptre and Reynolds 1994; Romanini et al. 2003), but there are only a few studies of primate population density in the Colombian Llanos. These reports mainly focus on howler monkeys (*Alouatta seniculus*), tufted capuchins (*Cebus* nee *Sapajus* (sensu Lynch-Alfaro et al. 2012) *apella*), white-fronted capuchins (*Cebus albifrons*), and dusky titi monkeys (*Callicebus ornatus*) (Carretero-Pinzón 2005; Defler 1981; Defler and Pintor 1985; Wagner et al. 2009). Data reported here is from eight-years of primate density surveys conducted at five forest fragments. Some possible explanations for species permanence in different sizes of fragments are explored.

Study Zones

This study was conducted near the town of San Martín de los Llanos, Department of Meta, in the Colombian Llanos, at two Zones: Santa Rosa-Arrayanes and Las Pampas (elevation 350 m; Fig. 12.1). These Zones have different sizes of forest fragments surrounded by pastures used for livestock. Some pastures are surrounded by fencerows to connect forest fragments. Five Neotropical primates: *Sapajus apella*, *Alouatta seniculus*, *Saimiri sciureus albigena*, *Callicebus ornatus*, and *Aotus brumbacki* live sympatrically in the area (Carretero-Pinzón 2005). This region was characterized by wet season (April–November) and dry season (December–March) with an annual average temperature of 26 °C (Carretero-Pinzón 2008). Plant

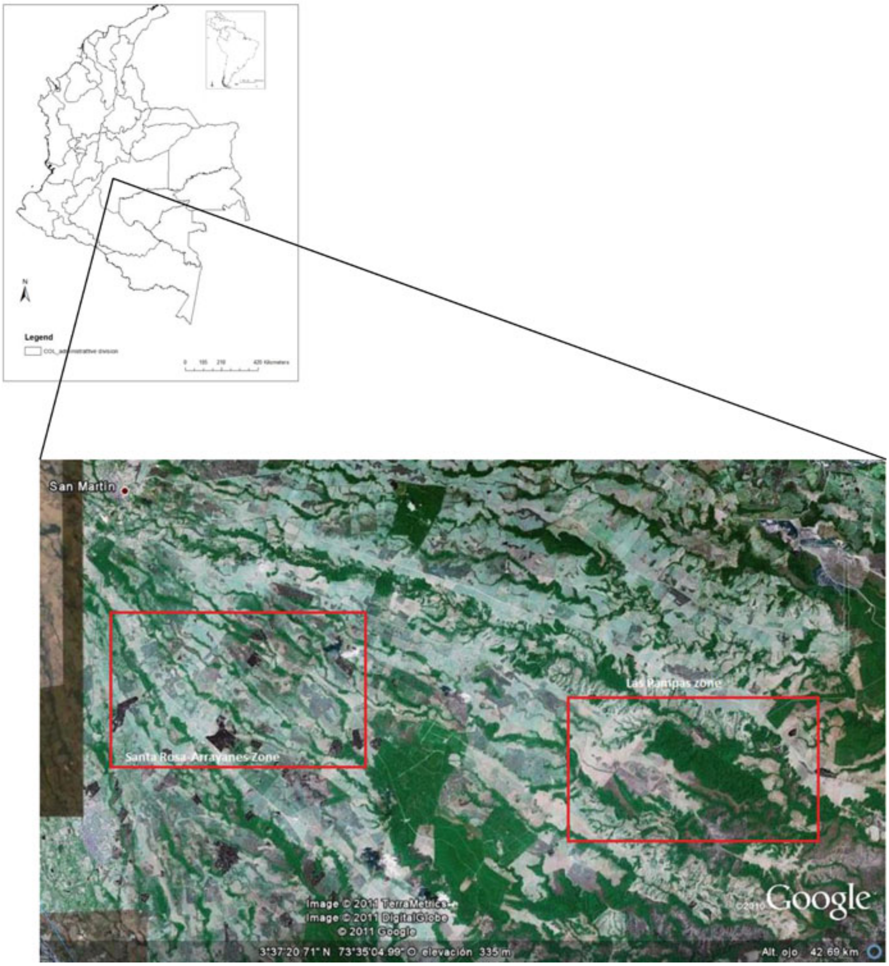
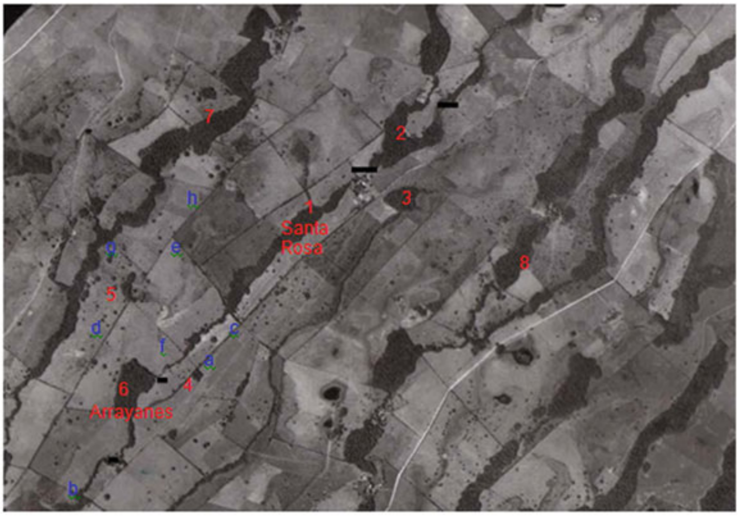


Fig. 12.1 General location of Santa Rosa-Arrayanes Zone and Las Pampas Zone (Google Earth image accessed on 15 June 2012)

a Santa Rosa-Arrayanes Zone



b Las Pampas Zone

Fig. 12.2 (**a**) Aerial Photograph from Santa Rosa-Arrayanes Zone (in 1997; scale 1:46,000, IGAC, Colombia): *Black lines* correspond to sites in which forest is fragmented now. *Red numbers* correspond to fragments connected by fencerows (Fragment 1: 21 ha; Fragment 2: 46.5 ha; Fragment 3: 11 ha; Fragment 4: 0.5 ha; Fragment 5: 2 ha; Fragment 6: 16 ha; Fragment 7: 120 ha; Fragment 8: 130 ha). *Blue words* correspond to fencerows where primates were observed. (**b**) Satellite image of Las Pampas Zone (Google Earth image): *Red numbers* correspond to fragments where primate species have been observed (Fragment 9: 1,050 ha; Fragment 10: 186 ha; Fragment 11: 155 ha; and Fragment 12: 222 ha)

species richness is different between fragments with some species shared (Stevenson and Aldana 2008).

Santa Rosa-Arrayanes Zone (*SRAZ*). Located at 3°3′30″N 73°35′40″ W. This Zone has small (1–10 ha), medium (10–100 ha), and large fragments (100–1,000 ha), most of them connected by fencerows and surrounded by pastures (Fig. 12.2).

Table 12.1 Plant species found at forest Fragments 1, 2, 3, and 6 at Santa Rosa-Arrayanes Zone

Fragment 1		Fragment 2		Fragment 3		Fragment 6	
Species	Family	Species	Family	Species	Family	Species	Family
27		30		11		24	
Schefflera morototoni	Araliaceae	*Schefflera morototoni*	Araliaceae	*Himatanthus articulatus*	Apocynaceae	*Annona sp.*	Annonaceae
						Duguetia sp.	Annonaceae
Guatteria ferruinea	Annonaceae	*Guatteria ferruginea*	Annonaceae	*Oenocarpus bataua*	Arecaceae	*Guatteria ferruinea*	Annonaceae
Xylopia polyantha	Annonaceae	*Xylopia aromatica*	Annonaceae				
		Xylopia polyantha	Annonaceae	*Unonopsis sp.*	Annonaceae	*Himatanthus articulatus*	Apocynaceae
Himatanthus articulatus	Apocynaceae						
		Himatanthus articulatus	Apocynaceae	*Arrabidaea sp2.*	Bignoniaceae	*Bombacopsis sp.*	Bombacaceae
Arrabidaea sp2.	Bignoniaceae						
		Arrabidaea sp2.	Bignoniaceae	*Protium sp.*	Burseraceae	*Protium sp.*	Burseraceae
Protium sp.	Burseraceae			*Trattinnickia cf. aspera*	Burseraceae	*Trattinnickia cf. aspera*	Burseraceae
Protium glabrescens	Burseraceae	*Bombacopsis sp.*	Bombacaceae				
Trattinnickia cf. aspera	Burseraceae			*Cecropia membranacea*	Cecropiaceae	*Cecropia membranacea*	Cecropiaceae
		Protium sp.	Burseraceae			*Pouroma bicolor*	Cecropiaceae
Clusia cf. palmicida	Clusiaceae	*Trattinnickia cf. aspera*	Burseraceae	*Pera arborea*	Euphorbiaceae		
Garcinia madruno	Clusiaceae					*Pera arborea*	Euphorbiaceae
		Cecropia membranacea	Cecropiaceae	*Ocotea oblonga*	Lauraceae		

(continued)

Table 12.1 (continued)

Fragment 1		Fragment 2		Fragment 3		Fragment 6	
Species	Family	Species	Family	Species	Family	Species	Family
27		30		11		24	
Combretum laxum	Combretaceae	*Cecropia sciadophylla*	Cecropiaceae			*Diospyros c.f pseudoxylopia*	Flacourtiaceae
				Byrsonima sp.	Malpighiaceae		
Pera arborea	Euphorbiaceae	*Clusia cf. palmicida*	Clusiaceae			*Ocotea oblonga*	Lauraceae
		Garcinia madruno	Clusiaceae	*Ficus americana*	Moraceae		
Diospyros c.f pseudoxylopia	Flacourtiaceae					*Bellucia pentamera*	Melastomataceae
Ryania speciosa	Flacourtiaceae	*Combretum laxum*	Combretaceae			*Bellucia grossularioides*	Melastomataceae
						Henriettella cf. goudotiana	Melastomataceae
Ocotea oblonga	Lauraceae	*Erythroxylon sp.*	Erythroxylaceae			*Miconia trinervia*	Melastomataceae
Bellucia pentamera	Melastomataceae	*Pera arborea*	Euphorbiaceae			*Enterolobium cyclocarpum*	Mimosaceae
Bellucia grossularioides	Melastomataceae						
Henriettella cf. goudotiana	Melastomataceae	*Ryania speciosa*	Flacourtiaceae			*Siparuna guianensis*	Moniminiaceae

Miconia sp3	Melastomataceae				
Miconia trinervia	Melastomataceae	*Ocotea oblonga*	Lauraceae	*Pseudolmedia laevis*	Moraceae
Siparuna guianensis	Moniminiaceae	*Bellucia pentamera*	Melastomataceae	*Iryanthera laevis*	Myristicaceae
		Bellucia grossularioides	Melastomataceae	*Virola sp1.*	Myristicaceae
Ficus americana	Moraceae	*Henriettella cf. goudotiana*	Melastomataceae	*Virola sp2.*	Myristicaceae
		Miconia elata	Melastomataceae		
Virola sp1.	Myristicaceae	*Miconia trinervia*	Melastomataceae	*Duroia hirsuta*	Rubiaceae
Virola sp2.	Myristicaceae	*Miconia sp3*	Melastomataceae		
Iryanthera laevis	Myristicaceae			*Vochysia lehmannii*	Vochysiaceae
		Enterolobium cyclocarpum	Mimosaceae		
Duroia hirsuta	Rubiaceae				
		Ficus americana	Moraceae		
Vochysia lehmannii	Vochysiaceae				
		Virola sp1.	Myristicaceae		
		Virola sp2.	Myristicaceae		
		Iryanthera laevis	Myristicaceae		
		Vochysia lehmannii	Vochysiaceae		

Plant species present in the study fragments ranged from 11 to 30 species (Table 12.1). Primate species were identified in eight fragments at SRAZ (Table 12.3). Census surveys focused on Fragments 1 (21 ha), 2 (46 ha), 3 (13 ha) and 6 (16 ha) at SRAZ (from 2004 to 2011). Fragments 4 (0.5 ha) and 5 (2 ha) have primates, but the sites are used only as dormitories or as fruit sources; groups using these fragments have their home range in other fragments (1 and 6). Fragments 7 (130 ha) and 8 (120 ha) at SRAZ have primate species, but census data hasn't been collected there due to logistical problems.

Las Pampas Zone (*LPZ*). Located at 3°34′51.93″N 73°27′02.56″W. This Zone has large (100–1,000 ha) and extra-large fragments (more than 1,000 ha) surrounded by pastures (Fig. 12.2). This Zone is a natural private reserve called Las Unamas Reserve surrounded by two other natural reserves, Rey Zamuro and Matarredonda (www.lasunamas.com). There were 197 plant species found in the study fragment (Table 12.2). Four fragments at LPZ have primates (Table 12.3), but Fragment 9 (1,050 ha) was the only one studied (from 2008 to 2011).

Population Information

Densities of primate species were estimated differently depending on fragment size defined by Marsh (2003). In small (1–10 ha) and medium (10–100 ha) fragments, population densities were calculated based on direct visual counts of individuals or groups between March 2004 and December 2011. For the larger categories, only Fragment 9 (1,050 ha) densities were calculated based on five line-transects of at least 1,000 m each. The other fragments at LPZ have insufficient data for density analysis. Surveys in all forest fragments were taken between 6:30 and 17:00 h to search for primate groups. These were conducted several times per month. At SRAZ, groups in each fragment were monitored and individuals identified. Group identification was facilitated by other behavioral studies conducted concurrently at this Zone (Beltrán 2005; Carretero-Pinzón 2008; Escudero 2004; Fajardo 2007; Ospina 2006; Ramos 2008; Torres 2005).

Population density at SRAZ was calculated based on the formula of ecological density: the number of individuals divided by the available or sampled area (Soini 1992). Population density at LPZ was calculated with Distance 6.0 (Thomas et al. 2002). At SRAZ, *Aotus* sleeping sites were searched according to literature, local references, and personal observations (Defler 2004). Data for *Aotus* at LPZ was insufficient for comment in this chapter. Group composition, census numbers (reproductive males and females), male to female ratio (number of adult males divided by number of adult females), and female to immatures ratio (number of adult females divided by number of juveniles and infants) were calculated based on 2011 sampling results for SRAZ and LPZ (Brito and Grelle 2006).

Table 12.2 Plant species found at forest Fragment 9 at Las Pampas Zone (http://www.lasunamas.com)

Fragment 9			
Specie	Family	Specie	Family
197			
Aphelandra sp	Acanthaceae	*Enterolobium schomburgkii*	Fabaceae
		Inga alba	Fabaceae
Tapirira guianensis	Anacardiaceae	*Inga brachyrhachis*	Fabaceae
		Inga cylindrica	Fabaceae
Annona sp1	Annonaceae	*Inga nobilis*	Fabaceae
Annona sp2	Annonaceae	*Inga thibaudiana*	Fabaceae
Duguetia cf. macrophylla	Annonaceae	*Inga villosissima*	Fabaceae
Guatteria cf. liesneri	Annonaceae	*Inga punctata*	Fabaceae
Guatteria recurvisepala	Annonaceae	*Inga velutina*	Fabaceae
Rollinia edulis	Annonaceae	*Andira surinamensis*	Fabaceae
Xylopia aromática	Annonaceae	*Clitoria cf. javitensis*	Fabaceae
Xylopia cf. sericophylla	Annonaceae	*Dioclea guianensis*	Fabaceae
		Derris pterocarpus	Fabaceae
Aspidosperma sp	Apocynaceae	*Machaerium quinata*	Fabaceae
Couma macrocarpa	Apocynaceae		
Fosteronia affinis	Apocynaceae	*Casearia javitensis*	Flacourtiaceae
Fosteronia graciloides	Apocynaceae	*Lindackeria paludosa*	Flacourtiaceae
Himatanthus articulata	Apocynaceae	*Ryania sp*	Flacourtiaceae
Lacmellea edulis	Apocynaceae		
Tabernaemontana sananho	Apocynaceae	*Heliconia hirsuta*	Heliconiaceae
Anthurium clavigerum	Araceae	*Vismia baccifera*	Hypericaceae
Monstera dilacerata	Araceae	*Vimia cayennensis*	Hypericaceae
Monstera gracilis	Araceae	*Vismia guianensis*	Hypericaceae
Spatiphyllum canaeifolium	Araceae	*Vismia macrophylla*	Hypericaceae
Dendropanax arboreus	Araliaceae	*Lacistema aggregatum*	Lacistemataceae
Dendropanax cf. caucanus	Araliaceae		
Schefflera morototoni	Araliaceae	*Aniba panurensis*	Lauraceae
		Nectandra membranacea	Lauraceae
Attalea insignis	Arecaceae	*Ocotea floribunda*	Lauraceae
Attalea maripa	Arecaceae	*Ocotea oblonga*	Lauraceae
Euterpe precatoria	Arecaceae	*Ocotea cf. oblonga*	Lauraceae
Mauritia flexuosa	Arecaceae		
Oenocarpus bataua	Arecaceae	*Eschweilera sp*	Lecythidaceae
Oenocarpus mapora	Arecaceae		
Socratea exorrhiza	Arecaceae	*Byrsonima crassifolia*	Malpighiaceae
Syagrus orinocensis	Arecaceae	*Byrsonima cf. stipulacea*	Malpighiaceae
		Mascagnia macrodisca	Malpighiaceae
Pollalesta discolor	Asteraceae		
Vernonia cf. Brasiliensis	Asteraceae	*Ischnosiphon arouma*	Marantaceae
		Maranta cf. friedrichsthaliana	Marantaceae
Anemopaema oligoneuron	Bignoniaceae	*Monotagma laxum*	Marantaceae

(continued)

Table 12.2 (continued)

Fragment 9			
Specie	Family	Specie	Family
197			
Arrabaideae cf. candicans	Bignoniaceae		
Arrabaidea sp	Bignoniaceae	*Norantea guianensis*	Marcgraviaceae
Jacaranda obtusifolia	Bignoniaceae		
Jacaranda copaia	Bignoniaceae	*Bellucia grossularioides*	Melastomataceae
Pleonotoma tretragonocaulis	Bignoniaceae	*Loreya strigosa*	Melastomataceae
		Miconia affinis	Melastomataceae
Eriotheca macrophylla	Bombacaceae	*Miconia dolichorrhyncha*	Melastomataceae
		Miconia elata	Melastomataceae
Cordia bicolor	Boraginaceae	*Miconia holosericea*	Melastomataceae
Cordia nodosa	Boraginaceae	*Miconia matthaei*	Melastomataceae
		Miconia tomentosa	Melastomataceae
Crepidospermum rhoifolium	Burseraceae	*Toccoca guianensis*	Melastomataceae
Protium aracouchini	Burseraceae		
Proptium glabrescens	Burseraceae	*Mendoncia lindavii*	Mendodonciaceae
Protium guianense	Burseraceae		
Protium cf. guianense	Burseraceae	*Abuta grandifolia*	Menispermaceae
Protium heptaphyllum	Burseraceae		
Protium cf. heptaphyllum	Burseraceae	*Siparuna guianensis*	Monimiaceae
Protium llanorum	Burseraceae		
Protium sagotianum	Burseraceae	*Brosimum cf. lactescens*	Moraceae
Trattinickia rhoifolia	Burseraceae	*Brosimum lactescens*	Moraceae
		Clarisia racemosa	Moraceae
Cecropia ficifolia	Cecropiaceae	*Ficus trigona*	Moraceae
Cecropia sciadophylla	Cecropiaceae	*Maquira cf. calophylla*	Moraceae
Coussapoa villosa	Cecropiaceae	*Perebea mollis*	Moraceae
Pouroma bicolor	Cecropiaceae	*Perebea xanthochyma*	Moraceae
Pouroma minor	Cecropiaceae	*Pseudolmedia laevis*	Moraceae
		Pseudolmedia cf. laviegata	Moraceae
Hirtella americana	Chrysobalanaceae	*Pseudolmedia oblicua*	Moraceae
Hirtella elongata	Chrysobalanaceae		
Licania cf. kunthiana	Chrysobalanaceae	*Iryanthera laevis*	Myristicaceae
Licania cf. subarachnophylla	Chrysobalanaceae	*Virola elongata*	Myristicaceae
		Virola sebifera	Myristicaceae
Calophyllum brasiliense	Clusiaceae	*Virola surinamensis*	Myristicaceae
Clusia sp	Clusiaceae		
Garcinia madruno	Clusiaceae	*Stylogyne cf. turbacensis*	Myrsinceae
Marila cespedeziana	Clusiaceae	*Myrsine guianensis*	Myrsinceae
Tovomita sp1	Clusiaceae		
		Myrcia sp	Myrtaceae
Cochlospermum orinocense	Cochlopemaceae		
Cochlospermum vitifolium	Cochlopemaceae	*Ouratea sp*	Ochnaceae

(continued)

Table 12.2 (continued)

Fragment 9			
Specie	Family	Specie	Family
197			
Buchenavia capitata	Combretaceae	*Peperomia cf. macrostachya*	Piperaceae
Combretum laxum	Combretaceae	*Piper obliquum*	Piperaceae
Terminalia amazonia	Combretaceae		
		Olyra latifolia	Poaceae
Connarus sp	Connaraceae	*Pariana sp*	Poaceae
Rourea cf. glabra	Connaraceae		
		Coccoloba sp.	Polygonaceae
Cayaponia granatensis	Cucurbitaceae		
Gurania eriantha	Cucurbitaceae	*Alibertia sp*	Rubiaceae
		Capirona decorticans	Rubiaceae
Asplundia moritziana	Cyclanthaceae	*Durota hirsuta*	Rubiaceae
		Duroia sp	Rubiaceae
Dichapetalum spruceanum	Dichapethalaceae	*Malanea sp*	Rubiaceae
		Geophila repens	Rubiaceae
Curatella americana	Dilleniaceae	*Psychotria casiquiaria*	Rubiaceae
Davila nítida	Dilleniaceae	*Psychotria muscosa*	Rubiaceae
Doliocarpus multiflorus	Dilleniaceae	*Psychotria poeppigiana*	Rubiaceae
		Posoqueria longiflora	Rubiaceae
Diospyros pseudoxylopia	Ebenaceae		
		Cupania scrobiculata	Sapindaceae
Sloanea aff guianensis	Eleocarpaceae	*Cupania sp*	Sapindaceae
		Matayba sp1	Sapindaceae
Erythroxylum macrophyllum	Erythroxylaceae	*Paullinia cf. faginea*	Sapindaceae
		Paullinia sp	Sapindaceae
Alchornea discolor	Euphorbiaceae	*Talisia intermedia*	Sapindaceae
Alchornea triplinervia	Euphorbiaceae	*Pouteria sp1*	Sapotaceae
Alchorneopsis floribunda	Euphorbiaceae	*Pouteria sp2*	Sapotaceae
Hyeronima alchorneoides	Euphorbiaceae	*Pouteria sp3*	Sapotaceae
Maprounea guianensis	Euphorbiaceae	*Sarcaulus brasiliensis*	Sapotaceae
Pera arborea	Euphorbiaceae		
Sapium laurifolium	Euphorbiaceae	*Simaba cedron*	Simarubaceae
Bauhinia guianensis	Fabaceae	*Solanum cyathophorum*	Solanaceae
Dialium guianense	Fabaceae	*Cyphomandra sp*	Solanaceae
Brownea ariza	Fabaceae		
Senna silvestris	Fabaceae	*Herrania nitida*	Sterculiaceae
Abarema jupunba	Fabaceae	*Sterculia guapayensis*	Sterculiaceae
		Teobroma glaucum	Sterculiaceae
		Vitex compressa	Verbenaceae
		Vochysia ferruginea	Vochysiaceae
		Vochysia lehmannii	Vochysiaceae

Table 12.3 Primate species present at forest fragments in Santa Rosa-Arrayanes and Las Pampas Zones

Fragment size (Ha)	*A. seniculus*	*S. apella*	*S. s. albigena*	*C. ornatus*	*A. brumbacki*
Santa Rosa-Arrayanes Zone (*SRAZ*)					
0.5	X	X	X	0	0
2	X	X	X	0	0
13	X	X	X	0	X
16	X	X	X	X	X
21	X	X	X	X	X
46	X	X	X	X	X
120	X	X	0	X	X
130	X	X	X	X	0
Las Pampas Zone (*LPZ*)					
155	X	X	X	0	0
186	X	X	X	X	X
222	X	X	X	?	?
1,050	X	X	X	X	X

Table 12.4 Primate densities of each fragment studied (average densities and annual densities for fragments at Santa Rosa-Arrayanes Zone and combined density for Fragment 9 at Las Pampas Zone)

	Alouatta (ind/km^2)	Sapajus (ind/km^2)	Saimiri (ind/km^2)	Callicebus (ind/km^2)	Aotus (ind/km^2)
Fragment 1: 21 ha					
2004	76.19	47.62	152.38	61.90	19.05
2005	76.19	52.38	152.38	61.90	19.05
2006	90.48	61.90	190.48	61.90	19.05
2007	85.71	52.38	190.48	61.90	19.05
2008	80.95	52.38	152.38	47.62	0.0
2009	76.19	52.38	147.62	52.38	0.0
2010	66.67	52.38	171.43	42.86	9.52
2011	76.19	52.38	204.76	47.62	19.05
Average	78.57	52.98	170.24	54.76	13.10
SD	7.2	3.97	22.30	8.05	8.73
Fragment 2: 46.5 ha					
2004	8.70	21.74	32.61	8.70	4.35
2005	30.43	39.13	0.0	8.70	4.35
2006	30.43	39.13	0.0	6.52	4.35
2007	23.91	21.74	0.0	6.52	4.35
2008	23.91	26.09	0.0	4.35	0.0
2009	23.91	30.43	0.0	8.70	0.0
2010	19.57	30.43	65.22	8.70	4.35
2011	23.91	30.43	65.22	10.87	4.35
Average	23.91	29.89	20.38	7.88	3.26
SD	6.87	6.75	29.87	1.99	2.01
Fragment 3: 13 ha					
2004	30.77	0.0	7.69	0.0	0.0

(continued)

Table 12.4 (continued)

	Alouatta (ind/km^2)	Sapajus (ind/km^2)	Saimiri (ind/km^2)	Callicebus (ind/km^2)	Aotus (ind/km^2)
2005	38.46	0.0	7.69	0.0	0.0
2006	38.46	0.0	7.69	0.0	0.0
2007	30.77	0.0	7.69	0.0	0.0
2008	30.77	0.0	0.0	0.0	0.0
2009	30.77	0.0	0.0	0.0	0.0
2010	30.77	0.0	0.0	0.0	0.0
2011	30.77	0.0	0.0	0.0	0.0
Average	30.77	0.0	3.85	0.0	0.0
SD	3.56	0.0	4.11	0.0	0.0
Fragment 6: 16 ha					
2004	0.0	0.0	0.0	0.0	0.0
2005	68.75	31.25	0.0	18.75	12.5
2006	75	43.75	0.0	25	6.25
2007	68.75	43.75	0.0	25	18.75
2008	62.5	31.25	0.0	12.5	6.25
2009	56.25	31.25	0.0	12.5	6.25
2010	50	31.25	0.0	18.75	12.5
2011	37.5	31.25	0.0	18.75	12.5
Average	52.34	30.47	0.0	16.41	9.38
SD	24.31	13.54	0.0	8.14	5.79
Fragment 9: 1,050 ha					
2008–2011	0.81	0.95	30.33	1,073	n.a

n.a: not applicable

Demographics

Average densities of primate species in the study area are shown in Table 12.4, for both Zones. SRAZ Fragment 1 (21 ha) was found to have the highest average density of all five primate species as compared to the largest fragment at LPZ (1,050 ha). All five species were found together in Fragments 1, 2 and 6 at SRAZ and at Fragment 9 and 10 from LPZ. However, a *Saimiri* group used both Fragment 1 and 6, thus a density of this species in Fragment 6 was not estimated to avoid double counting. For the duration of the study, Fragment 3 (13 ha) had only one group of *A. seniculus*. One individual of *S. s. albigena* was last recorded there in 2008. These densities varied only slightly between years for each fragment. Densities in Fragment 9 are the lowest for all fragments reported here.

Three types of group composition can be found: one male–one female (*Callicebus ornatus* and *Aotus brumbacki*), one male–two females (*Alouatta seniculus* and *Sapajus apella*), and multimale–multifemale (*Saimiri sciureus albigena*, Table 12.5). All groups contain several juveniles and infants. These types of group compositions were found in all fragments with variations in the number of juveniles and infants.

Table 12.5 Group size, composition and male: female and female: immature ratios for each primate species group differentiated in this study at both Zones (Data based on 2011 samplings)

		Adults			Subadults		Juveniles			Infants						
Primate Species	Group ID	Males	Females	Unknown	Males	Females	Males	Females	Unknown	Males	Females	Unknown	Total	Males: Females	Females: Immatures	Census number
Fragment 1																
Alouatta seniculus	1	1	2	0	1	0	0	0	0	0	0	1	5	0.5	1	3
Alouatta seniculus	2	2	2	0	0	0	0	0	1	0	0	1	6	1	1	4
Alouatta seniculus	3	1	1	0	0	0	0	0	2	0	0	1	5	1	0.33	2
Sapajus apella	1	1	1	0	0	0	0	0	3	0	0	0	5	1	0.33	2
Callicebus ornatus	1	1	1	0	0	0	0	0	1	0	0	1	4	1	0.5	2
Callicebus ornatus	2	1	1	0	0	0	0	0	1	0	0	0	3	1	1	2
Callicebus ornatus	3	1	1	0	0	0	0	0	1	0	0	1	4	1	0.5	2
Saimiri sciureus albigena	1	5	8	0	0	0	0	0	20	3	3	3	42	0.625	0.28	13
Aotus brumbacki	1	1	1	0	0	0	0	0	0	0	0	0	2	1		2
Aotus brumbacki	2	1	1	0	0	0	0	0	0	0	0	0	2	1		2
Fragment 2																
Alouatta seniculus	1	1	2	0	0	0	0	0	0	0	0	1	4	0.5	2	3
Alouatta seniculus	2	1	2	0	1	0	1	0	0	1	0	0	6	0.5	0.67	3
Sapajus apella	1	1	2	0	0	0	0	0	3	0	0	2	8	0.5	0.4	3
Sapajus apella	2	1	2	0	0	0	0	0	1	0	0	0	4	0.5	2	3
Callicebus ornatus	1	1	1	0	0	0	0	0	1	0	0	1	4	1	0.5	2
Saimiri sciureus albigena	1	3	5	0	0	0	0	0	7	0	0	0	15	0.6	0.71	8
Aotus brumbacki	1	1	1	0	0	0	0	0	0	0	0	0	2	1		2
Fragment 3																
Alouatta seniculus	1	1	2	0	0	0	1	0	0	0	0	0	4	0.5	2	3
Fragment 6																
Alouatta seniculus	1	1	2	0	0	0	0	0	1	0	0	0	4	0.5	2	3

Sapajus apella	1	1	1	0	1	0	0	0	2	0	0	0	5	1	0.33	2
Aotus brumbacki	1	1	1	0	0	0	0	0	1	0	0	0	3	1	1	2
Fragment 9																
Alouatta seniculus	1	1	2	0	0	0	0	1	0	1	0	0	5	0.5	1	3
Alouatta seniculus	2	1	2	0	0	0	0	1	0	0	0	1	5	0.5	1	3
Alouatta seniculus	3	1	2	0	0	0	0	0	2	0	0	0	5	0.5	1	3
Alouatta seniculus	4	1	2	0	0	0	0	0	0	0	0	0	3	0.5		3
Alouatta seniculus	5	2	3	0	0	0	0	1	0	0	0	0	6	0.67	3	5
Alouatta seniculus	6	1	2	0	0	0	0	1	0	0	0	0	4	0.5	2	3
Alouatta seniculus	7	1	2	0	0	0	0	0	0	0	0	0	3	0.5		3
Alouatta seniculus	8	1	2	0	2	0	1	1	0	0	0	0	7	0.5	0.5	3
Alouatta seniculus	9	1	2	0	0	0	0	0	0	0	0	1	4	0.5	2	3
Alouatta seniculus	10	2	2	0	0	0	0	0	2	0	0	0	6	1	1	4
Alouatta seniculus	11	1	2	0	0	0	0	1	0	0	0	0	1	0.5	2	3
Alouatta seniculus	12	2	2	0	0	0	0	0	0	0	0	0	4	1		4
Sapajus apella	1	1	2	0	1	0	0	0	3	0	0	1	7	0.5	0.4	3
Sapajus apella	2	1	1	0	0	0	0	0	2	0	0	0	4	1	0.5	2
Sapajus apella	3	1	2	0	1	0	0	0	2	0	0	0	6	0.5	0.67	3
Sapajus apella	4	2	2	0	1	0	0	0	2	0	0	2	9	1	0.4	4
Sapajus apella	5	2	3	0	0	0	0	0	3	0	0	2	10	0.67	0.6	5
Sapajus apella	6	1	2	0	1	0	0	0	2	0	0	2	7	0.5	0.4	3
Sapajus apella	7	1	2	0	0	0	0	0	2	0	0	2	7	0.5	0.5	3
Sapajus apella	8	1	2	0	1	0	0	0	2	0	0	2	8	0.5	0.4	3
Sapajus apella	9	2	2	0	0	0	0	0	3	0	0	1	8	1	0.5	4
Sapajus apella	10	1	2	0	0	0	0	0	2	0	0	1	6	0.5	0.67	3
Callicebus ornatus	1	1	1	0	0	0	0	0	1	0	0	0	3	1	1	2
Callicebus ornatus	2	1	1	0	0	0	0	0	1	0	0	0	3	1	1	2
Callicebus ornatus	3	1	1	0	0	0	0	0	1	0	0	0	3	1	1	2
Callicebus ornatus	4	1	1	0	0	0	0	0	0	0	0	0	2	1		2

(continued)

Table 12.5 (continued)

		Adults			Subadults		Juveniles			Infants						
Primate Species	Group ID	Males	Females	Unknown	Males	Females	Males	Females	Unknown	Males	Females	Unknown	Total	Males: Females	Females: Immatures	Census number
Callicebus ornatus	5	1	1	0	0	0	0	0	2	0	0	0	4	1	0.5	2
Callicebus ornatus	6	1	1	0	0	0	0	0	1	0	0	0	3	1	1	2
Callicebus ornatus	7	1	1	0	0	0	0	0	1	0	0	0	3	1	1	2
Callicebus ornatus	8	1	1	0	0	0	0	0	0	0	0	0	2	1		2
Saimiri sciureus albigena	1	4	9	0	0	0	0	0	17	0	0	0	30	0.44	0.53	13
Saimiri sciureus albigena	2	3	5	0	0	0	0	0	12	0	0	0	20	0.6	0.42	8
Saimiri sciureus albigena	3	4	6	0	0	0	0	0	10	0	0	0	20	0.67	0.6	10
Saimiri sciureus albigena	4	4	8	0	0	0	0	0	18	0	0	0	30	0.5	0.44	12

Solitary individuals were also observed in *A. seniculus*, *S. apella*, *C. ornatus*, and *S. s. albigena* in all fragments at both Zones. *S. s. albigena* also formed small bachelor groups in both Zones, but was not observed in all fragments. *S. s. albigena* group from Fragment 2 disappeared in 2005, was observed again in 2010, but no observations of solitary or bachelor groups were made during that time.

The census number (total reproductive males and females) for all primate species was low for forest fragments studied (Table 12.5). Male to female ratios for all species were high, while female to immature ratios were variable between species and groups (Table 12.5).

Population density reported at SRAZ is higher than that reported in other studies for *S. apella*, *C. ornatus, A. brumbacki*, and *S. s. albigena*. In contrast, *A. seniculus* densities fell between normal ranges reported previously (Table 12.6). At LPZ, population density of Fragment 9 was lower than that reported in continuous forest for *Alouatta*, *Sapajus*, and *Callicebus* probably as a consequence of a low study effort with respect to fragment size as mentioned by Buckland et al. (2010). *Saimiri* density in Fragment 9 was near to that reported for continuous forest (Table 12.6). However, densities reported here for LPZ seem to reflect that this area has populations similar to that of continuous forest compared with densities reported for SRAZ reinforcing the suggestion of Stevenson and Aldana (2008) that this area was a continuous tropical forest before human disturbance. On the other hand, fragmentation seems to have a tendency to increase densities in small and medium fragments with respect to extra-large fragments. A survey with a higher number of fragments of different sizes may be needed to clarify this tendency.

Several deaths were reported in this study, but only anecdotally and only at SRAZ (Table 12.7). Predator attacks were observed for *Sapajus* immatures by domestic dogs and tayras. Two *Alouatta* infant deaths were likely to be infanticide cases (Beltran 2005). One adult male of *Saimiri* was found dead by an unknown cause in 2009, although local people reported domestic dog attacks as the likely reason. An adult female *Aotus* was observed dead with unknown reasons in 2006; this individual was consumed by a *Sapajus* group as an opportunistic behavior (Carretero-Pinzón et al. 2008). Dead individuals of *Callicebus* were not found in this study, but incidents have been reported by local people to the author.

Fencerow Corridors

All species except *Aotus* used fencerows as biological corridors and/or as part of their home ranges. *Alouatta*, *Sapajus,* and *Saimiri* were often observed using fencerows as part of their home ranges and as corridors to travel between fragments during this study. *Sapajus* and *Saimiri* were also observed to use wire fences as corridors. In addition, *Alouatta*, *Sapajus* and *Saimiri* sometimes used pastures and natural savannas around forest fragments to travel between fragments. *Callicebus* were only found to use fencerows two times as part of their home range in 2006. *Aotus* were never found to use fencerows, but local people reported in 2006 an individual of this species using a fencerow apparently to disperse.

Table 12.6 Primate densities reported in this study for both Zones compared with densities reported in other studies

Species	Density reported in this study at Santa Rosa-Arrayanes zone	Density reported in this study at Las Pampas zone	Density reported in other studies	Authors
Alouatta seniculus	23.37–78.57 ind/km^2	0.81 ind/km^2*	35–55 ind/km^2	Gómez-Posada et al. 2007[a], Defler 2004[a,b]
Cebus (= *Sapajus*) *apella*	26.92–52.98 ind/km^2	0.95 ind/km^2**	5.8–6.2 ind/km^2	Carretero-Pinzón 2005[a]
			16–17 ind/km^2	Stevenson et al. 1991[b], Defler and Pintor 1985[a]
			5.8 and 8–10 ind/km^2	Defler 2004[a,b], Soini 1986[b]
Callicebus ornatus	7.61–54.76 ind/km^2	1.07 ind/km^2***	192.2–400 ind/km^2	Mason 1966[a], Wagner et al. 2009[a]
			3–8 ind/km^2	Robinson 1977[a], Polanco 1992[b], Carretero-Pinzón 2005[a]
Saimiri sciureus albigena	3.85–170.24 ind/km^2	30.33 ind/km^2****	50–80 ind/km^2	Klein and Klein 1974[b], Terborgh 1983[b], Soini 1986[b]
			4 ind/km^2	Defler 2004[b]
			1–6 ind/km^2	Carretero-Pinzón 2005[a]
			12.7 ind/km^2	Stevenson 2007[b]
Aotus brumbackii	3.26–13.10 ind/km^2	n.a.	3.3–9.9 ind/km^2	Carretero-Pinzón 2005[a]

n.a. not applicable, *ESW* effective strip width, *AIC* akaike information criterion, *%CV* coefficient of variation percentage

[a] Fragmented forest

[b] Continuous forest

*ESW 16.7, AIC: 474.93, %CV: 14.17

**ESW 15.31, AIC: 913.92, %CV: 9.28

***ESW 10.52, AIC: 156.25, %CV: 24.69

****ESW 14.9, AIC: 168.55, %CV: 38.25

Table 12.7 Dead individuals found at Santa Rosa-Arraynes Zone

Year	Month	Specie	Sex	Category	Fragment	Cause of death	Observer
2004	August	Alouatta		Infant	1	Unknown	Sandra
2005	April	Alouatta		Infant	1	Twins, possible infanticide	Martha
2006	January	Cebus	Male	Infant	2	Domestic dog attack	Alfredo
2006	February	Aotus	Female	Adult	6	Unknown	Xyomara
2006	November	Cebus	Male	Infant	1	Tayra attack	Xyomara
2008	March	Saimiri		Adult	Wire fence	Domestic dog attack	Pedro
2009	April	Alouatta		Juvenil	1	Unknown	Carolina
2009	April	Alouatta		Juvenil	1	Unknown	Carolina
2009	April	Saimiri	Male	Adult	1	Unknown	Carolina

Discussion

There are no clear distribution patterns of primates in the fragments reported here. SRAZ Fragment 1 showed the highest densities for all species as a result of a higher fruit production compared with other fragments (data of fruit production of Fragment 1 showed higher values than Fragment 6 from September 2005 to January 2007; Carretero-Pinzón 2008), and a high connectivity with other small and medium fragments, which increased access to food resources. However, the population of primate species in this region is lower than that estimated as viable (200–500 breeding individuals; Brito and Grelle 2006).

Alouatta

Adult sex ratios and mother–offspring ratios for *Alouatta* are currently stable. The number of adult males and females in each group found in this study is slightly different with previous literature (Crockett 1996; Defler 2004; Gómez-Posada et al. 2007; Izawa 1997) with a tendency toward more immature males than females in some years. This trend may lead this population to more males than females in the future, even though both males and females were observed to disperse.

Alouatta in SRAZ Fragment 1 frequently used fencerows as part of their home ranges to include small and medium fragments, as well as individual *Ficus* sp. trees within the fencerows themselves or isolated on the pasture matrix. Their use of the *Ficus* sp. fence trees was particularly important during times of seasonal fruit scarcity. Fencerows with trees of greater than 15 m in height assured some cover from predators; however, howlers who crossed open pastures to reach these areas were at high risk of encountering dangerous situations, not unlike howlers in other study sites (Pozo-Montuy and Serio-Silva 2007).

Saimiri

In the case of *Saimiri*, it seems that presence of fencerows increased the likelihood of presence in any fragment of any size, probably as a response to space requirements. In continuous forest, they average a 240 ha home range compared to 100 ha in this study (Carretero-Pinzón 2008; Carretero-Pinzón et al. 2009). This could be one reason why this species was absent from SRAZ Fragment 7, which while large, is isolated from the others. Small and medium fragments (SRAZ Fragments 1, 4, 5, and 6) were connected by fencerows and maintained a stable group of *Saimiri*. *Saimiri* densities reported here may be overestimated precisely because of their mobile nature. Group size and composition are typical of *Samiri* groups (Boinski 1999; Carretero 2000; Defler 2004; Mitchell 1990) in these fragments. For this subspecies solitary males and bachelor groups were observed moving between fragments through fencerows. Bachelor groups have been reported for other species of *Saimiri* (Boinski 1999; Mitchell 1990).

Callicebus

The cryptic behavior of *Callicebus* made it difficult to detect them in the LPZ Fragments 12 and 13. Based on group size of *Callicebus* groups at both Zones, Carretero-Pinzón (in press) showed that there was a tendency toward higher group numbers (4–5 individuals) in smaller and medium fragments compared to large and extra-large fragments (2–4 individuals). Group composition of this species was similar to other sites nearby (Polanco 1992; Wagner et al. 2009). Use of fencerows seemed rare for *Callicebus*, however this may have been underestimated since they were difficult to see on fencerows.

Aotus

Aotus densities reported might be higher due to a greater sampling effort made in this study. Information about this species in general is scarce and previous densities are not available for comparison (Defler 2004). In LPZ Fragment 10, presence of *Aotus* was difficult to determine during the study, but the reserve owner observed this species resting on an *Oenocarpus* palm (E. Enciso pers. comm., January 2012), suggesting their presence as likely. *Aotus* group size and composition was similar to that reported by Solano (1995) at Tinigua National Park. Higher densities in SRAZ Fragment 1 for this species can be explained by a higher number of available nest sites and higher overall fruit production. Solitary individuals observed were probably dispersing animals. *Aotus* weren't observed using fencerows, but more sampling may reveal their use. For instance, an *Aotus* group in SRAZ Fragment 6 has a nest near a fencerow with fruit trees. Additional surveys for *Aotus* must be conducted to further corroborate the apparent increased overall population.

Sapajus

Sapajus group size and composition were typical for this species in the greater Colombian Llanos (Defler 2004), but different from those studied at the Tinigua National Park, which is a more biodiverse site where there was a mean of 16 individuals (Izawa 1980; Stevenson and Aldana 2008; Stevenson et al. 1991). *Sapajus* males in the study area disperse more than females, as all solitary individuals were males.

Sapajus used fencerows regularly for access to small fragments (even less than 1 ha) with dormitory sites and *Ficus* sp., and like *Alouatta* and *Saimiri*, they were observed using wire fences as well as open ground. Their regular, yet seasonal use of fragments means not all sites are used equally. Use of fencerows and small fragments was not without risk particularly for immature individuals, as three predator attacks were observed: Two in a fencerow—one by a domestic dog and the other by a Crested Caracara (*Caracara cheryway*) and the other by a tyra (*Eira barbara*) inside Fragment 1.

Conclusion

In general, the future of *Alouatta*, *Sapajus*, *Callicebus, Saimiri* populations is uncertain, although their current population status appears stable, and *Aotus* appears to be increasing above predicted trends. The higher primate densities observed at Santa Rosa-Arrayanes Zone can be attributed to higher fruit availability as compared to other fragments. But isolation and increased fragmentation could lead to local extinction. Thus, fencerows proved to be invaluable for nearly all species as a means to increase home range, food availability, or sleeping sites. The network of fencerows and fragments is not without risk to the primates in the area, and the need for greater connectivity is apparent due to the lower numbers of the more isolated forest sites and the predation risk to individuals crossing through the matrix. *Saimiri* use fencerows as part of their home range and as biological corridors between fragments, which is an important tool for conservation of this endemic subspecies of squirrel monkeys.

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Chapter 13

A Critically-Endangered Capuchin (*Sapajus apella margaritae*) Living in Mountain Forest Fragments on Isla de Margarita, Venezuela

Natalia Ceballos-Mago and David John Chivers

Abstract There are currently only two islands in the Caribbean that harbour Neotropical primates, Isla de Margarita with an endemic capuchin *Sapajus apella margaritae*; and Trinidad with two endemic monkeys *Cebus albifrons trinitatis* and *Alouatta seniculus insulanus* and the recently introduced brown capuchin *Sapajus apella*. These Caribbean monkeys live in habitat islands surrounded by towns, agricultural areas and roads, and their main threats are habitat fragmentation and hunting. In this case study, conducted on a fragment scale on Isla de Margarita, we report on the Margarita capuchin distribution and encounter rates of monkey groups and signs, as well the location of introduced primates in the Margarita capuchin habitat. We conducted reconnaissance surveys and interviews with local people and hunters. Line-transect surveys by distance sampling were carried out in the forest fragments where capuchins were found. Margarita capuchins live in four forest fragments; two of them are protected areas. The abundance of introduced howler monkeys and wedge-capped capuchins in the mountains could not be quantified and it is assumed they are likely to be low, but generates concern about resource competition, disease transmission and hybridisation. Capuchins on Isla de Margarita seem to prefer the evergreen forest when this is available, but they also live in a forest fragment entirely covered by dry vegetation. Corridors have been proposed to increase the capacity of dispersal of primates among forest fragments as an important factor for their long-term survival on the island.

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Introduction

Currently, only two islands in the Caribbean harbour non-human Neotropical primates: Isla de Margarita in Venezuela, and Trinidad in the Republic of Trinidad and Tobago. The former has only one wild primate, the Margarita capuchin *Sapajus apella margaritae,* while Trinidad has the white-fronted capuchin *Cebus albifrons trinitatis*, the howler monkey (*Alouatta seniculus insulanus* (Hill 1962; Stanyon et al. 1995) or *A. macconnelli* (Groves 2001) and the brown capuchin *Sapajus apella*, that has been recently introduced (Narang et al. 2011). These primates are not well known, since only a very few surveys and studies have been conducted (Neville 1976; Ottocento et al. 1989; Márquez and Sanz 1991; Sanz and Márquez 1994; Agoramoorthy and Hsu 1995; Martínez et al. 2000; Phillips and Abercrombie 2003; Budgen and Goodwin 2007; Ceballos-Mago 2010; Ceballos-Mago et al. 2010; Ceballos-Mago and Chivers 2010; Narang et al. 2011), but due to their isolation, behavioural and genetic differences from their mainland conspecifics are expected (Phillips and Abercrombie 2003).

These Caribbean primates live in habitat islands surrounded by towns, agricultural areas, and roads and their main threats are habitat fragmentation and hunting (Sanz and Márquez 1994; Phillips and Abercrombie 2003; Ceballos 2008). Parts of their distribution are protected, but even in these areas they suffer from illegal activities. On Trinidad primates are heavily hunted, even within sanctuaries (Phillips and Abercrombie 2003; Agoramoorthy and Hsu 1995). On Isla de Margarita primates are not eaten, but hunting occurs for pest control and pet trade (Sanz and Márquez 1994; Martínez et al. 2000; Ceballos-Mago et al. 2010). Although hunting for pest control has partially decreased; recently the pet trade has rapidly increased (Moncada 2007; Ceballos-Mago et al. 2010). Howlers in Trinidad seems to have a stable population, following the expectations that howlers are adaptable and able to survive in small patches of forest (Phillips and Abercrombie 2003), but both endemic capuchins in the Caribbean are listed as Critically-Endangered (Morales-Jiménez et al. 2008; Rodríguez and Rojas-Suárez 2008, 1999; Ceballos 2008).

The Margarita capuchin, mono de Margarita or mono machín in Spanish (Fig. 13.1), is the only wild primate on Isla de Margarita, which lacks large predators. This case study is conducted on a fragment scale (Arroyo-Rodríguez and Mandujano 2009; Arroyo-Rodríguez et al. 2013). Although with this approach it is difficult to attribute the results to habitat fragmentation, because fragmentation per se is a landscape-scale process (Saunders et al. 1991; Fahrig 2003), the theoretical background in this area is useful to understand the dynamics in fragments. Here we report on the Margarita capuchin distribution and encounter rate, as well the evidence and location of pet primate species that have escaped or been released.

Fig. 13.1 Margarita capuchin, mono de Margarita or mono machín (local names), is one of the endemic sub-species of Isla de Margarita (Photograph by Natalia Ceballos-Mago)

Methods

Study Area

Isla de Margarita (1,071 km^2; 400,000 inhabitants) located in Venezuelan Caribbean (10°56′–11°06′ N; 64°10′–64°25′ W) (Fig. 13.2) is 23 km from mainland. This island has two National Parks and three Natural Monuments and three of these protected areas have been identified as Important Bird Areas (IBAs) (BirdLife International 2009a, b, c). At least seven of its 18 endemic terrestrial vertebrates are endangered (Rodríguez 2007; Sanz 2007). Thirty-one mammals, 158 birds, 42 reptiles and six amphibians have been found (Bisbal 2008), 28 species (including sub-species) of terrestrial vertebrates have been reported as endemic, endangered or habitat specialists with restricted distribution on Isla de Margarita, for which the current protected areas are insufficient to guarantee their viability (Sanz 2007). There are at least one Critically-Endangered species of mammal (Margarita deer, *Odocoileus virginianus margaritae*), and three subspecies are included in the Red List of Venezuelan Fauna, Margarita capuchin (*Sapajus apella margaritae*), rabbit (*Sylvilagus floridanus margaritae*) and squirrel (*Sciurus granatensis nesaeu*) (Rodríguez and Rojas-Suárez 2008). Isla de Margarita is one of the most important tourist destinations for Venezuelans and it is also visited by foreigners (Corpotur 2009).

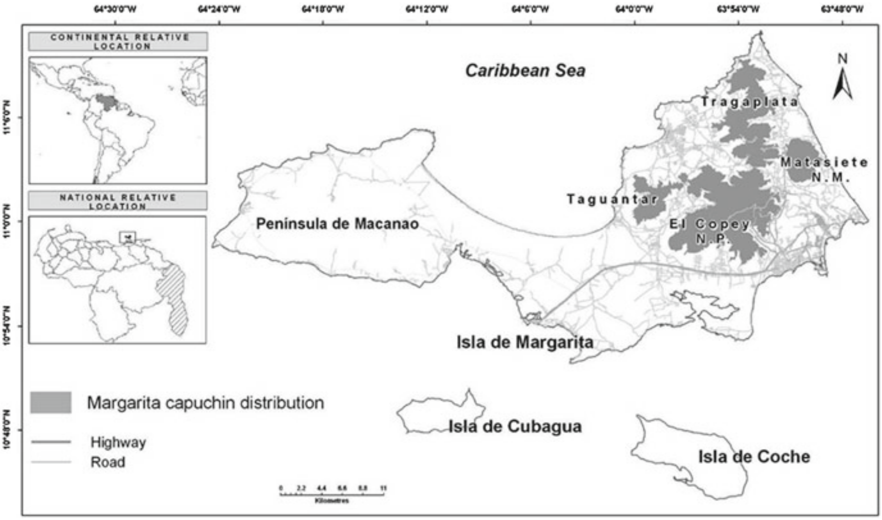

Fig. 13.2 Isla de Margarita (1,071 km^2; 400,000 inhabitants) is located 23 km from mainland in the Venezuelan Caribbean

Data Collection and Analysis

To determine the distribution of the Margarita capuchin, we conducted reconnaissance surveys and interviews with local people and we carried out systematic surveys, from November 2006 to April 2008, in the forest fragments where the monkeys were found. Line-transect surveys (distance sampling) (Buckland et al. 2001) and interviews with hunters were conducted. A total of 102 km were walked on 122 transects, that were located in the study sites using a stratified-random design (Quinn and Keough 2002). Stratification was carried out according to the two most contrasting types of vegetation (evergreen and dry). We collected data systematically along line transects, but every encounter with capuchins or another primate or their signs were also recorded. We recorded sighting and sign locations and altitude using GPS. We estimated encounter rate as groups (direct encounters and/or calls)/10 km walked on transects for the island and for each fragment. Count on transects of bromeliads eaten by capuchins were chosen to estimate encounter rate of capuchin signs (signs/10 km). Bromeliads were chosen because of their presence in the two vegetation types, compared to other signs of capuchins. All the bromeliads eaten in a diameter of 5 m were considered as one independent bromeliad-eaten unit on the transect. For this analysis return surveys were not considered to avoid bias, because most of the capuchins signs are detected the first time the transect was walked. Total transect length for sign counting was 65.5 km. Since the data were not normally distributed, even after transformation was conducted, non-parametric statistics were performed. All analyses were two-tailed tests, with the significance level at $p<0.05$.

Results

Distribution

The Margarita capuchin were only found on the east part of Isla de Margarita, as previously reported (Márquez and Sanz 1991; Sanz and Márquez 1994), but another mountain forest fragment (Taguantar) was added to the distribution of the species (Fig. 13.3). Local people had seen Margarita capuchins living in this fragment for at least 50 years, but the presence of this capuchin in Taguantar was formally

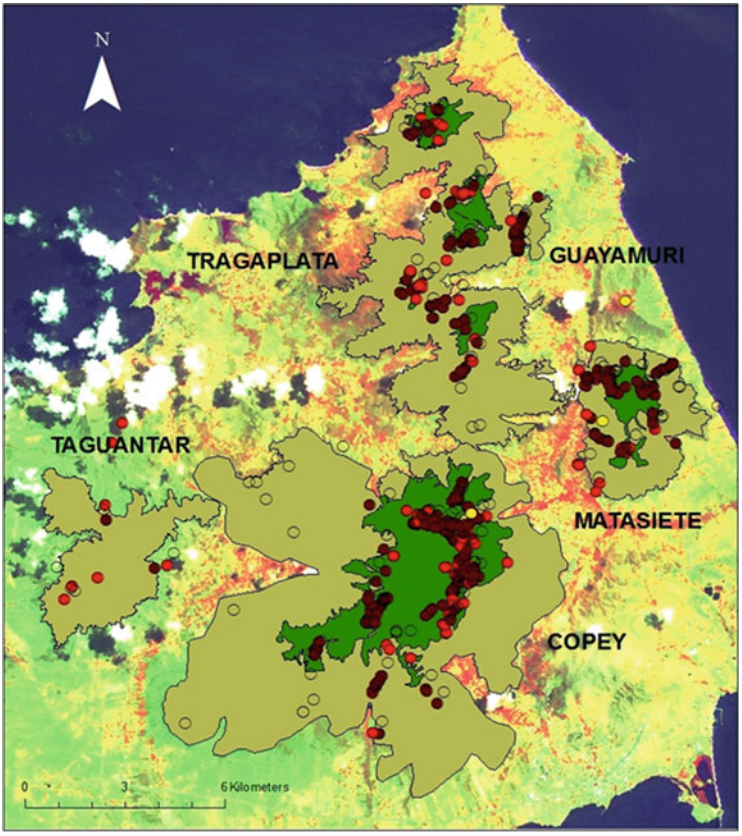

Fig. 13.3 Distribution of Margarita capuchin and introduced primates. Direct observations (*dark red dots*) and signs of Margarita capuchins (*light red dots*), other monkey species (*yellow dots*) and places surveyed with no observation recorded (*empty circles*). *Yellow dots* in Guayamurí and Copey were *Cebus olivaceus* and *yellow dot* in Matasiete was *Alouatta seniculus*. Key: evergreen forest (*dark green*), dry vegetation (*light brown*), *empty circles* are located in the coordinates of the starting points for line transects, *filled circles* represent both, observations during line-transect survey in the place where observation occurred, and observations *ad libitum*

determined and reported for the first time during this study. We recorded direct observations, calls and signs (bromeliads eaten) (Fig. 13.3).

Cerro El Copey National Park (71.3 km^2, highest peak 930 m a.s.l., IUCN II see Dudley 2008 for IUCN categories description), Cerro Matasiete (11.4 km^2, highest peak 660 m a.s.l.), which is part of Cerros Matasiete y Guayamurí Natural Monument (IUCN III), and the unprotected areas: Cerro Tragaplata (40 km^2, highest peak 680 m a.s.l.) and Cerro Taguantar (13 km^2, highest peak 500 m a.s.l) (Figs. 13.2 and 13.3) are the four mountain forest fragments for the Margarita capuchin. The three former mountain forest fragments support evergreen forest, contrasting with arid lowlands, while Taguantar is dry vegetation (Sugden 1986; González 2007). Capuchins were not restricted by the boundaries of the protected areas (that are in the contour line of 80 and 100 m a.s.l in Matasiete and Copey, respectively). They were found from 40 to 830 m a.s.l. Most of the reports of capuchins at low altitude (Fig. 13.3) were from monkeys eating in privately owned fruit trees.

Other Primate Species in the Forest Fragments

Direct observation, calls and signs of wedge-capped capuchins (*Cebus olivaceus*) and howler monkeys (*Alouatta seniculus*) were recorded in *ad libitum* sampling (Fig. 13.3). Their abundances could not be quantified in this study and it is assumed they are likely to be low, since they were not observed during line-transect surveys. We observed a wedge-capped capuchin in a group of Margarita capuchins in el Copey National Park and there were reports of at least 5 animals released in el Copey and Tragaplata during this study. Howler monkey calls were recorded in Matasiete and local people reported a group of four animals and a solitary living in two different sectors of this forest fragment. Signs of bromeliads eaten by capuchins were found in Cerro Guayamurí, which is part of Matasiete and Guayamurí Natural Monument. Cerro Guayamurí is not part of the distribution of the Margarita capuchin, but it is very close to it and movement of primates from Guayamurí to Matasiete could occur. We did not observe any primate in Guayamurí, but we have reports of wedged-capped capuchin pets released and observed in this forest fragment.

Encounter Rates of Margarita Capuchins

The encounter rate (encounters/10 km walked) was obtained counting the visual and aural encounters in line-transect surveys. The overall encounter rate for the island ± SE was 6 ± 1 (Table 13.1). When the results for all forest fragments are pooled, only a few encounters occurred in dry vegetation (2 enc./10 km walked), compared with evergreen forest (9 enc./10 km walked; $U = 3{,}226$; $p < 0.001$). In Copey there were no encounters in the dry vegetation and in Tragaplata only

Table 13.1 Encounter rates of Margarita capuchins (groups/10 km) by forest fragment and type of vegetation

Site	Vegetation type	Mean	SD	SE	Median	IR	Min	Max	*N*
All sites	Evergreen + dry	6	12.1	1.0	0	0	0	66	198
All sites	Evergreen	9	14.7	1.4	0	18.2	0	66	108
All sites	Dry	2	5.6	0.6	0	0	0	25	90
Copey	Evergreen	8	14.7	1.9	0	18.1	0	66	62
Copey	Dry	0	0	0	0	0	0	0	33
Tragaplata	Evergreen	11	16.0	3.1	0	28.1	0	40	27
Tragaplata	Dry	1	4.8	0.9	0	0	0	25	27
Matasiete	Evergreen	9	13.4	3.1	0	16.7	0	44	19
Matasiete	Dry	3	7.6	1.6	0	0	0	25	22
Taguantar	Dry	6	9.4	3.3	0	12.9	0	25	8

Only a few encounters occurred in dry vegetation, compared with evergreen forest
All sites evergreen—all sites dry $U = 3226$; $p < 0.001$
Copey evergreen—Copey dry $U = 726$; $p = 0.001$
Tragaplata evergreen—Tragaplata dry $U = 241$; $p = 0.002$
Matasiete evergreen—Matasiete dry $U = 164$; $p = 0.13$

Table 13.2 Encounter rates of Margarita capuchin signs (bromeliads) by forest fragment and type of vegetation

Site	Vegetation type	Mean	SD	SE	Median	IR	Min	Max	*N*
All sites	Evergreen + dry	21	47.9	4.2	0	19.0	0	269	127
All sites	Evergreen	32	61.1	7.9	0	44.1	0	269	71
All sites	Dry	12	29.8	3.9	0	0	0	139	60
Copey	Evergreen	38	67.7	10.2	0	55.1	0	269	44
Copey	Dry	2	8.9	1.9	0	0	0	43	23
Tragaplata	Evergreen	11	18.4	5.5	0	36.4	0	43	16
Tragaplata	Dry	34	45.0	10.3	16.9	46.9	0	139	19
Matasiete	Evergreen	16	39.8	12.0	0	16.7	0	133	11
Matasiete	Dry	0	0	0	0	0	0	0	13
Taguantar	Dry	4	8.2	3.7	0	9.2	0	18	5

Copey evergreen—Copey dry $U = 338.00$; $p = 0.004$
Tragaplata evergreen—Tragaplata dry $U = 113.50$; $p = 0.16$
Matasiete evergreen—Matasiete dry $U = 58.50$; $p = 0.6$

1/10 km walked). In Matasiete there were relatively more encounters in the dry vegetation (3/10 km walked), but the differences between type of vegetation were not significant (Table 13.1). Taguantar, with no evergreen forest, had the highest encounter rate in dry vegetation (6/10 km walked) compared to the other sites. Dry vegetation is the only habitat available in Taguantar.

Overall, a similar tendency to that observed in the encounter rate of capuchins occurred with the encounter rate of capuchin signs (Table 13.2). Nevertheless, signs of capuchins allowed detecting their presence in the dry forest in Copey. The overall encounter rate of signs for the island ± SE was 21 ± 4.2. When the encounter rates of signs were compared between type of vegetation for each site, the differences were significant only for Copey ($U = 338.00$; $P = 0.004$). In Matasiete there were no encounters in dry vegetation, but in Tragaplata the encounter rate of capuchin signs in this type vegetation was very high (34/10 km walked), with a higher encounter rate in the dry vegetation than the evergreen forest (Table 13.2). Regarding the results from *ad libitum* observation, most of the direct observations of capuchins and signs of their presence were found in the evergreen forest when this was available (Fig. 13.3).

Discussion

The origin and distribution of the capuchin species living on Caribbean islands remains unexplained. The Margarita capuchin was speculated to have been introduced during Pre-Columbian times (Linares 1998), but no evidence to support this is available. *Sapajus apella apella*, the other sub-species of brown capuchin in Venezuela, inhabits the Amazonas region, south of Venezuela, which is more than 800 km away from the island (Bodini and Perez-Hernandez 1987; Martínez et al. 2000). Boher-Bentti and Cordero-Rodríguez (2000) reported the nearest population of *Sapajus apella* as inhabiting the southern extreme of the Rio Orinoco delta. Nevertheless, this population in the Rio Orinoco delta seems to be a much smaller population that has probably been introduced (S. Boher-Bentti pers. comm). There is another report of *Sapajus apella* population in north Venezuela (Península de Paria), that should be investigated to determine its size and origin (Biord 1999). To clarify the taxonomic status of the Margarita capuchin, genetic studies is a priority. *Sapajus apella apella*, from the south of Venezuela, and *Sapajus apella fatuellus* from Colombia, are both claimed to be the ancestral population for this capuchin (Groves 2001). We propose that the *Sapajus apella* population from the Guyana Shield Eco-region (Guyana, Surinam and French Guiana), and populations reported in north Venezuelan mainland (Rio Orinoco delta and Península de Paria), should be also evaluated for this purpose.

The closer populations of *Cebus albifrons* are also very far from Trinidad. Hershkovitz (1972) (cited by Neville 1976), states that the Trinidad capuchin was almost certainly introduced. According to the fossil records, the New World monkeys once ranged more widely than currently, including in their distribution the Greater Antilles in the Caribbean (Horovitz and MacPhee 1999). There are four endemic and extinct Antillean primates recognised at present, *Paralouatta varonai* and *Paralouatta marianae* that occurred in Cuba, *Xenothrix mcgregori* in Jamaica and *Antillothrix bernensis* in Hispaniola (Horovitz and MacPhee 1999; MacPhee and Meldrum 2006). The reason for their extinction is not clear (MacPhee et al. 1989; Rivero and Arredondo 1991).

Regarding the distribution of the Margarita capuchin, two important implications arise from the observation of this monkey in Taguantar. First, this increased the known distribution of this capuchin and, second, this gives us information about the ecological flexibility of this sub-species. It was previously thought that their distribution on the island could be associated only with the wet forests (Márquez and Sanz 1991), since the three forest fragments where they were found before (Copey, Tragaplata and Matasiete) have wet-forest pockets in contrast to the surrounding arid lowlands (González 2007). Nevertheless, Taguantar is only dry vegetation. This is not a surprise, since capuchins are known for their ability to exploit a great variety of habitats (Fragaszy et al. 2004), but Taguantar is perhaps one of the few places inhabited by capuchins where dry vegetation is not combined with other habitat types.

The presence of any primate pets into the free-living Margarita capuchin habitat generates additional concern about resource competition, disease transmission and hybridisation (Chivers 1991; Martínez et al. 2000; Baker 2002; Fragaszy et al. 2004). There is a high numbers of *Cebus olivaceus* and other primate species kept as pets on the island and the impact of this pet trade on the wild Margarita capuchin has been discussed in Ceballos-Mago et al. (2010) and Ceballos-Mago and Chivers (2010). Measures should be taken to capture stray monkey and to prevent further pet primates from escaping or being intentionally released. The abundance of other primate species is assumed to be low, so competition between the Margarita capuchin and other primate species is not currently high, but this should be prevented.

The restricted distribution of the Margarita capuchin to forest fragments on the east side of Isla de Margarita has already been recognised as a threat to this capuchin (Sanz and Márquez 1994; Ceballos 2008; Rodríguez and Rojas-Suárez 2008, 1999). None of the forest fragments currently inhabited by the Margarita capuchin are connected. Unprotected and protected areas are becoming increasingly isolated within this human-dominated landscape matrix. Valleys with towns, agricultural areas and roads separate these remnants, causing "internal fragmentation," which is one of the most obvious anthropogenic impacts on the natural environment (Goosem 1997). It is highly probable that capuchins are living in completely-isolated populations in each forest fragment on Isla de Margarita, which increases concern about probabilities of extinction of this capuchin.

Overall, the encounter rates of capuchins in the four forest fragments on Isla de Margarita were higher than reported for *Sapajus apella* in other studies (Norconk et al. 2003; Moura 2007). Nevertheless, the population size of this primate is small (Ceballos-Mago 2010). Thus, this high encounter rate could be the result of a small population on monkeys that is concentrated in the evergreen patches of vegetation, because the food density or availability is also higher in this area, thus some patches or movement between them will be less preferred or profitable. This has been defined as Compression Effect (MacArthur and Wilson 1967; Augeri 2005). In general, encounter rates of capuchins and their signs were higher in the evergreen than in the dry forests. Thus, capuchins on Isla de Margarita seem to prefer the evergreen forest when this is available, but they also live in a forest fragment entirely covered by dry vegetation (Taguantar). From the vegetation assessment conducted, the cloud forest was the richest and most diverse, while the dry forest had the lowest species diversity (Ceballos-Mago 2010).

Due to this preference for the evergreen forest when this was available, it is also possible that capuchins within Tragaplata live in a metapopulation, due to internal fragmentation of the evergreen forest in this forest fragment (Fig. 13.3). Following the classic definition of metapopulation, it is a population grouped in patches, where there is continuous recolonisation and extinction (Levins 1970). If even one individual from a group can move between sub-populations, even sporadically, the hypothesis would be achieved for the metapopulation theory of sporadic immigration (Levins 1970; Hasting and Harrison 1994; Hanski 1996). Márquez and Sanz (1991) point out that, due to the apparent absence of monkeys on two of the peaks of Tragaplata, the capuchins on the other peaks could be isolated. We found capuchins on one of these peaks (Cerro los Micos (500 m a.s.l.), where Sanz and Márquez (1994) reported local extinction, but it was not possible to determine if the other groups are isolated. In Trinidad *Cebus albifrons* seems to no longer exist in the Central Range Wildlife Sanctuary, where it was reported in 1972 (Bacon and French 1972). The capacity of dispersal of primates among forest fragments is an important factor for their long-term survival on Isla de Margarita and Trinidad (Phillips and Abercrombie 2003; Ceballos-Mago 2010). For this purpose, dispersal corridors have been proposed for both islands (Phillips and Abercrombie 2003; Villarroel 2007).

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Section IV
Feeding and Behavioral Ecology Summary

Laura K. Marsh

Simply measuring the behavior of a group of primates within a fragment may prove effective to determine if animals can persist at all in that habitat. When the physical size of forest has been reduced to the point where survival at the metapopulation scale seems impossible (Section III), the information the authors in this section provide offers hope for primates who can modify their behaviors in such reduced forest landscapes.

Some early presumptions about survivability in fragments came from observing species other than primates, such as birds (Turner 1996). Since birds have the obvious mobile advantage that primates do not, it quickly became imperative that primatologists crack the code for what makes a primate survive to withstand initial isolation. For those that do persist, primates have been found to likewise impact the fragments they live in and can have effects on other species (e.g., plants, vertebrates; Marsh and Loiselle 2002; Feeley and Terborgh 2006), so that their ability to persist is not just a determinant of their own success, but potentially the success of any given fragment they inhabit over a longer period of time. When comparing primates to other mammals, such as carnivores (Michalski and Peres 2005) in their ability to remain in a degraded landscape, fragment size is important, but so is the nature of the matrix.

Nowak and Lee (Chap. 14) demonstrate that even for primates we identify as "specialists," defined with reference to their food or habitat preferences, can exist in fragmented habitats depending on their ability to be flexible in their resource use. The authors discuss how specialization may not be the best litmus test for extinction vulnerability until it is tested in a fragmented situation, as many specialist species have been found to adapt behaviorally to novel situations, including *Procolobus gordonorum*. This ability to adapt, for the short term and perhaps over time, will be the underpinnings of evolutionary traits we may see in the future for animals once thought to be extremely extinction-prone.

However, flexibility alone cannot determine the success of primates in a fragment. The foods must be available for them to put together a diet worthy of their survival. Several authors in this section indicate that while their animals are exploiting available resources, those resources may not always be available to them. Rodrigues Malta and Mendes Pontes (Chap. 17) show that for *Cebus flavius*, 60 % of their diet was provided for by six introduced species. The authors suggest that while in the short-term this is important for the groups within the Pernambuco Endemism Centre in northeastern Brazil, it is uncertain if this will meet their long-term needs.

Similarly, Cameron and Gould (Chap. 16) compare two similarly sized forest fragments in Madagascar housing *Lemur catta*. Both sites are similar in their surrounding the matrix, but one site receives more tourists than the other. Still, the behavior of the lemurs between the sites was significantly different, where the site with a higher density of introduced fruit trees and abundant drinking water had ringtails resting more and foraging less than those in the comparable site. Resource abundance drives behavior and in part, the ability of a species to be flexible or not.

In Central Uganda, fragment size was correlated with the abundance and size of native food resources for *Cercopithecus ascanius* (Baranga et al. Chap. 15). The authors show that the number of food tree species influenced the number of red-tailed monkeys in the fragment and that food tree species richness, total number of trees and basal area of the food trees increased significantly with fragment size. They also found that the number of groups and abundance overall declined in the fragmented forests as the human pressures increased in the surrounding matrix and within the fragments themselves.

Finally, Seiler et al. (Chap. 18) looked at sleeping sites for *Lepilemur sahamalazensis* in remaining forest fragments on the Sahamalaza Peninsula, Madagascar. They found in varying degrees of disturbance that the sportive lemurs chose different resting sites, tree holes or tree tangles that those with more intact forest found better sleeping sites (holes) and were presumed to be able to get more rest and thus be more active during daylight hours. The authors discuss predator avoidance scenarios with regard to the use of fragmented forests by these lemurs.

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Chapter 14
"Specialist" Primates Can Be Flexible in Response to Habitat Alteration

Katarzyna Nowak and Phyllis C. Lee

Abstract An increasing number of field studies on behavioral adaptations and learning suggest that a capacity for flexibility in local responses to disturbance could buffer some so-called specialists against that disturbance. We discuss how specialization, rather than an intrinsic species trait, appears to be moderated by flexible and learned behavior and may not represent a useful trait in comparative analyses of extinction vulnerability. Furthermore, the use of primate species as indicators of the effects of disturbance on communities needs to be balanced with data on their capacity to adjust behaviorally. We present recent examples of innovative and flexible behavior in primate taxa, some of which have traditionally been viewed as highly specialized, for example species of red colobus. We also highlight research gaps in the ecological specialization–behavioral flexibility domain.

Introduction

We have come a long way since thinking of animal behavior as instinctive or presuming that the behavior of an entire species can be described on the basis of a single study of one group at one location. Today, it has become fashionable to study "behavioral flexibility," but are we seeing more examples of it in nature? There is a rapidly growing literature on this topic associated with a proliferation of interrelated terminology: cognitive ecology (Dukas 1998), behavioral diversity (Whiten et al. 2001),

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behavioral plasticity (Pigliucci 2001; Wcislo 1989), behavioral geography (van Schaik 2003; van Schaik et al. 2008), ecotypic variation (Turesson 1922), and ecological fitting (Agosta and Klemens 2008). Following an early definition (Poirier 1969), here we define behavioral flexibility generally as adjustments of an organism in response to ecological conditions and changes.

There are several potential explanations for the current interest in behavioral flexibility in primatology: (1) When observing behavior, we measure performance and cannot detect the capacity for flexibility until it becomes manifest with changes in conditions, and given the increasingly mosaic, unpredictable, and dynamic environments inhabited by primates, we are now recording apparently novel behaviors under such changed and changing environments (Marsh 2003); (2) flexibility is masked by single-population studies that are then generalized to the species, and we now increasingly draw on multiple-group and multiple-population studies to make sense of observed variability (Chapman and Rothman 2009; Strier 2009); (3) we as observers are becoming more astute at detecting and identifying flexibility, in part thanks to emerging field methods and in part because of baseline and long-term datasets on which basis we can now recognize newly acquired behavior. We can still ask: Is this apparent increase in reports of flexibility substantiated—was flexibility always there or is it increasingly selected and evident as human disturbance becomes more widespread and primates inhabit anthropogenic ecotones, forest edges, or move into radically novel, but less disturbed habitats such as mangrove swamps? The importance of the existence or emergence of flexibility is illustrated in that if behavioral flexibility is the rule rather than exception, why has it not been considered in projections of primate extinction risk and why does it continue to be relatively neglected in ecological literature (Sol 2003), particularly when ecological specialization is suggested to be a major correlate of nonhuman primate extinction risk (Harcourt et al. 2002)?

These conflicting perspectives are highlighted in that broadly adapted species are thought to do well in anthropogenic environments and to resist extinction (birds: Bennett et al. 2005; primates: Harcourt 2000; Harcourt et al. 2002; bats: Boyles and Storm 2007) by comparison to niche specialists. However, other studies have failed to detect any relationship between specialization and extinction risk (birds: Sol et al. 2002; plant–pollinator communities: Vázquez and Simberloff 2002; mammals: Brashares 2003; bats: Safi and Kerth 2004). The latter studies analyzed specialization as an intrinsic trait using measures such as the number of habitat types occupied, niche breadth, diversity of interaction partners, species to genus ratio, maximum latitudinal range, and morphology (see Colles et al. 2009 for "ideal" identification of specialization). Comparative primate studies suggest that less specialized taxa have wider geographical ranges and that rarity (an "inevitable precursor to extinction"; Harcourt et al. 2002, p. 445) has only one correlate in the Primate order: dietary specialization. While a specific dietary guild predicts primates' use of and success in fragments (Boyle and Smith 2010), flexible and learned behavioral responses to dynamic ecosystems may capacitate resilience (Dukas and Ratcliffe 2009; Jones 2005; Reader and Laland 2003), although the links between specialization, behavioral flexibility, and extinction risk in primates remain unclear.

Primates may be able to "spread the risks" of extinction (Vázquez and Simberloff 2002) specifically through this behavioral flexibility.

Behavioral flexibility among primates in human altered environments includes dietary and habitat switching, use of invasive and nonnative plant species, opportunism, novel or more frequent interspecific and polyspecific interactions, and increased terrestriality. Dietary shifts appear to make up the majority of documented innovations (Reader and Laland 2003), with costs likely to differ across dietary guilds (e.g., fruits are less likely to contain toxins). Bigger-brained primates are more innovative (Reader and Laland 2002); but what remains to be examined is whether "specialists" are relatively less innovative and smaller-brained.

Large brains relative to body size are generally accepted as advantageous in facilitating behavioral flexibility for individuals facing novel or altered environments (the "cognitive buffer hypothesis"). For example, Sol et al. (2002, 2007) found that big-brained birds have higher invasion success and that big-brained mammals survive better following introductions (Sol et al. 2008). Yet again, the evidence is contradictory in that big-brained birds are not less extinction-prone (Nicolakakis et al. 2003). Even primates, such as lemurs with relatively small brain to body ratios, switch diets and habitats when faced with environmental disturbance or variation in abundance (e.g., *Lemur catta*, Soma 2006) which begets the further question: is there any causal relationship between relative brain size, dietary specialization, and the capacity for behavioral flexibility?

Leaving aside the question of cognitive capacity and ability to cope with environmental disturbance, at least 48 % of primate species and subspecies are already threatened with extinction (IUCN Red List 2010). Whatever categories of risk are used, no single measure will capture traits of both vulnerability and persistence. We suggest that the extent of behavioral diversity across populations and subpopulations of the same species indicate the ability to adjust responses and act adaptively in heterogeneous habitats. We refer to flexibility here as encapsulating behavioral modification of diet, exploitation of alternative food sources, and changing activity and typically used vertical strata in response to new foods or substrate opportunities. The ability to expand niche breadth via resource-switching is key to withstanding risks due to habitat modification (Lee 2003).

Recent Examples of Behavioral Flexibility

For many primates, local flexibility and reactive responses to habitat changes are broadly part of their selective history. Island or coastal populations have always been subject to catastrophic large-scale habitat modification due to tropical storms or hurricanes (Dittus 1985; Rebecchini et al. 2008). In many areas of low rainfall in Africa, nonequilibrium ecosystems are the norm (Niamir-Fuller 2002), again meaning that primates which live in such habitats probably have evolved to cope with the unpredictable and noncyclical dynamics of their habitats (de Vries 1992; Lee and Hauser 1998). Thus, we should not be wholly surprised by examples of major

Fig. 14.1 A Zanzibar red colobus (*P. kirkii*) eating a young coconut. Photo by Katarzyna Nowak

dietary shifts such as black-and-gold howlers (*Alouatta caraya*) preying on birds' nests in impoverished habitat fragments (Bicca-Marques et al. 2009), innovative fishing by long-tailed macaques (*Macaca fascicularis*) (Stewart et al. 2008), or prey-capture and meat-eating by Sichuan snub-nosed monkeys (*Rhinopithecus bieti*) in Yunnan, China (Ren et al. 2009).

The capacity to exploit nonnative species when natural species are limited is also common; for example hamadryas baboons (*Papio hamadryas*) use palm trees rather than cliffs as sleeping sites in Ethiopia (Schreier and Swedell 2008) and howlers (*Alouatta palliata*) forage in cacao plantations (Munoz et al. 2006) and inhabit shade coffee plantations (McCann et al. 2003). Black-and-white colobus (*Colobus guereza*) live in the Entebbe Botanical Gardens, Uganda eating novel foods without changing their species-typical home range size (Grimes and Paterson 2000), while the endangered lion-tailed macaques (*Macaca silenus*) can subsist off exotic food items such as tea, eucalyptus, and coffee in the Anaimalai Hills, India (Singh et al. 2001). A single population of Udzungwa red colobus (*Procolobus gordonorum*) in Tanzania, having lost the small isolated Kalunga forest to agriculture in the early 2000s, now inhabit an adjacent rubber (*Hevea brasiliensis*) plantation eating leaves, buds, and fruit; how long they can persist is open to question, as the decline of the subpopulation from an estimated 400 to 50 individuals since 2007 suggests that the plantation habitat is not ideal (Ehardt et al. 1999; Marshall et al. in press; pers. comm. with Ruth Steel and Andrew Marshall 2010). Like other red colobus which exploit habitats with low plant species diversity (Zanzibar red colobus *P. kirkii* in mangroves: Nowak 2008), these colobus crop-raid in the surrounding agricultural matrix to supplement their monotonous diet (Fig. 14.1). As a result, they are persecuted by people (Marshall et al. in press). Agro-forests are likely to be better refuges for wildlife, from birds to elephants and including primates, than are plantations

(Bhagwat et al. 2008), where even the most behaviorally flexible of species may not persist for long, at least not without access to other/additional habitat and vegetation types.

Although high dietary diversity is proposed to buffer primates against extinction (Harcourt et al. 2002), primates can and do exchange a high dietary diversity for reliability in availability. For example the Sulawesi Tonkean macaque (*Macaca tonkeana*) has a diet of >50 % palm fruits in fragmented forest (Riley 2007), while a Zanzibar red colobus population in a fragmented coastal forest have a diet that is >47 % mangrove (Nowak 2008). The white-collared lemur (*Eulemur cinereiceps*) eats fungi and nonnative plants such as the spicy fruits of Cameroon cardamon (*Aframomum angustifolium*) in highly degraded environments possibly avoiding competition with sympatric lemur species. "Such dietary flexibility and opportunistic behavior may prove to be the key to survival of this critically endangered lemur in an ever-changing and often challenging landscape" (Ralainasolo et al. 2008, p. 43). Again, no simple correlation between survival probabilities and dietary diversity exists. Dietary diversity may be better treated as facultative, rather than obligate, for many primates (Johns and Skorupa 1987).

The interplay between diversity and selectivity can result in greater risk when habitats change; species which are highly selective indeed suffer from the loss of key resources (e.g., vervet monkeys *Chlorocebus aethiops*: Lee and Hauser 1998, despite being generally considered to be opportunistic feeders with diverse diets). Low selectivity and high opportunism enhance resilience (Sichuan snub-nosed monkeys in commercially logged areas: Guo et al. 2008; Sulawesi Tonkean macaques in farms: Riley and Priston 2010).

Entirely new mechanisms for exploiting altered habitats are also widespread. Shifting from arboreal to terrestrial travel is a frequent response to fragmentation, especially if the risks of predation are relatively low (e.g., northern muriqui *Brachyteles hypoxanthus*: Mourthe et al. 2007). Ground travel by black howler monkeys (*Alouatta pigra*) has been observed in forest fragments in Mexico, as well as water foraging (Pozo-Montuy and Serio-Silva 2006). Water scarcity, which may present increasing challenges for primates with climate change, also prompts innovative behavior, for example *Acacia tortilis* pod-dipping by vervets (Hauser 1988). Extreme habitats lead to innovative reliance on water-collecting species like bromeliads for capuchins (*Sapajus apella*: Brown and Zunino 1990) or cycads for Zanzibar red colobus exploiting disturbed coral rag forest (Nowak and Lee 2011a, b). When alternatives to disturbed or degraded habitats are available (for example, mangrove swamps), even so-called specialists, such as red colobus, can successfully exploit these (Galat-Luong and Galat 2005; Nowak 2008). Facultative use of swamps and wetlands may become obligate if primates' upland, preferred habitats are heavily disturbed (Nowak in press; Quinten et al. 2009), suggesting that habitat preferences may be poor indicators of primary preferences, degree of disturbance, or flexibility (Pozo-Montuy et al. 2011). Enforced habitat shifts can benefit a population if the new habitat offers a safer, possibly less seasonal environment; the already swamp-obligate Allen's swamp monkey (*Allenopithecus nigroviridis*) may evade human disturbance for these reasons (of Least Concern; IUCN Red List 2010).

Fig. 14.2 Subadult *P. kirkii* grooming a calf. Photo by Katarzyna Nowak

Species which colonize unfamiliar forest patches or are translocated into areas outside their natal range may have to shift diets and foraging strategies to include novel foods (e.g., *Alouatta pigra*: Silver and Marsh 2003). The Zanzibar red colobus has been successfully translocated to a plantation forest and introduced to a novel, but protected, area on Pemba Island outside its natural range (Camperio Ciani et al. 2001). This species shows higher colonizing ability than would be expected given traditional models of colobus socioecology and the fact that red colobus cannot survive in captivity (Fig. 14.2).

How Constrained Are Primates by Their Physiology and Metabolism?

It has long been argued that gut physiology limits the capacity for primates to be both frugivorous and folivorous in equal proportions (Chivers 1994). However, evidence of alternative switching between digestive types (structural vs. simple carbohydrate) is more common than used to be thought. Southern muriquis (*Brachyteles arachnoides*) facultatively alter their digestive regimes from fruit to leaf as a function of food availability (Talebi and Lee 2008) and the digestively specialized frugivorous white-handed gibbon (*Hylobates lar*) subsists off leaf material in selectively logged areas (Johns 1986). Senegal red colobus (*Procolobus badius temmincki*) in Fathala's forest in the Saloum Delta National Park shift from folivory to frugivory where their habitat has become degraded and during times of food shortage; fruits represented up to 50 % observations of feeding, while the number of species in their diet decreased by 50 % (Diouck 2002). Translocated howler monkeys (*Alouatta pigra*) feed longer on fruit (Silver and Marsh 2003), and lianas are an important food source for brown howlers (*Alouatta guariba*) and southern muriquis in disturbed forests (Martins 2009). Innovations such as charcoal-eating by Zanzibar red colobus can potentially overcome the ingestion of toxins from nonnative plants, such as Indian almonds and mangoes (Struhsaker et al. 1997), and possibly from mangroves as well. Bamboo lemurs are exceptionally specialized and among the smallest herbivores in existence. However, the vulnerable rusty-gray lesser bamboo lemur (*Hapalemur meridionalis*) can supplement its bamboo diet by grazing on grass species (Poaceae), thus allowing it to forage outside forest habitats (Eppley and Donati 2009). Its digestive processing is faster than would be predicted for such a small and specialized herbivore.

Questions About Flexibility

The questions we raise are: Do specialist primates persist because:

1. They are not specialists? If so, we suggest that the definition of a specialist needs reconsideration, taking into account those examples where physiology, foraging behavior, dietary breadth, and exploitation of exotic, naturally disturbed or anthropogenic habitats varies over time with species persistence.
2. They are specialists and are at risk? Their flexible responses are short-term and transitory with a time lag between apparently flexible responses and their ultimate population collapse (Struhsaker pers. comm. 2008).
3. Do specialist primates persist because specialization is mediated by behavior (and especially learning in primates)? As noted above, opportunistic behavior, innovation, and social flexibility (e.g., uni-male howler monkey, *Alouatta palliata,* groups in shade coffee plantations, McCann et al. 2003; fission-fusion in the genera of red colobus inhabiting human-disturbed forests (*P. gordonorum,* Marshall et al. 2005; *P. kirkii,* Nowak 2007 and Nowak and Lee 2011a, b) can all allow for population persistence (Lee 2003).
4. Specialization is not a single "trait"? Rather it represents three separate but interacting components: ecological, behavioral, and functional or morphological (Irschick et al. 2005); each component represents phylogenetic and evolved responses to past environments but as these traits are not necessarily linked they thus can co-vary in response to environmental dynamics.
5. Does a relationship between specialization and population responses to disturbance at a species level exist (Vázquez and Simberloff 2002)? Rather, species may exhibit asymmetries, as well as variance, in their capacities to respond to disturbance. Generalists should therefore receive as much conservation attention as specialists (Colles et al. 2009).

Clearly, the relationships between behavioral flexibility, the specialist–generalist continuum, and extinction probability or risk require further exploration in both comparative analyses and at the population level. We need better measures of specialization, of resource dynamics and the ability to model the consequences for sociality (Chapman and Rothman 2009; Strier 2009) and for reproductive rates (Cowlishaw et al. 2009; Lee and Hauser 1998). In addition, we have almost no associations between habitat or diet type and reproductive rate or reproductive output for comparative analyses of resilience (Lee and Kappeler 2003; but see Ross 1992).

We know that many specialists can compensate for morphological specializations and that behavioral alternatives can evolve alongside established specializations (Wcislo 1989), rendering specialization alone inadequate in extinction forecasts; while specialization can be useful for predicting potential risks, the construct does not necessarily predict what happens while a population is at risk. Specialization, we suggest, is a local population phenomenon, rather than a species intrinsic trait (Fox and Morrow 1981) and specialists and generalists appear not to be types, but temporary states as a response, and fine-tuned, to local conditions (e.g., primate diets at local scales: Chapman and Chapman 1990, 1999; Chapman et al. 2002). Behavioral flexibility may be a mechanism for response generalization in specialists with relatively nonplastic traits (e.g., constraints due to body size, dental or skeletal morphology, locomotory mode).

Fimbel (1994) notes the hazard of generalizing about ecological correlates of species failure or success in disturbed habitats, emphasizing that such correlates are often site- or disturbance-specific. Furthermore, the ability to use human-modified habitats—although an alleged determinant of extinction proneness—has not been found to be associated with any single suite of traits (Laurance 1991). We might therefore learn more about extinction by studying populations that survive and persist following episodes of biological impoverishment than by searching for causes of extinction (Vermeij 1986). Investigating the significance of behavioral flexibility for survival in a systematic way could inform conservation action plans, and be valuable for the study of extinction biology (Strier 2009); however, as long as general patterns continue to be sought, we will carry on finding high variability and heterogeneity in primates' responses to disturbance at the species level (Cowlishaw et al. 2009). It has long been recognized that intraspecific comparative work is imperative before, if at all, any particular behavioral pattern is viewed as species-typical (Poirier 1969). How then can we compile reports of flexibility in ways that are useful and informative (Isabirye-Basuta and Lwanga 2008)?

If species are unable to change behavior sufficiently or rapidly enough in response to continuing habitat degradation, then we ask: "Does the future include a proliferation of opportunistic species or emergent novelties?" (Myers and Knoll 2001, p. 5390) and "will the environmental constraints humans place on surviving populations channel innovations toward properties we associate with pests?" If we see crop-raiding as innovative behavior, then the extent to which crop-raiding is widespread suggests the "creation" of pests in areas of high human density or where buffer zones between forests and farms are lacking. Yet again, we ask: do "generalists" crop-raid more than "specialists"? It would appear that, given opportunities, almost all species of primate will crop raid (Lee and Priston 2005).

More optimistically, “It is likely that there are adaptational ‘treasures’ that we have as yet failed to discover in primates, due partly to our own (hominid) biases in expectation” (Ganzhorn et al. 2003, p. 133). Behavioral flexibility, innovation, and reproductive plasticity are by and large the norm, rather than exception in primates, and we must collect data on primate responses to disturbance in more systematic ways that facilitate comparisons across not just taxa, but populations (Isabirye-Basuta and Lwanga 2008; Strier 2009). In an age where molecular biology is outpacing behavioral ecology and conservation biology (for example, we now recognize 24 species of *Lepilemur* yet know the conservation status of only three of them, the rest being “Data-Deficient”; IUCN Red List 2010), we also need to stimulate (and revive interest and investment in) ongoing field studies of behavior to seek to understand ramifications of continuing anthropogenic change to habitats and the capacity and expression of primate behavioral responses to this change. Primates, whether flexible or specialized, mostly frugivorous or folivorous, will be increasingly prone to extinction (see Conservation International’s “Top 25 Most Endangered Primate List”) unless there are both habitats and protection that safeguard their capacity for and existing expression of innovation and behavioral variability and flexibility.

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Chapter 15

Fragments and Food: Red-Tailed Monkey Abundance in Privately Owned Forest Fragments of Central Uganda

Deborah Baranga, Colin A. Chapman, Patrick Mucunguzi, and Rafael Reyna-Hurtado

Abstract Understanding the strategies that primates use to survive in fragmented forest landscapes is vital for constructing informed management plans for specific regions and to enable researchers to start to make generalizations. In a 15-month study, we investigated factors that influenced the status of red-tailed monkeys (*Cercopithecus ascanius*) and their plant food resources in 20 of the few remaining privately owned forest fragments in Central Uganda. We employed transect methods for vegetation assessments and censuses with a short stop upon sighting red-tails to establish demographics and food plants consumed. While the sample involved forests of very different successional stages, forest size was the most important factor influencing both red-tail population size and the number of groups per fragment. Number of food tree species influenced only the number of red-tail groups per fragment. Basal area of food tree species and food tree abundance per fragment were not related to red-tail population size or the number of groups per fragment. Food tree species richness, total number of trees, and basal area of food trees increased significantly with fragment size. Availability of food resources was

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affected by various factors including habitat area, the nature and intensity of human exploitation, and how fragments were managed. The number of groups and abundance of red-tail monkeys declined when anthropogenic consumptive activities increased. In the future, as these forests are further degraded, the availability of food resources will continue to decline, and thus, the probability that these red-tail populations will survive much longer seems unlikely.

Introduction

Increasing anthropogenic environmental change is recognized as a major challenge to global environmental systems (Chapman and Peres 2001; Patz et al. 2004). In the past 50 years, the size of the human population grew by 3.7 billion people (Potts 2007). Consequently, the demand for resources has increased, bringing about large-scale alterations of environmental conditions for wildlife populations. This has occurred to such an extent that nowadays the world is increasingly being dominated by human-modified ecosystems (Kariva et al. 2007). In the tropics, habitat degradation and forest conversion pose such a significant threat that widespread terrestrial species extinction is predicted to occur soon (Cowlishaw 1999; Sodhi et al. 2004). Our ability to conserve biodiversity in human-dominated systems increasingly requires research into mechanisms that can maintain species in fragmented and degraded landscapes. For example, the conservation of some biodiversity in degraded tropical landscapes may be assisted through the management of diverse agroforestry systems (Bhagwart et al. 2008; Gardner et al. 2009; Omeja et al. 2009). However, a detailed understanding of which species will be affected by different types of fragmentation, and which will benefit from different types of management systems remains largely unknown.

In Uganda, threats to biodiversity are similarly grave or worse than global averages. Closed-canopy tropical forest once covered 20 % of the country, but deforestation has reduced this to just 3 % (Howard et al. 2000). Uganda lost 18 % of this remaining forest between 1990 and 2000 (Howard et al. 2000), and the most recent estimate suggests that the annual rate of loss of tropical high forest in Uganda is 7 % (Pomeroy and Tushabe 2004). At the present rate, Uganda will have lost all its forested land by 2050 (NEMA 2008). Over 80 % of the land in Uganda is used for small-scale farming and nearly 80 % of the population are farmers (UBOS 2005), which means even small fragments are surrounded by people that need the resources found in forests—intact or not. In addition, Uganda's population is growing at approximately 3.3 % annually (2005–2010) which ranks 8th in the world (UN 2010). Even more alarming than the population growth rate is the fact that Uganda has the second youngest population of the world with 49 % below 15 years of age (PRB 2010). This high rate of human population growth is expected to increase forest fragmentation and

Fig. 15.1 A juvenile red-tailed monkey in a forest fragment in Uganda. Photo Credit—Colin Chapman

lead to a reduction in size and even complete loss of many forest fragments (Chapman et al. 2007). Increased demand for food, raw materials, and wood energy due to human population increase, amidst slow technological growth and a large rural population, will lead to the loss of forest habitat and the biodiversity therein (Jacob et al. 2008; Naughton et al. 2006; Naughton et al. 2011). The once large continuous forest in the Lake Victoria region now survives as small forest fragments. However, in spite of their sizes, they are still playing an important role in conserving biodiversity, including some primate species, among them the red-tail monkeys (*Cercopithecus ascanius*; (Baranga 2004a, b), if they can be maintained over the long-term (Fig. 15.1).

Here we investigate whether the forest fragments in the once large continuous forest surrounding the shores of Lake Victoria region can support viable red-tail monkey populations amidst increasing rates of human disturbance. Specifically we quantified the relationship between red-tail populations and the availability of potential food tree resources in the selected forest fragments in the Lake Victoria basin, Uganda.

Methods

This study was conducted in a 600 km^2 area of forest–savannah–agricultural mosaic dominated by human habitation and other human infrastructural development in central Uganda (Baranga 1995). We established two study sites within this large area from which we based our operations and sampled 20 fragments (Baranga 2004a). Site 1 had non-reserved forest fragments (0^0 05^0 N, 0^0 16^1 N and 32^0 30^1E, 32^0 38^1E) of which Zika Forest (Buxton 1952) was the largest and least disturbed, while the Kisubi Forests, owned by the Roman Catholic Church, constituted the majority of the other fragments. On the whole, 75 % of the fragments at this site were off-shore, 15 % were riparian, and 10 % were dry-mainland forest. Site 2 was based at Mpanga Forest Reserve (0^0 15^1 N, 32^0 15^1 E). It is a medium altitude moist evergreen forest (of about 4.5 km^2) considered a *Piptadeniastrum–Albizia–Celtis* forest by foresters (Howard 1991; Langdale-Brown et al. 1964). The fragments were at different stages of succession/maturity following disturbance. As a legally protected area, the Mpanga Forest Reserve was sampled to compare it to the other fragments.

Human activities and fragment size were determined directly. Stand structure was quantified by tree enumeration along 5-m wide transects divided into 10 m long plots to achieve the 'minimal area' based on the Brain-Blanquet concept (Kershaw 1973). Tree species classes (Richards 1996; Swaine and Hall 1986) were evaluated using the diameter at breast height (dbh), measured at a height of 1.3 m from the ground for all trees with a diameter of 10 cm girth and above. Tree stumps were enumerated and their diameters used to calculate tree basal area loss as an index of forest exploitation. The status of the forest fragments were assessed by allocating them scores: from 1 to 4 (1-fairly intact, 2-disturbed, 3-degraded, 4-highly degraded) based on presence or absence of distinct upper, middle, lower, and ground layers, thick undergrowth, presence of gaps, and human activities, such as tree cutting and forest clearing (Table 15.1).

As a means of describing similarities between fragments, cluster analysis (simple matching coefficient) and ordination (group average) were conducted on the basis of the woody species found in each fragment. We also did an ordination of all variables that include food tree species, forest fragment size, and number of groups and population size of red-tails in each fragment. For these analyses PC-ORD-VERSION 4 was used.

To facilitate evaluation of the red-tail populations in each fragment, a system of trails were set up so that each fragment could be searched with a minimum of disturbance to the animals. In the Mpanga Forest Reserve an existing trail system was used. Each month for 14 months, primate censuses were conducted over 2 days in each fragment with the exception of the Mpanga Forest Reserve that took 3 days each month due to its large size. During the census, the observer walked slowly (0.75 km/h) and when a group was detected the observer stopped for 20 min to estimate group size and when possible determine the age/sex composition of the group. We also determined breeding status of females and number of dependent young in each group to construct a breeding ratio. Finally, we evaluated what plant species and part red-tails were feeding on.

Table 15.1 Relationship between human activities, competition with vervets, and red-tail monkey residential status and demography in 20 selected forest fragments around Lake Victoria, Uganda

Category	Forest fragment	Major human activities	Competition with vervets	Status of groups	Groups	Popn.
1	Zika	Fuelwood collection	Present	R	3	23
	Kisubi Hospital	Fuelwood collection	Absent	R	2	14
	Kisubi Technical	Fuelwood collection	Absent	R	3	7
	Marianum Gogonya	Fuelwood collection	Absent	R	2	14
	Kisubi Kibale	Fuelwood collection	Absent	R	2	19
	Kisubi Nabinonya	Fuelwood collection	Absent	R	2	22
	Kisubi Girls	Fuelwood collection	Absent	R	1	24
	Wamala	Fuelwood collection for beer brewing	Absent	R	1	14
2	Mawanyi	Fuelwood collection + cultivation	Present	R	3	9
	Nganjo 3	Fuelwood collection + cultivation	Present	R	1	8
	Katwe	Fuelwood collection + cultivation	Present	0	0	0
3	Bunamwaya	Fuelwood collection + brick burning[a]	Present	SR	1	8
	Nganjo 1	Fuelwood collection+ poles+cultivation	Present	SR	1	7
	Sinzi	Fuelwood + tree cutting for canoes	Present	SR	1	8
	Kanywa	Fuelwood+clay quarrying+brick making	Absent	SR	1	3
4	Namulanda	Charcoal burning + water collection[a]	Absent	R	1	6
	Seguku	Paddock fencing + water collection[a]	Present	R	1	12
5	Nganjo 2	Fuelwood collection + cultivation[a]	Present	0	0	0
	Nalugala	Fuelwood collection + cultivation[a]	Present	SR	1	4
	Kisubi Paddock	Fuelwood collection + clearing	Absent	R	2	10

Key: *R* resident, *SR* semi-resident, *0* no red-tail
[a] Daily activities

We analyzed the data by performing parametric bivariate Pearson correlations among forest fragment size, food tree richness, food tree total abundance, and food tree basal area with red-tail population abundance and number of groups in each fragment. We ran additional analyzes between all the forest variables with the breeding ratio (number of dependent young/ breeding females) we found in each group. We ran these analyzes in SPSS 10.0.

Results

Contrasting Forest Fragments

Cluster analysis of the forest fragments based on the food tree species found in each fragment revealed four main clusters when 0.60 is used as a minimum index for defining the clusters (Fig. 15.2). Cluster one consisted of the Zika forest. Cluster two had nine forest fragments consisting of Namulanda, Kisubi, and Wamala sites. Cluster three included the Mpanga and Kituza forests only. Finally, cluster four had ten forest fragments consisting of the smaller unprotected forests.

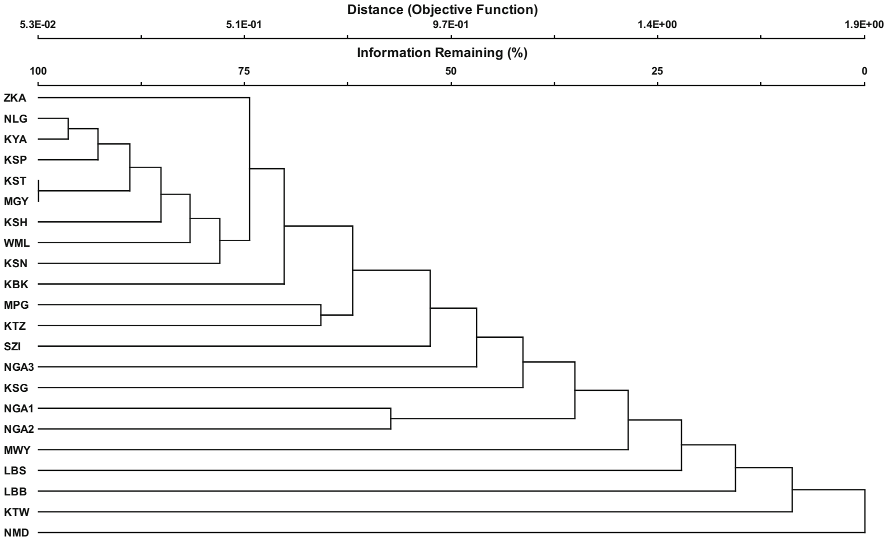

Fig. 15.2 Cluster Analysis based on food tree species in selected forest fragments around Lake Victoria Basin, Uganda. Key: Zika = ZKA, Mawanyi = MWY, Namulanda = NMD, Sinzi = SZI, Nganjo 1 = NGA1, Nganjo 2 = NGA, Nganjo 3 = NGA3, Nalugala = NLG, Kanywa = KYA, Kisubi padlock = KSP, Kisubi Kibale = KBK, Kisubi Technical = KST, Kisubi Hospital = KSH, Marianum Gogonya = MGY, Wamala = WML, Kisubi Nabinonya = KSN, Mpanga = MPG, Kituza = KTZ, Kisubi Girls = KSG, Lubowa Seguku = LBS, Lubowa Bunamwaya = LBB, and Katwe = KTW

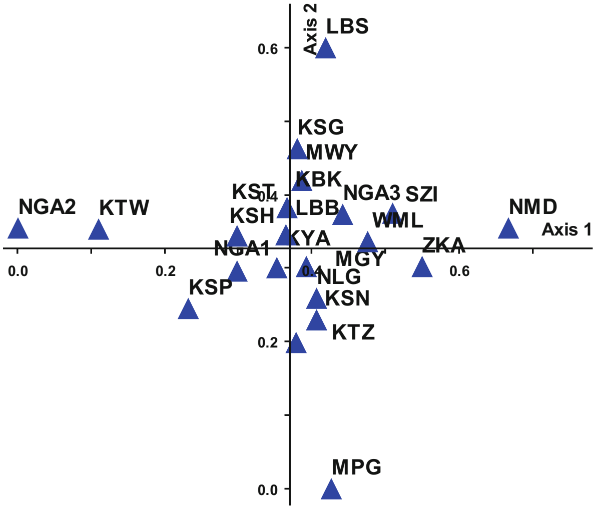

Fig. 15.3 Ordination based on the food tree species in selected forest fragments around Lake Victoria, Uganda. Key: Zika = ZKA, Mawanyi = MWY, Namulanda = NMD, Sinzi = SZI, Nganjo 1 = NGA1, Nganjo 2 = NGA, Nganjo 3 = NGA3, Nalugala = NLG, Kanywa = KYA, Kisubi padlock = KSP, Kisubi Kibale = KBK, Kisubi Technical = KST, Kisubi Hospital = KSH, Marianum Gogonya = MGY, Wamala = WML, Kisubi Nabinonya = KSN, Mpanga = MPG, Kituza = KTZ, Kisubi Girls = KSG, Lubowa Seguku = LBS, Lubowa Bunamwaya = LBB, and Katwe = KTW

Table 15.2 Fragment characteristics, the number of red-tail monkey groups, and population size for a series of fragments in the central area of Uganda

Forest type	Forest fragment size	Species richness	Pop size	Basal area	# of groups	#of redtails
Ziika	19.231	16	316	666782.9	3	23
Mawonyi	3.237	14	146	109460.9	3	9
Namulanda	0.747	10	69	128532.8	1	6
Sinzi	3.642	14	161	159792.2	1	8
Nganjo 1	1.925	11	114	67507.4	1	7
Nganjo 2	0.42	8	96	54065.5	0	0
Nganjo 3	2.295	14	140	118157	1	8
Nalugala	0.7	14	194	105914.3	1	4
Kanywa	3.187	15	251	151788.8	1	3
Kisubi Padock	3.645	13	274	244751.7	2	10
Kisubi Kibale	4.06	12	172	238038.6	2	19
Kisubi Technical	2.25	14	112	206805	3	7
Kisubi Hospital	3.55	12	157	306201.7	2	14
Marianum Gogonya	5.8	11	146	198614.3	2	14
Wamala	9.499	15	189	385396.4	1	14
Kisubi Nabinonya	7.462	14	95	125722	3	22
Kisubi Girls	3.392	11	225	140308.2	1	24
Lubowa Seguku	0.24	11	69	24768.8	1	12
Lubowa Bunamwaya	1.24	11	116	88384.5	1	8
Katwe	5.52	9	176	276380.7	0	0

Ordination analysis of food tree data from the 20 fragments revealed that in most fragments food tree species were common, with the exceptions of Namulanda, Katwe, Nganjo 2, and Mpanga that had few food tree species (Fig. 15.3; Table 15.1). The forest fragments with a higher number of food tree species were Zika ($n = 16$ species), Wamala (15), and Kanywa (15), and Mawanyi, Sinzi, Nganjo 3, Nalugala, Kisubi technical, and Kisubi Nabinonya each with 14 species (Table 15.2).

Ordination analysis of the relationship between forest size, food tree species, food tree abundance, basal area, and the number of groups and population size of red-tails in each fragment showed that Kisubi, Nabinonya, and Zika fragments conserve red-tail populations and their food tree species well and that Katwe and Nganjo2 were the worst fragments for conservation (Fig. 15.4).

In all fragments we found evidence of cutting of trees for the collection of fuelwood. Other activities present in some fragments, but not others, included: brewing beer, active cultivation, brick making, charcoal production, cutting large trees for timber or for making boats, and cutting of poles to build fences (Table 15.1). Since vervet monkeys (*Cercopithecus aethiops*) are potential competitors of red-tail monkeys, we determine in which fragments they were present (Table 15.1). The fragments with lower red-tail population size are Nganjo 2, Katwe, Nalugala, and Kanywa and there are more than two human activities in all these fragments (Table 15.1).

Food Tree Species

Twenty-two commonly consumed food tree species for red-tail monkeys were identified from observations made in all of the 20 fragments. These species were the following: *Harungana madagascariensis*, *Blighia unijugata*, *Measopsis emnii*, *Pseudospondias microcarpa*, *Pycnanthus angolensis*, *Trichilia drageana*, *Sterculia dawei*, *Manilkara dawei*, *Solanum mauritianum*, *Margaritaria discoideus*, *Chaetacme aristata*, *Alchornea cordifolia*, *Teclea nobilis*, *Ficus capensis*, *Pittosporum manii*, *Albizia coriaria*, *Sapium ellipticum*, *Antiaris toxicaria*, *Craterispermum laurinum*, *Ficus urceolasis*, and *Spondianthus preusii*. The forest fragments that had many of these 22 food tree species were: Zika (with 16 of the 22 food tree species) Wamala (15), Kanywa (15), Sinzi (14), and Kisubi Nabinonya (14). The food tree species that occurred in at least 75 % of the forest fragments were *H. madagascariensis*, *B. unijugata*, *M. eminii*, *P. microcarpa*, *P. angolensis*, *T. drageana*, *S. dawei*, *M. dawei*, *S. mauritanum*, ranging from 17 to 21 out of 22 species.

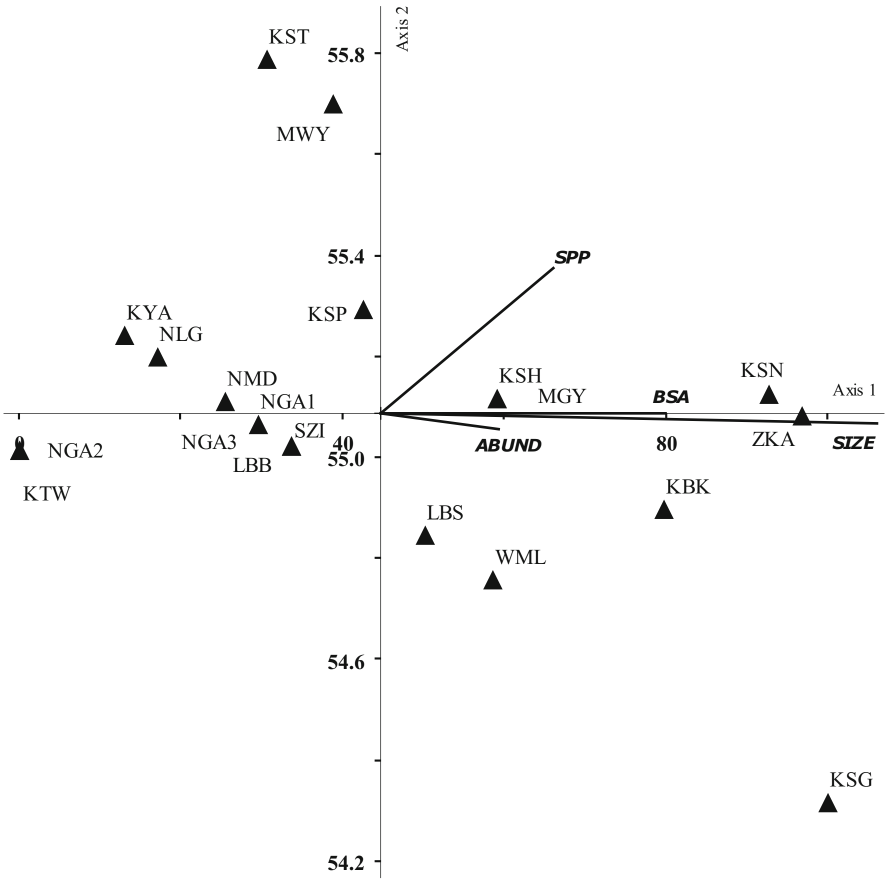

Fig. 15.4 Ordination of the relationship between forest size, food tree species, food tree abundance, basal area and the groups and population of red-tail monkeys in selected forest fragments around Lake Victoria, Uganda. KEY: Zika = ZKA, Mawonyi = MWY, Namulanda = NMD, Sinzi = SZI, Nganjo 1 = NGA1, Nganjo 2 = NGA, Nganjo 3 = NGA3, Nalugala = NLG, Kanywa = KYA, Kisubi padlock = KSP, Kisubi Kibale = KBK, Kisubi Technical = KST, Kisubi Hospital = KSH, Marianum Gogonya = MGY, Wamala = WML, Kisubi Nabinonya = KSN, Kisubi Girls = KSG, Lubowa Seguku = LBS, Lubowa Bunamwaya = LBB, and Katwe = KTW

Red-Tail Populations and Resources

As would be expected as fragment size increased, there was an increase in the number of food trees ($r = 0.601$, $p = 0.005$), food tree basal area ($r = 0.899$, $p = 0.000$), and the number of food tree species ($r = 0.503$, $p = 0.024$; Table 15.2). The number of red-tail groups per fragment increased with increased fragment size ($r = 0.488$, $p = 0.048$) and the number of food tree species ($r = 0.579$, $p = 0.008$). There was no significant increase in the number of red-tail groups with food tree basal area ($r = 0.377$, $p = 0.102$) or the abundance of food trees ($r = 0.172$, p = 0.468) in a fragment. The size of the red-tail populations in the fragments increased with forest size ($r = 0.571$, $p = 0.009$) and marginally so with basal area of food tree species ($r = 0.432$, $p = 0.057$). However, the populations did not increase as a function of the number of food trees ($r = 0.329$, $p = 0.156$) or with the food tree total abundance per fragment ($r = 0.282$, $p = 0.228$). As what might be expected, the higher the number of red-tails groups, the higher their population ($r = 0.569$, $p = 0.009$).

We also found that there were no correlations between forest size, tree species richness and abundance, and basal area with breeding ratio (number of breeding females/dependent young per site). However, there were significant correlations between number of juveniles and forest fragment size ($r = 0.481$, $p = 0.032$), number of breeding females with forest fragment size ($r = 0.525$, $p = 0.018$), and with total basal area ($r = 0.457$, $p = 0.043$). These last results likely reflect the fact that population size is highly correlated to forest fragment size per se as we demonstrated above. Finally, we found that forest fragment size, food tree number, and basal area, as well as total abundance of food trees, were highly correlated among themselves. This prevented us from performing a multiple regression analysis using these variables to predict red-tail population size or number of groups.

Discussion

With Uganda's high human population density and growth rate and the fact that a very large proportion of the population are small-scale farmers, forest fragments are almost inevitably surrounded by intensive human activities. Thus, our results suggest that if they do not receive some sort of protection that the fragments become rapidly and extensively encroached upon. The positive impact of protection is indicated by the segregation of the forest patches into the four major clusters that partly reflect the legal status that reflected the degree of degradation. Zika forest was a natural climax (under government institutional protection), while Cluster 2 mainly consisted of Kisubi forests which were on the whole mixed forests. Mpanga and Kituza forests were quite distinct from others as fairly large gazetted forests, with Mpanga being protected. The rest of patches were small and largely colonizing secondary forests with some of them (Nganjo 1 and 2, Kanywa, Sinzi, Namulanda, and Nalugala) in a retrogressive state due to cultivation. Since, most of the fragments were studies are not protected they are likely to be reduced in size in the future as anthropogenic activities such as fuelwood collection, cultivation, and collection of building poles take their toll.

Our study illustrates the importance of maintaining forest size since it was related to red-tail population size and the number of groups per fragment. In addition, forest size predicted other variables that might also be important for red-tail monkeys, such as the number of food trees, food tree basal area, and the number of food tree species. This produces a very simple management statement: the most effective means to protect red-tail populations in fragmented landscapes will be to protect fragments so that they are not reduced in size.

Since the majority of these fragments are privately owned or owned by organizations that will likely exploit them at some time (e.g., the Catholic Church), this calls for conservation strategies that will protect the fragments while at the same time meet the needs of the local people. The needs of the local people must be met since they are the owners of the fragments and thus have the right to exploit them. The goals of these strategies, protection and meeting the goals of local people, are in direct opposition to each other. The only way that we can see advances being made to satisfy both of these goals is if government or conservation agencies work with the local community to provide the resources that farmers would extract from the fragments from elsewhere. To make such an effort a success each member of the community, and particularly those families living directly opposite to the fragments, would have to agree not to exploit resources from the fragments if they were provided the resources from elsewhere. This of course raises a number of questions. The most important of which is, "Where would the replacement resources come from?" This is a landscape where all the land is officially or unofficially owned by someone (Naughton et al. 2011; Naughton et al. 2006). Other questions include: How does the government or conservation agency compensate landowners living adjacent to the fragment for crop-raiding done by animals like red-tail monkeys? How can cheating by community members be prevented? What justification can be given to the community to make a priority of protecting forest fragments when disease, poor nutrition, and lack of fees for school are more immediate priorities to most local farmers? How can an education program cover areas as large as 600 km^2? All of these questions would need to be addressed and the funding raised for the program before any plan that met both goals would have a good chance to succeed. We view that this is very unlikely to occur, and thus, the long-term future of these forest fragments and the red-tails they support looks grim.

Conclusions and Recommendation for Future Research

The few remaining forest patches in 'Kampala Area' are faced with different levels of human disturbance ranging from low in privately owned forests to high in forest on public land with minimal protection. With a range of common human activities and especially forest clearing and cultivation, forest size was on the decline, yet it was a crucial factor influencing key parameters (number of food trees, food trees species and their basal area, as well as the number of red-tails groups and their populations per fragment). Therefore, the continuing forest exploitation by the local communities around the forest fragments is likely to lead to diminishing or even complete elimination of the red-tail monkey populations. This will probably be through anthropogenic effects causing a decrease in fragment size that ultimately leads to scarcity in food resources and consequently declining red-tail populations. To reverse the present trends would require a major conservation effort, on a scale and of a nature that is not typically done. To stop the fragments from being cleared would require the cooperation of the local people, since this is their land or it is the community members that are using protected lands. Alternative sources of income would have to be found (e.g., ecotourism), fuelwood supplies from elsewhere would have to be made available (e.g., a large scale woodlot project), fuelwood demand would have to be reduced (solar or biogas stoves), and a great deal of effort would have to be placed in education and outreach to obtain the willing support of all the communities.

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Chapter 16
Fragment-Adaptive Behavioural Strategies and Intersite Variation in the Ring-Tailed Lemur (*Lemur catta*) in South-Central Madagascar

Alex Cameron and Lisa Gould

Abstract Behaviour, diet and population demography were sampled and compared between two forest fragment-living populations of wild ringtailed lemurs (*Lemur catta*) in south-central Madagascar. Both sites—a fragment in the Tsaranoro Valley near Andringitra National Park, and a more densely populated fragment at Anja, much closer to human habitation—are sacred forests (sites of human burial) surrounded by anthropogenically produced savannah, and are subject to traditional protective prohibitions (*fady*). Both sites attract tourists, but are operated differently, with Anja receiving considerably more tourists; the resources available to the *L. catta* also differ at each site, affecting their behaviour. *L. catta* at Tsaranoro spent more time feeding, and less time resting and engaging in social behaviour than those at Anja, where abundant fruit from introduced trees, as well as plentiful drinking water, are available and resource abundance is relatively higher. Although the fragments are of similar size and were expected to differ little, many significant behavioural and population differences were observed, suggesting the importance of the refinement of rapid assessment techniques for judging the habitat suitability and conservation value of small forest fragments.

Introduction

Madagascar is regarded as a conservation hotspot due to its intense biodiversity—nearly 80 % of Madagascar's flora and fauna are endemic to the island (Lourenco 1996; Goodman and Benstead 2003). Humans arrived on Madagascar roughly 2000 years ago, bringing slash and burn agriculture, and the process of forest clearing has

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been ongoing since then, fragmenting the island's forests and driving many species extinct (Burney et al. 2004). The fragmentation of forest threatens the island's remaining nonhuman primates, leaving them vulnerable in terms of both the immediate survival of populations and in terms of the genetic diversity of remaining populations (Ganzhorn et al. 2001; Mittermeier et al. 2008). In early 2009, a political coup resulted in increased economic instability and relaxed enforcement of logging restrictions in Madagascar, in many areas resulting in hardwood poaching and increased deforestation (Innes 2010). The area capable of supporting wild lemur populations is currently less than a tenth of the island (Mittermeier et al. 2008) and isolated forest fragments remain underrepresented among study sites due to the focus on continuous tracts in protected private reserves and national parks.

This is particularly true regarding the body of research on Madagascar's flagship nonhuman primate, the ring-tailed lemur (*Lemur catta*). In brief: *L. catta* is a medium-sized strepsirrhine averaging 2.2 kg (Sussman 1991; Gould et al. 2003). The species is found throughout parts of southern, south-western, and south-central Madagascar: *L. catta* range from Parc National de Kirindy-Mitea in the west; to the southwest and the southernmost point of the island (Cap Sainte Marie); east to Petriky and Parc National de Andohahela; and to the south-central region where our study occurred, with Anja Reserve likely the furthest northeast of their distribution (Goodman et al. 2006; Gould 2006). They are remarkably ecologically flexible, occurring in areas of gallery, xerophytic, brush and scrub, spiny, and dry deciduous forest as well as high-altitude ericoid bush (in the Andringitra mountain range) and rocky outcrop mixed vegetation forest surrounded by anthropogenic savannah (Goodman et al. 2006; Gould 2006; Jolly 2003; Sussman et al. 2003; Gabriel 2013). *L. catta* is the most terrestrial lemur, spending on average one-third of the time on the ground (Jolly 1966; Sussman 1974).

L. catta have been described as opportunistic omnivores (Sauther et al. 1999), feeding on fruit and other plant parts, insects, soil, and termitaria (Jolly 1966; Sauther 1992; Sauther et al. 1999; Sussman 1977). Seasonality of food resources is extreme in southern Madagascar, and droughts are common throughout *L. catta*'s range (Jolly 1966; Gould et al. 1999; 2003; Sauther 1992; Sussman 1977). As a result, *L. catta* embodies the traits expected in primate species that persist in fragments, as outlined by Marsh (2003): a low or flexible degree of frugivory, small or variable home range sizes, broad behavioural and dietary plasticity, and the capacity to move through or utilize matrix habitat surrounding the fragment (Gould et al. 1999; Gould 2006; Jolly et al. 1993; Jolly 2003; Sauther 1992, 1993 2002; Soma 2006; Gabriel 2013).

Although the species has been extensively studied for over 50 years, it is only rarely reported on at sites other than Beza Mahafaly Special Reserve (BMSR) in the southwest and Berenty Private Reserve in the far south, both largely gallery forest habitats (histories in Jolly 2012; Jolly et al. 2006; Sussman and Ratsirarson 2006; Sussman et al. 2012). This work has focused heavily on *L. catta*'s dry habitat adaptations in continuous tracts of gallery and scrub forests: correlations have been suggested between seasonality and behaviour, e.g., female dominance, ranging patterns (e.g., Jolly 1984; Jolly et al. 1993; Mertl-Millhollen et al. 2003; Sauther 1993), and seasonality and demography, e.g., rapid population recovery after extreme droughts, group size fluctuations (e.g., Gould et al. 1999; Jolly et al. 2002; Pride 2005; Sauther and Cuozzo 2008). These studies commonly lack comparative data from other habitats, because little has been generated (but see recent work on *L. catta* in spiny forest/spiny bush by Gould et al. 2011; Kelley 2011; LaFleur 2012).

This is particularly pertinent from the perspective of maintaining wild populations, as southern gallery forest, the predominant habitat type at both BMSR and Berenty, is considered among the most endangered types of forest on the island (Sussman et al. 2003). Livestock grazing and overcutting for agriculture have created narrow forest fragments running along river and stream edges, and this habitat has been considered optimal for *L. catta* (based on population densities, health profiles, population recovery in this habitat, and resource availability (Goodman et al. 2006; Gould et al. 1999, 2003; Jolly et al. 2002; Koyama et al. 2002). However, evidence of river shifts may hold implications regarding the efficacy of current efforts to protect these gallery forests (Blumenfeld-Jones et al. 2006; Koyama et al. 2006), which suggests the utility of studies aimed at determining the conservation potential of other sites and habitats. Particularly, many small fragments of other forest types exist throughout *L. catta*'s range (Sussman et al. 2003; Gould and Gabriel under review), and the work presented here was conducted at two such fragments. Few studies have been conducted to investigate how populations of *L. catta* in rocky outcrop fragments differed from conspecifics in terms of diet, demography, or behaviour (but see Gabriel 2013a), limiting our understanding of range of *L. catta*'s flexibility along these vectors, and leaving the conservation value of such sites unknown.

In this chapter, we present population densities, behavioural surveys and dietary data on two populations of *L. catta* living in south-central Madagascar, at a fragment in the Tsaranoro Valley and at Anja Special Reserve. Both small fragments remain intact due to past use by local Betsileo as a burial area, which renders the sites sacred, and subject to various *fadys* or taboos/restrictions on their use. The adherence to these traditional restrictions is a feature of tribal groups across the island, but the fadys themselves can vary intensely from area to area and village to village, as do the penalties, which may include divine retribution (as when the ancestors have forbidden the harvesting of a wild species, a very strict fady) or compensating the head of the village in which the violation occurred (in the areas where we worked this would generally be in the form of cattle or tree plantation). It has been suggested that fady, while not necessarily promoting sustainable resource management, are adhered to more than imposed, external conservation-oriented rules, and that the introduction of restrictions rooted in governmental and foreign authority may instead weaken the traditional safeguards against poaching and sacred site use (Jones et al. 2008).

Approximately 60 *L. catta* live in the Tsaranoro fragment in approximately 6–8 groups, ranging in size from 4 to ~20 individuals. During the study period, large groups of individuals appeared to fission and fusion, aggregating alternately throughout the day via contact calls between much smaller subgroups. There are approximately 225 *L. catta* living at Anja (Gould and Gabriel under review). Groups at this site average 16 individuals, although groups size ranges from 4 to 21

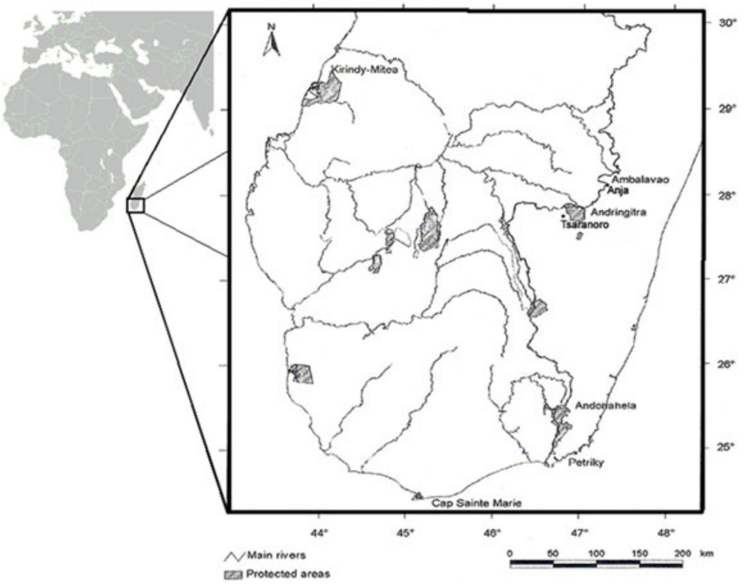

Fig. 16.1 Map of Southern Madagascar showing the study sites Anja and Tsaranoro

animals—no fusing of small groups was observed here, although large groups appear to time-share feeding sites peacefully and sometimes spread into slightly smaller groups while feeding.

Behavioural and dietary variations between these populations and *L. catta* studied elsewhere highlight this species' intense plasticity, suggesting the potential of small forest fragments for *L. catta*'s persistence in the wild. However, while comparisons with data from other habitats indicate that the two fragment sites are generally similar to one another, significant differences between the two populations in terms of behaviour and diet suggest that generalizing on the basis of habitat type and forest size is less useful for conservation planning than rapid assessment on a site-by-site basis.

Study Sites

Our study was conducted during the austral winter in June and July 2009 and July 2010, at a fragment in the Tsaranoro Valley (22°05′11 S, 46°46′ 14 E), and at Anja Community Reserve (21°51′12 S, 46°50′40 E), 55 km NE of Tsaranoro, and 13 km south of the town of Ambalavao, in south-central Madagascar (Fig. 16.1). Both fragments remain due to past use by local Betsileo as a burial area, which renders the sites sacred, and subject to various fady; hunting or harming lemurs is also considered fady by locals and thus *L. catta* are protected by traditional beliefs twice over. Malagasy guides are required for entrance into either fragment to ensure that these prohibitions are followed. At both sites the *L. catta* have not been previously studied but are habituated to human presence, although the Anja lemurs are far more habituated due to constant tourism since the designation of the fragment as a protected reserve in 1999 (http://anjacommunityreserve.netai.net/).

The major difference between sites is the presence at Anja of a human-made fish-farm lake surrounded by vegetable and tobacco gardens bordering the southwest corner of the forest. The lake also provides irrigation to rice terraces on the north side of the fragment. The broader area differs little from the Tsaranoro Valley in terms of water availability, but, fragment-to-fragment, water is much more accessible at Anja, as lemurs residing in the lower area of the reserve come down daily to drink at the lake, small ponds, or near the rice terraces, and there are small streams further up the mountain.

The Tsaranoro Fragment

The Tsaranoro Valley is 12 km east of Parc National Andringitra, and peak elevation in the fragment is 1,104 m (Google Earth 2012). Average cold season temperatures are similar (23–32 °C) to other *L. catta* sites in the south and south-west (Jury 2003; Sauther 1992; Sussman 1991). The Tsaranoro Massif makes up the western edge of the Tsaranoro fragment (Fig. 16.2a). The forest is 53.7 ha of continuous and semi-continuous rocky-outcrop vegetation, with a mix of temperate, rainforest (e.g., bamboo, some palms), and xerophytic scrub species similar to that found in southern Madagascar's spiny bush habitat.

The Anja Fragment

The Anja fragment is 13 km south of Ambalavao, located immediately adjacent to Route Nationale 7, Madagascar's main highway (Fig. 16.2b). The fragment area is 34 ha including continuous forest running up the mountain, with 3–5 *L. catta* groups living at this higher altitude. The reserve is bordered by large rock formations (sandwiching the fragment with the highway, which runs parallel). Maximum elevation of the mountain is 1,206 m (Google Earth 2012); but lemurs do not range above 1,020 m. The forest is more strictly rocky-outcrop vegetation than the Tsaranoro fragment (Fig. 16.3), and fruiting trees, especially *Melia azedarach and P. cattleianum* have become well established at Anja since the removal of large *Adansonia* and *Ficus* trees before the fragment was designated as a protected area (Razafimandimby, pers. comm.) (Fig. 16.4).

The majority of the forest grows around large boulders at the centre of the fragment, which has increased in size substantially from 8 ha in 1999 to 34 ha today (Rahaovalahy pers. comm.).

Tourists with guides are much more common at Anja; the reserve is maintained by the Anja-Miray Association as a community conservation and development effort. Tourism entrance fees go directly towards local projects such as the building

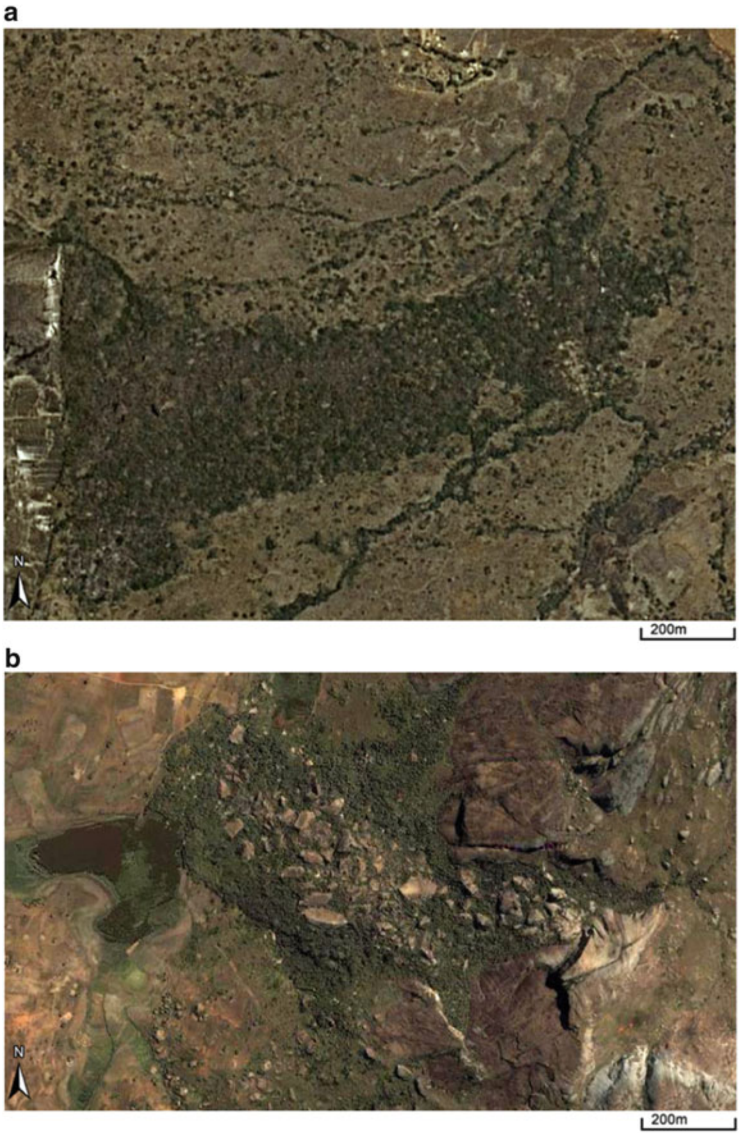

Fig. 16.2 (**a**) Map of the Tsaranoro fragment (Google 2012), showing adjacent tourist establishment to the north. (**b**) Map of the Anja fragment (Google 2012)

of a school, horticultural projects, reserve maintenance and guide wages (http://anjacommunityreserve.netai.net/, Rahaovalahy pers. comm.). Because Anja is located directly off a national highway, it attracts tourists interested in seeing easily accessible wildlife and purchasing crafts. Anja saw a much greater number of tourists, approximately 10 times the Tsaranoro fragment's daily average in 2009, and as

Fig. 16.3 Ring-tailed lemurs rock climbing in Tsaranoro. Photo by Alex Cameron

Fig. 16.4 *L. catta* sunning in the morning at the Anja fragment's northern edge, with rice terraces and fruiting *Melia* trees visible

of 2010, Anja received approximately 12,000 visitors/year (Raharovalahy 2012). The *L. catta* groups ranging in the lower portion of the reserve are highly habituated to human presence, groups further up the mountain, off the tourist circuit, are not.

Data Collection and Sampling Techniques

Due to the time available at each site during 2009, data collection was designed as a rapid assessment process (RAP), with methodological development, data collection, and site interpretation coordinated between three researchers (A. Cameron, L. Gould, D. Gabriel) assessing related variables at the same sites; data collection by each team member was assisted by the guides at each site. Often such studies focus on modelling the expansion of protected forest, i.e., assessing land use by wild species in terms of population density over large areas, for purposes of forming new governmentally recognized parks that optimize the park population's numbers. Our methodology was oriented toward generating predictive information about population status in preexisting (although more circumstantially established) reserves, in addition to obtaining general information on the ecological impact of different habitats and microhabitat features on these fragment populations.

Population counts were averaged after collection, with each researcher tallying the individuals in recognized groups at Tsaranoro and at Anja, via a coordinated walking survey of the fragment from group to group, counting individuals.

Behavioural data were collected by A. Cameron at the group level, noting behaviour (including food type when feeding) for each visible group member at intervals of 5 min. Data were recorded throughout the fragment and surrounding area, including the anthropogenic savannah as well as the gardened grounds of Camp Catta at the Tsaranoro site, which is visited regularly by at least one group of *L. catta*—data from this group are not included in these results as these individuals return nightly to remote sleeping trees to the north of the camp and likely never interact with fragment groups (Gabriel pers. comm.). Five minute group scan sampling (Martin and Bateson 1993) was chosen because it obtains data that are representative across all individuals, and allows for the rapid collection of data. In total, 3,598 observations of individual behaviour were recorded at Anja and 1,640 were recorded at Tsaranoro. Differences between the sites were measured in these data via two-tailed Pearson's chi-square test with significance level set at 0.05.

L. Gould collected phenological specimens of every type of food eaten during behavioural observations, and these were identified, when possible, by the guides at each site. Many were identified by vernacular name, and some by scientific names . Because we were unable to obtain identification for all plants consumed by the *L. catta* at the sites, food items were grouped as fruit, vegetation (leaves, vine, stems—at all stages of maturity) insects, or soil. Simplified plant-part categories allow for quick recording during behavioural sampling, and were used to observe broad trends in food resource use between sites and habitats.

Table 16.1 Demographic data for the Tsaranoro and Anja populations

Site	Number of groups	Population	Individuals/hectare
Tsaranoro	6	~60 individuals	1.1
Anja	15	~225 individuals	6.6

Table 16.2 Population-level time allocation data by percentage of behavioural observations, with significances listed to the right

	Site		
Behaviour	Tsaranoro	Anja	Significance
Feeding	21.94^a	17.14^b	$p=0.0054$
Resting	24.35^b	34.74^a	$p=<0.0001$
Locomotion	13.67	15.19	$p=0.754$
Sunning	3.66^a	0.42^b	$p=<0.0001$
Vigilance	6.45^a	3.45^b	$p=0.0003$
Vocalization	7.12	8.05	$p=0.4609$
Agonism	0.67^b	1.78^a	$p=0.0004$
Scent marking	0.19	0.33	$p=0.7335$
Drinking	0^b	1.04^a	$p=0.0023$
Autogrooming	1.7	2.78	$p=0.1035$
Allogrooming	0.77^b	2.49^a	$p=0.0018$
Resting in contact	18.9^a	11.66^b	$p=<0.0001$
Other	0.57	0.91	$p=0.4389$
Total	99.99	99.98	

[a] Significantly higher proportion than at the other site
[b] Significantly lower proportion than at the other site

Results

Population Demographics

These findings are summarized in Table 16.1.

Behaviour

Activity

The overall similarity and relatively close geographic proximity of the two fragments suggested that the populations would proportion their time similarly. Relative to other sites the two populations are generally similar in behaviour (Table 16.2). Following Rasamimanana et al. (2006), we grouped behaviours as active or inactive, with resting, sunning, and resting in contact as inactive behaviours and the remainder as active behaviours. Tsaranoro *L. catta* were inactive during 46.9 % of

Table 16.3 Proportion of diet (from feeding scan records) by food item class at Tsaranoro and Anja

Food item category	Tsaranoro	Anja	Significance
Fruit	45.61	58.6	$p = 0.0933$
Vegetation	37.72	40.19	$p = 0.7426$
Insect secretions	16.67[a]	0.24[b]	$p = < 0.0001$
Soil	0	0.97	$p = 0.3376$
Total	100	100	

[a]Significantly higher proportion than at the other site
[b]Significantly lower proportion than at the other site

scan records, and active for 53.1 % and Anja *L. catta* were inactive during 46.8 % of scan records, and active for 53.2 %, which suggests overall similarity between the populations in terms of balancing the conservation and expenditure of energy.

Statistical comparison between the sites' activity budget figures indicates that although the fragments are similar in size and habitat type, local-level differences cause divergences in the populations' allocation of time. Table 16.3 illustrates the percentage of feeding observations at each site according to food item class.

Diet

The difference in proportion of diet is significant in the case of the insect category ($\chi 2 = 68.374$, d$f = 1$, $p = < 0.0001$). The fruit and vegetation categories are not markedly different, and neither reached statistical significance ($\chi 2 = 2.816$, d$f = 1$, $p = 0.0933$ and $\chi 2 = 0.108$, d$f = 1$, $p = 0.7426$, respectively).

Discussion

Population Demographics

Population density has been seen as a vector for inferring habitat quality—for instance, the large populations supported by Berenty and Beza Mahafaly Reserves' gallery forests have been cited as indicating both that gallery forests have a high overall carrying capacity for *L. catta* and that this habitat is particularly suited to *L. catta* (Goodman et al. 2006; Gould et al. 1999, 2003; Jolly et al. 2002; Koyama et al. 2002). Table 16.4 compares the fragment populations' demographics to those from other sites.

The low population density of Tsaranoro suggests that rocky outcrop forest may be approximate in carrying capacity to dry and spiny forests, and that *L. catta* in regions increasingly dominated by cleared land and anthropogenic savannah are attracted to the remaining forest where they may become entrenched, with

Table 16.4 Between site comparison of broad population demographics

Site	Habitat	Number of groups	Average population	Individuals/hectare
Tsaranoro	Rocky outcrop forest	~6	~60 individuals	1.1
Anja	Rocky outcrop forest	~15	~225 individuals	6.6
Beza Mahafaly Special Reserve	Gallery and dry forest	9–11 in Parcel 1 of reserve	2006: 225 animals in 980 ha expanded reserve (Sauther and Cuozzo 2008) 2001: 1 04 animals in 80 ha (Parcel 1 of the reserve) (Gould et al. 2003)	0.23/ha for entire Beza Mahafaly are 1.3/ha in Parcel 1
Berenty Reserve	Gallery forest	8	~280	2–2.5
	Tourist front	10		
Berenty Reserve	Scrub forest	5–7	20–27 individuals	1–1.5
	Spiny forest	3–4		
Andringitra	Rocky outcrop Forest	Unknown	~300 individuals	0.23
Cap Sainte Marie	*Opuntia* forest	Possibly 5	~35	0.017

Tsaranoro and Anja: (Cameron 2010) and Gould and Gabriel (under review)
Beza Mahafaly Special Reserve: (Gould et al. 1999, 2003; Sauther and Cuozzo 2008)
Berenty Reserve gallery forest, tourist front, and scrub forest: (Jolly et al. 2002). Berenty spiny forest, (Gould et al. 2011)
Cap Sainte Marie: (Kelley 2011)

populations expanding extensively when resources allow, as they do at Anja. We suggest, however, that the extremely high density of the Anja population is an anomaly, and has grown rapidly (since the designation of the reserve as a protected area) as a function of excellent seed dispersal by the lemurs, particularly of the fruiting trees *M. azedarach* and *P. cattleianum,* the protected status of the reserve, year-round water availability, and access for some groups to village gardens which are planted at the edge of the lower reserve paths.

Gould et al. (1999) suggested that *L. catta* is an r-selected species, a strategy that aids in populations rebounding after decimation by a drought or other disaster . In small forests like our study fragments, this trait may inflate a population rapidly, possibly beyond the fragment's ability to sustain it. In the case of fragments isolated from other forests, such a trend may result in limited emigration, leading to stress due to population density and possibly to inbreeding depression. The availability of water year-round at Anja is unusual in *L. catta*'s geographic range, and this site-specific feature may decrease resource strain for this population, even as the crowding allowed may increase stress. A comparison of stress hormone levels in both populations is forthcoming (Gabriel 2013b), and a study of the population genetics at each site was conducted in 2012 (Clarke in prep).

Activity Budget

The patterning in activity budgets previously reported for *L. catta* across sites indicates that in habitats or microhabitats with low resource availability, *L. catta* have a higher resting-to-feeding-time ratio than conspecifics with greater resource access in the same season, as seen in studies at both Berenty, during the early hot season (Ellwanger 2007), and BMSR, during the cooler austral winter (Sauther et al. 2006). There is also a broad tendency to decrease the proportion of time devoted to affiliative social behaviour when resources are less available (Ellwanger 2007; Ellwanger and Gould 2011; Gemmill 2007; Sauther et al. 2006). As a species with a moderately low basal metabolic rate, *L. catta* spends a substantial portion of the day at rest or inactive (Rasamimanana et al. 2006). Comparison of activity budget, phenological, and dietary data across sites and habitats indicates activity decreases as habitat suitability increases, even as higher resource availability correlates with increased time spent feeding (Ellwanger 2007; Gemmill 2007; Gemmill and Gould 2008; Rasamimanana et al. 2006; Sauther et al. 2006). The two sites, while exhibiting significant intersite differences in the proportion of time allocated to particular behaviours, were very similar to one another relative to other habitats in the cold season (e.g., *Opuntia* forest (Kelley 2011), gallery forest at BMSR (Gemmill 2007)). This may be due to the overall greater continuity of forest type and size between the two fragments relative to the habitats in which previous studies have been conducted, despite local differences between the fragments such as tourist flow, isolation, and in particular the availability of water—although these factors likely contribute to the statistically significant intersite variation observed in some behaviours.

L. catta at Tsaranoro were observed feeding and resting less than *L. catta* at Anja (46.29–51.9 % respectively) in our cold season study, and both populations engaged in social behaviours (allogrooming, resting in contact, agonism) or locomoting in roughly one third of our scan record (33.6 % at Tsaranoro and 32.1 % at Anja). These patterns of time allocation suggests that *L. catta* at both sites were under low pressure to minimize energy expenditure. The Tsaranoro *L. catta* were inactive in 53 % of observations and active in 47 % and the Anja *L. catta* inactive in 46.8 % and active in 53.2 %, both echoing the figures from larger reserve sites considered to be near-optimal for *L. catta* (Rasamimanana et al. 2006).

Given the dense concentration of *L. catta* at Anja, agonism and scent marking were rare, and territoriality may be mitigated by the social flexibility of the species; low agonism and the relaxation of home range defence, including daily multigroup aggregations and fission, seem reasonable mechanisms for alleviating stress from crowding in an environment with ample resources. This flexibility has been observed sporadically in *L. catta*: groups at BMSR with overlapping home ranges meet in both benign and agonistic capacities (Gould and Overdorff 2002; Sauther 2002).

Diet

The results are in line with the similarity observed in activity budgets between sites. The majority of insects consumed were aphids and aphid secretions licked off of fig leaves (*Ficus baroni*), an extremely seasonal resource—during the austral winter. *L. catta* in the spiny forest at Berenty also include a relatively higher proportion of insects in their diet during the cold season (Gould et al. 2011), and *L. catta* in Berenty gallery forest begin to allocate increased feeding time to insects in July, peaking at 15.7 and 14.1 % of feeding time in November and December respectively, when preferred resources are low (Soma 2006). The greater number of regularly fruiting trees at Anja may mitigate the need to shift the diet toward insects at this site, where licking of aphid secretions was rare. Fruit consumption rates are expected to reflect total fruit availability, in which case the Tsaranoro and Anja populations appear to have much greater access to fruit compared with gallery and spiny forest *L. catta* sampled in the same season (Gould et al. 2011; Soma 2006). Concomitantly, naturally occurring vegetation makes up less of the Tsaranoro and Anja diets than those in the gallery and spiny forest at Berenty (Gould et al 2011; Soma 2006). Research conducted in 2010 (Gould and Gabriel under review) revealed that the groups residing in the lower part of Anja reserve regularly consume tomatoes from gardens planted along the lower edges of the reserve. One notable diet difference between the sites is that the Anja lemurs' diet is overwhelmingly made up of the fruit and leaves of *Melia azedarach*, an introduced tree to Madagascar, which is ubiquitous throughout the Anja reserve, even at higher altitudes (Gabriel 2013a). The abundance of fruit produced by this tree year-round is likely an important variable in the unusually high density of *L. catta* in this 34 ha site (Gould and Gabriel under review).

Summary

The variation in social structure, time allocation, and diet observed between sites during this study suggest that these fragment-dwelling populations of *L. catta* echo observations made of cercopithecoid primates that persist in fragments and exhibit high degrees of behavioural and dietary plasticity (Tutin 1999). The flexible home ranges, variable degree of frugivory (and variable diet in general), and willingness to utilize matrix habitat that were observed in the Tsaranoro and Anja populations fall in line with the other major traits of fragment living species (Bicca-Marques 2003; Estrada and Coates-Estrada 1996; Laurance 1991; Lovejoy et al. 1986; Marsh 2003; Onderdonk and Chapman 2000; Silver and Marsh 2003; Tutin and White 1999). The *L. catta* at Tsaranoro and Anja follow patterns of behaviour similar to conspecifics in high quality habitat, suggesting the attractiveness of small fragments of rocky outcrop forest as habitat under conditions of adequate food resources. Our population, diet, and activity budget data emphasize the importance of generating basic knowledge about population health in, and particularly gene flow between, these isolated populations.

The significant variations observed between the two fragments, despite their overall similarity to one another relative to other habitats in southern Madagascar's cool season (austral winter), indicate that site-specific assessments accounting for local differences in fragment management, and site-specific features (e.g., sources of water) are of greater practical use for conservation purposes than generalization on the basis of forest size or habitat type. Our research in these small fragments suggests the utility of a roughly standardized, broadly applicable rapid assessment methodology for fragment-living primate populations

A more detailed examination of diet, activity patterns and parasite loads of the *L. catta* populations at these two sites over an annual cycle is forthcoming (Gabriel 2013a; Gould and Gabriel under review). Future work at these sites should include phenological surveys, which will more clearly indicate resource availability in and the carrying capacities of the fragments by season. Endocrinological research conducted in 2010–2011 (Gabriel and Gould under review) further illuminates the interaction between resource bases, population density, stress, and population health and behaviour. The data collection protocols established in our study may be applicable in local level management efforts at other fragmented sites containing primate populations.

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Chapter 17
The Simplified Novel Diet of the Highly Threatened Blond Capuchin in the Vanishing Pernambuco Endemism Center

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Abstract Observations of a group of blond capuchins, isolated in three small forest fragments of the Pernambuco Endemism Center, located in the Atlantic Forest of North-eastern Brazil, revealed that the two most exploited food sources (ca. 50 %) were both introduced to the area, and were available throughout the study period. Out of 33 food sources observed, six introduced plant species were responsible for the bulk of the capuchins' diet (ca. 60 %). These capuchins exploited a highly restricted diet, the majority of which were introduced resources. They may have only been able to survive in these isolated forest fragments via the exploitation of novel foods, which in the long term may not assure their survival.

Abbreviation

CEPE	Pernambuco Endemism Center

Introduction

Capuchin monkeys, *Cebus* spp., are among the most generalist primate species of the tropics, feeding on a vast array of food types. They consume a variety of plant parts such as leaves, flower and fruit, seeds, pith, woody tissue, sugarcane, bulb, and exudates, among others, and are also highly carnivorous, including in their diet arthropods, molluscs, a variety of vertebrates, and even other primates (Izawa 1979;

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Freese and Oppenheimer 1981; Galetti 1990; Galetti and Pedroni 1994; Siemers 2000). Furthermore, they are characterized as truly innovative and "extreme" foragers because of their ability to acquire sustenance from a vast array of unlikely food sources (Fragaszy et al. 2004), which may assure them survival in habitats with extreme food limitation.

One group of 34 individuals of the critically endangered blond capuchin, *C. flavius* (Oliveira and Langguth 2006), whose taxonomy is still in dispute (cf., *C. queirozi* Mendes Pontes et al. 2006; Reeder et al. 2007; Silveira et al. 2008), was found totally isolated in a matrix of sugarcane plantations in the Pernambuco Endemism Center—herein CEPE (i.e., the sector of the Atlantic Forest located north of the São Francisco river, encompassing the States of Alagoas, Pernambuco, Paraíba, and Rio Grande do Norte). The group inhabits three very small forest patches that are very disturbed by human activities, such as wood gathering, selective cutting, hunting, and accidental fires from seasonal sugarcane harvest. The fragments are connected by a swamp that acts as a vegetation corridor and is an additional source of food.

The environment of the blond capuchin is characteristic of the CEPE (Prance 1982, 1987; Silva and Casteletti 2003; Silva Júnior and Mendes Pontes 2008), where astonishingly only 2 % of the forest remains and fragments are immersed within a matrix of sugarcane plantations, with most fragments measuring not more than 10 ha (Ranta et al. 1998), and where the single largest forest patch measures c.a. 3,000 ha. In this landscape, where all large and most medium-sized mammals are regionally extinct (Mendes Pontes and Soares 2005; Silva Júnior and Mendes Pontes 2008), these small forest fragments are highly simplified and homogenized—the "future flora" (Silva and Tabarelli 2000). The forest fragments have lost more than 50 % of the total tree species, and one-third of those large/very large-fruited, and large-seeded species (Oliveira et al. 2004; Santos et al. 2008), leaving very little food for large vertebrates. However, this is one of the most important biodiversity hot spots of the earth, and considered a priority for biodiversity protection (Myers et al. 2000).

Unfortunately, living in tiny fragments, in such a degenerated environment (Santos et al. 2008), highlights the serious threats that isolation represents for this species (Woodroffe and Ginsberg 1998; Silva Júnior and Mendes Pontes 2008). Thus, we evaluate how capuchins deal with the conditions found in these tiny "native" forest patches and, more specifically, if they were able to get enough food, and since these fragments now represent the totality of the remaining CEPE, to predict the future of other populations potentially living in the area.

Methods

The study area is located on private property, and comprises three small forest fragments immersed in sugarcane plantation and is in the Municipality of Ipojuca, southern coast of the State of Pernambuco, and is contiguous with an important tourist resort of Porto de Galinhas, 57 km from the capital city, Recife (Mendes Pontes et al. 2006). The group consists of 34 habituated individuals: 4 adult males, 5 adult females, 12 subadults (at least 3 males and 3 females), 8 juveniles, and 5 infants. The three forest patches that form their current home range are 39 ha of highly modified and disturbed secondary lowland tropical rainforest: (1) Mingu, 13.4 ha (08º 30′52″S and 35º 03′31″W); (2) Gengibre, 19.8 ha (08º 31'16″S and 35º 03′28″W); and (3) Bulandi, 6 ha (08º 32′06.2″S and 35º 02′51.5″W). The fragments are connected by a 94.2-ha swamp formed by stands of *Montrichardia linifera* (Araceae) of up to 5 m high, which act as corridors between the forest patches. Together the forest patches and swamp encompass an area of approximately 140 ha (Fig. 17.1).

The Queiroz family, who owns the Salgado mill, has protected this group for over 30 years (Mendes Pontes et al. 2006). The current head of the environment protection team at Usina Trapiche mill, Mr. De Assis, however, who has been the person responsible for environment issues at Usina Trapiche for an equal period of time, reported that the former area of the group was the Boca da Mata forest (08° 32′04″S; 35° 05′46″O) at Trapiche mill, located 3.9 km from where they are living now. He argues that the group fled from their former area some 30 years ago, as a result of persecution, and possibly resource scarcity (Mendes Pontes and Malta, unpublished data) (Fig. 17.1). He mentioned that there were many more forest fragments in the region, which may have served as stepping stones for the group until they reached their current area and subsequently became totally isolated.

The regional climate has distinct rainy (April and August) and dry (September and March) seasons. Mean annual rainfall is 185 mm during the dry season, and 324 mm during the rainy season. We carried out systematic observations for 97 days between January and October 2006. Observations started at dawn, when the group left their sleeping tree at approximately 05.00 h, until dusk, when they reentered their sleeping tree at approximately 17.30 h. A total of 896 h of direct observations were made.

Diet was recorded through instantaneous scan sampling of feeding every 10 min and ad libitum records of opportunistic feeding events (Altmann 1974; Lehner 1996). We considered animals to be feeding when handling, holding, licking, or chewing food items of plant origin, or capturing, handling, or ingesting animal matter. One feeding bout per food type was registered when at least one individual, a subgroup, or the group was found exploiting a food type.

Samples of food items consumed were collected and preserved in 70 % alcohol or dehydrated. Each was identified or sent to specialists for identification, and subsequently deposited at the carpological collection and Herbarium of the Federal University of Pernambuco, Brazil, respectively.

Results

Out of 33 food species recorded, 6 introduced plant species contributed 60.4 % of the feeding bouts ($n = 270$). Of the ten most exploited food species, four were introduced species. All of these foods were available in a minimum of 3 and a maximum

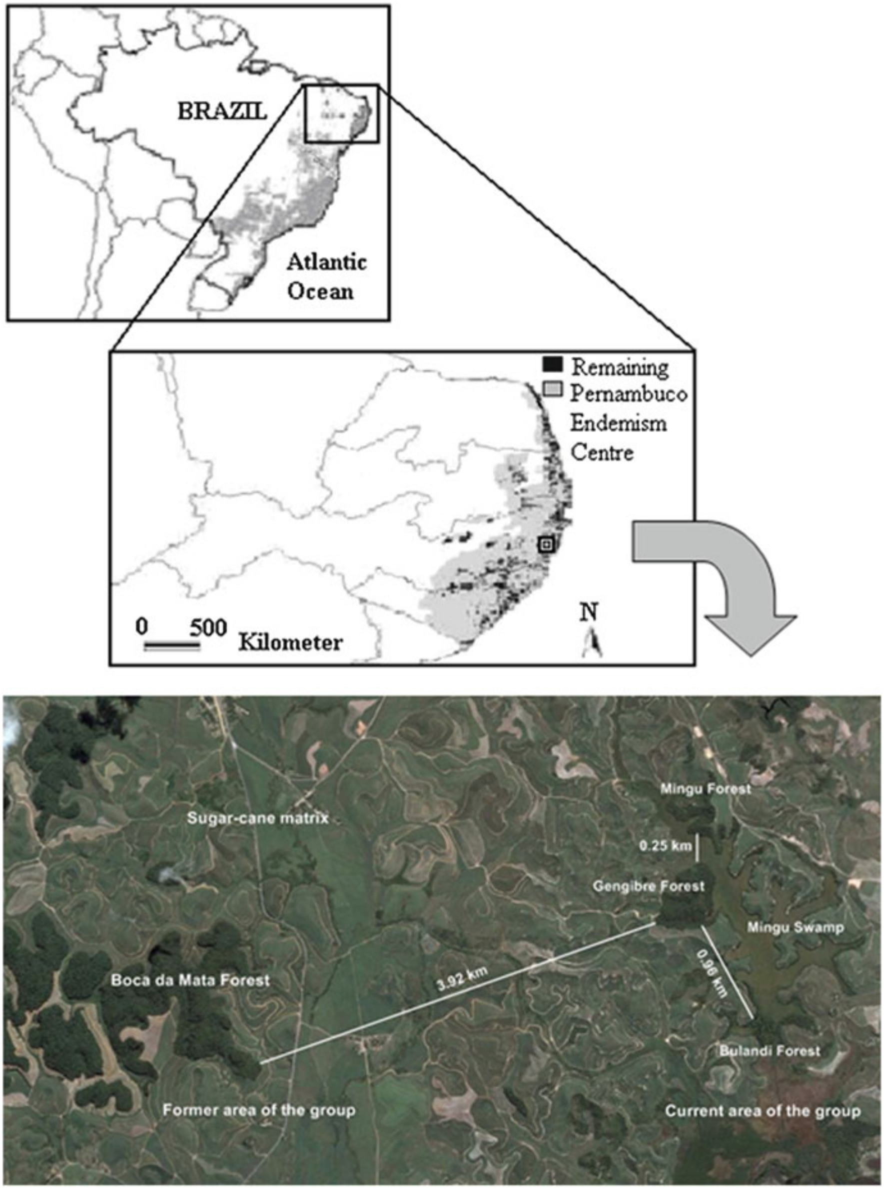

Fig. 17.1 Former and current home range of the studied group of blond capuchin at Usina Trapiche and Usina Salgado mills

of 10 months (when the study was discontinued). All food species were available in the smallest forest fragment, the Bulandi, but only three species were present in all of the three fragments, and of these, two were introduced and were among those most exploited (Table 17.1).

Table 17.1 Food items and their parts monthly exploited by the studied group of *Cebus queirozi*, the blond capuchin, their location and status, at Usina Salgado Mill, Pernambuco Endemism Center

Species	$n=270$	Status	Part eaten (%)	Month	Forest fragment	Habit
Anacardiaceae						
Mangifera indica L.	7	Introduced	Fr (drupe) (2.59)	Jan–Apr	Bul	Tree
Thyrsodium spruceanum Salzm	1	Native	Fr (drupe) (0.4)	Apr	Gen	Tree
Tapirira guianensis Aubl	1	Native	Fr (drupe) (0.4)	May	Min	Tree
Annonaceae						
Annona sp.	6	Native	Fr (syncarp) (2.2)	Jan–Feb, Apr	Bul	Tree
Araceae						
Montrichardia linifera Schott	8	Native	Fr (spadix) (0.4), Br (2.6) 3	Jan, Mar–Jun, Sept–Oct	Bul	Shrub
Anthurium sp.	1	Native	O (0.4)	Sept	Bul	Shrub
Phillodendron sp.	1	Native	O (0.4)	Sept	Bul	Shrub
Costaceae						
Costus spiralis (Jacq.) Roscoe	1	Native	Fl (0.4)	Apr	Min	Shrub
Clusiaceae						
Symphonia globulifera L.f.	25	Native	Fr (berry) (2.4), Fl (6.8) 9.2	Jan–May, Aug–Oct	Bul	Tree
Euphorbiaceae						
Sapium aubletianum Müll. Arg.	1	Native	Fr (capsule) (0.4)	May	Min	Tree
Heliconiaceae						
Heliconia psittacorum L.f.	1	Native	Fl (0.4)	May	Min	Shrub
Lecythidaceae						
Gustavia augusta L.	4	Native	Fr (capsule) (1.4)	Jan–Feb, Sept	Min, Bul	Tree
Eschweilera ovata (Cambess) Miers.	5	Native	Se (1.8)	Feb, Apr–May	Min, Bul	Tree
Marcgraviaceae						
Marcgravia cf. *umbellata* L.	4	Native	Fr (berry) (1.4)	Sept–Oct	Bul	Shrub
Mimosaceae						
Inga dysantha Benth.	3	Native	Fr (pod) (1.1)	Apr	Gen	Tree

(continued)

Table 17.1 (continued)

Species	$n = 270$	Status	Part eaten (%)	Month	Forest fragment	Habit
Inga cf. *edulis* (Vell.) Mart.	1	Native	Fr (pod) (0.4)	May	Min, Bul	Tree
Inga cf. *thibaudiana* DC	4	Native	Fr (pod) (1.4)	Apr–May	Bul	Tree
Inga sp.	15	Native	Fr (pod) (5.5)	Feb, Apr–May	Min, Bul	Tree
Moraceae						
Brosimum cf. *gaudichaudii* Trec.	1	Native	Fr (pseudo-fruit) (0.4)	Jun	Gen	Tree
Artocarpus integrifolia Lam.	6	Introduced	Fr (pseudo-fruit) (2.2)	Jan–Feb, Apr	Bul	Tree
Musaceae						
Musa paradisiaca L.	1	Introduced	Fr (berry) (0.4)	Apr	Bul	Tree shrub
Myristicaceae						
Virola sp.	1	Native	Se (0.4)	Apr	Gen	Tree
Palmae						
Acrocomia intumescens Drude.	1	Native	Fr (drupe) (0.4)	Jan	Bul	Tree
Attalea oleifera Barb. Rodr.	2	Native	Fr (nut) (0.7)	Jan, Apr	Min	Tree
Elaeis guineensis Jacq.	115	Introduced	Fr (drupe) (42.6)	Jan–Oct	Bul, Min, Gen	Tree
Passifloraceae						
Passiflora ovalis Vell.	8	Native	Fr (berry) (2.9)	Apr–May, Aug–Sep	Bul, Min, Gen	Vine
Passiflora alata Dryander	1	Native	Fr (berry) (0.4)	Jul	Gen	Vine
Poaceae						
Zea mays L.	1	Introduced	Se (0.4)	Feb	Bul	Erected-culm grass
Saccharum officinarum L.	33	Introduced	Sc (12.2)	Apr–Sept	Bul, Min, Gen	Erected-culm grass
Rubiaceae						
Genipa americana L.	2	Native	Fr (berry) (0.7)	Oct	Bul	Treelet

Sapindaceae							
Paullinia trigonia Vell.		1	Native	Fl (0.4)	Jul	Min, Gen	Vine
Sp.1		1	Native	O (0.4)	May	Gen	Herb
Sp.2		1	Native	Se (0.4)	Feb	Gen	Shrub
Sp.3		1	Native	Se (0.4)	Aug	Bul	–
Sp.4	1		Native	Fl (0.4)	Oct	Bul	–
Sp.5	1		Native	Se (0.4)	Sept	Bul	–
Sp.6	1		Native	Se (0.4)	May	Gen	–
Vertebrates							
Coereba flaveola	1		Native	N (0.4)	Apr	Min	Passarine
Cacicus cela	1		Native	N (0.4)	Apr	Min	Passarine

Food item: *Br* Leaf bud, *Fl* flower, *Fr* Fruit, *Se* Seed, *Sc* sugarcane (chewed stalk to drink the liquid), *O* Other, unknown, *N* Nest predation, eggs or siblings—not known

Forest fragment: *Bul* Bulandi, *Gen* Gengibre, *Min* Mingu

Fig. 17.2 The group of blond capuchin at Usina Salgado mill during foraging/feeding in a *Elaeis guineensis* palm, where they spent most of their time (photo by Cássia M. Rodrigues)

Only 270 feeding events were observed in 97 days (~3 per day) or 896 h of observation (<0.3 per hour). For the majority of feeding observations, the monkeys were found in the *Elaeis guineensis* (Fig. 17.2). This introduced species was located within the forest fragments in places where the pristine forest had been highly modified by human activity. The other major food, sugarcane, *Saccharum officinarum*, was located within the sugarcane matrix, which either formed a continuum with the forest border, or was separated from the forest fragments by roads. In the latter case, the animals travelled a mean distance of 5.5 m (4.5–6.5 m, $n=7$) on the ground between the forest fragments and the sugarcane plantations. These food types were available throughout the study from January to October (Table 17.1).

Fruit comprised 73 % ($n=198$) of the feeding bouts recorded in the three forest fragments. Excluding sugarcane (12 %, $n=33$) derived from the surrounding non-forested matrix, the summed contribution of other, non-fruit, food sources was only 14 % ($n=39$) (Fig. 17.3). Native species provided more different fruit parts (i.e., skin, seed) ($n=8$) than did introduced species ($n=3$), and the group exploited berries, drupes, and pods (Fig. 17.3; Table 17.1).

There was no statistically significant difference in the number of plant species fruiting between the two seasons ($t=0.137$, df$=8$, $p=0.44$). Two less marked peaks were recorded, one at the end of February, and the other at the beginning of the subsequent dry season in September (Fig. 17.4). These peaks did not significantly

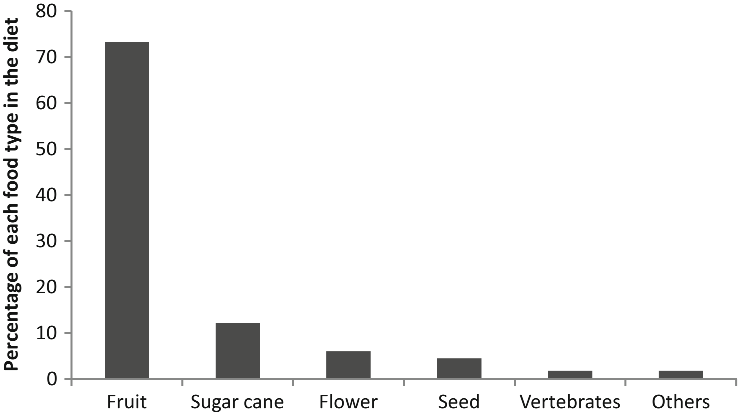

Fig. 17.3 The contribution of each food type to the diet of the blond capuchin at Usina Salgado, Pernambuco Endemism Center, Brazil

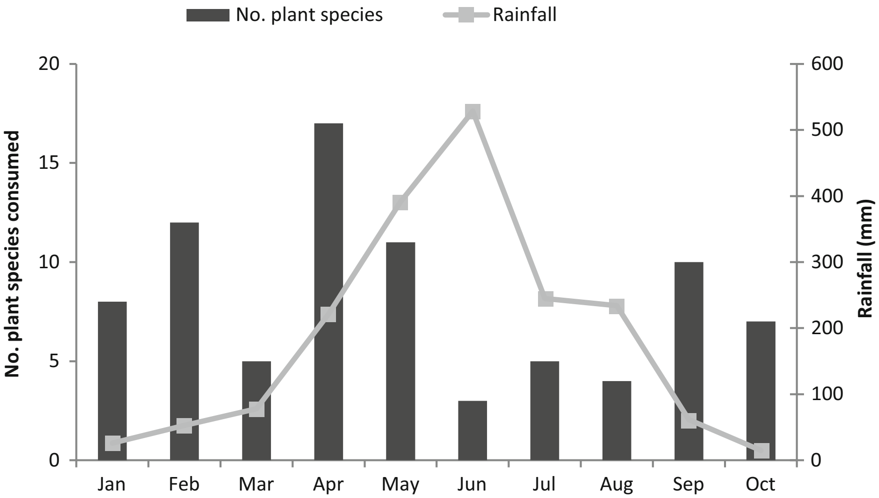

Fig. 17.4 Number of plant species exploited by the blond capuchin at Usina Salgado

differ in terms of number of species exploited (peak of the previous dry season vs. peak of the wet season: $X^2 = 0.862$, df = 1, $p = 0.46$).

The most diverse array of food items was recorded during the rainy season, especially at its end-of-April and beginning-of-June peak, when capuchins exploited all six of the separate items observed during the entire study. They exploited the fewest food items in the last 3 months of the dry season, when only fruit and seed or fruit and sugarcane were recorded in their diet (Fig. 17.5).

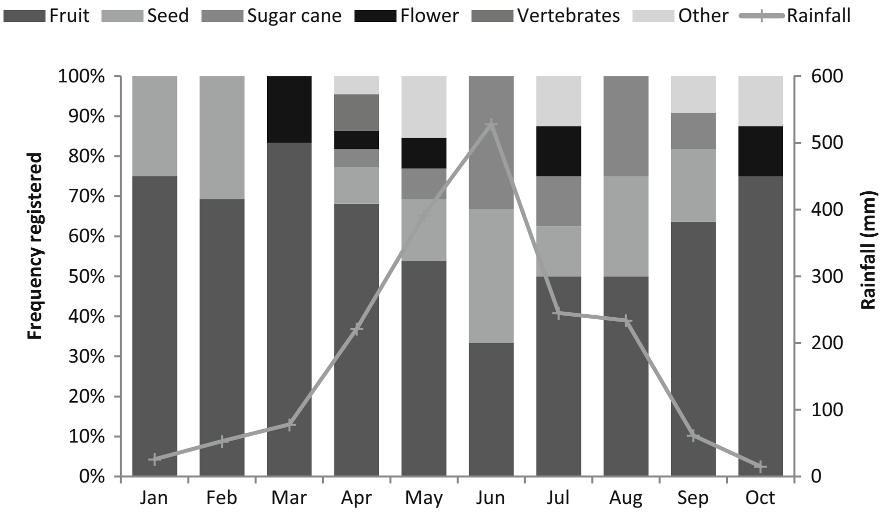

Fig. 17.5 Monthly contribution of each food type to the diet of the blond capuchin at Usina Salgado

Discussion

Human activity has effectively destroyed the CEPE. The tiny forest fragments of this important biodiversity hot spot, such as the ones in this study, comprise nowadays the so-called futura flora, which is highly impoverished and dominated by tree species dispersed by abiotic factors and tree species with very small fruit (Silva and Tabarelli 2000). These biotically simplified and homogenized forest fragments have lost 50 % or more of their tree biodiversity, and hold an additional 34 % of trees currently at the brink of extinction on the regional scale (Silva and Tabarelli 2000; Oliveira et al. 2004; Tabarelli et al. 2004). All large and most medium-sized mammals have been driven to regional extinction, and the remaining mammal communities are present at densities far below those of long-term sustainable populations (Soulé 1980; Silva Júnior and Mendes Pontes 2008). Given this catastrophic scenario, where native food resources are greatly scarce, the blond capuchins survived solely through the exploitation of introduced plant species, which are the African oil palm and sugarcane. Sugarcane was separated from the group's forest fragments and swamp by roads and open areas, making it potentially risky to exploit.

The importance of introduced species in sustaining this population is evidenced by the fact that six introduced species were responsible for ca. 60 % of the diet. Whether the group could be sustained solely from native species cannot be determined in the absence of further data on nutritional content and availability. Although there may be a preference for the nutrient-rich oil palm fruits (Hartley 1988) and for the sweet and easily processed sugarcane, we think that there were too few native species available to sustain the nutritional and energetic requirements of the group, leaving them with no choice, but exploit novel foods.

These capuchins had a restricted diet, with fewer plant parts, plant species, and animal prey taken, compared to other species of *Cebus* (e.g., Freese and Oppenheimer 1981; Robinson 1986; Galetti and Pedroni 1994; Williams and Vaugham 2001; Wehncke et al. 2004). The diet was predominately fruit, in common with observations of other species (Robinson (1986): 84 % of feeding bouts; Galetti and Pedroni (1994): 54 %; Ludwig et al. (2005): 68 %; Hladik and Hladik (1969): 65 %). In these studies, the remainder of the diet was complemented by an extensive array of other foods, including animal matter.

Animal matter in the blond capuchin's diet was also limited, with only two items recorded, compared to up to 16 items elsewhere (Izawa 1979; Freese and Oppenheimer 1981; Galetti 1990; Galetti and Pedroni 1994; Resende et al. 2003; Ludwig et al. 2005). The few comprehensive studies available suggest that the less disturbed the forest, the greater is the intake of animal prey: protected area: 55 % plant versus 33 % animal (Robinson 1986); disturbed: 77.3 % plant versus 22.7 % animal (Ludwig et al. 2005); and disturbed: 82.6 % plant versus 17.4 % animal (Williams and Vaugham 2001).

While these capuchins still had access to quantities of fruit, especially fresh fruit (berries), they also depended heavily on a few energy-rich foods from introduced plant species. The consumption of introduced species (even reliance upon them) has been reported for other capuchin species living in similar environmentally degraded or disturbed conditions (Freese and Oppenheimer 1981; Galetti and Pedroni 1994; Siemers 2000; Williams and Vaugham 2001; Moura and McConkey 2007), and may be the key adaptive response to survive in such highly modified environments.

Conclusions

We documented that (1) the diet of the group of blond capuchin studied was highly restricted to such a degree that additional human impact on their habitat may ultimately not allow long-term survival; (2) introduced plant species were likely to be important for their resilience in these tiny forest fragments; and (3) since this is the prevailing scenario of the entire CEPE, we predict that this and other future groups found in the CEPE will not just be critically endangered, but are living dead (Woodroffe and Ginsberg 1998; Mendes Pontes 2010). Their populations may only be able to survive in the long run if effective restoration measures are immediately put into practice by land owners and decision makers.

Acknowledgements We are grateful to the Queiroz family who has provided logistics and financial support for this study carried out in the premises of their property, and for having allocated one of their employees for this study full time. We also thank their forest engineer Mr. Marcel Franz, for support throughout the study. Dr. Marcondes A. de Oliveira (checked/identified plant species) and Mr. Diogo Araujo (identified the Passifloraceae). We thank the British Ecological Society—BES, UK, for the Small Ecological Project Grant No. 749/871, given to the first author. We are greatly indebted to the Silva family, especially Mr. Nanico and Mr. Sandro, for their care to the group, to us, and for field assistance. Mr. Assis and Mrs. Evânia provided information about the former range of the group and access to Boca da Mata forest at Usina Trapiche mill. Finally, we thank R. Gadelha, for having produced Fig. 17.2.

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Chapter 18
Effects of Habitat Alteration on Resting Behaviour of the Sahamalaza Sportive Lemur in North West Madagascar

Melanie Seiler, Marc Holderied, and Christoph Schwitzer

Abstract This study is the first to assess the impact of habitat degradation and fragmentation on sleeping site choice and activity budgets of the Sahamalaza sportive lemur (*Lepilemur sahamalazensis*), first described in February 2006 and exclusively confirmed for the remaining forest fragments on the Sahamalaza Peninsula. Seventeen individual Lepilemurs in forests of different degradation levels that used two classes of sleeping sites (tree holes vs. tree tangles) were observed for 606 h during the day and 324 h at night. 24-h activity budgets were quantified. Preliminary analyses show differences in the ratio of active to inactive behaviour: (a) between different types of sleeping sites, and (b) between differently degraded forest fragments. Individuals resting in tree tangles were active during 7.4 % of daylight hours, while those resting in tree holes were active for 25.4 % of the time. During the day, Lepilemurs never left their chosen resting site. Individuals in a young secondary forest fragment were active for 14.3 min/h during daylight hours, in mixed and mature secondary forest fragments 12.6 and 9.1 min/h, respectively, and in a degraded primary forest fragment 2.7 min/h. However, the latter group had a higher percentage of time out of sight. These differences are most likely predator avoidance strategies and highlight the importance of intact mature forests for this species. Further research into the diurnal habits of this nocturnal primate, investigating their anti-predator responses, and detailed habitat requirements is ongoing.

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Introduction

The deforestation rate of Madagascar continues to be enormous with a reduction of 33 % of primary forest types since the 1970s (Moat and Smith 2007) endangering all forest-dwelling organisms. The current rate of forest loss is roughly 1,500 km^2/year, which means that if this rate continues, all primary vegetation of Madagascar will be gone by 2067 (Moat and Smith 2007). The lemur superfamily Lemuroidea counts approximately 100 endemic species that are exclusively found in the forests of Madagascar. Members of the genus *Lepilemur* (family Lepilemuridae; Gray 1870), known as sportive lemurs, are small folivores (446–1,000 g) that have received notably little scientific attention (Groves 2001; Harcourt and Thornback 1990; Mittermeier et al. 2006; Tattersall 1982). Based on differences in mtDNA sequences, the number of *Lepilemur* species recently increased from a previous total of 7 species (Harcourt and Thornback 1990; Tattersall 1982) to 26 species (Andriaholinirina et al. 2006; Craul et al. 2007; Lei et al. 2008; Louis et al. 2006; Rabarivola et al. 2006; Ramaromilanto et al. 2009). Many of these *Lepilemur* species are only confirmed for single locations (Andriaholinirina et al. 2006; Craul et al. 2007; Louis et al. 2006; Rabarivola et al. 2006), and with the limited reproductive rates typical for similar-sized primates (female maximum reproductive output is one offspring/year; Randrianambinina et al. 2007) they are particularly vulnerable to human-caused disturbances.

The Sahamalaza sportive lemur (*Lepilemur sahamalazensis;* Fig. 18.1) is one of the numerous lemurs recently described (Andriaholinirina et al. 2006). Since it received species status, the Sahamalaza sportive lemur has been included on the World's Top 25 Most Endangered Primates 2006–2008 (Mittermeier et al. 2007).

Fig. 18.1 Sahamalaza sportive lemur (*L. sahamalazensis*) resting in a tree hole of the species *Bridelia pervilleana* during the day

L. sahamalazensis is the first *Lepilemur*, and the first nocturnal lemur, to be included on this list. It is currently red-listed as Data Deficient by the IUCN, but likely to be reassessed as Critically Endangered (Olivieri et al. 2008).

Taking into account their limited distribution, the small extent of remaining forest cover within their distribution range, as well as an average of 2.8 individuals found per hectare by Ruperti (2007), there are probably around 3,000 individual *L. sahamalazensis* remaining in their natural habitat. Although the range of this cat-sized, nocturnal primate is not precisely known, it is probably limited to the Sahamalaza Peninsula in northwestern Madagascar (Olivieri et al. 2007). This area has experienced rapid deforestation and habitat destruction over recent history.

Strictly arboreal species such as *Lepilemur*, who are unable to cross the non-forest matrix within their distribution range, will eventually become extinct when their habitat patches get too small and disconnected to support a viable gene pool/flow (Fahrig 2003; Frankham et al. 2002). The smallest forest fragment with confirmed *Lepilemur* persistence has been found to be 6 ha for *L. ruficaudatus* in western dry deciduous forest (Ganzhorn et al. 2000; Gibbons and Harcourt 2009). As an effect of a combination of all these and other factors, several *Lepilemur* species are now confirmed or thought to be at risk of imminent extinction (Bachmann et al. 2000; Mittermeier et al. 2007; Ravaoarimanana et al. 2001).

Besides deforestation and habitat fragmentation, general forest degradation (e.g. through selective logging, disturbance of sapling growth by zebu cattle, bush pigs, goats, other livestock) is an aggravating factor putting lemur populations under further stress. Habitat degradation might also mean easier access for predators and hence increased predation pressure (Andren and Angelstam 1988; Estrada and Coates-Estrada 1996; Wilcove 1985; Wilcove et al. 1986; but see Onderdonk and Chapman 2000). Better visibility and accessibility resulting from logging and fragmentation has been discussed as one reason for increases in some raptor populations, leading to the conclusion that fragmentation may be more disruptive to lemur populations than to predatory raptors (Colquhoun 2006; Karpanty 2003). Very little is currently known regarding how nocturnal primates respond to predation threats, especially when they are vulnerable to predators that have different daily activity patterns to them (Fichtel 2007). During the day, hawks and eagles may hunt sleeping nocturnal lemurs, like *Lepilemur*, as well as active diurnal lemurs, and fossas and boas hunt during day and night (Karpanty 2006; Wright 1998). In forests exposed to human activity, hunters are an additional predation threat for many lemur species. For sportive lemurs, the threat from humans is thought to greatly outweigh that from natural predators, such as the Madagascar harrier hawk (*Polyboroides radiatus*), the Fossa (*Cryptoprocta ferox*) and constricting snakes such as *Acrantophis madagascariensis, Acrantophis dumereli*, and *Sanzinia madagascariensis* (Colquhoun 2006).

The ability to develop foraging and resting strategies for risk avoidance is theorized to be an important factor in primate sociality (Janson and Goldsmith 1995; Janson and van Schaik 1993; Stanford 1995). Thus, the selection of an appropriate sleeping site may be essential for survival in primates (Rasoloharijaona et al. 2006). Sleeping sites should not only provide shelter from aerial and terrestrial predators but also protect from difficult climatic conditions like rain, wind, or temperature fluctuations in order to limit energy expenses for maintaining basal body metabolism (e.g. Anderson 1998). This might be particularly important for sportive lemurs, as they are known to exhibit the lowest known metabolic rates among mammals (Schmid and Ganzhorn 1996), and may profit particularly from sleeping site selection guided by metabolic constraints. Since the number of suitable sleeping sites is potentially limited, they are also considered as one factor shaping sociality in these primates (Rasoloharijaona et al. 2008).

Preliminary data from a study conducted by Ruperti in 2007 at Sahamalaza National Park suggested that factors associated with primary forest areas were vital for the continued existence of the Sahamalaza sportive lemur. In particular, a high density of large trees, extensive canopy cover, as well as the availability of vegetation tangles, tree holes, and food plants were correlated with higher densities of *L. sahamalazensis* (F. Ruperti, pers. comm.). Sahamalaza sportive lemurs were observed to react differently to aerial predators (*Polyboroides radiatus* and *Buteo brachypterus*) than to humans and other ground-dwelling animals (F. Ruperti, pers. comm.). The author of that same study commented that *L. sahamalazensis* was also easy and defenceless prey to humans because of its choice of exposed sleeping sites and therefore heavily hunted by natives. The combination of a very limited range, rapidly decreasing suitable habitats, and high hunting pressure thus renders this species particularly vulnerable to extinction (Olivieri et al. 2007).

Based on the preliminary data collected by Ruperti (2007), we hypothesised that the level of diurnal activity shown by Sahamalaza sportive lemurs differed in differently degraded forest fragments. Our prediction was that the animals were more active in more degraded fragments, as the latter would have less dense canopies and would thus demand a higher level of vigilance concerning aerial predators. Additionally, we hypothesised that the level of diurnal activity differed between different types of sleeping sites, and predicted that individuals were more active when they occupied tree holes than when resting in vegetation tangles.

Methods

Study Site

The Ankarafa Forest is situated within the UNESCO Biosphere Reserve and National Park on the Sahamalaza Peninsula, and is part of the Province Autonome de Mahajanga, NW Madagascar. It extends between 13°52′S and 14°27′S and 45°38′E and 47°46′E (WCS/DEC 2002; Fig. 18.2). The climate is strongly seasonal, with a cool, dry season from May to October and a hot, rainy season from November to April. The Ankarafa Forest lies within a transition zone between the Sambirano region in the North and the western dry deciduous forest region in the South, harbouring semi-humid forests with tree heights of up to 30 m (Schwitzer et al. 2006). The forests in this area include a mixture of plant species typical of the western dry deciduous forest as well as some typical of the Sambirano domain (Birkinshaw 2004) and comprise primary and secondary forest fragments.

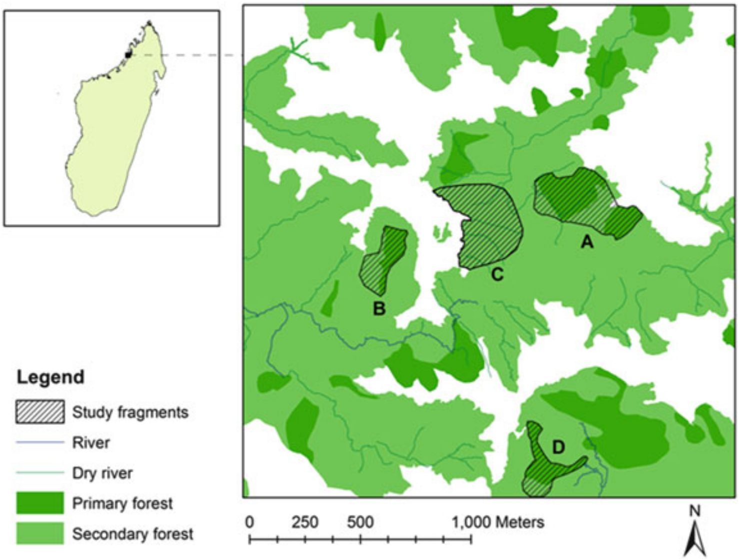

Fig. 18.2 Study fragments in the Ankarafa Forest, Sahamalaza Peninsula, northwest Madagascar: *A* = mature secondary forest, *B* = degraded primary forest, *C* = secondary forest, *D* = vegetation mosaic

There are no large connected areas of intact primary forest left on the Sahamalaza Peninsula, and the remaining fragments all show some degree of anthropogenic disturbance and/or edge effects (Schwitzer et al. 2007a, b). The forests and forest fragments are separated through grassland with shrubs. The Sahamalaza sportive lemur has so far been confirmed exclusively for this area. Other lemur species in Sahamalaza include the blue-eyed black lemur (*Eulemur flavifrons*), the aye–aye (*Daubentonia madagascariensis*), the western bamboo lemur (*Hapalemur occidentalis*), the giant mouse lemur (*Mirza zaza*), and an as yet unidentified species of dwarf lemur (*Cheirogaleus* sp.). The lemur species living in Sahamalaza are threatened by hunting and forest destruction (Schwitzer et al. 2006). The Ankarafa Forest is home to the Ankarafa Research Station, where previous research efforts in the region have taken place and which was also the research base for this study.

Selection of Forest Fragments

Within a 2 km radius from the field station there are several secondary forest fragments of various degrees of degradation, interspersed with small remainders of primary vegetation and separated by grass savannah and mosaics of low- to medium-height shrubs. Ruperti (2007) showed differences in forest characteristics of 1 ha plots between fragments as well as within different sections of larger fragments. She referred these differences to past and ongoing anthropogenic disturbance. For our study we selected three forest fragments based on Ruperti (2007) work and one additional fragment where *L. sahamalazensis* was also present (M. Craul, pers. comm.). After visual inspection on arrival at the field site in mid-2009 we ranked the four fragments along a degradation gradient A–D (with A being least and D being most degraded) based mainly on perceived tree density (see Gerwing 2002), which concurred with the results of Ruperti (2007) habitat description, where A = mature secondary forest, B = degraded primary forest, C = secondary forest, and D = vegetation mosaic (Fig. 18.1). The two fragments A and C as well as parts of the vegetation mosaic D were in the process of regeneration after significant human disturbance of the original forest vegetation over an extended period in the past. We considered them to be at least 35 years old, based on aerial and satellite images and GIS data (Harper et al. 2007), and to exhibit the key characteristics of post-abandonment secondary forest according to the definition by Chokkalingam and de Jong (2001). In order to confirm our visual assessment and to verify that there had not been any major changes to the forest structure since Ruperti (2007) study, a quantitative structural description and quantification of differences in forest characteristics between the fragments was one aim of this study.

Forest Characterisation

The four forest fragments were described using the Point-Centered-Quarter method (Ganzhorn 2003). For this, 252 points (63 points per fragment), distributed along line transects through the forest fragments with a distance of 25 m between them, were selected. Distance to the nearest small tree (5–10 cm DBH) and the nearest large tree (>10 cm DBH) was measured; trees were described in terms of species, DBH, height, and crown diameter. We calculated the density of trees per hectare as $10{,}000/d^2$, where d is the mean distance between the centre point and the nearest tree. Trees were identified to at least genus level by our local field assistants, referring to Schatz (2001) and to tree species identifications carried out by the Département de Flore at Parc Botanique et Zoologique de Tsimbazaza in Antananarivo as part of an earlier study in the same forest fragments by Schwitzer et al. (2007b). We identified 94.6 % of large and 93.7 % of small trees. During comprehensive but nonsystematic searches in the four forest fragments, each *Lepilemur* sleeping hole ($N = 25$) was marked and recorded using a handheld GPS device.

Behavioural Monitoring

During preliminary observations of four *L. sahamalazensis* during 2 days and 2 nights each in early July 2009, a basic ethogram of both diurnal and nocturnal behaviours was obtained using continuous focal animal sampling (Altmann 1974; Martin and Bateson 1993). Whenever new behaviours were encountered during subsequent data collection, they were added to the ethogram. From July to October 2009, 606 h of diurnal behavioural observations (06:00–18:00 h) and 324 h of nocturnal observations (18:00–06:00 h) were conducted on 18 sportive lemurs, 17 of which (3 males, 7 females, 7 individuals of unknown sex) were observed during the day and 4 (2 males, 2 females) during the night. The latter four individuals were fitted with radio tags (TW3 SM, Biotrack, Dorset, UK) and were followed using a portable TR-4 receiver (Telonics Inc., Arizona, USA) and a three-element yagi antenna (Biotrack, Dorset, UK). Diurnal and nocturnal behaviours and additional information related to spatial and ecological factors (e.g., location within the home range, climatic conditions) were recorded continuously during 6- or 12-h observation sessions using focal animal sampling. The exact time (hour, minute, second) of each activity was noted. Each individual was observed for a minimum of 3 days and 3 nights to quantify home range size, habitat use, food preferences, activity budget, social behaviour, anti-predator behaviour, vocal spectrum, and context of vocalisations. We compared the behaviour of individuals in differently degraded forest fragments and between different sleeping sites to assess the effects of habitat destruction and the influence of different day roosts. Here, we only refer to diurnal behaviour and resting site usage of the species.

Statistics

To test for differences in structural habitat characteristics and in diurnal activity levels between fragments of different degradation levels we used non-parametric Kruskal–Wallis ANOVA. When differences between fragments were statistically significant, we applied multiple Mann–Whitney *U* tests with Holm's Sequential Bonferroni corrections as post hoc tests. Units of statistical analysis were centre points in case of the habitat description ($n=63$ points/forest fragment) and individual sportive lemurs observed in case of the comparison of diurnal activity levels ($n=3$, 4, 4, and 7 for fragments A, B, C, and D, respectively). To compare diurnal activity levels between two different types of sleeping site we used non-parametric Mann–Whitney *U* tests. The significance level α was chosen as 5 % ($p \leq 0.05$). All statistical tests were carried out using SPSS 16.0 (SPSS Inc., Chicago, USA).

Results

Habitat Description

The four described forest fragments differed significantly in density of large and small trees, height of large trees, and crown diameter of small trees (Mann–Whitney *U* tests with Holm's Sequential Bonferroni corrections after Kruskal–Wallis ANOVA; $p \leq 0.05$; Table 1). Whereas the secondary forest fragment (C) had the highest tree density and largest crown diameter, the degraded primary forest fragment (B) contained the overall largest and tallest trees and had the highest species diversity (Table 1).

Diurnal Activity Budget in Differently Degraded Forest Fragments

During diurnal observations, 4.5–23.9 % of behaviours were considered active (i.e. autogrooming, resting vigilant, monitoring other species, biting/licking tree, and changing position), although the animals never left their sleeping sites. We found a trend towards higher levels of activity in secondary forest and vegetation mosaic than in mature secondary or degraded primary forest with the respective Kruskal–Wallis ANOVA approaching significance ($p = 0.082$; Table 2).

Diurnal Activity Budget at Different Types of Sleeping Sites

We found a significant difference in diurnal activity between two different types of sleeping site, with a higher level of activity in tree holes as compared to vegetation tangles ($p = 0.0008$, Mann–Whitney U test, two-tailed; Table 3).

Discussion

Our results showed significant differences in forest structure between the four study fragments, which were not consistent for all measured variables. Contrary to our expectations and our initial ranking, the secondary forest fragment (C) had the highest tree density and largest crown diameter, whilst the degraded primary forest fragment (B) contained the overall largest and tallest trees and had the highest plant species diversity. Thus, based on our results we would have to rank the secondary forest fragment (C) as the least degraded, followed by the degraded primary forest fragment (B), the vegetation mosaic (D), and finally the mature secondary forest fragment (A) as the most degraded. This sequence does not concur with the results of Ruperti (2007), who described the mature secondary forest fragment (A) as the least degraded one, whilst, as in our study, the degraded primary forest came out second. The differences between our results and those of Ruperti (2007) may be due to different methods of data collection. Whereas Ruperti and coworkers measured habitat structure variables inside 1-ha plots (one for each fragment), we worked along line transects that covered a considerably larger area and possibly greater detail of the respective forest fragments. After several centuries of anthropogenic and subsequent natural degradation, the forests of the Sahamalaza Peninsula seem to be heterogeneous on an increasingly small scale, which makes it difficult to assign entire fragments to existing categories such as primary or secondary forest. In order to measure habitat quality for a forest-dwelling species in a biologically meaningful way in forests such as those in our study area, it may make more sense to concentrate on areas known to be within the home ranges of the species in question, which in case of *Lepilemur* are usually below 1 ha of size (Albignac 1981; Hladik and Charles-Dominique 1974; Russell 1978; Warren and Crompton 1997; Zinner et al. 2003). Another factor that may have contributed to the differences between Ruperti et al. (2007) and our habitat description is ongoing habitat alteration, which has increased in magnitude since the political crisis in Madagascar in early 2009. Forest and bush fires have been occurring on the Sahamalaza Peninsula on an almost daily basis during recent years, and illegal logging of hardwoods is also a common occurrence. Due to the methodological differences between the two studies it is impossible to assess how much of a role these activities have played, however.

Based on the preliminary data collected by Ruperti (2007), we hypothesised that the level of diurnal activity shown by Sahamalaza sportive lemurs differed in differently degraded forest fragments. Our prediction was that the animals were more active during the day in more degraded fragments, as the latter would have less dense canopies and would thus demand a higher level of vigilance concerning aerial predators. We found a trend towards higher levels of activity in secondary forest and vegetation mosaic than in mature secondary or degraded primary forest. However, the results from our habitat description, which showed the mature secondary forest fragment to be the most degraded, disproved our prediction. Aligning structural habitat differences with differences in diurnal activity levels between the four study fragments, there was a trend for *L. sahamalazensis* to be less active in habitat with larger and taller trees and higher plant species diversity.

Additionally, we hypothesised that levels of diurnal activity differed between different types of sleeping sites, and predicted that individuals were more active when they occupied tree holes than when resting in vegetation tangles. We found a statistically highly significant difference in diurnal activity levels between lemurs resting in tree holes and such resting in tree tangles, with activity more than three times higher in individuals resting in tree holes. As almost the entire diurnal activity of *L. sahamalazensis* consisted of vigilantly scanning their surroundings, our results indicated a higher level of vigilance in those animals having chosen tree holes as resting sites. The observed Lepilemurs seemed to be more sensitive to birds of prey and moving leaves than animals or noise on the ground, suggesting that especially the individuals resting in tree holes, possibly due to the less dense cover of foliage in the immediate vicinity (tree holes were often found in dead trees of *Bridelia pervilleana*), are more vulnerable to aerial predators (M. Seiler, personal observation). The threat to *Lepilemur* from predation is however not restricted to birds of prey. Faecal analyses of fossa (*Cryptoprocta ferox*), Madagascar's largest mammalian terrestrial predator, revealed that *Lepilemur* are this species' most common mammalian prey item in the dry forests of Western Madagascar (Dollar et al. 2007). Ruperti (2007) speculated that the multitude of escape routes available from vegetation tangles rather than tree holes explained why many *L. sahamalazensis* were found in tangles during her study, even when tree holes previously used by *Lepilemur* were available nearby—similar to woolly lemurs (*Avahi* spp.), nocturnal lemurs similar in body size to *Lepilemur*, that prefer to sleep in tangled vegetation. Overall, the results of our study indicate that resting site type seems to be a more relevant constraint on diurnal activity levels of *L. sahamalazensis* than the degree of habitat degradation. The availability of suitable shelters for daytime use is also suggested to be associated with the distribution of the Milne-Edwards' sportive lemur *L. edwardsi* (Rasoloharijaona et al. 2003). There seem to be regional differences regarding the use of tree holes or vegetation tangles as resting sites by *Lepilemur* (Ruperti 2007). Both sexes of *L. edwardsi* use dense vegetation and holes in hollow trees high above the ground as shelters for sleeping during the day (Rasoloharijaona et al. 2008) with the majority of sleeping sites (92 %) being tree holes (Rasoloharijaona et al. 2003). The apparent preference of *L. edwardsi* for tree holes led Rasoloharijaona et al. (2008) to conclude that survival of this species will strongly depend on the availability of mature rain forests with suitable hollow trees. On the other hand, Charles-Dominque and Hladik (1971) found *L. leucopus* to sleep in tree holes only rarely. During strategic diurnal searches in Ankarafa by Ruperti (2007), only 7 % of *L. sahamalazensis* were found in tree holes and the great majority rested in vegetation tangles; the number of tree holes available inside the 1-ha study plots, which differed between differently degraded forest types, did not seem to have an influence on the percentage of individuals resting in this type of sleeping site in Ruperti's study. We did not count the number of available tree holes in any of the fragments in this study, since a comparative count of the number of available tree tangles was impossible due to insufficient knowledge on the species' criteria for the choice of tree tangles as resting sites.

The differences in *Lepilemur* diurnal activity levels between different types of resting sites and between differently degraded forest fragments are most likely predator avoidance strategies and highlight the importance of intact mature forests for this species. Further research into the diurnal habits of this nocturnal primate, investigating their anti-predator responses and detailed habitat requirements, is ongoing.

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Section V

Endemic, Endangered, and Nocturnal Primates Summary

Laura K. Marsh

Primates that are endemic, endangered, and/or nocturnal may be found in other chapters depending on the focus of study. However, we found it important to call out some of those animals that also have special status into a section of their own. Rarity in primates is largely due to habitat alteration and hunting, thus primates with a conservation status of Threatened or above will most likely be in a fragmented habitat. Currently, there are 633 recognized species of primates, and of those 54 % of them are Threatened, Endangered, or Critically Endangered (IUCN/SSC 2012). Almost every country housing primates has at least one endemic taxon. Except for Madagascar, where nocturnal primate species account for a large proportion of the species (45 %), nocturnal species richness in other regions account for significantly fewer of the total primate fauna: Americas—less than 10 %, Asia 15 %, and Africa 20 % (Harcourt and Doherty 2005). However, because they are nocturnal and can be easily overlooked, they are afforded particular interest.

De Vleeschouwer and Raboy (Chap. 19) have a unique situation with their study subjects; the endangered golden-headed lion tamarins (*Leontopithecus chrysomelas*) of southern Bahia, Brazil. Even though the animals need proper protection, they live in a variety of habitats including fragments, thus creating an opportunity for comparative methodological approaches. Fortunately for these lion tamarins, the scientists involved are interested in comparative work, studying behavior, ecology, demographics, habitat, genetics, and health. While it does not relieve the pressures facing these monkeys, a full understanding of their population dynamics makes a much stronger case for their survival into the future.

By comparison, in Manaus, Brazil, the endangered *Saguinus bicolor* resides in heavily fragmented forest patches within the largest city on the Amazonian frontier (Gordo et al. Chap. 23). This urban primate faces dying in traffic, attacks from domestic animals, electric shocks from power lines, and capture as pets by local residents. Where the lion tamarins of Chap. 19 are afforded some protection and numerous studies, the pied tamarins suffer in locations that have overwhelming social and economic pressures, making it almost impossible to implement meaningful regulatory measures. The authors describe the plight of this endangered primate and suggest possible ways to improve its status.

Another Brazilian, the Critically Endangered *Sapajus xanthosternos* in the northern Atlantic Forest was studied with regard to its ability to disperse seeds (Canale et al. Chap. 20). As is common throughout Mata Atlantica, the larger zoochoric fruit dispersing species have all but vanished, such that in southern Bahia, the primary dispersers are the capuchins. While they have habitat flexibility living in primary, old and young secondary forest, swamp, and *cabruca* (shaded cocoa plantations), they also feed on cultivars such as oil palm (*Elaeis guineensis*), jackfruit (*Artocarpus heterophyllus*), and cocoa (*Theobroma cacao*). The authors recommend that while the capuchins also disperse the seeds of the cultivars, that there be management for native food species. It brings up an interesting debate, one which needs to be continued: should critically endangered species be allowed to eat invasive or cultivated species if it means their survival—or do we work harder to manage the long-term viability of the habitat in terms of its original native flora despite the conservation status of the animals within it?

Countrywide surveys often include endangered and threatened species, such as the work conducted by Chalise in Chap. 22. Nepal has six primate species: *Macaca mulatta*, *Macaca assamensis* (Near Threatened), *Semnopithecus ajax* (Endangered), *Semnopithecus hector* (Near Threatened), and *Semnopithecus schistaceus*. Nepal is a small country with a high human population, resulting in increased contact and conflict with the local primate populations. The challenge is how best to protect important species who fall outside of the protected areas, and that are constantly interacting with humans.

Boonratana and Le (Chap. 21) studied the Critically Endangered Tonkin snub-nosed monkey (*Rhinopithecus avunculus*) in Vietnam. Historically in Vietnam there has been a push for land use that has resulted in fragmentation, to the point the snub-nosed monkeys were thought extinct. In the 1990s populations were rediscovered, and while the habitat remains critical, hunting pressures are the most recent assault on remaining populations. The authors suggest that while these populations remain in small, isolated forests that the monkeys may be able to persist for decades if effectively protected.

And finally, the nocturnal work on the endemic Sri Lankan *Loris tardigradus tardigradus* by Nekaris and Stengel (Chap. 24) demonstrates what type of habitat is most suitable for this species. The authors discuss the results of the modeling, which revealed that of the remaining suitable habitat—only 16 %—had any protection status making the fate of this night primate potentially critical.

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Chapter 19
Multilevel and Transdisciplinary Approaches to Understanding Endangered Primates in Complex Landscapes: Golden-Headed Lion Tamarins in Southern Bahia, Brazil

Kristel M. De Vleeschouwer and Becky E. Raboy

Abstract The effect of forest fragmentation on arboreal species can be measured and quantified at various scales using a variety of technical approaches. Multidisciplinary studies or networks of studies that integrate information across scales and fields of expertise provide the most comprehensive understanding of fragmentation. We illustrate the use of a multifaceted approach to assess the threats, and conservation status, of golden-headed lion tamarins (*Leontopithecus chrysomelas*, GHLTs), an endangered primate residing in a highly complex landscape of Southern Bahia, Brazil. Most remaining habitat is in the hands of private landowners. In the west, the cattle industry has contributed to the severe fragmentation of forests and led to small and extremely isolated fragments. Local GHLT extinctions are occurring quickly. In the east, declining market prices of cocoa and the rapid spread of a fungal disease have devastated cocoa production, and once rather contiguous expanses of shade-cocoa forests are rapidly being converted to unsuitable habitat. GHLTs have been studied at the population level, with increasingly more information being generated on their behavior, ecology, demographics, habitat, genetics, and health. GHLTs (and their landscapes) have also been studied at broader levels, yielding vital information regarding habitat change and fragmentation trends over time, predictors of the presence and absence, and viability and threat analysis via simulation modeling. Collectively, this information is giving rise to a more integrated sense of the mechanisms by which anthropogenic pressures are affecting GHLTs. Additional factors regarding the rich history of GHLT conservation efforts are discussed in this chapter. In an environment as

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spatially and temporally dynamic as Southern Bahia, a conservation management approach involving evaluation, adaptation, synthesis, and prioritization is critical towards developing efficient conservation action plans sensitive to the continuously changing socioeconomic context.

Introduction

Human-induced habitat degradation and fragmentation can influence the behavior, health, and ecology of animals, and lead to changes in the genetic structure, demography, and dynamics of animal populations—often in detrimental ways (Marsh 2003; Clarke and Young 2000). Documenting the changes that occur as a result of habitat degradation and fragmentation is essential for understanding a species' status and enabling conservation actions to ensure a species' long-term survival (Chapman and Peres 2001). Collective information on the landscape, habitat, genetics, health, population demographics, ecology, community interactions, behavior, and general biology of animals and their populations serve to better characterize the effects of habitat fragmentation and degradation than any one factor alone. Multidisciplinary studies integrating information across scales and implementing diverse techniques may provide the best understanding of fragmentation (Soulé 1985; Lindenmayer and Peakall 2000). Factors impacting species survival interact across scales and disciplines are cumulative in their influence on population dynamics (Gilpin and Soulé 1986). Studies that are spatially and temporally explicit, comparative in nature, and incorporate species perspective further aide in a holistic approach to understanding the factors affecting a threatened species. In this chapter we illustrate the use of such a comprehensive approach to assessing the conservation status of the golden-headed lion tamarin (GHLT, *Leontopithecus chrysomelas*), an endangered primate residing in the highly complex landscape of Southern Bahia, Brazil (Fig. 19.1).

GHLTs are small-bodied arboreal primates threatened by extreme habitat fragmentation and loss of the Atlantic Forest in Southern Bahia (Pinto and Rylands 1997; IUCN 2011). They are frugi-faunivores, live in small groups (5–7 individuals on average), and maintain home ranges that can be quite large (20–200 ha) (Rylands 1993; Raboy and Dietz 2004; Kierulff et al. 2002b; Oliveira et al. 2010). Generally one female per group breeds once or twice a year, usually producing twins, and infants are reared cooperatively by the group (French et al. 2002; Tardif et al. 2002; Raboy 2002). Populations range mostly in areas of secondary forest in various stages of degradation and some remaining tracts of mature forests (Pinto and Rylands 1997; Zeigler et al. 2010). In addition to mature and secondary forest, they use shade-cocoa plantations (Oliveira 2010). Pasture is generally unusable to GHLTs and anything more than a small field likely serves as a barrier for movement. The GHLTs' preference for epiphytic bromeliads for prey foraging and tree holes for sleeping likely limit their use of types of degraded habitats that lack such resources (Rylands 1996).

The geographic range of GHLTs is characterized by two distinct vegetation types: coastal humid forest in the east and semideciduous and mesophytic forest in the west

Fig. 19.1 Golden-headed lion tamarin. Photo by Leonardo Oliveira

(Pinto and Rylands 1997). These two distinct vegetation types coincide with two different predominant economic activities, cocoa cultivation in the east and cattle ranching in the west, resulting in different levels of forest fragmentation and disturbance (Figs. 19.2 and 19.3). The cattle industry has contributed to severe fragmentation of the western portion of the species' range (Pinto and Rylands 1997). Only small and extremely isolated fragments remain, yet they have considerable edge effect, and local GHLT extinctions are occurring quickly (Zeigler et al. 2010; Raboy et al. 2010; Fig. 19.2). Shade-cocoa plantations predominate in the east where some relatively large forest fragments still exist (Fig. 19.2). However, the decline of cocoa prices and the rapid spread of a fungal disease (witches' broom) devastated cocoa production, and many landowners are steadily converting their shade-cocoa plantations into cattle ranches or other crops, increasing the level of forest degradation and fragmentation and decreasing the amount of suitable interconnecting matrix habitat (Schroth and Harvey 2007; Cassano et al. 2009). Currently, over 90 % of the species' range is in the hands of private landowners. Shade-cocoa is the predominant usable habitat remaining for the GHLTs (Raboy et al. 2004; Oliveira 2010).

Techniques from diverse disciplines such as ecology (population, community, landscape), animal behavior, botany, veterinary science, and geography have all been used to study GHLTs. The more techniques and disciplines implemented, the more profound our understanding of the species has become.

Scale

Choice of scale can be critical for accurately documenting the effects of habitat fragmentation at relevant levels and reveal previously unknown aspects of a species' biology. Primates may be studied at all scales including individuals, groups, populations, or metapopulations—or at levels within an individual such as cells and DNA. Choice of scale is often inextricably linked to limitations of time, funding, techniques being implemented, and project feasibility, although ultimately it should be

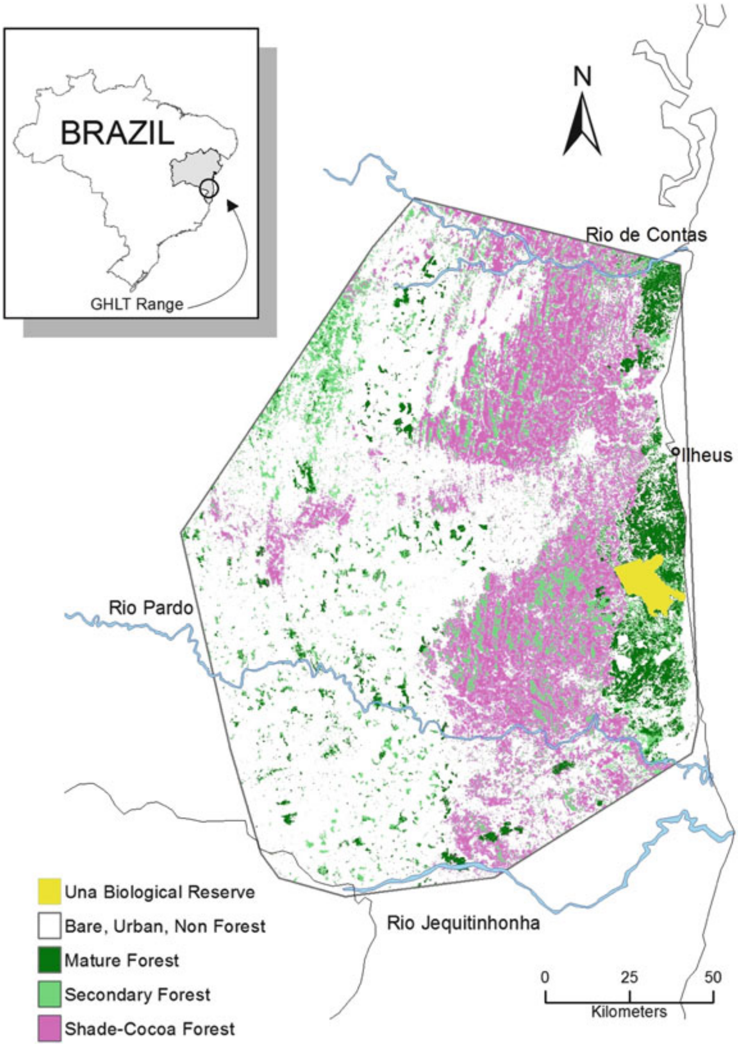

Fig. 19.2 Map of the GHLT distribution indicating main vegetation types. Bahia state is indicated in *gray* on the *inset*. Vegetation types were based on a reclassification of land cover at 30 m resolution published in Landau et al. (2003) from 1996 to 1997 Landsat data

determined by the research questions. Table 19.1 lists past and current research projects focused on in situ GHLT biology, the scale at which they were (or are) being implemented and the techniques used.

When results from lower scales are combined, they can provide detailed and multilayered insight into the large-scale impact of habitat fragmentation, particularly when multidisciplinary studies are involved. For example, a feeding ecology study can be relevant in a specific habitat and population, providing information on the type of food resources (and limitations therein) for that specific region (Rylands

Fig. 19.3 Aerial view of fragmentation over Una Biological Reserve and surrounding areas. Photo by James Dietz

1982; Raboy et al. 2004; Guidorizzi 2008; Catenacci 2008). But studying or comparison of data on the feeding ecology in different habitats and populations provides insight into the range of resources used by the various populations that compose the metapopulation, improves our understanding of how habitat fragmentation alters this aspect of the species' biology, and provides information to develop conservation actions both for specific populations and the metapopulation in general. Comparative work on ecology and demographics is in progress for five field locations where GHLTs have been studied (Table 19.2). Likewise, assessing a population's health status through biological sampling can lead to specific recommendations for that population (Monteiro et al. 2007), while comparing samples across populations can provide additional understanding on the impact of larger scale landscape factors such as proximity of human populations across the metapopulation (e.g., health assessment study by Catenacci et al.; Table 19.1).

Effective programs promoting primate conservation generally operate on larger spatial and temporal scales than those typically addressed by a single scientist, e.g., embracing a species' entire geographic region, or including a number of generations or scales sufficient to monitor ecosystem change (Chapman and Peres 2001). Setting up collaborative projects to analyze data or samples collected by studies at a smaller scale can prove useful to clarify issues at a larger scale and meet the demand for information at the scale needed for conservation purposes, provided comparability is maintained across studies. Examples of such collaborative projects for GHLTs that combine samples collected through studies conducted at the population level to investigate metapopulation questions include Grativol and Magro's genetic study and Catenacci et al.'s health assessment (Table 19.1) and spatiotemporal metapopulation modeling recently published (Zeigler et al. 2013) and in progress by authors drawing on multiple population studies.

Table 19.1 Overview of past and present studies on aspects of golden-headed lion tamarin biology, their duration, purpose, scale, number of study groups, size of study area, and techniques used

Scale[a]	Study region	Study	Length	Focus	No. of groups	Size of study area	Techniques
Metapopulation	Southern Bahia	Coimbra-Filho (1973)		Population survey	Multiple	n/a	Pioneering study: ad libitum observations of landscape and GHLT presence
	Southern Bahia	Pinto and Rylands (1997)		Population survey	Multiple	n/a	Survey (interviews, playback), GIS, landscape characterization
	Southern Bahia	Raboy and Zeigler[b]	2004–2008	Population survey, demographic and ecological modeling	Multiple	n/a	Survey (interviews, playback), remote sensing, GIS, landscape characterization
	Southern Bahia	Grativol and Magro[c]		Gene diversity, landscape genetics	Multiple	n/a	Study based on analysis of hair samples collected in individual population studies (Eastern and Western Una Biological Reserve, Fazendo Barro Branco, shade-cocoa)
	Western Una Biological Reserve, Fazenda Barro Branco, and shade-cocoas	Catenacci (unpublished)		Health assessment			Biological sampling (blood and feces)

Population	Eastern Una Biological Reserve (mature and degraded lowland moist forest)	Raboy and Dietz[d–h]	1991–2008	Ecology and behavior	16	700 ha	Behavioral observations, long-term monitoring, captures, biological sampling (health and genetics), vegetation transects and phenology, fecal sampling (studies on frugivory and seed dispersal), botanical sampling (species identification)
	Western Una Biological Reserve (degraded lowland moist forest)	De Vleeschouwer (unpublished)	2002–present	Ecology and behavior	6	1,400 ha	Behavioral observations, long-term monitoring, captures, biological sampling (health and genetics), vegetation transects and phenology, fecal sampling (studies on frugivory and seed dispersal), botanical sampling (species identification, morphological and nutritional analyses of fruits)
	Eastern and Western Una Biological Reserve	Monteiro et al. (1997)		Health assessment		900 ha	Biological sampling (blood and feces)

(continued)

Table 19.1 (continued)

Scale[a]	Study region	Study	Length	Focus	No. of groups	Size of study area	Techniques
Group	Shade-cocoas	Oliveira (2010)	2008–present	Ecology and behavior	7	Five areas between 22 and 84 ha	Behavioral observations, long-term monitoring, captures, biological sampling (health and genetics), botanical sampling (species identification)
	Lemos Maia experimental station (degraded lowland moist forest)	Rylands (1982)	1980 (4 months)	Ecology and behavior	1	40 ha	Behavioral observations, botanical sampling (species identification)
	Fazenda Barro Branco (semideciduous forest)	Guidorizzi (2008)	2006–2008	Ecology and behavior	2	450 ha	Behavioral observations, long-term modeling, captures, biological sampling (health and genetics), vegetation transects and phenology, botanical sampling (species identification)
	Eastern Una Biological Reserve	Cardoso (2008); Cardoso et al. (2011)	2007	Ecology and behavior	2	300 ha	Behavioral observations, community interactions (seed dispersal), botanical sampling (species identification)
	Western Una Biological Reserve	Catenacci (2008)	2006–2008	Ecology and behavior	2		Behavioral observations, community interactions (seed dispersal), botanical sampling (species identification)

[a] A population is defined by three or more groups studied in the same general area

[b] Zeigler et al. (2010)

[c] Moraes (2011)

[d] Raboy (2002)

[e] Raboy and Dietz (2004)

[f] Raboy et al. (2004)

[g] Dietz et al. (1996)

[h] Fontoura et al. (2010)

Table 19.2 Comparative summary of basic ecology between five study areas encompassing most representative habitats where the species occurs

Location	Forest type	Forest structure	No. of groups	Home range	Group size	Daily path length (m/day)	Plant species in diet	Most common plants (family)	% Fruit foraging	% Animal prey foraging
Eastern Una Biological Reserve (Raboy and Dietz)	Lowland, moist	Contiguous secondary and mature	3	123.4 ha	5.25 ± 1.8 ind	1,753	79 (32 families)	Myrtaceae, Sapotaceae	10.5 %	20 %
Western Una Biological Reserve (De Vleeschouwer, Catenacci)	Lowland, moist	Semi-contiguous, secondary in various stages of regeneration	2	n/a	n/a	n/a	92 (30 families)	Moraceae, Sapotaceae	10 %	15 %
Fazenda Barro Branco (Guidorizzi)	Mesophytic semideciduous	Fragment of secondary forest	2	68–71 ha	4.7 ind	1,342	39 (21 families)	Bromeliaceae and Myrtaceae (no. of species) In terms of visits: Bromeliaceae	15 %	25 %
Shade-cocoas (Oliveira)	Low–mid elevation, moist	Shade-cocoa agroforest	3	45 ha (22–84)	6.1	n/a	26	Bromeliaceae, Mimosaceae, Moraceae	n/a	n/a
		Mosaic forest	3	65 ha (64–65)	8.2	n/a	23	Moraceae, Mimosaceae	n/a	n/a

Fragmentation: Past, Present, and Future

Southern Bahia has had a complex series of socioeconomic stressors that created its current fragmented habitat (Câmara 2003; Young 2003). Historically, the landscape of Southern Bahia was influenced by timber harvesting, agriculture, livestock, and an increasing human population (Galindo-Leal and Câmara 2003). Cocoa cultivation in the traditional cabruca system has on one hand slowed down deforestation through preserving part of the native shade tree cover, but at the same time also caused conversion of large tracts of mature forest into secondary forest or agroforestry systems (Leão 2010). Since 1965, Brazil's forest legislation prohibiting logging of Atlantic forest and enforcing the establishment of legal reserves has allowed for a partial recovery of the Atlantic forest, though mostly in the form of secondary forest, while the area of mature forest continues to contract (Gonzalez and Marques 2008).

Estimates for the remaining amount of Atlantic forest cover vary greatly depending on the source, from 7–8 to 27 % (SOS Mata Atlântica/INPE 1993; 2008; Galindo-Leal and Câmara 2003; IESB et al. 2007). Ribeiro et al. (2009) analyzed fragmentation in the Atlantic forest in eight geographical subregions including a "Bahia region" (delineated as eastern Bahia and almost all of Espirito Santo and Sergipe) based on centers of endemism published in Silva and Casteleti (2003). In the Bahia region 16.7 % of original forest remained, and the largest fragment was 29,000 ha. Also within this region, 40–50 % of the forest was within 100 m of an edge (Ribeiro et al. 2009). SOS Mata Atlantica did similar analyses for the entire state of Bahia. They estimated 1.6 million ha of the remaining forest representing 8.38 % of the original Atlantic forest biome (Mata Atlântica and de Pesquisas Espaciais 2008). Raboy et al. (2010) characterized the forest located within the range of GHLTs. They found that 94 % of the patches ($N=784$) were <1,000 ha, and 52 % were <100 ha in size. Twelve patches reached sizes >10,000 ha. Comparisons of current and past forest cover convey a picture of recent pressures on the landscape. Zeigler et al. (2010) showed that forest cover loss in the GHLT distribution area between 1987 and 2007 was 145,796 ha (13 %). Zeigler et al. (2010) also noted 1,419 less fragments over the 20 years, and that mean patch size decreased by 10 ha.

In terms of how forest loss has affected population trends, survey work in combination with landscape analysis (Raboy et al. 2010) documented a range reduction for the GHLTs, in particular, from the west where fragments were found to be smaller and more isolated from one another. Predictive work demonstrated that Core Area Index (the proportion of core area to total patch size) and area of fragments were variables that could potentially explain GHLT's presence or absence. Both forest cover across the landscape and the GHLTs ranging on it have showed significant decline.

Predicting future trends is a vital tool for conservation practitioners. Changes in landscape structure as well as a species' response to such changes can be modeled to predict outcomes under various scenarios of future change. In the case of GHLTs, the likelihood of continued habitat loss is high. Recent changes to the Brazilian forest code reduce the level of protection for hilltop forests (the majority of the forest left in the western portion of the GHLT distribution area), and the margin of forest necessary to maintain along riverbanks. These changes will have a profound negative effect on the amount of remaining forest in the western of the GHLT range, and forest integrity and connectivity in the east, threatening region-wide conservation (Law No 12.727, of Oct. 17 2012).

Zeigler (2010) looked at predicted future vulnerability of forest loss throughout the GHLT landscape using the most significant predictors of past landscape change (distance from previously cleared areas, elevation, and human population density). Results indicated that most remaining habitat is highly vulnerable to future loss. Additional studies by the same team looked at what might happen to GHLTs in the future by conducting population viability analysis of the species throughout their entire distribution given no future landscape change (Zeigler et al. 2010) and of selected metapopulations in the western half of the species range given likely trends in future deforestation or reforestation (Zeigler et al. 2013). At current or increased rates of deforestation, most metapopulations suffer from increased extinction risk and decreased abundance and genetic diversity, indicating that major efforts to protect populations and tracts of habitat of sufficient size throughout the species' distribution will be important to protect the species from continuing decline and extinction (Zeigler et al. 2013; Raboy 2008).

Perspective

Better assessment and integration of species perspective into conservation biology and landscape studies may reveal novel ways to interpret fragmentation, its associated stressors, and potential solutions. For example, our impression of good habitat for GHLTs was initially biased by our human-centered view that secondary forest and human-altered habitats were inferior to mature forest for GHLTs. Studies showed though that GHLTs had affinities to degraded habitats for certain resources (Raboy et al. 2004; Catenacci 2008), and that shade-cocoa plantations were suitable habitats (Oliveira 2010). Connectivity is another point where perspective matters. Based on the concept of functional connectivity, traversable habitat (albeit lower quality according to some set specification) actually connects seemingly isolated forest patches into larger mixed-habitat patches. GHLT researchers have in the past used various definitions to classify fragments as isolated, ranging from 30 m to 1 km of isolation (Raboy et al. 2010; Zeigler et al. 2010). Zeigler et al. (2011) varied the resistance levels of the matrix habitat and identified the impact on functionally connected complexes in the GHLT range discovering the landscape becomes somewhat less fragmented the further GHLTs are capable of dispersing in matrix habitat. The maximal dispersal distance is unfortunately currently unknown.

Great emphasis has recently been placed on biodiversity conservation in lieu of single species conservation programs. Different species, even sympatric, may be differently affected by continued forest loss and fragmentation. Conservation efforts that are good for one species may not work for others, and such species-specific needs should not be overlooked when developing conservation actions for GHLTs, particularly for actions that affect relatively large regions encompassing diverse network of threatened species. For example, when mounting corridors or restoring degraded areas, factors such as the choice of vertical structure or species of fruit trees planted will have to take into account the needs of many species using the corridor, not just GHLTs. An approach to considering species perspective was taken by Paglia (2003) who considered population viability of three threatened Southern Bahian species including two primates, the GHLT, and the yellow-breasted capuchin (*Cebus xanthosternos*), as well as a parrot Red-browed Amazon (*Amazona rhodocorytha*). Forest patches of 2,700–3,600; 5,700–10,000, and 3,300–4,100 ha, respectively, were required to ensure a 95 % chance of surviving for 100 years given several assumptions for each species (Paglia 2003). As such, conserving forest patches, the size necessary for GHLTs, might aide parrots, but would not be sufficient for *Cebus*. In addition to differing needs in terms of the amount of forest necessary to survive in the future—each species will have varying abilities to traverse matrix habitat, and thus functional connectivity will be different for each.

Comparative Studies

Landscape and survey data show that GHLTs occur in a complex landscape, composed of different vegetation types (evergreen vs. semideciduous), under different forms of economic land use (agriculture vs. cattle ranching) and corresponding degree of fragmentation (Pinto and Rylands 1997). Habitat degradation and varying land use have resulted in a mosaic of various types of unsuitable (pasture, rubber tree plantations, urban and some other agricultural forms of land use) or suitable (swamp, mature, secondary forest in different stages of regeneration) habitat for GHLTs (Pinto and Rylands 1997). This landscape complexity presents a wide variety of threats, each of which impacts the different species in contrasting ways. Obtaining sufficient and comparable data for each of these different landscape and habitat configurations is extremely challenging, given the large spatial scale involved, yet this is imperative for making sound and adequate conservation actions for the entire metapopulation.

Setting up collaborative projects to analyze data or samples collected at the level of populations allows for comparing across populations, and addressing questions at the metapopulation level. Since the 1990s researchers spread across four projects have been studying GHLT behavior and ecology (sometimes simultaneously) in representative habitats through long-term monitoring (Table 19.2). Two projects were set up inside Una Biological Reserve, one in contiguous forest habitat and one in heterogeneous and patchy habitat. Two other projects were established outside of the reserve, one in an isolated semideciduous forest fragment and one in shade-cocoa agroforest, studying groups in shade-cocoa and mosaic forest. The data collection methods from these sites were similar which has thus far offered an insight into the range of food sources and sleeping trees used in each habitat, home ranges, densities, reproductive rates, and demographic parameters among others, across habitats (Table 19.2). Additional collaborative projects have been set up to compare certain aspects across study areas at the metapopulation level (i.e., genetics, vegetation studies and phenology, and health aspects such as infectious diseases and parasite load).

Valuable lessons about the impact of fragmentation on a species can also be learned by evaluating it in context to closely related species that share similar environmental stressors. There are three other species of lion tamarins: black lion tamarins (*L. chrysopygus*: endangered), golden lion tamarins (*L. rosalia*: endangered), and black-faced lion tamarins (*L. caissara*: critically endangered). While each of these species lives in different regions of the Atlantic forest and faces unique threats, basic biology and ecology are comparable (Kleiman and Rylands 2002a). All reside in heavily fragmented habitats (Holst et al. 2006). Of the four species, GHLTs have the largest amount of contiguous forest left (Holst et al. 2006). Looking at the patterns of fragmentation and species response that occurred for other lion tamarin species may help predict the GHLTs' future fate given further fragmentation. For example, Grativol et al. (2001) demonstrated loss of allelic diversity in and considerable genetic divergence between four recently isolated population of GLTs and Dietz et al. (2000) found that inbreeding increased infant mortality, posing a threat to the viability of all but one of the remaining wild populations of GHLTs. These are possible concerns for GHLTs too (Moraes 2011).

Synthesizing and Evaluating

GHLT researchers are convinced of the need for integrating work across scales and disciplines as evidenced by the wide array of collaborative projects in progress (Table 19.1) or being planned and publications integrating disciplines and scales will be soon available (e.g., Zeigler et al. 2013). Here we present some insights available from looking broadly across available studies.

Data on the species' feeding ecology and food sources used in different areas and habitats (Raboy and Dietz 2004; Catenacci 2008; Guidorizzi 2008; Oliveira et al. 2010) indicate that GHLTs use a large variety of food sources, which could serve as an advantage in an increasingly unpredictable landscape where plant species composition changes due to habitat modifications. In mature and heterogeneous forest, GHLTs use a large number of plant food species, whereas in semideciduous forest and shade-cocoa agroforest they rely on a smaller number of species as a key feeding resource (i.e., bromeliads in semideciduous forest, Guidorizzi 2008; exotic jackfruit in shade-cocoa agroforest, Oliveira et al. 2011). It's been suggested that the large plant diversity in the GHLT's diet reflects a tendency to diversify and use available resources when possible (Catenacci 2008), in which case the floristic composition of areas likely determines the diversity of the GHLT's diet. This seems true, given that vegetation transect studies have demonstrated a higher species diversity in older growth forest versus regenerating areas (Piedade and Maruim; Pessoa 2008) and the lists of species consumed in those two areas are extensive, but contain relatively few species consumed in both areas (Raboy and Dietz 2004; Catenacci 2008). So, the botanical composition of an area indeed seems to explain variation in the GHLT's diet composition. But does this mean that diets in semideciduous forest and modified areas, such as shade-cocoa, are nutritionally poorer? GHLTs captured in shade-cocoa weighed more than those in mature forest, suggesting good body condition, and thus adequate diet composition (Oliveira et al. 2011). Do GHLTs in shade-cocoa and semideciduous forest eat a low number of species because they can persist on a less diverse diet in these areas, or because low species richness of the area limits their choice of food plants? Does this then imply that these environments are more challenging for GHLTs, and that GHLTs are potentially more vulnerable to seasonal food shortage and changes in floristic composition in degraded and human-altered habitats? This is hard to answer without data on floristic composition in shade-cocoa and semideciduous forest, the total number of species available in each area, their nutritional value, and existing plant defense mechanisms that may make certain species unsuitable for GHLT consumption.

Both ecological and human-induced differences in resource availability exist among habitats, forcing GHLTs to adapt in different ways. Vegetation studies document lower species richness and more pronounced seasonal changes in fruit availability in the mesophytic forest in the western part of the species range compared to the coastal humid forest of the east (Guidorizzi 2008; Pessoa 2008; Pessoa et al. 2012). The existing ecological differences between east and west might have prompted GHLTs to evolve mechanisms to deal with food shortage. Landscape data have demonstrated more severe human-induced fragmentation of western compared to eastern forests (Raboy et al. 2010), and thus edge effects are expected to be more pronounced, all contributing to the floristic composition of an area and the choice of plants available to GHLTs. In shade-cocoa agroforest, agricultural management practices strongly reduce species diversity among shade trees (Sambuichi and Haridasan 2007; Schroth et al. 2011), affecting GHLT diet choice. In all, dietary flexibility versus specialization and the particular importance of key food species may have different relevance in the western mesophytic forest vs. the eastern humid forest, and in poor or modified habitats where species richness is low, due to ecological factors, human factors, or a combination of both. Integrated analyses of overall floristic composition and data on feeding ecology may answer some of these issues. Such comparisons will be instrumental for understanding whether in semideciduous forests and in degraded and modified habitats, GHLTs rely on key species because they prefer to, or because they have to, and improve our understanding of the species' vulnerability to alterations in vegetation composition due to ecological and human-induced habitat differences.

Ecological, demographic, and survey studies indicate that GHLTs are able to survive and reproduce in a variety of habitats, including older growth forest, heterogeneous degraded forests, shade-cocoa agroforest, and smaller isolated forests (Raboy et al. 2004; Oliveira 2010). Rapid degradation and increased amount of human-altered habitat may have forced GHLTs into using some of these areas more than they would have if more pristine habitat (the habitat in which they evolved in) still existed. While it is hard to tease apart preference from necessity, researchers have been documenting the extent to which GHLTs can use and thrive in different habitats. Birth rates and individual weights are higher in shade-cocoa (Oliveira et al. 2010). Yet, does this mean the species thrives there? More births seem like a benefit but population growth also requires low mortality and high reproductive success. How do differences in resource availability and predation risk between habitats affect birth and mortality rates? Mature forest may provide safer habitat, with lower predation risk and improved survival, whereas shade-cocoa provides abundant resources but at the cost of increased predation (Oliveira and Dietz 2011). Slower reproductive rates, steadier population growth, and long-term stability may be characteristics of more advanced forest, whereas high reproductive rates but larger population turnover may be more typical of modified habitats, leaving GHLTs (in particular small populations) in modified habitats more vulnerable to random factors affecting population growth. GHLT presence in isolated and degraded forest fragments in the west is probably the clearest case of GHLTs' use of suboptimal habitat and landscape. Comparative work comparing surveys 15 years apart indicates that local extinctions are common in the west; however, we still see GHLTs in surprisingly small and isolated fragments with extreme edge effect. The patches on which they persist may no longer be able to support healthy reproducing populations and those populations still present have entered a downward spiral to local extinction—a phenomena known as the extinction debt (Tilman et al. 1994).

Studies on seed dispersal and interspecies interactions have improved our understanding of the role of GHLTs in their community. Studies on associations between GHLTs and Wied's marmosets tested hypotheses on the benefits of interspecies associations in relation to ecological factors such as predation and food resources (Raboy 2002; Raboy and Dietz 2000; Oliveira and Dietz 2011). Interspecific associations with Wied's marmosets in shade-cocoa may be determined by predation risk, whereas those in more undisturbed habitat may be shaped largely by foraging benefits. Further, GHLTs seem crucial for the dispersal of bromeliad seeds, and thus may well be instrumental for maintaining one of their own principal food and foraging resources (Fontoura et al. 2010). GHLTs also help regenerate degraded forest, by dispersing seeds across vegetation types (Catenacci et al. 2009; Cardoso 2008; Cardoso et al. 2011). More studies on community ecology are particularly important for understanding how changes in behavior and population dynamics of GHLTs as a consequence of habitat modification might affect the ecological community. As we are beginning to understand the complex network of which GHLTs are part, we will gain a better understanding of how conservation actions directed towards one species may affect others, which will help us in developing species conservation plans that are adequate for not only GHLTs but also other Atlantic Forest species.

Integrated landscape and GIS research have helped dispel a false notion that GHLTs are relatively safe from threat. The last population estimates available for GHLTs (6,000–15,000; Pinto and Rylands 1997) presented an optimistic population estimate and implied a relative security in numbers for the species. Moreover, increased visibility of GHLTs and other forest species near farms and towns added to this notion that the species are more abundant than previously thought. However, increased sightings may actually be an effect of habitat modification, with GHLTs increasingly forced towards the limits of urban centers and agricultural zones, where they are more likely to be noticed. Thus, it can be harder to convince scientists, conservationists, and the general public that conservation actions are as pressing as formerly believed. Consequently, mounting conservation programs is deemed less critical and conservation funding is directed elsewhere. Recent multidisciplinary GIS and modeling studies have demonstrated GHLT range reduction, continuing and projected habitat degradation and destruction, decreased functional connectivity of habitat, and larger number of local extinctions for the species. The western populations of GHLTs have already reached the stage where intense management of individuals will likely be needed, but the eastern populations may be at a great disadvantage due to continued economic troubles, causing conversion of shade-cocoa to non-habitat. Eastern populations may still be saved principally through carefully thought-out landscape management, but actions are slow to take place. As Kleiman and Rylands (2002b) indicated, "we cannot, yet again, watch and wait as a threatened species reaches numbers so small that the species' survival becomes critically endangered."

The future is likely to provide us with many more insights, and more examples of the value of a comprehensive approach to GHLT conservation. For now, perhaps the most compelling example of how being comprehensive has helped us and can help us in the future is Raboy and Zeigler's integrated studies (Table 19.1) employing a range of different data, including GIS, demographic, and ecological data from a wide range of areas, and landscape analyses to provide not only an image of GHLT absence and presence in the current landscape, but also a basis for exploring future scenarios of landscape change, and potential conservation actions.

Evaluating, Prioritizing, and Creating an Action Plan

Brazil is one of the world's richest biodiversity regions and a world leader in biodiversity conservation (Mittermeier et al. 2005). The increasing cadre of conservation professionals has resulted in a national protected area system, the elaboration of threatened species lists, a large number of conservation NGOs, and a conservation system based on sound science involving capacity building of conservation scientists (Mittermeier et al. 2005). These elements have greatly facilitated lion tamarin conservation. As a result of a process of adaptation and reevaluation, over the years, GHLT research has moved from a generalized understanding of the ecology and demographics of GHLTs in the wild to understanding more specifically the influence of habitat on GHLT biology and the role landscape plays in all of this. In particular, conservation efforts for lion tamarins have been closely guided and evaluated through the International Committee for the Conservation and Management of the Lion Tamarins (ICCM; an official advisory organ to the Brazilian Government) and Population and Habitat Viability Assessments (PHVAs; Seal et al. 1990; Ballou et al. 1998; Holst et al. 2006). The PHVA Workshops use detailed data on species biology, genetics, and ecology integrated with estimates of human-based threats, such as current and projected land use patterns and sophisticated computer models to evaluate the risk of wildlife population decline or extinction under alternative future management scenarios. These models serve as tools for scientists and wildlife managers to develop detailed recommendations for conservation action focused on the most urgent problems. The resulting Action Plans (Seal et al. 1990; Ballou et al. 1998; Holst et al. 2006) served as a guideline for implementing both new research projects and conservation plans.

In response to the research needs defined during the 1990 PHVA, the first long-term research project in the relatively pristine eastern part of Una Biological Reserve was initiated, providing information on basic ecological parameters, in addition to detailed behavioral data. Following additional recommendations during the 1997–2006 PHVAs, Project BioBrasil was initiated in degraded and heterogeneous habitat in 2002, a project in semideciduous forest in 2006, and a project in shade-cocoa in 2008. During the 1990 workshop, conservationists were still under the assumption that the number of GHLTs in the wild was quite low. Conservation actions deemed necessary focused on securing and protecting habitat, conducting inventories and protecting wild populations, and establishing scientifically managed self-sustainable captive populations as a future source of animals to restock suitable habitat lacking tamarins. Then, following findings that the species also used shade-cocoa agroforest (Alves 1990), and a detailed species survey conducted in 1993–1994 (Pinto and Rylands 1997) suggesting a higher number of GHLTs remaining in the wild, conservation priorities defined for the GHLT conservation program during the 1997 PHVA changed considerably. Reintroduction no longer became an objective, the captive population was reduced in size, and it was decided that conservation actions should concentrate on forest protection and increasing forest connectivity (Ballou et al. 1998). In case suitable habitat became available, given the complications of reintroducing captive-held animals (Kierulff et al. 2002a; Beck et al. 2002), translocations, rather than the reintroduction of captive animals, would be preferred. In turn, research priorities as defined in 1997 and 2005 became strongly determined by the need to obtain the necessary data to develop adequate guidelines for landscape management, such as the identification of important forest fragments, and the construction of corridors as a means of increasing connectivity, and information on the use of shade-cocoa agroforest (Ballou et al. 1998; Holst et al. 2006). Further, the 2005 PHVA also emphasized the importance of research in other understudied habitats (semideciduous forest), as well as at the level of the landscape, in addition to genetic and health studies. Additional comparative research projects were set up in response to this (Table 19.1).

The work of the ICCM has been interrupted since the reorganization of IBAMA and ICMBio in 2007, prompting the lion tamarin programs to find other means of directing and evaluating its research and conservation actions. For example, in 2011, the GHLT research community organized a Research Symposium at the State University of Santa Cruz (UESC; Ilhéus, Bahia, Brazil) with the aim of sharing recent work and discussing potential future avenues for research. This allowed for the dissemination of information to the global GHLT community, compilation of recent advances in research, and identification of gaps in knowledge of GHLT biology, ecology, and conservation, which resulted in a list of research topics considered high priority for future research (Vleeschouwer et al. 2012).

Currently, the principal conservation planning instrument used by Instituto Chico Mendes, the Brazilian Federal institute for the Conservation of Biodiversity (formerly part of IBAMA), is the National Action Plans (NAPs), comprehensive action plans that address the conservation of Brazil's endangered species (ICMBio 2012). These NAPs propose and monitor the implementation of a series of actions that allow for a harmonic relationship between regional development and the preservation of regional biodiversity. Some are limited to one taxon only (e.g., *Brachyteles*; Jeruzalinsky et al. 2011), and others are cross-species action plans encompassing entire regions and their corresponding subset of endangered species, e.g., the NAP for the Conservation of Southeastern Mammals encompassing 27 species, including GHLTs and a series of actions from Southern Bahia, over Minas Gerais, Espirito Santo, Rio de Janeiro, and São Paulo states, up to the North of Paraná (PAN-MAMAC 2012). Obviously, this and other NAPs will have to incorporate species perspective and reconcile the needs of all species as a basis for formulating measures that benefit all species together and their landscape.

Conclusions: Future Directions in GHLT Conservation

Our current knowledge on the conservation status of GHLTs suggests that, due to population numbers in the wild still in the low thousands, conservation strategies to secure the long-term survival of the species are likely to be concerned primarily with the management of the landscape, ensuring safe-guarding of representative habitats and improving forest connectivity, and less with the management of individuals (Holst et al. 2006). This holds at least for the eastern part of the distribution that contains most of the remaining GHLT populations in the wild (Pinto and Rylands 1997). In the west, the intense degree of forest fragmentation means that extinctions are imminent (Zeigler et al. 2010) and conservation strategies aiming at restoring a healthy genetically viable western population of GHLTs will be more intense, almost certainly involving management of individual GHLTs and groups (e.g., translocations), in addition to management of forest and habitat linkage areas. This difference between east and west affects research priorities for each area within the distribution range (Vleeschouwer et al. 2012).

Recently, GHLT landscape and population data have been serving as a test case for the development of new conservation biology modeling paradigms and specific software in creation by the Chicago Zoological Society and the Conservation Breeding Specialist Group of the IUCN (Lacy 2012). A diverse network of collaborators have been working on ways in which to synthesize and computationally share knowledge across disciplines, linked through population viability analysis (PVA). Collaborators are in the process of developing a metamodel interface to run concurrent discipline-specific individually based simulation programs such as animal movement, epidemiology, PVA, and a social or life-history simulator, using shared and modifiable input/output and all connected to a GIS platform with supporting data that are spatially structured. For GHLTs the program is being implemented to model the consequences of developing corridors for forest connectivity in certain areas over others as measured by the long-term chances of population persistence and maintenance of genetic diversity given the species movement rules and demographic factors across a complex landscape. Such modeling paradigms and software will assist many conservation practitioners across the world and may have particular utility in multidisciplinary workshop settings.

Addressing future research and conservation priorities for GHLTs will require broad multidisciplinary research projects on a larger scale (across habitats) as well as the development of focused research questions in specific locations. The latter forms the building blocks of well-integrated research, addressing issues such as the impact of particular threats (e.g., predation risk in different habitats). Creating these building blocks is greatly assisted by long-term monitoring of critical ecological parameters in representative habitats, which can serve to identify specific pressures that may become the subject of shorter term or more focused studies (Wintle et al. 2010). Long-term monitoring is also critical towards investigating medium- to long-term effects of natural environmental variation and human-induced environmental modifications, including climate change, on population dynamics and GHLT behavior.

Finally, as we progress in understanding the factors that affect GHLT populations and what is needed to protect them, we should increasingly include additional disciplines, particularly those addressing social, political, and economic issues. An understanding of the economic factors behind particular threats, such as the impact of cocoa prices on the maintenance of shade-cocoa plantations, or political factors promoting economic development versus sustainability is essential for a full understanding of the underlying causes driving habitat modification. It is neither feasible nor desirable to maintain GHLTs in protected areas only. Saving GHLTs will involve the establishment of a network of collaborating private landowners who adopt sustainable forest management and biodiversity-friendly methods of land use, as a means of ensuring the maintenance and connectivity of critical tracts of forest. It is only through the integration of studies on genetics, ecology, resource management, economics, politics, and sociology that we can ever hope to achieve comprehensive effective long-term management of threatened species (Clarke 2000).

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Chapter 20
A Critically Endangered Capuchin Monkey (*Sapajus xanthosternos*) Living in a Highly Fragmented Hotspot

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Abstract Capuchin monkeys (*Sapajus* sp.) have cognitive skills and variation in morphological traits among different species that allow for a varied diet and flexible use of food resources. In the northern Atlantic forest, capuchins have been forced by fragmentation to live in human-altered environments; in addition, animal densities have been reduced by hunting and habitat loss, wiping out a number of large mammals that disperse zoochoric fruits. With the decrease in populations of other seed dispersers, yellow-breasted capuchins (*Sapajus xanthosternos*) are currently one of the largest fruit-eating mammals in the region. We provide frequency of feeding on invasive species (*sensu* Colautti and MacIsaac, Divers Distrib 10(2):135–141, 2004), and insights into how they might compete for seed dispersal with other species. *S. xanthosternos* had a high frequency of travelling and feeding on fruits. They ate fruits in primary, old- and young-secondary forest, swamp, and *cabruca* (shaded cocoa plantations). In addition, they fed on fruits of oil-palm (*Elaeis guineensis*), jackfruit (*Artocarpus heterophyllus*) and cocoa (*Theobroma cacao*); these cultivars compete with native species for seed dispersal by *S. xanthosternos*. We recommend the management of invasive fruiting species, especially in protected areas.

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Introduction

The Atlantic Forest of Brazil faces one of the higher extinction rates as compared to other biomes, due to its high species endemism, heavy historical and on-going habitat loss, increasing human population density (Laurance 2009), and increasing secondary forests in different levels of regeneration. The entire biome is threatened by deforestation and fragmentation with 83.4 % of forest fragments smaller than 50 ha. The northern Atlantic Forest is in a worse state of conservation than the southern part where the coastal areas of Bahia and Sergipe have less than 17 % of forest remaining (Ribeiro et al. 2009).

The yellow-breasted capuchin monkey (*Sapajus xanthosternos*) is endemic to the northern part of the Atlantic forest. Nowadays, remaining populations are extremely rare and restricted to small and degraded areas. *S. xanthosternos* is in critical danger of extinction due to habitat loss and hunting (IUCN 2010). The species has already disappeared over the major part of its original distribution (Kierulff et al. 2005). Thus, areas with the largest patches of forest and the largest number of capuchin groups are of great importance. Understanding how *S. xanthosternos* is coping with habitat disturbance is fundamental to future management of wild populations. Estimates of home range and habitat use are needed to establish the size of a suitable protection area and to determine management actions, such as connecting isolated fragments or expanding areas for the protection of a minimum viable population (Shaffer 1987).

Most of the large forest fragments harbouring populations of yellow-breasted capuchin monkeys are concentrated in southern Bahia Atlantic Forest (Kierulff et al. 2005). The presence of cocoa plantations in the agro-forestry system, with cocoa trees planted in forest understorey (called *cabrucas*), have helped to maintain a more forested landscape to preserve fauna and flora and to preclude a more dramatic change in microclimate and hydrological cycles (Mori et al. 1983), especially when compared to landscapes surrounded by pasture and extensive monocultures.

Cocoa (*Theobroma cacao*) was introduced in Bahia in 1746 from the Amazon and is still one of the most important commodities in southern Bahia Atlantic Forest (Purdy and Schmidt 1996). In the late 1980s, an economic crisis reached the region when a fungus, named witch's broom (*Moniliophthora perniciosa*), killed a vast area of cocoa plantations (Purdy and Schmidt 1996). This resulted in the conversion of old agro-forestry into pasture and other less environmental-friendly crops (e.g. manihot), and in the degradation of many of the forest remnants (Alger and Caldas 1994; Saatchi et al. 2001). Other exotic plants ubiquitous in Bahia Atlantic forest are oil-palm (*Elaeis guineensis*) that was introduced in Bahia in the late 1500s (Bastos et al. 2001), and abundantly used in Bahian cuisine, and jackfruit (*Artocarpus heterophyllus*), brought to Bahia for the first time in 1648 as an ornamental species (Ferrão 1993; Boni et al. 2009).

The classification of species as *exotic*, *invasive*, *introduced*, or *non-indigenous* has been currently discussed among invasion biologists and it is still subject to different views (Colautti and MacIsaac 2004; Richardson et al. 2000; Davis et al. 2001).

Here we consider cocoa, oil-palm and jackfruit to be invasive species in southern Bahia Atlantic forest, as all of them were introduced centuries ago from a different biome by humans, and today have a widespread distribution; also, they currently produce seedlings and might disperse longer distances if no management (removal and replacement by native species) is done. We follow a biogeographic approach and not taxonomic, i.e. the species per se is not invasive, but high dispersal capability and current distribution indicates their invasiveness in southern Bahia Atlantic Forest (Colautti and MacIsaac 2004; Richardson et al. 2000).

Sapajus are frugivore–insectivores (Robinson and Janson 1987) or faunifrugivores (Chivers 1998). Fruits, seeds, foliage (bromeliads), nectar and animal prey (including insects, birds, eggs, reptiles and small mammals) comprise their diet (Janson and Boinski 1992). Capuchin monkeys are able to feed on a wide range of food resources, not only due to their morphological and anatomical characteristics, but also because of their great manipulative and cognitive skills (Moura and Lee 2004; Canale et al. 2009). Crop use is common in environments with highly seasonal resources for primates (Freese and Oppenheimer 1981; Naughton-Treves et al. 1998; Di Bitetti 2001), but invasive plant species might be a threat to native species that also compete for seed dispersers (Gosper et al. 2005).

Methods

Study Site

Una Biological Reserve comprises one of the largest forest fragments in northern Atlantic forest, summing 18,500 ha (Fig. 20.1) It lies in southern Bahia, Brazil (15°06′–12′S, 39°02′–12′W) and its vegetation is composed by ca. 7,060 ha of mature and regenerating forests, broadly characterised as lowland moist tropical forest (Mori et al. 1983). Temperature averages 24–25 °C annually and rainfall is ca. 2,000 mm/year with no evident seasonality (Mori et al. 1983).

Behavioural Data Collection

We observed behaviour and ranging patterns of 14 individuals (two adult males, three adult females, two sub-adult males, two sub-adult females, two juvenile males, two juvenile females, and one infant) in one group of *S. xanthosternos* from September 2007 to December 2008 (Fig. 20.2a, b). The group was radio-tracked (Kierulff et al. 2005) and trapped individuals were dye-marked, but most of the animals of the group were recognised by coat patterns, and sex and age could be determined in most cases during behavioural observations. By the time we started the study, the capuchin monkeys were completely habituated to the observers.

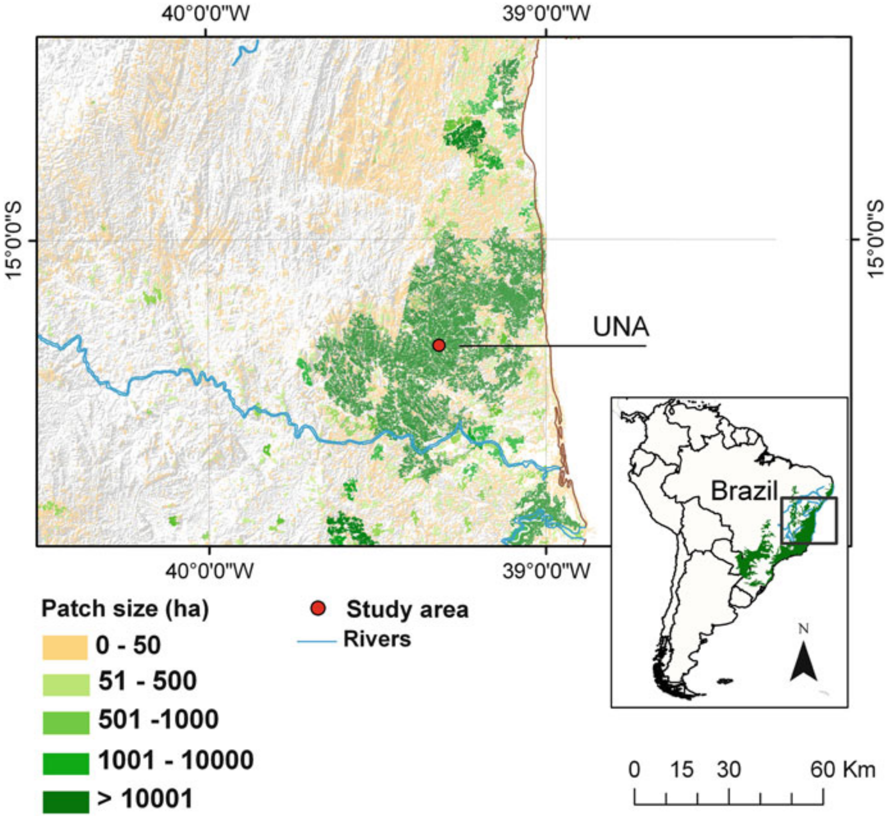

Fig. 20.1 Largest forest fragment in the Atlantic Forest of southern Bahia where is located Una Biological Reserve (UNA)

Behavioural data were collected during 3–5 days each month using scan samples at 15-min intervals (Martin and Bateson 2007). Groups were followed most of the time from dawn to dusk ($N=55$ full days); when we were not able to follow the groups the whole day, we completed the period not sampled in the following day ($N=42$ half days). We collected data on behaviour in a total of 2,598 scans. To avoid bias towards more conspicuous behaviours, we weighted each scan equally by dividing each observation by the total number of observations in a scan.

We scored the behaviours: travel, rest, social, feed and other. *Travel* involved horizontal and vertical movements. *Feeding* was recorded when animals were manipulating, chewing or swallowing dietary items (fruit, flowers, sap/gum, pith, leaves, bromeliad (foliar base), invertebrates, vertebrates, eggs). *Rest* was recorded if animals were lying or simply not moving. *Social behaviours* included affiliative and aggressive interactions. *Other* included behaviours that could not be coupled and alone represented less than 1 % (chest-rubbing, drinking water, urine-washing, vigilance).

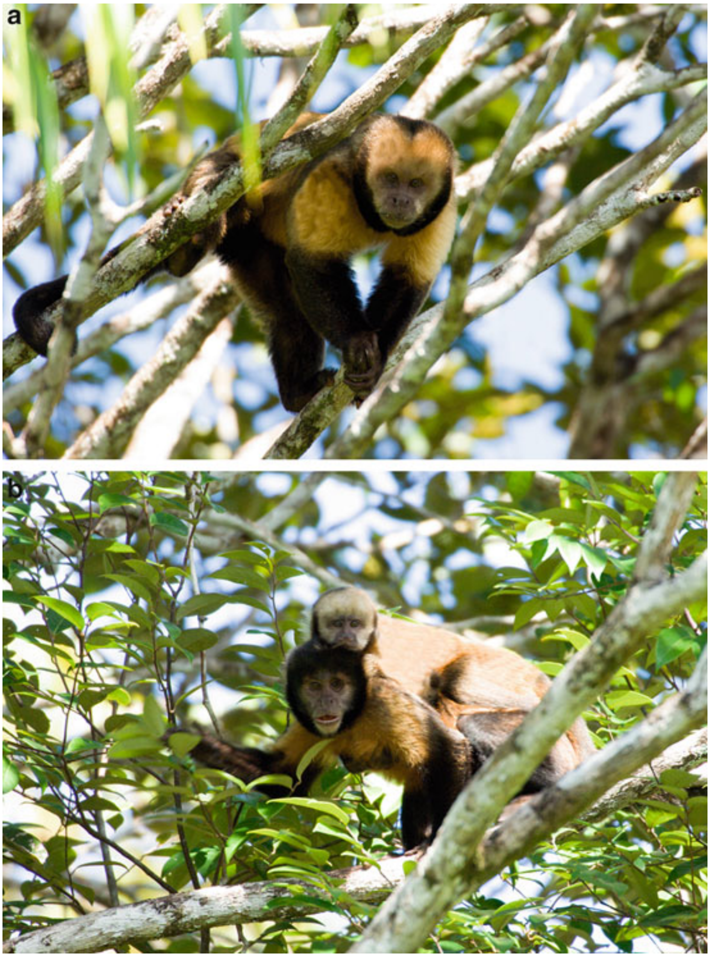

Fig. 20.2 (**a**) *S. xanthosternos* adult male. Photo by Luciano Candisani. (**b**) *S. xanthosternos* adult female and infant. Photo by Luciano Candisani

Results

Activity Budget

Yellow-breasted capuchins' home range was 969 ha based on Minimum Convex Polygon. When calculated by kernel (95 %) home range was 671 ha. Core area (25 %) was 75 ha (Fig. 20.3).

Capuchins spent on average 32.8 % (±4.9 %) of their time feeding, frequencies range from 25.9 to 40.5 %. Most of the time animals were travelling or feeding, both behaviours together summed 75.9 % (±4.0 %), on average reaching 81.5 % of total behaviour frequency in 1 month (Oct 2007) (Fig. 20.4).

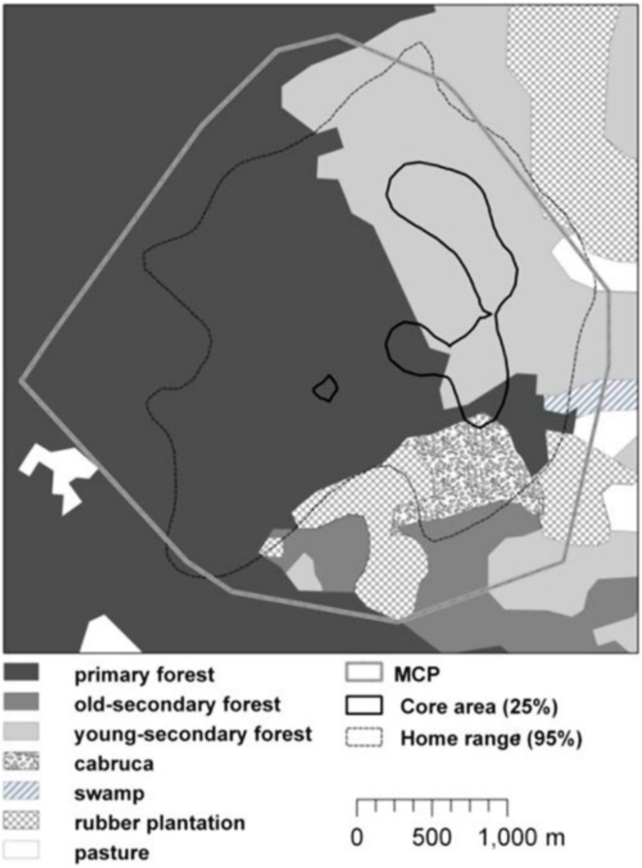

Fig. 20.3 Home range of a capuchin monkey group at Una Biological Reserve based on data collected from September 2007 to December 2008

Food Resources Availability

Fruits represent the bulk of *S. xathosternos*' diet. On average capuchins feed on fruits 38.3 % of total feeding frequency (±8.6 %, $N=14$ months) reaching up to 47.9 % of feeding frequency in February 2008. Invertebrates were the second most-frequent items in the diet, averaging 36.1 % (±6.6 %, $N=14$ months). In 4 months in 2008 (January, April, July and September) eating invertebrates was more frequent than eating fruits (Fig. 20.5), but there was no seasonal variation related to precipitation or fruit availability ($p>0.05$).

Capuchins feed on an average of 16.5 plant species/month. On average, 24.4 % (±15.6 %) of records of eating fruits were on invasive species (cocoa, jackfruit or oil-palm), but this went up to 47.1 % of fruit-feeding observations in 1 month (Oct 2007), and feeding on this three invasive species reached more than 25 % in 7 months ($N=14$ months) (Fig. 20.6).

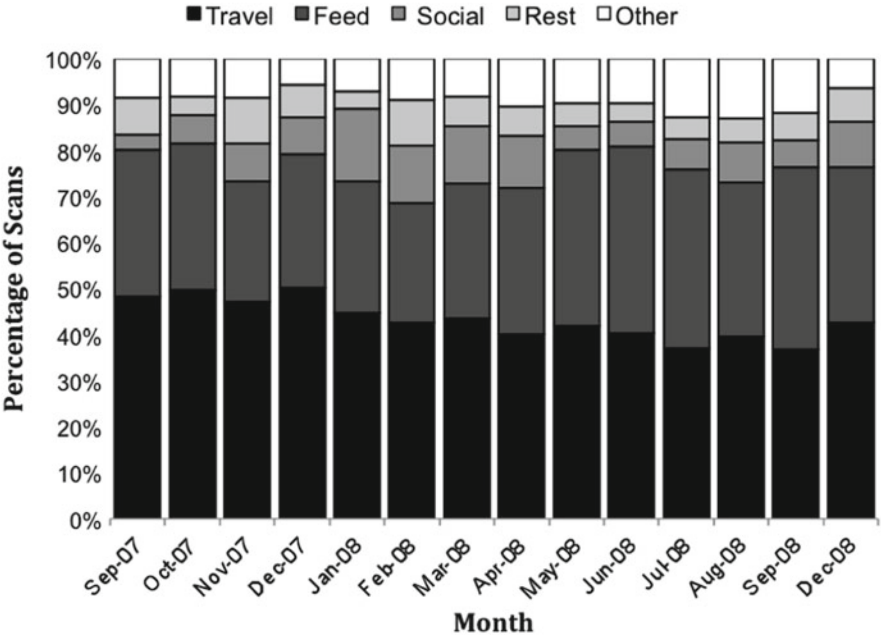

Fig. 20.4 Activity budget for *S. xanthosternos* group at Una Biological Reserve from September 2007 to December 2008 ($N = 14$ months)

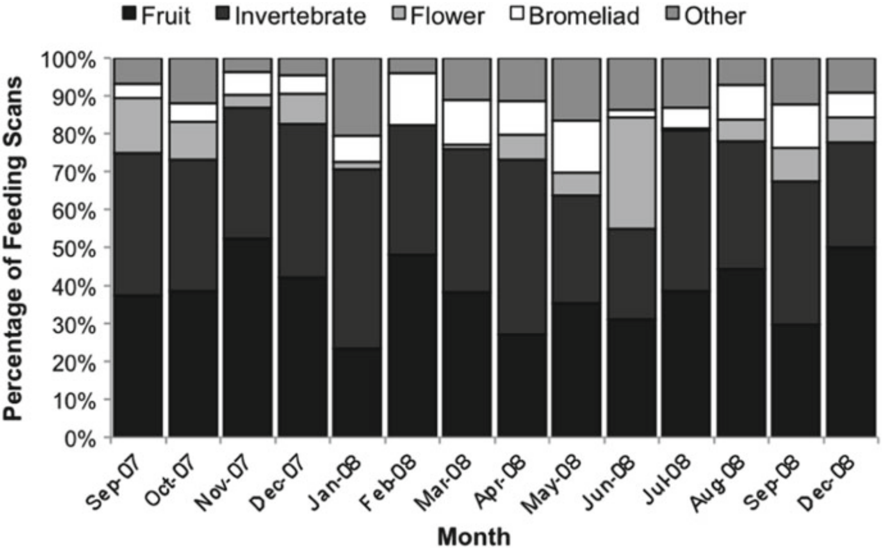

Fig. 20.5 Percentage of feeding scans on different items for *S. xanthosternos* group at Una Biological Reserve from September 2007 to December 2008

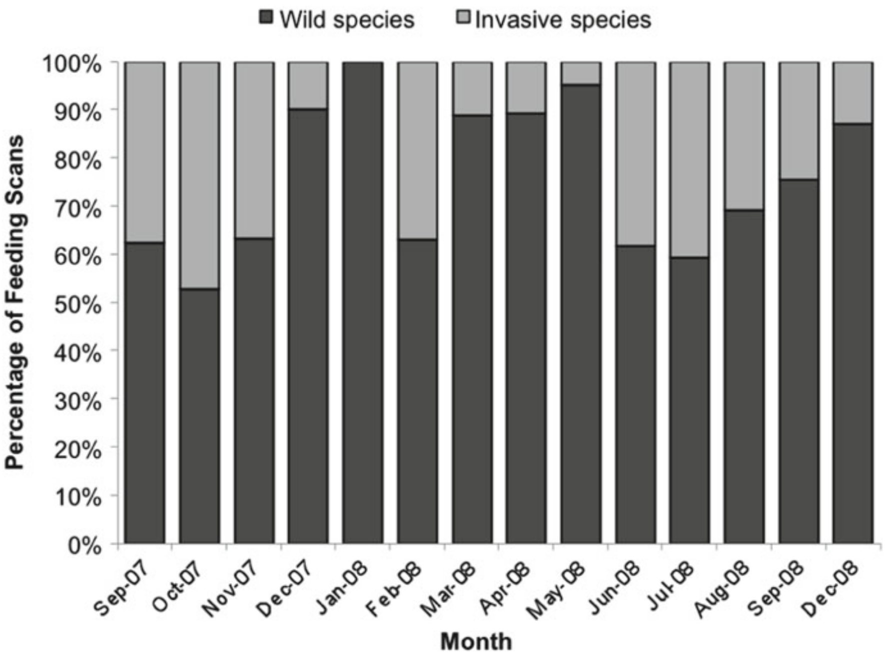

Fig. 20.6 Percentage of scans that individuals were feeding on fruits of invasive species and wild species of trees for *S. xanthosternos* group at Una Biological Reserve from September 2007 to December 2008

Table 20.1 Ten most-consumed plant species by *S. xanthosternos* in Una Biological Reserve from September 2007 to December 2008 (*N*=1,205 feeding records)

Family	Species	Feeding (%)	Status
Arecaceae	*Elaeis guineensis*	26.1	IN
Sapotaceae	*Manilkara longifolia*	14.1	ENA/EN
Menispermaceae	*Anomospermum reticulatum*	7.7	
Arecaceae	*Attalea funifera*	6.6	ENA
Mimosaceae	*Inga* sp.	4.1	
Sterculiaceae	*Theobroma cacao*	3.6	IN
Myrtaceae	sp.	3.2	
Moraceae	*Cecropia* sp.	3.1	
Melastomataceae	*Miconia prasina*	2.6	
	Artocarpus heterophyllus	2.4	IN

ENA endemic of northern Atlantic forest, *EN* endangered, *IN* invasive species

From all feeding records (*N*=1,205) oil-palm (*Elaeis guineensis*) was the most consumed item in their diet (26.1 %) and fruits of all invasive species summed 32.1 %. The second most-eaten fruit species was an endangered and endemic tree (*Manilkara longifolia*) (Table 20.1).

Discussion

Primates have flexible behaviours that reflect environmental changes, providing predictive responses to ecological alterations that may guide conservation strategies. In Bahia Atlantic Forest large-bodied primates are in peril due to hunting and habitat loss: howler monkeys and woolly spider monkeys are virtually extinct in the region (Canale et al. 2012). Yellow-breasted capuchins are the next in line, as they are the largest primates to survive in that region, even though they are constantly hunted for bushmeat.

Yellow-breasted capuchins had one of the largest home ranges ever reported for a *Sapajus* species (969 ha). This is an important result for conservation action for this critically endangered species, since decision-makers aiming to establish reserves and protected areas will have to consider *S. xanthosternos*' need for a large forest to support a viable population.

Capuchin monkeys spend a lot of time foraging in different vegetation types and at different heights (Zhang 1995; Siemers 2000). This is especially the case for those living in fragmented and/or degraded forests. Yellow-breasted capuchin monkeys visited five different vegetation types within their home range: primary forest, old-secondary forest, young-secondary forest, swamp and *cabruca*. Travelling from one vegetation type to another might have an important effect on seed-dispersal patterns.

Seeds of cocoa and jackfruit were found in *S. xanthosternos* faeces still intact, but yellow-breasted capuchin monkeys were never observed swallowing seeds of oil-palm. In fact, cocoa seeds (3.0 ± 0.09 cm) (Chandel et al. 1995) and jackfruit seeds (3.1 ± 0.2 cm) (Lazure et al. 2010) are on the upper-limit size of seeds ingested by *Cebus* (<3 cm, Wehncke et al. 2003), which might not be different from *Sapajus* due to their morphological similarities. It is possible they could be dispersing invasive species around a protected area. We have not followed the germination of cocoa and jackfruit seeds defaecated by *S. xanthosternos*, but together with oil-palm they are already a concern for seed dispersal of native fruit species, as these three invasive species are competing for one of the most important seed dispersers remaining in Bahia Atlantic forest.

Although invasive species should not be kept inside protected areas, removing them could affect native frugivores relying on these resources (Gosper and Vivian-Smith 2009). Other endangered and endemic species might be depending on invasive plants on our study area. For instance, golden-headed lion tamarins (*Leontopithecus chrysomelas*) eat jackfruit and oil-palm fruits (Raboy and Dietz 2004), Wied's black-tufted-ear marmosets (*Callithrix kuhlii*) feed on jackfruit (Raboy et al. 2008), and a reintroduced population of red-billed currasows (*Crax bluemanbachii*) were observed feeding on oil-palm in another site in the southern Atlantic Forest (Bernardo et al. 2011). We observed collared peccaries (*Pecari tajacu*) and coatis (*Nasua nasua*) frequently eating those fruits as well.

With the replacement of forested areas by human-modified landscapes, primate populations are getting closer to humans and crops are becoming part of primate diets all over tropical regions (Naughton-Treves et al. 1998; Chiarello 2003). Increase of crop-raiding is reported where there is a lack of wild fleshy-fruit species (de Freitas et al. 2008; Ludwig et al. 2006; Di Bitetti 2001). In this situation, crops could represent a fall-back food for primates (*sensu* Marshall and Wrangham 2007) as the use of non-indigenous species was related to low availability of wild fruits. Primates approaching crops only in times of low availability of wild food resources might not be related to low quality of crop foods compared to wild foods. In fact, most human crops are planted based on nutritional values, as much as edibility and palatability.

Feeding on crops is not always related to shortage of wild fruit species, as in some cases seasonal availability of wild fruits and crops coincides (Rímoli et al. 2008). In this study, there was no correlation between wild fruit availability and feeding on invasive species, probably because all crops were located inside forest fragments and mixed with wild tree species, reducing risk of predation by birds of prey. Even those crops close to humans and domestic animals were accessible through the canopy and mixed in dense wild vegetation. Alarm calls were given during human or dog approaches and the monkeys moved away quickly, back to forest patches far from human settlements. In fact, during interviews with local people harvesting cocoa, presence of capuchin monkeys was never reported in *cabrucas*, probably because capuchins retreat to the forest before being detected by humans, as observed by researchers following the capuchin group in this study.

The increase of crop-raiding during periods of wild fruit scarcity must be related to a trade-off between predation-risk and starvation. Crop-raiding must represent a high risk for primates, as they might be shot or harmed by humans and more easily predated due to reduced canopy cover (Naughton-Treves et al. 1998; Ludwig et al. 2006); even when crop-raiding in *cabrucas*, where canopy cover is mostly kept intact, capuchin monkeys are threatened by the constant presence of armed humans and dogs. During the lean season, however, primates must risk raiding crops to gain quality food. An extra risk is taken for crop-raiding by moving on the ground (e.g. sugar cane, maize and cassava); in these cases the attacks of domestic dogs seem to be fatal for *Sapajus* spp. (*S. nigritus*: Ludwig et al. 2006; *S. xanthosternos*: Canale, unpublished data).

Invasive species are not fall back foods for yellow-breasted capuchins, as they eat them all year around independently of wild fruit availability. They are indeed an important part of their diet, consumed independently of wild fruit availability. Thus, the common understanding of filler fall-back foods as low-quality foods eaten during periods of food shortage, does not apply to cocoa, jackfruit and/or oil-palm fruits in the yellow-breasted capuchin diet, as all of them are high-quality foods, clumped and of easy access. High-quality fruits could be used as staple fall-back foods (Marshall and Wrangham 2007). This would imply that those resources are used more often when there is lack of other preferable resources, which is not the case.

There is no general pattern in which invasive plants are consistently more appealing to frugivores than native species (Buckley et al. 2006). Thus, reforestation of degraded areas with native species that yield abundant fleshy fruits for local frugivores might reduce invasive plant species success in attracting seed dispersers

(Gosper et al. 2006). Managing invasive plants has received little attention from park managers (D'Antonio and Meyerson 2002; Gosper and Vivian-Smith 2009).

All in all, the long-term survival of large populations of these critically endangered primates must be currently dependent on the accessibility of nutritious invasive species; this must also be true to the other five species of capuchins leaving in highly degraded landscapes in the Atlantic Forest and in the *Cerrado*. Thus, the removal of invasive plant species should be carefully planned to avoid affecting animal populations; as they might suffer from the immediate reduction of food, and also, from drastic changes in the spatial–temporal availability of resources, which might affect use of space, ranging patterns, group encounter rates and, ultimately, group social stability.

Conclusions

S. xanthosternos feed all year around on invasive species, such as oil-palm (*Elaeis guineensis*), jackfruit (*Artocarpus heterophyllus*) and cocoa (*Theobroma cacao*), swallowing seeds of the latter two. These invasive species are competing for seed dispersal by yellow-breasted capuchins; moreover, seeds of jackfruit and cocoa are being brought to natural environments across crop boundaries and human settlements, posing a real threat to protected areas that have them nearby.

Although the removal of invasive species would seem to be a straight-forward solution, those trees were brought to Bahia Atlantic Forest more than 250 years ago and nowadays they are important sources of food for a large group of endangered animals, such as yellow-breasted capuchin monkey (*S. xanthosternos*), golden-headed lion tamarin (*Leontopithecus chrysomelas*), Wied's black-eared marmoset (*C. kuhlii*), red-billed curassow (*C. blumenbachi*) and many other seed dispersers, such as coati (*Nasua nasua*), and collared peccary (*Pecari tajacu*).

The presence of non-indigenous plant species inside protected areas is being seriously neglected by authorities and conservationists in the Atlantic Forest. Land-use is one of the main issues in this relentlessly fragmented and human-encroached environment. Its ordination and planning must consider not only cropland locations and natural environment protection, but also plant–animal interactions and indigenous and non-indigenous species associations. Gradual and carefully planned removal of exotic plant species with aggressive invasiveness capability should be considered for protected areas and their buffer zones.

Finally, yellow-breasted capuchins are living in a fragmented environment surrounded by cropland and other human-modified habitats, such as forest in distinct levels of degradation. Its ability to crop-raid and exploit secondary forest, normally altered by human activities, imposes a new peril to its survival. Crop-raiding may generate human–animal conflict, which leads rural producers to hunt crop-raiders, such as capuchins. In addition, capuchins in human-modified habitats, such as secondary forest, may be more prone to be hunted or attacked by domestic dogs.

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Chapter 21
Coping with Fragmented Forests: The Critically Endangered Tonkin Snub-Nosed Monkeys (*Rhinopithecus avunculus*) in Viet Nam

Ramesh Boonratana and Xuan Canh Le

Abstract The Tonkin snub-nosed monkey *Rhinopithecus avunculus* is a critically endangered colobine whose current distribution is largely restricted to tropical evergreen forest patches associated with karst limestone hills and mountains of northern Viet Nam. Five isolated extant populations have been identified since its rediscovery in 1992. The fragmentation of its habitats has primarily been the result of decades of expanding human population and increasing demands for scarce agriculturally lands. Habitat fragmentation has frequently been identified a major cause for declines of primate populations, including the Tonkin snub-nosed monkey. However, given that habitats of known Tonkin snub-nosed monkey populations were long fragmented prior to a pioneering study in 1993, the population decline over recent decades can likely be attributed to hunting activities. Comparative observations at two sites suggest that the Tonkin snub-nosed monkey, if effectively protected, is likely to persist for decades in small isolated, undisturbed forest fragments of even just 10 km^2. In addition, isolated forest fragments should be regarded as important refuges for biodiversity conservation, particularly in regions where little forest remains.

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Introduction

Globally, *Rhinopithecus avunculus* is categorized as Critically Endangered according to the 2011 IUCN Red List of Threatened Species (Le and Le et al. 2008), and is listed in the Appendix I of CITES (Fig. 21.1). In Viet Nam, the species is similarly categorized as Critically Endangered according to Viet Nam's Red Data Book (MoSTE 2000) and is listed in the Appendix I of GoV Decree No. 48/2002. An analysis in the early 2000s suggested *R. avunculus* to be one of the highest priority primate taxa in Viet Nam deserving immediate conservation action to ensure that they do not become extirpated or extinct (Boonratana et al. 2001). The conservation status of *R. avunculus* is so dire that it was considered to be amongst the most endangered primates worldwide and the most in need of urgent conservation measures at the fifth and sixth iteration of the biennial listing of a consensus of 25 primate species (Mittermeier et al. 2009).

Since its confirmed sighting in 1992 (Ratajszczak et al. 1992), there have been a number of commendable efforts to conserve the species, mostly in the form of status surveys, habitat protection, and conservation education (Hoang 2009). To date, the presence of *R. avunculus* is confirmed in only five totally isolated locations (Fig. 21.2), namely Tat Ke, Nam Trang-Ban Bung, Cham Chu, Khau Ca, and Tung Vai (Le et al. 2009), although Nam Trang-Ban Bung and Cham Chu require a reassessment to confirm their continued presence (Table 21.1).

Fig. 21.1 A Tonkin Snub-nosed monkey male in the Na Hang Nature Reserve. Photo by Dong Thanh Hai

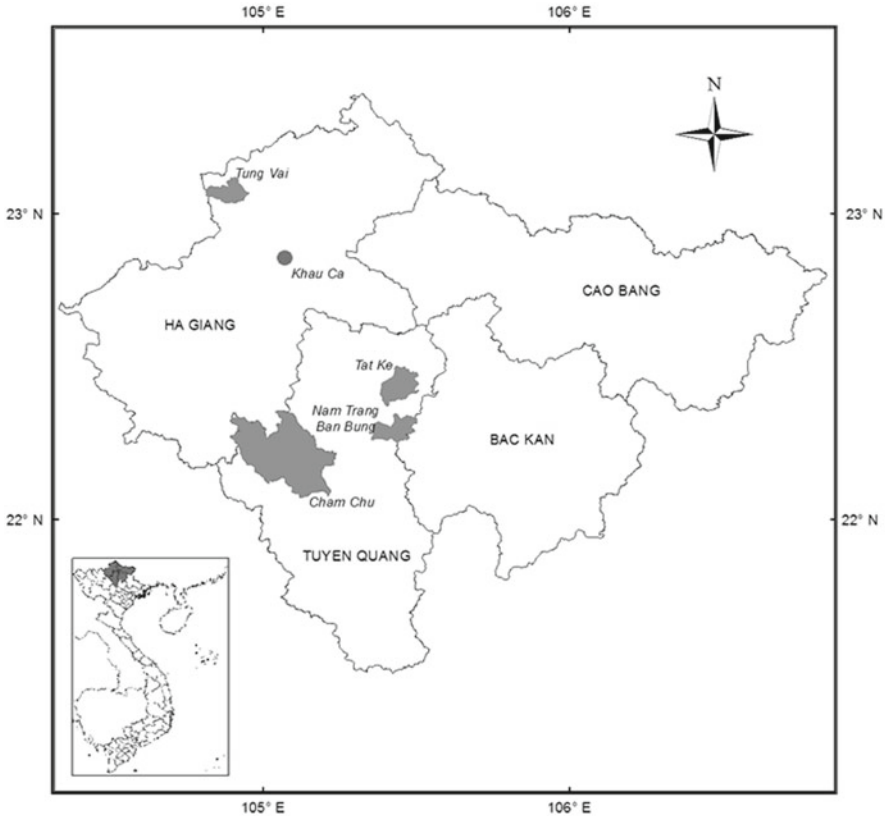

Fig. 21.2 Confirmed locations of *Rhinopithecus avunculus*

Given their rarity and the difficult terrain, very few studies have been carried out on this species. A pioneering 6-month study (Boonratana and Le 1994, 1998a,b) was carried out at Tat Ke and Nam Trang-Ban Bung in the early 1990s. Tat Ke and Nam Trang-Ban Bung are two separate sectors of the Na Hang Nature Reserve. Almost a decade-and-a-half later, a 2-year study was carried out at Tat Ke and Khau Ca (Dong 2007). Around the same time, another long-term research and conservation ongoing effort was initiated at Khau Ca which resulted in it being declared a Species Habitat Conservation Area (Covert et al. 2008). Despite the constraints, all these studies have resulted in providing valuable scientific information of this little known taxon.

Despite a long history of massive deforestation and land conversion throughout its distributional range, isolated populations of *R. avunculus* have somehow persevered, albeit being mostly restricted to forest habitats associated with steep karst limestone hills and mountains. This might be a testament to the species ability to cope, over several decades, with small, fragmented and isolated habitats. However, repeated observations at Tat Ke in 1993 (Boonratana and Le 1994, 1998a,b) and

Table 21.1 Number of *R. avunculus* reported at Tat Ke and other sites

Site	Year	Obs.[a]	Est.[b]	Remarks	Source
Tat Ke, Na Hang NR	1992	–	40–50	Interview data	Ratajszczak et al. (1992)
Tat Ke, Na Hang NR	1993	72	80	3 OMUs & 1 AMU	Boonratana and Le (1994, 1998b)
Tat Ke, Na Hang NR	1997	–	40	Villager report	Boonratana (1999)
Tat Ke, Na Hang NR	1998	13	16	1 OMU	Boonratana (1999)
Tat Ke, Na Hang NR	1999	–	30		Tinh in Nadler et al. (2003)
Tat Ke, Na Hang NR	2000	–	50		FPD,[c] in Le and Boonratana (2006)
Tat Ke, Na Hang NR	2001	–	40		FPD, in Le and Boonratana (2006)
Tat Ke, Na Hang NR	2002	–	30		FPD, in Le and Boonratana (2006)
Tat Ke, Na Hang NR	2004	–	40		Wolters (2004)
Tat Ke, Na Hang NR	2005	6	7	1 OMU	Boonratana (2005)
Tat Ke, Na Hang NR	2005	17	22	2 OMUs and 1 AMU	Dong (2007)
Tat Ke, Na Hang NR	2005	–	100	Guesstimate	Le Hong Binh, in Le and Boonratana (2006)
Nam Trang-Ban Bung, Na Hang NR	1992	12	90–110	Interview data	Ratajszczak et al. (1992)
Nam Trang-Ban Bung, Na Hang NR	1993	23	50		Boonratana and Le (1994, 1998b)
Nam Trang-Ban Bung, Na Hang NR	1996	4	–		Hill et al. (1996)
Nam Trang-Ban Bung, Na Hang NR	1998	35	–		Dinh Ngoc Luong in Boonratana (1999)
Nam Trang-Ban Bung, Na Hang NR	1998	–	20–30	Villager report	Boonratana (1999)
Nam Trang-Ban Bung, Na Hang NR	1998	–	40–50	Villager report	Boonratana (1999)
Nam Trang-Ban Bung, Na Hang NR	1999	–	40–45		Dang and Nguyen (1999)
Nam Trang-Ban Bung, Na Hang NR	2000	25	–		FPD, in Le and Boonratana (2006)
Nam Trang-Ban Bung, Na Hang NR	2001	23	–		FPD, in Le and Boonratana (2006)
Nam Trang-Ban Bung, Na Hang NR	2002	6	–		FPD, in Le and Boonratana (2006)
Nam Trang-Ban Bung, Na Hang NR	2005	–	50	Guesstimate	Le Hong Binh, in Le and Boonratana (2006)
Cham Chu NR, Tuyen Quang Province	1992	–	20–40	Interview data	Ratajszczak et al. (1992)
Cham Chu NR, Tuyen Quang Province	1999	–	22–25	Interview data	Dang and Nguyen (1999)
Cham Chu NR, Tuyen Quang Province	2001	8	70		Long and Le (2001)

(continued)

Table 21.1 (continued)

Site	Year	Obs.[a]	Est.[b]	Remarks	Source
Khau Ca SHCA, Ha Giang Province	2001	–	30–40	Interview data	La and Trinh (2001)
Khau Ca SHCA, Ha Giang Province	2002	–	50–60		Le (2002a)
Khau Ca SHCA, Ha Giang Province	2005	29	50	≥2 OMUs	Covert et al. (2008)
Khau Ca SHCA, Ha Giang Province	2006	81	90	5–6 OMUs and 1 AMU	Dong (2007)
Kien Thiet Forest, Tuyen Quang Province	1992	–	20–40	Interview data	Ratajszczak et al. (1992)
Khuoi Muoc & Khuoi Chang areas, Bac Kan Province	1999	–	18–20	Interview data	Dang and Nguyen (1999)
Tat Pet area, Bac Kan Province	1999	–	6	Interview data	Dang and Nguyen (1999)
Nam Xuan Lac SHCA, Bac Kan Province	1999	–	18–20	Interview data	Dang and Nguyen (1999)
Nam Xuan Lac SHCA, Bac Kan Province	2002	–	4–5	Interview data	Bezuijen and Trinh (2003)
Tam Tao PNR, Bac Kan Province	2000	–	5–7	Interview data	Le and Simmons (2002)
Yen Tu NR, Quang Ninh Province	2002	–	5–10	Interview data	Le (2002b)
Duc Xuan Commune, Ha Giang Province	1999	–	8–10	Interview data	Dang and Nguyen (1999)
Na Chi Commune, Ha Giang Province	2001	–	10–20	Interview data	Le (2001)
Tung Vai Commune, Ha Giang Province	2008	14	15–20	2 groups(?)	Le and Vu et al. (2008)

[a] Observed
[b] Estimated
[c] Forest Protection Department

later in 1998 (Boonratana 1999) and 2005 (Boonratana 2005; Le and Boonratana 2006; Dong 2007), showed a severe decline in *R. avunculus* population, although the forested habitats within the species known home range being relatively more mature and denser then when first observed in 1993.

Here we describe the nature of the habitat loss, fragmentation, and degradation in the Na Hang Nature Reserve, in comparison with studies at Khau Ca SHCA, and attempt to explain *R. avunculus* ability to cope with small, fragmented, and isolated forests. In addition, specific to studies at Tat Ke, we describe the observed population decline and the cause for the decline. We also describe changes in *R. avunculus* social organization and some of its behaviors and attempt to explain the underlying reasons to these changes. Moreover, we propose conservation implications of small and isolated forest fragments for *R. avunculus* populations, and the evolutionary implications of ecological pressures on the social organization of the species.

Study Area

The Na Hang Nature Reserve is located in Tuyen Quang Province, northern Viet Nam. It was declared a provincial protected area in 1994 by the Tuyen Quang People's Committee Decision No. 274/QD-UB to cover a total land area of 41,930 ha. This comprised 27,520 ha strict protection area, 12,910 ha forest rehabilitation area, and 1,500 ha administration and services area. The nature reserve consists of two noncontiguous sectors: Tat Ke in the north-western part of Na Hang District and Nam Trang-Ban Bung to the east. There is little surface water during the dry season and due to its limestone geology, much of the water is quickly drained into underground streams.

Biogeographically, the Na Hang Nature Reserve falls within the Tonkin subdivision of Delacour and Jabouille's (1931) classification, or Thailandian Monsoon Forest (unit 4.10.4) of Udvardy's (1975) classification, or South China (unit 6a) of MacKinnon and MacKinnon's (1986) classification for the Indo-Malayan Realm. The natural vegetation comprises mostly tropical lowland and lower montane broadleaf mixed evergreen and semievergreen forests (Le et al. 2004). Most of the habitats in the two sectors, however, have been disturbed to different degrees, resulting in a mosaic of habitat types. This includes remnants of fragmented tropical primary evergreen forests, largely confined to the steeper limestone hills and mountains, patches of secondary growth, human settlements, and areas of permanent and shifting cultivation. The steep rugged limestone hills and mountains cover about two-thirds of the nature reserve. The altitude at Tat Ke ranges from 200 to 1,200 m and the forest cover in 1993 was estimated to be about 6,000 ha. The altitude at Nam Trang-Ban Bung ranges from 300 to 1,150 m and the forest cover was estimated to be about 12,000 ha (Boonratana and Le 1994, 1998a).

The climate in the nature reserve is typically influenced by the southwest monsoon during the wet season (April to September), with a total rainfall recorded at more than 1,600 mm, and the cold northeast winds in the dry season (October to March). Temperatures typically range from 10 to 38 °C.

Observations

Habitat Loss, Fragmentation, and Degradation

Much of the Na Hang Nature Reserve has been partially logged and subjected to various forms of land clearance. Although logging operations ceased in the early 1980s, old logging tracks remain visible, and evidence of occasional log poaching was observed right into the mid-2000s (Boonratana and Le 1994; 1998b; Boonratana 1999; Dong 2007). Dinh (1998, in Boonratana 1999) reported local inhabitants' extraction of timber ranging from 1 to 1.5 m^3/annum, 70 % of which was traded.

In addition, a number of loggers remained behind and established small settlements. These and other settlements in and around the nature reserve typically practice cultivation in the valleys and along the gentler slopes that further reduced and fragmented the remaining habitats.

A strong cultural preference among some communities for shifting cultivation practices and allowing their livestock range freely has exacerbated habitat fragmentation and degradation. Observations in the mid-2000s indicate that enforcement over the years has been successful in curtailing shifting cultivation practices, and no new clearance was observed (Boonratana 2005). Until 1994, gold prospecting was common in Nam Trang and areas suspected to contain gold deposits were cleared and excavated, mostly within the valleys, along rivers and intermittent streams. At times these activities affect areas as large as 100 ha (Boonratana and Le 1994, 1998b).

In late 2002, work on a 342-MW hydroelectric dam project was initiated along the Gam River, close to Pac Ta Mountain. The Na Hang Dam having a 92-m rock fill and 718-m crest length was expected to have a flood control reservoir of more than 81 km^2. In addition, it is expected that the surface area, when fully inundated, would cover approximately 57 km^2 (UNEP 2007), and cause Na Hang Nature Reserve to lose about 220 ha to the raised water level (Scott Wilson Asia Pacific Ltd. 2000). New settlements and infrastructure development that accompanied the hydroelectric dam construction, such as new roads or accommodation, have further fragmented and degraded parts of the nature reserve. Explosives used for the hydroelectric dam construction that could be heard and felt all the way to the Na Hang town, are likely to cause undue stress to *R. avunculus* located nearby.

NTFP Collection and Wildlife Poaching

Collection of non-timber forest produce (NTFP) was common throughout the initial studies (Boonratana and Le 1994, 1998b; Boonratana 1999), but reduced somewhat during the later study (Boonratana 2005). Bamboo in particular was collected for constructing homes and shelters, and for making household utensils. Bamboo shoots, rattan, and honey were regularly harvested for local use and trade in nearby townships, whereas fruits of *Dracontomelon duppereanum* (Anacardiaceae) and *Canarium album* (Burseraceae) were harvested for trade in major towns. Fruits were frequently harvested by felling the trees. Dinh (1998, in Boonratana 1999) reported local inhabitants' average consumption of fuelwood ranging from 30 kg/household in summer to 50 kg/household in winter. Information on NTFP harvested from the Na Hang Nature Reserve for 1998 (Dinh 1998; Nguyen et al. 1998) are detailed in Boonratana (1999).

In 1993, wildlife trapping and hunting were widespread throughout the nature reserve, and although species harvested varied among the ethnic groups, literally all mammal and most reptiles and amphibians present in the nature reserve were harvested. The meat of *R. avunculus*, although not considered particularly appealing to some ethnic groups, are eaten by some groups while others particularly prize the stomach along with its contents of digested plant matter. Occasionally the body parts are prepared to treat fatigue, or the bones prepared into a medicinal balm for curing chronic musculoskeletal disorders. Throughout its current range, the animal, its body parts, or finished medicinal products are traded both domestically and to neighboring China.

In the latter part of 1993, the authors communicated the issue of wildlife poaching to the Na Hang District People's Committee and this has largely succeeded in curbing hunting and trapping activities. Although some hunting was still reported in 1998 (Boonratana 1999), it was at relatively lower levels compared to that initially reported in 1993. However, observations from September 2004 to August 2005 showed that hunting had increased dramatically, with five to seven gunshots heard daily (Boonratana 2005; Dong 2007). The relative density of large mammals was generally low and the distribution appeared patchy, all primate species previously recorded were rarely observed, if ever. In an earlier study, Nguyen et al. (2003) reported wildlife hunting in the Na Hang Nature Reserve appeared to be under control and attributed this to the gun collection program in 2001. Details on wildlife harvested from the Na Hang Nature Reserve (Dinh 1998; Nguyen et al. 1998) are provided in Boonratana (1999) and on traded wildlife species are provided in Nguyen et al. (2003).

The increased hunting reported by Boonratana (2005) and Dong (2007) was very likely due to an increased demand for wild meat created in part by the sudden presence of more than 10,000 hydroelectric dam construction workers in Na Hang. This was evidenced by a high number of restaurants in the towns offering wild meat on their menu and wine concoctions containing whole wildlife or their body parts. An evaluation on the wildlife trade in the district town made similar observations and assessment (Nguyen et al. 2003). Wildlife poaching was probably made worse by the easier and uncontrolled access into the nature reserve, and between Na Hang and other major towns, including Hanoi. Moreover, to supplement their income to meet rising costs of necessities and other goods associated with the influx of construction workers, local inhabitants living in around the nature reserve have had to rely more on the forest produce, including wildlife.

Findings and Discussion

Given the short duration of the initial work (Boonratana and Le 1994, 1998b), no quantitative data on the structure and composition of the vegetation was obtained. Nevertheless, a qualitative assessment in 2005 show trees to be more mature and denser as compared to 1993 (Boonratana 2005). Apparently a ban on shifting cultivation and better enforcement has been effective in curtailing this activity, and to a lesser extent, in curtailing illegal timber extraction.

A comparison of the vegetation data collected at Tat Ke and Khau Ca (Dong 2007) provides support to the qualitative observations described above, as both sites represent isolated remnants of *R. avunculus* forest associated with karst limestone habitats. By measuring trees 6 cm dbh (diameter at breast height), Dong (2007) determined that in 0.64 ha there were 612 trees with a mean basal area at 21 cm dbh, and 151 species from 50 families at Tat Ke. Thus, the tree density was 956.25 trees/ha and the total basal area was 58.95 m^2/ha. At Khau Ca, Dong (2007) measured 512 trees with a mean basal area at 17.4 cm dbh, and 136 species from 49 families in 0.58 ha, giving a tree density at 882.76 trees/ha, and the total basal area at 34.77 m^2/ha. The differences in the mean and total basal areas and the tree density between the two sites shows that the forested habitats at Tat Ke are more mature and denser, even if the baseline data at Tat Ke of the 1990s were not available.

The basic social structure of *R. avunculus* comprises the one-male unit (OMU); with extra males forming a loosely bonded all-male unit (AMU), and different units frequently coming together to form a larger band (Boonratana and Le 1994, 1998a). Repeated censuses of *R. avunculus* groups, comprising three OMUs and one AMU, and two complete counts of the band at Tat Ke over 3 months in 1993 yielded a population of 80 individuals (72 minimum; Table 21.1). Although reliable counts of one OMU in 1998 and another OMU in 2005 were obtained, these numbers were unlikely to be representative of the population. Nonetheless, reliable population estimates post-1993 until 2004 suggest that the population has been reduced by half. Supported by a small team, Dong (2007) carried out repeated censuses of *R. avunculus* groups and the band over a year and could only determine the presence of at least 17 individuals and no more than 22 individuals. Hence, between 1993 and 2005, there has been a drastic decline in *R. avunculus* population at Tat Ke. In the same year, Le Hong Binh (personal communication in Le and Boonratana 2006) estimated a population of 100 individuals present at Tat Ke, but this is a crude estimate since no reliable verification could be made. Data for other sites collected at different times suggest changes to the population size (Table 21.1).

The drastic population decline at Tat Ke in those 13 years cannot be attributed to habitat loss and fragmentation, although Tat Ke has lost some area to the hydroelectric dam construction, this area was outside the population's recorded area of use (Boonratana and Le 1994, 1998a). Having completely overlapping home ranges, and exhibiting intergroup tolerance and an absence of defense for widely distributed food resources (Boonratana and Le 1994, 1998a) would not necessitate *R. avunculus* persisting at a lower population size to compete for food resources. Habitat fragmentation and isolation of *R. avunculus* populations occurred long before the species was rediscovered in 1992, when Tuyen Quang Province was reported by De Koninck (1999) to have only 7.2 % natural forest cover remaining. The *R. avunculus* habitats at Tat Ke in 2005 were more mature and denser than in 1993, and the forests at Khau Ca, despite having lower mean and total basal areas, could support a much higher *R. avunculus* population, resembling that at Tat Ke in 1993. All of these observations lead us to reject the notion that this decline is due to habitat loss. Hence, the most plausible explanation causing *R. avunculus* population at Tat Ke to decline drastically is hunting. The lack of evidence and sighting of other large mammals strongly suggested that species previously recorded in the early 1990s were either persisting at very low densities or are extirpated. Sightings of *Macaca assamensis* and *M. mulatta* were extremely rare, and *M. arctoides* were no longer observed (Boonratana 1999, 2005; Dong 2007). Hunting is very likely causing the reported decline in *R. avunculus* populations elsewhere. Many published and unpublished reports cited hunting being common in areas where *R. avunculus* have been recorded, and cite that *R. avunculus* were rarely encountered, if at all, during surveys. In addition, although *R. avunculus* is not a species targeted for local use or trade, the increased demand for wildlife meat caused by the sudden increase in human population, and the species behavior of not fleeing immediately upon human contact, places them at a very high risk of being opportunistically killed by hunters.

Besides reducing the population size, a long history of hunting has apparently affected the social organization and behavior of *R. avunculus* at Tat Ke. This population exhibits a smaller group size and a lower frequency at which groups exhibited intergroup associations. While still exhibiting a multilevel society, comprising OMUs, AMUs, and the band, later observations (Le and Boonratana 2006; Dong 2007) showed the mean OMU size at Tat Ke had reduced by more than half (Table 21.2). Had there been no decline in mean OMU size at Tat Ke due to hunting, it might have been possible to attribute the difference with Khau Ca to a higher availability of food (Wilson 1975), larger size of food sources (Clutton-Brock and Harvey 1978), large patches of uncontested food resources (Wrangham 1987), and large clumped food sources (Struhsaker and Leland 1979) there. However, this was not the case.

Various studies have shown primates adopting one or more strategies to avoid predation. In group-living primates, predation is proposed to lead to larger group sizes to improve detection or reduce the probability of being captured (Dunbar 1988; Krebs and Davies 1993). However, evidence of *Panthera pardus*, the only predator recorded in Tat Ke large enough to predate on *R. avunculus*, was last reported in 1993 (Boonratana and Le 1994). Hunting of *R. avunculus* by humans cannot be considered the same as natural predation and may lead to different responses. All researchers, villagers, and hunters report that *R. avunculus* do not immediately flee upon detecting humans. Instead, they start uttering loud and rapid alarm calls, and some individuals, particularly the resident male, would approach the people. This behavior, unfortunately, makes them more susceptible to hunters. Hence, we suggest that the small group sizes now observed is due to a continuous hunting pressure, rather than a strategy to cope with hunting.

The mean ratio of OMU adult male to adult females has similarly reduced. A lower mean adult male to adult females sex ratio in OMUs suggest low numbers of extra males, therefore threat from harassment, male takeovers, and infanticide is lower (Grueter and van Schaik 2010). It is also interesting to note that the mean ratio of OMU adult male to adult females at Khau Ca (Dong 2007) was similar to that observed at Tat Ke in 1998 and 2005 (Table 21.2). Paucity of comparative ecological data does not allow this similarity to be explained. However, it should be noted that data at Khau Ca was based on four OMUs with reliable age/sex composition, out of the five or possibly six OMUs observed at Khau Ca (Dong unpublished data); hence, the actual mean OMU size and mean ratio of OMU adult male to adult females might be different than that reported.

Table 21.2 Age/sex composition of *R. avunculus* OMUs reported at Tat Ke and other sites

Year	A♂	A♀	SA♀	OJ♂	OJ	YJ	J♀	J	I	?	Obs.	Est.	$\bar{x}$	A♂:A♀	Site	Source
1993	1	7	2	1	4	–	–	3	6	–	24	24	15.2	1:5.7	Tat Ke	Boonratana and Le (1994, 1998b)
1993	1	6	–	–	3	–	–	3	5	–	18	20				
1993	1	4	1	–	1	–	–	–	4	–	11	16				
1994	1	4	–	–	–	–	–	6	–	2	13	20	11.5	1:3	Nam Trang-Ban Bung	Boonratana and Le (1994, 1998b)
1994	1	3	–	–	–	–	–	–	–	6	10	20				
1998	1	3	1	–	–	–	–	3	1	4	13	16	13	1:3	Tat Ke	Boonratana (1999)
2005	1	3	–	–	–	2	–	–	–	–	6	7	6	1:3	Tat Ke	Boonratana (2005)
2005	1	4	–	–	–	–	–	–	1	–	6	–	7	1:3.5	Tat Ke	Dong (2007)
2005	1	3	–	–	–	–	–	4	–	–	8	–				
2006	1	2	1	–	–	–	3	–	1	–	8	–	11.3	1:3.8	Khau Ca	Dong (2007)
2006	1	5	2	–	–	–	3	–	2	–	13	–				
2006	1	6	1	–	–	–	3	–	4	2	15	–				
2006	1	2	2	–	–	–	1	–	1	–	7	–				

$\bar{x}$ based on observed numbers only

A = adult; SA = subadult; OJ = older juvenile; YJ = Young juvenile; J = juvenile; I = infant; ♂ = male; ♀ = female; ? = age/sex indeterminate

In 1993, Boonratana and Le (1994, 1998a) reported observing different *R. avunculus* units frequently forming large aggregations at sleeping sites and feeding trees and sometimes travelling together. Similarly, various researchers at Khau Ca all reported groups forming aggregations of various sizes and Dong (unpublished data) reported band sizes ranging from 22 to 81 individuals. These data imply that intergroup associations were common, and that banding was likely an aggregation to exploit large food sources that were very unpredictable in space and time (Boonratana 2003; Homewood 1978; Kirkpatrick et al. 1999), or that there was weak intergroup competition for food resources (Isbell 1991). However, the rarity at which groups were observed to band together at Tat Ke during a later study (Boonratana 2005; Dong 2007) might be due to a lack for a need to form temporary aggregations for exploiting localized and seasonally unpredictable food resources, to improve harvest efficiency, or for avoiding predators. Nevertheless, with the absence of intergroup competition for food resources, their occasional aggregations might simply be a response to their needs to socialize.

Detailed observations on intergroup associations are needed to provide better explanations to banding behavior. Nevertheless, infrequent banding might also confer some benefits to small populations, possibly by reducing the rate at which the population would become genetically less diverse, the chances of being detected, intergroup competition for resources (food, shelter, and mates), or the pressure to increase group sizes. Similarly, there are a number of possible benefits to having smaller group sizes. This might include a prolonged male tenureship, decreased chances of being detected, reduced intra-group competition for food and shelter, reduced female-female competition to access the resident male, reduced social stress, and male investment in parental care. Although not quantified, Boonratana (unpublished data) observed in 1998 and 2005 that *R. avunculus* groups were apparently less gregarious compared to when observed in 1993 and 1994. Whether *R. avunculus* groups have become cryptic in response to hunting pressure, or simply exhibiting behaviors that are normal to small social units needs further investigation.

In 1993, Boonratana and Le (1994, 1998a), estimated the population density of *R. avunculus* at Tat Ke at 7.2–8 individuals/km^2 or at an estimated biomass up to 48 kg/km^2, but later observations (Dong 2007) show a population density of 1.7–2.2 individuals/km^2 or at an estimated biomass up to 13.2 kg/km^2. However, observations at Khau Ca (Dong 2007), which had less dense and mature tree composition, exhibited a population density of 8.1–9.0 individuals/km^2 or at an estimated biomass up to 54 kg/km^2, slightly higher than at Tat Ke in 1993. Although differences in plant species composition and phenology have to be taken into account, observations suggest that small isolated forest fragments of at least 10 km^2 can support a viable population of 80–90 individuals. If reports of the presence of up to 200 individuals prior to 1990s were correct, then such small isolated forest fragments can support up to 20 individuals/km^2 or at an estimated biomass up to 120 kg/km^2 (Boonratana and Le 1994, 1998b). Thus, the conservation value of small isolated forest fragments serving as important refuges for the critically endangered *R. avunculus* should not be underestimated.

Conclusion

The continued existence of *R. avunculus* populations in small remnant habitats that have been totally isolated for several decades is evidence that the species is able to cope with forest fragmentation over this timeframe, but only if certain conditions are met. Specifically, this includes having at least 10 km^2 of intact habitat free from anthropogenic pressures, particularly from hunting. The species continued existence is statement to the conservation value of small, isolated forest fragments.

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Chapter 22
Fragmented Primate Population of Nepal

Mukesh K. Chalise

Abstract Loss of natural habitat due to the expansion of crop fields is inevitable in a country with more than 83 % of the rural agriculture-based human population dependent upon natural resources for their livelihood. Nearly 25 % of Nepal is officially protected habitat, but these protected areas are fragmented and not all are suitable for primates. Deforestation drives the dispersal of primates increasingly into areas of human settlement and agricultural lands, and ultimately leads into conflict—as is frequently reported in local newspapers. The intact wild areas of Nepal are fragmented due to physical infrastructure with highway and human settlements poured around and through the forests, further exacerbated by extreme fuelwood and timber extraction. One of the driving forces behind land use issues is national politics. Six species of monkeys are from Nepal: the macaques—Rhesus (*Macaca mulatta*) and Assamese (*Macaca assamensis* 2 species?) and the Hanuman Langurs—*Semnopithecus ajax, Semnopithecus hector*, and *Semnopithecus schistaceus*. These monkey species are found in different phyto-ecological zones from the lowland Tarai plain to the valleys of high mountains. This chapter reports on census data across Nepal obtained from different research activities, including historical records since the 1970s, and discusses habitat composition with respect to the human–primate conflict throughout the agroforestry landscape.

Background

Nepal is situated on the southern slopes of the central Himalayas and occupies a total area 147,181 km^2. The country is located between latitudes 26°22′ and 30°27′ N and longitudes 80°40′ and 88°12′ E (Fig. 22.1).The average width of the country

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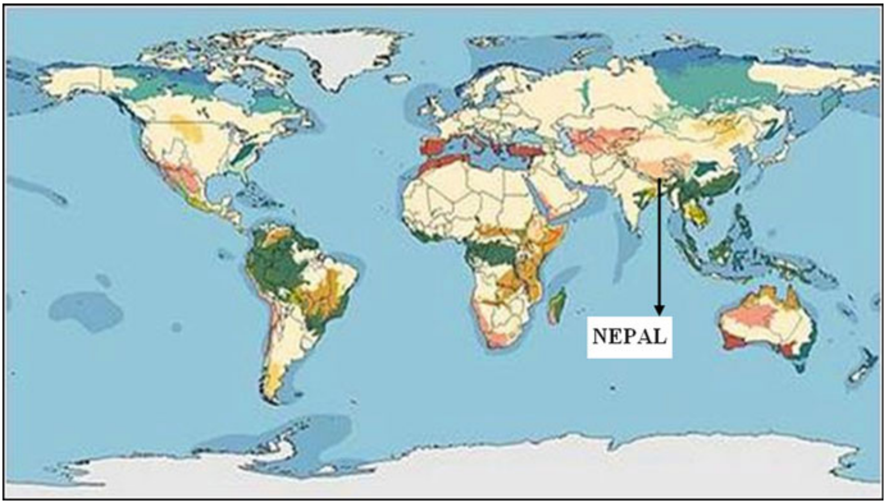

Fig. 22.1 Location of Nepal

is 885 km from east to west and the length varies from 145 to 241 km with a mean of 193 km north to south. Hills and high mountains cover about 86 % of the total land area and the remaining 14 % are the flatlands of the Tarai, which are less than 300 m in elevation. Altitude varies from some 60 m above sea level in the Tarai to Mount Everest (Sagarmatha) at 8,848 m, the highest point in the world. Nepal's biodiversity is a reflection of its unique geographic position, altitudinal, and climatic variations. Nepal's location in the central portion of the Himalayas places it in the transitional zone between the eastern and western Himalayas. It incorporates the Palaearctic and the Indo-Malayan biogeographical regions and the major floristic provinces of Asia (the Sino-Japanese, Indian, western and central Asiatic, Southeast Asiatic, and African Indian desert), creating a unique and rich terrestrial biodiversity.

Wide altitudinal variations and diverse climatic conditions have resulted in four main physiographic zones and seven climatic conditions in Nepal. The extreme altitudinal gradient has resulted in seven bioclimatic zones from tropical to nival within a short horizontal span (Table 22.1).

Historic Primate Research in Nepal

Primate research in Nepal was started in the 1970s on rhesus monkeys (*Macaca mulatta*) in urban areas mostly near religious places and latter, on the langurs. The first publication on monkeys in Nepal was in Southwick and Siddique (1974). Earthwatch group, U.K. and Nepali students for the partial fulfillment of M. Sc. thesis under the Central Department of Zoology at Tribhuvan University, Nepal did some researches around 1980s on the behaviours of rhesus monkeys (*M. mulatta*)

Table 22.1 Physiographic zones of Nepal. *Source*: LRMP (1986)

Physiographic zone	Area (%)	Elevation (m)	Climatic zonation	Species
High Himal (Northern parts)	23	above 5,000	Tundra-type and Arctic	–
High Mountains (North/Mid)	20	4,000–5,000	Alpine	–
		3,000–4,000	Subalpine	Langur
Mid-hills	30	2,000–3,000	Cool temperate monsoon	Assamese, Langur, Rhesus
		1,000–2,000	Warm temperate monsoon	Assamese, Langur, Rhesus
Lowlands (Tarai and Siwalik Hills) (South parts of country)	27	500–1,000	Hot monsoon and Subtropical	Assamese (?) Langur, Rhesus
		below 500	Hot monsoon and Tropical	

around Kathmandu. A report on the monkeys of Nepal was also published by Adit (1979). The research on the *Presbytis entellus* in Nepal was accomplished by American primatologists (Chalise 1995; Bishop 1975; Curtin 1975; Boggess 1976)) studying on langurs of high altitude areas of Melamchi and SoluKhumbu, Nepal. In 1990, Dr. Paul Winkler (Institute of Anthropology, University of Gottingen, Germany) started research on the Hanuman langur monkeys (*Semnopithecus entellus*) living around Ramnagar village of Chitwan, Nepal. This preliminary research led to the establishment of the Ramnagar Monkey Research Project (RMRP) in 1991 by Prof. Dr. Christian Vogel (Institute of Anthropology, University of Gottingen, Germany) in collaboration with the Natural History Museum, Tribhuvan University, Nepal. One Nepali joined this project in March 1992, to collect the data on langurs' sex differences in feeding behavior and finished by 1995. The aim of the RMRP project was to study the ecology and sociobiology of the langurs in the Sal (*Shorea robusta*) forest around Ramnagar living in multi-male groups. The result was supposed to compare with data on langurs living around Jodhpur, India in predominantly one-male groups (Chalise 1995). The influence of ecological factors on the evolution of social organization was instigated in this research: "By now, the one-male troops and all-male bands of the common langurs are well studied; whereas, some information is available on multi-male troops and causes for social flexibility in langurs are not yet understood" (Borries, et al. 1993).

Primates of Nepal

*Langur (*Semnopithecus *sp.)*

The vernacular names of Langurs in Nepal are Langoor, Kalomukhe Bandar, Lampuchhre Bandar, Phetawal Bandar, Kaldhaure, and Guna. Collectively in English they are referred to as the "Hanuman" langurs. The genus was formerly

Fig. 22.2 *Semnopithecus hector* (Tarai), *S. schistaceus* (mid-mountains), and *S. ajax* (higher elevation of the Himalaya). Photos by: M. K. Chalise

known as *Presbytis*; however, it is recently changed to *Semnopithecus*. Three distinct species were identified by the Conservation Assessment and Management Plan (CAMP) workshop 2003 for Nepal (Chalise 2003a, b, 2010a, b) are: the Western Himalayan Langur (*Semnopithecus ajax*)—Endangered, the Lesser Hill Langur (*S. hector*)—Near Threatened, and the Nepal Grey Langur (*S. schistaceus*)—Least Concern (Fig. 22.2). *S. ajax* is reported from East Langtang, Melamchi area, *S. hector* from Central to West Nepal in outer Tarai, and *S. schistaceus* is reported from south to north in Central Nepal (Chitwan, Kathmandu, Langtang).

These are the largest primates in Nepal reaching up to one meter of head and body length alone, with the addition of the tail to over two meters. Males are larger and heavier than females and range between 7 and 20 kg. Largely folivorous, but because of their size and terrestriality, they can be fierce crop raiders.

*Rhesus Macaque (*Macaca mulatta*)*

The local vernacular names of rhesus monkeys are Rato Bandar, Hajariya, Aule, and Bandar (Fig. 22.3). The IUCN categorizes these species as Least Concern since their pan-Asian metapopulation is quite large. Males have body length 48–64 cm and weigh 6.5–12 kg; whereas, females have body length 45–55 cm and weigh 5.5 kg on average. They mostly feed on fruits, seeds, roots, green leaves, inner barks and small invertebrates.

As the most common primate species in the world, the rhesus monkey exhibits considerable adaptability. They occur from low-lying flat lands to the foot of the Himalayas up to 4,000 m. They are found in temperate coniferous, moist and dry

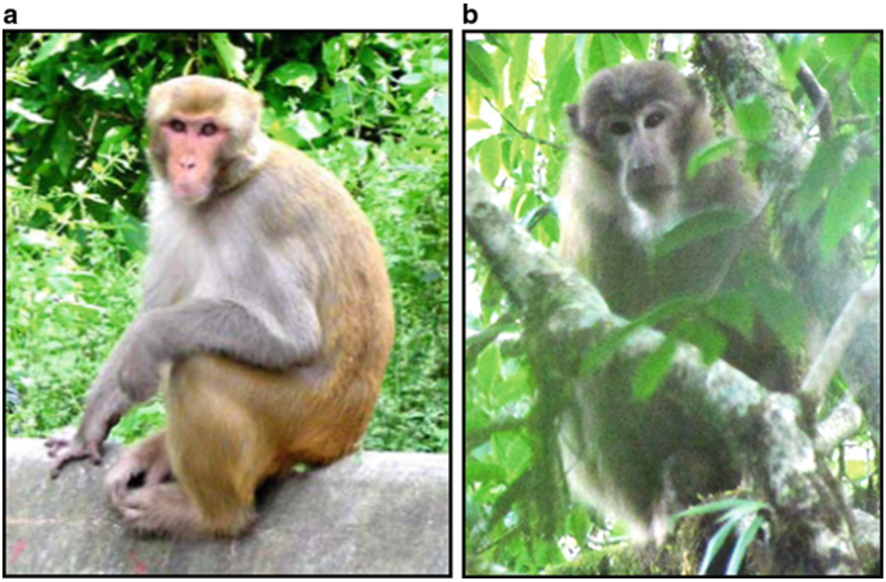

Fig. 22.3 Males of (**a**) *Macaca mulatta* and (**b**) *M. assamensis*

deciduous forest, mangrove, scrub, rain forest, cropland, human habitation, temples, mixed and bamboo forest. They can tolerate vast climatic and vegetative zones (Roonwal and Mohnot 1977), and are numerous throughout Nepal.

*Assamese Macaque (***Macaca assamensis***)*

The local vernacular names of the Assamese monkeys are Kalo Bandar, Pahare Bandar, Pupa, Timnyau, and KalaGanda. Considered distinct and likely endemic to Nepal, they are referred to as the "Nepal Population" by CAMP (2003), as they are awaiting taxonomic revision (Sanjay et al. 2003; Chalise 2008). It is also possible that within Nepal two forms may occur with a distinct difference found between the higher elevation and lower elevation populations between 380 and 2,350 m (Chalise 2003a, b, 2008). At present they are grouped within the larger Assamese metapopulation and are classified as Near Threatened by the IUCN. Assamese monkeys are similar to rhesus in a generalized "macaque" way, but locals describe them as "missal" or mixed for their color variation within groups. Assamese monkeys tend to be larger and heavier than rhesus, with males and females weighing more than 12 kg on average, and having a head and body length greater than 60 cm.

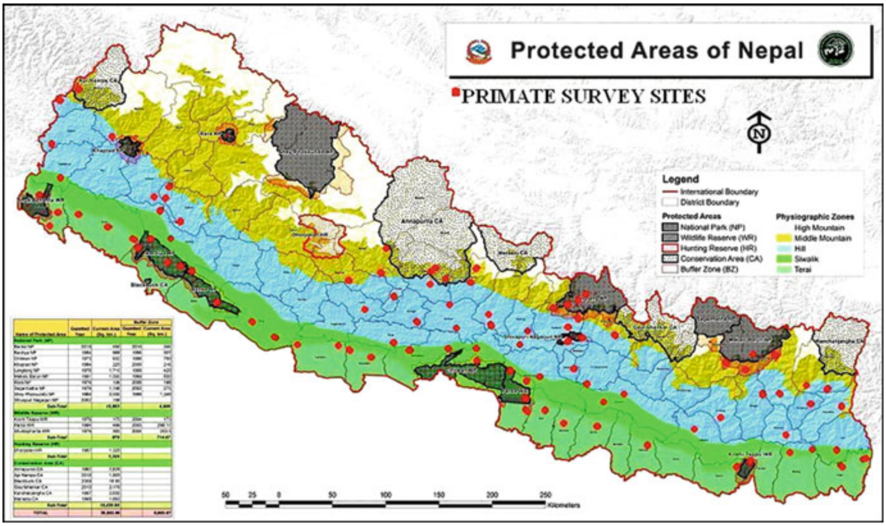

Fig. 22.4 Primate Population study sites with physiographic zones and Protected Areas of Nepal (DNPWC 2011 map with *red* spots by Chalise)

Assamese monkeys inhabit in the mountains and hills along the Himalayas. Like rhesus, they are flexible in habitat types in Nepal from river basins to subtropical hills of Sal forests, mixed deciduous forest, temperate broadleaved forest with rocky outcrops, and along the steep sloped forests along rivers above altitude.

Census of Primates in Nepal

Of some 186 mammals listed for the country, 27 have been declared “protected” by the Wildlife Act 2029 (1973) of His Majesty’s Government and the Assamese monkey is one of them (HMGN 1973). Nepalese primates, however, have yet to be systematically surveyed to determine their actual countrywide conservation status. This chapter is among the first to summarize primate populations throughout the country (Fig. 22.4).

Countrywide Primate Population Surveys

The population survey was carried out by applying scan sampling with continuous recording of numbers, age, and sex in each observed group (Martin and Bateson 1993). Counts of group size and composition were carried out repeatedly in each observation. Daily observation lasted up to 8 h. All occurrences of other events and interesting behaviors of any group members were recorded whenever they were

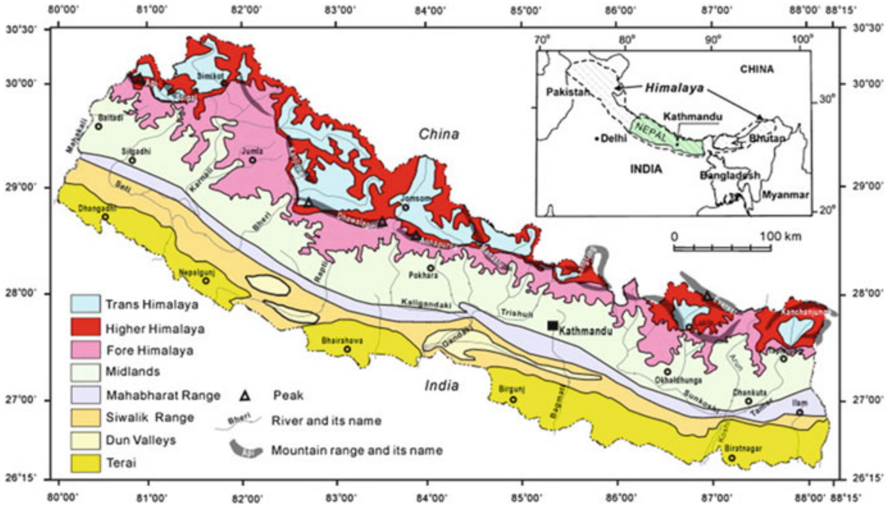

Fig. 22.5 Map of the seven habitat divisions. Modified from Hagen (1998) in Dahal and Hasehawa 2008

seen. The survey revealed the information on group composition, habitat use, and primate occurrence. Data for all regions and species are in Appendices I–III.

The population counted during different biodiversity research projects and primate explorations are listed here from east to west Nepal. It might be helpful to understand general information and dispersal pattern of monkey species in the diverse topography of Nepal. Beside the population count, we are projecting some of the habitat and topographic characteristics as collected for different areas and districts. Some of the population census results are already indicated in published papers (Alicia et al. 2012, Chalise 1997a, b, 1999, 2000a, b, 2003a, b, 2006, 2008; 2010a, b; Chalise and Ghimire 1998; Chalise et al. 2001, 2005; Koenig et al. 1997; Sanjay et al. 2003). Hagen (1998) described Nepal with seven divisions from south to north: Tarai, Siwalik Hills zone, Mahabharat Lekh, Midlands, Himalaya, Inner Himalaya, and Tibetan marginal mountains (Fig. 22.5), and primates were surveyed in four of these divisions. The Himalaya (above 4,000–6,000 m), Inner Himalaya (above 3,600 m), and Tibetan Marginal Mountain Range zones do not have any record of primates yet.

Lowlands, Including Tarai and Siwalik Hills: Hot Monsoon and Subtropical/Tropical

The lowland of Nepal lies in southern part of the country stretching from east to west. This biotic zone is characterized by hot climate with prevailing monsoon rains with annual temperature ranges from 15 to 45 °C and rainfall up to 500 mm.

The Tarai belt is a flat and valuable stretch of fertile agricultural land, which forms part of the alluvial Gangetic plain. It lies at an altitude of 60–300 m between the Indian border and the outer foothills. The original forest cover in the Tarai was dense and this is still so in western Nepal, but in other parts there has been a great deal of habitat destruction and ruthless felling of trees.

The Siwalik Hills Zone, which rises abruptly from the Tarai plains and reaches an elevation of between 700 and 1,500 m is wider in the western and far-western regions and narrower in the east. It is mainly composed of sedimentary rock and big boulders. The Bhabar rises from the Tarai in the north and comprises a narrow but continuous belt of forest, locally known as *Char Kose Jhadi*, which is about 8–12 km wide. The Bhabar is formed by the accumulation of gravel, boulders, stone, and sand that are washed down from the foothills. Water is scarce in these parts throughout the year except during the monsoon, when sizeable streams often rise up. The Bhabar is not an entirely independent range since in some areas the Mahabharat Lekh, which lies behind it to the north, merges into the Siwalik Hills Zone. The two ranges are separated by broad, gently sloping valleys called the Dun valleys. Important Dun valleys are the Dang Valley in the west, the Chitwan Valley in central lowlands, and the Trijuga Valley in the east. Dun valleys are under intensive cultivation, and due to the removal of forest cover, serious soil erosion has been a problem particularly in recent years.

The region is predominantly composed of *Shorea robusta*. *Acacia catechu–Dalbergia sissoo* forests replace *Shorea* forests along streams and rivers, while other commonly found species include *Terminalia alata*, *Adina cordifolia*, *Dillenia pentagyna*, *Lagerstroemia parviflora*, *Bombax ceiba*, *Toona ciliata*, *Mallotus philippinensis*, *Albizzia lebbeck*, *Trewia nudiflora*, *Salix tetrasperma*, *Spatholobus parviflorus*, and *Bauhinia vahlii*. *Shorea* forests are replaced by *Terminalia–Anogeissus* forests in the western foothills.

A total of 752 rhesus, 529 langurs (*S. hector*), and zero Assamese monkeys were recorded for the region as a whole.

Churiya hills of Ilam, *East Nepal*. During a wildlife survey of the Churiya range of Morang and Jhapa districts, there were three sites where langurs, rhesus, and suspected Assamese were observed. The area was heavily encroached by the locals and landless tenants. The area is meant for fuelwood collection for both market and personal use.

Ramnagar, *Chitwan*. Ramnagar lies 150 km southwest of Kathmandu city and 5 km to Narayangadh market, at an altitude of about 300 m. It is situated in the northern fringe of the Chitwan valley (inner Tarai) on the southern lap of Kabilas hill of Mahabharat range. The eastern part of this area is connected with the protected forests for rhino (*Rhinoceros unicornis*) and in western, Narayani river flows as natural boundary line. The area of Ramnagar was cleared for settlement about 70 years ago by the mountain communities and ex-army. The Gorkha-Narayangadh highway was constructed in 1979–1980. This highway along with high potential electrical lines passes through the forest area and the village. The village area is flat and forest area is uneven with denudated gullies and steep slopes with some meadows and waterholes (Chalise 1995). The forest in the west is relatively small and with thinner vegetation than in the east. Langurs and rhesus groups are found in the western part while most of our known troops are in the eastern part, including Ramnagar village. The population census shows there are 19 troops of langurs in the local forest area: the largest troop had more than 40 individuals, and the smallest, 8 individuals (Appendix II). Total number of langurs is more than 300. There are no records of all-male bands. Additionally, we observed more than 125 individuals of rhesus monkeys in the Ramnagar Forest (Chalise 1995). In the limited area of northern part of Chitwan National Park, we observed in *Shorea–Terminalia–Bombax–Albizia* forest more than 177 rhesus monkeys. They were trying to invade nearby village store and hotel garbage.

East-West Highway. Censuses were conducted from the east city of Dhalkebar to Dang in the west. Western highway census is recorded under the heading of districts Banke, Bardia, Kailali and Kanchanpur (Appendix I). The eastern survey started at Chapur and Dhalkebar area and went to Lalmatia of Dang district. The eastern sector covering Dhalkebar to Pathalaiya consisted of 11 troops with 139 individuals of rhesus monkeys. The census done along the highway passing from Nabalparasi, Rupandehi, Kapilbastu, and Dang recorded 59 langurs with in four groups in Nabalparasi and one group each in Kharkatti of Rupandehi.

GhodaGhodi Tal, *Kailali*. This wetland is situated in the Kailali district of far-west Nepal just east of Kanchanpur. Around the lake there is degraded Sal forest where we observed 50 rhesus monkeys in two troops along the highway and in the temple area.

Suklaphanta and Jhilmile Tal, *Kanchanpur*. Kanchanpur is far-western Tarai district bordered with India by Mahakali River. Suklaphanta wildlife reserves harbor many animals, including endangered swamp deer (*Cervus devoucelii*). A troop of rhesus monkeys with 35 individuals was observed inside the reserve, and 50 individuals were seen approaching a nearby army garbage ground. Astonishingly the langurs, generally very common to the Tarai forest in large groups, were only observed once with a small band of 12. Three troops of rhesus monkeys with more than 30 individuals each were observed near the highway and west parts of Arjuni phanta, while a troop of langurs were observed in Hirapur phanta at the lap of Churiya forest. Jhilmile Tal (lake) lies in the northern part of the park across the highway at the Churiya hills. On the way to this lake, at the ridge of Churiya we observed a group of langurs with 35 individuals.

Mid-Hills, Including Mahabharat Lekh and Midlands: Warm and Cool Temperate Monsoon

Mahabharat Lekh lies between the Siwalik Hills to the south and the Midlands to the north. The range is well developed in eastern and central Nepal and underdeveloped in western Nepal. It is composed of granite or quartzite and limestone. The elevation of the Mahabharat Lekh is from 1,500 to 2,700 m. Major rivers, namely, the Bagmati, Babai, and Rapti, flow from the northern to the southern edges of the Mahabharat range.

The Midlands lie north of the Mahabharat and occupy the central region of the country. The average altitude is 2,000 m with elevations ranging from 600 to 3,500 m. The Midlands comprise the high valleys of Nepal, of which the most important with very dense human populations are the Kathmandu, Pokhara, Trishuli, and Banepa (Kavre) Valleys. The midlands are rich in schist and quartz rocks, and hence, agriculture is intensive in this part of the country where the farmers have made terraces on the steep hillsides, sometimes up to the very tops of the high hills. Forests have been severely degraded in this region and the rate of soil erosion is alarming. All the rivers that flow from the Himalayas down to the plains combine their waters into three great rivers, the Sapta Koshi in eastern, the Narayani in central, and the Karnali in far-western. The vegetation of mid-mountain region has been categorized into four types: (1) Lower mixed hardwood forests, (2) Chirpine forests, (3) Oak forests, and (4) Upper mixed hardwood forests. The major plant species found are *Schima wallichii*, *Castonopsis indica*, *Pinus roxburghii*, *Myrica esculenta*, *Pyrus pasia*, *Quercus* sp., *Rhododendron arboreum*, and *Juglans regia*. The other common species are *Alnus nepalensis* mostly in degraded and eroded areas. The floral division is categorized as *Schima–Castanopsis* forest type.

A total of 2,113 rhesus, 564 langurs (*S. schistaceus*), and 1,099 Assamese monkeys were recorded for the region as a whole.

Lakuwa, *Makalu Barun National Park* (*MBNP*). Lakuwa is a small Rai village of Sankhuwasabha district of east Nepal. It is the buffer zone of the MBNP with steep mountain forest in its surroundings ranging from 980 to 2,300 m asl. We observed rhesus, and Assamese monkeys, and highland langur species (*S.e. schistaceus*). We recorded 173 individual Assamese monkeys, 115 rhesus, and 148 langurs in and around Lakuwa village forests, Khonglewa river gorge, and Sintup village forest. West of Khonglewa River along the eastern facing slopes of Dankhila village, at least 104 Assamese monkeys were recorded. We counted 67 Assamese during a transect walk and survey along the Apsuwa river basin of Arun tributary. On the way to our study site outside the conservation area, we observed 15 unidentified monkeys, likely Assamese in Heluwabeshi foraging in the Sal Forest of Arun River along with 30 rhesus monkeys. Finally, around the confluence of Arun and Sankhuwa Rivers, in the forest of Bhumlingtar, we observed three Assamese monkeys.

Balthali, *Kavre*. During the investigation of Assamese monkeys of mid-hills of Nepal, we observed two troops of rhesus monkeys with 55 individuals in Balthali area, near the Panauti hydropower station of Kavre district of central Nepal, 35 km east of capital city Kathmandu.

Kathmandu. The rhesus monkeys in the capital city Kathmandu live in close human commensalism fostered by religious beliefs. One population of approximately 400 monkeys in 7–8 social groups lives at Swoyambhu, a Buddhist and Hindu temple site over 2,000 years old, on the western edge of the city. During the census, a group of all males was recorded along with a set of twin infants were recorded (Appendix I). Another population of 350 monkeys, where twinning is not uncommon, lives near Pashupatinath, a Hindu temple and parkland on the east side of the city, close to the international airport. Several times rhesus caused problems at the airport, not only as a nuisance to passengers, but to the take-off and landing of planes. These two nearby populations (5 km apart) have been censused at least once a year, with very little fluctuation in the populations. Due to human carelessness in August 1996, a rhesus group lost sixty-six percent of its population when 41 individuals were electrocuted in Pashupati area in barbed fence. A total loss of 18 adults was recorded in the succeeding September census. These temple-dwelling primates benefit from supplemental feeding, freedom from predation, and other natural causes of death, but are pressured into a restricted home range, crowding and harassment from humans, and the disease and parasite exchange from people and feral animals. In Swayambhu, many rhesus monkeys are found with large tumors, malnourished, and disabled. Many have scars and fractures from people throwing stones at them. Several times there was record of twins and triplets infants in Pashupati forest. Forest is ever decreasing in the region in part for the construction of walking trails, a cemetery and public facilities.

A fragmented population of about 40 rhesus monkeys resides near the Thapathali area, and about 100 monkeys are in Sankhu-Bajrajogini. Thapathali area consists of temples and old houses. This area is almost treeless and no natural food and shelter is available for monkeys. They rest inside the roof of the houses and at the top of temples. Sankhu groups have good connection with wild forest in its one fringe and have less human pressure due to the distant from the city. The langur population was never encountered in Kathmandu valley; however, people reported some in Shivapuri forest. Assamese monkeys were also reported from Godawari forest at the Phulchoki slope, but are unconfirmed.

Shivapuri Nagarjun National Park, (*alt. 1350–2,732 m*). Primate census of Shivapuri recorded at least 120 rhesus monkeys in six different troops. We observed 83 Assamese monkeys in four different bisexual troops ranging the terrain between 1,458–1,949 m asl. Local people report crop-raiding behavior in both primate species. In Nagarjun forest area, except the western slope, we observed Assamese monkeys inside the forest at 1,355–1,530 m with three troops and a total of 83 individuals, where the largest troop was 35 individuals with seven adult males. Nagarjun area also harbors 223 rhesus. Two troops were frequently observed along the Balaju Garden and army camp area near the highway, and other two troops were observed along the Okarpauwa, one km north. Frequently lonesome adult and juvenile males are seen along the highway from the Nagarjun forest area. Rhesus regularly invaded human properties and crops at the marginal areas of the forest prior to the release of captive breed monkeys in 2010–2011, but now the problem of nuisance monkeys and conflict with people in the park is increasing,

Hariharpur. We observed a group of 11 individuals along the river of Bagmati in Tapke Danda of Hariharpur area. It lies in Makawanpur district of Central Nepal. The Assamese monkeys observed in this area were smaller and very shy compared to Assamese of other observed sites.

Dhading District of Central Nepal. Along the Trishuli River and its tributaries, we recorded Assamese monkeys with five troops with 78 individuals; near the northern Mugling 32 individuals, and near the forests of Jogimara, Kirtan village area we observed an additional 78 monkeys. Local people reported that during the hot season, these monkeys are capable of crossing the Trishuli River. They stated that monkeys were frequently visiting crop fields and crossing the highway.

Tanhun: *Taprek and Abukhaireni*. Surveys in Taprek recorded: 99 individuals *Semnopithecus* species (*S. schistaceous*?), 40–50 of rhesus monkeys, and 3 of Assamese monkeys. Abukhaireni is a market place and highway crossroads of Tanahun district. Near the market along the highway 2 km east, 32 Assamese monkeys were recorded scavenging into market garbage site.

Pokhara. In the eastern part of Medical College along the mountain slope of the Kali River more than two troops of 125 rhesus monkeys were recorded.

Beg Khola, *Myagdi*. A troop of 20 Assamese monkeys were observed across the Kali Gandaki River on the slope of the mountains. They were eating petioles of *Holarrhena* species.

Kopche Pani, *Myagdi*. A troop of 12 langurs (*S. schistaceus*) were observed above the tea shops' slope. They were eating *Machilus odoratissima* leaf and licking greenish rock.

Palpa. A mid-hill district of west Nepal lying south of Kaligandaki River at 152–1,936 m asl. The study of rhesus monkeys was initiated at Bandipokhara. A census around the Matindanda village in a community forest revealed a total of 67 rhesus monkeys in three troops. Similarly, in northern parts of this village development committees (VDC), there were 40 rhesus monkeys in a troop around the government forest of Ghiunsibas village. At Brangdi VDC there were 25 rhesuses at the south bank of KaliGandaki River in Phanta, Khanigaun VDC. A famous RaniMahal area, Baugha Gumba VDC in the bank of same river, a very shy troop of langurs was noticed, but the count was incomplete. Ramdi Area near the highway is a small settlement in Palpa District along the KaliGandaki River where we counted 30 Assamese individuals. In Gulmi district along with 128 rhesus monkeys in four troops, a sympatric langur troop of 14 individuals were also observed.

Sworgadwari, *Pyuthan*. Famous for its ancient temple situated at the top of a mountain with the elevation of 2,121 m asl, three troops of 70 individuals *Semnopithecus schistaceus* species were observed in the surrounding protected forest. They spent most of their time in the forest; however, one troop was observed raiding the food from the temple and its surrounding gardens.

Langtang National Park: Cool Temperate Monsoon and Subalpine

Langtang National Park is located in the central Himalayan region of Nepal and can be reached by road driving 132.2 km north of Capital City Kathmandu. The park borders Tibet and is a challenging, multi-altitudinal landscape where different primate species are found at different elevations. At 1,545–1,980 m asl, at least 62 Langurs were counted from four different troops at Bokajhunda-Sole, Trishuli Bridge, Sebrubeshi-Dovan, and Bamboo. Due to topographical obstacles and the shy nature of the langurs, counting infants was completely impossible. During a snow leopard study, 68 individuals from four different troops of langurs were observed at 1,800–2,200 m asl. Langur groups were encountered, but not counted between Shyabrubeshi to Bamboo area along the Langtang River. They were observed one group each at 1,466, 1,834, 1,906, and 1,967 m. On the return trek we observed four troops of langurs from 1,950 m to down 1,824 m. In other occasion, a Langur troop of 20 individuals of *S. ajax* was observed at the height of 3,400 m asl around Langtang village.

Assamese monkeys totaling 148 individuals from six different troops inhabited the steep slope forest at 1,500–1,700 m along the Trishuli River basin at Ghattekhola of Dhunche and Chilime bridge of Sebrubeshi. Along the Langtang valley at Thulo Bharkhu village area, a troop of Assamese monkey was observed. They were raiding the young green wheat leaf in the crop field. Between Shyabrubeshi to Bamboo along the Langtang River, a troop of Assamese monkeys were observed at 1,466 m asl. Along the same trek just above 1,932 m, troops of Assamese were observed. A lonesome Langur and an Assamese monkey were observed at 2,007 m.

Conclusion

Primates are distributed from urban temples to wilder areas in different ecological zones of Nepal. Primate censuses were never thoroughly conducted in Nepal. Therefore, this chapter represents the most current summarized information for the country.

The Assamese monkeys were observed in habitat from Sal forest to mixed deciduous and temperate broadleaved forest, and in various climates, such as warm and cool temperate monsoon and subalpine. Estimated populations are roughly 1,000 Assamese along the mid-mountains in roughly 2,000 square km. The lowest elevation of occurrence was 300 m in Seti River basin while highest elevation of occurrence recorded was around 2,500 m in Langtang area.

The three Hanuman langur species covered almost all vegetative and climatic zones of Nepal, except alpine and above. The highest record of occurrence was around 3,400 m above sea level in Langtang village area of mid-Nepal. In total, more than 1,000 individuals of Hanuman Langurs of all species combined were counted in different climatic zones of Nepal, with approximately 20 *S. ajax*, 529 *S. hector*, and 564 *S. schistaceus* (not genetically confirmed, morphological differences only).

The rhesus monkeys are common around Nepal from human settlement to the wilder habitat. The temple rhesus monkeys are densely populated in Kathmandu valley with more than 1,000 individuals. The wild habitat consists of more than

1,800 individuals around the country in different ecological zones, except alpine and cold regions.

The biggest threat to all of the primates in Nepal is persistent human encroachment. Rhesus macaques have adapted the most to human presence, but even so, human interaction is starting to take its toll in terms of disease and injury to some populations. Taxonomic revision of the Assamese monkeys and conservation status of all langur species are immediate research needs for Nepal.

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Appendix 1: Rhesus Monkey Census in Nepal

	Adult		Young		Immature		Total		
Area/GPS location	Male	Female	Male	Female	Juve	Infant	Indiv	Group	Remarks Info
A. Tarai and Siwalik Hills (hot monsoon and subtropical hot monsoon and tropical, below 500–1,000 m asl)									
1. Ilam/Jhapa East Nepal									
ChulaChuli VDC Barhgothe village Kause Danda and Bagdwar area N 26°42′32″ E 87°46′30″; 300 m asl							10	1	Total count was done, new born baby in winter (December)
Sakphara VDC, Jare forest area N 26°46′20″ E 87°41′30″; 580 m asl							15	1	
Danabari VDC, Sanokholsi forest N 26°44′50″ E 87°54′50″; 300 m asl							10	1	
Danabari VDC, Kilathoke Chuli N 26°44′50″ E 87°43′45″; 380 m asl							20	1	
2. *Pathlaiya–Dhalkebar*, *East-West Highway* N 27°11′55″ E 84°58′57″ –N 26°59′54.8″ E 85°54′35.2″							139	11	Single male two places, Counted along the edge of Highway forest area
3. *Chitwan NP*, Baghamara BZCF N 27°35′16.7″ E 84°28′30.1″; 170 m							76	(8 ?)	5–25 members in a troop (subgroup ?)
Kumrose Community Forest N 27°37′9.0″ E 84°28′7.2″	5	8	4	4	6	5	32	1	Near Office building, riverside habitat
Gaida Camp Hotel N 27°36′18.3″ E 84°27′7.1″	5	10	1	3	7	3	29	1	East of Bees Hajari Tal road
4. *Ramnagar*, *Chitwan* N 27°44′14″ E 84°25′9.1″							125	2	Area covered east to rhino post from Highway
5. *Nabalparasi to Dang*									Along East-West Highway

(continued)

(continued)

	Adult		Young		Immature		Total		
Area/GPS location	Male	Female	Male	Female	Juve	Infant	Indiv	Group	Remarks Info
Arunkhola, Nawalparasi 120 m asl N 27°36′49.5′ E 83°56′40.8″	2	3	2	2	3	2	14	1	One Adult male fractured leg
Daunne, Nawalparasi 187 m asl N 27°32′52.4″ E 83°50′24.3″	2	5	2	3	2	2	16	1	
Bhutaha, Nawalparasi 105 m asl N 27°34′8.7″ E 83°44′9.5″	2	3	-	-	3	1	9	1	
Kharkatti, Nawalparasi 122 m asl N 27°37′0.5″ E 83°37′0.8″	6	11	5	8	5	8	43	1	
Dharampur, Nawalparasi 92 m asl N 27°34′7.9″ E 83°36′10.1″	1	-	-	-	1	-	2	1	Male subgroup
Devdaha, Rupandehi 121 m asl N 27°39′23.5″ E 83°33′15.4″	2	5	2	2	5	3	19	1	
Bhaluhi, Rupandehi N 27°36′4.5″ E 83°28′49.1″	1	3	-	-	1	2	7	1	
Gorusinge, Kapilvastu 105 m asl N 27°39′7.8″ E 83°02′8.4″	2	4	1	2	3	2	14	1	
Lalmatiya, Dang 285 m asl N 27°50′8.4″ E 82°44′12.3″	2	3	1	2	3	1	12	1	
6. GhodaGhodi Tal, *Kailali* N 28°41′03″ E 80°56′43″							50	2	Highway south and north, temple area
7. Suklaphanta WLR N 28°56′21.8″ E 80°09′2.9″							85	2	Inside the Wildlife reserve, Majhgaun
Arjuni Phanta N 28°55′6.7″ E 80°18′43.0″							10	1	Near army barrack in Nagarjun Com. Forest
East of Daiji N 28°54′5.4″ E 80°22′51.7″							15	1	Along highway
Subtotal							752	42	

B. Mid-hills (warm temperate monsoon; cool temperate monsoon 1,000–3,000 m asl) rhesus count cont.									
8. Makalu Barun NP 980 m asl *Lakuwa* N 27°31′49.9″ E 87°5′7.3″							75	3	
Shiva Makalu Barun NP 1,500 m asl N 27°32′0.8″ E 87°5′31.6″							40	1	
9. Heluwabeshi, 380 m asl 27°26′01″ N 87°08′04″ E							30	1	Fringe of conservation area
10. Balthali, *Kavre* N 27°30′ E 85°30′							55	2	
11. Kathmandu Valley									
Thapathali, *Singh Temple* N 27°41′23.3″ E 85°18′52.8″	4	17	3	1	6	12	43	1	Along Bagmati river, in Shingh Temple
Swoyambhu Stupa forest 27°42′54.4″ N 85°17′24.9″ E	40	152	18	11	93	128	442	8	Additionally All male band of 8–15 members
Pashupati temple forest 27°42′28.9″ N 85°21′06.3″ E	46	152	17	12	102	113	441	7	Several time twins and quadruple recorded
Nilbarahi forest Madhyapur N 27°41′47.0″ E 85°23′31.5″	10	11	3	8	5	5	42	1	Recently its population increased to double
Gokarn Safari forest N 27°43′36.7″ E 85°23′38.8″							38 + 25 + 30	3	Around the hotel area, a few (20) are in forest
Sankhu-Bahrajogini N 27°44′36.7″ E 85°28′0.9″	8	28	11	6	20	23	96	2	Bajhrajogini forest and temple area
Shivapuri Sundarijal forest N 27°47′25.9″ E 85°25′32.9″	11	25	22	10	31	21	120	6	Mainly southern face of Shivapuri and top
Nagarjun Balaju forest area N 27°45′2.4″ E 85°16′16.1″	13	49	35	20	69	37	223	7	Problem of raiding house store, cornfield and shops
12. Tanhun, *Thaprek* N 28°05′17.1″ E 84°09′22.6″							40	1	
13. Pokhara N 28°15′10.3″ E 83°59′14.5″							125	3	Near Kali khola former Manipal Hospital

(continued)

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	Adult		Young		Immature		Total		
Area/GPS location	Male	Female	Male	Female	Juve	Infant	Indiv	Group	Remarks Info
14. Palpa District									
Matin Danda 1,100 m asl N 27°51′0.2″ E 83°31′32.3″	15	19	8	10	8	7	67	3	Community forest
Ghiunsibas, *Barangdi*, 1,040 m asl N 27°53′13.7″ E 83°33′5.5″	2	9	6	7	8	8	40	1	5 km N of Tansen
Phanta, *Khanigaun* 980 m asl N 27°54′59.6″ E 83°33′3.6″	1	5	4	5	6	4	25	1	9 km N of Tansen, four rhesus electrocuted 05′
15. Gulmi District									
Sitheni-Gurunggaun 465 m asl 28°27′ N 83°35′	10	25	22	17	35	19	128	4	
Aslewa Bote Gaun 514 m asl	12			7	5	4	28	1	
16. Dailekh, 651 m asl N 28°56′29.9″ E 81°27′2.2″							25	1	Bank of Karnali, near shops, 610 m asl
N 28°57′18.9″ E 81°26′44.9″							30	1	651 m asl, Karnali River
17. Achham 1,000 m asl N 28°55′0.2″ E 81°26′12.8″							20	1	Hill top, near Chyurikand area
18. Darchula, Mahakali 750 m asl N 29°45′59.3″ E 80°24′7.0″							11	1	Highway to Darchula Headquarter above river
Subtotal							2,217	60	
Rhesus grand total							2,993	103	

Appendix 2: Hanuman Langur Monkey Census in Nepal

	Adult		Young		Immature		Total		
Area/GPS location	Male	Female	Male	Female	Juve	Infant	Indiv	Group	Remarks Info
A. Tarai and Siwalik Hills (Hot monsoon and Subtropical Hot monsoon and Tropical below, 500–1,000 m asl)									
1. Ilam/*Jhapa*, *East Nepal*									
ChulaChuli VDC Barhgothe village Kause Danda and Bagdwar area N 26°42′32″ E 87°46′30″; 300 m asl							10	1	Yellowish tint fur at abdomen
Sakphara VDC, Jare forest N 26°46′20″ E 87°41′30″; 600 m asl							30	2	
Danabari VDC, Sanokholsi forest N 26°44′50″ E 87°54′50″; 300 m asl							15	1	
2. *Ramnagar*, *Chitwan* 250–300 m asl N 27°44′ E 84°25′ –N 27°43′ E 84°29′							300	19 (8–40)	Area covered east to rhino post from Devghat
3. *Nawalparasi* 114 m N 27°33’61”3 E 83°46’7.3”	1		1				2		Male band (?)
Birta, Nawalparasi 104 m N 27°33′48.7″ E 83°46′38.8″	4	9	3	5	3	4	28	1	

(continued)

(continued)

	Adult		Young		Immature		Total		
Area/GPS location	Male	Female	Male	Female	Juve	Infant	Indiv	Group	Remarks Info
Dumkibas, Nawalparasi, 125 m asl N 27°34′59.8″ E 83°51′34.5″	1	-	1				2		Male band (?)
Daunne Hill, Nawalparasi, 187 m asl N 27°32′52.4″ E 83°50′24.3″	3	4	2	1	2	2	14	1	Near Temple area
4. *Rupandehi*, Kharkatti	2	5	1	1	2	2	13	1	
5. *Bardia NP*, Babai river 150 m asl N 28°25′16.3″ E 81°22′49.9″							21	1	Near the park elephant stable at the south side
Lalmati cross road and Chisapani N 28°36′44.7″ E 81°16′46.6″; 160 m asl	3	7	2		2	5	19	1	Near the Karnali bridge, army post
6. *Suklaphanta WLR* N 28°56′21.8″ E 80°09′2.9″	3	4				3	10	1	Inside the Wildlife reserve, Majhgaun
Hirapur phanta N 28°56′38.9″ E 80°23′40.2″							App. (30)	1	Few adult male and female identified.
7. *Jhilmile Tal* 511 m asl N 27°33′61″3 E 83°46′7.3″	5	12	2	2	7	8	35	1	North of Mahendranagar, Langurs mostly whitish fur
Subtotal							529	31	

B. Mid-hills (warm temperate monsoon; cool temperate monsoon, 1,000–3,000 m asl)									
8. *Makalu Barun NP* 1,600 m asl *Lakuwa*, N 27°32′16.0″ E 87°5′9.9″							79	4	Langurs were mostly to the Achamkha Hill slope (59)
Shiva MBNP 1,500 m asl N 27°31′46.8″ E 87°5′40.6″							27	1	Langurs were along the Sankhuwa river slope (13)
9. *Langtang NP and Buffer zone*									
Bokajhunda, Sole, 1,980 m N 28°05′41.1″ E 85°16′43.6″							<15	1	
Dhunche, South Brabal 2,025 m asl N 28°06′04.4″ E 85°17′42.8″							30+	1	New Infants in autumn
Trishuli Bridge, 1,900 m N 28°06′41.2″ E 85°20′36.4″	2	5	3	3	-	-	13	1	Near market place
Sebrubesi east 1,466 m asl N 28°09′47.5″ E 85°20′37.9″							10+	1	
Way to Dovan 1,545 m N 28°09′24.7″ E 85°21′02.2″	4	5	4	-	3	3	19	1	Reached Thulo Sebru Village
Pahiro 1,838 m asl N 28°09′22″ E 85°22′98″	3	5			5	1	14	1	
Bamboo forests N 28°09′15.4″ E 85°23′09.9″	3	6	3	-	1	2	15	1	Bamboo south

(continued)

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	Adult		Young		Immature		Total		
Area/GPS location	Male	Female	Male	Female	Juve	Infant	Indiv	Group	Remarks Info
Bamboo, 1,802 m asl N 28°09′15.4″ E 85°23′09.9″	2	3	1				6	1	Across Langtang river in the cliff
N 28°09′12.7″ E 85°23′11.5″; 1,824 m–N 28°09′15.6″ E 85°23′40.1″; 1,950 m							40	4	Each group (10+)is 30 m asl apart average
Bamboo 2,116 m asl N 28°09′18.4″ E 85°23′51.6″							7+	1	Leaf harvesting
Bamboo south forests N 28°09′17.4″ E 85°24′16.0″	2	5				1	8	4	
Bridge 2,141 m asl N 28°09′19″ E 85°24′32″	6	13			5	2	26	1	One male lame
Rimiche down 2,206 m asl N 28°09′23″ E 85°24′41″	6	12			2		20	1	
East of Lama Hotel, 2,610 m asl N 28°10′14.2″ E 85°26′13.7″							8+	1	Area covered by snow
Ghodatabela, 2,892 m asl N 28°12′95.3″ E 85°27′36.9″	1	2					3	1	Eating leaves
10. Tanhun, Thaprek N 28°05′17.1″ E 84°09′22.6″							99	2	Groups is scattered into small subgroups

11. *Lamjung*, *Sattale*, 1,455 m asl N 28°26′39.6″ E 84°22′51.2″	3		1				4	1	Male only, eating stem pith of dry grass.
Tagring, Syange, 1,602 m asl N 28°23′47.0″ E 84°24′0.2″	4	10	2		3	6	24	1	Above the Syange market
12. *BaughaGumba*, *Palpa* 1,060 m asl N 27°54′59.6″ E 83°31′16.1″	1						1		Single adult male seen 6 km North of Tansen
13. *Gulmi* Sitheni-Gurunggaun 465 m asl 28°27′ N 83°35′	1	2	3	2	4	2	14	1	
14. *Myagdi*, *Kopche Pani*, 1,950 m asl N 28°35′50.4″ E 83°38′44.4″	2	4	1	1	1	3	12	1	Eating along the trail side
15. *Pyuthan*, Sworgadwari2,100 m asl N 28°07′16.0″ E 82°40′26.9″							70	3	One troop (25) around the temple at North-East slope
Subtotal							564	35	
C. High Mountains 3,000–4,000 Subalpine									
1. *Langtang* village area, 3,430 m asl N 28°12′85.5″ E 085°34′54.7″							20+	1	Eating tree fruit/many infants, very white fur, crown, fair abdomen
Highest altitude of primate observed									
Subtotal							20	1	
Langur grand total							1,113	67	

Appendix 3: Assamese Monkey Census in Nepal

	Adult		Young		Immature		Total		
Area/GPS location	Male	Female	Male	Female	Juve	Infant	Indiv	Group	Remarks Info
B. Mid-hills (warm temperate monsoon; cool temperate monsoon 1,000–3,000 m asl) cont.									
1. *Makalu Barun NP* 980–2,300 m asl *Lakuwa*, N 27°32′16.0″ E 87°5′9.9″	39	66	4	3	23	38	173	8	Censused around Lakuwa and Sintup village forest
Dankhila, 1,320 m asl N 27°30′25.7″ E 87°5′1.2″	24	38	3	-	19	20	104	4	West of Sankhuwa River
Apsuwa River 600–1,200 m asl N 27°29′9.5″ E 87°9′59.4″	11	23	2	-	15	16	67	4	Mostly along the Arun River valley
Bhumlingtar, 465 m asl N 27°27′3.0″ E 87°8′24.1″	1	2					3	1	Along the trail to Tamku
Heluwabesi 350 m asl N 27°25′55.9″ E 87°7′38.9″	2	6			3	4	15	1	South of Heluwa besi at the Sal forest
2. *Dhankuta*, *Mulghat* 380 m asl N 26°55′59.7″ E 87°19′29.8″							30	1	In the first turning loop of Highway, Tamor river
3. *Langtang NP and Buffer zone*									
Melung	4	10	1	2	5	8	30	1	*Transect walk and count*
Pranjal	2	5			2	3	12	1	
Dahalphedi	1	2			1	1	5	1	
Sole-Brabal 2,025 m asl N 28°06′04.4″ E 85°17′42.8″	7	13	3	1	8	4	36	1	
Ramche 1 h from road 1,719 m asl N 28°02′21.6″ E 85°12′31.9″	4	9	3		2	7	25	1	
Chutrabesi, Dhunche-4, 1,450 m asl N 28°05′48.2″ E 85°16′02.3″	3	7	5		3	4	22	1	
Pahiro 1,820 m asl N 28°09′41.4″ E 85°25′55.2″	2	11			5	8	26	1	Summer

Chilime/Sano Bharkhu 1,520 m N 28°09′01.5″ E 85°19′33.4″	4	7	6		4	6	27	1	
Sebrubeshi, 1,450 m asl N 28°09′47.6″ E 85°20′37.3″	5	11	2	1	7	6	32	1	Near large stone boulder wheat field
Sebrubeshi to Bamboo 1,466 m asl N 28°09′47.5″ E 85°20′37.9″							(20)	1	
Ronga bridge 1,455 m N 28°10′56.0″ E 85°20′22.2″	3	5	2		3	3	16	1	
Tarsa, Sebrubeshi, 1,690 m N 28°11′49.5″ E 85°20′54.1″	3	7	3		4	4	21	1	Ghoral was playing with immature monkeys
Phewyolung, Timure Bridge 1,662 m N 28°13′34.8″ E 85°21′42.0″	1						1		Male only
Ghattekhola 1,710 m N 28°15′49.0″ E 85°22′23.0″	9	11	4		5	7	35	1	One male was far from group may be alone
Thulo Bharkhu 1,860 m asl N 28°07′47.0″ E 85°18′22.9″	4	9	3		4	3	23	1	
Thulo Bharkhu Village 1,875 m asl N 28°07′54.3″ E 85°18′56.2″								1	Crop-raiding, 3 km from Dhunche
4. Shivpuri Nagarjun National Park									
Alche/Sikre khola 1,550 m asl N 27°49′50.9″ E 85°22′23.6″	3	5	16			3	27	1	
Rholche/Cha-gaun 1,525 m asl N 27°49′49.2″ E 85°24′42.2″	2	2	9			2	15	1	
Sinche, 1,980 m asl N 27°49′8.7″ E 85°21′8.1″	5	6	14			4	29	1	
Fulbari gate 1 500 m asl N 27°46′45.0″ E 85°21′6.6″	9	7	12			7	35	1	
Mahabhir 1,830 m asl N 27°49′34.1″ E 85°25′45.3″	4	4	3			1	12	1	

(continued)

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Area/GPS location	Adult		Young		Immature		Total		Remarks Info
	Male	Female	Male	Female	Juve	Infant	Indiv	Group	
Sanagaun-Mudkhu, 1,460 m asl N 27°45′45.6″ E 85°16′9.0″	3	5	6			3	17	1	
Raniban 2,000 m asl N 27°44′35.9″ E 85°15′30.9″	9	7	10			4	31	1	
5. *Lalitpur*, *Phulchoki* 1,960 m asl N 27°34′39.9″ E 85°23′14.6″	3	6	5		2	3	19	1	Above the Naudhara area, large loop road
6. *Dhading district Mid Nepal*									
Kintang 1,800–2,000 m asl N 28°01′26.4″ E 85°03′7.3″	2	4	3		1	3	13	1	
Reegau, 2,145 m asl N 28°01′26.4″ E 85°03′7.3″	3	4	2		1	2	12	1	
Jogimara, 500–700 m asl N 28°7′27.4″ E 84°59′34.7″	6	9	4		3	4	26	1	
Fisling west 400 m asl N 27°52′34.7″ E 84°35′02.08″	4	8	5		6	4	27	1	
7. *Tanhun Bajhgra* 330 m asl N 27°57′15.5″ E 84°13′20.7″	2	4	2	2	2	3	15	1	Eating Ban Peepal fruits along Seti river
8. *Lamjung Chyamse* 1,493 m asl N 28°26′25.4″ E 84°23′24.1″	2	4	2	1	2	3	14	1	Visiting the hotel garbage
9. *Gorkha*, *Abukhaireni* 300 m asl N 27°53′54.1″ E 84°32′20.6″	2	12	6	2	2	8	32	1	Visiting Urban dumping site 1 Juvenile lame
10. *Myagdi*, *Begkhola*, 1,150 m asl N 28°25′55.4″ E 83°36′01.1″	3	6	2	2	3	4	20	1	Along the Kaligandaki River
11. *Ramdi*, *Palpa* 420 m asl N 27°54′8.4″ E 83°38′1.6″							32	1	Eastern forest patch above the Highway
Total							1,099	51	

1. Rhesus monkey Census in Nepal
   A. Tarai and Siwalik Hills (Hot monsoon and Subtropical Hot monsoon and Tropical, below 500–1,000 m asl)

      Subtotal 880 individuals among 46 troops

   B. Mid-hills (Warm temperate monsoon; Cool temperate monsoon 1,000–3,000 m asl)

      Subtotal 2,113 individuals among 59 troops

   Grand Total Rhesus 2,993 individuals in 103 troops
2. Hanuman Langur monkey Census in Nepal
   A. Tarai and Siwalik Hills (Hot monsoon and Subtropical Hot monsoon and Tropical below 500–1,000 m asl)

      Subtotal 529 individuals among 31 troops

   B. Mid-hills (Warm temperate monsoon; Cool temperate monsoon, 1,000–3,000 m asl)

      Subtotal 564 individuals among 35 troops

   C. High Mountains 3,000–4,000 Subalpine

      Subtotal 20 individuals in one troop

   Grand Total Langur 1,113 individuals in 67 troops
3. Assamese monkey Census in Nepal
   B. Mid-hills (Warm temperate monsoon; Cool temperate monsoon, 1,000–3,000 m asl)

   Grand Total Assamese 1,099 individuals in 51 troops

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Chapter 23

The Challenges of Survival in a Concrete Jungle: Conservation of the Pied Tamarin (*Saguinus bicolor*) in the Urban Landscape of Manaus, Brazil

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Abstract The ongoing growth of the Brazilian city of Manaus—the largest urban center in the central Amazon basin—has led to extremes of habitat fragmentation and the local extinction of many animal and plant species. One species in particular—the pied tamarin (*Saguinus bicolor*) is threatened by this process more than most, considering that its 7,500 km^2 geographic range coincides with the Manaus City region. This situation has led to the classification of the species in the endangered IUCN category, although it has previously been considered critically endangered. Dozens of small fragments of forest can still be found within the urban area of Manaus, and tamarins survive at many of these sites. In most cases, the urban matrix—with busy roads, power lines, and domestic animals—is virtually impenetrable, while the rural area to the east of the city is becoming increasingly fragmented. The reduced size and poor quality of most forest fragments and the eventual need for the dispersal of surplus individuals has highly deleterious implications for the survival of most populations. The ongoing deforestation of fragments for the establishment of residential areas has led to the death of many individuals and the reduction of remaining populations. In some cases, fragments are occupied by no more than one or two individuals although larger fragments, such as that of the UFAM campus, which covers 700 ha may contain dozens or even hundreds of *S. bicolor*. Dispersing animals risk dying in traffic, attacks from domestic animals, electric shocks from power lines, and capture as pets by local residents. For example, the access road to the UFAM campus that passes through the forest is responsible for the death of approximately 5 % of the local population per year. The generalized disrespect for environmental legislation and the lack of effort on the

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part of public authorities for the protection of this species and its habitats combine to create a bleak outlook for the remaining urban populations of *S. bicolor*, especially considering that even the largest remnants may not be viable over the medium to long term. The survival of these populations will depend on a concerted effort, integrating research, education, environmental monitoring, metapopulation management, and the development of adequate public policies for the protection of *S. bicolor* within the urban matrix of Manaus.

Introduction

The Amazonian callitrichids—the small-bodied tamarins and marmosets—are a diverse group of primates with at least 30 species distributed in five genera (*Callibella*, *Cebuella*, *Mico*, *Saguinus*, and *Callimico*) found throughout the Amazon basin (Hershkovitz 1977; Hirsch et al. 2002; van Roosmalen and van Roosmalen 2003; Ferrari et al. 2010). Most of these species have relatively ample geographic ranges, although some newly discovered marmosets, including *Callibella*, appear to occupy much smaller areas of the order of tens of thousands of square kilometers.

However, these marmosets are all found in relatively remote and sparsely populated areas of the lower Madeira basin where they are under little pressure from local human populations. In stark contrast, the pied tamarin, *Saguinus bicolor*, not only has one of the smallest geographic ranges of any Amazonian primate, but this range is centered on the metropolitan area of Manaus, the second largest conurbation of the Amazon basin inhabiting more than two million. The city became a free trade zone in 1967, which resulted in intensive industrialization and explosive population growth over the course of the subsequent four decades and increasingly intense fragmentation of remaining forest habitat within an urban matrix. Colonization of the surrounding rural areas has intensified proportionally due to the increasing local demand for agricultural produce. The Manaus area thus represents one of the “hotspots” of deforestation in the Brazilian Amazon basin, albeit on a slightly smaller scale than those of the southern rim, ranging from the state of Rondônia in the west to Maranhão in the east (Fearnside 2005).

In ecological terms, most callitrichids can be characterized as pioneer species which are not only able to tolerate habitat fragmentation, but tend to thrive in disturbed and marginal habitats due to features such as their small body size, rapid reproductive rates, and ability to exploit resources such as large arthropods, in particular orthopterans, and plant gums (Sussman and Kinzey 1984; Ferrari 1993). These specializations enable the animals to colonize landscapes subject to intensive anthropogenic habitat fragmentation which are virtually uninhabitable for most other platyrrhines. In many regions, populations may even be found in urban environments (Poveda and Sanchez-Palomina 2004; Goulart et al. 2010), the most extreme cases being the colonization by common marmosets (*Callithrix jacchus*) of cities such as Florianópolis in southern Brazil located outside the natural range of the Callitrichidae (Santos et al. 2007).

As a typical callitrichid, *S. bicolor* has been able to survive in the urban landscape of Manaus, but its remaining populations face ever-increasing habitat loss, degradation, and isolation. The urban matrix is characterized by reduced permeability and very little potential for regeneration or the formation of corridors. On the more positive side, the urban setting may have a number of benefits for the management of remnant populations, in particular, the lack of dependence of local residents on natural resources for their subsistence and the potential for the development of effective monitoring and conscientization programs.

The combination of these factors has resulted in a unique challenge for the conservation of *S. bicolor*, which is listed as endangered by the IUCN (Mittermeier et al. 2008) based on ongoing rates of population decline, and critically endangered in the Brazilian red list (Gordo 2008). Recognition of the mounting threats faced by the species led to the establishment of the Pied Tamarin Project (Projeto Sauim-de-Coleira) in 2002 (www.projetosauim.com). This pioneering program, which is coordinated by the Federal University of Amazonas (UFAM), combines ecological and biological research (e.g., Santos 2005; Gordo et al. 2008; Maia da Silva et al. 2008) with educational and political activities (Vidal and Gordo 2008) with the overall aim of guaranteeing the survival of the species within the areas of greatest anthropogenic impact and creating an effective network of protected areas.

The Pied Tamarin

Saguinus bicolor (Fig. 23.1) is a typical tamarin with an adult body weight of approximately 500 g (Pied Tamarin Project, unpublished data) and a distinctive two-tone coloration pattern. Social groups contain as many as 12 members and are highly territorial. Breeding is restricted to a dominant pair and, in typical callitrichid fashion, the female normally gives birth to twins raised cooperatively by the members of the group. The diet is also typical of the tamarins and is based on fruit and invertebrates, complemented by nectar, small vertebrates, and some plant exudates (Egler 1992; Gordo et al. 2008).

With the exception of isolated populations in northwestern Colombia and southern Panama, the genus *Saguinus* is essentially restricted to the Orinoco/Amazon basin with the exception of the Xingu-Madeira/Jiparaná interfluvium, south of the Amazon (Hershkovitz 1977; Hirsch et al. 2002). In the Amazon basin, the geographic ranges of most species tend to coincide with major interfluvia and are mostly of the order of hundreds of thousands of square kilometers in area. By contrast, the geographic range of *S. bicolor* is restricted to the south by the Negro/Amazon rivers, to the west by the Cuieras/Negro, and to the east by the Rio Urubu, and appears to extend no more than 50 km north of the Amazon between these two rivers (Fig. 23.2). Within these limits, the totally area occupied by the species would be less than 10,000 km^2. The whole of this area is delimited by the geographic range of the red-handed tamarin, *Saguinus midas*, which is distributed throughout the northeastern Amazon basin.

Fig. 23.1 A pair of adult pied tamarins in the garden of a residence in Manaus

Early surveys of the distribution of *S. bicolor* indicated that the species occurred east of the Rio Urubu, as far east as the Rio Uatumã (Hershkovitz 1977; Ayres et al. 1982; Egler 1983), although Röhe (2006) found no evidence of its presence east of the Urubu. While the evidence is sketchy, a number of authors, beginning with Ayres et al. (1982) and most recently Röhe (2006), have suggested that this apparent shift in the eastern limit of the species is a relatively recent phenomenon resulting from the competitive exclusion of *S. bicolor* by *S. midas* within the context of increasing anthropogenic impacts on local forests. If this is true, the presence of *S. midas* to the north of the current range of *S. bicolor*, where their ranges are not separated by physical barriers to dispersal, would appear to constitute an additional problem for the survival of *S. bicolor* over the long term.

The only other Amazonian tamarin that has a geographic distribution comparable in size to that of *S. bicolor* is *Saguinus martinsi*, a closely related member of the bare-faced tamarin group, once considered to be a subspecies of *S. bicolor* (Hershkovitz 1977). This species is found to the east of the Uatumã River, where it was almost certainly parapatric with *S. bicolor* at some time in the recent past.

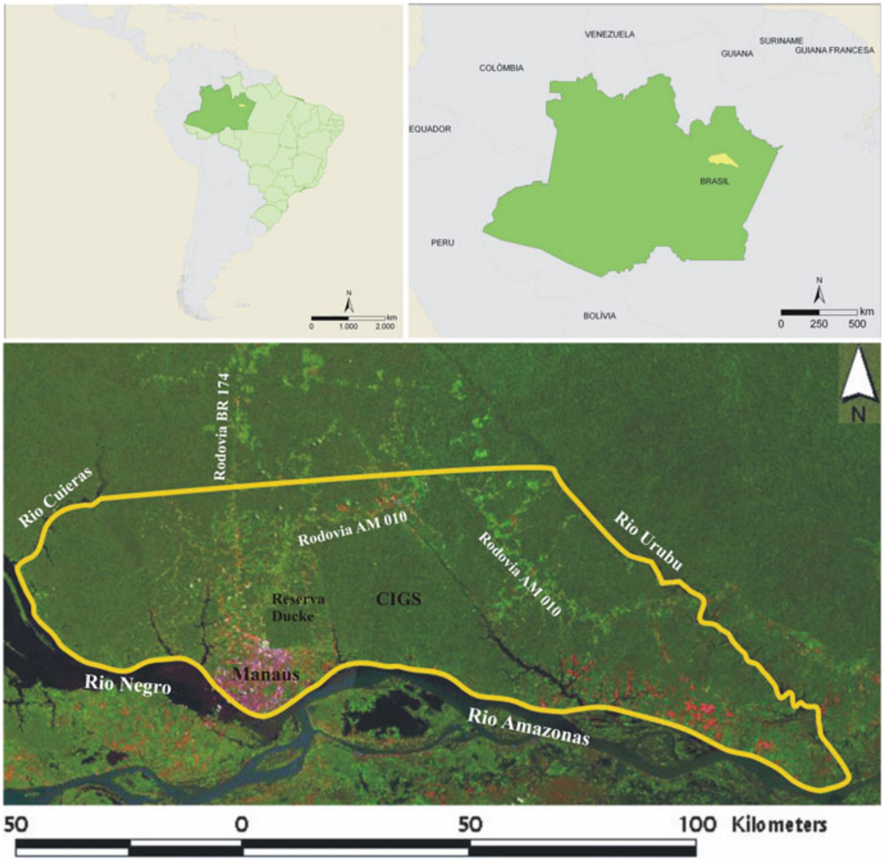

Fig. 23.2 Estimated geographic range of *S. bicolor*, based on Röhe (2006)

Given its close affinity with *S. bicolor* and the similarities of its geographic range, in terms of its size and configuration, it would seem reasonable to assume that *S. martinsi* is, intrinsically, at least as vulnerable to habitat disturbance as *S. bicolor*. However, the species' range is still relatively sparsely populated and has suffered only limited deforestation which has contributed to the classification of species as Least Concern by the IUCN (Rylands et al. 2008).

The Urban Matrix and Rural Frontier

While some parts of the geographic range of *S. bicolor* remain relatively intact (Fig. 23.2), the whole area must be considered to be under some degree of threat by deforestation due to their proximity to Manaus and its potential for both urban and rural growth. The potential threat of high human densities is an increasingly important factor in the evaluation of threats to the survival of species (Harcourt and Parks 2003).

Fig. 23.3 Composite Landsat images showing the expansion of the urban area of Manaus (*red spectrum*) between 1986 and 2010. The square area to the northeast of the city is the 10,000 ha (10 km × 10 km) Adolpho Ducke Reserve

The city of Manaus had fewer than five hundred thousand inhabitants prior to the installation of the free trade zone in the 1960s by the federal government as part of a coordinated strategy for the occupation and development of the Brazilian Amazon region. The fiscal incentives provided by the government have resulted in the installation of a major industrial complex in the city, in particular the electronics sector, including the Suframa agricultural zone that created extensive deforestation within the local rural frontier (Bierregaard et al. 2001).

The free trade zone represents more than 90 % of the economy of the Brazilian state of Amazonas which covers a total area of 1,570,746 km^2 and is the region's principal hub for urban migration. Over the past 40 years, the city's population has increased to almost two million inhabitants, resulting in the expansion of the urban area, and an increasingly intense occupation of this area (Fig. 23.3). This mostly unregulated urban growth has resulted in the decimation of much of the original forest cover, with the disappearance of many areas and the isolation of most remaining fragments. In the rural zone, expansion has involved the growth of neighboring towns, increasing deforestation rates, logging activities, and hunting pressure.

While many of the larger fragments are protected within the urban zone—some are conservation units, while others are owned by public institutions such as the Federal University and the Brazilian Army—most of the smaller areas are subject to intense pressure from adjacent communities and some have already been earmarked for development as building land. In addition to the variation in their size, the fragments also differ considerably in their format, habitat quality, and degree of isolation. However, whatever their specific characteristics, all the fragments share the same types of problems, to a greater or lesser degree.

Population Dynamics

In Manaus, groups of *S. bicolor* can be found in practically all the remaining fragments of natural habitat of at least 5 ha, and there are some records of groups of three or four individuals surviving in even smaller patches. In one extreme case, an

Fig. 23.4 Typical landscape in central Manaus, showing a remnant patch of forest, of 55 ha, surrounded by roads, housing and water courses, some of which encompass corridors of forest. Extracted from Google Earth Images

adult male was found in the garden of a house in a heavily built-up area of northern Manaus that contained four small trees in an area of less than 25 m^2 (Gordo 2012).

Most of the urban fragments are very isolated, especially in relation to areas of more continuous forest. Where fragments are linked, the corridors tend to be relatively long and tenuous, and are almost invariably affected by problems such as their proximity to inhabited areas, interruptions by thoroughfares, watercourses, or transmission lines, and sectors of reduced vegetation cover (Fig. 23.4).

This obviously reduces the potential for dispersal between fragments, but despite these difficulties, a number of dispersal events have been recorded during almost 10 years of monitoring in which some of the animals successfully crossed busy roads or heavily populated areas during their migrations. In one of these cases, a group of three animals migrated from the UFAM campus to that of the National

Table 23.1 History of the composition of six *S. bicolor* groups monitored by the Pied Tamarin Project between 2003 and 2009

Fragment/group	Fragment size (ha)	Number of members present 2003	2004	2005	2006	2007	2008	2009
Ducke/Central	10,000	8	6–7	6	6	6	6	6
UFAM/Galerosos	650	2–6	5	4–5	5–6	4–5	–[a]	4–5
UFAM/Acariquara	650	8	7	8	6–7	6–8	4–6	4–5
UFAM/Periférico	650	6	6–7	6–7	–	–	–	–
UFAM/Coroado1	650	–	–	3–4	4–5	0–6[b]	†	†
UFAM/Coroado2	650	–	–	–	–	4–7	4	4–6
SESI/Rosa	75	11	10–11	11	11–12	10–11	11	9–11

[a] Group not monitored

[b] Five members killed by traffic between January and September, the surviving animal subsequently disappeared

†Extinct group

Amazon Research Institute (INPA) which required crossing a busy four-lane freeway. Four solitary animals (three males and one female) were encountered in residential gardens at least 190–300 m from their probable fragments of origin (Gordo 2012). In addition, the home ranges of at least 11 groups are crossed by major avenues traversed frequently during the group's daily activities. However, it seems likely that successful dispersal is relatively rare.

The demographic characteristics of the pied tamarin populations in 30 of the urban fragments—varying in size from 4 to 776 ha—have been recorded over the past 7 years. Most of the fragments contain between one and four groups, and even the largest areas have relatively small populations, from the perspective of long-term conservation and management. The 776 ha fragment of the UFAM campus, for example, supports a total of 24 groups with a population of around 145 individuals, or a density of approximately 18 individuals per km^2. Population density nevertheless tends to be much higher in fragments—in the Ducke Reserve (Fig. 23.3) which is 15 times larger than the UFAM campus is still partly linked to neighboring areas of continuous forest, but has a population density of only around six individuals per km^2 (Gordo et al. 2008; Gordo 2012), less than half that of UFAM.

Seven groups were monitored systematically between 2003 and 2009 using radio-telemetry revealing considerable oscillations in size in some cases (Table 23.1). Much of this variation is likely due to premature mortality resulting not only from dispersal between fragments, but primarily local movements within the group's home range, which may often involve some form of contact with the anthropogenic matrix, such as roads (Fig. 23.5) or transmission lines (Fig. 23.6), or even residential gardens, where the potential for contact with domestic predators, such as cats and dogs is accentuated. Obviously, such contact tends to be more frequent in smaller or more irregularly shaped fragments, whereas some groups inhabiting the interior of the larger fragments may have little or no contact with man-made environments.

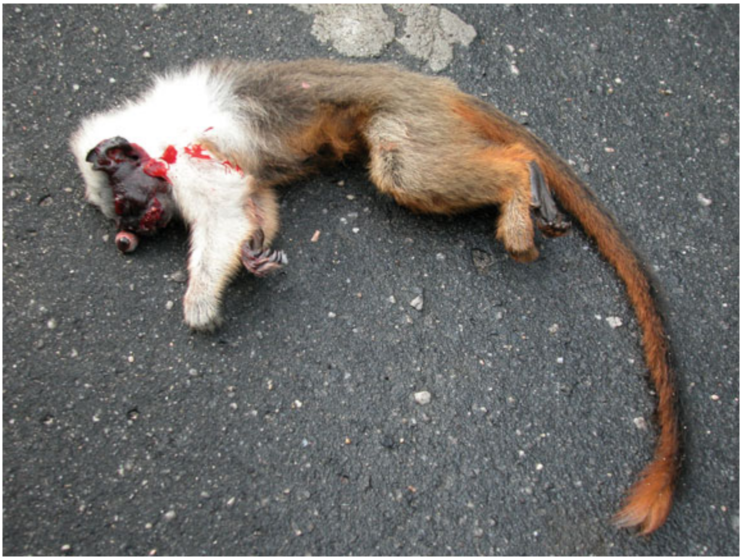

Fig. 23.5 Body of a juvenile male pied tamarin found on the main service road crossing the UFAM Campus in central Manaus

Fig. 23.6 Pied tamarin caught on transmission lines near the UFAM campus

Traffic is a major problem for many groups because, while the tamarins will approach the roadside with caution, as they would any open area, they appear to be unable to perceive the danger posed by oncoming vehicles and will often attempt to cross a road en masse in front of traffic. This behavior, combined with the relatively high speed of the traffic on many urban thoroughfares, represents a major source of mortality. The main road through the densely forested UFAM campus is 5 km long, and has been monitored for the past 10 years during which at least 6–10 tamarins have been run over annually, representing between 5 and 10 % of the total population (Gordo 2012). In 2007, five of the six members of one of the UFAM groups were killed by traffic in a period of less than 9 months.

Similar mortality rates may affect groups in marginal locations where the tamarins visit gardens regularly to feed on fruit or leftovers provided by humans. Ironically, many local residents—often the same people who contribute to the degradation of fragments by extracting wood, plant parts, and even soil, as well as depositing their refuse—welcome the tamarins as visitors and provide them with food. While this provisioning may constitute an important resource for groups in small and highly degraded fragments it is also conceals a number of potential risks, not least by increasing the probability of contact with domestic predators. And while disease transmission has not been reported, there is the possibility for interspecific diffusion of disease when primates and humans are so close (Maia da Silva et al. 2008). Habituation of the animals is an additional problem, given that the animals may become more vulnerable to negative interactions with malevolent residents who may wish to harm or capture them. Fortunately, while some tamarins are kept as pets, the species does not appear to be very popular as a domestic animal.

Despite the apparent resilience of the species, contact with the urban matrix tends to have a significant degrading effect, not only on the fragments themselves, but also on the tamarin populations in particular through increased mortality rates. While fragments of relatively small size may be able to support tamarin groups at least over the short term, a number of groups have disappeared completely since monitoring began. Twelve cases have been documented in which groups of between two and eight tamarins have disappeared from fragments of less than 10 ha. In half of these, the process occurred over a period of 4 or 5 years, as the fragment was degraded gradually and progressively. In the other six cases, the process took only a few months as the whole fragment was destroyed.

The examination of animals captured in highly degraded areas has revealed evidence of nutritional deficiencies, such as reduced levels of calcium and iron in the blood and fractured teeth. Some animals also appear to exhibit abnormal behavior patterns, such as an extended activity period. Preliminary genetic analyses have revealed potentially harmful loss of genetic variability (Santos 2005; unpublished data), which will be crucial to the long-term survival of the urban metapopulation.

Urban Conservation

Up until now, there has been limited official interest in the development of a systematic conservation program for the pied tamarin within the urban area of Manaus, although the Pied Tamarin Project has received federal funding through UFAM which supported basic research and preliminary activities in environmental education. While the project has developed working ties with the federal environment institute (IBAMA), and has established a conservation committee with the National

Primate Protection Center (CPB—ICMBio), initial plans for a federal conservation unit have been placed on hold, and if such a unit is implemented eventually, it is unlikely to be located within the urban zone.

The municipal government of Manaus has been involved in a number of initiatives related to the conservation of the urban populations of *S. bicolor* over the past decade, although this has had little practical effect on the rate of habitat loss. A number of important policies were nevertheless implemented, such as a municipal law which obliges construction companies to provide an inventory of the fauna of any area to be deforested, as well as a rescue or management plan for the displaced animals. Fiscal incentives have also been provided for the creation of privately owned reserves within the area of the municipality. Municipal legislation regulating the creation of protected areas has also been passed, and an ecological corridor has been established along the central sector of the Mindú drainage basin.

The city also created, and then amplified the 40-ha Mindú Municipal Park in response to the initiative of local residents, who campaigned for the protection of their native population of *S. bicolor*. One other urban protected area, the 51-ha Sumaúma State Park (Fig. 23.4) was established by the Amazonas state government in 2003, although its primary objective is not the protection of *S. bicolor*, even though a population does exist in the park. A number of private reserves have also been set up by individual citizens or corporations, but all are small in size and mostly unconnected with other areas of habitat. While potentially important in symbolic terms, these reserves are far too small to play more than a supporting role in the conservation of the species.

In perhaps the most emphatic demonstration of support for the species, Manaus adopted *S. bicolor* as the city's official animal in 2005 giving it the name "Manaus Tamarin" (*sauim-de-Manaus*). Despite all these initiatives, practical measures such as the recuperation of degraded habitats or the consolidation of protected areas are nonexistent and habitat loss—some of which is caused by government works—continues virtually unabated throughout the city.

There is considerable potential for the development of environmental education programs in the urban setting, but while schools and local clubs or residents' associations will often seek the support of the Pied Tamarin Project for the development of educational activities, there is currently no official, universal program. This is despite the pioneering campaign of the late Márcio Ayres who first brought the pied tamarin to the public's attention through the local media in the 1980s, and two subsequent programs developed in the 1990s by the local NGO Fundação Vitória Amazônica. In 2004, however, only 4 years after the last of these campaigns, interviews with 400 local residents (unpublished data) revealed that a quarter knew nothing of the species, while a similar proportion was unfamiliar with its characteristics.

Modeling the Future

While Brazil is a pioneering nation in terms of its environmental legislation, it is also infamous for its impunity and lack of effective regulation. In the urban setting of a burgeoning metropolis like Manaus, overwhelming social and economic

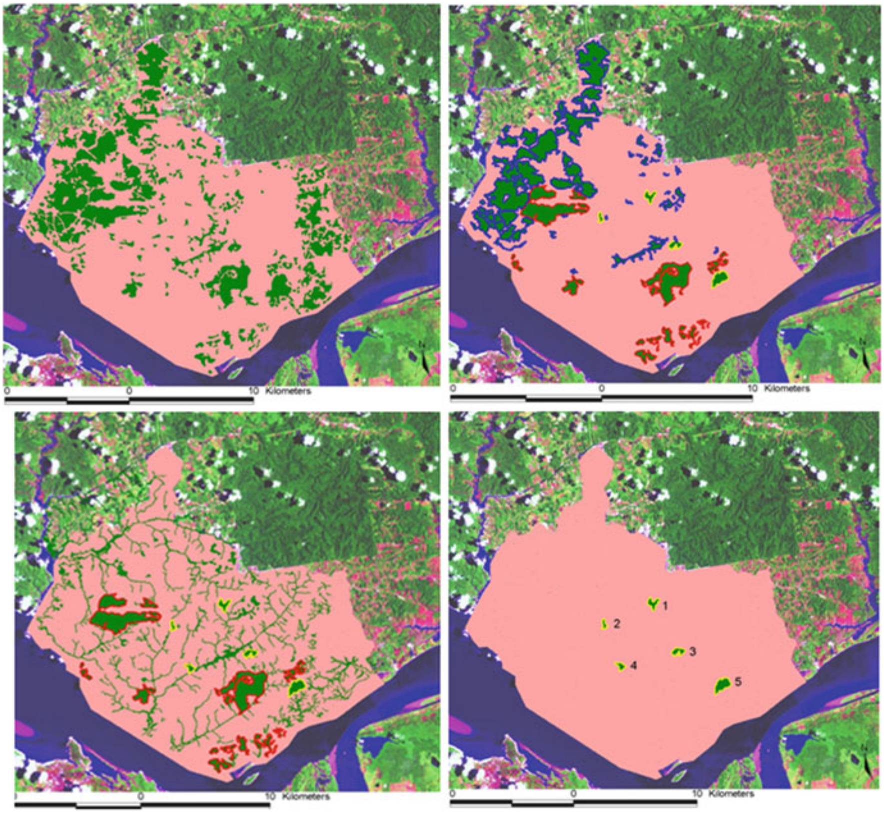

Fig. 23.7 Potential scenarios for the evolution of the urban populations of *S. bicolor* in Manaus, from the 2008 baseline (*upper left*): principal fragments (protected areas, public lands, and large fragments) without corridors (*upper right*); all areas linked by corridors (*lower left*); only protected areas remain (*lower right*)

pressures make it almost impossible to implement adequate regulatory measures. In particular, it seems unlikely that the present-day scenario might be altered in any significant way, such that habitat loss or degradation could be halted or even reverted.

An analysis of the possible consequences reveals three primary scenarios for the long-term future of *S. bicolor* in the urban landscape of Manaus (Fig. 23.7). At one extreme, the most favorable situation would depend on the effective (but unlikely) preservation of habitat corridors, primarily along water courses. This would require considerable efforts at all levels of government and society (Vasconcelos 2008), and seems almost impossible on a universal scale. At the opposite extreme, only the officially protected areas remain in total isolation with greatly reduced potential for the long-term survival of the species. This is the most likely scenario at the current rate of progress.

Despite the extremes of habitat degradation and predation pressure faced by the remnant populations of pied tamarins in the urban landscape of Manaus, one overwhelming advantage of the species is its ability to survive within this highly unfavorable environment. However, the small size of the urban populations, and their increasing isolation means that they are probably doomed to extinction over the long term, even if effective metapopulation management can be put into place in the immediate future.

In absolute terms, the consolidation of protected areas within the rural portion of the species' range will likely be more cost effective over the long run, but the value of the tamarins in Manaus as a flagship for conservation programs and a model for the development of management strategies in the urban landscape cannot be underestimated. The ultimate irony is the fact that, while the conservation of the Amazon Forest has received so much attention and investment from governments and non-governmental organizations alike in recent years, one of its most endangered, but potentially most conspicuous species has gone almost totally unnoticed.

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Chapter 24
Where Are They? Quantification, Distribution and Microhabitat Use of Fragments by the Red Slender Loris (*Loris tardigradus tardigradus*) in Sri Lanka

K.A.I. Nekaris and Carrie J. Stengel

Abstract The red slender loris is a nocturnal primate species endemic to Sri Lanka's biodiversity—rich, yet anthropogenically disturbed "Wet Zone". Until the '00s virtually nothing was known about the distribution or conservation status of this cryptic species. We present population data in relation to ecology from eight sites, and relate these data to an ecological niche model using MAXENT in order to predict what type of habitat is suitable for this species. Lorises were present at only six of eight sites, and density varied from 3.4 to 28 lorises/km^2 with an overall density across all sites of 32 lorises/km^2. Ecological niche modelling revealed that of the suitable habitat available for the species, only 25 % remained, and only 16 % of this is protected. Combining the population estimates, about 100,000 red slender lorises may remain in Sri Lanka, but most of these are outside the protected area network. Based on continued habitat declines and the species' total reliance on larger patches that are not exacerbated by humans, we suggest that the species be up-listed to Critically Endangered and that the protected area network in the Wet Zone be extended as soon as possible.

Introduction

The Endangered red slender loris (*Loris tardigradus tardigradus*) is a nocturnal primate endemic to Sri Lanka's Wet Zone, a biodiversity hotspot characterised by forest loss and increasing human population growth (Kumar et al. 1999;

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Fig. 24.1 (**a**) Red slender loris (*Loris tardigradus tardigradus*) sleeping group. Photo by K.A.I. Nekaris. (**b**) *L. t. tardigradus* eating an insect. Photo by K.A.I. Nekaris

Myers et al. 2000) (Fig. 24.1a, b). Sri Lanka's population growth increases by 1.4 % annually and is especially high in the biologically rich areas of the southwest where human density reaches 700 people/km^2 (Pethiyagoda 2005). Less than 5 % of original rainforest remains in Sri Lanka, spread across a heavily fragmented landscape (Gunawardene et al. 2007). Habitat loss, fragmentation, soil erosion and pollution have negatively effected primate populations and previous studies found the red slender loris to be in low abundance or absent from several sites within their traditional range (Douglas et al. 2007; Nekaris and Jayewardene 2004; Pethiyagoda 2005).

The red slender loris is affected by habitat size, composition and quality. Despite its small size of 100–180 g, it makes use of home ranges that average 2.6 hectares (ha) for males and 3.7 ha for females and as large as 3.4 ha for males and 6.9 ha for females (Nekaris and Bearder 2012). Dissimilar from primates that can leap over large forest gaps, lorises tend to inhabit areas with continuous canopy, allowing for primarily arboreal movement so they can avoid travel on open ground where they are vulnerable to predation (Nekaris et al. 2007; Singh et al. 1999). During a one-year radio tracking study in an extremely disturbed fragment of 1,028 ha, red slender lorises avoided edges as much as possible (Bernede et al. 2012).

To locate, study and conserve the red slender loris, data on the few field studies available of this elusive species can be combined with computer-generated models to highlight important research and conservation areas. In this chapter, we present data from field research on abundance and microhabitat variables combined with data from ecological niche models to analyse habitat in and around eight forest patches in Sri Lanka's Wet Zone. Combining field research with computer-generated models allows researchers to image and reinterpret data to focus field and conservation efforts.

Methods

Study Area

Sri Lanka's Wet Zone exhibits high levels of biodiversity, greater than many countries in Asia in terms of species per unit area and endemism (Gunatilake 1998; Kumar et al. 1999). The country has a strong tradition of conservation and a relatively high proportion of total land cover under protection at 25 % (Gunawardene et al. 2007). Despite this, little natural habitat has survived the last two centuries of agricultural expansion and many endemic flora and fauna are currently threatened (Pethiyagoda 2005), particularly in the southwest, an area to which the red slender loris is endemic. To assess the status of the red slender loris, we collected data from June to August 2004 at eight forest reserves in Sri Lanka's Southern Province (Fig. 24.2). These reserves have been established since the 1930s, yet all exhibit signs of anthropogenic disturbance and closely border villages and/or roads.

Field Research

We estimated loris abundance at each site using line transects selected at random. Because no maps were available to us, randomisation was done by entering the study site, glancing at the second hand on a watch, and following a compass bearing 100 m. At that point, a stone tied in flagging tape was then thrown, and the transect was started from the point where the stone landed. By this manner, transects were not always started in "clearings". We walked from either sunset to midnight or midnight to sunrise (Sutherland 2002). Researchers using halogen head lamps with red filters scanned all levels of the vegetation at a walking pace of 500 m per hour (Nekaris et al. 2008). We derived transect lengths using a laser rangefinder and confirmed with GPS reference points. We used the program Distance to determine a global density across fragments, and to determine density within fragments, we determined strip width by excluding the furthest 10 % of observations on either side of the line. Only confirmed visual sightings of slender lorises were included in the data.

We recorded characteristics of the microhabitat using the point-quarter method for vegetation sampling (Southwood and Henderson 2000). We took random samples within 15 m of an area where lorises were spotted; to establish habitat at sites where lorises were not seen, we established vegetation plots using a random number table. Variables collected included canopy continuity and undergrowth continuity using the Braun-Blanquet scale, substrate size and angle availability at 3.5 m (the preferred height of red slender lorises), and complexity between a sampled tree and its nearest neighbour (Lacher and Cleber 2001; Nekaris et al. 2005). We transformed percentage data into ordinal values to create independent variables for analysis and ran Komolgorov–Smirnov tests to test for data normality. All the data were normal and we used parametric tests for the analyses where appropriate (Zar 1999).

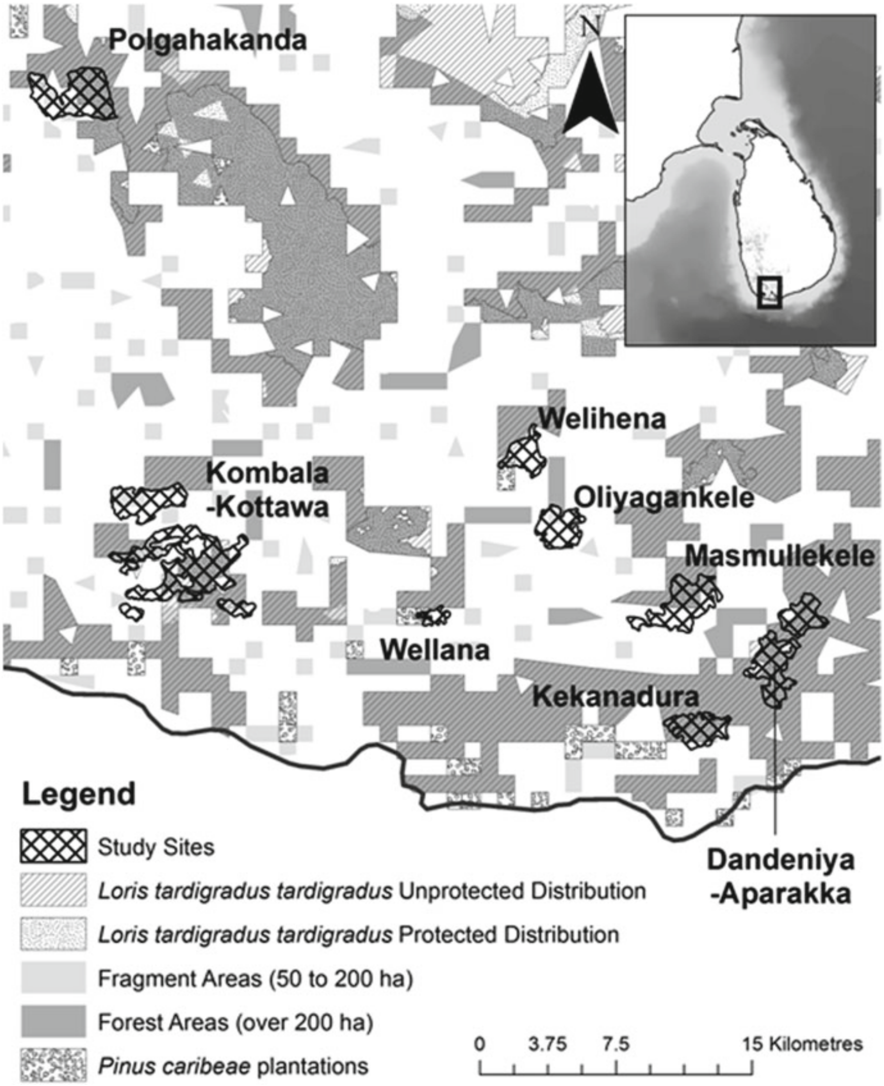

Fig. 24.2 Map of Sri Lanka showing the surveyed study sites in relation to other protected areas in Sri Lanka's Wet Zone; the study sites neighboured by forests (forested areas greater than 200 ha) and fragments (forested areas greater than 50 ha)—note that many of these neighbouring forests are planted *Pinus caribeae* plantations and thus not suitable for slender lorises

Ecological Niche Modelling

Niche-based modelling is a method for describing species distribution and several studies illustrate the useful application of these programs for primate research (Buckingham and Shanee 2009; Stengel et al. 2009; Thorn et al. 2009). Ecological niche modelling (ENM) combines known species occurrence information with environmental variables to create a model of the ecological conditions within which a species can persist (Anderson et al. 2003; Pearson et al. 2007). For this study, we generated a predictive model of red slender loris distribution using the ENM program Maxent and analysed it using Geographic Information System (GIS) software.

Maxent has proven to be successful at highlighting potentially unknown species populations and areas of high habitat suitability (Pearson et al. 2007; Thorn et al. 2009). Maxent uses presence only data and environmental variables to compute a probability distribution of "maximum entropy," meaning that which is most spread out or closest to uniform, across a defined area. For a full description and mathematical definition of the program see Phillips et al. (2006). In comparison to other ENM programs Maxent has been statistically more successful in creating useable models (Elith et al. 2006; Hernandez et al. 2006; Pearson et al. 2007; Phillips et al. 2006).

We collected presence data from natural history museum collections, published literature and reports; the majority of these data were ground-truthed during surveys undertaken by the Nocturnal Primate Research Group at Oxford Brookes University, and additional points were gleaned from these surveys. To build models, we obtained environmental data layers comprising temperature, precipitation and altitude from Worldclim (www.worldclim.org). As most of the locality data for this study were ground-truthed (e.g. Nekaris and Jayewardene 2004) and therefore considered highly reliable, the "lowest presence threshold" setting was used because it maintains a zero omission error in building the model (Pearson et al. 2007). We tested models for statistical accuracy using a receiver operating characteristic (ROC) curve and analysed them using ArcGIS 9.2. We turned results from a range of probability into a binary prediction of presence/absence using an objective threshold of 50 %. We chose this threshold because it produced a result consistent with the locality data and, as the information is to be used for conservation assessment and planning, it is best to use a generous distribution (Anderson and Martinez-Meyer 2004; Liu et al. 2005). We clipped the predicted distribution model by a suitable habitat layer to reflect forested areas where the species may persist. We then analysed variables including total area of protected site, average elevation, presence and number of close unprotected habitat fragments/forests, their total size and the distance to these areas from the edge of forest reserves.

Results

Field Research

Over 72 days of field effort we walked nearly 100 km and found red slender lorises at six out of eight forest reserves. We encountered 44 animals with clear visual sightings. We heard the distinctive *Loris* loud whistle vocalisation at all six sites more often than animals were seen. Density estimates ranged from 3.4 to 28 lorises/km^2 with linear encounter rates ranging from 0.1 to 1.1 lorises/km (Table 24.1).

Table 24.1 Comparison of densities as well as microhabitat features across sites by presenting the average and standard deviation, or the category represented by the highest percentage

			Tree height	% tree cover	Canopy continuity	No. vines	Branch size	Sub-strate angle
Study site	Loris/km	Loris/km^2	F	χ	χ (%)	F	χ (cm)	χ
Masmullah ($n=123$)	1.1	28.0	7.1 ± 5.7	0–25	0–25	0.8 ± 1.2	>30	Vertical
Dandeniya ($n=75$)	0.8	21.7	4.7 ± 2.8	0–25	26–50	2.4 ± 1.6	1–5	Oblique
Kottawa ($n=78$)	0.7	20.8	5.1 ± 3.4	26–50	0–25	0.9 ± 1.2	>30	Vertical
Kakanadura ($n=93$)	0.5	14.7	6.8 ± 5.0	0–25	26–50	1.2 ± 1.6	>30	Vertical
Oliyagankele ($n=126$)	0.2	4.3	6.3 ± 4.3	0–25	0–25	1.5 ± 1.4	>30	Vertical
Wellana ($n=80$)	0.1	4.1	4.9 ± 2.7	26–50	26–50	0.9 ± 1.3	1–5	Vertical
Bangamukande ($n=50$)	0.1	3.4	12.0 ± 0.4	0–25	0–25	0.7 ± 1.4	>30	Vertical
Polgahakande ($n=80$)	0	0	5.6 ± 3.9	26–50	0–25	1.9 ± 1.8	1–5	Vertical
Welihena ($n=80$)	0	0	5.4 ± 3.0	0–25	0–25	1.4 ± 1.5	1–5	Vertical

"n" refers to number of trees in each plot. Both analysis of variance (F) and chi-square cross tabulation tests (χ) revealed that sites differed significantly in these microhabitat components at $p \leq 0.001$

Table 24.2 Areas and percentages of predicted, remnant, protected and unprotected habitat for the red slender loris

Species	Predicted distribution	Remnant distribution	Remnant habitat	Protected area	Protected	Unprotected area	Unprotected
L. t. tardigradus	11,705 km^2	2,919 km^2	25 %	459 km^2	16 %	2,460 km^2	84 %

As the fragments in our study would have historically been connected and had similar habitat types (see below), we used the program Distance to determine a universal density across all sites. The best fit model, using the lowest AIC value generated by the program Distance (AIC = 173.30), based on a half-normal cosine model, generated a density across all sites of 31 lorises/km^2 with a detection probability of 0.45 (confidence intervals 0.48–0.63). Extrapolating to TOTAL area across sites (not taking into consideration extreme disturbance in most patches, making large areas of many patches unsuitable to lorises), 1,293 red slender lorises are estimated to occur within the surveyed areas, with a range between 882 and 1,894. Patch size does really seem to matter, because in some of the smaller patches, if the species does occur, it probably does so at very low densities, such as at Welihena and Polgahakande, where it was neither seen nor heard. Although we conducted all transects within forest boundaries, we also constantly searched for lorises and other nocturnal mammals along hedgerows, forest edges, and roads whilst travelling to and from the forest, either on foot or from a slow-moving (<10 miles per hour) tuk-tuk (three wheel vehicle), yielding an approximate effort of 126 km. Lorises were only seen within the boundaries of forest reserves and never spotted along roads or other human-dominated areas.

All sites exhibited a low percentage of canopy continuity and sapling ground cover; yet they differed significantly from each other for all microhabitat variables measured. Forest patch size strongly correlated with loris encounter rate (Pearson's $r = 0.778$, $p \leq 0.01$). We removed this variable to test the independent effects of microhabitat variables on loris encounter rate via an ANCOVA analysis. We observed a significant negative relationship between the complexity of vines and lianas and loris encounter rate (ANCOVA: $F_{2,6} = 18.65$, df = 2, $p \leq 0.005$), explaining 93 % of the variance in loris encounter rate.

Ecological Niche Modelling

We selected 35 species localities for model building after accounting for spatial autocorrelation. Maxent produced a highly significant model for the red slender loris (AUC = 0.854). Analysis of the predicted and remnant distributions show the red slender loris has lost a significant proportion of its potential habitat and less than 20 % of the remaining habitat is under protection (Fig. 24.2; Table 24.2).

The eight study sites where field research was conducted were analysed in relation to the predicted distribution model to calculate protected area, unprotected fragment area and proximity, and unprotected forest area and proximity (Table 24.3).

Table 24.3 Results from GIS model analysis of red slender loris habitat in and around the eight study sites where field research was conducted

Forest reserve (alternate name)	Latitude	Longitude	Total area (ha)	Average elevation (m)	Nearby fragment	Total fragments	Fragment size (ha)	Distance to fragment (km)	Nearby forest	Total forests	Forest size (ha)	Distance to forest (km)
Masmullah (Masmullekele)	6° 2′ 6.18″	80° 35′ 30″	718	35	No	0	Null	Null	Yes	2	1,028	Adjacent; 0.13
Dandeniya (Dandeniya-Aparakka)	6° 0′ 47″	80° 38′ 30.8″	950	83	No	0	Null	Null	Yes	1	1,766	Adjacent
Kottawa (Kombala-Kottawa)	6° 3′ 38.5″	80° 20′ 24.6″	2,118	65	Yes	4	77	0.41	Yes	3	1,397	All Adjacent
Kakanadura (Kekanadura)	5° 58′ 23.7″	80° 35′ 57.4″	456	45	No	0	Null	Null	Yes	1	604	Adjacent
Oliyagankele	6° 4′ 22.3″	80° 31′ 49.8″	439	33	Yes	1	58	0.37	Yes	2	605	Adjacent; 1
Wellana	6° 1′ 44.7″	80° 28′ 7″	99	52	Yes	1	85	0.79	Yes	1	828	Adjacent
Polgahakande	6° 17′ 16.7″	80° 17′ 26.″	891	118	Yes	1	70	0.5	Yes	1	892	Adjacent
Welihena	6° 6′ 33.4″	80° 30′ 48.8″	339	46	No	0	Null	Null	Yes	2	956	Adjacent; 1

Fragments were considered to be areas of suitable habitat greater than 50 ha and less than 200 ha; areas of greater than 200 ha were defined as forests. Only fragments and forests within 1 km of forest reserves were considered for inclusion in analysis, as areas further than this would not be accessible to lorises. Four of the eight study areas do not have fragments in close proximity, three have one nearby, and one area has four. All fragments are small, with total areas adding up to less than 1,000 ha. All eight forest reserves have at least one forest greater than 500 ha adjacent to them. Four reserves have more than one sizeable forest within a 1 km radius (Fig. 24.2). If we consider our remnant distribution of approximately 3,000 km^2, and combine this with our universal detection function of 31 lorises/km^2, we can estimate that at best fewer than 100,000 red slender lorises remain.

Discussion

Combining density estimates of red slender lorises at the eight study sites with predictive analyses presents a complex picture for the conservation of this species. Our definition of "forest" in this study (e.g. a forested area greater than 200 ha) is much smaller than that given for "fragment" in many other chapters in this volume. All forest fragments are small, degraded, and impacted by humans, and some neighbouring forests are made up completely of planted non-native Caribbean pine (*Pinus caribeae*) (Ashton et al. 2001). The presence of other "fragments" and "forests" around the study sites may be encouraging for the species, but is marked by complex issues as discussed below.

The linear results obtained in this study ranged from 0.1 to 1.0 animals/km. These estimates are comparable to the lower figures obtained for encounter rates of slender lorises in India and Sri Lanka (Nekaris and Jayewardene 2004; Kumara et al. 2006; Singh et al. 1999, 2000), and to Southeast Asian slow lorises in general (Nekaris et al. 2008). At two sites (Watahena, Bangamukande), only one animal was seen during 19 days of surveying and local people were surprised that we were able to find the species at all. At Bangamukande, the smallest fragment, the loris may have even been a transient individual, as only two others were ever seen during three other intensive field seasons (Bernede and Nekaris 2004). Unlike many of Sri Lanka's mammals, including giant squirrels, common palm civets and purple-faced langurs, which are able to use agro-forested gardens as corridors between forest patches (e.g. Nahallage et al. 2008), this does not seem an option for the red slender loris. During 100s of hours of surveys as well as during a 1-year radio-tracking study, not once yet has a loris been seen to enter a home garden (Bernede et al. 2012; Nekaris and Bearder 2012), meaning each fragment contains an isolated population. This does not mean that entering gardens is not impossible; it just means that it would be the exception to the rule.

Most fragments exhibited a combination of low canopy and undergrowth cover, and predominantly vertical substrates that are less suitable for lorises than those found in their preferred habitat (Nekaris and Jayewardene 2003), potentially explaining why loris encounter rate and density was relatively low when compared to other studies. A characteristic that we expected to be positively associated with loris presence, arboreal complexity as exhibited by number of vines and lianas connecting trees, was in fact negatively correlated. Increased vines and lianas also can indicate severe anthropogenic disturbance, usually caused by logging and unrestricted and open accessibility of the forest (Bhuyan et al. 2003). Complexity can be related to the tangled vegetation characteristic of disturbed areas and tree fall zones (Molino and Sabatier 2001; Nekaris et al. 2005). In Sri Lanka a main cause of forest loss is human encroachment, including use of forest for rice paddies, cattle grazing and cutting of branches for firewood (Ashton et al. 2001). For example, several hectares of Masmullah where Nekaris et al. (2005) conducted their study in 2002, and which held a large population of slender loris, had been burnt down in 2005 and replanted with crops. The overriding factor influencing presence of lorises was fragment size; when fragment size decreased, and human disturbance increased, loris numbers were low or they disappeared entirely.

A similarly grim picture was painted when we applied known distribution data to our ENM. Due to the steady conversion of natural habitat to human-dominated landscape, Maxent predictions do not always reflect current species persistence. Therefore, it was necessary to generate remnant distributions to quantify current distribution areas and percentages of loss. These remnant distributions image the fundamental niche, indicating areas of high habitat suitability and therefore are not confirmations of actual species presence (Anderson et al. 2003; Peterson 2001). Areas identified by models may not hold a species due to a lack of colonisation, extinction, or competition (Anderson et al. 2003).

Considering these constraints, Maxent predicted a highly significant model for *L. t. tardigradus*. Clipped to current forest cover the species persists in 20 % of its potential distribution area, approximately 3,500 km^2. This prediction supports the field data presented here showing that the species is limited to small forest fragments and severely impacted by human activity (Nekaris and Jayewardene 2003; Nekaris et al. 2005). Care must be taken to select, statistically analyse, contextualise and apply generated results appropriately. This is especially the case if results are going to be used to make conservation recommendations, as incorrect maps may encourage ill-informed decision-making.

Specific locality data points were carefully selected with ground-truthed data prior to the modelling process. These points were critically analysed for relevance and many were clipped to mitigate the effects of spatial autocorrelation. The results of this study support previous research that Maxent is able to produce statistically viable models with a few as five localities (Hernandez et al. 2006; Pearson et al. 2007). This has positive implications for the future applicability of Maxent in modelling rare species with small datasets.

Even statistically sound models can be misleading and generated outputs are only as good as the data relied upon in the modelling process (Pearson et al. 2007). Species localities, environmental data, and unknown confounding geographic variables can have significant effect on the accuracy and applicability of models. Species localities, especially from natural history museum records, can be faulty due to transcription error or species misidentification (Pearce et al. 2001; Gaubert et al. 2006). As this study relied on expert opinion to select data points prior to modelling, the locality data used here are considered reliable and representative of loris distribution.

Environmental data used in the model building process can be subject to error as layers may not completely describe a species' fundamental niche (Phillips et al. 2006). The Worldclim layers used in this study are generally accepted to be the most comprehensive and reliable suite of environmental data available, which are applicable across species and study regions (Hijmans et al. 2005). Additional environmental errors may come from the forest layer used in determining remnant distributions. A global landcover layer from 2003 was the most current data source available to take forest cover information from. Nine years of habitat fragmentation and the potential effects of civil war on wildlife suggest that remnant areas within Sri Lanka may be smaller than those predicted by this study. Additional factors not considered in modelling mean species rarely occupy all areas within suitable environments (Pearson et al. 2007). Other unknown biogeographical elements may restrict species' ranges such as rivers, mountains, predator–prey relationships, and competition (Anderson et al. 2003; Peterson 2001). These elements are difficult to account for when generating predictive models and highlight the need to confirm predictions through field surveys. In the case of the red slender loris, these confounding variables suggest the predictions we present here are optimal, and may overestimate their current distribution.

Even with potential over-estimation, our results suggest that the IUCN designation for *L. t. tardigradus* needs to be changed to Critically Endangered. Based on predicted remnant distributions, it can be inferred that a population size reduction of over 80 % may occur within three generations. Projected population decline will be due to a decrease in area of occupancy, extent of occurrence, and deteriorating quality of habitat. As habitat loss and reduced extent of occurrence have repeatedly been documented in the Wet Zone (Douglas et al. 2007; Nahallage et al. 2008; Parker et al. 2008; Rudran 2007), it is recommended that conservation action be undertaken immediately.

Slender lorises are threatened by multiple factors, not limited to deforestation, including use in traditional medicines and ritual compounding the need for conservation intervention (Nekaris et al. 2010). We clearly show that habitat loss and decreasing patch sizes over time have contributed to their continual population decline. An unremitting trend due to agricultural and logging demands will probably lead to short-term local extinctions of red slender lorises in Sri Lanka. Habitat protection and expansion of the protected areas network are essential for the survival of the remaining wild populations of red slender lorises.

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Section VI
Genetics, Disease, and Parasites Summary

Laura K. Marsh

Every year new methods with increased accuracy have been employed to solve genetic questions regarding effective population size, parentage, relatedness, sex, dispersal, population structure, population assignment, and gene flow in wild primates (Ferreira da Silva et al. 2012). For primates in fragments, we need to understand inbreeding, genetic drift, and hybridization potentials, as well as molecular indicators of stress that can lead to disease. Likewise, our understanding of disease and parasites is a burgeoning contribution to managing the welfare of wild primates, particularly in fragmented landscapes. The authors in this section discuss ways we are increasingly expanding our knowledge of primates in fragments with readily available technology.

Knapp (Chap. 25) discusses the various tools and means for genetic analysis particular to primates in fragments. One of the biggest challenges to the genetic study of wild primates has been the gathering of material to analyze. Fortunately, technology is making it easier to extract genetic material from hair and feces. And while not all genetic markers are the same, and they can be quite variable especially if the sequences are too short, having the knowledge base for the options is very useful. But even as Knapp provides this information, she cautions that while genetics will not save primates in a fragmented landscape from extinction, it can provide additional data that can ultimately lead to their protection.

Glenn and Bensen (Chap. 27) discuss how an introduced, bottlenecked species, *Cercopithecus mona*, rebounded genetically after 200 years of isolation on the islands of Sao Tome and Principe in the Gulf of Guinea and in Grenada in the Caribbean. These primates were originally carried to the islands on slave ships. Genetic studies indicate that the mona population in the Caribbean was started by a single founding female originally from the Sao Tome stock. Interestingly, the Grenadine monas show no inbreeding effects and might be an example of genetic purging, where deleterious genes are weeded out of small populations if the animals breed quickly enough to rebound. Since these monkeys are habitat generalists, the populations, while fragmented, demonstrate the potential conservation gains that can result from protecting small, isolated populations.

A detailed molecular study was conducted in Argentina on *Alouatta caraya* in fragmented forests and continuous forest to compare the genetic structure of these populations (Oklander and Corach, Chap. 26). The authors found that in the fragmented forests, the groups were genetically differentiated; whereas, in the continuous forest they were not. Males and females dispersed in continuous forest, and adults were not closely related. In the fragmented forests it was the opposite, where the males dispersed more than females, and the adult females were closely related. The authors emphasize that using genetic tools greatly facilitates understanding of social organization and behavioral patterns that may eventually lead to genetic problems.

De la Torre et al. (Chap. 29) used genetic analysis to determine whether group size in *Callithrix pygmaea* was impacted by fragmentation in San Pablo, Amazonian Ecuador. The authors found that there was no impact of fragmentation on group size as compared to intact habitat, but that some groups exhibited non-random mating. However in the fragments, a nomadic behavior reported for the first time in this chapter was noted where individuals used small core areas that they continuously moved between.

Dias et al. (Chap. 28) studied natural hybridization between *Alouatta palliata* and *A. pigra* in Tabasco, Mexico to determine if any habitat attributes were responsible for the hybridization. When they compared the genetic and morphometric differences between the purebred species and hybrids as assessed by habitat metrics such as number of fragments, size, isolation, and shape, they found that fragmentation is more severe where hybridization takes place. They discuss that in a fragmented landscape where conspecific occur, the need for both populations to use available habitat creates a situation where the primates increased their encounters as they moved more frequently through remnant patches looking for resources.

Genetics as a field continues to advance by leaps and bounds, but even with all of this new knowledge, we still know very little about what actually causes deleterious genetic effects in primates. We have evidence that hybrids can reproduce and continue into the future in a healthy manner (Detwiler 2003), demonstrating that hybridization per se may not be detrimental. Hybrids may not signal a loss of genetic diversity as once feared, but may represent resorting—in that we are witnessing the creation of new species—something that has taken place for millions of years in continuous forest, but is potentially forced as forest is fragmented and conspecifics vie for available resources (Detwiler et al. 2005, Chap. 28).

Diseases and stress go hand in hand, and fragmentation as a stressor on the molecular level persists at higher levels as compared to primates in continuous forest, and it can be measured directly in cortisol levels or as parasite loads. Behie and Pavelka (Chap. 30) discuss not only the roles of diet, cortisol levels, and parasites in a population of endangered *Alouatta pigra* living in fragmented forests of southern Belize, but the same animals before and after a hurricane which wiped out 80 % of the original population. Their multi-factorial approach uncovered issues with malnutrition post-hurricane and this physiological stress resulted in multispecies parasite infections in the population. Understanding the correlations between habitat, behavior, resources, and subsequent infections all influence primate population dynamics.

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Chapter 25
Molecular Genetic Tools for Evaluating the Consequences of Habitat Fragmentation

Leslie A. Knapp

Abstract Fragmentation and loss of habitat is a serious problem facing the conservation of biodiversity. Habitat fragmentation can lead to reduction in the connectivity between primate populations and ultimately isolation of populations. Decreased levels of gene flow among small populations can lead to decreased genetic variability and concomitantly a reduced ability to adapt to changing environments. Habitat fragmentation may also lead to increased inbreeding, reduced reproductive success, reduction in survival and an increased probability of extinction. Using molecular genetic tools, scientists can measure genetic diversity within and between populations and investigate genetic differentiation between populations of primates living in fragments. Theory predicts a positive correlation between genetic variation and population size and between genetic differentiation and geographic distance among populations. Using genetic data, statistical methods, and computer programs, it is possible to test these predictions and to evaluate the consequences of fragmentation on primates. This chapter reviews the genetic tools available to primatologists interested in evaluating the consequences of habitat fragmentation. Since reduced genetic variation can also potentially lead to increased susceptibility to disease, it is increasingly important to determine what regions of the genome are affected by reduced gene flow and to understand the mechanisms by which genetic diversity changes in association with habitat loss and fragmentation. These are new and important challenges for primate geneticists in the coming decade.

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Introduction

While the earliest molecular genetic studies of natural populations of primates provided simple characterizations of individual animals, researchers can now go far beyond basic descriptions of genetic diversity and can instead use sophisticated molecular genetic tools and statistics to determine genetic structure and evaluate the consequences of habitat fragmentation in primates. These tools, combined with the use of noninvasive genetic sampling (e.g., extracting DNA from feces or hair), provide great potential for research, assessment, and even management of natural populations of primates. With 35 % of all primate species threatened by extinction (IUCN Red List 2010), the need to evaluate the consequences of habitat fragmentation, especially in small populations of endangered primates, is greater than ever.

Empirical studies in other mammals show that habitat fragmentation can reduce genetic variation, which can adversely influence fitness, increase susceptibility to disease, and decrease population viability. However, it appears that not all fragmentation events lead to genetic losses and different parts of the genome may respond differently. In some circumstances, fragmentation has been known to increase gene flow and break down local genetic structure. To evaluate the consequences of fragmentation in primate populations, researchers must be able to identify the presence of rare or elusive species, to count and identify individuals, and to use biological samples to evaluate genetic diversity and determine population structure. Since habitat fragmentation typically reduces the size and increases the spatial isolation of populations, it is essential to determine the extent and rate of erosion of genetic variation and increased interpopulation genetic divergence due to increased random genetic drift, elevated inbreeding, and reduced gene flow in fragments.

The goal of this chapter is to present an overview of the genetic tools available to primatologists interested in evaluating the consequences of habitat fragmentation, to review selected examples of the successful application of these tools, to briefly address potential pitfalls in the application of the methods and to touch upon less common, but equally appropriate, approaches that can be used in light of the growing threats, particularly health and disease-based threats, to many wild primate populations.

Choosing and Using Genetic Markers

Habitat fragmentation can lead to genetic changes and there are many ways to measure, and monitor changes in genetic variation. Before the advent of the polymerase chain reaction (PCR) researchers typically focused on the detection of genetic differences that resulted in major molecular changes, usually at the level of the protein. For example, allozyme gel electrophoresis can be used to measured differences in amino acid composition of allozyme proteins encoded by different alleles found at a single genetic locus. This method detects differences in amino acid composition,

Table 25.1 Software programs commonly used to evaluate the consequences of habitat fragmentation (for more information see Excoffier and Heckel 2006)

Program	Statistic(s) or analysis	Website
Arlequin	F_{ST}, F_{IS}, F_{IT}, G_{ST}, AMOVA	http://anthro.unige.ch/software/arlequin/
FSTAT	R_{ST}, θ	http://www2.unil.ch/popgen/softwares/fstat.htm
Genepop	F_{ST}, F_{IS}, F_{IT}, R_{ST}	http://genepop.curtin.edu.au/
GeoDis	NCPA	http://darwin.uvigo.es/software/geodis.html
MIGRATE	Estimate gene flow	http://popgen.sc.fsu.edu/Migrate/Migrate-n.html
PHYLIP	Phylogenetic trees	http://evolution.genetics.washington.edu/phylip.html
SPAGeDi	F_{ST}, R_{ST}, D, $\delta\mu^2$	http://ebe.ulb.ac.be/ebe/Software.html
STRUCTURE	Evaluate population structure	http://pritch.bsd.uchicago.edu/structure.html

caused by one or more mutation, and differences appear as different protein bands in a gel matrix. Although variation may be limited within a population, differences between individuals can be used to evaluate gene flow and population structure. One major disadvantage of this technique is that allozyme assays require collection of whole blood samples. Therefore researchers must trap and/or sedate study subjects to obtain genetic data. While this may not be the method of choice, some studies of the genetic consequences of habitat fragmentation in primate have focused on allozyme variation (Table 25.1).

Noninvasively collected samples, such as feces, urine, shed/plucked hairs, or food wadges, generally do not contain large numbers of nucleated cells but they are usually much easier to collect. With these samples, specialized DNA extraction methods can be used and then followed up with molecular genetic methods such as polymerase chain reaction (PCR) amplification of DNA sequences to measure and monitor genetic variation. A number of publications have described the problems and difficulties associated with molecular genetic studies of noninvasively collected samples (Jefferey et al. 2007; Morin et al. 2001; Vigilant 2002). The same methods used to study noninvasively collected samples can also be used to study DNA extracted from whole blood or tissue (such as ear punches or skin samples) taken from sedated or live-trapped primates.

Microsatellites, or short simple tandemly repeated sequences of DNA (such as $TGTGTG_n$ or $AATAATAAT_n$), are frequently used to evaluate the consequences of habitat fragmentation. Microsatellites (msats) are widely dispersed throughout the eukaryotic genome and each one is usually characterized according to its genetic locus. For example, a human microsatellite locus might be called D6S260 because it can be pinpointed to human chromosome 6. Microsatellites have many features that make them ideal for evaluating genetic variability in fragmented primate populations. First, microsatellites are codominant markers, which mean that one allele is inherited from each parent, can be traced from parent to offspring and therefore heterozygotes (or individuals with two different alleles) can be recognized. Microsatellites are also highly variable (i.e., polymorphic) due to variation in the number of repeat unit found in different individuals. This hyper-variability is especially useful for researchers interested in assessing the consequences of habitat fragmentation and there are even specific statistical calculations that account for potentially high rates of microsatellite evolution over time. Finally, while the development of microsatellite genotyping in less well-studied primate species might have been a laborious and time consuming process in the past, many laboratories have developed (nearly) universal sets of microsatellite markers for apes and Old World monkeys and recent studies of New World monkeys and lemurs promise similar benefits for other researchers in the near future.

Other regions of the nuclear genome can also be used to determine genetic structure and evaluate the consequences of habitat fragmentation in primates. The Y chromosome, while transmitted only along the paternal line, offers researchers the opportunity to evaluate the consequences of habitat fragmentation on males of a species. It is also used to detect signs of male-specific migration between fragments. The typical Y chromosome marker is a microsatellite and there are several dozen to choose from in most primates. Some microsatellite loci are highly polymorphic, with 12 or more alleles.

Other, less common, regions of the nuclear genome used for measuring genetic variation within and between populations and for assessing the consequences of habitat fragmentation include intronic sequences and even single nucleotide polymorphisms (also known as SNPs). Introns are usually unaffected by natural selection and therefore expected to exhibit some degree of polymorphism. SNPs can only have one of the four nucleotides at any one position but when several SNPs are considered together, they represent useful genetic markers for assessing genetic diversity in populations.

Researchers have also begun to consider how fragmentation affects functionally important genes such as the major histocompatibility complex (MHC) (Sommer 2008). Some researchers have even started to assess the levels of diversity of functional genes by studying RNA sequences (Perry et al. 2012). In the case of the MHC, loss of genetic diversity due to genetic drift or reduced gene flow between fragments can lead to negative consequences for disease resistance and ultimately fitness (Knapp 2005). The study of these genes in light of fragmentation is relatively new but this research may become increasingly important in the future of primate conservation research.

Molecular data from the mitochondrial genome can also yield important insight about the genetic uniqueness and genetic diversity of population fragments. The data obtained from the mitochondrial genome differs from the nuclear genome, as mitochondria are maternally inherited. Differences in mitochondrial DNA (mtDNA) may be detected as different PCR fragment lengths, different bands in a gel matrix, or different DNA sequences. For the simplest tests, it might only be necessary to determine if two individuals share the same mitochondrial genotype (also known as haplotype), which would suggest that they share common ancestry along the maternal line. With in-depth and detailed data, such as nucleotide sequences, it may be possible to construct phylogenetic relationships between individuals, and establish ancestral relationships. Like msat and other nuclear markers, mtDNA data can also be used for the population genetic analyses described below.

Statistical Measures

The genetic consequences of habitat fragmentation depend on the level of migration, or gene flow, which occurs between the population fragments. Not surprisingly, gene flow is affected by the number, size, and pattern of fragments, as well as the distance and nature of the terrain (or matrix) between fragments and the time since fragmentation. If there is restricted gene flow, fragmentation usually leads to loss of genetic diversity within fragments and greater inbreeding. In these fragments, greater genetic differentiation can lead to greater risk of extinction.

Genetic differences between population fragments are commonly estimated by using one of several statistics to evaluate population structure and estimate gene flow between population fragments. These statistics are convenient estimates but they make a number of simplistic, and unrealistic, assumptions, such as no selection and that migration is random. Estimates of population subdivision and genetic variation within and between population fragments (or what appear to be fragments) are typically calculated using F-statistics. Wright's (1969) F_{ST} or Nei's (1978) coefficient of gene variation (G_{ST}) is often used. Slatkin's R_{ST} (1995) is comparable to Wright's F_{ST} but assumes a high-stepwise rate of mutation that is common for microsatellite loci. Weir and Cockerham (1984) developed a theta (θ) estimator which corrects for sample size and number of populations (fragments) examined. All of these values are calculated by determining the amount of heterozygosity (or haplotype diversity) within and between populations, based on differences in allele (or haplotype) frequencies. Detailed equations and derivations of formulae can be obtained in the original references or in recent discussions of the use of these statistics (Meirmans and Hedrick 2010; Whitlock 2011). Computerized programs (Table 25.2) are available for quickly and easily calculating these statistics even when researchers have large data sets containing many individuals with many loci consisting of many alleles. If the researcher has knowledge about generation time of the species studied at several sites, it is possible estimate the rate at which genetic diversity will be reduced due to the prior loss of alleles in a population (i.e., genetic erosion) in the fragmented populations under study (Srikwan and Woodruff 2000). Values of F_{ST}, G_{ST}, R_{ST}, and θ vary from 0 to 1, with higher values implying considerable differentiation between population fragments. Traditionally, an F_{ST} above 0.15 is considered to indicate significant differentiation among fragments (Frankham et al. 2002).

Although its use has been criticized in recent years (Neigel 1996; Neigel 2002), F_{ST} is a frequently encountered value in the primate literature (Table 25.2). G_{ST} in particular has a number of useful properties: it can be used for one or many loci,

Table 25.2 Selected examples of nonhuman primate studies using molecular genetic markers and statistical tests to evaluate the consequences of habitat fragmentation

Species	Genetic marker	Statistic	Reference
Propithecus	msats	F-statistics	Lawler et al. 2003
Microcebus	MHC	F_{ST}	Sommer 2008
Alouatta	msats	F-statistics, *D*, and G_{ST}	Ruiz-Garcia et al. 2007
Brachyteles	allozymes	F-statistics	Pope 1998
Papio	mtDNA	AMOVA, ML trees	Winney et al. 2004
Pongo	msats	F_{ST}, Bayesian analyses	Goossens et al. 2006
Gorilla	msats	STRUCTURE, GENECLASS	Bergl and Vigilant 2007
Pan	mtDNA and Y chromosome msats	AMOVA, NETWORK analyses	Eriksson et al. 2006

mutation rates do not alter the statistic significantly, the exact number of populations need not be specified, and the statistic is relatively responsive to changes in allele frequencies in time. R_{ST} is especially advantageous when analyzing highly variable microsatellite loci. Although each of these statistics has important conceptual differences, in practice F_{ST} and G_{ST} are used in similar fashion as indices of genetic difference among populations (Crow 1986). Frequently, several statistics can be found together in a single publication, used for comparative purposes.

F_{ST} can, in general, be considered a measure of genetic distance between population fragments. It is not the only genetic distance tool for evaluating the consequences of habitat fragmentation. Genetic distance is a traditional measure of divergence among populations (or species), which can be used to infer whether populations, or fragments, are reproductively independent or not. Scatterplot comparisons of pairwise genetic versus geographic distance (Fig. 25.1) may yield interesting insight about the degree and extent of isolation between some population fragments. There are many different quantitative approaches to measuring genetic distance and many different statistics can be found in the primate literature. These are generally considered analysis of molecular variance (AMOVA) statistics (Excoffier et al. 1992). AMOVA statistics are also appropriate for use with uniparentally inherited markers such as mitochondrial DNA sequences and Y chromosome microsatellites. Delta mu ($\delta\mu^2$) (Goldstein et al. 1995), is comparable to R_{ST} and is also used to assess microsatellite data. A classic statistic for estimating genetic distance is Nei's *D* (Nei 1978) and a number of computer programs can be used to conduct these analyses (Table 25.2). Detailed discussions and reviews of these methods can be found elsewhere (Meirmans and Hedrick 2010; Whitlock 2011).

There are other F-statistics (Wright 1969) that can be used to measure population fragmentation. F_{IS}, for example, estimates the amount of inbreeding within a fragment. F_{IS} values range from −1 to 1, where 0 represents random mating within the population fragment and a positive F_{IS} represents at least some mating among related individuals. For individuals living in fragmented habitats and isolated populations, estimating the amount of inbreeding, and determining if there is an

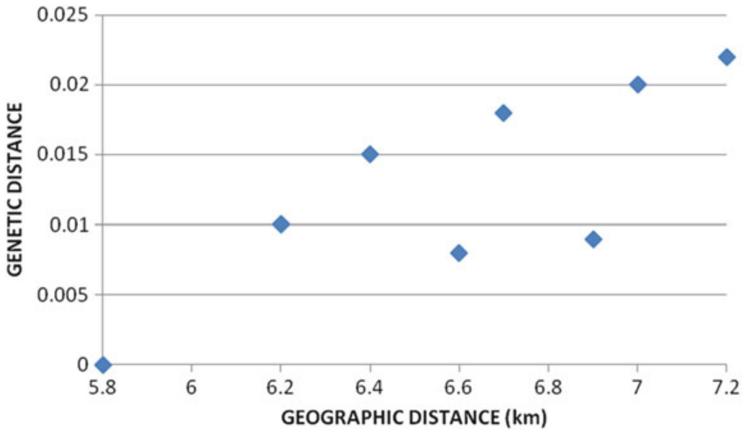

Fig. 25.1 Example relationships showing the extent of genetic differentiation and geographical distance between pairs of populations. In this hypothetical example, geographical distance (in km) is plotted on the horizontal axis and a measure of genetic distance [$F_{ST}/(1-F_{ST})$] is plotted on the vertical axis for pairs of populations. As predicted, the most geographically distant populations are generally the most genetically dissimilar. When fragmented populations are surveyed, they often exhibit greater levels of genetic distinctness ($F_{ST}>0.25$) even when they are not geographically distant from each other

inbreeding depression, is an urgent conservation requirement. F_{IT} estimates the amount of inbreeding within all fragments together and like F_{IS}, values range from −1 to 1. These statistics are frequently calculated at the same time as F_{ST}, as the values are easily determined once F_{ST} is known. Other measure of relatedness within populations can also be calculated. IR is a measure of parental relatedness (Amos et al. 2001) and the estimated mean individual inbreeding coefficient is IDB (Raymond and Rousset 1995). A high mean F_{IS}, IDB, and IR reflects inbred individuals in fragments.

New and Alternative Approaches

Anyone who has ever observed natural populations of primates knows that the assumptions of F-statistics are unrealistic. In most primate societies, sexual selection is a major factor in breeding success. We also know that sex-specific migration occurs in many primate species. F-statistics are still the hallmark of many conservation genetics studies (Neigel 2002), but a number of new methods have become available in recent years and it is likely that we will see more of these statistics in the literature in the future.

Populations may not be discretely distributed due to unidentified barriers to gene flow. Groups of individuals may have different geographical locations, behavioral patterns, or phenotypes and these may not be immediately apparent to the researcher. Pritchard et al. (2000) developed a novel software program called STRUCTURE which delineates clusters of individuals on the basis of their genotypes at multiple loci using a Bayesian approach. Maximum likelihood estimators based on allele frequencies represent another way to infer rates of gene flow for subdivided populations (Rannala and Hartigan 1996). Nested clade phylogenetic analysis (NCPA) approaches (Templeton 2004) offer researchers the opportunity to test hypotheses about historical events and evaluate current population structure of species or even groups of populations. Alternatively, migration rates can be estimated using the genealogies of sampled individuals (i.e., coalescent theory). While the calculation of migration rates may be difficult, there are specific programs designed to do this and some are specifically designed to calculate long-term rates using coalescent theory (e.g., MIGRATE, Beerli and Felsenstein 2001). Readers interested in the background and basic assumptions of these approaches are encouraged to consult the references suggested above, in particular see Beerli, 2009.

Conclusion

Biological samples are difficult to collect, preserve, export, and store. Genetic data may be difficult and costly to generate, replicate and analyze. However, these are the data we need to determine the population structure and approximate the rate of gene flow between population fragments. Using the genetic tools only briefly described in this chapter, researchers can determine the conservation status and make recommendations for endangered species management. Genetics will not save species from extinction, but the data we generate can be used to make informed decisions that would not otherwise be possible.

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Chapter 26
Kinship and Dispersal Patterns in *Alouatta caraya* Inhabiting Continuous and Fragmented Habitats of Argentina

Luciana Oklander and Daniel Corach

Abstract Black and gold howler monkeys (*Alouatta caraya*) still inhabit degraded and fragmented forests in southern South America. This fact raises questions regarding the real capacity of the howler's long-term survival under such conditions. A detailed molecular study was carried out with the aim of evaluating how the continuous processes of habitat reduction and fragmentation affect the genetic structure of howler monkey populations. Two populations exposed to differences in forest continuity were compared using molecular markers: one inhabiting an undisturbed and continuous forest (CF) and the other a fragmented forest (FF). FF and CF showed differences in kinship relations and dispersal patterns. The groups in the FF were genetically differentiated; in contrast, there was no differentiation between groups in the CF. Moreover, both males and females disperse in the CF; accordingly, most groups were composed of adult individuals that were not closely related, whereas in the FF, males disperse more than females and groups were composed of closely related adult females. These results suggest that habitat fragmentation modifies the dispersal patterns of black and gold howler monkeys and might reflect a trend towards a reduction in their ability to disperse. This study underscores the use of molecular genetic data as a tool of utmost importance for conservation purposes to better understand social organization and behavioral patterns.

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The Species

Black and gold howler monkeys (Primates, Platyrrhini, Atelidae) have been intensively studied for decades in a variety of habitats including degraded and fragmented forests throughout their distribution (Fig. 26.1a, b). There is available data of the populations inhabiting northern Argentina on demography, social structure, diet, and many behavioral patterns (Rumiz 1990; Rumiz et al. 1986; Kowalewski and Garber 2010; Zunino and Kowalewski 2008). Nowadays, entire fragments of forest are being clear-cut for agriculture and cattle ranching in the southern limit of the geographic range of *A. caraya*, covering the Argentine provinces of Formosa, Misiones, Salta, Corrientes, and Chaco (Brown and Zunino 1994; Peres 1997; Zunino et al. 2007). Several studies mention the survival ability of this species in fragmented and impoverished habitats such as those that have suffered selective logging (Bicca-Marques 2003; Bicca-Marques et al. 2009; Zunino et al. 2007). For example Zunino et al. 2007 studied groups inhabiting forests that have been under continuous logging for the past 20 years and found that the ecological density and the number and composition of groups have remained constant. Although *A. caraya* groups still inhabit degraded and fragmented forests, the real capacity of howlers to endure under these levels of habitat degradation in the long-term is still unknown. The ultimate goal of this research was to address this issue.

The Approach

Molecular genetic methods have been increasingly applied in studies of behavioral ecology and conservation of primates (Di Fiore 2009; Fischer et al. 2006; Hernandez et al. 2007). In particular, the use of microsatellites has allowed the description of

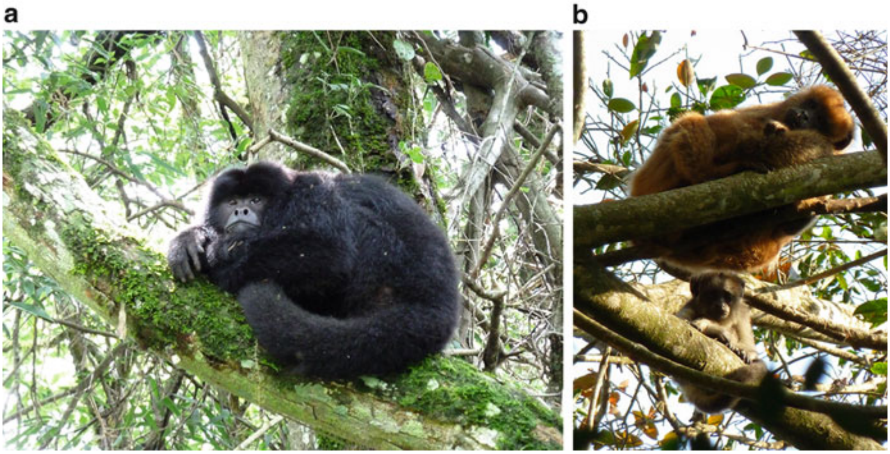

Fig. 26.1 (**a**) Male *Alouatta caraya*. (**b**) Female and juvenile *Alouatta caraya*

primate population characteristics such as mating systems, dispersal patterns, and levels of inbreeding that were difficult to detect by observational studies. Microsatellites are short tandem repeats (STR) of genomic DNA sequences dispersed all over the genome that are highly polymorphic because of variation in the repeat number. These markers are co-dominantly inherited, since the alleles of both parents are detectable in the offspring, thus are useful for population genetic studies and kinship determination.

In sharp difference with research carried out on apes where human-specific polymorphic genetic markers can be employed, most of these markers were not useful in the analysis of more evolutionarily distant species such as Platyrrhines. The underlying reason for this restriction is the lack of homology between human-derived primer sequences and Neotropical primate-genomes. Therefore, in order to investigate the population dynamics of black and gold howlers, the first step to accomplish was to detect, isolate, and characterize suitable polymorphic genetic markers for this species. Accordingly, prior to this research we identified eleven polymorphic DNA microsatellite markers for the *A. caraya* (Oklander et al. 2007), allowing the opportunity to study kinship relations and gene flow in this species.

Few data were available on the influence of habitat fragmentation on genetic variation in free-ranging Neotropical primates. Loss of genetic variation and inbreeding depression, typically expected outcomes of forest fragmentation, are likely to have highly deleterious implications for the long-term viability of animal populations.

In this study we examine by molecular methods how habitat fragmentation impacts the genetic structure of black and gold howler monkeys (*A. caraya*) populations in northern Argentina. For this purpose, fixation indexes (Fst and Fis), kinship relationships between members of each group, and paternity/maternity identification of juvenile and subadult individuals were analyzed for each population: one inhabiting an undisturbed continuous forest (CF) and the other a fragmented forest (FF). We expected to find related individuals within the groups, but highly differed among groups in the FF, as a consequence of the restriction for dispersal caused by habitat fragmentation.

The Populations Studied

Two populations of black and gold howlers located 20 km apart on the boundary of Corrientes and Chaco provinces in Northern Argentina were studied. These two populations inhabit sites that were exposed to similar temperature, precipitation, and photoperiod patterns (Argentina's National Meteorological Service), but display differences in forest continuity. One of the populations included a set of groups living in an undisturbed and continuous forest (CF) located on Brasilera Island that has 292 ha with no permanent human settlements (27° 18′ S, 58° 38′ W). The other population inhabits a fragmented forest (FF) located in the surroundings of the Corrientes Biological Field Station (27° 30′ S, 58° 41′ W) (EBCo;

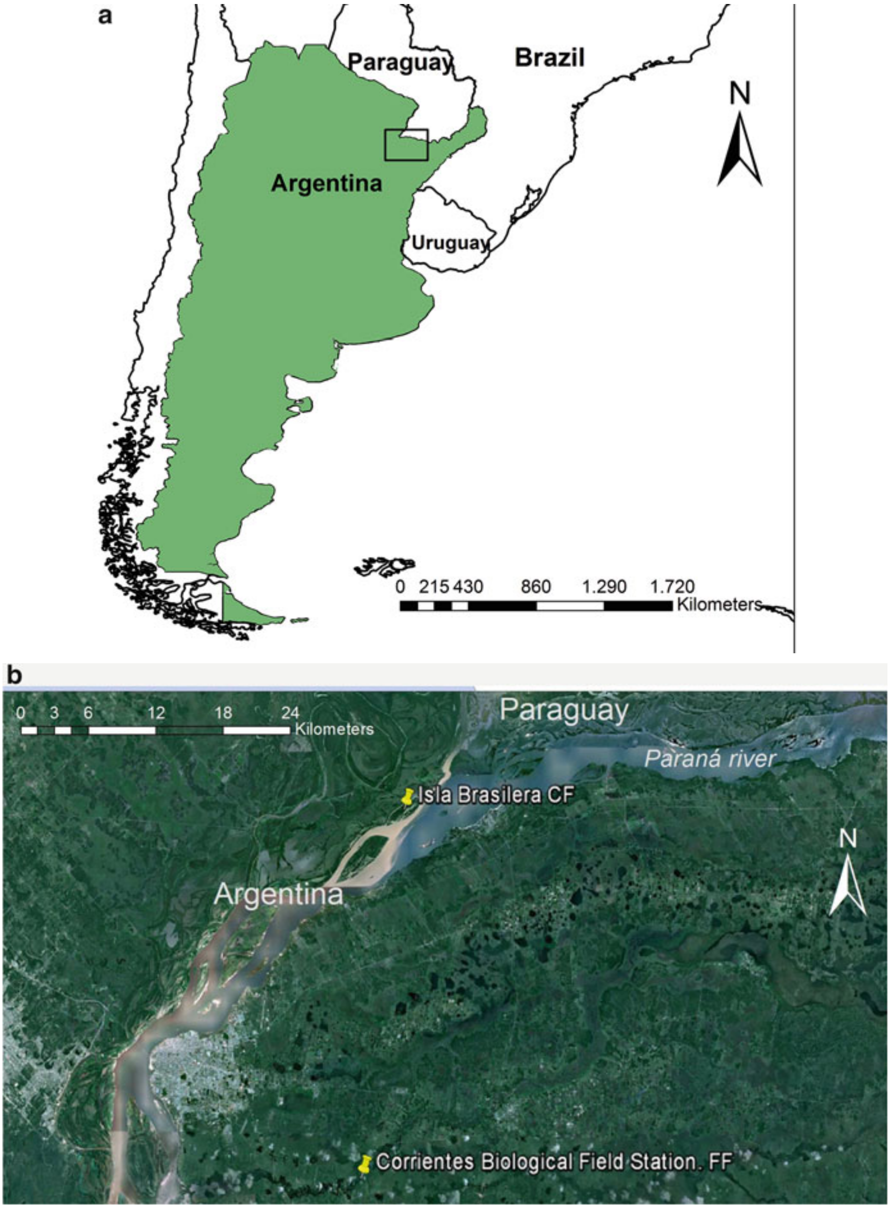

Fig. 26.2 (**a**). Location of the study area in Argentina. Photo by Luciana Oklander. (**b**) Location of Isla Branca continuous forest site and Corrientes Biological Field Station fragmented forest site. Photo by Luciana Oklander

MACN-CONICET) (Fig. 26.2a, b). Groups studied in the FF were dispersed in forest fragments interrupted by grassland in a total area of 306 ha. In general, there was only one group associated with each fragment. Individuals from 7 groups in the CF and from 11 groups in the FF were studied (Table 26.1).

Table 26.1 Composition of 7 groups in the CF and of 11 groups in the FF

CF groups	EM (11)	NF (9)	G (10)	LR (11)	MK (7)	VC	X (10)				
Individuals	AM[a]	AM[a]	X AM[a]	X AM[a]	AM[a]	AM[a]	X AM[a]				
	AM[a]	AM[a]	AM[a]	AM[a]	AM[a]	AM[a]	AM[a]				
	AM	AF[a]	AM[a]	AF[a]	AF[a]	AM	AM[a]				
	AF[a]	AF[a]	AF[a]	AF[a]	AF[a]	AF[a]	AF[a]				
	AF[a]	AF[a]	AF	AF[a]	SAF[a]	AF[a]	AF[a]				
	AF	SAF	AF	AF[a]	JF	AF	SAM				
	AF	JM[a]	AF	SAM[a]	IM	SAM	SAM[a]				
	SAM	IM	SAM[a]	SAF[a]		SAF[a]	SAF[a]				
	JM	IF	SAM[a]	JF[a]		JM	JF[a]				
	JF		SAM	JF[a]			IM				
	IM		JM[a]	JF[a]			IF				
				JM							
FF groups	CC (7)	CV (6)	EV (9)	H (8)	L1 (5)	L2 (5)	ML (8)	PZ (7)	RS (9)	NN (5)	ZN (6)
Individuals	AM[a]	AM[a]	AM[a]	AM[a]	AM[a]	AM[a]	AM[a]	AM[a]	AM[a]	AM[a]	AM[a]
	AF[a]	AF[a]	AF[a]	AM[a]	AM[a]	AF[a]	AM[a]	AF[a]	AM[a]	AF[a]	AM[a]
	AF[a]	AF[a]	AF[a]	AF[a]	AF[a]	AF[aa]	AF[a]	AF[a]	AF[a]	AF	AF[a]
	SAF	SAM	AF[a]	AF	AF[a]	SAM	AF	SAM[a]	AF[a]	JF	AF
	JM	JM	AF	SAM	SAM[a]	JM	AF	SAF	AF[a]	IM	SAM[a]
	JF	IF	SAF	JM[a]			SAF[a]	JM[a]	AF[a]		JF[a]
	IF		JF[a]	JM			JM	JF[a]	SAM[a]		
			JM[a]	IM			JM		SAF[a]		
			IM						JM[a]		

A adults, *SA* sub-adults, *J* juveniles, *I* infants; *X* corpses (dead individuals), *F* females, *M* males, ( ) number of individuals in the group (not considering dead individuals)

[a] Sampled individuals

Research Strategy

A. caraya individuals of both populations were under permanent observation as part of a multidisciplinary research (Oklander et al. 2004; Zunino et al. 2007; Kowalewski and Garber 2010; Kowalewski et al. 2010). Accordingly, captures were frequently required for individual identification.

Capture

Black and gold howler monkeys inhabit the top of trees, up to 20 m high, and rarely come down to ground level. Therefore, one way to capture them was by darting. This procedure was carried out by shooting darts with a Pneu Dart Model 179B Air Pump Rifle, Sheridan. The darts were 1 cc Pneu Dart type "P" with collared needles. A combination of medetomidine hydrochloride (Domitor, Pfizer Corporation) and Ketamine hydrochloride 50 mg/ml (Ketalar, Parke Davis) was used as anesthetic. Dosage was 150 mg/kg medetomidine hydrochloride combined with 4 mg/kg of Ketamine. When the darted animals were under anesthetic effect and ready to fall, stretched nets were placed under them in an attempt to catch them before they reached the ground. The average anesthesia period was approximately 60 min. Once the effect of anesthesia subsided, animals were maintained in a safe place until their complete recovery. Behavioral observations assured this condition prior to animal release into their habitat. All procedures were supervised by veterinaries from the Universidad Nacional del Nordeste, Argentina. Ear tagging and ankle color identification bracelet fittings (same material as commercial pet collars) were applied to the narcotized animals.

Sampling

Ear tissue obtained during tagging was used as a DNA source. A total set of 43 individuals from 7 groups (Table 26.1) were captured and sampled in the CF in 2005. In addition, tissue samples from three monkey corpses found during behavioral studies within the research area in 2004–2005 were gathered and used in the analysis (Table 26.1). In 2004, a set of 50 individuals from 11 social groups (Table 26.1) were captured and sampled for analyses in the FF. Tissue samples from captured individuals and corpses found in the study sites were conserved at room temperature in solid NaCl (Oklander et al. 2004) until DNA extraction in the laboratory. The study complied with current Argentine laws (permissions from the National Resources Board, Subsecretariat of Fauna and Flora, Corrientes Province, Argentina).

Lab Procedures

DNA was extracted from ear tissue samples using the standard procedure SDS/ Proteinase K digestion followed by phenol–chloroform organic extraction (Sambrook et al. 1989). Amplifications of 11 microsatellites characterized for *A. caraya* were subsequently performed for each sample as described in Oklander et al. (2007). In all cases, DNA extraction and PCR amplification reactions included negative controls. Allele sizes of PCR products were determined using an ABI 310 Genetic Analyzer and Genescan software version 3.1, using GS-500 TAMRA as size standard (Applied Biosystems, Foster City, USA).

Fixation Indexes

Fixation indexes (F statistics; Wright 1965) were used in order to measure genetic variability within populations. These indexes were based on heterozygosity measures and were used to evaluate the reduction in expected heterozygosity for random mating at any one level of a population hierarchy relative to another more inclusive level of the hierarchy (Hartl and Clark 2007).

Arlequin 3.0 (Excoffier et al. 2005) and Fstat (Goudet 2001) software packages were used to estimate Fst and Fis indexes within and between each population of *A. caraya* by means of the analysis of variance of allele frequencies—AMOVA (Analysis of Molecular Variance; Weir and Cockerham 1984). These programs use parameters of the statistical *F* that allow to make inferences even when there were differences in the number of sampled individuals in each subpopulation, or in the subpopulation number within each population. The frequency of null alleles in each locus was also considered by the Cervus software (Marshall et al. 1998).

The statistical Fst is a measure of population genetic structure that allows estimates of gene flow among populations under the hypothesis of neutral alleles (Hartl and Clark 2007). In fragmented habitats, Fst values can estimate the proportion of gene flow among fragments. It is considered that if high gene flow exists among subunits, Fst values should not be significantly different from 0. Therefore, at low rates of gene flow, Fst values were increased. High Fst implies a considerable degree of differentiation among populations or groups (Hedrick 2005). Fst was also used to analyze possible sex bias in dispersal patterns. Dispersions generally happen in juvenile or subadult states (Pusey and Packer 1987). For this reason, only adult individuals were considered for sex-bias analysis. Allele frequencies of individuals of the dispersant sex should be more homogeneous than those of philopatric sex individuals; therefore, the Fst of the philopatric sex in each population is expected to be higher than that of the dispersant sex in each population (Goudet et al. 2002). Fis (inbreeding coefficient) is the proportion of the variance in the subpopulation contained in an individual. High Fis usually implies a high degree of inbreeding (Hartl and Clark 2007).

Kinship Relationships

Kingroup software (Konovalov et al. 2004) was used for the estimation of kinship relationships among the individuals that compose the groups in both howler populations (Table 26.2). This program calculates kinship coefficients (*r*) based on analysis of maximum likelihood, even evaluating the genetic similarities for progeny with a small number of samples (Goodnight and Queller 1999). Paternity and maternity of juveniles and subadults were also evaluated by Mendelian inheritance between candidate's parents and offspring (Table 26.3). Whenever one allele in all loci analyzed was also detected in the candidate's parent, statistical likelihood analyses were performed in order to obtain the Paternity Index (Edwards 1972). For this estimation we used the Cervus software (Marshall et al. 1998). Those individuals who achieved paternity indexes higher than 97 % were considered to be the parents of the juvenile/subadults in the sample.

Table 26.2 Kinship relations and FIS for groups in CF and FF

CF groups	*r* adult individuals (average)	*r* adult female dyads	*r* adult male dyads	FIS
EM	0.230	0.2	0.29	0.094
NF	0.102	0.0/0.0/0.35	0.29	−0.063
GR	0.048	–	0.0/0.01/0.05	−0.014
LR	0.117	0.0/0.0/0.1/ 0.2/0.38/0.64	0.0	0.015
MK	0.142	0.0	0.43	0.056
VC	0.027	0.0	0.0	−0.055
XZ	0.157	0.0	0.0/0.0/0.39	−0.057
Average	0.118	0.144	0.133	
FF Groups				
CC	0.227	0.58	–	−0.036
CV	0.2	0.46	–	−0.018
EV	0.19	0.24/0.35/0.5	–	−0.256
HT	0.49	–	0.72	−0.148
L1	0.12	0.53	0.0	−0.173
L2	0.32	0.66	–	−0.241
ML	0.35	–	0.05	−0.260
PZ	0.317	0.27	–	−0.272
RS	0.24	0.33/0.34/0.39/0.41/0.51/0.67	0.46	−0.176
NN	0.0	–	–	0.188
ZN	0.15	–	0.15	−0.136
Average	0.237	0.447	0.276	

r: Kinship coefficient

Table 26.3 Juveniles and subadults maternity and paternity

Population	Group	Age/sex	Individual	Mother	M Group	Father	F Group	LOD	PI
CF	[a]NF	JM	ME25	HE20	NF	M17	VN	6.12E+14	99.78
CF	G	JM	Huevo	Orejas	G	Marley	GR	5.60E+14	99.57
CF	LR	JF	Mireya	China	LR	TomX	LR	1.66E+14	99.75
CF	LR	JF	Lila	–	–	Mazzi	LR	5.34E+14	98.36
CF	LR	JF	Milica	China	LR	TomX	LR	3.40E+14	99.92
CF	X	JF	Gordita	Gorda	X	Gatti	XZ	1.89E+14	99.87
CF	G	SAM	Hermoso	–	–	MuertoM	GR	3.43E+14	98.65
CF	[b]LR	SAM	Julio	Orejas	G	Jose	GR	5.66E+14	99.98
CF	[b]X	SAM	Alf	Lola	G	Jose	GR	4.91E+14	99.81
CF	[b]G	SAM	Primo	–	–	M207	XZ	3.92E+14	97.92
CF	MK	SAF	HMuk3	–	–	208Muk	MK	2.03E+14	98.64
CF	VC	SAF	HVec18	HV7	VC	–	–	2.60E+14	98.93
CF	LR	SAF	Migui	Chile	LR	Mazzi	LR	4.79E+14	99.95
CF	X	SAF	Gorda	–	–	M207	XZ	2.09E+14	98.46
FF	EV	JF	H25	H12	EV	M3	EV	3.14E+14	98.10
FF	EV	JM	M21	H10	EV	M3	EV	9.18E+14	99.02
FF	H	JM	M1	–	–	M15	HT	3.40E+14	97.60
FF	PZ	JM	M36	H35	PZ	M32	PZ	3.42E+14	97.33
FF	[c]PZ	JF	H19	H35	PZ	M33	PZ	8.14E+14	98.67
FF	RS	JM	M24	H17	RS	M12	RS	6.22E+14	99.02
FF	ZN	JF	H1	H15	ZN	M16	ZN	6.63E+14	98.34
FF	PZ	SAM	M33	H35	PZ	M32	PZ	7.08E+14	98.79
FF	ML	SAF	H6	–	–	M6	ML	5.15E+14	98.59
FF	L1	SAM	M14	H21	L1	–	–	3.83E+14	98.22
FF	RS	SAF	H4	–	–	M12	RS	4.88E+14	97.03
FF	RS	SAM	M8	H17	RS	M12	RS	8.45E+14	99.00
FF	ZN	SAM	M7	H15	–	M16	–	3.62E+14	98.97

Includes: Group, age, sex, mother's group (M Group), father's group (F Group), LOD, and paternity index (PI) values

[a] Extragroup paternity

[b] Dispersant subadults

[c] Incest case

What Genetic Markers Tell Us About Habitat Fragmentation

Population analysis of the 11 microsatellites in the FF and the CF suggested many differences between the two populations. AMOVA results in the CF population showed nonsignificant values in *F* indexes (Fst = 0.050, $p = 0.173$, Fis = –0.012, $p = 0.627$). In addition, the analyses of Fis values for each group were not statistically significant (Table 26.2). Moreover, the analyses of Fst by sex showed similar values (Female Fst = 0.056, Male Fst = 0.055, $p = 0.981$), indicating that neither females nor males from different groups were genetically differentiated. Nonsignificant *P* values mean that Fst values were also similar between sexes.

On the other hand, the AMOVA results for the FF population showed Fst values that suggested significant genetic differentiation among groups (Fst = 0.139, AMOVA $p < 0.001$). However, significant values were not observed for Fis = −0.153, $p > 0.05$. Therefore, these results do not support inbreeding in the FF. Although the Fis analyses of each group were not significant ($p > 0.05$), most of them showed higher negative values than those in the CF (Table 26.2). Fst analyses by sex showed significant differences (Female Fst = 0.233, Male Fst = 0.079, $p = 0.036$) suggesting that females were genetically differentiated between groups, being their differentiation higher than that observed among males from different groups.

Average kinship relationships among adult females and males composing the groups showed similar and relatively low values in the CF (female $r = 0.144$; male $r = 0.133$, $p = 0.905$). These results suggest that there were no differences in kinship relationships among adult males and females in the groups. Average kinship relationships in each group are shown in Table 26.2. On average, individuals from each group in the CF were related by $r = 0.118$ (not closely related). In the analysis of paternity/maternity of juvenile and subadult individuals of the CF we found a juvenile male individual whose father belonged to a neighboring group (MJ from group NF, Table 26.3). Additionally, it was found that three out of eight analyzed subadults were living in different groups from those of their parents (male subadult from group LR and, male and female subadults from group X, Table 26.3). This data shows that three from the eight analyzed subadults (37.8 %) dispersed from their natal groups.

In the FF, in contrast, average kinship relationships among adult females and males showed significant differences (female $r = 0.447$; male $r = 0.276$, $p = 0.047$). These results indicate that differences exist in female and male grouping in this population. Adult females in the groups were more closely related among each other than males. Females also present higher genetic differences among groups. Average kinship relationships in each group are shown in Table 26.2. Individuals of each group in the FF have an average kinship coefficient of $r = 0.237$. This relationship coefficient was twice as high as observed in the CF. Furthermore, it was found that all juvenile and subadult individuals analyzed for paternity and maternity in the FF were in the same group as their progenitors; therefore, they had not dispersed yet (Table 26.3). In addition, we detected an incest case of a female who had an offspring (identified as individual H19) with her son (Table 26.3).

Diverse Genetic Landscapes Reflect Habitat Fragmentation

Habitat fragmentation may isolate populations and limit dispersal opportunities. By analyzing the genetic variability of the two groups of howlers with differences in their habitat quality, we were able to discern the strategies used to cope with habitat fragmentation and estimate long-term consequences. Microsatellite marker analysis allowed evaluation of fixation indexes, kinship relationships, and the comparison of black and gold howler groups inhabiting undisturbed and fragmented forests underscoring many clear differences.

The CF population exhibits a genetic variability that was almost entirely found in all of the studied groups, since only 5 % (Fst = 0.05) of the variation was due to differences among groups. CF analysis by sexes indicates that both sexes disperse in this population. As a result, groups were composed of mature females and males that were not related by kinship, demonstrating that these groups were composed of immigrant individuals. These data were also supported by paternity analyses that confirmed three subadult individuals whose progenitors reside in a different group. Additionally, a case of extra-group paternity was found in the CF, which indicates that, either due to extra-group copulation or male turnover in the groups, there was gene flow among groups. Prior behavioral data on the same groups confirm a high degree of extra-group copulation during potentially fertile periods (Kowalewski 2007). These data would strongly suggest that extra-group fathering might occur. The results of the Fis index were close to 0 in all the groups, showing that neither heterozygosis deficiency nor excess was observed in any of the groups. Summarizing, these results suggest that considerable gene flow exists among groups in the CF population and that there was no indication of inbreeding.

Conversely, the FF population shows significant differences in Fst, indicating that the genetic variability in the FF population was distributed among groups and consistent with a recent genetic differentiation. On average, only 86 % (Fst = 0.14) of the total population variability was shared by the groups, suggesting a reduction in the dispersal rate between groups residing in different fragments. Isozyme marker analysis in another howler species (*Alouatta seniculus*) also indicated an influence of habitat fragmentation on gene flow decrease (Pope 1990, 2000). Mature individuals analyzed by sexes in the FF indicate dispersal biased towards males. Females that compose groups in the FF were highly related within groups and highly differentiated between groups. The relationship coefficient among them was 0.45, a value expected only among mothers and daughters or sisters. Accordingly, females in this habitat seem to be philopatric. Males showed a relationship coefficient of 0.28. Although this magnitude was significantly smaller than that for females in this population, it was twofold higher than that found in the CF for both sexes. These results show that males constitute the dispersing sex in this habitat, but their dispersal into other groups occurs about 50 % less frequently than in the CF.

Paternity analysis in the FF showed that individuals of the same group fathered all studied individuals. Fis analyses of the FF groups mostly showed high negative values. These results usually indicate heterozygosity excess, and therefore absence of inbreeding. But in the FF, mature females were highly related within the groups and their gametes represent a differentiated portion of the gene pool. Gametes from any male coming from other groups might cause heterozygosity excess in the first offspring generation when joining these females (Chesser 1991; Pope 1992), which makes potential inbreeding situations extremely difficult to detect by the Fis index in this situation.

Another approach to estimate inbreeding was by kinship relationship coefficients. These values averaged 0.24, indicating that most individuals within groups would be closely related—a value expected for uncles, cousins, grandsons, or half siblings. The increase in philopatric behaviors increases the chances of inbreeding. In FF one case of incest was found, where a female had a son whose father was another of her sons, which indicates consanguineous mating. Hence, inbreeding was occurring in this habitat.

Studies carried out on many taxa have indicated that inbreeding is expensive (Briskie and Mackintosh 2004; Crnokrak and Roff 1999; Foerster et al. 2003), even to the point that the extinction risk rises significantly (Nieminen et al. 2001). Inbreeding may cause fitness reduction due to a series of genetic factors such as exposing deleterious recessive alleles because of homozygosis increase, heterozygosis decrease, and/or loss of isoenzyme variability (Crnokrak and Roff 1999). Although the inbreeding depression level varies depending on the species, local conditions and reproductive history, in all cases, the costs of inbreeding increase with the relationship coefficient among reproductive couples (Paul and Kuester 2004). The incest case in the FF was a clear example of inbreeding with very high relationship coefficients among progenitors. This fact, plus the high genetic differentiation among groups, and the permanence of juvenile and subadults in their natal groups suggest reduced gene flow in this habitat, revealing that increasing habitat fragmentation may severely limit the howler's ability to disperse.

The inbreeding avoidance hypothesis proposes that individuals will avoid inbreeding because of its fitness costs. Dispersal patterns reduce inbreeding probability in primates (Field and Guatelli-Steinberg 2003). Limited dispersal or high costs of dispersal may explain that howlers reproduce with the only individuals present in their habitat, whether they were closely related or not, when their reproductive success was compromised. Altogether, these results suggest that habitat fragmentation modifies the dispersal patterns of black and gold howler monkeys.

Conclusion

Northeast Argentinean forests are suffering continuous human modifications that may isolate populations and limit dispersal opportunities. If fragmentation and clearing of forest fragments continue as a consequence of uncontrolled deforestation and landscape modification, there will be an isolation of different subsets of howler populations. The increase in isolation levels may be translated into loss of genetic diversity resulting in an inability to respond to selective pressures. Moreover, loss of genetic variability associated with a decrease in the availability of food and a higher risk of diseases could possibly lead to local extinction. This study underscores the use of molecular genetic data as a tool of utmost importance for a better understanding of modifications of behavioral patterns produced by habitat fragmentation, offering a new approach for optimizing wildlife conservation strategies.

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Chapter 27
The Mona Monkeys of Grenada, São Tomé and Príncipe: Long-Term Persistence of a Guenon in Permanent Fragments and Implications for the Survival of Forest Primates in Protected Areas

Mary E. Glenn and Keith J. Bensen

Abstract Forest dwelling mona monkeys (*Cercopithecus mona*) were introduced to the Caribbean island of Grenada and the Gulf of Guinea islands of São Tomé and Príncipe 200–500 years ago and have remained isolated from their African mainland conspecifics for at least 200 years. All three island populations provide insight into the possible medium-term future of small populations of African forest guenons isolated in forest fragments due to deforestation and human hunting. The forest habitats on the three islands range in size from 5,000 to 25,000 ha. Genetic studies indicate that the Grenada population originated from potentially a single female and is a subset of the São Tomé population, which had a larger founding size. The Grenada population now numbers in the thousands, as do the populations on São Tomé and Príncipe. The Grenada monas appear to have suffered no inbreeding effects and may be an example of genetic purging, the process where deleterious phenotypes are weeded out of very small populations if they are allowed to rapidly rebound. Monas are ecological generalists and thus may have been conferred additional survival benefits on each island by their ability to take advantage of completely novel forest habitats. The Grenada monas, in particular, demonstrate that it may not be a lost cause to conserve very small populations of forest primate species in habitat fragments, if they can be immediately protected from further depredation and if the species has some ecological flexibility.

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Introduction

Extremely small numbers of African mona monkeys, *Cercopithecus mona*, were introduced to the Caribbean island of Grenada 200–350 years ago and a larger number of monas were introduced to the West African islands of São Tomé and Príncipe approximately 350–500 years ago (Fig. 27.1). Mona monkeys continue to thrive on all three islands today with each island population numbering in the thousands (Glenn 1996; Glenn et al. 1999; Horsburgh et al. 2002) (Fig. 27.2). Only two other species of primates have been introduced to islands hundreds of years ago that still thrive today, long tailed macaques (*Macaca fascicularis*) on the Indian Ocean island of Mauritius (Sussman and Tattersall 1986) and green monkeys (*Chlorocebussabaeus*) on the Caribbean islands of Barbados, St. Kitts and Nevis (Sade and Hildrech 1965). Unlike the semi-terrestrial long-tailed macaques or green monkeys, however, mona monkeys are restricted to living in forest habitats (Booth 1956; Struhsaker 1969; Oates 1988). On Grenada, São Tomé, and Príncipe, suitable, contiguous mona monkey habitat currently exists only in the central highland rainforests of each island. These forest areas have been protected for hundreds of years due to either their preservation as watersheds (Grenada: Caribbean Conservation Association 1991) or because the terrain is too steep for timber harvest or land conversion (São Tomé and Príncipe: Interforest 1990). There are approximately 2,500–5,000 ha of contiguous forest on Grenada suitable for mona monkeys (Caribbean Conservation Association 1991; Glenn 1996), 35,000 ha of

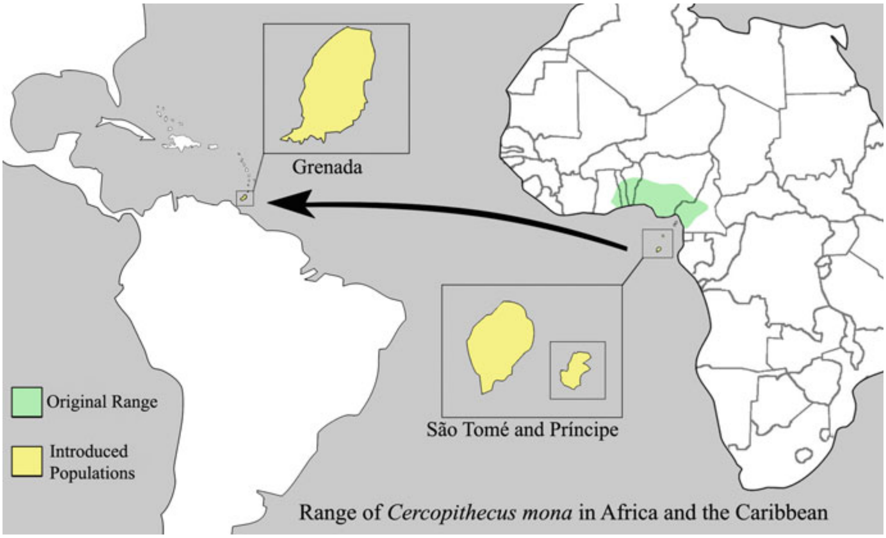

Fig. 27.1 Range of *Cercopithecus mona* in Africa and the Caribbean

Fig. 27.2 *Cercopithecus mona* in Grenada. Photo by Mary Glenn

contiguous forest on São Tomé, and 4,000 ha of contiguous forest on Príncipe (ECOFAC unpublished data; Glenn et al. 1999).

Many forest *Cercopithecus* (and other guenon) species, particularly in west and central Africa, are currently suffering from a double negative impact. First, forest primate habitat is being fragmented through intensive clear cut logging. Second, the *Cercopithecus* populations within those fragments are being reduced due to greatly increased human hunting pressure brought on through the construction of roads built to access and remove the timber, as well as the persistent "bush meat" trade (Butynski 2002). If some of these habitat fragments can be preserved as protected areas and human hunting can be eliminated, are there circumstances or certain characteristics that will allow different species to be more capable of recovering and persisting within the protected fragments? Our field studies of mona monkeys on Grenada (Glenn 1996), São Tomé and Príncipe (Glenn et al. 1999) as well as others' studies of monas in Benin in the western mainland mona monkey range (Matsuda Goodwin 2007) and in Cameroon in the eastern mainland mona monkey range (Howard 1977), coupled with our genetic comparisons between the island and mainland mona monkey populations (Horsburgh et al. 2002), finally allow for a much broader examination of the possible impacts of hundreds-year-long isolation. The island monas provide an example of what may happen to other small populations of forest monkey species surviving in protected habitat fragments and which species may be more or less vulnerable to extinction over the medium term.

History of Mona Monkey Introduction to Grenada, São Tomé and Príncipe

The native range of *C. mona* in west Africa stretches from just west of the Volta River in Ghana eastward and southward beyond the southern bank of the Sanaga River in Cameroon (Booth 1955, 1956; Struhsaker 1970; Oates 1988; Fig. 27.1). The islands of Grenada, São Tomé and Príncipe are volcanic in origin and have never had a dry mainland connection. No native terrestrial mammals exist on any of the three islands. São Tomé and Príncipe were never settled by any humans until Portugal established a colony on São Tomé in the late 1480s and on Príncipe by 1500 (Thomas 1997). Grenada was settled by a series of Amerindian peoples from South America thousands of years ago. The French established a colony on the island in 1649 (Brizan 1984). No trade existed between Africa and the Caribbean until Europeans had established colonies in the region. Thus, before Grenada, São Tomé and Príncipe were colonized by Europeans, there were no means for mona monkeys to get from mainland Africa to the three islands.

Trade, primarily in slaves, began between São Tomé and Príncipe and mainland Africa immediately upon colonization of the two islands. Throughout the Atlantic slave trade era, it was common for exotic African animals, including monkeys, to be traded or kept by sailors as pets (Eaden 1931). Shipping records containing accounts of monkeys are rare, however, because only a few monkeys were ever carried at one time (Denham 1982, 1987). Unfortunately, we have yet to find a written historical account of the arrival of mona monkeys to São Tomé or Príncipe. There is, however, documentation of an unknown species of monkey being on São Tomé by 1804. One of the last English slave trading ships' captains kept a personal log which mentions collecting several monkeys from São Tomé before heading to the Caribbean (Denham 1982, 1987). The species was not described. On Príncipe, a secondary historical compilation by Thomas (1997) regarding the Atlantic slave trade mentions that monkeys were present on the island by at least the 1700s. The species and the primary historical source are not described. Despite not having direct historical evidence, a range of dates can be developed based on the current information available and from the pattern of trade between the two islands and mainland Africa. Throughout the 1500s, the Portuguese islanders traded heavily along the Gold Coast and Niger River delta of West Africa. The African range of mona monkeys extends throughout this region (Fig. 27.1). In the 1600s, the Portuguese, and the islanders themselves, started trading more heavily in the Congo and Angolan region to the south, outside of the range of *C. mona*. The islands eventually ceased being a slave trade center in 1842 with the international ban of sea trade of African slaves (Thomas 1997). Trade between the two islands and Africa decreased dramatically after the cessation of the slave trade. Thus, it can be assumed that mona monkeys could have been introduced as early as 500 years ago to São Tomé and Príncipe and that it is highly unlikely they arrived later than 160 years ago. In addition, some species of introduced monkey (presumably *C. mona*) existed on Príncipe at least 250 years ago and on São Tomé 190 years ago (Thomas 1997).

The slave trade between Grenada and Africa began in the late 1600s (Brizan 1984). The height of the African slave trade to Grenada occurred between 1735 and 1779 when sugar cane production in the Caribbean was at its peak. The slave trade and virtually all trade between Africa and Grenada ceased in 1807 (Brizan 1984). The first mention of monkeys on Grenada was from a travelogue written by Ober (1880) about his hunting trips in the late 1870s. Though he did not know the species, his descriptions match that of mona monkeys. The most likely scenario, then, is that mona monkeys were introduced to Grenada sometime between the late 1600s and 1807, but with the highest probability during the mid-1700s.

Founding Population Size of Island Monas and Genetic Relationship to Mainland Africa Monas

Our collaborative genetic study of the Grenada mona monkeys (Horsburgh et al. 2002) used a mitochondrial DNA analysis to determine the number of founding mtDNA lineages and the origins of those lineages as they relate to the mona populations on São Tomé Príncipe, and mainland Africa. It is expected that the genetic diversity of an island population will generally increase with the size of the founding population and with any subsequent introductions (Tajima 1990). We discovered that the monas on Grenada originated from an extremely small population, possibly stemming from a single female. Using Nei's (1987) gene diversity index (h), Grenada presented an h factor of 0–0.186, while the São Tomé Principe, and mainland monas presented an h factor of 0.790–0.970, depending on the length of sequences utilized. Based on the history of the trade in pet monkeys to the Caribbean, it is very likely that an equally small number of male monas were introduced to Grenada. It is reasonable to assume that the total founding population was extremely small.

The phylogenetic analysis (using the computer programs PAUP 4.0—Swofford 1999 and MODELTEST—Posada and Crandall 1998) resulted in only one tree, and thus a simple evolutionary model could be legitimately applied (Horsburgh 2000). Two distinct clades appeared, with the Grenada monas having come from São Tomé. The monas on the island of Príncipe also came from São Tomé, but with possible multiple introductions. The São Tomé monas appear to have originated from a very diverse cross section of the mainland population and may even have hybridized with another guenon species whose phenotype has now been eliminated from the population (Horsburgh et al. 2002). Due to the high diversity of the São Tomé mona population, it is likely that the founding population was significantly larger than the founding Grenada population.

Inbreeding Effects in the Grenada Mona Monkey Population and Ramifications for Small, Isolated Populations of Primates

Beyond the overall decrease in resources, risk of a stochastic event (e.g., infectious disease outbreak, natural disaster, exotic invasive species competition) or heightened predation pressure due to edge effects, one of the primary threats that is commonly believed to affect the persistence of very small forest primate populations found in permanently fragmented habitats is deleterious change brought on by inbreeding and lack of gene flow (Pope 1996). Due to the relatively long generation times of primates, deleterious genetic changes may not express themselves for decades or even centuries and so are hard to measure in species currently suffering from habitat fragmentation and population loss. Interestingly, the population of mona monkeys on Grenada now numbers in the thousands (Glenn 1996, 1998) and has survived for possibly 350 years after having experienced a severe genetic bottleneck (Horsburgh et al. 2002). That fact demonstrates that inbreeding depression has not reduced fecundity, one of the genetic traits thought to be most at risk when effective breeding populations are radically decreased (Hedrick and Kalinowski 2000). The monas on Grenada instead may be an example of what may happen to a small isolated population if it is protected and allowed to rebound. The Grenada monas may have gone through a process that is known as "genetic purging" where during the first few generations after a genetic bottleneck, a population will rapidly lose deleterious phenotypes because intense inbreeding will cause those phenotypes to be more readily expressed and subsequently selected out of the population (Saccheri et al. 1996; Amos and Balmford 2001).

The Grenada monas thus provide an example that can be pointed to when arguments are made that an isolated forest primate population has become too small to save. If protected, small populations can rebound and remain healthy. The key, however, is that a population is allowed to rebound soon after having been reduced. The longer a population is kept at small numbers, the much greater the chance that inbreeding depression and even "mutational meltdown" (the inability of a continually small population to weed out deleterious mutations because too few variations exist to allow selection to eliminate the bad phenotypes) will negatively affect fecundity and even survivorship (Hedrick and Kalinowski 2000; Amos and Balmford 2001).

Beyond their obvious survival success, the Grenada monas also appear to have not experienced deleterious genetic changes when compared to their mainland counterparts. These types of changes may occur due to genetic drift or a loss in neutral variability. Lack of change was to be expected, however, because neutral variability degrades very slowly (Amos and Balmford 2001) and, as stated above, the effects of genetic drift decrease if a population rapidly expands. For example, vocal repertoire is a genetically driven trait in primates (Jurgens 1979, 1990; Gautier and Gautier 1977; Newman and Symmes 1982; Brockelman and Schilling 1984). Mona monkeys, like all guenons, have a wide variety of unique vocalizations. And, interestingly in terms of inbreeding, monas even have a relatively rare copulation call (Glenn et al. 2002). However, the gross vocal repertoire (types of calls given), including the copulation call, of Grenada monas (Glenn 1996) has not changed when compared to the repertoire of monas on São Tomé and Príncipe (Glenn et al. 1999), Benin (Matsuda Goodwin 2007), or Cameroon (Struhsaker 1970; Howard 1977). Additionally, the gross bodily morphology of the Grenada monas has not significantly changed when compared to the other studied populations (Glenn and Bensen 1998).

Ecological Traits of a Successful Fragment Survivor

Mona monkeys span the greatest range of habitat types of any forest guenon including primary and secondary rainforest, seasonal dry forest, gallery forest, and freshwater and mangrove swamp (Booth 1956; Happold 1987; Oates 1988; Dunn 1993). Their range in food types is equally broad and consists primarily of fruits, seeds, arthropods, leaves, nectar, and flowers, but monas will occasionally even consume lizards, birds' eggs, birds, and bats (Howard 1977; Glenn 1996; Matsuda Goodwin 2007). The importance of the primary food types also varies greatly depending upon different habitat rainfall seasonality. In the wet forests of Cameroon and Grenada, fleshy fruit dominates the mona diet (Howard 1977; Glenn 1996), while in the seasonally dry forest of Benin, monas will switch to a seed dominated diet during dry months (Matsuda Goodwin 2007). Dietary flexibility, however, is not an exclusive ability of mona monkeys and has been recorded in a variety of other forest guenons (Chapman et al. 2002). The extraordinary ecological flexibility of monas, however, is further demonstrated by the fact that when they were introduced to Grenada, São Tomé, and Príncipe, they were confronted with a wide range of foods that they had never been exposed to within their native range on mainland Africa. The biota on São Tomé and Príncipe is highly endemic with 16 % of the plants and 41, 71, and 100 % of the birds, mammals (bats), and amphibians found only on the two islands, respectively (Jones 1994). The indigenous Grenadian flora and fauna are equally alien to mona monkeys, having originated wholly from the western hemisphere (Fritsch and McDowell 2003). None of the potential food sources on any of the three islands had evolved in conjunction with a relatively large arboreal mammal. This is readily apparent from the small size of the fruits on native trees. None of the native tree species evolved large fruits to attract monkeys to disperse their seeds. In addition, the monas on all three islands had to survive in an ever shrinking forest habitat as European colonists cleared native forest for agricultural production (Caribbean Conservation Association 1991; Interforest 1990). Mona monkeys, however, are able to utilize domestic tree crops as a food source, as is widely demonstrated by their crop raiding abilities (Glenn 1996; Glenn et al. 1999). Thus, even when confronted with a very different environment, monas find sustenance.

From an ecological standpoint, it appears that being a generalist confers many benefits for forest guenons remaining in isolated habitat fragments. The island monas can maximize the use of all resources, even in a spatially limited environment (i.e., they can gain more calories per hectare of occupied habitat as compared to an ecological specialist species). Second, the island monas have proved that they are able to exploit new and novel food sources. Presumably, as competing ecological specialist species become extinct in forest fragments, generalist species such as monas should be able to move into newly opened niches and obtain more resources, again, increasing their chances for survival. The ecological applicability to conservation biology from the island mona example is that a primate species that has the opposite traits of monas would be a high conservation priority because they would be so much more prone to extinction due to fragmentation. Conversely, in a thoroughly devastated forest habitat fragment, it may not be a lost cause to try to conserve the area for a generalist primate species.

Summary

African forest mona monkeys were most likely introduced to the Gulf of Guinea islands of São Tomé and Príncipe sometime between 500 and 350 years ago and to the Caribbean island of Grenada sometime between 300 and 200 years ago. Since then the island monas have been isolated from their African counterparts and have thrived in each islands' central rainforests where they now number in the thousands. The Grenada and Príncipe mona populations originated in São Tomé and the Grenada founding population was extremely small with possibly only a single female as shown from mitochondrial DNA analysis. The São Tomé and Príncipe founding populations were much larger and the São Tomé population originated from a wide cross section of the mainland range of mona monkeys. The Grenada mona population does not to appear to be showing any deleterious inbreeding effects when compared to mainland Africa mona populations found in both rainforest and seasonally dry habitats. The Grenada monas' fecundity has not been negatively impacted and their gross bodily morphology and vocal repertoire are the same as their African conspecifics. Mona monkeys are very ecologically plastic as evidenced by the wide variety of forest habitat types they inhabit and their broad and variable diet. The applicability of the Grenada mona monkey "story" to forest guenons, and even to the conservation biology of other forest primates, is that it may not be a lost cause to attempt to save a tiny population of an ecological generalist primate living in a habitat fragment. Small isolated populations of primates may be able to survive and even thrive for hundreds of years, if given the chance.

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Chapter 28
Landscape Attributes Affecting the Natural Hybridization of Mexican Howler Monkeys

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Abstract Natural hybridization can be affected by genetic and environmental factors. For instance, genetic incompatibilities may impede the formation of hybrids, or cause infertility of hybrid offspring, whereas anthropogenic habitat disturbance can promote the contact between formerly isolated species, and therefore, increase the probabilities of hybrid formation. Although there are a number of studies addressing endogenous factors affecting hybridization, little is known about the effects of environmental factors, such as habitat fragmentation, on hybridization in animals. Here we evaluate whether habitat configuration in a fragmented landscape affects the process of natural hybridization between Mexican howler monkeys (*Alouatta palliata* and *Alouatta pigra*), and which attributes of the fragmented landscape, if any, are likely responsible for this effect. Based on the genetic and morphological identification of purebred and hybrid individuals, we assessed the relationship between several metrics of habitat configuration (number of habitat fragments, fragment size, fragment isolation, and fragment shape) and the demographic characteristics and occupancy patterns of groups in areas where exclusively purebred individuals occur and in areas of hybridization in Macuspana, Tabasco. Our results indicate that forest fragmentation is more severe where hybridization occurs, where there is a larger number of small, though less isolated, fragments. Additionally, there are differences in group size and composition between purebred groups in areas with just purebred animals and in areas where hybridization is occurring. In areas of hybridization, purebred groups tended occupy the largest fragments,

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whereas in the only area where groups of the two parental species and hybrids coexist, groups that included hybrid individuals tended to occupy more isolated fragments than groups of purebreds. These results are congruent with the hypothesis that hybridization between Mexican howlers is facilitated in fragmented landscapes. Although we could not discover the mechanisms that underlie this hypothesis, it is possible that in a landscape with more fragments, which are also smaller but rather connected, individuals move more frequently between forest remnants, increasing the probabilities of interspecific encounters.

Introduction

Hybrid zones are affected by both endogenous (hybrid viability and fecundity) and exogenous (environmental) selection (Arnold 1997). It is has been long assumed that most hybrid zones are maintained by a balance between dispersal of parental genotypes into the zone and selection against hybrids (Barton and Hewitt 1985). However, it is also recognized that the habitat configuration may play an important role in structuring hybrid genotypes within a hybrid zone (Cruzan and Arnold 1993). In areas where the habitat has been disturbed due to natural or anthropogenic events, hybridization may be favored (Anderson 1948) and hybrids can use niches unoccupied by purebred individuals, or even compete with parental forms if hybrids are equivalent to, or more fit than, the parental taxa (Arnold 1997).

Many instances of hybridization associated with human disturbance have been reported in both plants (Bleeker and Hurka 2001; Lamont et al. 2003) and animals (Docker et al. 2003; Heath et al. 2010; Keller et al. 2008; Schwarz and McPheron 2007). In primates, anthropogenic factors have also been suggested to augment the incidence of hybridization (Detwiler et al. 2005). However, further research based on field-based studies is required to understand how habitat configuration affects primate hybridization, and which particular spatial metrics affect this process in fragmented landscapes.

An excellent opportunity to investigate the effect of habitat configuration on hybridization in primates is the natural hybridization occurring between the two species of howler monkeys in Mexico (Cortés-Ortiz et al. 2007). These species (*Alouatta palliata* and *Alouatta pigra*) have allopatric distributions in most of their range, but live in sympatry in a small region in the state of Tabasco (Smith 1970). The landscape in this area has been severely transformed by human activities and the remaining habitat is highly fragmented (Sánchez-Colón et al. 2009).

The two species of Mexican howler monkeys diverged approximately 3 mya (Cortés-Ortiz et al. 2003), and can be distinguished on the basis of genetic (Cortés-Ortiz et al. 2003), cytogenetic (Steinberg et al. 2008), and morphological characters (Smith 1970). Additionally, they present marked differences in their social systems. For example, group size and sex ratios are higher in *A. palliata*, and unimale groups are common among *A. pigra* in contrast to the typical multimale groups of *A. palliata* (Di Fiore and Campbell 2007). Genetic studies on a number of populations of *A. palliata* throughout Mesoamerica show a clear decline of genetic variation from south to north, implying a recent expansion in that direction (Cortés-Ortiz 2003; Ellsworth and Hoelzer 2006), and suggesting a secondary contact as the origin of the hybrid zone between these species (Cortés-Ortiz et al. 2003).

The fact that many cases of primate hybridization have occurred in areas where the habitat is fragmented due to human disturbance (Detwiler et al. 2005) raises the questions of whether human-induced forest fragmentation promotes the contact and subsequent hybridization between different primate species, and if so, which attributes of the landscape affect the hybridization process. In particular, Cortés-Ortiz et al. (2007) noted that human-induced forest fragmentation may promote contact between *A. palliata* and *A. pigra*, by confining members of both species to small areas and limiting access to conspecific mates. Under this scenario, natural hybridization of Mexican howlers would be facilitated in highly fragmented landscapes.

Here we examine the process of hybridization between *A. palliata* and *A. pigra* by comparing landscape configuration (see Chap. 2) and group size and composition of howler groups of the Macuspana hybridization area (HY) to those in the adjacent areas where only purebred *A. palliata* or *A. pigra* occur (PB). We expect that, if hybridization is facilitated in highly fragmented landscapes, the following conditions should be met: (1) Forest fragments in HY should be smaller, more isolated, and more irregular—attributes usually associated with a high degree of fragmentation (Fahrig 2003). (2) If fragmentation is more severe in HY, (A) groups of purebred *A. palliata* and *A. pigra* should be smaller than groups in PB. This is because, as Arroyo-Rodríguez and Dias (2010) report, in fragmented habitats population size of howler monkeys decreases, dispersion rates are reduced, groups are smaller and grouping patterns are altered. Also, as group size is reduced while male to female ratios are maintained, (B) a larger proportion of unimale groups should occur in HY than in PB for both species (as has been observed in fragmented habitats for *A. palliata* by: Clarke et al. 2002; McCann et al. 2003; and for *A. pigra* by: Estrada et al. 2002; Van Belle and Estrada 2006). (3) If habitat configuration affects the contact between parental species, (A) groups containing hybrid individuals should occupy smaller, more isolated and more irregular fragments than purebred groups in the same area (HY), and (B) hybrid groups should exhibit similar group size and composition among themselves. Additionally, (C) the spatial attributes that predict the probability of fragment occupancy by purebred or hybrid groups should differ.

Methods

Study Sites

This study was carried out in the state of Tabasco, which is located in southeastern Mexico (Fig. 28.1). Its original vegetation included large tracts of tropical evergreen and semievergreen forests (Rzedowski 2006), but native vegetation has been severely disturbed and destroyed due to human activities. Currently, the remaining

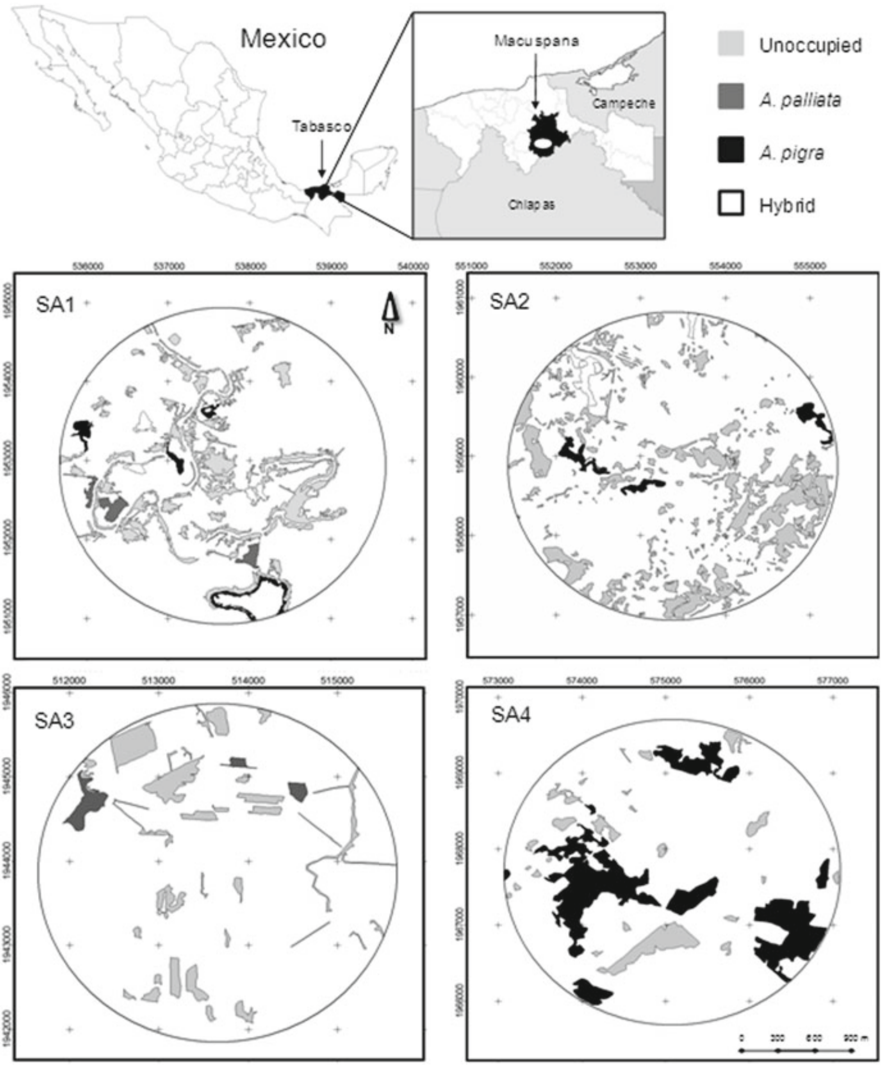

Fig. 28.1 Location of the four sampling areas (SA) studied in the Macuspana area, Tabasco. Occupation of forest fragments by purebred and hybrid groups is indicated in the map. Coordinates provided at the edge of the maps are in UTM

tropical forests in the area are immersed in a matrix of pasturelands, agricultural fields, and human settlements (Sánchez-Colón et al. 2009).

Previous surveys of *A. palliata* and *A. pigra* in their contact zone, and the associated genetic evidence suggested that the Macuspana hybridization area follows a southwest (*A. palliata*)–northeast (*A. pigra*) gradient (Cortés-Ortiz et al. 2007, LCO unpublished). Therefore, we selected four sampling areas following this gradient:

two sampling areas where sympatry and hybridization have been confirmed (sampling area 1 and sampling area 2 in Fig. 28.1), and two sampling areas where only purebred individuals have been found (sampling area 3 for *A. palliata* and sampling area 4 for *A. pigra*, Fig. 28.1). In each sampling area, we positioned a 2 km-radius circle that included at least one location for which we had genetic evidence for purebred or hybrid individuals, resulting in an area of 1,257 ha per sampling area. Sampling areas were approximately 20 km apart.

Spatial Attributes of Sampling Areas

We digitized vegetation fragments in the four sampling areas with ArcGIS 9.3.1 (ESRI Inc., Redlands, CA, USA), using orthophotos (1:10,000, resolution 1 m) taken between 2004 and 2008 and obtained from the National Institute of Statistics and Geography of Mexico (INEGI). We corroborated the current presence of fragments with field surveys. We defined a fragment as a patch of forest with a surface area ≥0.5 ha. This choice was based on previous studies that have identified a 0.5 ha criterion as the minimum habitat requirement for fragment occupation by howler monkeys (Arroyo-Rodríguez et al. 2008; Cristóbal-Azkarate et al. 2005). However, we also digitized and visited smaller patches of vegetation to confirm the absence of howler monkeys. We calculated size, isolation, and shape of each fragment using Patch Analyst 3.12 for ArcView 3.2 and Patch Analyst 4.2 for ArcGIS 9.3.1, as well as self-developed geostatistical processes created in ModelBuilder for ArcGIS (ESRI Inc., Redlands, CA, USA). Three isolation metrics were used: (1) distance to the nearest fragment, (2) number of fragments in a radius of 200 m from each fragment, and (3) the amount of available habitat in the neighborhood of each fragment within a 200 m radius. The 200 m criterion was used because this distance has been previously defined as a maximum threshold for interfragment dispersion of howler monkeys in other populations (Mandujano and Estrada 2005). In addition, we calculated the shape of each fragment using the index proposed by Forman and Godron (1986): $\mathrm{SI} = P/\sqrt{A\pi}$; where P is the perimeter and A is the area of the fragment. This index varies from 1, for a circular shape, to 5 for a highly irregular shape. Irregular fragments can be colonized more easily than compact (e.g., round) patches, as they have a proportionally greater amount of edge, increasing the likelihood that a patch will be encountered by a moving individual (Ewers and Didham 2006).

Sampling of Howler Monkey Populations

Genetics. We captured and collected blood samples from 40 individuals in HY (for a description of the capture and handling techniques that were used see Rodríguez-Luna and Cortés-Ortiz 1995). All individuals were genetically characterized based on sequence data for the mitochondrial control region, the SRY gene

Table 28.1 Number and identity of groups sampled in the hybridization area

Sampling area	Species/group	No. of groups
1	*A. palliata*	3 (1)
1	*A. pigra*	4 (2)
1	Hybrid	3 (3)
2	*A. pigra*	4 (2)
2	Hybrid	2 (2)

Numbers in brackets denote the number of groups for which genetic data was available

and genotype data from 20 microsatellite loci (Cortés-Ortiz et al. 2007, 2010). Individuals with discordant mtDNA and SRY haplotypes were considered hybrids. To identify hybrid individuals based on their microsatellite genotype, we used the Bayesian methods implemented in the program STRUCTURE v2.3 (Pritchard et al. 2000). We used this method to assign individuals to one of two populations ($K = 2$). The program was run with 100,000 iterations as burn-in period and 100,000 iterations for convergence. Individuals were classified as hybrids if they had an assignment value ≤ 0.90. Analyses were carried out using the groups as the unit of study. Groups where considered as "pure" if they only contained purebred individuals of one of the species, and "hybrid" if they contained at least one genetically confirmed hybrid individual. We could only capture 62.5 % of all groups (Table 28.1). Within HY, groups that were not captured were classified based on their phenotype. Given that the phenotype usually resembles the genotype (Cortés-Ortiz et al. 2007), phenotypic identifications are reasonably confident.

Demography. Between May and August 2010 we visited all fragments in the four sampling areas. Two trained observers walked slowly around and inside each fragment between 6:00 and 19:00 h, to detect visual cues (e.g., movement in the canopy, feces, consumed food items) or vocalizations of howler monkeys. Once a group was located, we recorded the species, and the number of adult males, adult females, subadults, juveniles, and infants following the age–sex classifications of Balcells and Veà (2009) for *A. palliata*, and Rosales-Meda (2003) for *A. pigra*.

Data Analyses

To compare the proportion of available habitat and the number of fragments between PB and HY, we used chi-square tests for similar expected frequencies. To compare the spatial attributes of fragments between PB and HY, we used ANODEV with generalized linear models corrected for overdispersion. In these models, we nested fragments within sampling areas to control for spatial dependency of measures taken from fragments belonging to the same sampling area. To compare group size and composition of purebred groups between PB and HY, and of hybrid groups between sampling areas, we used Mann–Whitney tests, and to compare the percentage of unimale groups of purebreds between PB and HY, we used *Z* tests for two proportions. We compared the spatial attributes of fragments occupied by purebred and hybrid groups in HY with Kruskal–Wallis ANOVA (sampling area 1) and Mann–Whitney tests (sampling area 2). Finally, to identify the spatial attributes that explained the probability of occupancy (i.e., presence/absence of groups) of fragments by purebred and hybrid groups in HY, we used logistic regressions with generalized linear models. We used the Akaike's information criterion to first select the most parsimonious model, that is, the combination of spatial attributes that better explained the probability of a fragment being occupied (Motulsky and Christopoulos 2003). We then reran the regressions with the selected variables to generate occupancy models for purebred and hybrid groups.

Results

Prediction 1: Difference in landscape attributes between HY and PB

We sampled a total of 349 fragments for the presence of howler monkey groups; 196 fell within the category of forest fragments (i.e., ≥0.5 ha). None of the fragments with less than 0.5 ha was occupied. The proportion of available habitat was similar between PB and HY ($\chi^2=0.155$, $p=0.693$), but the number of forest fragments was significantly higher in HY ($\chi^2=41.32$, $p<0.001$). All spatial variables differed significantly between PB and HY (Table 28.2). In PB fragment size and distance to nearest fragment were larger, whereas in HY the number of neighboring fragments, available habitat and shape index were higher.

Prediction 2: (A) Group size and composition of purebred groups differ between HY & PB, and (B) there is a larger proportion of unimale groups in HY than in PB

We found *A. palliata* groups in sampling area 1 (3 groups, 15 individuals) and sampling area 3 (3 groups, 30 individuals). In sampling area 3 (i.e., PB for this species) groups were significantly larger ($Z=1.993$, $p=0.046$) than in sampling area 1, and included more females ($Z=1.993$, $p=0.046$) and subadults ($Z=2.121$, $p=0.034$;

Table 28.2 Comparisons of landscape spatial attributes between HY and PB

	Hybridization	Purebred	χ^2	*P*
Proportion of remaining habitat	15.1 %	12.9 %	0.155[a]	0.693
Number of fragments	143	53	41.32[a]	<0.001
Fragment size (ha)	2.7 ± 3.2	6.2 ± 12.2	13.51[b]	<0.001
Distance to the nearest fragment (m)	42.6 ± 74.6	114.8 ± 118.2	22.12[b]	<0.001
Number of neighboring fragments	4.5 ± 2.5	1.6 ± 1.3	71.04[b]	<0.001
Available habitat in the neighborhood of each fragment (ha)	5.2 ± 3.4	1.9 ± 2.1	49.78[b]	<0.001
Shape index	2.9 ± 1.1	2.2 ± 1.2	11.31[b]	<0.001

[a] Analyzed with chi-square goodness-of-fit tests
[b] Used in GLM analysis

Table 28.3 Group size and composition of purebred and hybrid groups

	Alouatta palliata		*Alouatta pigra*		
	HY	PB	HY	PB	Hybrid
Group size	3.7 ± 1.2	11.3 ± 5.9	4 ± 1.7	5.3 ± 1.7	5.4 ± 3.4
No. of males	1.3 ± 0.6	2.3 ± 0.6	1.1 ± 0.8	1.1 ± 0.4	1 ± 0
No. of females	1.3 ± 0.6	4.3 ± 1.5	1.5 ± 1.1	1.6 ± 0.7	2 ± 1.4
No. of subadults	0	1.7 ± 1.2	0.1 ± 0.4	0.8 ± 0.9	0.8 ± 0.8
No. of juveniles	0.7 ± 0.6	2 ± 1.7	0.5 ± 0.8	1.3 ± 0.5	0.8 ± 0.8
No. of infants	0.3 ± 0.6	1 ± 1	0.8 ± 0.7	0.5 ± 0.8	0.8 ± 1.3
% unimale groups	33.3	0	42.9	87.5	100

Table 28.3). In sampling area 1, 33.3 % of the groups were unimale and 66.7 % had two adult males. In sampling area 3, 66.7 % of the groups included two adult males and 33.3 % included three adult males.

We observed *A. pigra* in sampling area 1 (4 groups, 16 individuals), sampling area 2 (4 groups, 16 individuals) and sampling area 4 (PB for this species, 8 groups, 42 individuals). There were significantly more juveniles per group in PB ($Z = 2.176$, $p = 0.029$; Table 28.3) than in HY. In HY, 42.9 % of the *A. pigra* groups had only one male, 42.9 % had two males and 14.2 % did not include adult males; whereas in PB, 87.5 % of the groups were unimale and a single group had two males. Nonetheless, the proportion of unimale groups did not significantly differ between PB and HY ($Z = 1.281$, $p > 0.05$).

Prediction 3: (A) Groups containing hybrids use smaller, more isolated and more irregular fragments than purebred groups; (B) groups that include hybrids have similar size and composition, and (C) different attributes of landscape configuration predict the occupancy of hybrids and purebred groups in HY

We observed groups that included hybrid individuals in sampling area 1 (HY, 3 groups, 15 individuals) and sampling area 2 (HY, 2 groups, 12 individuals). In sampling area 1—the only one that includes both hybrids and both species of purebreds—, hybrid groups occupied fragments that had higher DNF than fragments occupied by purebred groups ($H_{2,\ 10} = 6.746$, $p = 0.034$). In sampling area 2, there were no differences between *A. pigra* and hybrid groups in the spatial attributes of occupied fragments (all Mann–Whitney tests $p > 0.05$). There were no significant differences in group size and composition among hybrid groups between sampling areas (all Mann–Whitney tests $p > 0.05$). All hybrid groups were unimale.

When modeling the data with Akaike's information criterion to identify the attributes that better explain the probability of fragment occupancy in HY, the most parsimonious model explaining the occupancy of fragments by hybrid individuals retained four variables: fragment size, number of neighboring fragments, available habitat, and shape. The logistic model including these four variables was significant ($\chi^2_{4,\ 143} = 9.791$, $p = 0.041$, $R^2 = 0.23$), but only size ($\chi^2_{1,\ 143} = 4.14$, $p = 0.041$, estimate $= -0.33$), number of neighboring fragments ($\chi^2_{1,\ 143} = 5.53$, $p = 0.019$, estimate $= 0.81$), and available habitat ($\chi^2_{1,\ 143} = 4.72$, $p = 0.029$, estimate $= 0.82$) had significant effects on occupancy. Therefore, the probability of fragment occupancy by hybrid groups increased in smaller fragments that had more neighboring fragments and available habitat. For *A. pigra*, fragment occupancy was best explained by fragment size and available habitat ($\chi^2_{2,\ 166} = 19.928$, $p < 0.001$, $R^2 = 0.19$). However, only fragment size had a significant positive effect on the model ($\chi^2_{1,166} = 9.56$, $p = 0.002$, estimate = 0.16), indicating that fragment occupancy by *A. pigra* in HY increased with fragment size. Finally, for *A. palliata* fragment occupancy depended on fragment size, number of neighboring fragments and shape ($\chi^2_{3,102} = 9.429$, $p = 0.024$, $R^2 = 0.21$). Yet, again, only fragment size had a significant positive effect on the model ($\chi^2_{1,166} = 3.95$, $p = 0.047$, estimate = 1.49) indicating that in HY, the probability of finding *A. palliata* groups increased in larger fragments.

Discussion

We found evidence suggesting that in the Macuspana area, hybridization between *A. palliata* and *A. pigra* is likely associated with particular attributes of the habitat configuration. First, there were differences in spatial attributes of the landscape between the hybridization area (HY) and the areas where only purebred individuals occur (PB). Although the proportion of total available habitat was similar between HY and PB, in HY there were more fragments, which were smaller and more irregular. However, in contrast to our prediction, in HY forest fragments were less isolated, as distance to nearest fragment was shorter and number of neighboring fragment and available habitat were larger. Second, as predicted, we found differences in group size and composition of purebred groups between HY and PB. For *A. palliata*, PB groups were larger mainly due to a significantly higher number of females and subadult individuals; whereas *A. pigra* groups in PB were similar in size to *A. pigra* groups in HY, but included more juveniles. Third, in the sampling area 1 (HY), where *A. palliata*, *A. pigra* and hybrid groups where present, hybrid groups occupied more isolated fragments than purebred groups. Also, there were differences between purebred and hybrid groups in the spatial attributes that predicted their occupancy patterns: whereas purebred groups tended to occupy larger fragments, hybrid groups were usually present in smaller fragments that had higher values for number of neighboring fragments and available habitat. These results are consistent with our hypothesis that hybridization in howler monkeys is affected by habitat configuration associated with human-induced habitat fragmentation; however which mechanisms are responsible for these associations is still unclear.

Comparing the landscape of the sampled areas with studies of Mexican howler monkeys in other fragmented areas, both HY and PB are severely disturbed. For instance, the proportion of available habitat is significantly lower in our study area than in fragmented landscapes in Veracruz occupied by populations of *A. palliata* (Arroyo-Rodríguez et al. 2008), or in southeast Tabasco occupied by *A. pigra* (Pozo-Montuy et al. 2008). Although the origin of the hybrid zone in Mexico is likely the product of a secondary contact between two species that have not achieved complete reproductive isolation (Cortés-Ortiz et al. 2003; Smith 1970), the current occurrence of hybridization in HY might be facilitated by the presence of a highly disturbed landscape with a large number of small fragments in close proximity. In smaller fragments the access to food for howler monkeys is constrained (Arroyo-Rodríguez and Dias 2010), and as a consequence, groups will have to move between fragments to meet their dietary requirements (Asensio et al. 2009). Such movements would be facilitated in HY by the large number of fragments and their proximity. Thus, individuals of both parental species living in sympatry in this landscape would have higher probability of encounter than those living in a less disturbed setting.

There is evidence that group size is positively related to fragment size in howler monkeys (Arroyo-Rodríguez and Dias 2010), so it is expected that in HY fragments may only sustain small groups of purebreds. For *A. palliata*, group size was nearly three times smaller in HY, whereas in PB group size was similar to that reported for both extensive and fragmented forests (12.9 individuals; Chapman and Pavelka 2005). However, for *A. pigra* there were no differences in group size between PB and HY, and the observed values are similar to those reported for this species in both extensive and fragmented landscapes throughout its distributional range (reviewed in Van Belle and Estrada 2006). Consequently, the small fragment size in HY seems to pose a major effect on group size and composition to groups of *A. palliata*, limiting the number of potential mates. Therefore *A. palliata* groups in HY may experience increased intraspecific competition that would drive *A. palliata* individuals to leave their natal groups, and promote higher rate of encounter with *A. pigra* groups. Furthermore, even when there were no significant differences in size between *A. pigra* groups in HY and PB, there remains an observed trend (Arroyo-Rodríguez and Dias 2010) that in smaller fragments there are smaller groups. Therefore, the small size of fragments in the area could also restrict the potential number of mates for *A. pigra*. The additive effects of lower food availability and fewer reproductive opportunities must therefore promote higher rates of natal and secondary dispersal by individuals in HY, facilitating encounters between individuals of the two parental species and favoring the occurrence of interspecific matings.

Another important consideration is the possible influence of interspecific differences in responses to disturbance and competitive abilities. In agreement with what has been suggested by Van Belle and Estrada (2006), habitat size seems to have limited effects on the grouping patterns of *A. pigra*, probably because small group sizes have been evolutionarily favored in response to conspecific competition (Chapman and Pavelka 2005). In contrast, group size in *A. palliata* was severely reduced in small fragments. This suggests that, given their usually large size, *A. palliata* groups are more likely to change their social organization in response to habitat constraints than *A. pigra* groups. Thus, when facing similar environmental conditions, group size and composition tend to be similar for both species, as it is shown in the present study. A social element that is likely to play a role in the dynamics of the hybridization in this fragmented landscape is the fact that howler monkey males employ alternative mating tactics, which usually involve evading female-guarding by dominants (Horwich et al. 2000; Jones 1995). Such opportunities are reduced in small groups, as the effectiveness of mate-guarding is expected to increase when group size is reduced (Nunn 1999). However, given that *A. pigra* are significantly larger in body mass than *A. palliata* individuals (Kelaita et al. 2011), it is possible that the former are at an advantage during interspecific encounters. This could result in the eviction of *A. palliata* males from their own groups by *A. pigra* males in the context of group takeovers, facilitating hybridization, as well as the displacement of *A. palliata* groups from preferred fragments (i.e., larger and less isolated fragments).

Even if some of the groups that were classified morphologically as purebreds included hybrid individuals, the fact that hybrid groups were mainly present in the smallest and more isolated fragments in the area where groups of both of purebred species exist, suggests that either (1) hybridization occurs in fragments where it is less probable to find purebreds, (2) that hybrids may be more fit to occupy highly disturbed habitat than purebreds, or (3) that hybrids are displaced by purebreds from better quality fragments. To understand the mechanisms that are determining the distribution of hybrid groups and individuals within this fragmented landscape, we are expanding our genetic and demographic samplings and establishing long-term behavioral and demographic investigations of howler monkeys in the area.

In conclusion, we found evidence concordant with the hypothesis that natural hybridization between Mexican howlers is associated with highly fragmented landscapes in the Macuspana area, as groups that included hybrid individuals were present in small and more isolated fragments. Furthermore, these findings suggest that the genetic makeup of this hybrid zone is affected by the configuration of the habitat, and that the prevalence of hybridization in the area may be a consequence of repeated encounters between parental species favored by a landscape where the movements of individuals between forest fragments are more frequent, and influenced by the social dynamics among *A. palliata*, *A. pigra* and hybrid individuals.

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Chapter 29
Preliminary Evaluation of the Effects of Habitat Fragmentation on Habitat Use and Genetic Diversity of Pygmy Marmosets in Ecuador

Stella de la Torre, Pablo Yépez, Diego Nieto, and Hernán Payaguaje

Abstract We evaluated the effects of habitat fragmentation on group size, home range size, and genetic variability of pygmy marmosets *Callithrix pygmaea*, from May 2008 through February 2010, in three wild groups in the San Pablo population in Ecuadorian Amazonia. Forest remnants in this area are surrounded by pasture and fields of plantain, corn, and manioc, and have been considerably reduced in the past decade. We used scan samples to record data on group size and home range size. We collected fecal samples from the groups to analyze n-DNA. The increase in habitat fragmentation in San Pablo did not appear to affect group size; the mean group size recorded during the study was similar to that obtained in previous years. A "nomadic" behavior not previously reported in any of our studied populations or elsewhere for this species was seen in the study groups. This behavior was characterized by the short-term use of small core areas and a continuous movement among them. The results of the genetic analyses suggest that nonrandom mating may be occurring in some groups. Genetic distances between groups appeared to be related to the linear distances between core areas. Overall, our results suggest that population responses to fragmentation are more complex than we initially expected.

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Introduction

Habitat fragmentation is one of the most important ecological phenomena and one of the greatest threats to primate conservation (Arroyo-Rodríguez and Mandujano 2009; Cowlishaw 1999; Marsh 2003); as such, it is receiving increasing attention by scientists and conservationists worldwide. However, there is still a lot we need to know about the effects of fragmentation on the 20 primate species in Ecuador, the smallest (253,000 km^2) megadiverse-country in South America, which has a deforestation rate of about 190,000 ha/year (SENPLADES 2007). One of these 20 species is the pygmy marmoset *Callithrix pygmaea*; a small (120 g) primate that inhabits gallery forests along rivers and lakes in the Upper Amazonia, from about 220 to 450 m above sea level, feeding mainly on exudates of certain plant species (de la Torre 2000; Yépez et al. 2005; Fig. 29.1). These habitat and diet specializations may make it particularly vulnerable to human impacts since riparian habitats are widely used by humans in Ecuadorian Amazon and elsewhere. Based on these considerations, pygmy marmosets have been recently included in the list of vulnerable mammal species in Ecuador (Tirira 2011).

The effects of fragmentation on pygmy marmosets are difficult to predict. Considering the small home ranges of the groups, usually of less than 1 ha (de la Torre et al. 2009), we may expect that marmosets could resist relatively high levels of fragmentation. However, in previous studies we have reported the absence of pygmy marmosets in disturbed habitats, from grasslands and areas of intense agriculture to small forest patches affected by selective logging (de la Torre et al. 2009). Of the nine populations of pygmy marmosets we have studied since 1996, the San Pablo population, on the margins of the Aguarico River, has been the most affected by fragmentation. Forest remnants in this area are surrounded by pasture and fields of plantain, corn and manioc and have suffered a considerable reduction in the last 10 years.

Based on the results of previous studies of primates in fragments (Arroyo-Rodríguez et al. 2008; Cristóbal-Azkarate and Arroyo-Rodríguez 2007; Pope 1998; Wieczkowski 2004; Zunino et al. 2007), and our knowledge of the ecology and behavior of pygmy marmosets (de la Torre et al. 2000, 2009; Yépez et al. 2005) we expected that pygmy marmosets in San Pablo would show changes in home range size, ranging patterns, dispersal and genetic variability as a result of habitat fragmentation. In this chapter, we present the evidence we have gathered in recent years, to test some of our expectations.

Methods

Study Area

The area of the San Pablo population (UTM, 18 Zone, Datum PSAD 56 341767 E, 9969737N) was originally a varzea forest with an altitude of 220 m above sea level. When we began our study of pygmy marmosets in this population in 2001, the

Fig. 29.1 Adult pygmy marmoset. Credits: Pablo Yépez

combined area of forest patches, which included the home ranges of our four studied groups, was of 3.3 ha; mean forest patch size at that time was estimated in 1.10 ha ± 0.40. By 2005, this area was reduced by 85 % to only 0.5 ha (mean forest patch size 0.17 ha ± 0.12) and by 2009 the area decreased to 0.32 ha (mean forest patch size 0.11 ha ± 0.08). Forest remnants have been gradually converted into fields of corn, manioc and plantain.

Despite the high rate of fragmentation, this area could be considered a “refuge” for pygmy marmosets since the Secoya families who owned the land had purposely avoided to cut most of the exudate trees known to be used by the groups and did not capture or hunt marmosets. The behavior of these families towards the marmosets may have been influenced by a program on environmental education we developed since 2002 (de la Torre and Yépez 2003) and is different from that of people in neighboring areas.

Observations of Groups

From May 2008 through May 2009 we observed and followed three groups of pygmy marmosets in San Pablo for a total of 240 h of direct observation. The marmosets in each group were classified by size and other morphological characters into approximate age classes (Soini 1988). Sex determination was possible for adult and some subadult animals. Group size and composition were determined by observations and counts of group members early in the morning or late in the afternoon. We used scan samples (Martin and Bateson 1994) every hour to gather data on habitat use. Home range size was estimated by connecting the extreme location points of group members during the study; the periphery that enclosed all points was considered as the home range perimeter (de la Torre et al. 2000; Yépez et al. 2005).

Genetics

We collected fecal samples from the groups (P1, P2 and P4) from September 2008 through February 2009. Large leaves of banana (*Musa × paradisiaca*) and heliconia (*Heliconia* spp.) were placed very early in the morning under the feeding tree of a group before the marmosets began their daily activities. Animals were observed by one field worker in periods of 3 h from 0600 to 0900 and from 1500 to 1800. The leaves were checked continuously during the observation periods. Due to the collection methods, we could not accurately assign a particular fecal sample to a given animal in a group; however, based on our observations, we are confident that the collected feces belonged to at least three different animals in each group. Fecal samples from each group were taken in a single period of observation (2 weeks to 2 months) when the focal group was occupying a core area (see below).

We stored the collected feces on filter paper and placed them in a flask with a desiccant (silica gel). The closed flasks with the samples were dried with controlled sunlight (avoiding drastic rises of temperature) over 1 or 2 days to reduce the probability of contamination of the feces with fungi. The samples were later transported to Quito and placed in a freezer at −20 °C (Nieto et al. 2010).

We obtained DNA from the samples using the QIAamp DNA Stool Mini Kit (QIAGEN). We used Polymerase chain reaction technique to amplify nDNA microsatellites. We tested primers established by Nievergelt et al. (1998) for *Callithrix jacchus*. The PCR amplification was performed in a 25 μL reaction volume which include buffer 1×, 1.5 mM of $MgCl_2$, 0.2 μM of dNTPs, 0.24 μM of each primer, 0.5 U of Taq polymerase (Invitrogen) and 5 ng of sampled DNA. The amplification program consisted of an initial denaturation of 3 min at 95 °C; 40 cycles of denaturation for 1 min at 94 °C, annealing for 1 min at optimum temperature, an elongation during 1 min at 72 °C; and a final elongation at 72 °C during 5 min. Polyacrylamide 6 % and urea 5 M gels were used to separate DNA bands (Nieto et al. 2010).

For the statistical analyses, we used five of the nine loci tested (CJ-1, CJ-7, CJ-11, CJ-12, and CJ-15) because they showed a higher number of amplified samples (>10 amplified samples per primer). We used GenAlEx 6 (Peakall and Smouse 2006) to obtain allele frequencies to carry out Hardy–Weinberg equilibrium analysis from observed (H_o) and expected (H_e) heterozygosity and to calculate Nei's (1987) genetic distance; with this last variable we did a Principal Coordinate Analysis (PCoA) (Nieto et al. 2010).

Results

Group Size and Home Range Size

Group size varied from three individuals (P1) to seven individuals (P4; mean group size 5.2 individuals/group ± 1.04; Table 29.1). Infants were observed in June 2008 in groups P1 and P2, and in January 2009 in group P4.

Table 29.1 Mean group size, home range (core area) size, and exudate species of the studied groups of pygmy marmosets

Group	Mean group size (±SD)	Home range (core area) size (m^2)	Exudate species (# of individuals)
P1	4 ± 1.40	2,000	*Inga marginata* (1) *Inga ruiziana*
P2	5.5 ± 0.71	400	*Sterculia apetala* (1) *Cedrela odorata* (1)
P4	6 ± 1.40	400	*Sterculia apetala* (1) *Spondias mombin* (1)

Estimations of home range size were extremely difficult since groups occupied small core areas (mean 0.075 ha ± 0.08) for short periods (2 weeks to 2 months), with periods of up to 6 weeks when no records of the animals were obtained. Due to this “nomadic” behavior it was difficult for us to correctly identify a group once it appeared again in a core area; we did so based on a combination of individual recognition of some animals, group size and location matching. We were not able to follow groups when they left a core area, partly because of the wary behavior of the marmosets and also because of logistic limitations. Some animals were sporadically observed rapidly traveling across plantain fields. We never observed marmosets traveling through open areas with houses. All the core areas were forest remnants, some of them highly disturbed, and included exudate sources used by the groups in the past 10 years (Table 29.1) (Fig. 29.2).

Groups P1 and P2 were the most distant, separated by open areas, houses and plantations (closest linear distance between P1 and P2 core areas: 250 m), whereas 200 m of open areas and cultures separated the home ranges of groups P2 and P4. The closest distances occurred between groups P1 and P4 (linear distance: 165 m); since the beginning of the study until August 2008, there was a disturbed, secondary forest connecting the core areas of these two groups.

Genetic Variability

Forty-two fecal samples were collected (P4 = 23 samples, P2 = 12, P1 = 7). DNA samples from group P4 showed various alleles at the five loci tested, samples from group P2 showed alleles at three loci, and samples from group P1 showed alleles at four loci (samples from this group showed fixed alleles at two loci). The observed heterozygosity (H_o) ranged from 0.556 to 1.000 (Table 29.2). In all groups the observed heterozygosity values were greater or equal than the expected ones, with the exception of locus CJ-1 in group P4 (mean $H_o = 0.59$, mean $H_e = 0.40$). The results from the Hardy–Weinberg equilibrium test suggested nonrandom mating in group P4 since three polymorphic loci showed frequencies that were significantly different from the expected values.

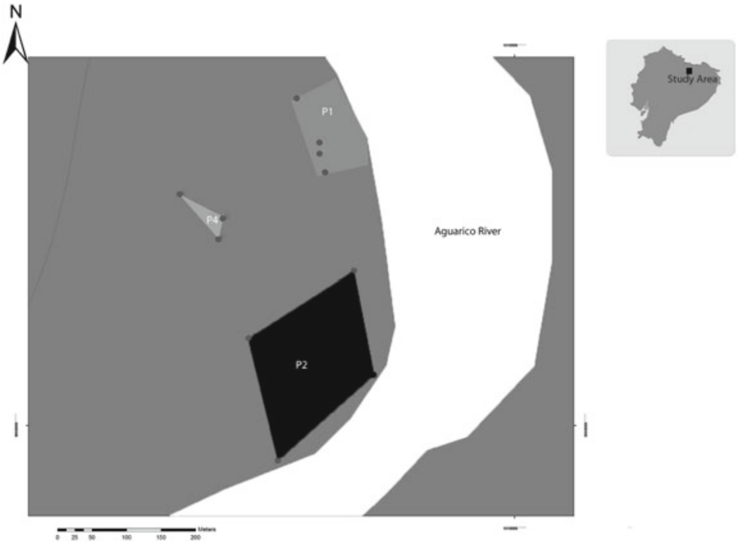

Fig. 29.2 Study area—location of the pygmy marmoset groups in the San Pablo population. *Gray circles* show the location (without scale) of the core areas used by the groups at different times during the study period

Table 29.2 Observed (H_o) and expected heterozygosity (H_e) at the five loci for the three pygmy marmoset groups P1, P2, and P4 (primers were established by Nievergelt et al. 1998 for *Callithrix jacchus*)

Group	Locus	# Samples	# Alleles	H_o	H_e
P1	CJ-1	1	1	0.000	0.000
	CJ-7	1	2	1.000	0.500
	CJ-11	0	0	0.000	0.000
	CJ-15	1	1	0.000	0.000
	CJ-12	3	2	1.000	0.500
P2	CJ-1	0	0	0.000	0.000
	CJ-7	1	2	1.000	0.500
	CJ-11	0	0	0.000	0.000
	CJ-15	3	2	1.000	0.500
	CJ-12	3	4	1.000	0.722
P4	CJ-1	9	8	0.556	0.815
	CJ-7	8	3	1.000	0.625
	CJ-11	9	4	0.667	0.512
	CJ-15	8	7	0.750	0.836
	CJ-12	12	2	1.000	0.500
Mean		–	–	0.589	0.40

Nei's (1987) genetic distance between groups P1 and P2 was 1.211, whereas the distance of group P4 with group P2 was 0.612 and with group P1 was 0.485. The PCoA using Nei's (1987) genetic distance showed that groups P1 and P4 differed 93.02 % from group P2, considering Axis 1, and 6.98 %, considering Axis 2.

Discussion

Group Size and Home Range

The increase in habitat fragmentation in San Pablo did not appear to affect group size, the mean group size recorded during the study (5.2 individuals/group ± 1.04) was similar to that obtained from 2001 to 2005 (5.4 individuals/group ± 0.2) (de la Torre et al. 2009). This result suggests that factors other than fragmentation, such as capture and hunting, may be related to the disappearances of groups reported in our previous studies (de la Torre et al. 2009).

The effects of fragmentation on the ranging patterns and habitat use of the marmosets may have caused the "nomadic" behavior not previously reported in any of our studied populations or elsewhere for this species. By 2005, two of the three studied groups of pygmy marmosets in San Pablo moved away from their original home ranges within a period of 1–6 months after the forest remnant was disturbed by selective logging (de la Torre et al. 2009). Since then, groups have occupied small core areas of their original home ranges for short periods, moving continuously among them. This new behavior may be related to the scarcity of exudate sources. The core areas contained only old exudate sources, which may be temporarily exhausted, forcing the marmosets to move. Until now, we have not been able to adequately measure the productivity of exudate sources; however, based on our records since 2001 and on the number of old, not-used holes in these trees, we believe that this explanation is plausible.

Genetic Variability

Although the results of this pilot study have to be interpreted with caution because the number of samples for each group was small and not equal for all groups and the number of loci analyzed was also low (five loci), it appears that nonrandom mating may be occurring in some of the groups. The results of the Hardy–Weinberg equilibrium test point in that direction, as well as the fixed alleles found in groups P1 and P2. The cooperative breeding system characteristic of pygmy marmosets where offspring are slow to disperse and often stay with their natal group to help care for offspring, is related to low rates of immigration, high rates of recruitment after births and a possible transfer of reproductive status between related females.

These factors may cause a high degree of relatedness among members of the group and, as a consequence, some inbreeding and low genetic variability (Nievergelt et al. 2000).

In addition to these natural factors, our results suggest that habitat fragmentation may be affecting the dispersal of individuals and influencing the genetic variability of the groups. According to the Nei's genetic distances, groups P1 and P4 differed more from group P2, suggesting that physical barriers for the dispersion of the groups are influencing genetic diversity. Groups P1 and P2, the most genetically different, have the most distant home ranges, separated by open areas, houses and several plantations. On the other hand, groups P1 and P4, the more genetically similar, had a secondary forest connecting their home ranges areas (Nieto et al. 2010).

These preliminary results suggest that population responses to fragmentation are more complex than we initially expected. We are currently analyzing the genetic variability of other pygmy marmoset population less affected by fragmentation to complement these findings. Combining behavioral data with molecular genetics may allow us to better understand the magnitude of the impact of habitat fragmentation on this and other Ecuadorian primate species. Meanwhile, there is an urgent need to restore the riparian habitats used by the marmosets to reduce the risk of local extinctions. In San Pablo, about 4 years ago we began a reforestation program with some Secoya families; we hope that this program, complemented with an on-going campaign of environmental education, may eventually improve the conservation status of the pygmy marmoset population in this and the surrounding areas. Marmosets have a number of characteristics that should help them survive, including a plasticity in behavior that is consistent with our previous findings of inter-population differences in vocalizations (dialects) and feeding preferences in this species (de la Torre and Snowdon 2009; Yépez et al. 2005). We hope that we are still in time to be as plastic as they are, changing our own behavior to reduce our impacts on this and other primate species.

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Chapter 30
Interacting Roles of Diet, Cortisol Levels, and Parasites in Determining Population Density of Belizean Howler Monkeys in a Hurricane Damaged Forest Fragment

Alison M. Behie and Mary S.M. Pavelka

Abstract Primates in fragments, because of their increased vulnerability to stochasticity, are in double jeopardy with the expected increases in severe weather patterns due to global climate change. It is thus increasingly important to have a better understanding of how severe weather events affect primate populations, especially those in fragments. This study explores the interacting effects of diet, cortisol levels, and parasites on the density of a black howler (*Alouatta pigra*) population following a major hurricane. In October 2001, Hurricane Iris made landfall in Southern Belize resulting in substantial damage to the 96-km^2 Monkey River watershed forest fragment and a loss of nearly 80 % of the population by 3 years after the storm. Late in 2004 the population stabilized and began to recover. From 2001 to 2006, demographic, behavioral, and dietary data along with fecal samples were collected from six monkey groups in an 86-ha study site in the Monkey River forest. Changes in population density over the 5-year period were explained primarily by fruit consumption both directly through inadequate fruit intake leading to energy malnutrition and indirectly through physiological stress (measured through fecal cortisol). Cortisol levels had a lesser direct effect on population density and were affected not only by low fruit consumption, but by multispecies parasite infections. This study highlights the importance of taking a multifactorial approach to understanding population density and shows how diet, stress, and parasites can have interacting effects in influencing primate population dynamics.

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Introduction

As part of the Northern Atlantic Cyclone Basin, the Caribbean along with Central and South America are frequently hit by hurricanes, averaging six hurricanes and two tropical storms per year. The Central American country of Belize is no exception and has been hit by over 16 hurricanes and 17 tropical storms since 1930. While hurricanes are frequent, studies on their effects on forest ecosystems are less so. Documented studies on changes to forest structure have found that following hurricanes, the majority of trees are at the very least defoliated and many suffer more severe damage ranging from minor delimbing to complete uprooting (Brokaw and Walker 1991; Elmqvist et al. 1994; Tanner et al. 1991, Walker et al. 1992; Whigham et al. 1991). Tree mortality rates are also know to dramatically increase following wind storms, with mortality rates ranging from 35 % following Hurricane Iris in Belize to 41.5 % following Hurricane Hugo in Puerto Rico (Lugo 2000). Of the trees that die, many are upper canopy or emergent trees that may be more vulnerable to wind damage (Dittus 1985; Pavelka and Behie 2005), leaving these forests with lower average canopy heights than other forests. The loss of these large trees also creates many forest gaps that allows for the rapid growth of fast-growing pioneer species, which can result in changes to overall forest composition. For example, following Hurricane Hugo, 13 new tree species established themselves in the forest while four of the ones previously there disappeared (Brokaw and Grear 1991).

Due to the severe and sudden changes to forest structure that result from natural disasters primate species living in such habitats often alter their diet to include less preferred or exotic species. Following such disturbances ring-tailed lemurs (*Lemur catta*; LaFleur and Gould 2009; Ratsimbazafy et al. 2002), ruffed lemurs (*Varecia v. editorium*; Ratsimbazafy 2006), and black howlers (*Alouatta pigra*; Behie and Pavelka 2005) altered their diets to include plant parts and species not previously ingested, some of which were exotic to the region or were located outside of the regular forest habitat. These changes in diet often have snowballing effects, potentially interacting with other body systems to result in changes to population density or population dynamics.

One thing that may be influenced by changes in diet is the production of cortisol in the body. Cortisol levels are often higher for primates living in disturbed habitats, potentially due to nutritional stress associated with lowered food supply (Chapman et al. 2006; Martinez-Mota et al. 2007). Cortisol is a glucocorticoid that is released from the adrenal cortex to help the body handle and recover from stressful situations by helping to restore homeostasis. Regardless of the type of stimuli, stress will induce the flight or fight response, which serves to mobilize glucose from cells and tissues into the bloodstream for immediate use (Sapolsky 1992). The metabolic goal of the stress response is to free up energy to be used by the body until the stressor passes. While this mechanism is beneficial in the short term, if it is activated too often or for too long it can have deleterious effects on the body, as energy is constantly being removed from other systems. Persistently high cortisol levels can lead to tissue and muscle breakdown, immunosuppression, decreased growth rates and lower reproductive rates (Abbott 1987; Avitsur et al. 2001; Bercovitch and Ziegler 2002; Saltzman and Abbott 2009; Sapolsky 1992; Ziegler et al. 1995). When a low quality diet is ingested, cortisol may be produced to increase glucose release for use by malnourished animals (Muller and Wrangham 2004; Behie et al. 2010).

As with stress, increased parasitism in disturbed habitats is also linked to diet because low food availability in fragments may limit nutrient intake and possibly compromise the immune function. In red-tailed monkeys (*Cercopithecus ascanius*; Gillespie et al. 2005) and Milne Edward's sifakas (*Propithecus edwardsi*; Wright et al. 2009) living in disturbed habitats, parasite levels were higher, which the authors interpreted as a possible side effect of malnutrition. For red colobus (*Procolobus rufomitratus*) in Uganda, the prevalence of four parasites was higher in fragments than continuous forests and five additional parasites were found in fragments that did not appear in continuous forest (Gillespie and Chapman 2008). Black howlers living in disturbed forests had increased *Controrchis* spp. infections that may be explained through their consumption of pioneer species that grow in disturbed areas and are home to ants that may be an intermediate host for this parasite (Kowalzik et al. 2010; Vitazkova and Wade 2007).

Nutritional status and parasitism can have a synergistic effect with food shortages increasing parasite burdens, which in turn can increase nutritional demands on the host and further accentuate the effects of the food shortages (Coop and Holmes 1996). Malnutrition can also act in conjunction with stress as both will interfere with immune response (Coop and Holmes 1996). Chapman et al. (2006 and 2007) found that both increased fecal cortisol and periods of low food availability were associated with increased parasite levels in *C. guereza* and that decreased food availability led to population declines both directly through malnutrition and indirectly through increased parasitism. A 68-month study of howler monkeys (*Alouatta palliata*) and parasitic bot flies (*Alouattamyia baeri*) determined that the annual pattern of howler mortality was due to a combination of factors including both the physical condition and larval burden of the parasitized individual (Milton 1996). Similarly, Gulland (1992) found that during population crashes Soay sheep (*Ovis aries*) were emaciated, had high nematode burdens, and showed signs of protein-energy malnutrition. These studies suggest that population declines are rarely due to a single factor and stress the importance of considering multiple variables when looking at patterns of population change.

In 2001, Hurricane Iris caused severe damage to the 96-km^2 Monkey River forest fragment in Belize that is home to a well-studied population of *A. pigra*. In the first year following the hurricane the population declined by 54 % and this decline continued for another 2 years until the population reached a low of 22 % of its pre-hurricane size (Pavelka et al. 2007). The population then stabilized for 2 years between 2005 and 2006, and began increasing in 2007. In this chapter, we examine the interacting effects of diet, stress and parasitism in population recovery patterns following Hurricane Iris.

Methods

The Monkey River study site is an 86-ha site in southern Belize, Central America that is part of a larger 96-km^2 forest fragment composed of semievergreen broadleaf riparian forest (Fig. 30.1). The study population consists of six howler groups from which behavioral and ecological data have been collected since 1999. Population characteristics within this site have been shown to be representative of the larger forest fragment (Pavelka et al. 2007), thus population density was determined

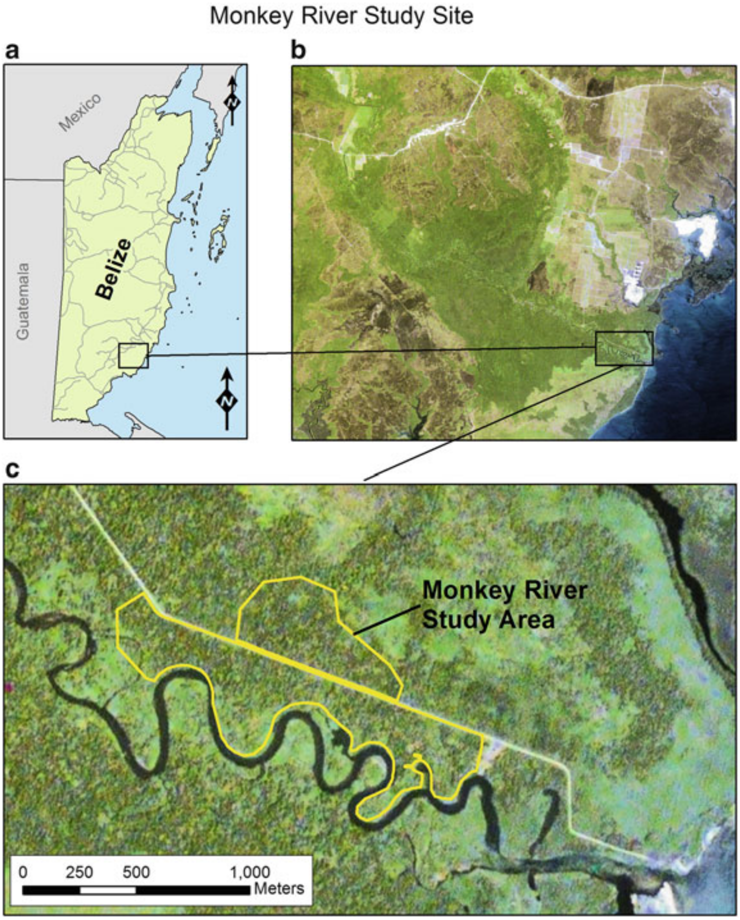

Fig. 30.1 Location of the Monkey River study, where (**a**) shows the location of the larger Monkey River watershed fragment in the country of Belize, Central America, (**b**) shows the location of the Monkey River study site within the larger forest fragment, (**c**) shows a close-up view of the exact area in which the study monkeys live

through true counts of all monkey groups within the study site. At least 3 days per week each known group was located and monitored to determine any changes to group size and composition. Fruit consumption (percentage of feeding time devoted to fruit) was calculated from 1,710 h of focal animal data collected from 2001 to 2008. Fruit consumption in this species is known to be directly correlated with fruit availability (Behie, unpubl. data; Silver et al. 1998).

Fecal cortisol levels and parasite measures were determined via fecal sampling. We collected 350 fecal samples over a 4-year period (May–July 2004, January–July 2005, and February 2006–May 2007; a total of 21 months). One sample was collected each month from the 16 recognizable adults living in the six groups. Steroids were extracted from the fecal samples following the protocol of Ziegler et al. (1995) and stored in Prevail SPE C18 cartridges (Alltech Associates, Inc.) out of sunlight until they were transported to the USA for analysis. Samples from 2004 to 2005 were sent to the Wisconsin National Primate Center for analysis and samples from 2006 to 2007 were taken to the behavioral endocrinology lab at the University of Nebraska at Omaha for analysis. Both labs used the same extraction techniques and assay reagents were obtained from the same source (Coralie Munro, UC Davis). Duplicate samples run at each lab produced virtually identical results and there was no statistical difference between mean cortisol values from samples analyzed at each lab (lab 1 N: 149; Mean: 13.35 ng/g; lab 2 N: 201; Mean: 13.41 ng/g; Mann-Whitney U; $Z = -0.952$; $P = 0.356$). For parasites, fecal samples were analyzed using floatation to determine the presence of helminth eggs and larvae.

Our objective was to determine if changes in the population density of black howlers living in a hurricane-damaged forest fragment was influenced by the following predictor variables: fruit consumption, cortisol levels, parasite prevalence (the proportion of individual samples that are infected with a parasite), and multispecies parasite infections (the proportion of the population infected with >1 species of parasite) to see if any of these variables were interacting to have a more pronounced effect. A path analysis (LISREL 8.72) is the most useful technique to determine the effect of multiple independent predictor variables as the path coefficients among the variables allow the determination of the magnitude of both direct and indirect effects. We first constructed a path diagram showing the expected relationships among the variables based on a priori knowledge (Mathur et al. 2007). For this study, we based our diagram on changes in fruit consumption, which was previously found to have a direct effect on population size (Behie unpubl. data) and could have further indirect effects on the population via increased stress or parasite infections (Fig. 30.2). The path (beta) coefficients presented are standardized regression coefficients that allow us to compare the relative effect of each predictor variable (fruit consumption, cortisol levels, parasite prevalence, multispecies parasite infection) on each other and on the dependent variable (population density). Results were significant ($p = 0.05$) when the path coefficient divided by the standard error was greater than two.

Results

Our path analysis revealed that fruit consumption had a significant direct and positive effect on population size (BETA=0.53; SE=0.20) (Fig. 30.2). However, as seen by the dotted line in Fig. 30.2, there was also a negative relationship between fruit consumption and cortisol, indicating that fruit consumption also had an indirect effect on population size through this negative influence on cortisol levels (BETA=−0.58; SE=0.23). In other words, when fruit consumption was low, cortisol levels increased, which had a smaller, negative effect on population density (BETA=−0.23; SE=0.11) than fruit consumption. Parasite prevalence did not have either a direct or indirect affect on population density; however, as seen in Fig. 30.2, multispecies parasite infections did have a positive effect on cortisol (BETA=1.20; SE=0.51). When individuals were infected with more than one parasite species they had higher cortisol levels in the following month, indicating that along with fruit consumption, multispecies parasite infections had an indirect affect on population density through increasing cortisol levels.

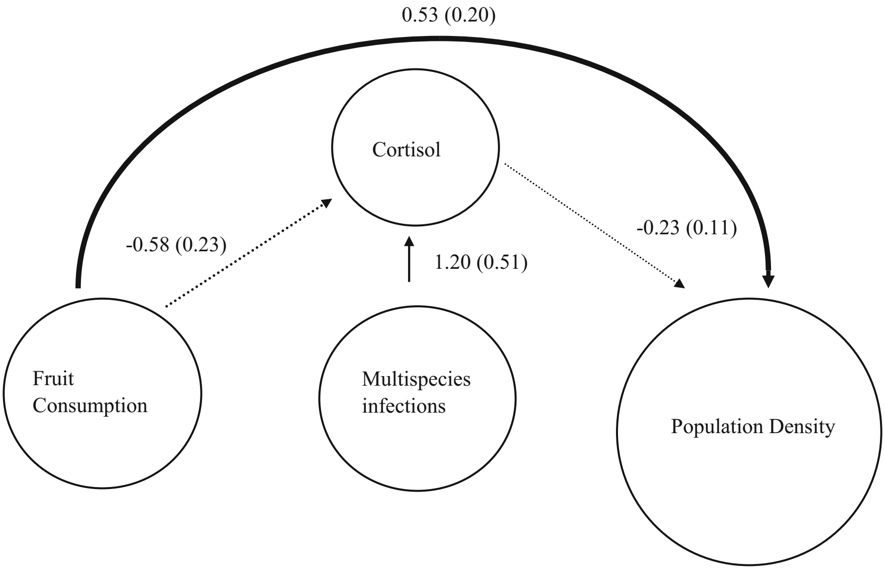

Fig. 30.2 Path analysis diagram of predictor variables found to significantly predict population density ($p=0.05$) for a black howler monkey population living in a hurricane-damaged forest fragment. A variable has a significant effect if the T value is ≥2, where T=BETA/Standard Error. BETA is the first number provided in each path coefficient and the standard error is the number in brackets. *Solid lines* represent positive relationships, while *dashed lines* represent negative relationships. Stronger relationships are shown by *thicker lines*

Discussion

Many primates are living in fragmented habitats and these populations are especially vulnerable to stochastic environmental events, such as severe weather, which is expected to increase in both frequency and severity with global climate change. Understanding the effects of fragmentation and severe weather patterns are hampered by the unpredictability of the latter and thus the unlikelihood of having pre-disaster data for any given site. Because a category four hurricane hit an on-going *A. pigra* study site in Belize, we were put in the somewhat unique position to be able to document population change in response to an environmental catastrophe.

These data suggest that the consumption of fruit had the biggest effect on population abundance. Due to the fact that folivorous primates, like howlers, can rely on leaves for extended periods of time, they are expected to be less sensitive to habitat disturbance than other primates. In fact, folivores may even increase following disturbance, as they may ingest pioneer species that grow in disturbed habitats and offer high quality leaves that are both high in protein and low in fiber (Chapman and Chapman 1999; Estrada et al. 2002; Rosales-Meda 2007). This reliance on pioneer species was documented in Monkey River following Hurricane Iris with the increased consumption of *Cecropia peltata*; however, despite the consumption of these high quality leaves the population continued to decline until fruit consumption returned to the 40 % pre-hurricane levels. It is hypothesized that due to their lack of a specialized foregut, howlers use fruit as their main source of readily available energy (Milton 1982). However, some populations of howlers are able to subsist on much less fruit than what was required by the Monkey River population. For example, a population of *A. fusca* eats as little as 5 % fruit annually (Chiarello 1994) and populations of *A. caraya* and *A. palliata* eat less than 25 % fruit each year (Bravo and Sallenave 2003; Julliot 1996). Our results support the idea that *A. pigra* eat “as much fruit as possible and as many leaves as necessary” (Silver et al. 1998, p. 273). We suggest that the importance of fruit in the diet of folivores has been underestimated and may play a much bigger role in determining population abundance than previously believed.

Fruit consumption was not only found to directly influence population density, but also to indirectly affect it through its effect on cortisol. When animals ate a low quality diet, their fecal cortisol levels increased, indicating nutritional stress. When animals are nutritionally stressed, they are generally not taking in enough energy to meet demands, putting the body in a situation where it needs to rely on existing glucose stores for energy. In this situation the body releases cortisol over night as a means to mobilize glucose from these stores for use the next day. This form of physiological stress has been reported in other nonhuman primates, and often it is associated with primates living in fragments with deceased food availability (Chapman et al. 2007; Foerster and Monfort 2010; Martinez-Mota et al. 2007; Muller and Wrangham 2004). It is likely that similar to what is seen in degraded forest fragments, cortisol levels increased in the howler monkeys following Hurricane Iris in response to the ingestion of a primarily folivorous diet that is low in readily available sugar-causing nutritional stress.

In the post-hurricane Monkey River population, cortisol levels were also affected by multispecies parasite infections; when individuals were infected with more than one species of parasite their cortisol levels increased, a result also found in red colobus monkeys (*Piliocolobus tephrosceles*) living in fragmented habitats (Chapman et al. 2006, 2007). While reports on the occurrence of multispecies infections are common in vertebrates, the same is not true for reports on the morbidity and mortality of these infections (Petney and Andrews 1998). Our results suggest that one of the potential outcomes of multispecies parasite infections is increased cortisol levels which over the long term can cause immunosuppression and decreases in reproduction. When the body is parasitized by more than one species there is likely greater physiological stress on the body as the parasites would be competing for nutrients and using more of the host's energy. This physiological stress is something that would also be accentuated by the consumption of a low quality diet, as was the case following Hurricane Iris. Similar results were found in mantled howlers where Milton (1996) determined that the annual pattern of howler mortality due to botfly infection was due to a combination of factors including both the physical condition of the individual and larval burden of the parasitized individual.

As both forest fragmentation and natural disasters increase, primate populations are becoming increasingly vulnerable to extinction. It is therefore crucial that we understand how primates in fragments respond to severe environmental changes. This study highlights the importance of understanding the way that different factors often associated with forest fragmentation, including lower food availability, higher cortisol levels, and increased parasitism, interact to influence primate populations. Studies such as this that are multifactorial in nature will provide our best tool for understanding how these factors both directly and indirectly influence population abundance.

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Section VII
Conservation and Ecology: Threats and Management Summary

Laura K. Marsh

While we gather our forces for a synthesis that can be used to formulate future research and conservation needs in the final chapter (Marsh et al. Chap. 34), authors in this section offer case studies from very interesting and differing perspectives. Boonratana (Chap. 31) discusses endangered *Nasalis larvatus* populations in the extremely fragmented lower Kinabatangan River in Sabah with regard to historic deforestation and current pressures, including tourism. Riverside habitats are critical to this species, which almost exclusively stays along waterways, rarely using dipterocarp or swamp forests. Ecotourism was touted since the 1980s as a means to a conservation end: "sell" the concept of primates as a tourist attraction and the funds generated by tourism will go to locals to help protect the animals. Proboscis monkeys are shown to play a significant role in generating revenue for the state, businesses, and local communities, but without careful management the tourism industry will destroy the very thing it depends on as they build more hotels and remove more habitat so that the tourists are accommodated. Because this species is not particularly flexible in their habitat usage, there are significant conservation challenges ahead.

In Chap. 32, Ramos-Fernandez et al. use an experimental algorithm to predict available habitat and distribution based on climate change scenarios for two species of Mexican primates *Ateles geoffroyi* and *Alouatta pigra* in the Yucatan peninsula. They used surveys from 78 locations as inputs for the program, and two strategies for estimating the potential distribution for the primates in the year 2020. They found for all variables and for both species that while forested and protected areas, such as the Calakmul Biosphere Reserve, would prove important habitat, the vast majority of predicted distribution of the primates would fall outside of protected areas, particularly in the northeastern Yucatan peninsula, resulting in less than 20 % of potential distribution for these species falling within protected status. Simulation models such as these are useful in planning the future for primates across a region.

From the large-scale to the start-up, Wallace et al. (Chap. 33) focused their efforts on two endemic, largely unstudied titi monkeys in naturally fragmented habitat in Bolivia: *Callicebus modestus* and *C. olallae*. The authors investigated the distributional limits of both species, determined their phenotypic characteristics, conducted preliminary analyses of genetic differences between the two species, estimated population densities, described the composition and structure of the habitats where they occur, and documented the behavioral ecology of both species. As a result of their work, they are able to put forth conservation recommendations in coordination with government offices and local municipalities.

Finally, the question has been raised throughout the science community and should be no different in ours: Who is science for and how can science reach disenfranchised populations (Shanley 2006) to make meaningful changes in the way we conduct conservation, in our case, for primates in fragments? We continue to hope that the work we do large-scale, small scale, theoretical, and hands-on will result in changes for our global primate populations. The authors in this section continue to work toward the goal that so far has been maintained, of zero primate extinctions in the modern era.

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Chapter 31
Fragmentation and its Significance on the Conservation of Proboscis Monkey (*Nasalis larvatus*) in the Lower Kinabatangan, Sabah (North Borneo)

Ramesh Boonratana

Abstract Timber extraction from the lowland forests of the Lower Kinabatangan floodplain was widespread since the early 1980s and was the major threat to *Nasalis larvatus* populations. Since then, much of the region has been clear-felled to make way either for cocoa and oil palm plantations or for smaller government-sponsored farming projects. Such clearances not only led to a severe loss of habitats for *N. larvatus*, but also fragmented the remaining forests. Then beginning in the early 1990s, interests and the relative ease in viewing proboscis monkeys and other wildlife in the Lower Kinabatangan led to a booming tourism industry in parts of the region. This further fragmented *N. larvatus* habitats and threatened their survival, particularly given that the prime areas for tourist accommodations and associated facilities typically comprising riverside habitats are critical to the species. *N. larvatus* sleeping sites are determined by the presence of standing trees adjacent or overhanging large water bodies; therefore, loss of those trees or loss of access to those trees have several socio-ecological and conservation implications. Here I describe fragmentation of *N. larvatus* habitats in the Lower Kinabatangan and the implications of such fragmentations on their long-term survival.

Introduction

Proboscis Monkey *Nasalis larvatus* (Wurmb) is a large, sexually dimorphic, monotypic arboreal “odd-nosed” colobine, endemic to the island of Borneo, where it is largely restricted to riverine, peat swamp, and mangrove forests of the coastal lowlands. Globally, *N. larvatus* is categorized as Endangered according to the IUCN Red List of Threatened Animals, and listed on CITES Appendix I (Meijaard et al.

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Fig. 31.1 *Nasalis larvatus* group, adult female in the center

2008) (Fig. 31.1). It is legally protected by national and state/provincial laws throughout its distributional range (Meijaard and Nijman 2000). In Sabah, *N. larvatus* is a totally protected species under the 1997 Wildlife Conservation Enactment, and populations of the species are found in the Kabili-Sepilok Forest Reserve, Klias National Park, Kulamba Wildlife Reserve, Lower Kinabatangan Wildlife Sanctuary, and the Ulu Segama Reserve. Despite the legal protection throughout its range, the species population is nevertheless declining, primarily because much of its habitats are favored for timber extraction, cultivation, and human settlements. Hunting of *N. larvatus* for food or traditional medicine does occur, but it is a less serious problem when compared to habitat loss.

The root causes to habitat loss, fragmentation, and degradation in the Lower Kinabatangan are all of anthropogenic origins. The oldest record of human settlement along the Kinabatangan River dates back to 1410 (The Brunei Annals in Scholz 2008). Since then the local human population have expanded, resulting in small clearings for agriculture and settlements along the river, fragmenting the forested riverine habitats. From the 1980s, many small clearings, ranging from 0.5 to 4 ha, were associated with government-sponsored farming projects (Boonratana 1993; Boonratana and Sharma 1994).

The Lower Kinabatangan region has been subjected to commercial logging and varying degrees of disturbance from the early 1950s, and virtually all of the forests of the Kinabatangan area have been logged at least once (Payne 1989). Old skidder roads exist until today and partly contribute to habitat fragmentation. In the early 1980s, logging of mangroves in eastern Sabah was widespread, mainly for woodchips, but later banned in early 1987 (Bennett 1991). In addition, large quantities of rattan (Arecaceae), a traditionally important local trade item, were collected from the region, mainly along the long stretches of flat land along the banks of the

Fig. 31.2 Isolated forest fragment compressed between a river and oil palm plantations

Kinabatangan River and its tributaries. Most of the harvesting was within a kilometer of the waterways (Khoo 1981). Until 1989, all the rattan harvested from the region was wild, after which, most was cultivated by the Sabah Forestry Development Authority (Payne 1989).

Conversions into oil palm plantations to the 1990s (Boonratana 1993, 2000b; Boonratana and Sharma 1994; McMorrow and Talip 2001; Teoh et al. 2001) have exacerbated habitat loss, fragmentation, and degradation and it is estimated that oil palm plantations have replaced at least 85 % of the original habitats (Maginnis and Jackson 2002) (Fig. 31.2). Five-meter wide ditches up to 3 km or more in length were dug to drain the swampy parts of the oil palm plantations, and electric fencings placed around them to deter large mammals from damaging the crops (Boonratana 1993; Boonratana and Sharma 1994) (Fig. 31.3). In addition to fragmenting the remaining habitats, these ditches and fencings have significantly disrupted the ranging patterns of many terrestrial animals and their movements between the forest fragments (Boonratana 1993; Boonratana and Sharma 1994).

Simultaneously, in the early 1990s, interests and relative ease in viewing *N. larvatus* and other wildlife along the Kinabatangan River lead to a booming tourism industry in parts of the region. Sukau Village alone was reported to attract about 2,000 tourists per month (Teoh et al. 2001) and up to 60,500 in total for 2006 (Fletcher 2009). Numerous infrastructure and tourism development projects (e.g., roads, accommodations, boat landings) accompanied the booming tourism industry, further clearing and fragmenting the remaining forested habitats or reducing connectivity between them (Boonratana, unpubl. data; Sha et al. 2008). Moreover, a number of tourism accommodations and associated boat landings are located at sites previously occupied by *N. larvatus*.

Here I report on a 2-year field study on the ecology and behavior of *Nasalis larvatus* at Sukau and Abai along the Kinabatangan River (Fig. 31.4) that was

Fig. 31.3 Swamp drainage for oil palm plantation growth

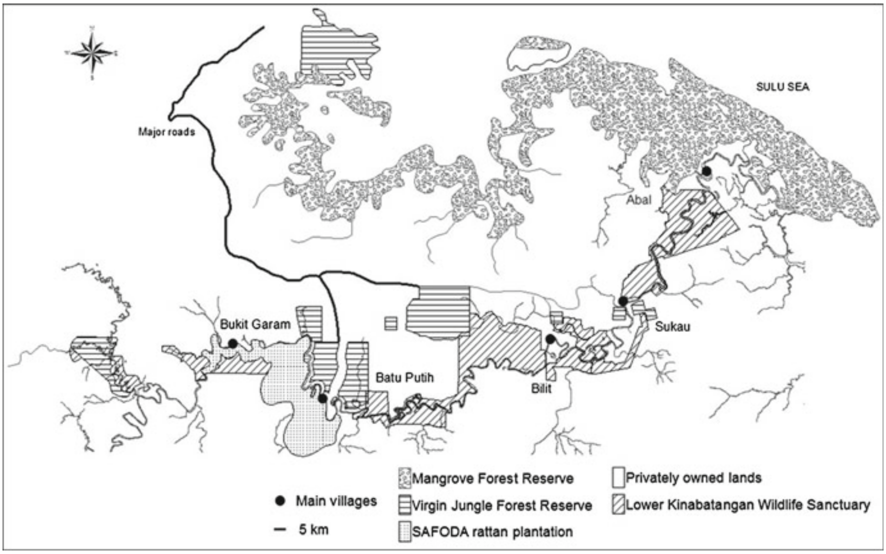

Fig. 31.4 The Lower Kinabatangan Floodplain

conducted between January 1990 and December 1991 prior to the extensive conversion to oil palm plantations and mass tourism. These results contrasted to later studies carried out at the same area to identify changes in the ecology and behavior of *N. larvatus* in the context of habitat loss, fragmentation, and degradation.

Study Area

The Kinabatangan River is Sabah's longest river at a length of 560 km and it has a catchment area of 16,800 km^2 (Scott 1989). The Lower Kinabatangan River meanders through a large flat floodplain, much of which is subject to seasonal flooding, resulting in low-stature forest with little timber of commercial value. This floodplain, measuring approximately 280,000 ha, is the largest and possibly the most important wetland in Sabah (Scott 1989).

The region has a humid tropical climate with an average annual rainfall of about 2,600 mm and mean diurnal temperatures from 22 to 32 °C (Scott 1989). This climate results in the natural vegetation in the flood-prone areas at Sukau to comprise principally riverine forest and freshwater swamp forest, peat swamp forest, and some open reed swamps. In the flood-free zone, cocoa and oil palm plantations, and remnants of pristine lowland dipterocarp forest, logged-over swamp forest, and burnt lowland dipterocarp forest dominate. At Abai, the principal vegetation is mangrove forest with extensive stands of *Nypa fruticans* (Arecaceae) at the inland edge and the upper tidal limit of the estuaries.

Methods

This study was carried out at Sukau (N5°30′, E118°17′) and Abai (N5°41′, E118°22′) from January 1990 to December 1991 and comprised monthly census surveys, full day follows, botanical studies, and phytochemistry analysis. In addition, I made opportunistic observations between mid-1994 to late 1996, and after 1996 I obtained information from various published and unpublished manuscripts and from personal communications with researchers working in the area (Table 31.1).

N. larvatus is highly dependent on waterways and the adjoining forests. Although wide-ranging, *N. larvatus* groups return to sleep in trees by the water bodies every night (Bennett and Sebastian 1988; Boonratana 1993, 2000a; Rajanathan and Bennett 1990; Yeager 1989). By travelling along the rivers before dusk and just after dawn, it was possible to observe most groups. Each month, five survey-nights were carried out along the Menanggul River at Sukau and another five survey-nights at Merah River at Abai. Opportunistic surveys were also conducted in the estuaries of the Kinabatangan River, along the Kinabatangan River from Mumiang to Bilit, and the various tributaries and ox-bow lakes located between Mumiang to Bilit. From April to November 1991, my field assistants were assigned ten survey-nights

Table 31.1 Summary of comparative studies in the Lower Kinabatangan

Author	Site	Year of study	Reference
Boonratana	Kinabatangan Floodplain (including Sukau and Abai)	Jan. 1990–Dec. 1991	Boonratana (1993, 2000a, b, 2002, 2003)
Boonratana and Sharma	Kinabatangan Floodplain (including Sukau and Abai)	Jan. 1990–Dec. 1991	Boonratana and Sharma (1994)
Goosens et al.	Kinabatangan Floodplain	May 2002	Goossens et al. (2002)
Murai	Sukau	Feb. 1999–Oct. 2001	Murai (2004)
Leasor	Sukau	Jun. 2003–Jul. 2004	Leasor (2008)
Sha et al.	Kinabatangan Floodplain	Jun.–Nov. 2005	Sha et al. (2008)
Matsuda	Sukau	May 2005–May 2006	Matsuda (2008)
Matsuda et al.	Sukau	May 2005–May 2006	Matsuda et al. (2009a, b, 2010)

per month to conduct systematic census surveys along Tenegang Besar, Sapasidom, and Menanggul Rivers, and at Kelandaun and Kelananap Lakes.

River surveys were made using a small boat, and the age–sex composition and location were recorded every time a group was encountered. The surveys began at 16:30 and usually ended at 18:30, between the time when *N. larvatus* arrived at the river and when it was too dark to count well. Cruising speed was maintained at no more than 5 km/h, and about 10–15 min was spent observing each group encountered. The surveys were repeated the next morning at 05:45 following the same route taken the previous evening and ending at 07:15. This allowed two attempts at group counts, obtaining their locations, and age/sex identifications for any one night (Bennett and Sebastian 1988; Boonratana 1993; Rajanathan and Bennett 1990).

Scan samples were recorded during a 2-min period every 15 min from dawn to dusk during every full day follow and encompassed all members of the group that could be observed. At Sukau, a focal OMU (one-male unit) was identified and observed. Observations were made from the boat in the morning before the focal OMU moved away from the river, and in the evening after it returned to the river. During the day when the focal OMU moved into the forest, it was followed on foot. Whenever the focal OMU could not be located, observations were made on other *N. larvatus* OMUs. A continuous network of trails based on a grid system (100 m × 100 m) was established to allow positions to be accurately plotted every 15 min, or whenever its position changed at least 20 m. At Abai, it was not possible to observe an OMU continuously throughout the day. This was partly due to the shyness of the animals, but mainly due to the forest being flooded during high tide. The ground was very soft and muddy during low tide, making it impossible to follow in a noiseless manner. The presence of *Crocodylus porosus* in the area was also a deterrent. Thus, almost all observations were made from the boat when the OMUs were by the river. An OMU was observed for as long as possible, and then another OMU was located when the first OMU was no longer visible.

Botanical transects were established at Sukau and Abai to describe the structure and tree species composition of the forest and to monitor tree phenology. The number of trees of at least 30 cm girth at breast height (gbh) within the botanical transects totaled 1,378 at Sukau and 300 at Abai. At Sukau, the crowns of 500 trees and at Abai all 300 trees were examined monthly for the presence of mature and young leaves, ripe and unripe fruits, and flowers.

Results

Population Size and Density

In replicated census surveys over 2 years, I counted at least 832 individuals in the Kinabatangan Floodplain (Table 31.2). A decade later, using non-replicate surveys, Goossens et al. (2002) estimated 3,430 individuals by extrapolating from the numbers observed for the surveyed stretch of river. In 2005, Sha et al. (2008) counted 1,454 individuals but similarly employed non-replicate surveys.

Using replicate census surveys, I obtained a minimum count of 146 individuals along the first 10-km stretch of the Menanggul River (a tributary of the Kinabatangan River) or at 14.6 individuals/km of river. Using comparable methods, Leasor (2008) counted 14–108 individuals along the first 5-km stretch of the river (12.2 individuals/km of river for an average of 61 individuals per census survey); Murai (2004) counted 171–174 individuals along the first 6-km stretch of the river (averaging 28.5–29 individuals/km of river; and Matsuda (2008) counted 21–218 individuals along the same 6-km stretch (giving 3.5–29.8 individuals/km of river). Thus over time the ranges of different estimates overlapped completely. With respect to density, I obtained an estimate of 34.0 individuals/km^2 and Matsuda et al. (2009b) obtained 29.8 individuals/km^2.

Social Organization

All long-term studies at the Sukau reported the social structure of *N. larvatus* as flexible, comprising relatively stable OMUs, all-male units (AMUs), and predominantly male units (PMUs). PMUs refer to loosely bonded predominantly male unit with at least one female member. I recorded 17 individuals as the average OMU size at Sukau (Table 31.2). Murai (2004) reported an average OMU size of 18 individuals and Matsuda (2008) reported 13.6 individuals. I obtained the OMU adult male to adult female sex ratio at 1:7.3, whereas both Murai (2004) and Matsuda (2008) reported a lowered sex ratio, at 1:4.9 and 1:5 respectively; and I obtained the adult

Table 31.2 Population size, group size, adult sex ratio, and home range of *N. larvatus* in the Lower Kinabatangan area

Location	Survey length (km)	*N*[a]	No. of individuals/ km[b]	Density (individuals/ km^2)	Average OMU size[c]	Adult sex ratio (OMU)	Adult female/ infant ratio (OMU)	Home range (ha)	Day range length (m)	Source
Kinabatangan Floodplain	206.5	832	4	–	–	–		–	–	Boonratana (1993)
Mumiang to Abai[d]	40	82	2.1	–	–	–		–	–	Boonratana (1993)
Kuala Kinabatangan Besar to Abai[d]	40	82	2.1	–	–	–		–	–	Boonratana (1993)
Abai to Sukau[d]	50	128	2.6	–	–	–		–	–	Boonratana (1993)
Sukau to Bilit[d]	35	154	4.4	–	–	–		–	–	Boonratana (1993)
Merah River	12	84	7.0	10	14.6 (8–22)	1:7.1	1:0.14	315	–	Boonratana (1993)
Resang/Sapasidom River	6	44	7.3	–	–	–		–	–	Boonratana (1993)
Menanggul River	10	146	14.6	34.01	17 (14–20)	1:7.3	1:0.1	221	910 (370–1,810)	Boonratana (1993)
Tenegang Besar River	12	95	7.9	–	–	–		–	–	Boonratana (1993)
Kelananap Lake	1.5	17	–	–	–	–		–	–	Boonratana (1993)
Kinabatangan Floodplain	103.1	3,430	33.3	6.86	–	–		–	–	Goossens et al. (2002)
Menanggul River	6	171–174	28.5–29	–	18 (8–34)	1:4.9	–	–	–	Murai (2004)
Menanggul River	5	14–108	12.2[e]	13	11.9	–	–	–	–	Leasor (2008)
Resang River	0.9	56	16.7[e]	–	–	–	–	–	–	Leasor (2008)
Tenegang Besar River	3.5	11–97	12.2[e]	–	–	–	–	–	–	Leasor (2008)
Kinabatangan Floodplain	–	1,454	7.89	–	–	–	–	–	–	Sha et al. (2008)
Menanggul River	6	21–218	3.5–29.8	29.8[f]	13.6 (2–29)	1:5	1:0.34	138.3	799 (220–1,734)	Matsuda (2008)

[a] Boonratana (1993): minimum numbers observed using replicate surveys; Goossens et al. (2002): extrapolated from non-replicate surveys; Murai (2004); Leasor (2008); Matsuda (2008): maximum numbers observed using replicate surveys; Sha et al. (2008): maximum numbers observed using non-replicate surveys

[b] Linear measurements

[c] Range given in parentheses

[d] Along the Kinabatangan River

[e] Obtained from average count per survey

[f] Highest density given

female to infant ratio at 1:0.1, whereas Matsuda (2008) reported a higher ratio at 1:0.34.

In addition, the same studies reported *N. larvatus* further exhibiting intergroup associations, indicating a multilevel society, with fission–fusion of stable OMUs within bands. Previously, I have reported the focal OMU spending 43.8 and 54.2 % of its sleeping nights within 50 and 100 m, respectively of another OMU (Boonratana 1993, 2002). Murai (2004) reported one OMU spending up to 71.2 % of its sleeping nights within 100 m of another OMU, and Matsuda et al. (2010) reported the focal OMU spending 36.6 and 63.4 % of its sleeping nights within 50 and 100 m, respectively of another OMU.

Activity Budget and Feeding Behavior

Comparing my study in 1990 and 1991 to Leasor's (2008) conducted in 2003–2004 revealed a drop in the percent time OMUs spent engaged in vigilance, but an increase in percent time OMUs travelling, resting, and vocalizing (Fig. 31.2). When behaviors were recategorized to match those of Matsuda et al. (2009b), Leasor (2008) showed little difference to my earlier study in the percent time OMUs spent resting and feeding. On the contrary, compared to my study, Matsuda et al. (2009b) reported a major decline in the percent time OMUs spent travelling, while the percent time spent resting and feeding increased by 20 and 10 %, respectively. Matsuda et al. (2009b) further reported significant lowered percent time spent grooming and sexual copulation.

I documented that 72.7 % of the OMUs annual diet comprising young leaves, whereas flowers (including flower buds) and fruits (including seeds) comprised 8.3 and 10.7 %, respectively (Fig. 31.3). Matsuda et al. (2009b) reported the annual diet of the mature members of a focal OMU comprising 65.9 % young leaves, 7.7 % flowers (including flower buds), and 25.9 % fruits (including seeds).

Ranging Behavior

I found that *N. larvatus* used the natural riverside habitats almost exclusively, and was rarely observed in the lowland dipterocarp and the freshwater swamp forests. No animals were seen entering agricultural lands or the large areas by the Kinabatangan and Menanggul Rivers that comprised mainly tall grass and scrub, but they occasionally travelled on the ground between tree patches (distance between patches recorded at not more than 20 m). Later observations also showed that *N. larvatus* avoided using or sleeping in those riverside habitats where tourist accommodations and associated boat landings were established (Boonratana, unpubl. data; Matsuda, pers. comm.). Boonratana (1993) previously recorded those sites as their sleeping areas and part of their range. All studies at Sukau reported that

N. larvatus have completely overlapping home ranges and that they returned to sleep by the rivers every evening. Matsuda et al. (2010) further reported observing *N. larvatus* sleeping in inland habitats on nights when the area was flooded, along old skidder roads or forest gaps. However, only on nine out of the 34 nights when they were considered to sleep inland could be confirmed.

Compared to my study, the home range size and average day range length of OMUs reported by Matsuda et al. (2009a) declined by about 40 and 12 %, respectively (Table 31.2). I found no correlations to suggest that the use of specific areas in the OMU's home range was influenced by the phenology or their consumption of young leaves (expressed as the monthly mean number of one ha quadrats). However, there were positive correlations between the abundance of fruits and flowers in the OMU's diet and its range use (i.e., the OMU occupied particular areas of its home range more when feeding on fruits and flowers). I found no correlations to suggest the influence of phenology or fruits and flowers in the diet on the monthly mean day range lengths of the focal OMU, but the focal OMU travelled farther when there were higher proportions of young leaves in its diet. Matsuda et al. (2009a) reported a negative correlation between day range lengths of his focal OMU and the availability of fruits, but no correlation with the availability of flowers and young leaves.

I observed that whenever tourist boats inadvertently prevented river crossings, *N. larvatus* would travel farther upriver or downriver to once again attempt crossing. Occasionally, several unsuccessful attempts were required before a successful crossing could be made. *N. larvatus* were also observed moving away whenever tourist boats attempted to get too close for better viewing and photography. On some occasions, *N. larvatus* would move inland and cross the river after some hours when the tourist boats had gone. Matsuda (2008) reported seeing an average of 12 tourist boats and 70 tourists per day during the peak tourism season, sometimes interfering with *N. larvatus* river crossings. He further reported disruption from loud and noisy boat engines and camera flashes, and that some guides shouted to attract *N. larvatus* to facilitate their tour groups in taking better views or photographs.

Discussion

Population Size and Density

Unfortunately, the census survey I did in the Kinabatangan Floodplain is not comparable to those of Goossens et al. (2002) and Sha et al. (2008), thus the current population status urgently needs to be reassessed, particularly in the light of extensive habitat loss and fragmentation. Reduced number of individuals/km of river surveyed and density reported by Leasor (2008) along the Menanggul River suggests the influence of habitat changes. Although Murai (2004) reported an increase in the number of individuals observed per kilometer of river, but this is likely a response to a loss or degradation of natural habitats, forcing *N. larvatus* to occupy the remaining habitats, thus this density may not be sustainable. In addition, the wide range of individuals per kilometer reported by Matsuda (2008) suggests that he did not take into account when *N. larvatus* slept upriver beyond his study area or along the Kinabatangan River. Reduction of population densities also suggests the influence of habitat changes. Hence, reduced and degraded habitats, reduced access to other forest fragments, and increased competition for food resources very likely caused the population size and density to decline. Reduced, degraded, and fragmented habitats can be viewed as impoverished habitats, and several studies have shown that population density declines as habitats become increasingly impoverished (Bennett 1986; Freeland 1979; Marsh 1981; McKey and Waterman 1982; Struhsaker and Leland 1979).

Social Organization

The average OMU size at Sukau reported by Matsuda (2008) was closer to the average OMU size I recorded at the Merah River in Abai, which had comparatively lower food availability. Reduced habitats, diminished access to other habitat fragments, the distribution, size, and availability of food sources, and higher competition for limited food resources have likely resulted in *N. larvatus* opting for smaller group sizes. The small difference observed by Murai (2004) could possibly be that *N. larvatus* was, at that time (Feb. 1999–Oct. 2001), still able to access different habitat fragments. In addition, the reduced sex ratio of OMUs reported by Murai (2004) and Matsuda (2008) is probably a response to habitat loss and fragmentation.

Activity Budget and Feeding Behavior

No explanations could be provided for the differences in activity budgets observed by Boonratana (1993) and Leasor (2008), although there is a possibility that increase in percent time travelling is a response to avoiding tourists, particularly when *N. larvatus* needed to cross the river. The negative correlation between the number of tourist boats present on the river and the number of *N. larvatus* sighted per kilometer of census reported by Leasor (2008) suggests *N. larvatus* might be actively avoiding large human presence.

The higher percent time spent vocalizing (Leasor 2008) cannot be explained without looking into the context in which the vocalizations were emitted. Comparing across the three datasets (Fig. 31.2), habitat loss, fragmentation, and degradation are likely causing *N. larvatus* to have limited area for travelling; therefore, more time was spent on feeding and resting. Moreover, more time spent feeding was possibly to compensate for the reduced access to more diverse or preferred foods. With less diverse foods, *N. larvatus* may require more time for resting to reduce a buildup of potential toxins from any one species (Boonratana 2000a, 2003; Waterman 1984).

The increased time needed for feeding and resting could have led to a decline in time spent grooming, which can possibly have severe long-term implications on *N. larvatus* physiological health (Freeland 1976; Vayro 2009) and intra-group social relationships (Coelho et al. 1983; McKenna 1978; Seyfarth 1980). More observations are needed to see if these are consequences of having to cope with reduced and fragmented habitats. A higher percent time feeding on fruits (Matsuda et al. 2009b) is not likely attributable to habitat loss and fragmentation, but a possible mast fruiting during study might result in *N. larvatus* spending more time consuming rare food items.

Ranging Behavior

Habitat loss and fragmentation have not changed *N. larvatus* tendency to use riverside habitats, but reduced habitats and access to forest fragments have apparently resulted in reduced home range size, average distance travelled in a day, and availability of and possibly competition for the remaining sleeping sites. As to the habit of sleeping inland on flooded days, it has been proposed that *N. larvatus* sleep inland to minimize perceived threats from terrestrial predators (Matsuda et al. 2010) or increased tree falls due to flooding (Yeager 1993). However, it is more likely that inland forest gaps and abandoned skidder roads, when inundated, resemble small lakes and narrow rivers, and studies have shown *N. larvatus* sleeping along the smaller tributaries and the ox-bow lakes. Use of such newly created sleeping sites could possibly be a means of avoiding intergroup competition for limited sleeping sites and provide a temporary refuge from human disturbance associated with poorly managed tourism.

A 40 % difference in home range size, albeit of different OMUs, is suggestive of the impacts of reduced habitats and reduced opportunities to access other fragments, or availability of food sources. Boonratana (1993, 2000a) proposed that *N. larvatus* travelled farther on days when there were higher proportions of young leaves in the diet, to reduce potential toxins from any one species by accessing different plant species located in different parts of their home range. Accordingly, the lack of influence of young leaves in the diet on *N. larvatus* average day range lengths reported by Matsuda et al. (2009a) might be attributed to a decline in plant species diversity with habitat loss.

Several studies have shown that size, availability, and distribution of food sources do influence home range size and patterns (Bennett 1986; Boonratana 2000a; Marsh 1981; McKey and Waterman 1982; Freeland 1979; Struhsaker and Leland 1979). Extending such suggestions, Matsuda et al. (2009a) proposed that *N. larvatus* were apt to occupy a smaller range in fruit-abundant seasons to explain the observed negative correlation between the day range lengths and fruit availability. In the context of habitat loss or fragmentation, this was likely because the fruit sources in the study area were unevenly distributed and highly clumped (Boonratana 1993, 2003). Nevertheless, long-term observations are needed to verify this, as some studies have shown that home range size decreases as food sources become more abundant (McKey and Waterman 1982; Terborgh 1983).

Tourist boats disrupting river crossings likely affects *N. larvatus* ranging patterns and access to food or other resources. The disrupting behaviors of some tourists or guides are likely to cause undue stress to *N. larvatus*, and alter their behaviors.

Protection and Conservation

Most of the local inhabitants in the Lower Kinabatangan are Muslims and therefore do not hunt or trap *N. larvatus* and the species are not regarded as pests since they do not raid crops or incur any other grievances to the local human population (Boonratana 1993; Boonratana and Sharma 1994). Occasional pirate raids right into the early 1990s apparently discouraged outsiders from hunting around the estuaries (Boonratana 1993; Boonratana and Sharma 1994). Although there have been no reports of the species being hunted at the study sites, there were unconfirmed reports of the species being hunted as exotic meat in the mangrove habitats of the Sandakan Peninsula in the 1980s and early 1990s by nearby town inhabitants (Boonratana 1993; Boonratana and Sharma 1994). With expansion of oil palm plantations, there has been an influx of migrant laborers, many of whom are not Muslim by faith, and there have been reports of hunting or trapping of wildlife, including primates (BirdLife International 2009; Fletcher 2009).

Although efforts to legally protect the natural fauna and flora of the Lower Kinabatangan began in the 1980s, it was not until 2005 that the 27,800-ha lower Kinabatangan Wildlife Sanctuary was finally gazetted under the 1997 Wildlife Conservation Enactment. The sanctuary comprise ten forest lots, some totally fragmented while others connected by a narrow strip of forest cover. Some of these forest lots link with Virgin Jungle Forest Reserves of varying sizes (Fig. 31.4). There is an initiative to develop corridors linking these fragments by adding another 11,000 ha (Ambu in Chiew 2009; WWF-Malaysia 2007). Even back in the early 1990s, when boundaries were being drawn, Boonratana and Sharma (1994) cautioned that the size and shape of the proposed protected area are far from adequate in providing long-term protection of *N. larvatus* and its habitats, and that much of the *N. larvatus* areas of occupancy were not included in the proposal. Thus, had there been serious considerations paid to the original proposal and scientific studies, much of the current conservation issues would not have existed and efforts and funds could now be directed to management and livelihood improvement activities instead of new planning. Nevertheless, to conserve *N. larvatus* effectively, it is imperative to ensure that all natural riverside habitats are protected, and this will require restoring some of those habitats by reclaiming areas cleared for oil palm plantations and by relocating detrimental tourism infrastructure. To sustain wildlife populations, Ancrenaz (in Chiew 2009) proposed corridors of at least 500 m wide along major rivers and 250 m wide along major tributaries be established. However, based on long-term *N. larvatus* studies, an absolute minimum of 1,000-m forested strip is needed along the Kinabatangan River and its tributaries to allow connectivity between forest fragments and to ensure availability and access to food and other resources, including critical sleeping sites. In addition, ensuring effective protection to the forest corridors and fragments would require an additional 500-m forested strip to serve as a buffer zone.

N. larvatus plays a significant role in generating revenue for the state, businesses, and local communities, but without careful management the tourism industry in the Lower Kinabatangan will destroy the very thing it depends on. Management will require addressing the location of tourism infrastructure, the behavior of tourists and their guides, the limits of acceptable capacity, and preferably providing some "time-off" for *N. larvatus*, such as restricting entry up the tributaries at specific times during the day or closing the tributaries for specific periods (e.g., mating and birth seasons). In addition, tourism in the Lower Kinabatangan Floodplain is currently offered as ecotourism, although most do not adhere to the concept and principles of ecotourism, merely using it as a marketing tool. Hence, it is imperative for the relevant government agencies and businesses to distinguish which products, activities, and services qualify to be branded as ecotourism to allow consumers a choice and to encourage good practices.

Conclusion

Continued existence of *N. larvatus* in the Lower Kinabatangan Floodplain is evidence of the species resilience to habitat changes, but loss of critical habitats and inability to access different fragments have allowed the species to persist only at lowered population size and densities, and with likely changes to their behavior and ecology. However, their ability to survive is currently constrained by unmanaged tourism activities and habitat conversion. Hence, in addition to reforesting critical habitats and linking forest fragments, it is very important to promote responsible practices among the stakeholder tourism businesses and imperative that management is based on sound science.

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Chapter 32
Potential Distribution of Primates in the Yucatan Peninsula, Mexico Under Current and Climate Change Scenarios

Gabriel Ramos-Fernandez, Celene Espadas-Manrique, and Juan Carlos Serio-Silva

Abstract The distribution of primate species, under current and climate change scenarios, constitutes crucial information for their successful conservation. In areas with limited information on their distribution, simple extrapolations based on historical records may not reflect the actual distribution of a species. Here we model the potential distribution, under a current and a climate change scenario for the year 2020, of the two species of ateline primates that inhabit the Yucatan peninsula, in Mexico: spider (*Ateles geoffroyi*) and howler monkeys (*Alouatta pigra*). Data from a recent survey in 78 locations throughout the Yucatan peninsula were used as inputs for the DOMAIN algorithm, which estimates the similarity between the predictor variables found in the surveyed locations and those in the potential range of the species. The distributions estimated using this algorithm can be considered as being similar to the surveyed locations with a given degree of certainty (in this case, we used thresholds of 95, 97, and 99 %). We have used two different strategies for estimating the potential distribution of howler and spider monkeys in the Yucatan peninsula. The first strategy employed biophysical variables as predictors and obtained areas of potential distribution for both species that range from 19 to 81 % of the region's extent, depending on the threshold. The second strategy began by using the

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same biophysical variables to generate potential distributions for important trees in the diet of both primates, and then used the similarity values thus obtained as predictors of the potential distribution of monkeys. This strategy yielded somewhat smaller areas with similarity values above the threshold, comprising between 11 and 75 % of the region's extent. Semievergreen forest, the most abundant original vegetation cover in the Yucatan peninsula, was not the most abundant vegetation within the potential distribution areas, although it became more important as the threshold of habitat similarity was increased from 95 to 99 %. Protected areas, particularly the Calakmul Biosphere Reserve, include a small proportion (between 8 and 18 %, depending on the species, predictor variables and similarity threshold) of the species' potential distribution. Climate change scenarios predict a slight increase in the extent of similar habitat for both species in 2020, particularly in the south-central portion of the peninsula. Less than 20 % of the extent of potential distribution under current and climate change scenarios lies within protected areas. For both species, the largest extent with similarity values >97 % lies in the northeastern Yucatan peninsula, an area with little protection, subject to high pressures for development and that could become less hospitable for both primate species under a climate change scenario.

Introduction

Almost half of the primate species of the world are threatened (IUCN 2012). For most of these species the main threat to their survival is habitat loss and degradation (Schipper et al. 2008). The Atelidae family in particular (which includes howler, spider and woolly monkeys) is one of the primate families with the highest proportion of threatened species (Schipper et al. 2008). The Mexican portion of the Yucatan peninsula, with a surface of around 140,000 km^2, is home to two species of atelidae species: black howler monkeys (*Alouatta pigra*) and black-handed spider monkeys (*Ateles geoffroyi*). This region is important for biodiversity conservation both because of its relatively large portions of well-preserved forest and for the relatively fast rates of deforestation in recent decades (Mas et al. 2004). Together with the more threatened areas in the Gulf of Mexico, the Yucatan peninsula is part of the northernmost distribution of Neotropical primates. Howler and spider monkeys are particularly vulnerable to habitat loss and degradation, as they tend to occur in low numbers, have low fecundity rates, rely on patchy food resources such as ripe fruit and young leaves and, in the case of spider monkeys, have relatively large home ranges (Lovejoy et al. 1986; Difiore and Campbell 2007; Ramos-Fernandez and Wallace 2008).

The distribution of a species is a fundamental piece of information for conservation planners. The design of conservation strategies, including the creation of protected areas and the management of non-protected habitats, should ideally be based on accurate knowledge about the location and extent of those areas that would ensure long-term persistence of conservation targets, be they species, populations, or highly diverse ecosystems (Margules and Pressey 2000; Margules and Sarkar 2007). However, even in the case of conspicuous species, such as diurnal primates, some regions where they occur are clearly understudied, as is the case

Fig. 32.1 A female and infant *Ateles geoffroyi* search for water in a cement *olla* in an unprotected fragment. Photo by Gabriel Ramos-Fernandez

of the Yucatan peninsula (Estrada et al. 2006). Moreover, climate change is modifying species distributions in ways that conservation strategies must consider if they are to be successful (Walther et al. 2002) (Fig. 32.1). In the face of urgent decisions and actions, species distribution models (SDM) are an increasingly common tool used to infer the potential distribution of a species (Guisan and Thuiller 2005). SDMs can also be used to generate hypothetical species distributions under different scenarios of future climate change (e.g., Peterson et al. 2002; Williams et al. 2003).

Here we use DOMAIN, a correlative type of SDM (sensu Soberon and Peterson 2005), to develop habitat similarity maps for howler and spider monkeys living in the Yucatan peninsula. As inputs for the model we use the results of a relatively recent (2000–2002) survey performed using the same methodology in 78 locations throughout the region (Serio-Silva et al. 2006). We predict the current distribution using two versions of the model: one with biophysical variables as predictors and another with the results of a separate SDM on the potential distribution of important food plants as predictors. The first version of the model assumes that, by whichever mechanism, the presence of monkeys is affected by biophysical variables, while the second version assumes that biophysical variables affect the presence of trees that are important for the monkeys, and these in turn affect the presence of monkeys. The latter assumption is supported by studies demonstrating the relationship between plants and primates (Milton 1981; Robins and Hohmann 2006) and the dependence of primate distribution on fruit productivity (Kay et al. 1997). Also, we compare the potential distribution before and after a climate change scenario, using only biophysical variables as predictors.

Materials and Methods

Survey Location Data

We modeled the potential distribution of howler and spider monkeys using the results of a survey carried out between January 2000 and April 2002 in the three states of the Mexican portion of the Yucatan peninsula (Fig. 32.2; Serio-Silva et al. 2006). Briefly, experienced observers walked along transects for a total length of 716 km in 78 different sites, which were selected on the basis of historical records of the presence of primates, current vegetation maps and protected status of various locations. Observers recorded information about the sex/age composition of the group and its location. 66 out of the 78 surveyed locations contained either species: 25 contained both howler and spider monkeys, 24 contained only howlers and 15 contained only spiders (Fig. 32.2).

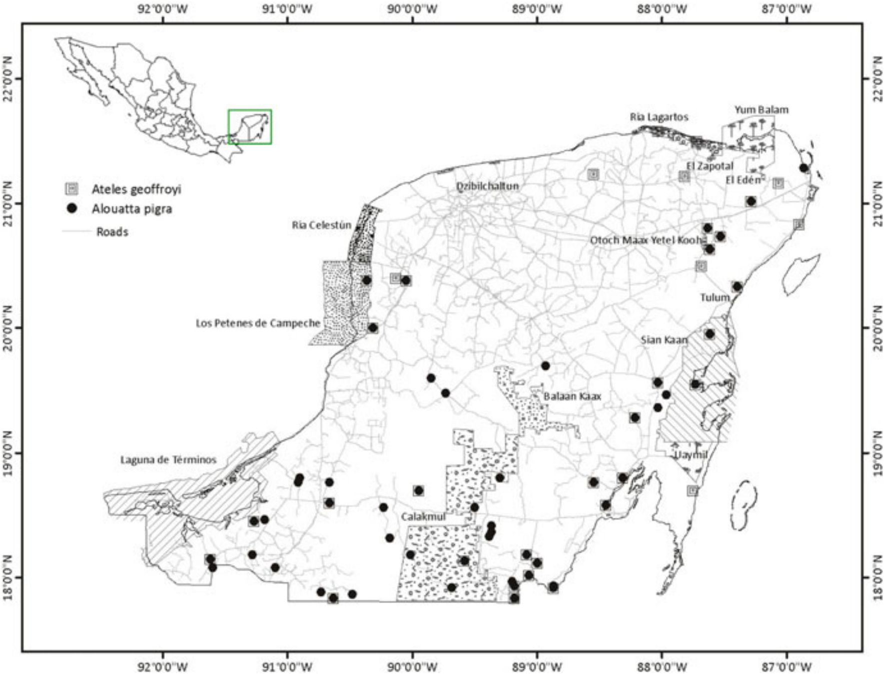

Fig. 32.2 Map of the study region, showing its location within Mexico (*insert*), roads and protected areas (*textured polygons*). Locations used as inputs for modeling the potential distribution are shown in *dark circles* (*Alouatta pigra*) and *empty squares* (*Ateles geoffroyi*)

Modeling the Potential Distribution

We modeled the potential distribution of the two species using DOMAIN (Carpenter et al. 1993), which estimates the similarity between the attributes of those locations where the species was observed and the areas where it could potentially occur. We ran two versions of the model, which differed in the type of predictor variable used by DOMAIN to estimate the similarity. In the first one, the predictor variables were biophysical variables and in the second, the predictor variables were the results of a separate DOMAIN modeling exercise of the potential distribution of the most important food plants in both primate species' diets as a predictor. In other words, the second model used the potential distribution of important tree species as the predictor for the presence of primates.

Biophysical Variables as Predictors

We divided the study area with a grid of 5×5 km cells. In the first modeling strategy, we used eight different biophysical variables as predictors, assigning their values to each of the 3,038 cells. Four of these variables were related to the monthly variation in precipitation and were obtained by analyzing ombrothermic climatic diagrams (temperature and precipitation across time) from 48 climatological stations throughout the Yucatan peninsula (Orellana et al. 2002). These variables were *water surplus* (total amount of rain exceeding 100 mm during the year); *humid condition* (amount of rain below 100 mm during the rainy season which maintains the soil close to permanent humidity); *water deficit* (amount of rain below the humid condition insufficient to maintain humidity in soil); and *mid-summer drought* (the period with the most pronounced water deficit). In addition, four more variables related to other biophysical features of the environment: *geomorphological characteristics* (Garcia-Gil et al. 2004); *soil types* (Garcia-Contreras et al. 2004a); *potential vegetation* (Garcia-Contreras et al. 2004b); and *soil humidity* (SPP 1986). All source maps from which we extracted the values of biophysical variables were at a 1:250,000 scale, with the exception of the map of soil humidity, which was at a 1:1,000,000 scale.

Potential Distribution of Food Tree Species as Predictor

In the second modeling strategy, we used the potential distribution of important food plants in both primate species' diet as a predictor of the potential distribution of the primates themselves. We identified important food plants from published work (spider monkeys: 10 species (Ramos-Fernández and Ayala-Orozco 2003); howlers: 14 species (Pozo-Montuy and Serio-Silva 2006; Rivera and Calmé 2006; Stoner and Gonzalez Di Piero 2005). Using location data from the CICY Herbarium database (which contains over 65,000 records of vascular plants from the region) we generated potential distributions of each of these food trees (Fig. 32.3), using the

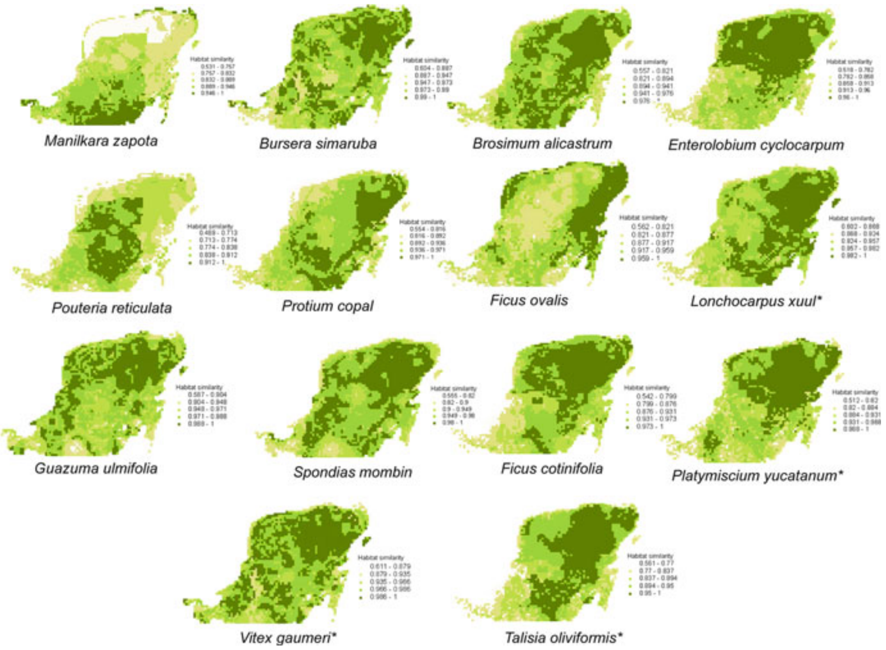

Fig. 32.3 Potential distribution of plant species important in the diet of howler and spider monkeys. Different similarity values are shown in different colors. Species with an *asterisk* were only used as important food items for *Alouatta pigra*. All others are important in the diet of both species

same biophysical variables listed above. Each of the 3,038 cells in the area thus acquired the similarity values of each of the important food plants for each species (10 values per node in the case of spider monkeys, 14 in the case of howlers). Then, we used the similarity values of these potential distributions as predictors of the potential distribution of primates.

Calculating Similarity Indices

In both models, we superimposed the survey location data on the cell grid, using the computer program Idrisi Kilimanjaro (Eastman 2004). This yielded a multidimensional matrix that contained, in each cell, the survey location data and the values of the predictor variables. We then applied the DOMAIN algorithm to calculate a similarity value for each cell, which essentially consists of the reciprocal of the distance between the predictor values at a given cell and those at the nearest known location site. In other words, the higher the resemblance between a given cell's predictor variables and those in a known location site, the higher the similarity value for that cell. Then, we chose three threshold similarity values (95, 97, and 99 %) to define the potential distribution. Locations with similarity values above the threshold are those where the predictor variables did not vary over more than the variation above the threshold (in this case, 5, 3, and 1 %, respectively). It is important to note that the potential distribution thus defined does not consist of probability of presence values (e.g., where the species would have a chance to occur), but of sites where there is a given level of confidence that the predictor variables will be similar to where the species was observed (Carpenter et al. 1993). Hereafter, similar habitat will be defined as the areas with similarity values higher than the specified threshold in each case.

Analysis of Protected Status and Vegetation Types Within the Potential Distribution

To calculate the extent of the potential distribution of each species under protected status, we superimposed the resulting potential distribution under each of the predictor variables and similarity thresholds on a map of the federal and state protected areas in the Yucatan peninsula (CONANP 2007). Similarly, we used a map of current vegetation (Garcia-Contreras et al. 2004b) to calculate the vegetation cover within the potential distribution of each species.

Modeling the Potential Distribution Under a Climate Change Scenario

We modeled the potential distribution under a climate change scenario using only biophysical variables. We generated two potential distributions for each primate species: one under the actual 1961–1991 climate conditions and another under an assumption of climate change occurring by the year 2020. We created the 1961–1991 baseline scenarios with data from 48 climatological stations throughout the peninsula for the period 1961–1991 (Orellana et al. 2009). We analyzed these data to obtain the following climate variables: rainfall/temperature index of Lang, aridity index, mean annual temperature, total annual precipitation and percentage of winter precipitation. Our climate change scenario for the year 2020 was based on the HADCM3B21 version of the HADLEY general circulation model, which assumes moderate increases in emissions (Solomon et al. 2007). This is the model that predicts the largest increase in mean temperature for the Yucatan peninsula, between 1 and 2 °C from 1961 to 1991 to 2020 (Orellana et al. 2009). The predicted increase in mean temperature is more pronounced in the southwestern portion of the region and less pronounced, although significant, for the northeastern portion. This model also predicts large annual precipitation deficits for most of the region, between −200 and −600 mm, with the only exception of the northeastern tip which would either remain with the same annual precipitation or increase by 100 mm (Orellana et al. 2009). We estimated the climate variables of this scenario using the same approach as for the baseline scenario.

Results

Using biophysical variables as predictors and a 95 % habitat similarity threshold, the potential distribution of both species comprises a large proportion of the study region (80 and 78 % for howlers and spider monkeys, respectively; Fig. 32.4), with the exception of northern areas close to the coast (which seem less suitable for howlers) and the drier regions in the center and south-central Yucatan peninsula (which seem less suitable for spider monkeys). Under a more stringent definition (97 % habitat similarity threshold), the potential distribution of both species is shifted to the eastern and southern portions of the peninsula (53 and 52 % for howlers and spider monkeys, respectively). Finally, under the most stringent definition of habitat similarity (99 %), only 19 and 18 % appears as similar for howlers and spider monkeys, respectively. Using this threshold, the largest continuous area

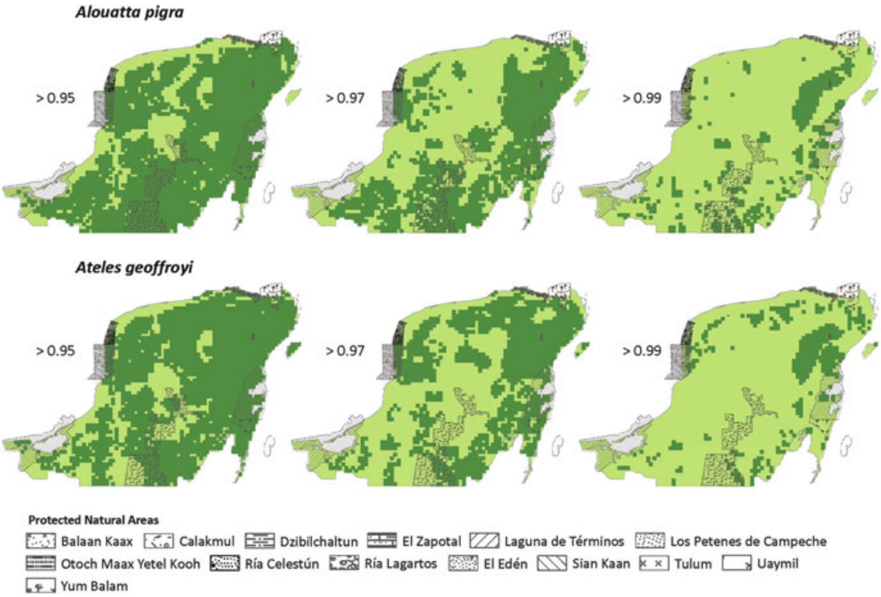

Fig. 32.4 Potential distribution of both primate species, using biophysical variables as predictors. Shown in dark green are the resulting distributions under three different similarity thresholds: 95, 97, and 99 %. *Shaded areas* correspond to the protected areas shown in Fig. 32.2

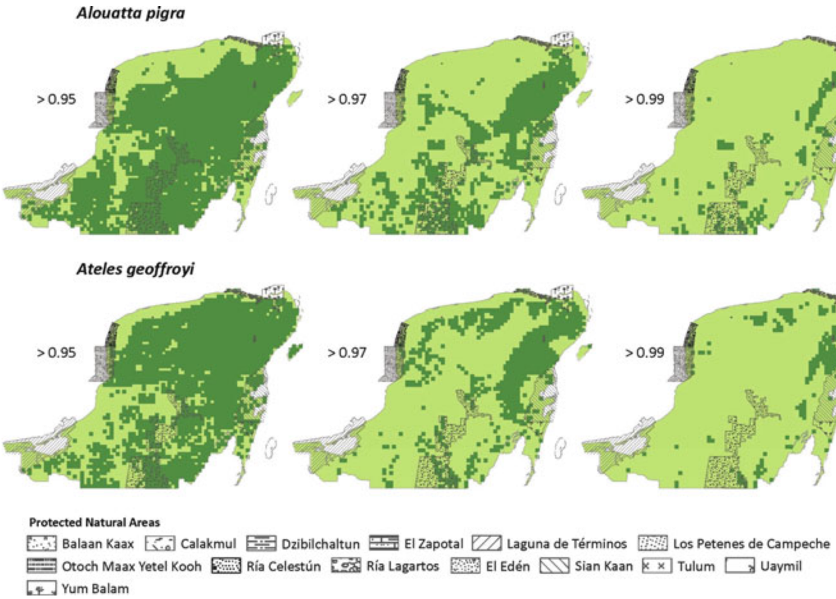

Fig. 32.5 Potential distribution of both primate species, using the similarity values of the potential distribution of important food plants (Fig. 32.3) as predictors. Shown in dark green are the resulting distributions under three different similarity thresholds: 95, 97, and 99 %. *Shaded areas* correspond to the protected areas shown in Fig. 32.2

of similar habitat for both species appears in the northeastern portion of the peninsula. It is noteworthy that, under any threshold of habitat similarity, the south-center portion of the peninsula seems less suitable for spider monkeys than for howlers, while the reverse is true for the north-center portion of the region.

Figure 32.5 shows the potential distribution obtained using the similarity values in the potential distribution of both species' most important food trees as predictors. Overall, this model version yields smaller areas for the potential distribution of both species. Under the most stringent definition of habitat similarity (99 %), only 11 and 10 % of the study area seems similar for howlers and spider monkeys, respectively. Under both the 97 and 99 % thresholds, the northeastern portion of the peninsula shows the largest portions of highly suitable habitat, particularly for spider monkeys.

Superimposing the potential distributions shown in Figs. 32.4 and 32.5 with a map of current vegetation (Fig. 32.6), it can be seen that similar habitat includes a greater proportion of relatively well conserved, semievergreen forest, but agricultural/human use and secondary vegetation also constitute a large proportion of the potential distribution of both species, regardless of the predictor variables or the threshold used to define habitat similarity. In all cases, despite the large reduction of the total area of potential distribution when increasing the similarity threshold, the

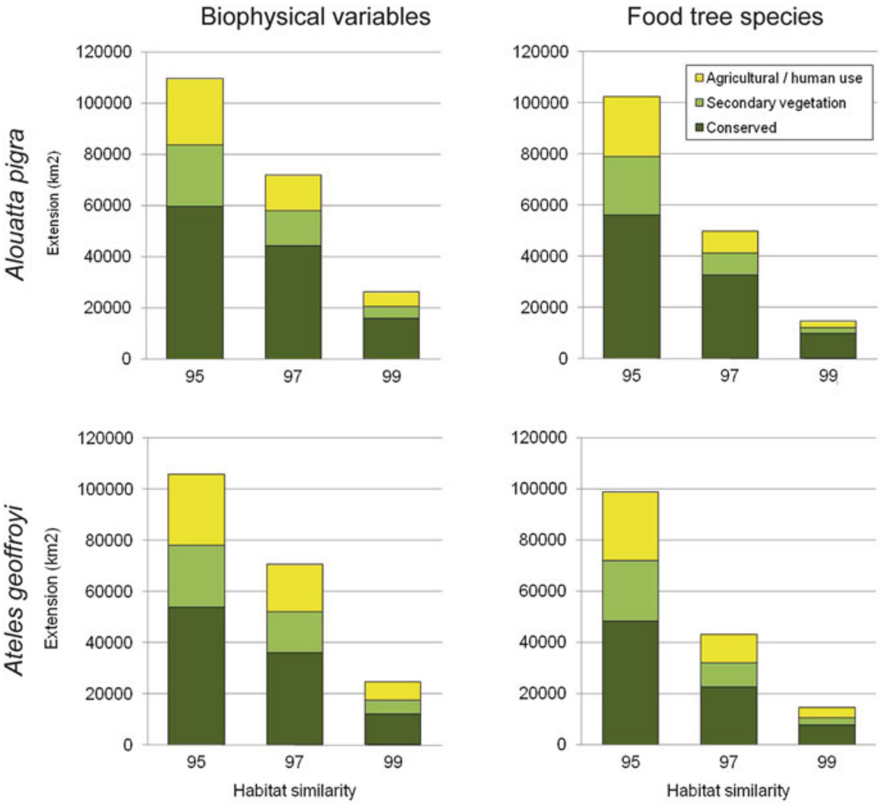

Fig. 32.6 Total extent (in km^2) and vegetation types in the potential distribution of both primate species, using both modeling strategies

proportion of conserved forest increases. The increase is even larger in the case of using the potential distribution of food tree species as predictors (Fig. 32.6).

Table 32.1 shows the proportion of each potential distribution area that falls in unprotected land or within state or federal protected areas (CONANP 2007). Between 81 and 92 % of the area in the potential distributions is unprotected, depending on the primate species and the version of the model. The Calakmul and Sian Ka'an Biosphere reserves, in the south center and southeastern portions of the peninsula, respectively, account for the largest percentages of the potential distribution, with Balan Ka'ax, Los Petenes, and Uaymil (Fig. 32.2) protecting around 1 % of the potential distribution of both species. All other protected areas include less than 1 % of the potential distribution of each primate species in each of the modeling versions, and together comprise no more than 4 % of the potential distribution.

Table 32.1 Total extension and proportion of the potential distribution in different protection status, for different primate species, modeling strategies and similarity thresholds

Habitat similarity	95 %	97 %	99 %
Alouatta pigra, biophysical variables			
Total extension (km^2)	109,693.33	72,052.11	26,372.52
Unprotected	86.0	83.8	81.7
Calakmul	6.6	8.5	10.4
Sian ka'an	3.2	4.5	6.1
Los petenes	–	1.3	1.0
Others <1 %	4.2	1.9	0.7
Ateles geoffroyi, biophysical variables			
Total extension (km^2)	105,962.56	70,842.93	24,740.12
Unprotected	88.7	88.6	89.2
Calakmul	4.0	3.3	3.5
Sian ka'an	3.2	4.1	4.0
Los petenes	–	1.4	1.9
Uaymil	–	1.1	–
Others <1 %	4.1	1.4	1.4
Alouatta pigra, food tree species			
Total extension (km^2)	102,524.62	49,797.54	14,786.66
Unprotected	87.7	85.4	80.8
Calakmul	6.8	9.2	14.1
Sian ka'an	2.7	3.0	3.6
Balan ka'an	1.2	1.2	–
Los petenes	–	–	1.1
Others <1 %	2.0	1.1	0.3
Ateles geoffroyi, food tree species			
Total extension (km^2)	98,920.22	43,046.52	14,524.65
Unprotected	89.6	88.7	91.8
Calakmul	4.8	5.6	3.4
Sian ka'an	2.4	2.4	1.8
Los petenes	–	–	1.4
Others <1 %	3.3	3.3	1.6

Regarding the predicted effects of climate change on the potential distribution of both primate species, Fig. 32.7 shows the distributions predicted for the 1961–1991 baseline compared to the HADCM3B21 climate change scenario for the year 2020. As can be seen, climate change would shift the distribution of both species in a southwest direction, toward the warmer and drier areas. The total extent of similar habitat, however, would not change significantly after climate change in the case of howlers and, in the case of spider monkeys, would in fact be larger after climate change, particularly under the 95 and 97 % similarity thresholds (Fig. 32.8). It is noteworthy that the largest increases in the distribution of spider monkeys would occur in the south center portion of the region, an area that under the climate change scenario would become warmer and drier by the year 2020.

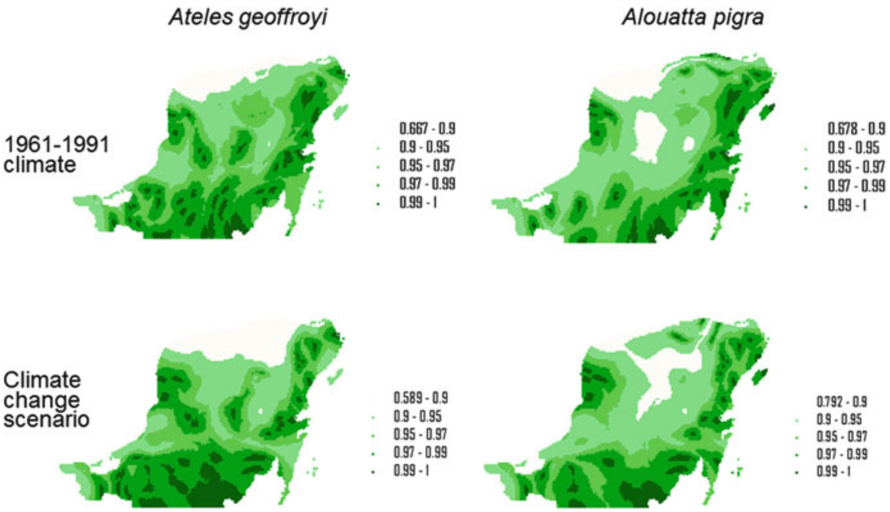

Fig. 32.7 Maps of the potential distribution of each primate species predicted for the 1961–1991 baseline compared to the HADCM3B21 climate change scenario for the year 2020. Shown are areas with different similarity values

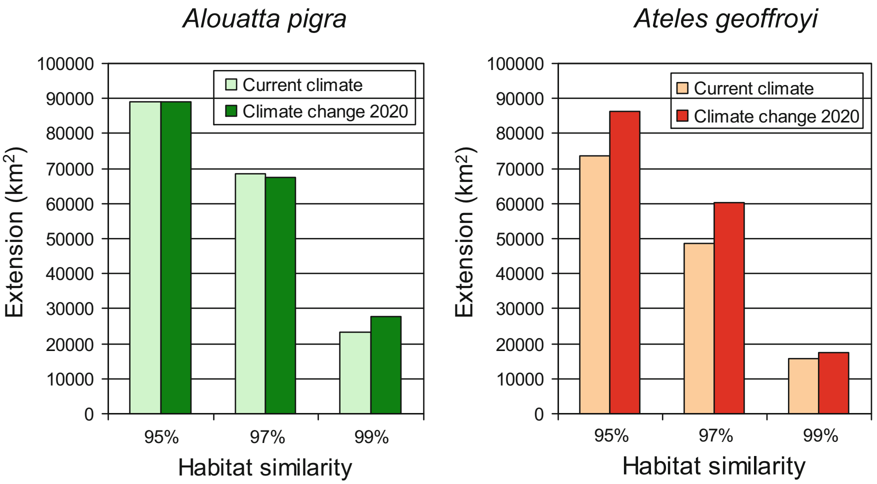

Fig. 32.8 Total extent (in km^2) of the potential distribution of each primate species predicted for the 1961–1991 baseline compared to the HADCM3B21 climate change scenario for the year 2020, for different similarity thresholds

Discussion

Species distribution models (SDMs) constitute a common method for inferring the distribution of a species of concern and use it as a basis to plan conservation action (Rodríguez et al. 2007). Given the urgency of conservation measures in many regions, and the lack of information on where a given species could successfully be preserved, it is likely that the use of potential distributions estimated through SDMs will be increasingly common. However, some authors have argued for a more careful and critical use of SDMs in conservation planning, based on several grounds (Guisan and Thuiller 2005; Loiselle et al. 2003). One important criticism to SDMs is that by focusing only on climatic variables as predictors, SDMs ignore biotic interactions and dispersal as determinants of a species' distribution (Davis et al. 1998); Pearson and Dawson 2003; Araújo and Luoto 2007). Another criticism of SDMs is the assumption that species distributions are in equilibrium with biotic and abiotic determinants (Pearson and Dawson 2003; Guisan and Thuiller 2005). This assumption is particularly problematic in correlative-type models based exclusively on historical or museum records, which may have been collected at a time when the species distribution was very different to its current distribution due, among other things, to anthropogenic disturbance occurring since then.

In this study, we made an explicit attempt to deal with the aforementioned criticisms. First, we used two strategies to model the potential distribution, one in which predictors consisted mostly abiotic factors as predictors (biophysical variables) and the other in which biotic factors were included as predictors (potential distribution of important food plants). Even though the distribution of food plants is in itself a prediction based on biophysical variables, by taking into account the similarity values for the most important food sources for both species of primates, we believe we are incorporating a crucial intervening variable between abiotic factors (which to a large extent determine the distribution of food trees) and the distribution of primates. Secondly, by using occurrence data from a recent survey that used the same methodology to detect presence of howler and spider monkeys, we have avoided the problem of the lack of correspondence of historical records with actual conditions. This allowed us to include current vegetation cover among the biophysical variables, because it can be assumed that the surveyed locations had the vegetation specified by the map. Had we used historical locations from collections, the current vegetation may not have been an accurate representation of the vegetation types at the time data were collected.

It is interesting to compare the results of both modeling strategies. While using food plants as predictors yielded smaller potential distribution areas than using biophysical variables, both strategies highlighted the same areas as important for each species (see below). The smaller extent of potential distribution when using food plants as predictors is also associated with an increase in the proportion of semievergreen forest as the threshold increases. This could be due to the fact that several of the food plant species used by both primate species are restricted to semievergreen forest in the Yucatan peninsula (Pennington and Sarukhan 2005). On the other hand, the coincidence of important areas of highly similar habitat predicted by both strategies could be a result of the fact that the two strategies are not completely independent: the potential distribution of plants was actually modeled with the same biophysical variables as those used as predictors in the first strategy.

There are important differences in the potential distribution of howler and spider monkeys. While the total extent of potential distribution predicted by model type and similarity threshold is similar, the location of similar habitat is not. The south-central Yucatan peninsula seems to be more important for howler monkeys than for spider monkeys, while the northeastern portion of the peninsula seems to be the most important region of the peninsula for both species, when potential distribution is defined with a 97 of 99 % similarity threshold. The importance of the south central portion of the peninsula for howler monkeys is evident from the results of the survey itself (Fig. 32.2). Most of the locations where howler monkeys were observed without spider monkeys are concentrated in this portion of the peninsula. Thus, the model is finding similar habitat to these locations for howlers, but not for spider monkeys. Additionally, the diet of howler monkeys includes the two species that are potentially distributed in the south-central, more than in the northeastern, portion of the peninsula (*Manilkara zapota* and *Pouteria reticulata*, Fig. 32.3), while spider monkeys' diet only includes the first of the two species.

Climate change, modeled here assuming a moderate increase in carbon dioxide emissions over the next 7 years, would not alter the extent of similar habitat in the potential distribution of howler and spider monkeys. However, the location of similar habitat would be modified by climate change. Both primate species would find more similar habitat in the south-central portion of the Yucatan peninsula, while the northeastern portion, found to be especially important for spider monkeys in the absence of climate change, would not remain as suitable after climate change.

Which similarity threshold should one consider as the most appropriate definition of potential habitat for these primate species? Our similarity indices are an indication of "habitat suitability," which is not a binary variable but rather a continuous representation of the similarity between observed and potential habitat in a given location. As Carpenter et al. (1993) pointed out, DOMAIN does not produce areas with probability of presence values, but degrees of confidence that the predictor variables are similar between the locations with known presence and the rest of the area. Also, because DOMAIN is a presence-only method, its performance cannot be evaluated using the standard procedures which evaluate the success of the predicted distributions by comparing frequencies of presence/absence in the observed and predicted locations (Liu et al. 2005). Therefore, the decision on which threshold to consider as an accurate prediction of the distribution of a species is, in the end, a question of interpretation (Soberon and Peterson 2005).

If these results are to be useful for conservation, one must consider that conservation planning is a perfect example of a post-normal scientific problem (Ravetz 1999): stakes are high, uncertainty is high, and a diversity of values are confronted. Precisely because the decisions on what and how to conserve will more often than not be taken by nonscientists with different backgrounds and worldviews, it is necessary for scientists to spell out the uncertainties inherent in their own results

(Berkes 2004). In the case of this study, recommendations for conserving primate habitat in the Yucatan peninsula must consider the different thresholds used to infer the species' potential distribution *as degrees of uncertainty* about how similar the predictor variables are between the observed and the potential locations. Therefore, one could say that from a species conservation standpoint, the 99 % threshold distributions are giving the most similar habitat and therefore highlighting those areas which would be the most important for conserving primates in the region; but from an ecosystem conservation perspective, the 95 % of 97 % threshold distributions can be used to justify the protection of area which may include suitable habitat for monkeys, provided that the confidence level with which is being assumed is explicitly considered.

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Chapter 33
Conservation Challenges Facing Two Threatened Endemic Titi Monkeys in a Naturally Fragmented Bolivian Forest

Robert B. Wallace, Jesus Martinez, Heidy Lopez-Strauss, Julia Barreta, Ariel Reinaga, and Lesly Lopez

Abstract The south-western Beni forest–grassland mosaic in central western Bolivia, a natural fragmented forest area, is home to two Bolivian primate endemics: the Beni titi monkey (*Callicebus modestus*) and the Olalla brothers titi monkey (*Callicebus olallae*). Despite extremely low sample sizes ($n=1$ and $n=2$, respectively), these species have been consistently recognized in taxonomic reviews of the genus since their discovery and description in the late 1930s; however, no new field data was available until 2002. In this chapter, we present a summary of our efforts to: describe the distributional limits of both species, determine their phenotypical characteristics in the field, conduct preliminary analyses of genetic differences between the two species, estimate population densities, describe the composition and structure of the naturally fragmented forest habitats where they occur, and document the behavioral ecology of both species. We also report the threats facing

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these two range restricted endemics through informal questionnaires with local actors and deforestation studies. Additionally, we detail efforts to conserve these species to date, such as local outreach campaigns, coordination with national government offices, and assistance to local municipalities for inclusion of these species requirements in municipal development plans and their prominence in the justification for the creation of a Municipal Protected Area in the Santa Rosa municipality. Finally, we identify priority conservation actions for the future.

Introduction

In 2002, the Wildlife Conservation Society "rediscovered" Bolivia's two endemic primate species, the Beni titi monkey (*Callicebus modestus*) and Olalla's titi monkey (*C. olallae*) (Felton et al. 2006), for whom no field data existed following their original collections in 1937 and 1938 (Lönnberg 1939). Subsequently, we have concentrated research efforts on determining the distribution of these range restricted primate endemics (Felton et al. 2006; Martinez and Wallace 2007), determining their genetic diversity (Barreta 2007), and taxonomic status (Martinez and Wallace 2007), assessing their conservation status (Mercado and Wallace 2010; Veiga et al. 2008a, b), estimating their natural abundance (López-Strauss 2008; López-Strauss and Wallace, submitted), describing their basic ecology (Arnez 2012; López 2011; Martinez and Carvajal, unpublished data; Martinez and Lopez, unpublished data), and assessing the threat of forest destruction, fire, and increased forest fragmentation in the southwestern Beni Department (Reinaga et al. unpublished data). In this paper we summarize results to date and assess the overall conservation challenges facing these threatened and endemic titi monkeys in a naturally fragmented Bolivian rainforest.

Synopsis of Biological Information

Field observations of phenotypic traits (Felton et al. 2006; López 2011; López-Strauss 2008; Martinez and Carvajal, unpublished data; Martinez and Lopez, unpublished data; Martinez and Wallace 2007) support historical taxonomic reviews (Hershkovitz 1990; Kobayashi 1995; van Roosmalen et al. 2002) that have consistently maintained a species status for both endemics (Figs. 33.1 and 33.2).

Genetic information on six loci derived from collected scats of wild *C. modestus* and *C. olallae*, and blood samples from one captive specimen of *C. donacophilus* clearly demonstrate that both *C. modestus* and *C. olallae* differ significantly from the allopatric *C. donacophilus*. Parameters of genetic differentiation between *C. modestus* and *C. olallae* are sufficiently large ($F_{ST}=0.12$) to warrant distinct subspecies status (Barreta 2007) although falling just short of the rule of thumb ($F_{ST}=0.15$) for automatic genetic qualification for species status. However, when considered in combination with distributional and phenotypic data, as well as

Fig. 33.1 Beni titi monkey (*Callicebus modestus*), Photograph: Mileniusz Spanowicz/WCS

Fig. 33.2 Olalla brothers titi monkey (*Callicebus olallae*), Photograph: Jesus Martinez/WCS

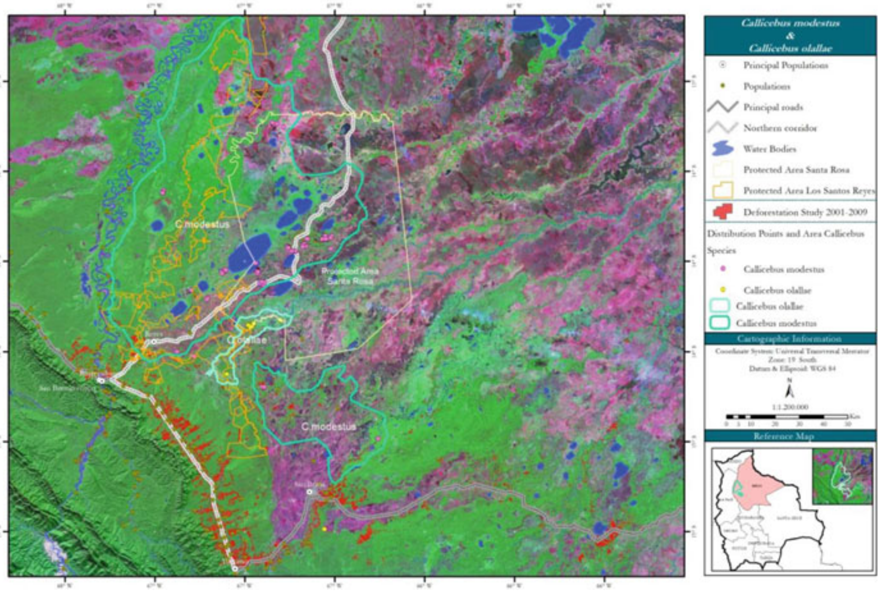

Fig. 33.3 Distribution of *Callicebus modestus* and *C. olallae* and deforestation pattern in southwestern Beni Department

incorporating a conservation perspective that tends to consider the phylogenetic concept of species definition, we continue to recommend full species status for *C. modestus* and *C. olallae*.

Callicebus olallae and *C. modestus* were originally described from one and two specimens respectively, and each known from one location separated by just 65 km (Lönnberg 1939). Subsequent field efforts have broadened the distributional knowledge for both species (Felton et al. 2006; Martinez and Wallace 2007, 2013; WCS, unpublished data) with *C. modestus* distribution defined by the Beni River in the west, the Maniqui River in the east, the beginning of the Andean piedmont forest in the south, and the beginning of true Amazonian forest near the Candado community in the north (Martinez and Wallace 2007, 2013) covering a total area of approximately 8,966.4 km^2 (Fig. 33.3).

Callicebus olallae has an even smaller overall distribution of 267.4 km^2 occupying riverine forests and associated forest along the Yacuma River between the headwaters of the Yacuma river and the area near Santa Rosa del Yacuma itself (Martinez and Wallace 2007; Fig. 33.3). One additional and isolated record exists for *C. olallae* along the Maniqui River to the east although this requires further confirmation, especially because of observed heavy hunting pressure in this area.

For both species the total areas reported above are significant overestimates of the potential distributions for two reasons. Firstly, the natural savanna-forest complex in which they occur means that forest habitat is only a percentage of the overall polygons detailed above: approximately 41.7 % in the case of *C. modestus* and 36.6 % in the case of *C. olallae* (WCS, unpublished data). Secondly, distributional surveys have revealed that titi monkey distribution is far from ubiquitous within the forested portion of the landscape (Felton et al. 2006; Martinez and Wallace 2007, 2013; WCS, unpublished data). Current studies are focusing on a finer-scale analysis of forest cover and vegetation type as well as predictive models of distribution using field information on presence, confirmed absence and probable absence of both species (WCS, unpublished data).

In the dry season of 2006, the abundance of both species was estimated using an adapted point count methodology for primate vocalizations (López-Strauss 2008; López-Strauss and Wallace, submitted). Seven selected locations were sampled for each endemic species, and distances to detected vocalizations were measured over four sample days at each location. Results revealed that minimum density estimates on the basis of observed and verified groups were 2.91 groups/km^2 (SD ± 2.2) for *C. olallae* and 2.65 groups/km^2 (SD ± 2.06) for *C. modestus*. Estimates on the basis of all groups detected through vocalizations were approximately double the minimum densities: 5.94 groups/km^2 (SD ± 3.50) for *C. olallae* and 4.93 groups/km^2 (SD ± 4.58) for *C. modestus* (López-Strauss 2008). Average observed group size is 2 individuals (SD ± 1.06) for *C. olallae* and 2.64 (SD ± 1.19) for *C. modestus* (López-Strauss 2008). Groups for both species generally consist of monogamous pairs, pairs and their offspring from 1 or 2 years, or solitary individuals (López-Strauss 2008; Martinez and Wallace 2007).

Finally, between 2007 and 2008, we conducted a behavioral ecology study on two groups of *C. olallae* (López 2011; Martinez et al. unpublished data), and between 2010 and 2011, we conducted a similar study on two groups of *C. modestus* (Arnez 2012; Martinez et al. unpublished data). Preliminary analyses have provided important management information for both species. For *C. olallae* observations of terrestrial movements of 5–40 m between patches of forest in the natural fragmented forest (Martinez and Wallace 2011) as well abandoning territories in direct response to fire (Martinez and Wallace, unpublished data) have important implications in terms of interpreting forest fragmentation and associated threats from the perspective of these monkeys. There are also observations of *C. olallae* fleeing in the presence of other primate species including *Aotus azarae*, *Sapajus apella* and *Saimiri boliviensis*, suggesting that interspecific competition may also be an important limiting factor for this species.

Preliminary analyses of dietary information demonstrate that *C. olallae* is frugivorous–folivorous, only incidentally insectivorous, with the diet shifting from fruit to leaves as a function of fruit availability in the forest (Martinez et al. unpublished data). Mampuesto (*Tabebuia nodosa*) was the most consumed species including leaves, flowers, and fruits. Other species such as a liana (*Machaerium* sp.) and the bibosillo (*Coccoloba* sp.) provided significant annual percentages of observed fruit consumption.

Observations of terrestrial movements were also registered for *C. modestus* during movements in their territory, as was fleeing behavior in the presence of *Sapajus apella*, though not *Aotus azarae*. Observed diet to date suggests that *C. modestus* is slightly more frugivorous than *C. olallae*, possibly due to a greater overall fruit availability at the study site including motacù (*Attalea phalerata*) and tutumilla (*Coussarea hydrangeaefolia*). Folivory is also important for this species, and insectivory of grasshoppers, caterpillars, stick insects, ants, and termites has also been observed markedly more frequently than for *C. olallae* (Arnez 2012; Martinez et al. unpublished data).

Summary of Threats and Human Activities

Bolivia is the 28th largest country in the world, but has a small population (80th in the world), and as a result has an extremely low national population density (216th in the world). As such, Bolivia has large tracts of intact wilderness in good conservation condition as demonstrated in a national conservation status evaluation (WCS, unpublished data). The conservation status of the southwestern Beni Department in this national evaluation is generally considered between good and moderate. Specific information regarding human activities and threats in the distribution area identify cattle ranching and associated fires and deforestation as the major threats (WCS, unpublished data), and observations during research in the area have verified this assessment (Felton et al. 2006; Martinez and Wallace 2007, 2011, 2013).

More recently, a specific analysis of deforestation within the distribution of both *Callicebus* endemics (Reinaga et al. unpublished data) revealed that for *C. modestus* deforestation rates between 2001 and 2005 were 0.71 %; whereas, between 2005 and 2009 there was actually a process of forest growth (0.27 %) resulting in an overall annual forest loss of 0.17 % between 2001 and 2009 representing 28.6 km^2 or 1.49 % of the maximum distribution (forest cover within known distribution = 1,914.7 km^2) for this endemic primate. This is well below the national average for the period 2000–2010 (0.5 % annual loss); however, it is important that forest regeneration between 2005 and 2009 does not necessarily signify an increase in habitat for *C. modestus*, at least not in the short term.

Due to the extremely restricted distribution of *C. olallae* the situation is even more dramatic with annual deforestation rates between 2001 and 2005 at 0.11 % increasing markedly to 0.67 % between 2005 and 2009 for an overall annual rate of 0.39 % between 2001 and 2009 representing 3.15 km^2 or 3.1 % of the maximum theoretical distribution in 2001 (forest cover within known distribution = 101.7 km^2) for this endemic primate. This is also below the national average for the period 2000–2010.

Conservation Opportunities, Priority Actions, and Future Challenges

In 2007, the Santa Rosa del Yacuma municipal government declared the creation of the Pampas del Yacuma Municipal Reserve, the largest municipal reserve in Bolivia covering 616,453 ha. Similarly in 2008, the neighboring Reyes municipality also created the Los Santos Reyes Municipal Reserve covering 505,591 ha.

These reserves do not have the same protection status as national protected areas; for example, land tenure is not largely in favor of the protected area. In addition, the large size of the Municipal Reserves has resulted in major management and administration challenges for the municipalities. Nevertheless, the two municipal reserves do cover the vast majority of the known distribution areas of both *Callicebus* endemics and as such represent a huge opportunity for their conservation.

Only Santa Rosa del Yacuma municipality has any kind of presence in the reserve, largely because the Yacuma River is a major ecotourism location with more than 15,000 tourists a year. Neither municipal reserve has a management plan to date. A priority action for the next five years will be to develop management plans in a participative manner with local stakeholders that include specific considerations for the endemic primates and their habitat. Given that much of the area within the reserves overlaps with existing cattle ranches, a key local stakeholder group will be the cattle ranching community. Encouraging them to retain forest patches within their ranch management schemes and manage pasture fires accordingly and/or switch to alternative pasture improvement techniques represents a major conservation action priority.

An imminent and game-changing infrastructure development project—el Corredor del Norte or Northern Corridor road improvement—is another huge challenge for the forests of southwestern Beni. In 2011, the road paving process was already underway for the adjacent Yucumo–Rurrenabaque section and the consultation process has begun for the Rurrenabaque–Santa Rosa del Yacuma section that bisects the distribution of both species (Fig. 33.3). The paving of this road is expected to increase pressures on remaining adjacent forests including forest loss due to colonization, agroforestry, and cattle ranching, all well-known phenomena observed at sites across the Amazon (Fleck et al. 2006, 2007).

Only elegant mitigation actions specifically designed for the Corredor del Norte will avoid significant habitat loss for both endemic species, a potentially catastrophic outcome for the extremely range-restricted *Callicebus olallae*. As such researchers and conservationists must work with the Bolivian national road authority (Autoridad Boliviana de Carreteras) to develop specific recommendations to reduce the risk of deforestation related to potential expansions in colonization, slash and burn agriculture, and intensified livestock production.

In the meantime, conservationists have prioritized local and national outreach campaigns regarding the existence of the virtually unknown *Callicebus modestus* and *C. olallae*, their endangered and endemic status, and ecology and habitat requirements. To date, at a national level this has consisted in a series of newspaper articles and the production of posters for each species as well as informing the scientific and environmental community in professional settings. At a local level, preliminary outreach activities included distribution of the aforementioned posters, as well as meetings with local communities, ranchers and schoolchildren to provide basic information on the habitat needs of these range-restricted endemics (Fig. 33.4). These local outreach activities have been intensified by a group of outstanding young Bolivian conservationists who are focused on raising local awareness about the endemic primates (Carvajal et al. unpublished).

Fig. 33.4 Conservation outreach activities for *Callicebus modestus* and *C. olallae* at a primary school in southwestern Beni Department, Photograph: Jesus Martinez/WCS

Conclusion

In 2002, the very existence of Bolivia's two endemic primates was in question. A decade later and both phenotypically distinct and apparently valid species are now exponentially better off in terms of available information, and even more encouragingly, local people in the Santa Rosa and Reyes municipalities are now aware and proud of their existence. This change has been achieved with a total investment of less than $150,000. The challenge of how to manage this naturally fragmented tropical forest–savanna landscape in the face of forthcoming threats will require more significant investment in the future, but the data summarized here will hopefully ensure that the conservation requirements of these endangered titi monkeys are appropriately considered therein.

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Chapter 34

Primates in Fragments 10 Years Later: Once and Future Goals

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Introduction

In 2010, the Food and Agriculture Organization of the United Nations (FAO) estimated that 16 million hectares of forest per year were lost globally in the 1990s (FAO 2010), and approximately 12.5 million hectares/year were lost in countries with primate populations, an area just smaller than Greece or the US State of Mississippi (Chapman and Peres 2001; Chapman and Gogarten 2012). In contrast, in the last decade (2000–2010), the rate of deforestation has decreased globally by approximately 5.2 million hectares/year, and reforestation and natural expansion of forests in some countries significantly reduced the net loss of forest (FAO 2010). This may be in part due to the lack of resonance in satellite imagery between secondary and primary forest regions, particularly in the tropics. Unfortunately, the increase in forested lands has principally affected temperate regions of Europe and eastern Asia (e.g., China, Japan), but deforestation of most tropical forests has continued steadily (e.g., annual loss: 0.5 % in Africa, 1.2 % in Mesoamerica, 0.5 % in South America, 0.4 % in southeastern Asia; FAO 2011).

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Of course, whenever sweeping calculations of loss or gain are reported, it is worth a note of caution in responding to the results. Puyravaud (2003) cited: “Deforestation is a non-homogeneous process and it is of interest to focus on the worst affected area in order to understand and predict its dynamics and correlate it to socio-economic trends at different scales (Lambing 1994). At the local level, the annual rate of change can be much higher than the global average because of the unprotected status of the forest, or due to economic or legal reasons (Ramesh et al. 1997).” An increasing number of primate populations are located in isolated forest fragments, and for some species these fragment-dwelling populations are the only

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ones that remain. Thus, the need to understand the effects of forest fragmentation on primates is still paramount.

Since the publication of the original *Primates in Fragments* book, we have the unique opportunity to reflect on what has been accomplished in the last decade. In 2003, Marsh and her colleagues ended the final chapter by discussing what they perceived as future research needs in the field to facilitate conservation decisions regarding the value of forest fragments to primates. They arrived at five topics: (1) disease, (2) regional comparisons (scale), (3) fragment size, (4) genetic studies, and (5) climate change (Marsh et al. 2003). In response, this volume includes chapters on all of these issues, bringing a considerable amount of clarity to the fate of primates in fragments.

Progress on Previous Research Priorities

Disease

Work in Africa (Chap. 7), Central America (Chap. 30), Southeast Asia (Lane et al. 2011), and Madagascar (Wright et al. 2009) have all demonstrated that anthropological changes in fragmented landscapes can be associated with increased disease levels in primates, which are thought to result in greater mortality. Fragmentation can also increase disease transmission between nonhuman primates and humans, posing a serious threat to wildlife conservation and human health. For example, Goldberg et al. (2008) found that humans living near forest fragments harbored *Escherichia coli* bacteria that were on average 75 % more similar to bacteria from primates in those fragments than to bacteria from primates in nearby undisturbed forests. Likewise, habitat degradation in forest fragments has been related to increases in stress in primates (usually assessed by fecal glucocorticoids), which can have a negative effect on immune function (Chaps. 7 and 30, Sapolsky 2002). A dramatic example of this is cortisol levels in red colobus (*Procolobus rufomitratus*) in forest fragments. They are so elevated that the lowest level recorded in the fragments is higher than the highest level documented in continuous forest (Chapman et al. 2006a, b, 2007). Dunn et al. (in press) suggest that an increase in daily travel time, which is related to increased folivory in primates in fragments, is the most important factor predicting cortisol levels in howler monkeys (*Alouatta palliata*). This highlights the potential conservation significance of studies showing that habitat loss and fragmentation can increase travel time in primates (e.g., Donati et al. 2011; Dunn et al. 2009, 2010; Gonzalez-Zamora et al. 2011; Hardus et al. 2012). However, for most primate species, the proximate causes of increases in stress remain to be identified. We know of several studies currently in progress or that have been published recently that directly examine disease issues in fragments and are trying to identify the causal factors of elevated levels of stress and disease (D. Gabriel unpublished data, Irwin et al. unpublished data, R. Ghai unpublished data, Hodder and Chapman 2012).

Hunting and habitat loss are major drivers of extinction in primates, and ecotourism and academic research projects have been widely promoted as a means of providing alternative value for primates and their habitats (e.g., Butinski and Kalina 1998). However, several diseases, including viruses, bacteria, and whole parasites have been shown to move from humans to wild primates during such projects (e.g., Köndgen et al. 2008) raising concerns that disease transmission risks might outweigh benefits.

Regional Comparisons

Landscape Ecology has emerged as an important intellectual field that can play a central role in conservation, and we have seen clear advances in the last decade considering scale. Chapter 2 by Arroyo-Rodríguez and colleagues clearly illustrates the importance of considering fragmentation as a landscape level process. However, this chapter also quantifies that there is still a great deal of work to be done in this area, as all reviewed fragmentation studies ($n = 100$ studies) were at the fragment scale, which means that extrapolations to the landscape scale were not possible. In fact, 25 % of the 100 studies did not describe the amount or configuration of the surrounding habitat nor the matrix, and hence, these studies cannot test the impact of processes operating at the landscape scale (e.g., neighboring effects, source-sink dynamics, landscape supplementation, landscape complementation; Dunning et al. 1992; Arroyo-Rodríguez and Mandujano 2009). Considering scale issues with respect to how conservation plans are made (i.e., at species distribution, regional, national levels), we do not see great progress, as management or action plans are typically operationalized at the national level (Chaps. 4 and 22). Generally, this is not a problem as whenever a primate species is endangered at a national level, small-scale action is advocated by the nation in question. However, this does point to the need for international NGOs and agencies such as the United Nations (as illustrated in the work by GRASP—http://www.un-grasp.org/) (Nelleman et al. 2010; Wich et al. 2011) to play a larger role, so that conservation dollars can be used in the most effective way.

Fragment Size

A great deal of research has been done on how fragment size influences the probability of primate survival both in the short- and long-term (Chaps. 3, 5 and 7). Although Arroyo-Rodríguez and his colleagues (Chap. 2) found that most fragmentation studies with primates are focused on assessing the effect of fragment size on primates, the effects of fragment size on populations and species can strongly vary among landscapes with different configuration (Pardini et al. 2010); and hence, the effects of fragment size on primates needs to be assessed in landscapes with different spatial configuration before we will likely be able to produce clear generalizations (Chap. 2). In this sense, despite over a decade of research at many sites (e.g., Chap. 6), large gaps in our knowledge exist (Chap. 4). We are still largely unable to state beforehand which species are more threatened in forest fragments, which was a conclusion drawn 10 years ago as well (Marsh et al. 2003). For example, blue monkeys (*Cercopithecus mitis*) are found in forest fragments throughout East and South Africa (Lawes et al. 2000) and near Budongo Forest Reserve, Uganda. Yet while they are found near Kibale National Park, Uganda, they never occur in any forest fragment, irrespective of fragment size (Onderdonk and Chapman 2000). Understanding the root causes of such issues is a challenge where the key point is time since isolation relative to the generation time of the study species in question. If we want to understand this (which species will disappear first?), we need multiple fragments that have been isolated for considerable periods of time. For primates these datasets are simply few and far between (but see Chap. 5). The way forward is for primatologists to start learning from other zoological fields where we have more species with shorter generation times.

Genetic Studies

Genetic methods have advanced significantly in the last 10 years, and research using these methods has contributed a great deal to our understanding of the consequences of breaking apart populations in forest fragments (Chap. 25). Since many primate species living in fragmented landscapes are endangered, one of the most important methodological advances has been discovering and perfecting tools to noninvasively extract DNA from feces, urine, hair, and saliva (Goossens et al. 2003). In general, habitat fragmentation reduces connectivity between forest-dwelling primate populations, decreasing gene flow among small populations, which can result in decreased genetic variability (Bergl et al. 2008). And while we surmise that this decrease reduces the ability of the population to respond to change, be that climate change or further anthropogenic change, it can be confounded by the additive, amplified effects of fragmentation per se (Ewers and Didham 2005). Populations' isolation can also lead to increased inbreeding and reduce reproductive success, which increases the chances that the population in the fragment will die out. Goosens et al. (2006) were the first to show that genetic data can be used to detect and quantify the effect of human-induced deforestation and habitat fragmentation on an endangered species after the demographic collapse of the orangutan population in North Eastern Borneo.

The increasing interest in genetic approaches to study fragmentation is illustrated by the number of authors using these methods in the current volume (six) as compared to the 2003 book (only one). There are studies in this volume that use genetic approaches to examine issues of reduced genetic variability and population health (de la Torre et al., deVleeschower and Raboy), hybridization and species status (Dias et al., Wallace et al.), dispersal and relatedness of individuals in fragments (Oklander and Corach), and to discover the origin of populations (Glenn and Benson). However, in general these studies assess the impact of population isolation on primate genetic profiles at local scales, without evaluating (nor controlling) the impact of the landscape spatial context (e.g., landscape forest cover, number of forest fragments, edge density, matrix permeability). This limits our ability to predict future scenarios for alternative management practices: an important challenge in conservation biology and land management (c.f., Feinsinger 2001).

Climate Change

There is mounting data available at both the academic and policy level for the effect that climate change has on biodiversity (Hannah et al. 2002; Lovett et al. 2005a, b; McClean et al. 2005). Some estimates suggest that in this century the climate could warm by up to 5.8 °C (IPPC 2001). Already, there have been numerous documented cases of shifts in the distribution, population abundance, life history, and even survival of species in response to climate change (Pounds et al. 1999; Hannah et al. 2002; Parmesan and Yohe 2003; Malcolm et al. 2006). With primate populations increasingly isolated in protected areas, or in forest fragments surrounded by agricultural land that often supports high human densities, the loss of habitat as the climate changes is of obvious concern as they have nowhere to disperse to (Dunbar 1998; Cowlishaw and Dunbar 2000; Chapman et al. 2006a; Gonzalez-Zamora et al. 2011). As well as direct effects of climate change on primate populations, individuals or groups may be affected by either the loss of particular plant species or changes in the phenological cycles of plant communities. Through a series of modelling exercises, McClean et al. (2005) studied the impact of projected climate change on the distribution of 5,197 African plant species. For 97 % of these species, areas of suitable climate were projected to decrease in size and/or the species would shift location, many to high altitudes, and 25–41 % of species would lose all their area by 2085.

Ramos-Fernandez and colleagues (Chap. 32) modeled the distribution of spider (*Ateles geoffroyi*) and howler (*Alouatta pigra*) monkeys under a current and projected climate change scenario for the year 2020 for the Yucatan peninsula in Mexico. The model suggests that climate change will lead to a slight increase in the extent of similar habitat for both species, but less than 20 % of the extent of potential distribution under current and climate change scenarios lies within protected areas. These models can provide important guidelines to predict what will happen and what must be planned for; however, they are based on sets of assumptions that are largely untested. For example, the models use either biophysical variables or the potential distribution of the most important food plants currently in use by the primates in question. As we have seen both for spider and howler monkeys (Silver and Marsh 2003; Bicca-Marques 2003; Ramos-Fernandez and Ayala-Oozco 2003; González-Zamora et al. 2009; 2011), and several other taxa (Chaps. 14, 17 and 20) primates can adjust to novel habitats, thus potentially confounding even our best modelling assumptions. What we can glean for conservation purposes is a fact mentioned repeatedly throughout this volume: that primates outside of protected areas are at risk for numerous reasons, climate change being only one of them. But even protected areas that house primates might be impacted by climate change, and that is a much broader challenge.

There are suggestions from Kibale National Park that climate change may have affected some fruiting tree pollinators, a variable that is difficult to consider (Chapman et al. 2005). The Kibale region receives approximately 300 mm more rainfall/annum than it did at the start of the century, droughts are less frequent, the onset of the rainy season is earlier, and the average maximum monthly temperature is 3.5 °C hotter than it was 25 years ago. Using a phenology data set that extends almost continuously from the 1970s to the present, Chapman and colleagues (2005) documented changes in fruiting patterns that they speculated were caused by declines in the pollinator populations. For example, *Pouteria altissima* and *Parinari excelsa* exhibited a relatively regular pattern of fruiting during the 1970s; however, they rarely have fruited since the 1990s (Chapman et al. 2005). It is possible that changes in fruiting patterns are responsible for progressive declines in some primate species (e.g., *Cercopithecus mitis*: Chapman et al. 2010; Lwanga et al. 2011), but this speculation requires further study.

Finally, changes in land use, forest loss and fragmentation, and elevated atmospheric CO_2, all of which are implicated in climate change, have been shown to be associated with large-scale structural changes in tropical forests. The most apparent of these may be the increase in the abundance and biomass of lianas (Schnitzer and Bongers 2011). Lianas are thought to be important fallback foods for many primate species (Dunn et al. 2012; Onderdonk and Chapman 2000; Marshall et al. 2009) and play an important role in primate ecology, including niche partitioning, home range use, reproductive behavior, ranging behavior and grouping patterns (Arroyo-Rodriguez et al. 2013). However, as the structure of tropical forests continues to be modified by climate change, it will be crucial to understand the responses of primates to their changing habitats.

Fragmentation Science and the Future

By examining primates in fragments on a global scale it has become evident that fundamental information is needed to construct informed plans for the adequate management and conservation of primate populations in fragmented landscapes. In other words, we still cannot predict how a primate community would respond to an upcoming anthropogenic change or what the most important variables are for determining long-term survival in a fragmented landscape (Arroyo-Rodríguez and Mandujano 2006, 2009; Chap. 2). To start to rectify this knowledge gap, we would like to end this volume by discussing two important issues: (1) how scientific thought has shifted in the last decade; and (2) what we see as research priorities for the next decade and beyond.

Changing Trends

Ways of thinking about primate research has shifted in the last decade, moving in a direction favoring research on primates in fragments (see Fig. 2.1). In the early studies of primate behavioral ecology, there was an emphasis placed on studying primates in their native environment often with the goal of understanding the selective pressures that shaped their social organization. For example, in John Terborgh's (1983) classic book, *Five New World Primates*, he spent a considerable amount of text explaining how remote the study site was. In 2012, tourists can fly to Puerto Maldonado from Lima or Cusco, drive 10 minutes, to a launch site at Tambopata River Port, and take a speedboat for 2.5 hours until they reach the comfortable lodge at Tambopata Reserve (Go2Peru.com). In part precisely because there is greater ease for reaching remote sites, and that continuous sites are becoming ever more encroached upon, we can clearly see a shift more inclusive of research in disturbed habitats.

This is reflected when comparing the two volumes of *Primates in Fragments*. In the current volume, there are chapters dealing with primates in villages (Carretero-Pinzon), large cities (Gordo), around Buddhist temples (Aggimarangsee), and other sacred sites (Cameron and Gould). There are now a number of studies in Central America that are focusing on highly modified landscapes, such as those that demonstrate that howler monkeys walk along barbed wire, forage In isolated trees, sleep in living fencerows, or use or use introduced *Eucalyptus* plantations (Asensio et al. 2009; Serio-Silva et al. 2006; Bonilla-Sanchez et al. 2012; Chap. 8). And while we certainly touched on some of those topics in the first volume, it is clear that they are now dominating the discussion.

There is a growing tendency for empiricists and theoreticians to work together often leading to modelling the real world, which has facilitated greater understanding and thus drives primatology to be more predictive. Chapman et al. (Chap. 7) demonstrated that metapopulation models may not be of value in dynamic landscapes, where extinction of fragmented populations corresponds to fragment disappearances. But predictive models can contribute to the way we approach conservation on the front end before further damage is levied on already disturbed primate populations. Models rarely used in primate conservation work, such as Agent-Based Simulations would allow for capturing all of the "moving parts" in a fragmented ecosystem, including the human elements, in a way that would describe layered details often not reported in our field. Our continued dialog about modelling may be one of the best avenues we have on the path to making real impacts in maintaining fragmented primate populations.

Lastly, there is a growing appreciation of the value of long-term research at field sites (Chap. 6, Kappeler and Watts 2012). It is now very clear that addressing many of the most important questions in behavior, ecology, and evolution requires data that extends over decades (Clutton-Brock and Sheldon 2010). Primates were some of the first animal species where individuals were followed over a significant period of their lifetimes, and this contributed a great deal to understanding the selective advantages of different behavioral and life-history strategies. In the study of fragmentation, we need projects that will clearly illustrate the long-term fate of the primate population, the habitat itself, and the shifts in human-created matrices.

In the last decade there has been an increasing realization that the taxonomic diversity within the Order Primates is significantly larger than ever thought. The number of recognized species has increased from some 230 in 1993 (Groves 1993), to close to 400 in 2005 (Groves 2005), and 480 in 2012 (Mittermeier and Wilson 2012). While some may see this as “taxonomic inflation” (Isaac et al. 2004), the reality is that, certainly from a management perspective, we have more primate species to deal with than ever before. Unfortunately for us as diurnal primates, many of the newly described species are nocturnal, including galagos in eastern Africa, slow and slender lorises in Asia, lemurs in Madagascar, and tarsiers in Southeast Asia (Mittermeier and Wilson 2012). While often even the most basic data are lacking it appears that many of these primates have exceedingly small geographic ranges (Nekaris 2012a, b). To the untrained eye many of the nocturnal species look similar being the primate equivalent of what is known amongst birders as “little brown jobs”; there is, however, no reason to assume these myriad of cryptic species respond in the same manner to anthropogenic pressures. Some may thrive while others may wither. Matching forest distribution maps with the known or inferred distribution ranges of these newly described nocturnal primates suggests that there is plenty of work to be done when it comes to understanding the impact of fragmentation on nocturnal primates.

Where Do We Go from Here?

We would like to end this chapter by outlining what we see as research priorities for the next decade with respect to primates in fragments.

Definition of Fragments

We have discussed the issues surrounding scale, fragment definitions for primate studies, and the need for a commonality in the terms we use in fragmentation science, but in a world of ever continuing deforestation, climate change, habitat modification, human population growth, and pollution it is worth stressing the need for our professional consensus. There is still a qualitative shift necessary in how primates perceive fragmentation (Arroyo-Rodríguez and Mandujano 2009): is everything fragmented? Is it truly a mix of fragmented habitat and continuous? Are there large tracts of continuous forest anywhere in primate habitat countries, and if so, by what definition? It is not only a matter of scale, it is a matter of definition of what it means to be *continuous* more than what it means to be *fragmented*. Definitions of this kind exist, but they have been modified to meet the shifting needs of habitat conversion into a human-dominated landscape (c.f., Chap. 1). What is important to

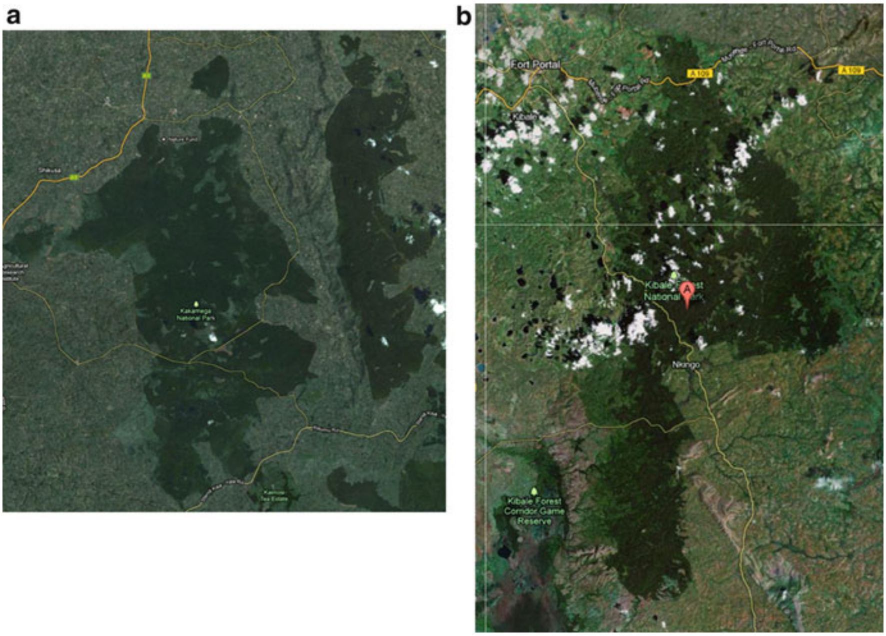

Fig. 34.1 Two national parks in East Africa: (**a**) Kakamega in Kenya and (**b**) Kibale in Uganda

us is a definition within primate science that is consistent no matter the kind of study, that is, whether it is a targeted “fragment” question or not.

We often find studies that compare fragmented habitat to “continuous” forest that lies within a reserve, national park, or other protected area. Similarly, we often find that primate studies on behavior, resource use, or a myriad of other questions are conducted within reserves that are considered “continuous,” but are not. We should think of fragmentation as “an unnatural detachment or separation of expansive tracts of suitable habitat into smaller patches, which are spatially segregated by a matrix of non-habitat areas” (Forman 1995; Farina 2007). Ultimately, questions regarding how large is a small patch will depend on the largest known habitat tract in which the species in question is found, and on the ecological, reproductive, and/or behavioral requirements of the species.

There are numerous examples of “continuous forests in a national park” (see Fig. 2.4b, Chap. 2), but two are illustrated here (Fig. 34.1). Now that satellite imagery is so readily available, it is more and more obvious that our perceptions of what we traditionally describe as continuous may need revision.

Landscape Scale

Studies of primates in fragments usually conclude that fragmentation negatively affects some aspect of their biology or ecology (Chap. 2). Nevertheless, the definition and quantification of fragmentation vary considerably among studies, resulting in contradictions and results that are difficult to interpret (Arroyo-Rodríguez and Mandujano 2009). It is important to consider that what happens at the fragment scale could be the consequence of processes that interact at various spatial and temporal scales. Fragmentation per se is a landscape scale process (Fahrig 2003), and hence, future fragmentation studies with primates should consider adopting a landscape approach, that is, using landscapes as the independent units of observation (McGarigal and Cushman 2002; Fahrig 2003). Because complete landscapes are very difficult to sample, the fragment-landscape approach (sensu McGarigal and Cushman 2002) can be used to assess the relative impact of both fragment (e.g., fragment size, isolation, shape) and landscape spatial attributes (e.g., number of fragments, forest cover, edge density, connectivity, matrix type) on primates. This approach implicates that fragments are the experimental units, but the independent variables include not only fragment metrics, but also spatial characteristics of the landscape within a specified "neighborhood" distance surrounding the fragment (i.e., within a buffer zone or landscape). With this experimental design and appropriate statistical models (c.f., Smith et al. 2009) we will be able to identify the spatial attributes (including fragmentation per se) with stronger influence on primates.

Taxonomy

Simply put, if you do not know what it is you cannot study it, compare it, or save it. Bortolus (2008) found that biology, ecology, biodiversity, genetics, and like disciplines, tend to disregard reporting the taxonomic pedigree of the species in question resulting in "a cascade of errors with negative consequences for the development of scientific knowledge, as well as for biodiversity and human welfare." He concluded that, "a single incorrect taxonomic identification has a great potential to be assimilated into many different biological and ecological studies and then in several environmental management studies and programs, multiplying its impact synergistically." He maintained that these kinds of errors are likely to have a variety of negative consequences, such as identifying population as homogeneous and monospecific when it is actually recognized as a complex assemblage with completely different geographic distribution patterns. At a minimum, cascading errors in taxonomy in our field are annoying and inaccurate, at worse they are impacting our ability to do good science, conserve species, or get funding (Marsh in press). When it comes to primates in fragments, the need is even greater for taxonomic clarity because we are frequently encroaching where scientists have never been, are working in difficult habitats like swamps or flooded forest, or are studying nocturnal species. Thus, the likelihood for finding new taxa or forms becomes greater the harder it is to study them.

We all need to do a better job in the reporting on nomenclature and taxonomy of primates. We follow Wagele et al. (2011) in proposing that "whenever a species name is used, the author(s) of the species hypothesis be included and the original literature source cited, including taxonomic revisions and identification literature, which is nothing more than what is done for every other hypothesis or assumption included in a scientific publication." Because it cannot be said enough, a reliable taxonomy is among the major factors guaranteeing the accurate identification of biodiversity hot spots, wilderness areas, endangered species, and areas of greatest concern, including fragments, that impact the entire Order (Marsh in press).

Evolution of Behavioral Flexibility

The study of primate responses to fragmentation is unfortunately still at the stage where we cannot make predictive statements about how different primate communities will respond to different scenarios of fragmentation. The example given earlier where blue monkeys are commonly in fragments across East and South Africa, but not near Kibale National Park is just one of many. A primary reason for the failure to predict responses is that the information is not currently available on which species or populations are sufficiently behaviourally flexible to shift diet, behavior, or social system to changing environmental conditions (Chapman and Rothman 2009). That said, considerable levels of behavioral flexibility have been documented. For example, redtail groups (*Cercopithecus ascanius*) within Kibale varied in the amount of time they spent foraging for leaves (13–35 %), fruit (36–60 %), and insects (15–31 %), and when comparing redtails in different regions, this variation increased (leaves 7–74 %, fruit 13–61 %, and insects 1–16 %) (Chapman et al. 2002; Chap. 15). Likewise, a summary of *Alouatta* species across the Neotropics by Bicca Marques (2003) showed this genus to be extremely flexible overall, with various species relying in some cases almost entirely on invasive or human introduced food species. So while examples exist for taxa that can almost have predictive qualities for survival in fragmented landscapes, there are always exceptions both ways (c.f., Arroyo-Rodríguez and Dias 2009; Cristobal-Azkarate and Dunn for fragment habitability by howlers in Los Tuxtlas, Chap. 6).

Primates in fragmented habitats are almost always surrounded, if not entirely, by human created matrices whether of small villages, timber, firewood, non-timber forest product extraction, cattle, mono-cultural cash crops and other mixed-crop farming or more intensive landscapes with cities, roads, hydroelectric dams, mining, or some combination of all of the above. Primates have been found to live within all of these systems and show some degree of habitat flexibility (c.f., virtually all chapters in this volume, but in particular: Chaps. 8, 11, 12, 15, 19, 20, 21, 22, 23, 31). Primate flexibility for resource use in fragments then, is in part due to their proximity and tolerance of humans, and ultimately, vice versa.

Estrada et al. (2012) reviewed the literature on primates in agroecosystems and found that 57 primate taxa used agroecosystems as temporary or permanent habitats, including 16 species from the Neotropics, 16 from South East Asia, 15 from Sub-Saharan Africa, and 10 from Madagascar. The degree of terrestriality in primates is likely a principal reason we see so much more overt crop-raiding behavior throughout Asia-Africa, but it may also be related to the kinds of crops available.

In Estrada et al. (2012) Table 1, they identified 38 different kinds of agroecosystems (although they missed chimpanzees, baboons, and others species in sugar cane, c.f., Reynolds et al. 2003). But of those identified, there were only 7 of 38 (18 %) overlapping between Old and New World tropics: shade coffee, shade cacao, cacao and *gliricidia*, eucalyptus, banana, oil palm, and mango. And of those, only three: eucalyptus, shade coffee, and cacao/*gliricidia*, were the closest in use between regions, the others did not even nearly compare. Of the overlapping crops, dominant use by Neotropical primates was cacao, and for Asia/Africa banana and oil palm. The authors point out that while use can include primates acting as crop-raiding pests, there are occasions when primates might benefit the farmers by acting as fertilizers, pollinators, seed dispersers, insect control, or tourist attractions (Estrada et al. 2012). In the Neotropics, primates may be successfully incorporated into the agroecosystem culture in ways that may benefit the primate's survival in fragmented habitats because on average, they cause less damage to crops. But it is a fine line where primates are perceived as pests to be hunted (either for food or control) or animals to be tolerated, if not actively conserved. There is a great need to study the primate's flexibility to use these systems for resources and the human ability to allow it.

While our understanding of issues has increased over the last 10 years, our ability to actually develop actions has not. We are not at the stage where it is possible to rigorously quantitatively determine which primate lineages are flexible in ways that facilitate them to respond to fragmentation and those lineages that are not. The main reason for this is that for most species or taxonomic groups we lack a robust number of comparable studies conducted across different spatial or temporal scales to get an understanding of which primates are flexible and positively respond to change, and which are not. Obtaining such an understanding will take us a long way toward predicting response to different scenarios of fragmentation and thus to the development of appropriate conservation plans.

Studying Disease Transmission Using Genetic Tools

There is a critical need for using genetic tools to determine if diseases are being transmitted between humans and nonhuman primates. In Marsh et al. (2003), we pointed out clear zoonotic transmissions, such as ebola, AIDS, and other pandemics between primates and humans, but greater detail is needed in terms of genetic inclusion. The value of genetic analysis to determine if interspecific disease transmission has occurred has been demonstrated by Gasser et al. (2009). They demonstrated that studies employing coproscopic analysis suggested that there was transmission of nodular worm (*Oesophagostomum* sp.) among nonhuman primates and humans, and thus that primates posed a health risk to people. In contrast, genetic analysis suggested that *O. bifurcum* in humans was genetically distinct from populations in nonhuman primates and that these primates did not pose a health risk to people (de Gruijter et al. 2004; Gasser et al. 2006). Similarly cross-species transmission of avian blood parasites has been confirmed by using both PCR (polymerase chain reaction), direct sequencing, and RAPD (random amplified polymorphic DNA) methods (Waldenström et al. 2002). Genetic methods have also been used to highlight the dangers of primate bushmeat infected with SIV and other diseases (e.g., Peeters et al. 2002).

Climate Change

Climate change was highlighted as a research priority in Marsh (2003) as well. We consider climate change is such a complex issue of which so little is understood that it should remain a research priority in the coming decades for primate science and, in particular, fragmentation science. There is no doubt that climatic change is affecting plant and animal populations around the globe in very apparent ways, such as the loss of geographic range (Dunbar 1998). Yet most changes are likely to be subtle and difficult to detect. For example, in the instance discussed above, primates were likely to be affected by the cessation of fruiting of some species of tropical trees, which the researchers speculated was due to the effect of climate change on pollinators (Chapman et al. 2005). For folivorous primates, one potential consequence of climate change is a decline in nutritional composition of leaves (Coley 1998). Greenhouse experiments have found that elevated CO_2 levels result in a 15–50 % reduction in leaf nitrogen, a 25–30 % increase in fiber (Staudt et al. 2001), and an increase in plant defense chemicals like phenolic compounds (Coley et al. 2002), including a 19 % increase in condensed tannins (Peltonen et al. 2005). All of these changes would be expected to negatively affect folivorous primates, but much more research must be done on the entire range of issues that climate change bears on primate populations (Rothman et al. Submitted).

Restoration of Plant and Animal Communities

For the smallest fragments and most isolated primate populations, managing the species in situ has been proposed (Marsh 2003). However, in general, for primate populations that only occur in fragments, conservation strategies often involve restoring the connectivity among fragments or enlarging the habitat to facilitate the growth of the population. These represent two contrasting management options, and to identify which is the most appropriate for designing successful primate conservation plans we first need to assess the relative impact that habitat loss and fragmentation per se may have on each primate species (Fahrig 1999). As effects and species characteristics can be additive in terms of their ability to remain in a fragmented landscape (Ewers and Didham 2005), often a “both-and” strategy is suitable. If species are more vulnerable to habitat loss, the increment in habitat amount should be the best management option, but if the species are negatively impacted by increasing fragmentation levels, the best management solution for this species/population should be the creation of vegetation corridors (Fahrig 1999).

While these and other suggestions were made 10 years ago in the first *Primates in Fragments* book, very little has been done to move toward a more direct "hands on" approach at this level of conservation effort. To accomplish any significant impact on the long-term survival of fragmented populations, the scientific community will need an in-depth understanding of methods for restoring plant and animal communities. Restoration of primate communities requires knowledge of the determinants of primate abundance (Feinsinger 2001); however, understanding and predicting factors that affect the abundance of particular species have proven extremely difficult (Chapman et al. 2010; Lwanga et al. 2011). Even so, Silver and Marsh (2003) demonstrated that reintroduction of howlers into a natural habitat that once carried them was successful.

Issues of connectivity were addressed by deVleeschower and Raboy (Chap. 19) where they inform that newer studies take into account the species perspective, since our concept of connectivity is not necessarily the same as the animals'. Lessons from throughout the tropics on living fences, hedgerows, crop borders, agroecosystems, and arboreal forest corridors suggest there are numerous, inexpensive low-tech means of increasing the arboreal surface area for primates (e.g., Asensio et al. 2009). But restoration is not simply creating connectivity or increasing food resources. Long-term viability calls for understanding the mechanisms for ecosystem health beyond primates and fragments that include basic systems, such as seed dispersal, seedling and sapling recruitment, pollination, and abiotic conditions (Marsh and Loiselle 2001). This kind of approach must be handled with the expertise of a larger conservation community involving landscape level ecologists, biologists (species specific experts depending on the region), botanists, soil scientists, local experts from the immediate area, and funding agencies. Restoration will be a useful path in the future of primate conservation, but is one that must take care to involve as many disciplines as possible to incur success.

Incorporating Primates into Humanized Landscapes

In Marsh et al. (2003), we had a separate section entitled, "Politics," to recognize the importance of dealing with the human dimensions associated with fragmentation, and the conservation of primates in humanized landscapes. In the last decade there has been an increased recognition that to address any conservation issue it is necessary to use tools and skills from a number of different disciplines. Ten years ago we stressed that working across disciplines was key, and particularly when it came to habitat areas without protection, it was mandatory. We continue to stress that alliance here: that biologists specializing on other taxonomic groups, social anthropologists, economists, and local and national leaders need to work with primate researchers to aid us in understanding the human element if progress in conserving primates in fragments is to be achieved. An example of the complexity of issues is the trend in declining human fertility rates and abandonment of rural land as a result of urbanization. If these continue, they will signal a globally significant transformation offering possible conservation opportunities in some regions. This kind of transformation is evident in a number of countries (FAO 2011; Aide et al. 2012), and projections suggest it may occur in the future in many developing nations (Wright and Muller-Landau 2006; Jacob et al. 2008). Such dramatic changes in the human dimension have powerful impacts on primate habitat conservation.

There is a relatively easy means by which academics can incorporate people into change that benefits conservation of primates in fragments. The first is through formal education in urban schools. Ten years ago, we supported education in source countries of rural community members, students, and teachers and numerous examples flood the literature of successes. And while, and while we still believe in both formal and informal education in rural regions, focusing on urban education is key. Of the world's most populated cities, 18 of the top 25 (72 %) are primate source countries, with New York (#19) and London (#21) further down the list (http://en.wikipedia.org/wiki/List_of_cities_proper_by_population). Over 50 % of the world's population lives in cities, and likely a huge majority have little understanding of forest dwelling animals. Educators in cities can often reach hundreds of students a year, and through lectures and lessons, can provide not only appreciation, but a solid basis for understanding the natural world. The impact of this is staggering, especially if we can convince our schools that courses in ecology, biodiversity, and conservation are mandatory. It is true that the majority of students will not become committed to conservation in countries harboring primates, but they do vote, they buy products, and they go on vacation—often to primate rich regions if they are not already from a source country. Educated students would have a better ability for understanding political issues of the day, in terms of how they might impact the environment in their nation, as well as the global environment which ultimately impacts primates. Nations in North America, Europe, and Asia are some of the most rabid consumers on the planet, but with mandatory environmental education, their choices for consumption can become less deleterious.

Further, we can support a growing field of Tropical Urban Ecology. An excellent example is Programa Macacos Urbanos in Porto Alegre, Brazil, where scientists and students work with local landowners in and around a major city to provide knowledge for incorporating wildlife, but especially primates, into urban parks. They also provide education to farmers and ranchers in the extended area on how best to manage their land in a way that aids primates. Where primates are subsumed within cities (Chap. 23), we are seeing action groups popping up to find creative solutions for their safety and long-term management. There are small projects like this all over the world, but the ideas are clear: primates and humans must find a way to co-exist.

Conclusions

It is apparent that there are great challenges ahead of the scientific community if we are to formulate effective conservation plans for primates living in fragments. We still have a great deal to do: we must integrate approaches across disciplines, develop effective predictive models of how species will respond to change, and we must understand how to effectively influence policy. In another decade's time, we hope to report that all of these needs have been met, and the challenges have been embraced to drive our knowledge of primates in fragments toward the broadening goal of never losing a single primate species to extinction.

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