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Landscapes of change: the ecology of white-faced capuchins over space and time

by

Fernando A. Campos

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Abstract

As global change accelerates, there is a growing imperative to understand how wild animals respond to changing environments. I investigated how environmental variability, both in the short term (seasonality and habitat differences) and the long term (changing climate and habitats), shapes the behavioral ecology of white-faced capuchins (*Cebus capucinus*) in a highly seasonal dry forest mosaic in Costa Rica. I used a multi-scale approach with the ultimate goal of gaining a more complete understanding of how individual-level selective pressures scale up over space and time to affect group and population dynamics.

Perceived predation risk, based on alarm-call responses to distinct predator classes, varied among habitat types and was greatest in mature forest. The capuchins adjusted their anti-predator vigilance behavior to changing levels of perceived risk. Feeding efficiency varied over both space and time and was greatest during the wet season and in mature forest habitats, which were both associated with higher energy intake rates and lower energy expenditure rates. The hot dry season also favored smaller home ranges, with high-use zones concentrated around patches of mature evergreen forest. These findings demonstrate that environmental variability plays a key role in driving the spatial ecology of capuchin individuals and groups. Because the dry season is associated with greater energetic deficits, the capuchins' increased preference for mature forest and more compact use of space during the dry season may be a behavioral adjustment aimed at maximizing use of the most productive foraging areas and reducing travel, perhaps at the expense of safety.

Finally, I examined spatial and demographic patterns in the growing capuchin population over multiple decades in relation to quantitative information on how the environment changed over the same period. The availability of evergreen habitats varied with the strength of the previous wet season, which in turn was strongly coupled with global climatic and oceanic cycles. Following extreme drought periods, population growth slowed, mean group size decreased, and reproductive rate declined. Future work will aim to develop a deeper understanding of how climate change will affect primate populations and to expand the scope and generality of this research to a global scale.

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Contents

ABSTRACT	ii
ACKNOWLEDGMENTS	iii
TABLE OF CONTENTS	v
LIST OF TABLES	ix
LIST OF FIGURES	x
I GENERAL INTRODUCTION	1
1.1 Theoretical framework	1
1.2 Research aims and questions	2
1.3 Significance	3
1.4 An introduction to the study system	4
1.4.1 Brief history of the site	4
1.4.2 Climate of Santa Rosa	5
1.4.3 Habitats in Santa Rosa	6
1.4.4 Study species and groups	9
1.4.5 Why SSR is an appropriate site for this study	10
1.5 Organization of the thesis	11
2 SPATIAL ECOLOGY OF PERCEIVED PREDATION RISK AND VIGILANCE BEHAVIOR IN WHITE-FACED CAPUCHINS	14
2.1 Introduction	14
2.2 Methods	17
2.2.1 Study site	17

2.2.2	Data collection	19
2.2.3	Data analysis	23
2.3	Results	26
2.3.1	Alarm-calling bouts and predator guilds	26
2.3.2	Perceived risk landscapes	27
2.3.3	Vigilance and predation risk	27
2.4	Discussion	30
2.4.1	Predator encounters and perceived danger	30
2.4.2	Spatial characteristics of alarms and risk zones	31
2.4.3	Is vigilance behavior predictive?	33
2.4.4	Implications and future directions	35
3	ENERGY RETURNS ON FORAGING IN WHITE-FACED CAPUCHINS, <i>Cebus capucinus</i>	38
3.1	Introduction	38
3.2	Methods	41
3.2.1	Study subjects and site	41
3.2.2	Data collection	41
3.2.3	Data analysis	44
3.3	Results	49
3.3.1	General observations	49
3.3.2	Energy expenditure rate	51
3.3.3	Energy intake rate	51
3.3.4	Net energy return	51
3.4	Discussion	53
3.4.1	Extrinsic effects on foraging energetics: season and habitat	53
3.4.2	Intrinsic influences on foraging energetics: sex and group mass	56
3.4.3	Implications	58
4	DRIVERS OF HOME RANGE CHARACTERISTICS ACROSS SPATIOTEMPORAL SCALES IN A NEOTROPICAL PRIMATE, <i>Cebus capucinus</i>	59
4.1	Introduction	59
4.1.1	Predictions	60
4.2	Methods	62
4.2.1	Study site	62
4.2.2	Study species and subjects	62

4.2.3	Data collection	64
4.2.4	Data analysis	66
4.3	Results	74
4.3.1	Home range size	74
4.3.2	Home range composition	77
4.4	Discussion	77
4.4.1	Determinants of home range size	77
4.4.2	Intensity of use and forest maturity	81
4.4.3	Implications for capuchin behavioural ecology and conservation	83
4.4.4	The importance of scale	84
5	A MULTI-DECADE INVESTIGATION OF PRIMATE POPULATION DYNAMICS: THE EFFECTS OF CLIMATIC OSCILLATIONS AND FOREST REGENERATION	86
5.1	Introduction	86
5.2	Materials and methods	89
5.2.1	Study system	89
5.2.2	Data collection	90
5.2.3	Data analysis	94
5.3	Results	98
5.3.1	Demographic trends	98
5.3.2	Climatic trends	98
5.3.3	Landscape trends	99
5.4	Discussion	101
5.4.1	Changes in capuchin population size and structure	101
5.4.2	Effects of variable climate	104
5.4.3	Changes in the availability of critical capuchin habitat	105
5.4.4	Drivers of spatial heterogeneity	107
5.4.5	Conservation and management implications	109
6	GENERAL DISCUSSION	111
6.1	Overview	111
6.2	Review and synthesis of key empirical results	112
6.2.1	Predation risk over space and time	112
6.2.2	Foraging efficiency over space and time	112
6.2.3	Home ranges over space and time	113

6.2.4	Population dynamics over space and time	114
6.3	Theory and policy implications	115
6.3.1	Implications for primate behavioral ecology	115
6.3.2	Implications for biological anthropology	115
6.3.3	Implications for conservation and restoration ecology	116
6.4	Unresolved questions, limitations, and directions for future research	117
6.4.1	A more synthetic approach to studying individual fitness landscapes	117
6.4.2	Applying resource selection analyses to understand space use patterns	117
6.4.3	A more quantitative approach to linking climate with population dynamics . .	118
6.5	Conclusion	119
REFERENCES		120
APPENDIX A SUPPLEMENT TO CHAPTER 3		149
A.1	Screening the movement data	149
A.2	Energy estimates for per-bite food items	150
A.3	Determination of energy expenditure for different activity states	151
APPENDIX B SUPPLEMENT TO CHAPTER 4		154
B.1	Justification for using the Biased Random Bridge (BRB) home range method	154
B.2	Parameterization of the BRB home range method	155
B.3	Calculation of the fruit availability index	156
APPENDIX C COPYRIGHT PERMISSION LETTERS		157

List of Tables

2.1	Candidate model set and model selection for the occurrence of vigilance behavior.	16
2.2	Variables obtained for each instantaneous scan during focal samples.	25
2.3	Pearson's chi-squared goodness-of-fit tests comparing observed and expected predator encounter frequencies among microhabitat categories.	33
3.1	Overview of variables used in the analysis of foraging energetics.	47
4.1	Data summary and group sizes.	62
4.2	Temporal scale definitions and biological interpretations.	65
4.3	Candidate model set and model selection for home range area.	73
4.4	Candidate model set and model selection for mean forest maturity index.	76
4.5	Summary of home range characteristics at four temporal scales.	78
4.6	Descriptive statistics of home range predictor variables.	80
4.7	Post-hoc tests for forest age as a function of usage intensity.	83
5.1	Landsat surface reflectance Climate Data Record products.	93
5.2	Class-level metrics of landscape spatial pattern.	97
5.3	Edge contrast matrix specifying the magnitude of contrast for edges between each pairwise combination of land cover classes.	99
5.4	Similarity matrix specifying the similarity values between each pairwise combination of land cover classes.	99

List of Figures

1.1	Location of the study site and groups.	2
1.2	Seasonal variationin temperature, relative humidity, and daily aggregate rainfall.	6
1.3	Examples of different habitat types in the study area.	8
1.4	Adult female and adult male <i>Cebus capucinus</i>	10
1.5	Precipitation seasonality over the entire geographic range of <i>Cebus capucinus</i>	11
1.6	Landscape features and distribution of habitat types in the primary study area.	13
2.1	Predator encounter densities and habitat use density used to construct the perceived risk maps.	15
2.2	Proportion of samples coded as vigilant for each focal animal.	18
2.3	Proportion of samples scored vigilant in different microhabitat categories.	21
2.4	Relationship between proportion of time vigilant and group size.	22
2.5	Number of encounters and number of participants for encounters with different predator guilds.	24
2.6	Observed and expected number of encounters in different vertical level and height categories categories.	28
2.7	Log-relative risk functions for each predator guild.	29
2.8	Risk zones plotted over a habitat map of the study area.	30
2.9	Coefficient plot for models of vigilance behavior.	32
2.10	Ecological characterization of risk zones for different predator guilds.	34
2.11	Observed and expected number of encounters in different habitat categories.	36
2.12	Number of alarm-calling bouts provoked by different species.	37
3.1	Concurrent changes in the energetic resource base and travel velocities.	43
3.2	Comparison of travel distances during focal samples among groups and sexes.	45
3.3	Activity budgets of males and females during the focal samples.	49

3.4	Temporal representation of female reproductive status during the study.	50
3.5	Model-averaged regression coefficients and relative variable importance for linear mixed models related to foraging energetics.	52
3.6	Seasonal comparisons of energy expenditure rate, energy intake rate, and net energy return.	54
3.7	Estimated fruit biomass of fruit trees visited during the study period in different habitats and seasons.	55
3.8	Relative differences in the use of specific body postures in early, intermediate, and mature forest habitats.	57
4.1	Habitat map with multiyear home ranges.	63
4.2	Illustration of the movement-based kernel method.	67
4.3	Data coverage for home range estimation.	68
4.4	Home range area, fruit biomass, and temperature.	70
4.5	Home range area at three spatial scales and four temporal scales.	71
4.6	Home range area at three spatial scales and four temporal scales.	74
4.7	Coefficient plot for models of home range area.	75
4.8	Coefficient plot for models of home range composition.	79
4.9	Coefficient plot for models of usage zone maturity.	81
4.10	NDVI-based forest maturity indices at different spatiotemporal scales.	84
5.1	Changes in habitat from 1985 to 2011.	88
5.2	Makeup of the capuchin population from 1983 to 2013.	90
5.3	Demographic trends in the capuchin population from 1983 to 2013.	92
5.4	Estimated number of animals in each of the six sub-regions of the park for each census year.	95
5.5	Population density in sub-regions of the park for each census year.	96
5.6	Yearly rainfall totals from 1979 to 2013.	100
5.7	Relationship between rainfall and Southern Oscillation Index.	101
5.8	Maps of NDVI-based vegetation evergreenness from Landsat images.	102
5.9	Time-series analysis of Southern Oscillation Index and monthly rainfall.	103
5.10	Relationship between MODIS NDVI values and total rainfall in the previous wet season.	104
5.11	Dry season MODIS NDVI profiles for weak vs. strong preceding wet seasons.	106
5.12	Trends in class-level landscape metrics from 1985 to 2011.	108

1

General introduction

1.1 THEORETICAL FRAMEWORK

Animal ecology is fundamentally concerned with space and time. Each interaction that an animal has with its environment happens at some particular place and time, and so to study why an animal behaves the way that it does is inherently to pose a spatiotemporal question: *why here and why now?* Of key importance for answering this question is heterogeneity in the animal's physical environment. Every animal has a specific set of essential requirements: food, water, shelter, and mates, as well as other biotic and abiotic factors that enable the animal to exploit these resources efficiently. However, because all natural landscapes vary over space and time, the task of finding these essential resources is a continuous challenge. Common sources of environmental variability can differ greatly in their scale and intensity, and may include the diurnal cycle, seasonality, macroclimatic patterns, climate change, topography, soils, vegetation structure, and exogenous disturbance. If they are to survive, animals must cope with these and other changes by making behavioral and physiological adjustments. One of the primary ways that animals deal with spatiotemporal variability in their environments is by moving (Holden, 2006; Nathan et al., 2008), and of particular interest is how animals use and distribute themselves relative to available habitat. "Habitat" is the set of resources and conditions that enables an organism to occupy a particular area (Hall et al., 1997); the term implies more than simply vege-

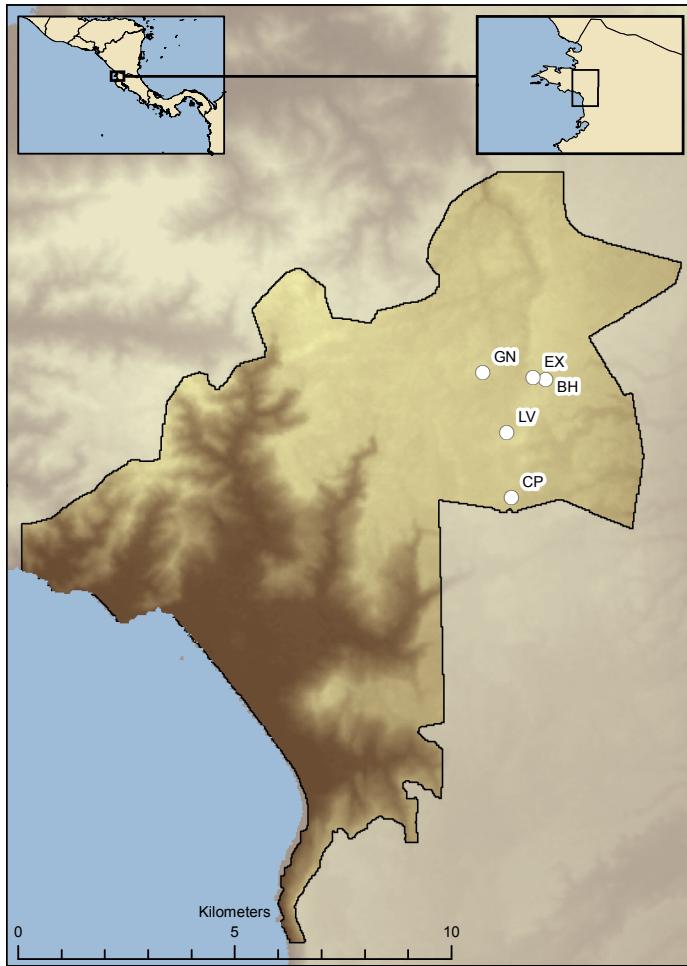


Figure 1.1: Location of the study site and groups. The region outlined in black is Sector Santa Rosa. The points show approximate centroids of each study group's home range during the study.

tation structure, although vegetation may be the key determinant of a particular area's resources from many animals' perspectives. Animals' movement patterns and differential use of habitats can provide important insights into the ecological and conservation value of different landscape elements as well as the animal's ability to persist under different disturbance scenarios. Therefore, a complete understanding of an animal's ecological role requires detecting and characterizing spatial patterns in the environment, determining why such patterns exist, measuring how the patterns change over time, and examining how the animal responds to the changing conditions.

1.2 RESEARCH AIMS AND QUESTIONS

The central aim of this thesis is to provide a comprehensive study of responses to environmental variability and ecosystem recovery in the white-faced capuchin (*Cebus capucinus*), a Neotropical pri-

mate, across a range of spatial and temporal scales. I collected behavioral data during 18 months of fieldwork in Sector Santa Rosa (SSR), a highly seasonal mosaic of regenerating tropical dry forest in northwestern Costa Rica (fig. 1.1). In this thesis, I combine my behavioral observations with long-term census and demographic data, satellite-based assessments of landscape spatial pattern, climate records, and botanical measurements to investigate several prominent questions about how primates cope with ecological change.

Research question 1: How does predation risk for individual *C. capucinus* vary with the spatial and temporal heterogeneity of the current landscape they inhabit, and what behavioral adjustments do they make to mitigate these risks?

Research question 2: What environmental and intrinsic factors are responsible for differences in foraging efficiency over space and time?

Research question 3: How do groups of *C. capucinus* adjust their use of space to meet the collective and individual challenges of growth, survival, and reproduction? What role does environmental variability play in mediating this response?

Research question 4: How do climate and land cover change in the study area since the park was established relate to concurrent patterns of *C. capucinus* population growth and demography, and what can we infer about ecological recovery processes from this study system?

1.3 SIGNIFICANCE

Primates' responses to environmental variability are vital issues for diverse scientific disciplines, including ecology, ethology, anthropology, and conservation. All environments are dynamic to some degree, but there is abundant evidence that the pace of environmental changes worldwide is accelerating due to the ramifications of human population growth (McKee et al., 2004) and human-induced climate change (Burrows et al., 2011; Loarie et al., 2009). These changes will pose a growing existential threat to many plants and animals (Sala et al., 2000), and nowhere are these challenges more acute than in Neotropical dry forests (Hansen et al., 2013). In the Neotropics as a whole, 66 % of the tropical dry forest biome has been already been cleared for cattle ranching and agricultural development (76 % has been converted in Costa Rica), and many forest remnants exist in small, disjunct fragments that are incapable of supporting high biodiversity in the long term (Portillo-Quintero and Sánchez-Azofeifa, 2010). Ecological restoration—the intentional or guided recovery of an ecosystem to something approaching its original state—provides a beacon of hope. Pioneering restoration

projects have demonstrated that Neotropical dry forest can be “regrown” naturally with minimal intervention (Janzen, 1987, 1988), but we can expect such recovery to affect species differently. To maximize its efficacy, ecological restoration must therefore be backed by sound knowledge of species-level recovery processes (Clewel and McDonald, 2009). Currently, there is virtually nothing known about the long-term dynamics of expanding primate populations in variable, mosaic habitats. This information is difficult to obtain because (1) primates are relatively rare and have long life-history patterns, and (2) the majority of natural primate populations are either stable or declining as their habitats become increasingly fragmented (Cowlishaw and Dunbar, 2000; Marsh, 2003; Mittermeier and Cheney, 1987).

Primates’ responses to environmental variability are also of key importance for understanding human origins. Current evidence suggests that environmental change and landscape heterogeneity were key components driving the evolution and diversification of early hominins (Kingston, 2007; Potts, 1996, 1998; Vrba, 1980, 1985). However, the spatiotemporal resolution of archeological and paleoenvironmental data is often too coarse to examine selective pressures acting at the local, individual level at which natural selection operates (Kingston, 2007). For example, the fitness landscapes associated with individual foraging strategies, ranging behaviors, daily activity patterns, and habitat and resource utilization depend critically on interactions between individuals and the particular biotic and abiotic elements of their local surroundings and can probably never be fully contextualized within a reconstructed ancient environment based on archeological data. One approach to dealing with these limitations is to use extant nonhuman primates as models (Whiten et al., 2010). In particular, the influence of landscape change and heterogeneity on the behavioral, demographic, and spatial characteristics of early hominin populations can be explored by studying the responses of nonhuman primates to seasonality, habitat heterogeneity, and environmental change (Brockman, 2005).

1.4 AN INTRODUCTION TO THE STUDY SYSTEM

1.4.1 BRIEF HISTORY OF THE SITE

The relevant history of heavy human disturbance at the study site begins in the late sixteenth century with the establishment of Hacienda Santa Rosa, one of the oldest and largest ranches in Costa Rica. Though its borders were imprecisely defined, the original ranch covered a vast area of around 100 000 ha that extended from the Pacific Ocean in the west across a broad coastal plateau covered by tropical dry forest and stretched eastward to the densely forested slopes of the volcanic mountain chain known today as the Cordillera de Guanacaste (Janzen, 2000). Over the next four centuries, most of the dry-forested plain was cleared for cattle, timber, and crops. Ranchers set fires annually

during the dry season to keep pastures free of encroaching woody vegetation, and over time, the repeated cycle of annual burning—in combination with relentless logging, cattle grazing, and an aggressive introduced pasture grass (*Hyparrhenia rufa*) that choked out native seedlings—eliminated or extensively modified nearly all of the original vegetation (Janzen, 2000). Because of its long history and its role in various international battles, the government of Costa Rica established a national monument at Hacienda Santa Rosa in the mid-1960s in recognition of its cultural significance. Shortly thereafter in 1971, Santa Rosa National Park was established on the recommendations of some pioneering Costa Rican conservationists. This event marks the beginning of what would grow to become one of the world’s foremost endeavors in restoration ecology, the Área de Conservación Guanacaste (ACG), which was inscribed as a UNESCO World Heritage Site in 1999. The conservation area has expanded from its original boundaries to encompass neighboring wildlands and marine ecosystems, and the original conservation area decreed in 1971 surrounding the old Hacienda Santa Rosa is now called Sector Santa Rosa. A variety of management practices begun in the 1970s and 1980s have aided forest recovery in SSR, including aggressive fire suppression and the removal of hunters, squatters, cattle, and horses (Janzen, 1983, 1988, 2000). However, the biota itself has been allowed to regenerate via natural reseeding and dispersal, unaided by tree planting, soil conditioning, or other land reclamation measures (Janzen, 1987).

1.4.2 CLIMATE OF SANTA ROSA

Climatic seasonality is a cornerstone of my research. Here, I provide an overview of the major climatic changes that occur in SSR over a typical annual cycle. Annual changes in temperature are generally slight in this tropical region, being driven largely by changes in cloud cover, solar radiation, and the cooling effect of strong trade winds (Taylor and Alfaro, 2005). Trade wind activity—specifically, the atmospheric convection that follows when the trade winds diminish—also mediates rainfall seasonality and some anomalous rainfall events (Peña and Douglas, 2002). Throughout the early dry season from November to March and again in during a short dry period in mid-July (the “veranillo”), strong trade winds blow westward off the Caribbean and cross over the low peaks of the Cordillera de Guanacaste, losing their moisture on the volcanos’ windward slopes, and finally sweep down into the Pacific lowlands, scouring the coastal plain with cool and dry gusts of air (Peña and Douglas, 2002; Taylor and Alfaro, 2005). Midday temperatures peak during the late dry season (April and early May) as trade wind activity decreases before the onset of the wet season. The 6-month-long wet season in SSR (mid-May to mid-November) is generally characterized by frequent rainfall, very high relative humidity, and warm temperatures (fig. 1.2). Annual rainfall shows a bimodal distribution, with peaks in June and September/October, but annual totals are highly variable

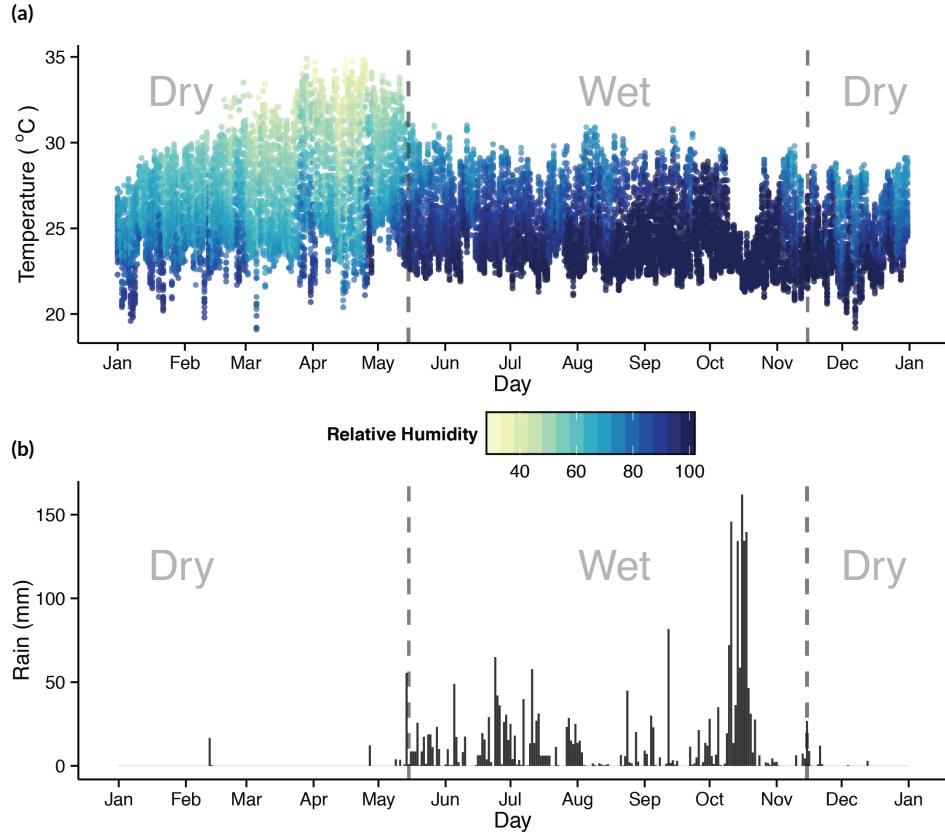


Figure 1.2: Seasonal and day-to-day variation during 2011 in (a) temperature and relative humidity, and (b) daily aggregate rainfall. The temperature and relative humidity data consist of 48 measurements per day taken at regular 30-min intervals on each day of the year. For each point in (a), calendar date is indicated by the horizontal axis, temperature by the vertical axis, and relative humidity by the hue.

(range: 818 mm to 3498 mm, mean: 1497 mm, median: 1764 mm, $n = 35$ years). The dry season (mid-November to mid-May), in contrast, is typified by a near-total lack of rainfall, relatively low humidity, high midday temperatures, and scarce surface water (fig. 1.2).

1.4.3 HABITATS IN SANTA ROSA

Land cover, and the primate habitat that it provides, is another key component of this thesis. Here, I provide detailed descriptions of the four main habitat categories that I distinguish in my analyses: scrub and open grassland, early stage successional forest, intermediate stage successional forest, and mature forest (fig. 1.3). Definitions of these habitats follow previous categorizations (Arroyo-Mora, Sanchez-Azofeifa, Kalacska, et al., 2005; Kalacska, Sanchez-Azofeifa, Calvo-Alvarado, et al., 2004; Kalacska, Sanchez-Azofeifa, Rivard, et al., 2007), and further details on their species compositions and structural and spectral characteristics can be found in those studies. The four habitat categories blend continuously into each other in some areas, but there remain many abrupt ecotones along the

edges of former pastures and recently burned areas and alongside rocky streambeds. The heterogeneous nature of past disturbances makes some classifications ambiguous. For example, some large evergreen trees that are typical of mature forest were left in old pastures to provide shade for cattle, producing a present-day mix of trees whose species are typically restricted to either early-stage or mature forest. There is, of course, a great deal of variation within each of these broad categories, but they are each differentiated by structural attributes and typical species makeup.

SCRUB AND OPEN GRASSLAND

Though it once covered much of the study area, the scrub and open grassland habitat class (fig. 1.3b) is presently almost absent from the upland region of SSR, persisting only in recently-burned areas, around buildings, and in several firebreaks. This habitat class represents tropical dry forest in its earliest stages of regeneration, as on a recently abandoned pasture. A different sort of mixed scrubland covers a significant proportion of the steep rocky valleys and ridges in the southwestern portion of SSR, where very thin, nutrient-poor soils naturally support only woody scrub and native grasses, and there are few intact forest remnants nearby to provide wind-borne seed rain. Although these scrublands are similar in appearance to the very early stage of regeneration in the upland region of SSR, the two habitats differ fundamentally in their ecology, species makeup, and growth trajectories. However, from the capuchins' perspective, they are likely to be functionally similar (i.e., equally hostile).

EARLY SUCCESSIONAL STAGE FOREST

The early successional stage (fig. 1.3c) consists of a single stratum of woody vegetation, mostly juvenile trees and shrubs, not exceeding 6 m to 8 m in height. This habitat is species-poor, being dominated by wind-dispersed trees with hardy seedlings capable of colonizing open pasture. Deciduousness is near-complete. Most of the present-day early-stage forest around the primary study area exists in the upland regions on reclaimed pastureland that was burned for the last time in the 1980s (Castillo-Núñez et al., 2011).

INTERMEDIATE SUCCESSIONAL STAGE FOREST

The intermediate successional stage (fig. 1.3d) encompasses a broad range of vegetation communities that have been disturbed to varying degrees, primarily by fire damage and logging. The hallmark of this habitat class, at least in terms of its spectral reflectance, is an intermediate degree of deciduousness, with 50 % to 80 % of the canopy becoming leafless during the dry season. The vegetation



Figure 1.3: Examples of different habitat types in the study area: (a) recent burn; (b) scrub and open grassland; (c) early successional stage forest; (d) intermediate successional stage forest; (e) mature or late successional stage forest. All photos from peak dry season.

is typically arranged in two vertical strata, the uppermost reaching 15 m, and is often covered with densely tangled lianas and vines. The intermediate stage supports a markedly more diverse set of tree species compared to the early stage. However, stands of monodominant oak forest (dominated the tropical live oak, *Quercus oleoides*) are spectrally similar to the intermediate stage of tropical dry forest. Oak forests were formerly widespread in this region of Costa Rica, and a few sizable patches remain in the northeastern corner of SSR (Klemens et al., 2011). However, these were uncommon in the primary study area and were infrequently used by my study groups.

MATURE OR LATE SUCCESSIONAL STAGE FOREST

The mature or late successional stage forest class (fig. 1.3e) is characterized by a tall, two- or three-tiered canopy structure, the uppermost of which reaches 30 m and consists of a high proportion (>50 %) of overlapping evergreen crowns. The understory is deeply shaded and relatively open year-round, supporting a diverse assemblage of shade-tolerant shrubs and juvenile trees. Mature forest is relatively uncommon and localized in SSR, with one major unbroken patch in the northwestern portion of the primary study area and a few other extensive patches near the coast and along steep escarpments.

1.4.4 STUDY SPECIES AND GROUPS

The capuchins comprise two closely-related genera: *Cebus* and *Sapajus* (Lynch Alfaro et al., 2012). Capuchins show many behavioral and anatomical convergences with great apes and humans, including a large brain-to-body size ratio, long life spans, violent coalitionary aggression, the capacity for tool use, and social traditions (Perry, 2011). Their remarkable ability to exploit varied and varying environments has enabled capuchins to thrive in a diverse range of natural biomes—tropical rain forest, tropical dry forest, premontane and montane evergreen forest, and mangroves—as well as some human-modified ecosystems. Although all capuchins are omnivorous, the makeup of their diets is highly variable even within populations. They are therefore commonly described as generalists both in terms of habitat requirements and diet, and this supreme adaptability has made capuchins one of the most successful and widespread radiations of New World monkeys (Fragaszy et al., 2004). They live in multi-male multi-female social groups with male dispersal and female philopatry. Social group size is typically in the range of 15 to 20 animals, but groups including as many as 45 animals are not uncommon. Sexual dimorphism is pronounced: adult females have smaller canines, slimmer head and shoulders, and body mass roughly 70 % that of adult males (fig. 1.4) (Ford and Davis, 1992; Masterson and Hartwig, 1998; Smith and Jungers, 1997). The taxon that inhabits SSR is the white-faced capuchin (*C. capucinus*), which is distinguished from other capuchins by its strik-



Figure 1.4: (a) Adult female and (b) adult male *Cebus capucinus*.

ing black-and-white pelage. This species is distributed from northern Honduras south through the Isthmus of Panama, along the Pacific coast of South America west of the Andes to northern Ecuador (fig. 1.5) (Causado et al., 2008).

Most of my data collection focused on five neighboring social groups of *C. capucinus* (BH, CP, EX, GN, and LV) during 18 months in 2010 and 2011. Group CP underwent a fission shortly after I completed my fieldwork, and I include some location data from the two fission products, AD and RM, in chapter 2. The study groups were located in the relatively flat upland region of SSR near the administrative center of the ACG (fig. 1.6). Because chapter 5 deals with long-term trends in the larger population, it includes census data from all other groups within the borders of SSR.

1.4.5 WHY SSR IS AN APPROPRIATE SITE FOR THIS STUDY

As perhaps the oldest and most celebrated example of ecological restoration in the Neotropics, SSR is an ideal site for this study. Its complex mosaic landscape and resident primates have been monitored intensively over multiple decades. SSR therefore offers an exceptional opportunity to investigate primates' long-term responses as their environment slowly transitions from a patchwork agroecosystem to whatever old-growth condition lies in its future. Moreover, the strongly seasonal climate and resulting phenological changes in SSR (Frankie et al., 1974) enable studies of short-term behavioral adjustments to ecological change. Indeed, across the entire geographic range of *C. capucinus*, precipitation seasonality reaches its peak in northwestern Costa Rica (fig. 1.5). Using *C. capucinus* as a model, I aim to develop a fuller understanding of primate-focused ecological recovery processes to enable informed conservation decisions, promote the welfare of our closest living relatives, and gain insights into our own evolutionary past.

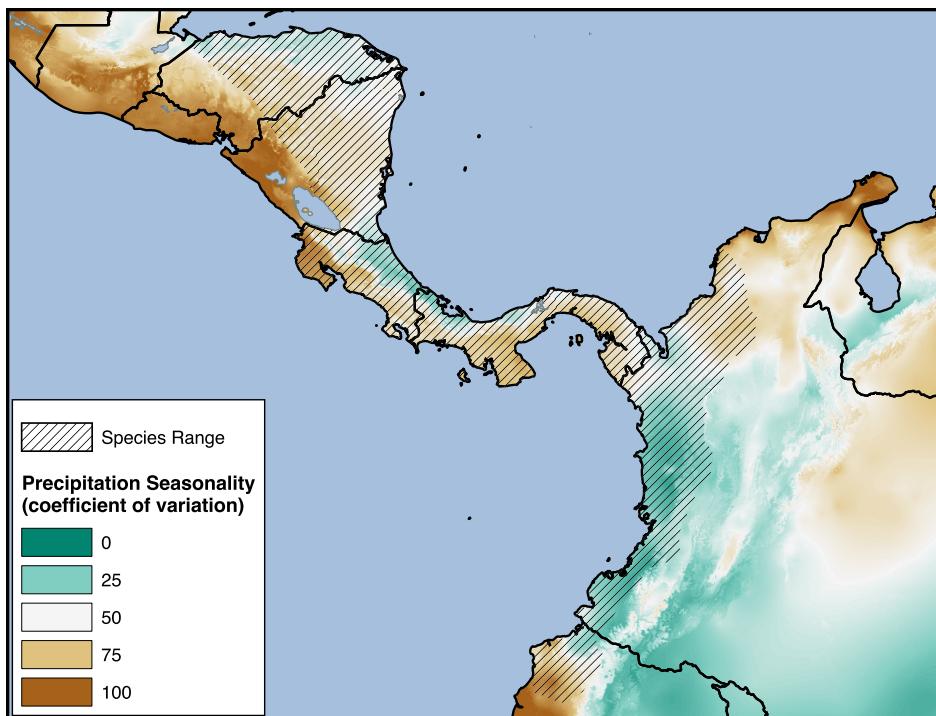


Figure 1.5: Precipitation seasonality over the entire geographic range of *Cebus capucinus*.

1.5 ORGANIZATION OF THE THESIS

The four chapters that follow (chapters 2 to 5) were originally written as independent articles for publication, each with its own account of the study system and relevant field protocols. Accordingly, there is considerable repetition in the methods sections of these chapters.

In chapter 2, I infer characteristics of the predation pressures faced by white-faced capuchins based on the spatial pattern of their alarm calls directed toward three classes of predators: snakes, aerial raptors, and terrestrial quadrupeds. By relating these “landscapes of fear” to underlying patterns of space use, I create maps of perceived predation risk, and I characterize “high” and “low” risk zones in terms of habitat and microhabitat attributes. Finally, I develop and evaluate predictive models for vigilance behavior that are informed by these relative risk functions. This study has been published in *Behavioral Ecology* and is cited throughout this thesis as Campos and Fedigan (2014).

In chapter 3, I investigate the energetics of foraging behavior over space and time. I quantify both energy intake and energy expenditure to calculate net energy returns, and I examine how these currencies vary relative to habitat type, season, sex, and group size. Because foraging efficiency is widely held to be a fundamental target for natural selection, this chapter’s primary goal is to understand how the capuchins’ variable environment molds this important component of individual fitness. Macken-

zie L. Bergstrom contributed to this chapter by collecting fruit samples for nutritional analysis and organizing all aspects of the nutrition data. I designed the study, collected and analyzed all other data, created the figures and tables, and wrote the manuscript.

Chapter 4 investigates the spatiotemporal dynamics of capuchins' home ranges. I examine how seasonal fluctuations in climate, food resource abundance, and group mass affect variance in home range area and the maturity stage of forest used by capuchins. By approaching these questions from a range of spatial and temporal scales, I explore the home range concept itself and how biological inferences in home range studies may depend on spatiotemporal scale. This study has been published as a multi-authored article in *Animal Behavior* and is cited throughout this thesis as Campos, Bergstrom, et al. (2014). The following authors contributed to the study (in alphabetical order): Mackenzie L. Bergstrom, Andrew Childers, Jeremy D. Hogan, Katharine M. Jack, Amanda D. Melin, Monica S. Myers, Krisztina N. Mosdossy, Nigel A. Parr, Elizabeth Sargeant, Valérie A.M. Schoof, and Linda M. Fedigan. These authors provided data (location points, weather, phenology and demography) collected during separate projects and edited the manuscript. Amanda D. Melin and Nigel A. Parr collected the transect data used for calculating available fruit biomass. As the lead author, I designed the study, collected data, carried out the analysis, created the figures and tables, and wrote the manuscript.

Chapter 5 draws together various long-term data sets to examine how climatic fluctuations and changes in landscape structure and spatial pattern have affected the capuchin population at my study site over a 30-year period. I draw on the individual- and group-level analyses in chapters 2 to 4 to infer links between the capuchins' changing environment, likely fitness outcomes, and population-level consequences. This manuscript was written in collaboration with Katharine M. Jack and Linda M. Fedigan, who made major contributions to organizing and collecting the census data.

In chapter 6, I conclude by discussing how the findings I have presented in this thesis advance our current understanding of how primates respond to environmental variability, and I discuss the implications of this knowledge in broader ecological, evolutionary, and anthropological context.

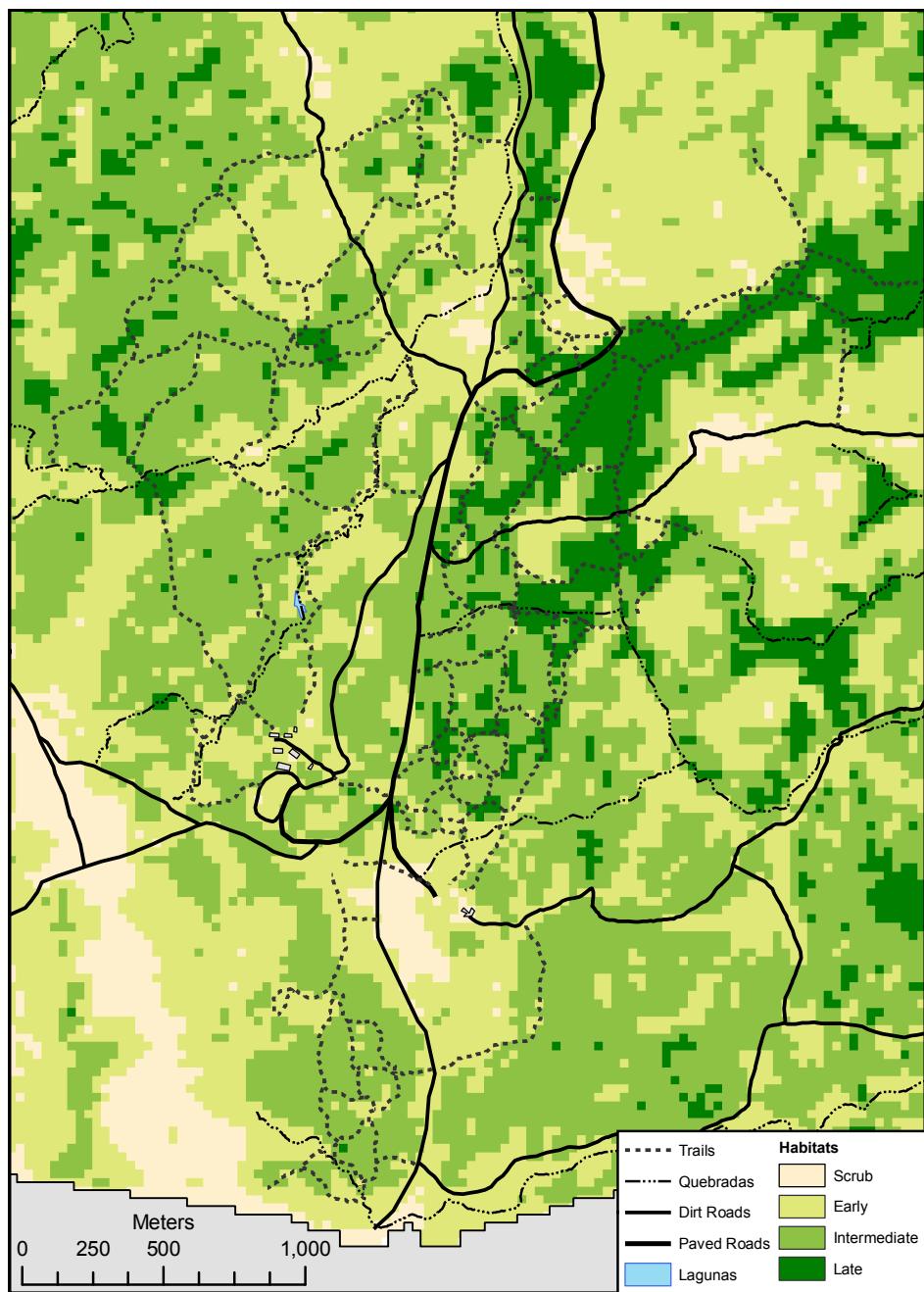


Figure 1.6: Landscape features and distribution of habitat types in the primary study area.

During any given day, an animal may fail to obtain a meal and go hungry, or it may fail to obtain matings and thus realize no reproductive success, but in the long term, the day's shortcomings may have minimal influence on lifetime fitness. Few failures, however, are as unforgiving as the failure to avoid a predator: being killed greatly decreases future fitness.

Steven L. Lima and Lawrence M. Dill, 1990

2

Spatial ecology of perceived predation risk and vigilance behavior in white-faced capuchins

2.1 INTRODUCTION

Predation has long been considered a fundamental selective pressure over evolutionary time scales, but growing evidence has demonstrated that predation risk—the likelihood of falling prey to a predator’s attack—can strongly affect an animal’s behavior patterns and space usage over shorter, “ecological time” scales (Lima, 1998; Lima and Dill, 1990). Even among animals that are rarely preyed on, predation risk may exert a powerful influence on behavior because a single failure to avoid a predator can have absolute and ruinous effects on individual fitness (Lima and Dill, 1990; Stanford, 2002). Predation risk can be operationalized in different ways. *Intrinsic risk* is the expected predation rate holding antipredator behavior constant or at zero (Janson, 1998), whereas *perceived risk* is the animal’s own assessment of the likelihood of an attack, which is based on past experiences and imperfect knowledge (Bouskila and Blumstein, 1992; Hill and Dunbar, 1998). Though they may differ from each other considerably (Lima and Dill, 1990), both assessments of risk are informative from the ecologist’s perspective. Intrinsic risk is likely to drive the evolution of predator defense strategies over evolutionary time scales (Janson, 1998), whereas perceived risk is likely to underlie short-term be-

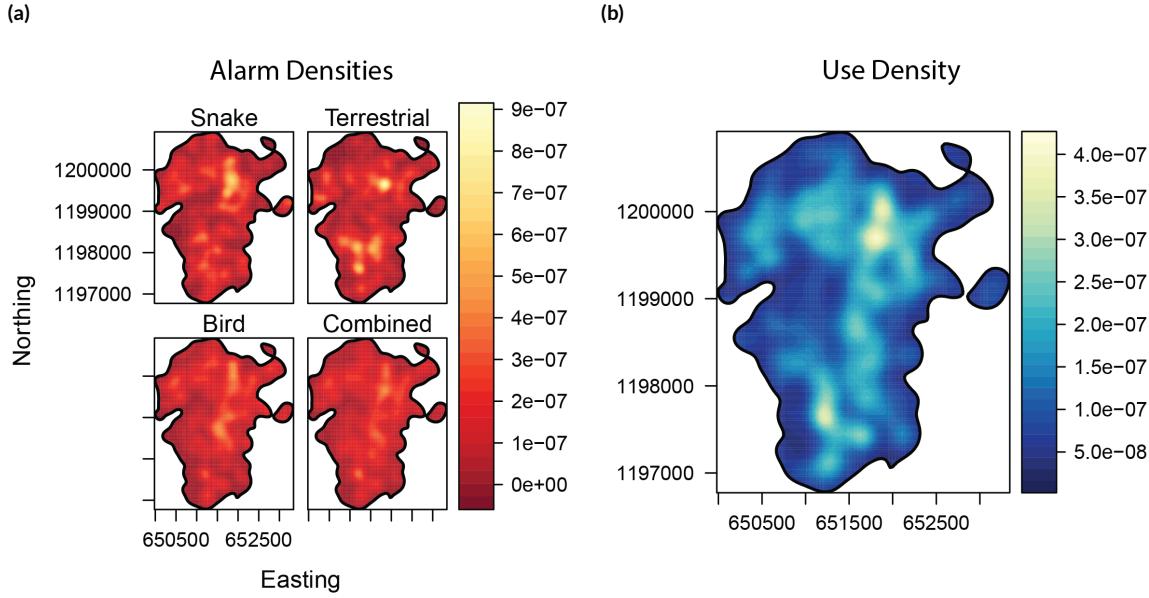


Figure 2.1: (a) Predator encounter densities for the different predator guilds, based on all-occurrence sampling of the locations of guild-specific alarm calling bouts. (b) Space use density, based on systematic scans collected at 30-min intervals.

havioral decisions aimed at reducing individual risk (Lima, 1998). Predictive antipredator behavior occurs when animals act on their perception of local risk in the absence of an immediate threat. Such behaviors may have opportunity costs if the animal must forego opportunities to find food, mates, or other important resources in order to reduce mortality risk (Lima and Dill, 1990). If those opportunity costs are negligible, animals may benefit from continually overestimating intrinsic risk, and may thus be relatively insensitive to fluctuating levels of intrinsic risk (Bouskila and Blumstein, 1992). However, when the opportunity costs of predictive antipredator behavior are significant, animals should benefit from the ability to make accurate judgments about spatial and temporal heterogeneity in intrinsic risk and to respond appropriately. Therefore, an animal's behavioral responses to variation in perceived risk can provide important insights about predation intensity, the opportunity costs of antipredator behavior, the reliability of predator cues for accurate risk assessments, and predator-prey ecosystem dynamics (Bouskila and Blumstein, 1992; Luttbeg and Trussell, 2013; Ripple and Beschta, 2004).

Predictive antipredator behaviors vary with the characteristics of the prey species and the hunting tactics of the predator species, and may include vigilance (Elgar, 1989), aggregation (Banks, 2001; Elgar, 1986; Link and Di Fiore, 2013), and selection for particular habitats (Creel et al., 2005; Willems and Hill, 2009) or microhabitats (Cruz et al., 2013; Thomson et al., 2006). Studies that have examined the function of vigilance in diurnal, gregarious nonhuman primates often conclude

Table 2.1: Candidate model set and model selection for the occurrence of vigilance behavior.

Model	Fixed effects	<i>K</i>	AICc	ΔAICc	w_i	Ev. ratio	Rank
m1	Null model (intercept only)	3	10 146.6	44.31	$\sim 10^{-10}$	$\sim 10^9$	15
m2	Habitat type	5	10 149.7	47.37	$\sim 10^{-11}$	$\sim 10^{10}$	14
m3	Snake risk	4	10 147.6	45.24	$\sim 10^{-10}$	$\sim 10^{10}$	16
m4	Terrestrial risk	4	10 147.8	45.45	$\sim 10^{-10}$	$\sim 10^{10}$	17
m5	Bird risk	4	10 137.5	35.21	$\sim 10^{-8}$	$\sim 10^7$	13
m6	Combined risk	4	10 130.0	27.72	$\sim 10^{-6}$	$\sim 10^6$	12
m7	Vertical level	5	10 117.2	14.92	$\sim 10^{-4}$	1734	6
m8	Vertical level + Habitat type	7	10 120.8	18.43	$\sim 10^{-4}$	$\sim 10^4$	5
m9	Vertical level + Snake risk	6	10 118.6	16.24	$\sim 10^{-4}$	3360	8
m10	Vertical level + Terrestrial risk	6	10 118.3	15.97	$\sim 10^{-4}$	2935	7
m11	Vertical level + Bird risk	6	10 107.8	5.47	0.048	15.4	3
m12	Vertical level + Combined risk	6	10 102.3	0	0.745	1	1
m13	Vertical level \times Habitat type	11	10 125.9	23.62	$\sim 10^{-5}$	$\sim 10^5$	11
m14	Vertical level \times Snake risk	8	10 122.0	19.66	$\sim 10^{-5}$	$\sim 10^4$	9
m15	Vertical level \times Terrestrial risk	8	10 122.1	19.81	$\sim 10^{-5}$	$\sim 10^4$	10
m16	Vertical level \times Bird risk	8	10 110.8	8.52	0.011	70.93	4
m17	Vertical level \times Combined risk	8	10 105.0	2.69	0.195	3.83	2

All models include the random effects focal sample number and focal animal. The model with the greatest empirical support (m12) is shown in bold. Estimated coefficients for the gray-shaded models are plotted in fig. 2.9. *K*: number of parameters; AICc: corrected Akaike's Information Criterion; ΔAICc : change in AICc between each model and the best model (m12); w_i : Akaike weight; Ev. ratio: evidence ratio

that vigilance serves a variety of functions, some of which are not related to predator detection, including within-group or extra-group conspecific monitoring, food search, and planning travel routes (Stanford, 2002; Treves, 2000). We investigate predator encounter frequencies, perceived risk, and vigilance behavior in an arboreal primate, *Cebus capucinus*. We report encounter frequencies with different predator guilds based on alarm calls and direct observation, and we characterize these encounters using a range of ecological variables. Our major goals are to develop a spatial model of perceived predation risk for *C. capucinus* in this study system and to determine whether this risk is informative for predicting the occurrence of a putative antipredator behavior, vigilance.

We make no attempt to test or distinguish between functional explanations for vigilance in general, as this question has been addressed for capuchin monkeys elsewhere (Gould et al., 1997; Hirsch, 2002; Pannozzo et al., 2007; Rose and Fedigan, 1995; van Schaik and van Noordwijk, 1989), and our data set would not have offered any improvement over these previous studies. Although measuring intrinsic risk in a complex multi-predator system is fraught with challenges (Janson, 1998), perceived predation risk can be estimated relatively easily in some nonhuman primates (Willems and Hill, 2009) due to their distinct and easily recognizable alarm-call responses to different predator

guilds (Cheney, 1987; Digweed et al., 2005; Fichtel et al., 2005; Seyfarth et al., 1980; Zuberbühler, Noë, et al., 1997). Using an approach introduced by Willems and Hill (2009), we relate the spatial distribution of alarm calls to the spatial distribution of systematically collected ranging data to predator guild-specific estimates of perceived predation risk, and we explore the distribution of these risk functions across the heterogeneous landscape. Finally, we investigate whether incorporating these risk functions into predictive models of vigilance behavior improves prediction relative to null models of uniform risk or habitat-specific risk.

2.2 METHODS

2.2.1 STUDY SITE

We conducted the study in the Santa Rosa Sector (SSR), one of several sectors that make up the Área de Conservación Guanacaste UNESCO world heritage site in northwestern Costa Rica (Janzen, 2000). The SSR was a functioning cattle ranch from the late 1500s until the mid-1960s; today, after nearly 50 years of ecological restoration following centuries of anthropogenic burning and logging, the SSR contains 108 km² of varied habitat that stretches from a forested coastal plateau at about 300 m above sea level to the Pacific Ocean (Janzen, 2000). Our study area was located on the plateau, and it comprised an irregular complex of heterogeneously damaged tropical dry forest, including some small patches of semi-evergreen forest, deciduous dry forest in various stages of regeneration, and some very young woody succession on recently reclaimed cattle pastures (Fedigan and Jack, 2012). Canopy height varied markedly among these habitats, from 30 m in small pockets of mature forest to about 6 m in the early successional stage forest (Kalacska, Sanchez-Azofeifa, Calvo-Alvarado, et al., 2004). Rainfall and leaf cover in the SSR are strongly seasonal, with a six-month-long dry season from November to May during which most plants shed their leaves, especially those in the younger successional stages. Total yearly rainfall at the site averages 1710 mm (Fedigan, Carnegie, et al., 2008). There are a variety of commonly encountered species in the SSR that could potentially prey on capuchin monkeys, all of which have been observed multiple times by members of L.M.F.'s research team. These species include five felids (*Panthera onca*, *Puma concolor*, *Leopardus pardalis*, *Leopardus wiedii*, and *Puma yagouaroundi*); two canids (*Canis latrans* and *Urocyon cinereoargenteus*); one large mustelid (*Eira barbara*); several large raptors (*Leptodon cayanensis*, *Micrastur semitorquatus*, *Pulsatrix perspicillata*, *Geranospiza caerulescens*, *Chondrohierax uncinatus*, *Buteogallus anthracinus*, and *Herpetotheres cachinnans*); and two large snakes (*Boa constrictor* and *Crotalus simus*) (personal observations; Rose, Perry, et al., 2003).

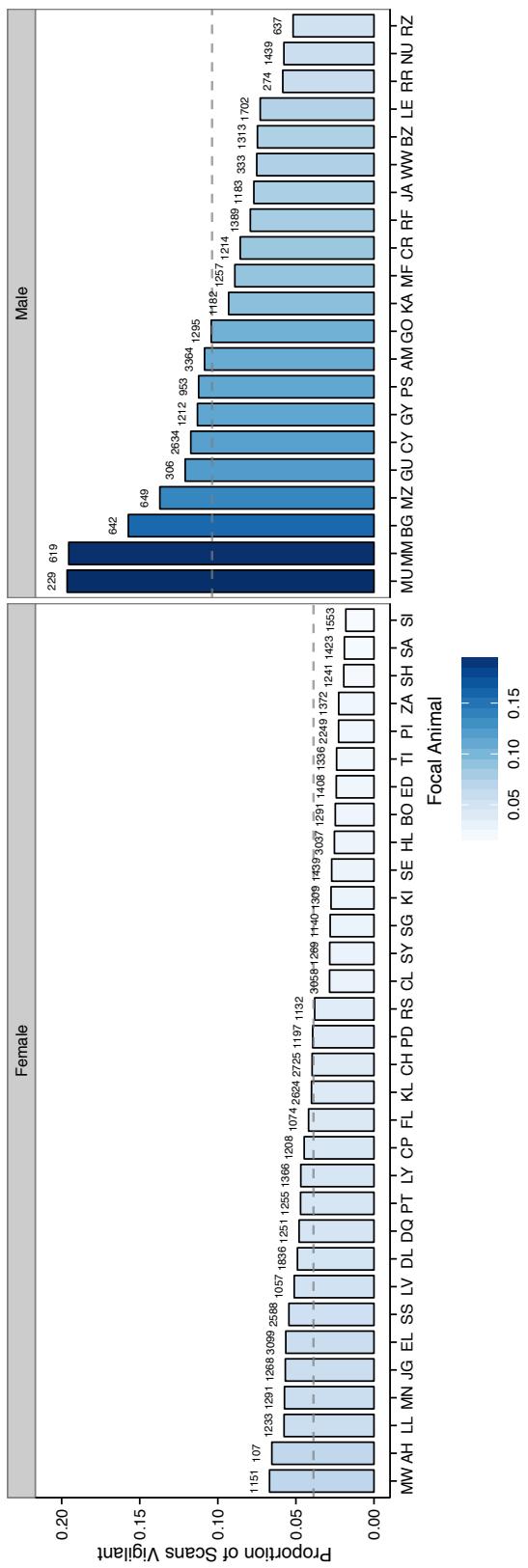


Figure 2.2: Overall proportion of samples coded as vigilant for each focal animal. Horizontal dashed lines indicate the mean value for each sex. Vigilance clearly makes a greater contribution to males activity budgets.

2.2.2 DATA COLLECTION

STUDY ANIMALS AND OBSERVATION SCHEDULE

FAC and six field assistants collected data on five social groups (BH, CP, EX, GN, and LV) of white-faced capuchins during two study periods: January to May 2010 and January to December 2011. Group sizes ranged from 10 to 40 animals in total, and all animals were fully habituated to human observers. The training period for each field assistant lasted 3 to 5 weeks and ended when FAC and the assistant reached 100 % agreement on individual identification and 90 % agreement on all other recorded data. After the assistants began collecting data independently, FAC continued to overlap regularly with each assistant to ensure that the inter-observer reliability established during training remained consistent. We typically followed two groups simultaneously with between one and three observers in each group. We followed each group from sleep tree to sleep tree whenever possible. We rotated among groups after a fixed five-consecutive-day schedule, with a mean \pm standard error of $74.7 \text{ h} \pm 3.39 \text{ h}$ of contact time per group per month.

FOCAL ANIMAL SAMPLING

We recorded individual vigilance behavior and microhabitat usage during 15-min focal animal samples on all sexually mature individuals ($n = 53$) in the five social groups. We selected focal animals in a pseudo-random order: the individual order for each round of samples was opportunistic, but we sampled each focal animal once before beginning the next round. During focal sampling, we recorded instantaneous samples (Altmann, 1974) on the focal animal at 1-min intervals, noting the focal animal's activity state and vertical position above the ground. We classified the focal animal's activity state at the instantaneous sample as vigilant or nonvigilant, which could be any other activity state, including foraging, feeding, socializing, traveling, resting, and self-grooming. We defined vigilance as scanning intently at long range while alert and stationary. We noted the animal's vertical position above the ground using two alternative methods. First, we estimated absolute height above the ground in 5-m intervals with the endpoints 0–4 m, 5–9 m, 10–14 m, 15–19 m, 20–24 m, and >25 m. Second, we recorded a relative height category ("vertical level" hereafter) by visually dividing the vegetation layer into equal thirds and assigning the animal to the low, middle, or high third. The depth of the three vertical levels therefore varied in proportion to the total height of the canopy, which was typically greater in mature forest. Although this is an unusual method of codifying height, classifications scheme based on absolute height above the ground fail to capture the increased exposure to the sky near the top of a low-canopy forest ($\sim 6 \text{ m}$), which might fall entirely in an "understory" height category. Thus, the high vertical level was always more exposed to the sky

than the ground, whereas the low vertical level was always more exposed to the ground than the sky, regardless of differences in vegetation structure or maximum canopy height at that location. We obtained the GPS location for each instantaneous sample from track points recorded automatically at 10-s intervals throughout the focal sample by matching the time of the sample with the most temporally proximal track point.

PREDATOR ENCOUNTER DATA

On encountering a predator, white-faced capuchins often engage in mobbing responses that may involve repeated alarm-calling by multiple individuals (Digweed et al., 2005; Fichtel et al., 2005; Rose, Perry, et al., 2003). We defined an alarm-calling bout as the period of time including all the alarm calls directed at the perceived threat, regardless of whether the observers could confirm that a threat was actually present. Perceived threats could include single or multiple allospecific animals (e.g., one snake or a group of tayras, *E. barbara*) as well as “false alarms” given by startled animals. We excluded alarm calls that were clearly directed at conspecific animals, such as those given during extraordinarily severe agonism and during between-group encounters (Fichtel et al., 2005). We also excluded rare alarm calls at humans, which were typically given only in response to harassment by unfamiliar humans or sudden unexpected movements by observers. We recorded contextual information for all occurrences of alarm-calling bouts that were apparently directed at a perceived allospecific threat. This included the absolute height category and vertical level for the animal who initiated the alarm-calling bout at the moment of discovery. Due to the chaotic nature of many alarm-calling bouts, as well as other data-collection requirements, we were unable to record the total number of alarm calls or the identities of all the animals involved.

We used a combination of the acoustic characteristics of alarm calls, behavioral responses, and direct observation of potential predators to categorize each alarm-calling bout into one of four predator guild categories: snake, other terrestrial animal, bird, and unknown. Alarm calls by white-faced capuchins can be separated into two easily distinguishable acoustic classes: first, those given in response to aerial predators and unfamiliar conspecific animals; and second, those given in response to snakes and other terrestrial animals such as felids (Digweed et al., 2005; Fichtel et al., 2005). We considered alarm-calling bouts of the first acoustic class as bird alarms if they were not followed by the conspicuous behaviors associated with between-group encounters in this species. For calls of the second acoustic class, we distinguished between the snake and other terrestrial animal guilds only in cases when the target was directly observed or when the capuchins’ behavior made the distinction unambiguous. For example, mobbing behavior that followed a quickly moving but unobserved target clearly indicated the terrestrial animal predator guild, as all dangerous snakes at this site are slow-moving.

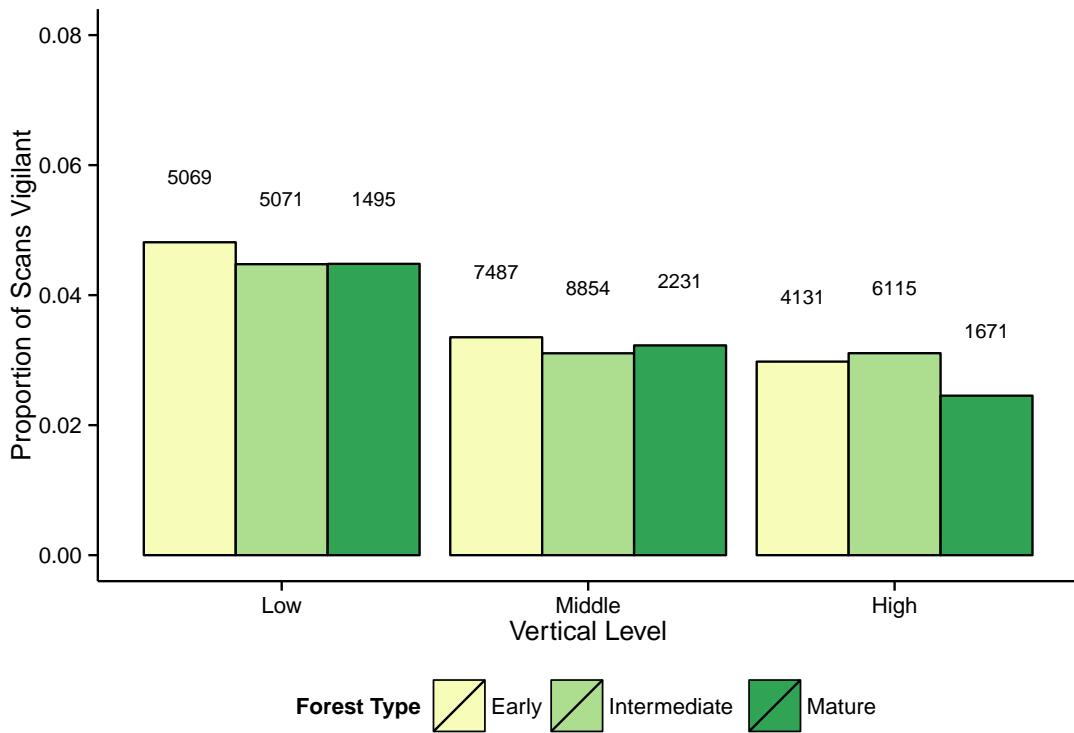


Figure 2.3: Proportion of samples scored vigilant in the reduced focal data set across vertical levels and forest types. Animals were more likely to be vigilant in the low vertical level compared to the middle and high levels, which did not differ from each other. There were no consistent, obvious differences in vigilance behavior according to forest type. Total number of scans for each condition indicated above the bar. Grassland and Early Forest habitat types combined due to low number of samples in grassland habitat.

Whenever the observers were unsure of the alarm type for any reason, we considered the predator guild category unknown. If the observers could confidently identify the animal that provoked each alarm-calling bout, we also recorded the animal's species.

HABITAT AND MICROHABITAT USAGE

We recorded the focal group's geographic location every 30 min on the half-hour using handheld GPS receivers (Garmin GPSMAP 62s). At the time of the group scan, we recorded the "predominant group height," which we defined as the absolute height category that contained the greatest number of visible animals. Finally, we recorded the "predominant group vertical level," which we defined as the vertical level that contained the greatest number of visible animals at the time of the group scan. We used a categorical map of land cover and a continuous map of normalized difference vegetation index (NDVI), both obtained from a multispectral Landsat 5 TM satellite image of the study region acquired during peak dry season (6 March 2011). We describe the creation and vali-

dation of these maps elsewhere (Campos, Bergstrom, et al., 2014). The land cover map consisted of four habitat categories, defined as in Kalacska, Sanchez-Azofeifa, Calvo-Alvarado, et al. (2004), including open grassland and bare soil, early successional stage forest, intermediate successional stage forest, and mature forest. Dry season NDVI in this seasonal forest indicates the degree of evergreeness of the vegetation represented by the pixel. Previous research in the SSR has demonstrated that dry season NDVI values can effectively discriminate among maturity stages of dry forest (Arroyo-Mora, Sanchez-Azofeifa, Kalacska, et al., 2005; Kalacska, Sanchez-Azofeifa, Calvo-Alvarado, et al., 2004), which becomes more evergreen as it matures (Sorensen, 1998). We use the term “forest maturity index” hereafter to refer to these NDVI values.

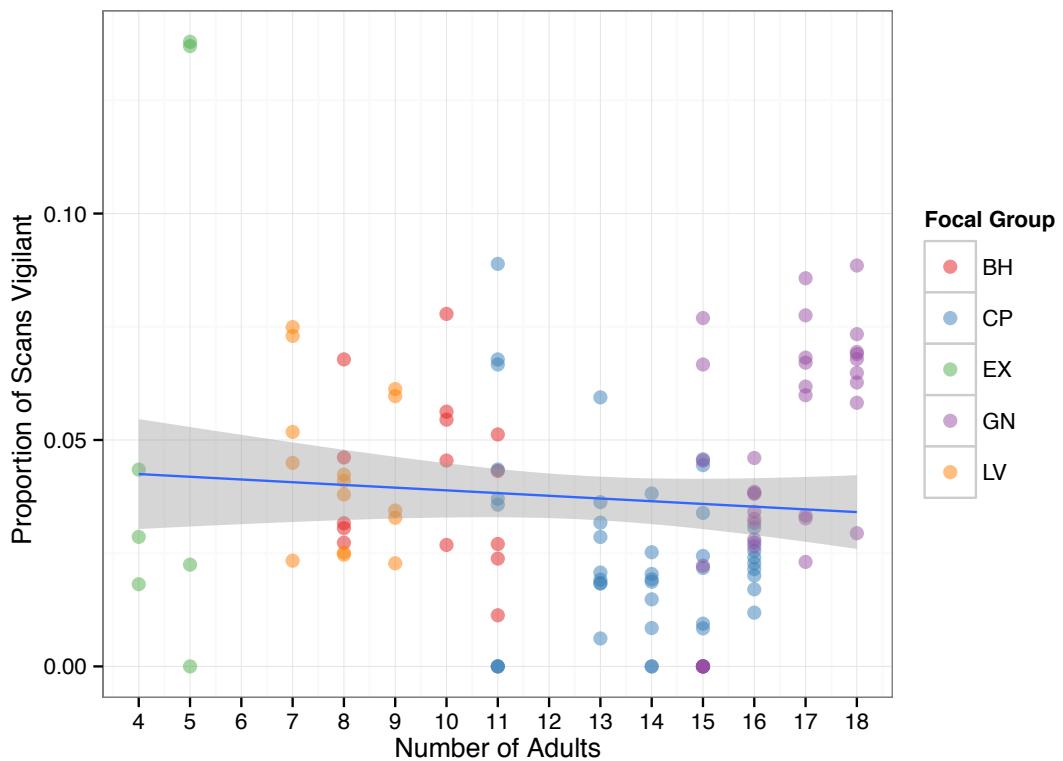


Figure 2.4: Total proportion of samples coded as vigilant for each group, with all individuals pooled together, at different group sizes. Gray shaded area shows 95 % confidence interval around the regression line. Regression coefficient \pm standard error: 0 ± 0.0079 , $F \approx 0$, $P \approx 1$, adjusted $R^2 = -0.00427$. Vigilance behavior shows no clear linear relationship with group size.

2.2.3 DATA ANALYSIS

ENCOUNTER FREQUENCIES AND MICROHABITAT ASSOCIATIONS

We calculated expected encounter frequencies for each predator guild in each vertical level, absolute height, and habitat type category by multiplying the total number of encounters for each guild by the proportion of systematic group scans in each vertical level, absolute height, and habitat type category (i.e., overall usage). We evaluated the observed and expected frequency distributions with Pearson's chi-squared goodness-of-fit tests. We grouped the infrequently used grassland habitat category with early-stage forest due to very small expected frequencies. Because the expected counts remained small in some categories, we computed the P values for these tests via Monte Carlo simulations with 10 000 replicates. When the global chi-squared test was significant, we performed pairwise comparisons among categories, and we adjusted the P values for multiple comparisons using the Holm-Bonferroni method (Holm, 1979).

PERCEIVED RISK LANDSCAPES

To understand how the risk of encountering predators of different guilds varied over the study region, we used a technique commonly used in spatial epidemiology for mapping disease risk from case-control data (Bithell, 1990). We calculated a “perceived risk landscape” (Thomson et al., 2006) for each predator guild as the ratio of predator encounter densities (the “cases”, fig. 2.1a) to usage densities (the “controls”, fig. 2.1b). The resulting maps represent the probability of encountering a predator given the underlying pattern of habitat use by the study animals. We calculated the predator encounter and usage densities from the locations of alarm-calling bouts and systematic group scans, respectively (following Willems and Hill, 2009). Based on an exploration of various candidate bandwidths, we used fixed kernel smoothing with a bandwidth of 100 m for smoothing the density estimates. We implemented boundary correction for all datasets following the procedure developed by Diggle (1985). We defined the boundary of the study area as the 95 % isopleth of the kernel density estimate based on all systematic group scan points. A small number of encounters on the outermost fringes were therefore excluded from the analysis; we feel this is appropriate to reduce possibly spurious results in areas that were used very infrequently. We identified subregions with significantly elevated or lowered risk by delineating upper- and lower-tailed adaptive asymptotic tolerance contours (Davies and Hazelton, 2010) at the 0.05 significance level using the R package *sparr* (Davies, Hazelton, and Marshall, 2011). Having delineated these “hot spots” and “cool spots” of perceived predation risk for each predator guild, we were interested in characterizing these zones relative to the surrounding landscape. First, we calculated the proportion of the landscape within each zone (high

risk, low risk, and neither) represented by each of the four habitat classes. Second, we visually examined differences in the medians, interquartile ranges, and probability densities of the forest maturity index values contained within each zone using violin plots and box plots. In addition to the three predator guilds, we carried out these analysis steps for a “combined risk” landscape, which included the alarm-calling bouts for all three guilds plus all the bouts that could not be confidently assigned to a particular guild.

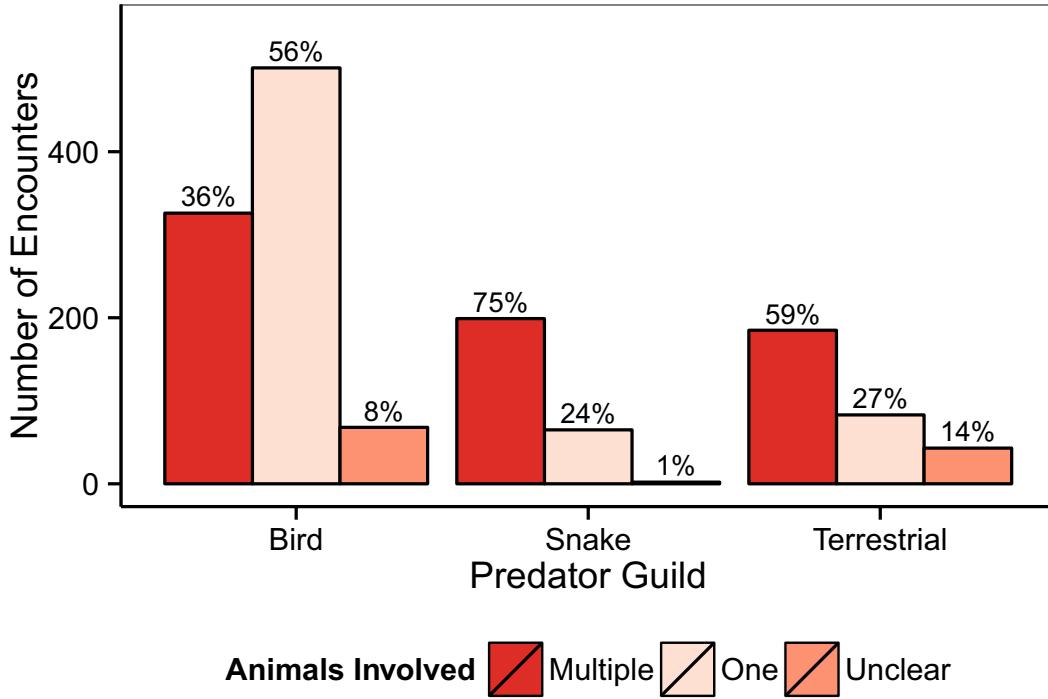


Figure 2.5: Total number of encounters (i.e., distinct alarm calling bouts) for snake, terrestrial, and bird predator guilds that involved one vs. multiple alarm-calling animals. The “unclear” category refers to cases in which the number of animals involved was not obvious. Predator guild-specific percentages for each encounter type are shown above the bars.

VIGILANCE MODELS

We were interested in assessing the evidence for predictive antipredator vigilance; that is, if vigilance behavior that was not clearly related to monitoring social partners or perceived threats varied in relation to the perceived risk landscape. Because vigilance is multi-functional, we took steps to reduce the influence of potentially confounding social vigilance and “reactive” antipredator vigilance in our analysis. First, adult male vigilance in this population is strongly influenced by the likelihood of en-

Table 2.2: Variables obtained for each instantaneous scan during focal samples.

Name	Description
Vertical level	Relative height above the ground (low, middle, or high), obtained by visually dividing the vegetation layer into equal thirds.
Absolute height	Absolute height above the ground in 5 m intervals.
Group size	Total number of individuals in the focal group at the time of the sample.
Habitat type	Vegetation type delimited over a grid with 30 x 30 m pixels. Categories include open grassland, early successional stage forest, intermediate successional stage forest, and mature forest.
Forest maturity	A continuous index of evergreenness measured over a grid of 30 x 30 m pixels. The values are based on peak dry season normalized difference vegetation index (NDVI).
Perceived snake risk	Value of the perceived snake risk landscape, calculated as log (snake encounter density / habitat use density).
Perceived terrestrial risk	Value of the perceived terrestrial predator risk landscape, calculated as log (terrestrial animal encounter density / habitat use density).
Perceived bird risk	Value of the perceived bird risk landscape, calculated as log (bird encounter density / habitat use density).
Perceived combined risk	Value of the combined perceived risk landscape, which includes encounters with all three predator guilds listed above and encounters for which the guild was uncertain.

The first three variables were recorded in the field, whereas the remaining variables were obtained by overlaying the location of the scan with the relevant map. Encounter densities for the different predator guilds are based on all occurrence sampling of the locations of guild-specific alarm-calling bouts. Based on data exploration, we excluded the gray-shaded variables from the models of vigilance behavior.

countering extra-group males (Rose and Fedigan, 1995), and our data also support a strong sex difference (fig. 2.2). We therefore limited our analysis to data from adult females only ($n = 32$). Second, we defined vigilance to exclude scanning that was clearly aimed at food resources or social partners. Such restrictive definitions of vigilance have been criticized (Treves, 2000), but in our case, we had no a priori expectation that food-related or social vigilance should be responsive to the perceived risk landscapes, nor that their exclusion would produce biases in the occurrence of outwardly-directed, non-food vigilance. We do not claim that we have eliminated social vigilance from our data set, but rather we have reduced it as much as possible. Third, we excluded all samples occurring less than 10 min after an alarm-calling bout, during which heightened vigilance is likely to be reactive (i.e., monitoring a threat that is physically present at that moment). This 10-min time threshold is equal to the thresholds used in previous studies to characterize heightened antipredator vigilance following an alarm call (Blanco and Hirsch, 2006; Gaynor and Cords, 2012). We also considered longer 30- and 60-min time thresholds, but the results were qualitatively identical.

We analyzed vigilance behavior using generalized linear mixed models (GLMMs) with binomial error structures and logit link functions, implemented in the R package lme4 (Bates and Byrne, 2009), with parameter estimates obtained by the Laplace approximation. We used instantaneous

samples ($n = 42\,124$) during focal samples ($n = 2905$) as the unit of analysis. For all models, the response variable was the focal animal's activity state at the time of the instantaneous sample, coded as 1 (vigilant) or 0 (not vigilant). These binary responses were organized in groups of approximately 15 serial observations collected over the duration of one focal sample (we excluded focal samples with fewer than 10 observations). To account for within-focal-sample and within-focal-animal correlation in the response variable for this repeated-measures design, we fit a unique focal sample ID number and the focal animal's identity as random effects in all models. We began by constructing a null model of uniform risk (m1) and models for habitat-specific risk (m2), guild-specific risk (m3–m5), and combined risk (m6), all measured at the location of the instantaneous sample (table 2.1). Based on data exploration (fig. 2.3) and research by others (De Ruiter, 1986; Hirsch, 2002; Rose and Fedigan, 1995; van Schaik and van Noordwijk, 1989), we had reason to believe that the focal animal's vertical level would influence the occurrence of antipredator vigilance and that it could potentially interact with habitat type or the perceived risk landscapes. Therefore, we also considered a vertical-level model (m7), additive models that included vertical level and the different risk scenarios (m8–m12), as well as models with interactions between vertical level and risk (m13–m17) (table 2.1). We omitted variables that were somewhat redundant with this set of variables, including absolute height category and forest maturity index. We also omitted group size from the models because our exploratory analysis suggested that vigilance behavior did not vary linearly with group size (fig. 2.4), which is consistent with previous findings at this site (Rose and Fedigan, 1995). All variables included or considered for this analysis are summarized in table 2.2. We calculated model ranks, Akaike weights, and evidence ratios on the basis of AICc values (Burnham and Anderson, 2002; Burnham, Anderson, and Huyvaert, 2011).

2.3 RESULTS

2.3.1 ALARM-CALLING BOUTS AND PREDATOR GUILDS

Alarm-calling bouts directed at birds were approximately three times more frequent than alarm-calling bouts directed at snakes or other terrestrial animals (fig. 2.5). Most alarm-calling bouts directed at snakes or other terrestrial animals involved multiple animals (75 % and 59 %, respectively), but fewer bouts directed at birds involved multiple animals (36 %) (fig. 2.5). The global chi-squared goodness-of-fit tests comparing observed and expected frequencies of alarm-calling bouts among vertical levels and absolute height categories deviated significantly from null expectations for all predator guilds (table 2.3). Pairwise comparisons of observed predator encounter frequencies among absolute height categories and vertical levels revealed several noteworthy deviations from expected frequencies.

Consistent with expectations, alarm-calling bouts directed at the bird predator guild were more likely to originate in the high vertical level and absolute height categories and less likely to originate in the low vertical levels (figs. 2.6a and 2.6b) and absolute height categories (figs. 2.6c and 2.6d). An opposite pattern was evident for both the snake and terrestrial mammal predator guilds. For habitat type, the chi-squared tests revealed that encounters with the bird predator guild were less frequent than expected whereas encounters with the terrestrial predator guild were more frequent than expected in early-stage forest (table 2.3, fig. 2.11).

2.3.2 PERCEIVED RISK LANDSCAPES

The perceived risk landscapes for each predator guild and for combined risk are presented in fig. 2.7 (see also figs. 2.1 and 2.8). For the bird and combined predator guilds, high-risk zones showed greater proportional coverage of mature forest and lesser proportional coverage of grassland and early forest than low-risk zones (fig. 2.10a). For the terrestrial predator guild, high-risk zones showed greater proportional coverage of the younger habitat classes, but the pattern was not as clear as in the case of bird risk or combined risk (fig. 2.10a). For the snake predator guild, the different risk zones did not clearly differ in their habitat composition (fig. 2.10a). These patterns were corroborated by examining the distributions of forest maturity indices in each zone. For the bird and combined predator guilds, high-risk zones were more mature and low-risk zones were less mature, whereas the opposite was observed for the terrestrial predator guild (fig. 2.10b).

2.3.3 VIGILANCE AND PREDATION RISK

Table 2.1 summarizes the model selection on our candidate set of models for vigilance behavior. No model that included an interaction effect was supported over a simpler, otherwise identical model without the interaction effect. Therefore, we do not consider the subset of models with interaction effects further (m13–m17). All models that included vertical level were supported over all models excluding this variable. The estimated coefficients for the subset of models that include vertical level, one guild or habitat risk scenario, and no interaction effects (m8–m12) are shown in fig. 2.9. The highest-ranked model, m12, included the fixed effects vertical level and combined risk landscape (table 2.1). Among the remaining models, only m11, which included both bird risk and vertical level, was identified as remotely plausible (m11: $\Delta \text{AIC}_c = 5.47$; all other models: $\Delta \text{AIC}_c > 14$). However, m12 had considerably more empirical support. Consistent with our exploratory analysis (fig. 2.3), animals were more likely to be vigilant in the low vertical level compared with the middle and high levels, which did not differ from each other. Furthermore, higher combined or bird risk landscape values predicted greater occurrence of vigilance. Habitat type and the risk landscape

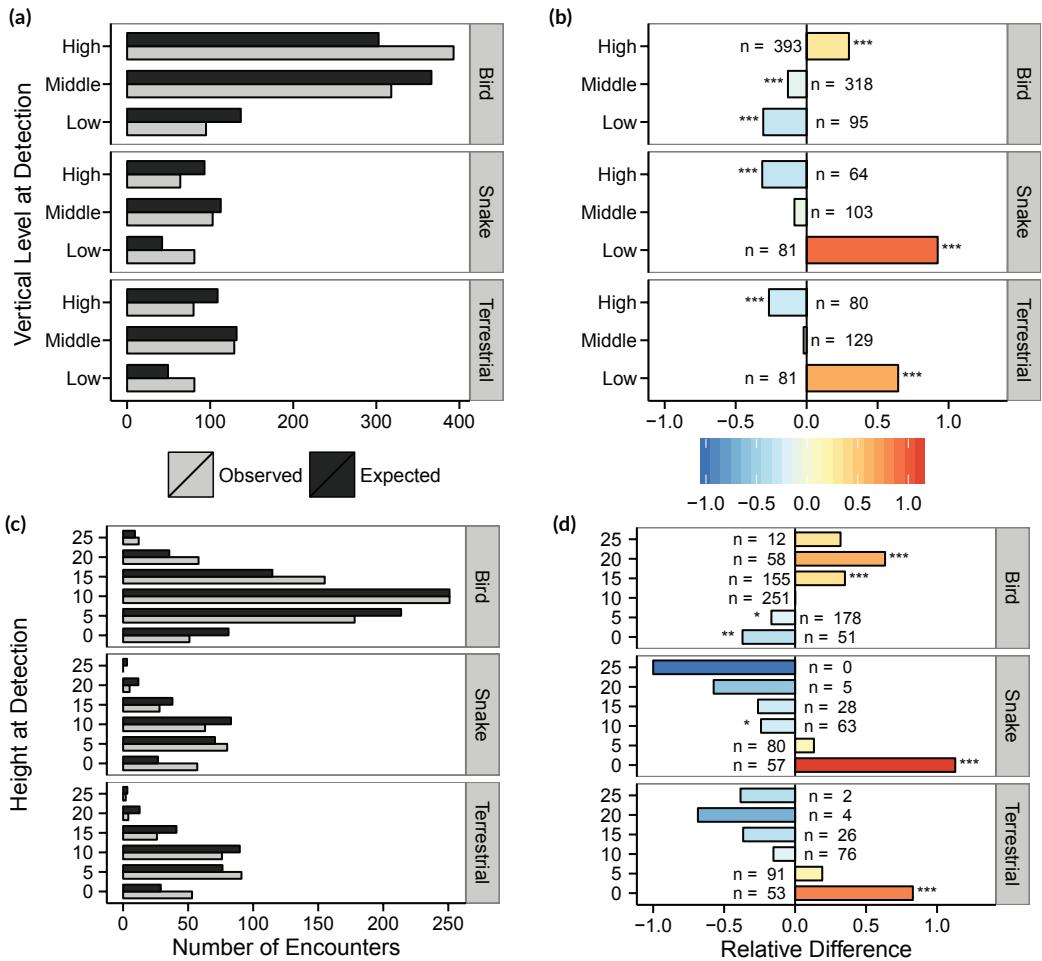


Figure 2.6: Observed and expected number of encounters (i.e., distinct alarm-calling bouts) for snake, terrestrial, and bird predator guilds, stratified by (a) vertical level and (b) absolute height above ground (in 5-m increments). Expected values are based on the proportional use of each vertical level or absolute height category during systematic sampling. Relative difference calculated as (observed – expected)/expected for (c) vertical level and (d) absolute height category. Sample sizes in the relative difference plots indicate the observed number of encounters for that condition. Significance stars indicate adjusted P values for pairwise comparisons among categories (* P_{adj} < 0.05, ** P_{adj} < 0.01, *** P_{adj} < 0.001).

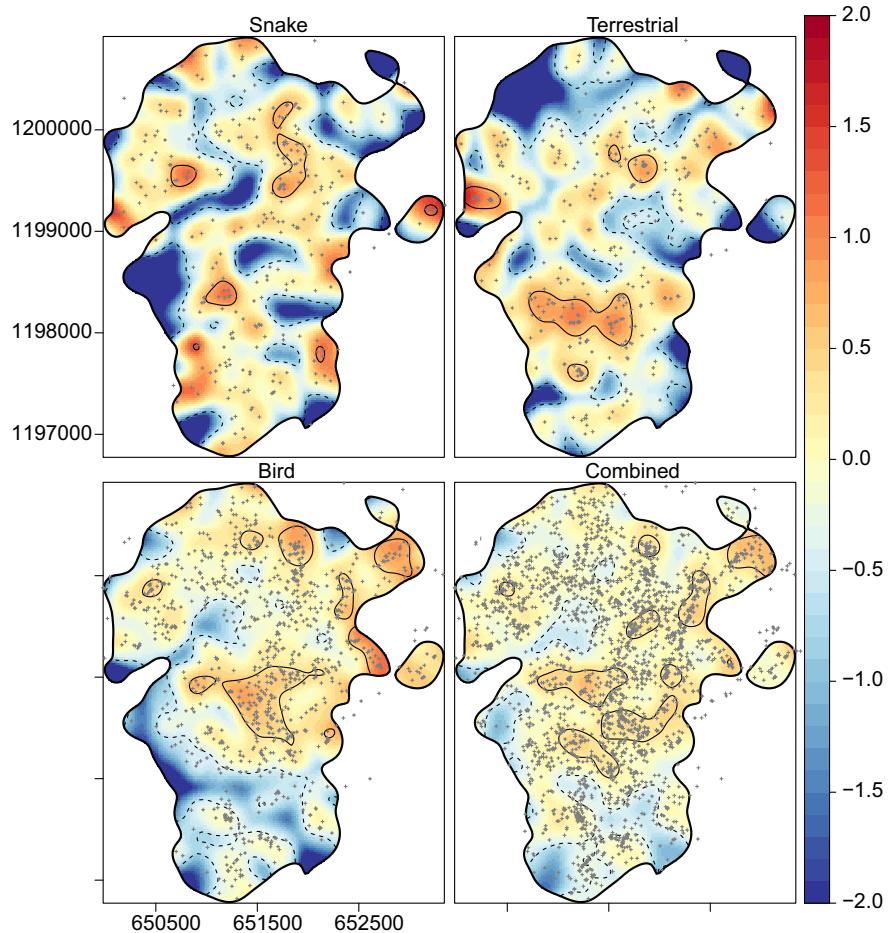


Figure 2.7: Log-relative risk functions for each predator guild based on alarm-calling data and given the underlying pattern of habitat usage, with asymptotic tolerance contours showing zones of heightened risk (solid) and reduced risk (dashed). Small gray crosses indicate the locations of recorded alarm-calling bouts. The “combined” guild includes the other 3 guilds as well as all alarm-calling bouts that could not be confidently assigned to a guild.

values for snakes and terrestrial animals were consistently poor predictors of vigilance behavior, and their inclusion did not improve model performance compared with a null model of uniform risk. For the highest-ranked model (m12), the marginal and conditional R^2 , as defined by Nakagawa and Schielzeth (2013) for GLMMs, were $R^2_{GLMM(m)} = 0.0147$ and $R^2_{GLMM(c)} = 0.415$. The corresponding interpretation is that in the best model, 1.47 % of the variance in vigilance was explained by the fixed factors, and 41.5 % of the variance was explained by both fixed and random factors.

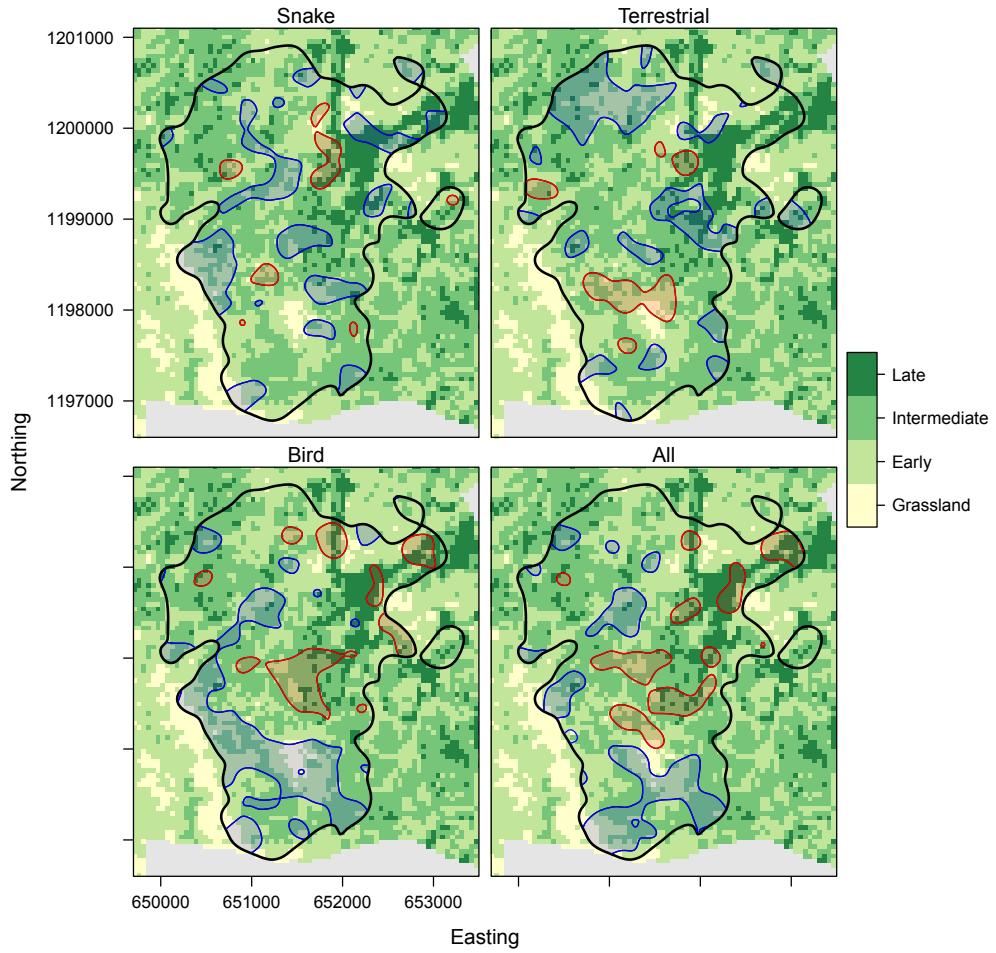


Figure 2.8: High-risk zones (red) and low-risk zones (blue) for each predator guild plotted over a categorical habitat map. The thick black line encloses the study area.

2.4 DISCUSSION

2.4.1 PREDATOR ENCOUNTERS AND PERCEIVED DANGER

As others have noted (Isbell, 2005; Janson, 1998), observations of predator encounters and alarm-calling are not reliable indicators of intrinsic risk, which requires long-term mortality data and/or independent observations on predator species to evaluate accurately. However, our data suggest that there was considerable variability among predator guilds in how reliably the occurrence of an alarm call signified actual danger. Many bird alarms for which we were able to identify the target were directed at presumably nondangerous species such as crested guans (*Penelope purpurascens*), vultures (*Coragyps atratus* and *Cathartes aura*), and raptors too small to pose a legitimate threat (e.g., double-

toothed kite, *Harpagus bidentatus*) (fig. 2.12). To a lesser extent, this was also true for the terrestrial guild. By contrast, snakes were encountered less frequently, but there were relatively few alarm calls given to nondangerous snakes. It seems likely that flying birds would be more readily misidentified by the monkeys because they are fast moving and possibly farther away than potential threats in the snake or terrestrial guilds. There may be negligible cost to erring on the side of caution by emitting an alarm call whenever the animal is startled by a large bird flying nearby, even if most such cases involve nondangerous birds.

It is striking that despite the frequent “false-alarms” at non-dangerous birds, vigilance behavior was more responsive to the perceived risk landscape for birds than for snakes or terrestrial animals. Raptors are the primary predators of many neotropical primate species (Ferrari, 2009; Hart, 2000, 2007). Our finding that proportionally fewer bird encounters involve multiple calling animals is consistent with a previous study (Fichtel et al., 2005) and with the idea that neotropical primates are less likely to mob raptors than other types of predators, perhaps because mobbing is relatively ineffectual against raptors (Ferrari, 2009). The true impact of raptor predation on our study animals may be reduced relative to some sites because all of the large-bodied raptor species that are preeminent primate hunters are absent from SSR, including the harpy eagle (*Harpia harpyja*), crested eagle (*Morphnus guianensis*), and hawk-eagles (*Spizaetus* spp.) (Ferrari, 2009; Fichtel, 2012; Hart, 2000, 2007). Nonetheless, aerial predators appeared to contribute more substantially to the combined perceived risk landscape than did the other predator guilds, which reinforces the idea that raptors exert major selective pressures on neotropical primates (Hart, 2007). We avoid making further quantitative inferences about the degree of perceived risk posed by the different predator guilds because we do not know if the monkeys attribute equal weight to each alarm-calling bout, as we have done. For example, we do not know if “false alarm” bouts by startled monkeys at nondangerous species are quickly forgotten, or if, by raising the specter of a legitimate threat, such bouts make real contributions to shaping the perceived risk landscape. The challenge of attributing meaningful “weights” to different alarm-calling bouts, each of which is unique in its own way, may be a fruitful direction for future studies of perceived risk in primates.

2.4.2 SPATIAL CHARACTERISTICS OF ALARMS AND RISK ZONES

The spatial distribution of alarm-calling bouts did not reveal straightforward relationships between habitat type and guild-specific risk. High- and low-risk zones for snakes were entirely undifferentiated from the surrounding landscape in terms of habitat composition, which indicates that the likelihood of encountering snake predators did not vary with habitat type (see also fig. 2.11). The picture was slightly more complicated for bird and terrestrial predation risk, and by extension, for all

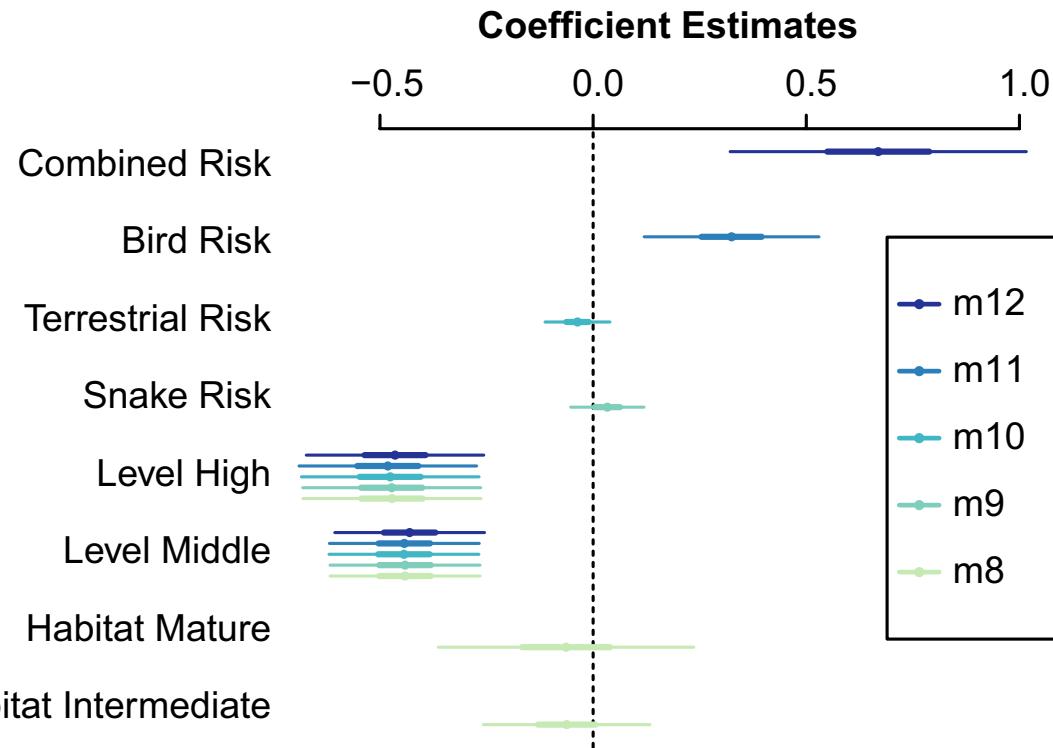


Figure 2.9: Estimated coefficients for the subset of models for the occurrence of vigilance that include vertical level, 1 guild or habitat risk scenario, and no interaction effects (m8–m12). Estimates are relative to the baseline categories “Low” for vertical level and “Early Forest” for habitat. Vigilance was coded as 1 (vigilant) or 0 (not vigilant). All models include the random effects focal sample number and focal animal. Thick lines show ± 1 standard deviation; thin lines show ± 2 standard deviations. Model m12 received greatest empirical support.

guilds combined. For birds, early-stage successional forest carried reduced encounter risk (fig. 2.11). This could reflect the habitat preferences or densities of birds that are likely to elicit alarm-calling responses by the monkeys. For example, several of the large bird species that were commonly encountered (e.g., crested guans, *P. purpurascens*) or that provoked intense alarm responses (e.g., collared forest falcon, *M. semitorquatus*; gray-headed kite, *L. cayanensis*; spectacled owl, *P. perspicillata*) seemed to be most common in mature forest, and there appeared to be few suitable perches for such species in very young, low-canopy forest. The tendency for young forest to carry greater risk for the terrestrial guild (fig. 2.11) may appear somewhat puzzling, but we believe that this result was heavily influenced by very frequent encounters with some non-dangerous species that sometimes elicited alarm-calling bouts and were common in young forest, including white-nosed coatis (*Nasua narica*), white-tailed deer (*Odocoileus virginianus*), and agoutis (*Dasyprocta punctata*) (fig. 2.12). However, we lack independent location data for these and other potentially threatening species to analyze their habitat associations. In a system with fewer predator species, it may be possible to tease apart species-level contributions to the perceived risk landscape that may have been obscured by our use of multi-

Table 2.3: Pearson's chi-squared goodness-of-fit tests to determine whether observed predator encounter frequencies among microhabitat categories differ from expected frequencies, which are based on systematically-sampled usage. Due to small sample sizes for some categories, the p-values for these tests were computed via Monte Carlo simulations with 10 000 replicates. Where this global test is significant, we show the results of pairwise comparisons among categories using asterisks in fig. 2.6 and fig. 2.11.

Microhabitat Variable	Predator Type	χ^2	P-value
Vertical level	Bird	46.077	< 0.001
	Snake	45.864	< 0.001
	Terrestrial	28.217	< 0.001
Absolute Height	Bird	46.422	< 0.001
	Snake	49.595	< 0.001
	Terrestrial	36.755	< 0.001
Habitat Type	Bird	9.589	0.009
	Snake	0.725	0.693
	Terrestrial	6.177	0.046

species predator guilds. Taken together these findings suggest that, for our study system, habitat type is not a particularly accurate cue on which to base behavioral decisions for reducing predation risk for any of the three guilds.

2.4.3 Is VIGILANCE BEHAVIOR PREDICTIVE?

The predictive model that incorporated the perceived predation risk function for all guilds combined was strongly supported over null models of uniform risk or habitat-specific risk for predicting the occurrence of vigilance. This finding suggests that vigilance behavior was heightened in higher-risk areas in the absence of an actual threat, and is therefore at least partly predictive. Moreover, the combined risk model had considerably more empirical support than any of the guild-specific risk models, which suggests that the “true” perceived risk landscape is built by integrating information about risk from multiple predator guilds. However, the marginal and conditional R^2 values of the highest-ranked model provide an important insight that must be considered: most of the data variability existed in the random effects, whereas the amount of variation explained by the fixed effects—vertical level and risk landscape—was rather small (1.47 %). Does this mean that the effects of the predictor variables on vigilance behavior in our most-supported model are in fact trivial? Abelson (1985) discusses the disparity between the magnitude of R^2 values and their practical meaning in cases where small, chronic influences produce meaningful cumulative outcomes. Because long-distance scanning is a relatively brief, low-cost behavior, the animals may benefit from continually overestimating perceived risk (Bouskila and Blumstein, 1992), weakening the linkage between fluctuating levels of

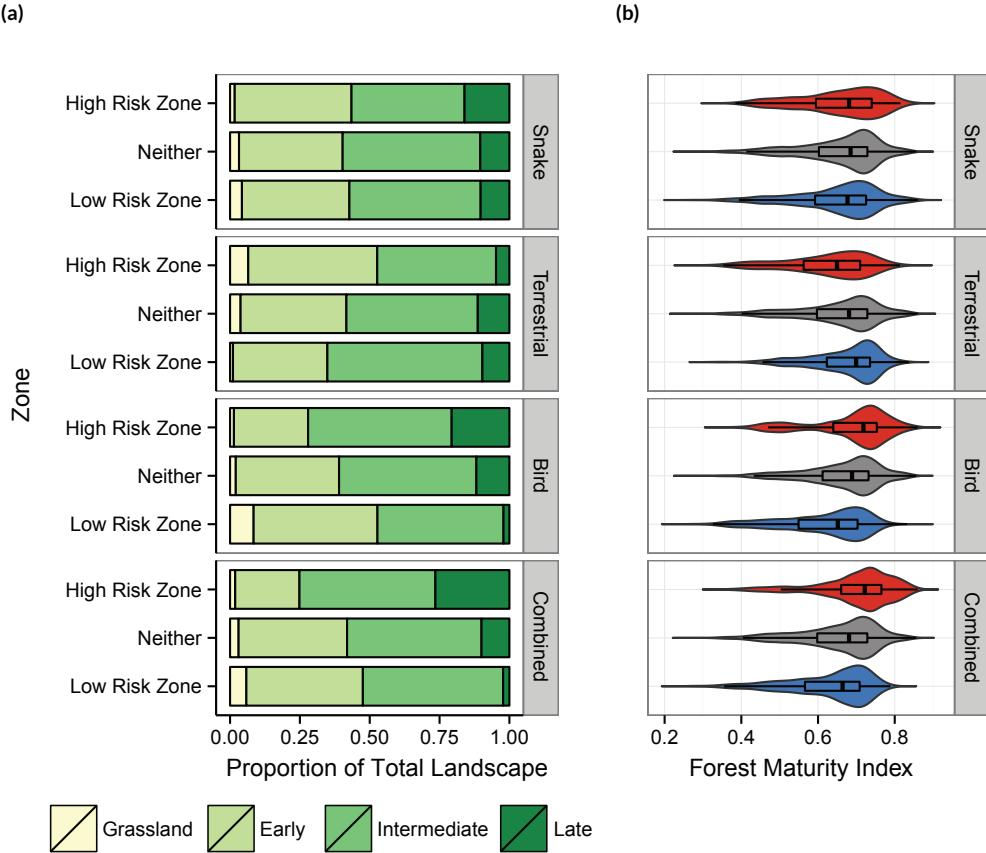


Figure 2.10: Ecological characterization of high-risk, low-risk, and neither zones (neither heightened nor reduced risk) for snake, terrestrial, bird, and combined predator guilds, including (a) proportional coverage of four different habitat categories; and (b) violin plots showing the probability densities of forest maturity indices within each zone. Black boxplots show medians (thick vertical bars) and interquartile ranges (box hinges), and 1.5 times the interquartile range (whiskers).

perceived risk and predictive vigilance behavior. Below, we discuss two additional reasons why our best vigilance model may have had low explanatory power.

First, we have not considered the role that different predator encounter histories and risk perceptions among individual animals might play in modulating vigilance behavior. Although some primates adjust alarm-calling behavior based on the degree of danger (Casar et al., 2012; Papworth et al., 2008) or the ignorance of other group members (Crockford et al., 2012; Papworth et al., 2008; Wich and de Vries, 2006), we believe it is unlikely that information about every alarm-calling bout will be shared perfectly among all group members. Accordingly, there is probably significant inter-individual variation in perceived risk landscapes. Accounting for such variation by tracking individual encounter histories was beyond the scope of this study, but future work may improve on our

findings by relating the informational environment to variation in individual risk perceptions and behavioral responses.

Second, it is widely acknowledged that vigilance in primates serves a variety of functions (Gaynor and Cords, 2012; Treves, 2000). Realistically, we should not expect vigilance behavior to be finely tuned to any single predictor variable, including a perceived risk landscape, which is likely to be an imprecise abstraction to the animals themselves and which we can only estimate inexactly. Our goal in this study was to determine whether spatially explicit perceived risk functions provide meaningful information for predicting the occurrence of antipredator vigilance. Due to data limitations and for the sake of simplicity, our vigilance models have not accounted for many other purported influences on primate vigilance behavior, including dominance relationships, kinship, number of neighbors (Gaynor and Cords, 2012), spatial position relative to the group center (Hirsch and Morrell, 2011), and the likelihood of an intergroup encounter (Rose and Fedigan, 1995). Although we took steps to limit the effects of some of these factors, we have no doubt that substantial variability remained in the data due to factors that we did not consider. Thus, the low marginal R^2 suggests that our best model was an oversimplification of a complex biological reality, but it does not invalidate our primary conclusions. Given that the estimated effects of vertical level on vigilance behavior agreed with our intuition and with previous studies (De Ruiter, 1986; Hirsch, 2002; Rose and Fedigan, 1995; van Schaik and van Noordwijk, 1989), and that the estimated effects of the combined perceived risk landscape on vigilance were significantly positive in our highest-ranked model, our results demonstrate predictive antipredator vigilance that varied in response to a perceived risk landscape.

Behavioral strategies to mitigate perceived predation risk can reveal important information about predator-prey dynamics. Here we have shown that in white-faced capuchins, one such behavior, vigilance, varies with spatial fluctuations of perceived risk, albeit loosely. Our analytical approach could be improved with more detailed ecological characterization of risk zones, independent data on predator distributions, and finer quantification of perceived risk for each encounter. Future work may build on these results by incorporating perceived predation risk into predictive models of space use and habitat selection, which may in turn shed light on a wide range of ecological processes. For example, Willems and Hill (2009) have shown that, in vervet monkeys (*Chlorocebus pygerythrus*), the effects of perceived risk may exceed those of resource distribution in driving space use patterns.

2.4.4 IMPLICATIONS AND FUTURE DIRECTIONS

In view of the SSR's unique history as a pioneer project for large-scale habitat restoration (Janzen, 2000), the findings of this study also have implications for restoration ecology, because they highlight spatial variability in the pressures faced by a primate population as it repopulates a regenerating,

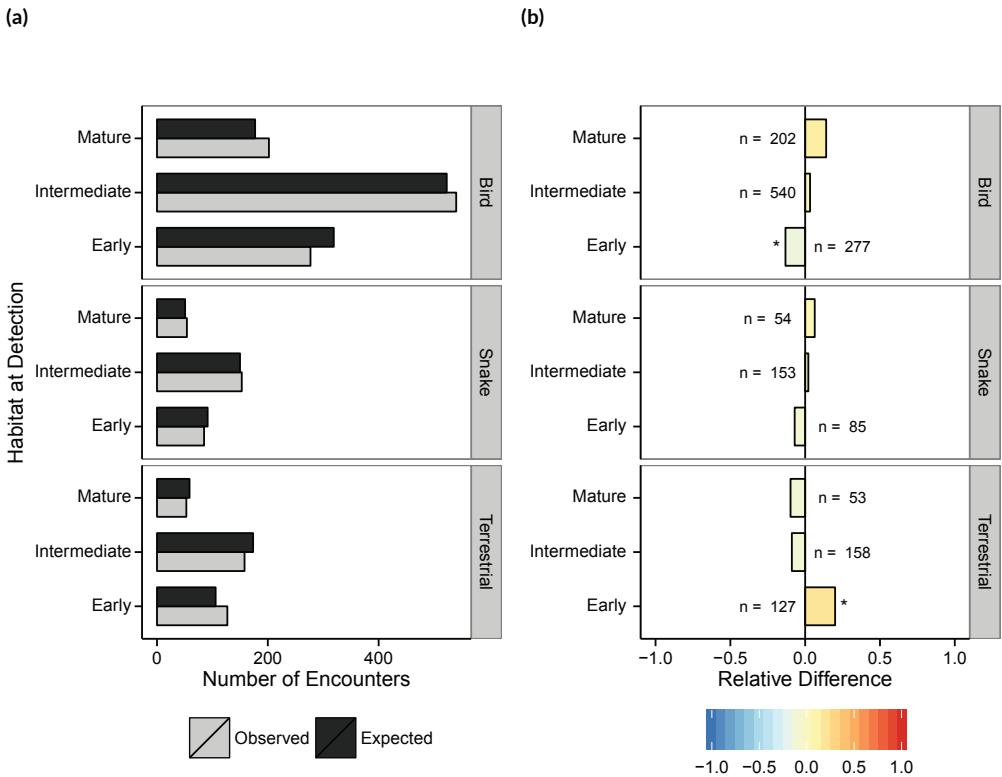


Figure 2.11: (a) Observed and expected frequencies of alarm-calling bouts for snake, terrestrial, and bird predator guilds, stratified by habitat type. Expected frequencies are based on the proportional use of each habitat type during systematic sampling. (b) Relative difference calculated as $(\text{observed} - \text{expected}) / \text{expected}$. Sample sizes in the relative difference plot indicate the observed number of alarm-calling bouts for that condition. Significance stars indicate Holm-Bonferroni adjusted p-values for pairwise comparisons among categories (* $p_{adj} < 0.05$).

mosaic habitat. Previous research in the SSR has found that while sympatric primate species *Alouatta palliata* and *Ateles geoffroyi* are largely confined to mature forest, *C. capucinus* readily exploits a wide range of regenerating habitats including forest as young as 14 years (Sorensen and Fedigan, 2000) and open, grassy areas. Our results suggest a possible benefit to *C. capucinus* from exploiting these disturbed habitats: perceived predation risk from aerial predators and overall predator encounter rates are reduced in younger habitats. Thus, the ability to exploit disturbed buffer or edge habitats, which are often given low conservation priority, may provide unexpected advantages to adaptable species, such as refuge from some types of predators.

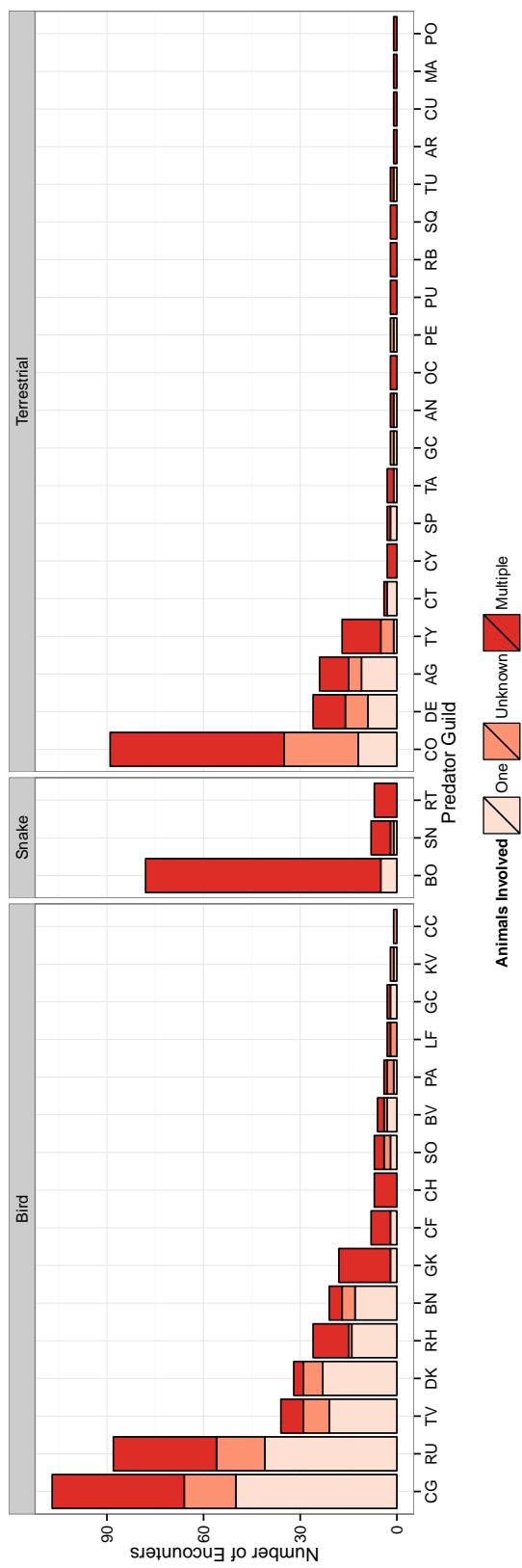


Figure 2.12: Number of alarm-calling bouts provoked by different species. All encounters for which the target species could not be identified are excluded. Note that these counts are biased against secretive species such as felids. **Birds:** CG: crested guan (*Penelope purpurascens*), RU: unidentified diurnal raptor, TV: turkey vulture (*Cathartes aura*), DK: double-toothed kite (*Harpagus bidens*), RH: roadside hawk (*Rupornis magnirostris*), BN: non-dangerous bird (e.g. dove, woodpecker, etc.), GK: gray-headed kite (*Leptodon cayanensis*), CF: collared forest falcon (*Micrastur semitorquatus*), CH: crane hawk (*Geranospiza caerulescens*), SO: spectacled owl (*Pulsatrix perspicillata*), BV: black vulture (*Coragyps atratus*), PA: parrot (subfamily Arinae), LF: laughing falcon (*Herpetotheres cachinnans*), GC: great curassow in tree (*Crax rubra*), KV: king vulture (*Sarcogyps calvus*), CC: crested caracara (*Caracara cheriway*). **Snakes:** BO: boa (*Boa constrictor*), SN: non-dangerous snake (Colubrids), R: rat-tailed deer (*Odocoileus virginianus*), AG: agouti (*Dasyprocta punctata*), DE: white-tailed deer (*Odocoileus virginianus*), DE: white-tailed deer (*Odocoileus virginianus*), DE: Baird's tapir (*Tapirus bairdii*), GC: great curassow walking on ground (*Crax rubra*), CY: coyote (*Canis latrans*), SP: spider monkey (*Ateles geoffroyi*), TA: Baird's tapir (*Tapirus bairdii*), GC: great curassow walking on ground (*Crax rubra*), AN: anteater (*Tamandua mexicana*), OC: ocelot (*Leopardus pardalis*), PE: collared peccary (*Pecari tajacu*), PU: puma (*Puma concolor*), RB: rabbit, SQ: squirrel (usually *Sciurus variegatoides*), TU: turtle/tortoise, AR: armadillo (*Dasyurus novemcinctus*), CU: cat of unknown species, MA: margay (*Leopardus wiedii*), PO: porcupine (*Sphiggurus mexicanus*).

One way to think of an animal is as an energy processor: it acquires energy from its environment and allocates this energy among maintenance, growth, and reproduction, with the end result that a portion of the ingested energy is converted into (somatic or reproductive) biomass.

P. Yodzis and S. Innes, 1992

3

Energy returns on foraging in white-faced capuchins, *Cebus capucinus*

3.1 INTRODUCTION

A distinguished body of theoretical work predicts that natural selection should strongly favor efficiency in individual foraging behavior (Emlen, 1966; MacArthur and Pianka, 1966; Pyke, 1984; Pyke et al., 1977; Schoener, 1971). The degree of optimality in foraging behavior may be evidenced most clearly by the animal's decisions of which food items to consume, which food patches to visit, how long to spend in a given patch, and how to move between food items or patches (Pyke et al., 1977). Although we expect that animals should forage efficiently, their actual performance is subject to constraints imposed by their physical, ecological, and social environments, as well as by intrinsic factors such as cognitive ability (Janson, 2000; Janson and Byrne, 2007; Poucet, 1993; Zuberbühler and Janmaat, 2010), individual foraging history (Janmaat, Ban, et al., 2013; Janmaat, Byrne, et al., 2006), sex (Key and Ross, 1999; Lees et al., 2012), and life stage (Gittleman and Thompson, 1988). As a consequence of these complex and interrelated factors, the study of foraging efficiency by animals in natural settings is notoriously problematic. Nonetheless, our growing understanding of locomotor energetics and recent advances in nutritional ecology (Rothman et al., 2012) have facili-

tated field-based studies of one fitness currency related to optimal foraging theory: the flow of energy (Brown et al., 2004; Houston and McNamara, 2014; Humphries and McCann, 2014).

The fundamental currencies on which selection operates to hone foraging efficiency may differ in their details across species, but there is little doubt that energy budgets—defined by the intake of metabolizable energy relative to its expenditure—are universally important fitness currencies throughout the animal kingdom (Yodzis and Innes, 1992). For example, yellow baboon (*Papio cynocephalus*) individuals whose diets maximize daily energy gain have longer reproductive lifespans, higher survival rates, and greater lifetime reproductive output than group mates who forage less optimally (Altmann, 1991). As in other animals, primates gain energy from the macronutrients contained in the foods that they eat (Chapman, Rothman, et al., 2012; Lambert, 2011; Rothman et al., 2012). The energetic costs of basic life processes fluctuate over time, but another important source of variability arises from changes in the animal's behavior (Goldstein, 1988). For most primates, the activity budget is a major determinant of costs in the energy balance equation: animals are expected to expend more energy per unit time the more active they are and the farther they move (Leonard and Robertson, 1997). The locomotor energy costs associated with traveling and foraging can be substantial for arboreal quadrupeds (Hanna and Schmitt, 2011). Janson (1988) estimated that capuchins (*Cebus* and *Sapajus* spp.) expend approximately twice as much energy per unit time when feeding/foraging than when resting, and on top of this basal cost, every 15 m of travel further expends the equivalent of 1 min of resting time. Arboreal travel presents a unique set of circumstances that increase transport costs compared to terrestrial travel on flat ground: frequent changes in vertical height (e.g., climbing) (Hanna, Schmitt, and Griffin, 2008); increased use of energy-demanding postures on oblique, vertical, or flexible substrates (Garber, 2011); and loss of momentum during the takeoffs and landings associated with gap-crossing (Demes et al., 1995). For example, in squirrel monkeys (*Saimiri boliviensis*), the energetic cost of transport during climbing is more than double the cost of walking on a horizontal surface, and this cost-of-transport ratio for climbing increases with body mass (Hanna and Schmitt, 2011).

In view of these potentially large locomotor costs, it is commonly assumed that the movement strategies used by animals during foraging are, if not optimal, then at least verging on an efficient solution to maximizing their energy balance, given their current environmental and intrinsic constraints (Dickinson, 2000; Nathan et al., 2008). Thus, strong and consistent variation in energy expenditure rates or energy intake rates during foraging could reveal important information about the nature of these constraints and their effects on the organism's biology. For example, the locomotor costs for an arboreal animal may vary among habitats due to the differential availability of canopy-to-canopy linkages, preferred substrates, and foliage for concealment. In strongly seasonal environ-

ments, habitat-specific microclimates that facilitate or impede efficient movement may be exacerbated by such seasonal differences in plant phenology. Among studies that deal with the foraging efficiency of primates, most attention has focused on the effects of the social environment (e.g., group size, dominance rank, competitive regimes) and/or the distribution of food resources (e.g., food patch spatial configuration, size, abundance, predictability) (reviewed by Oates, 1987 and Chapman, Rothman, et al., 2012). Consequently, climatic and structural constraints are perhaps underappreciated influences on primates' small-scale movement patterns and foraging efficiency.

Here, we quantify rates of energy expenditure and intake to examine influences on net energy returns during foraging in a Neotropical primate, the white-faced capuchin (*Cebus capucinus*). To meet our goal of assessing the importance of various predictor variables, our analyses focus on the possible effects on energy return of climatic seasonality, habitat, sex, and social group size. Previous studies on the balance between energy gain and expenditure in primates have generally considered the question from coarse or dissimilar spatiotemporal scales. For example, energy intake rates are typically calculated from brief focal-animal samples whereas expenditure rates have been calculated from groups' daily travel distances and activity budgets over monthly (or longer) time periods (Janson, 1988; Wright, Robbins, et al., 2014), metabolic indicators in urine (Grueter et al., 2014; Knott, 1998), body appearance (Heesen et al., 2013), or some combination of these methods (Miller et al., 2006). This longer scope has the advantage of treating energy balance as a persistent physical condition over a fitness-relevant time period. However, the time-scale disconnect between the intake and expenditure components in the currency calculation raises questions about how well such approaches are matched to the biological system that they are modeling. In contrast, our study treats brief foraging bouts as the unit of analysis for both components of the currency calculation: we quantify intake using the energy content of all ingested foods, and we quantify expenditure using estimates of basal and locomotor energy costs during the bout based on continuous changes in activity and time-matched movement trajectories. The small spatiotemporal focus of our study differs in scope from these studies in that we do not seek to quantify energy balance as a general, integrative condition for specific individuals over an extended time period. Rather, the question addressed by our study is: how does the net energetic return during a typical bout of foraging vary according to season, habitat type, sex, and group size?

3.2 METHODS

3.2.1 STUDY SUBJECTS AND SITE

We studied five groups of white-faced capuchins from January to December 2011, with 404 group-observation days spread approximately evenly among groups and months. The groups occupied adjacent home ranges in the Santa Rosa Sector (SSR) of the Área de Conservación Guanacaste in north-western Costa Rica. Strong climatic seasonality in this region brings about extensive phenological changes in the deciduous tree species that dominate the study area (Janzen, 1988). Selective logging, clearing, fire damage, and other human activities were common in the study area until the 1980s (Janzen, 2000). The spatially variable impact of these past disturbances shaped the current landscape, producing large areas of early- and intermediate-stage regenerating forest, smaller patches of old-growth semi-evergreen forest, and a few areas of very young grassland/scrub (Campos, Bergstrom, et al., 2014).

3.2.2 DATA COLLECTION

OBSERVATIONAL DATA

FAC and eight field assistants recorded individual foraging paths and feeding data from sexually mature animals ($N = 46$) using focal animal sampling in which one or two observers followed a single animal for 15 min. FAC trained the assistants to collect data independently and carried out regular checks of inter-observer reliability (see Campos and Fedigan, 2013, 2014, for further details). During focal sampling, one observer recorded the focal animal's movement path using the track logging function on a handheld GPS receiver (Garmin GPSMAP 62s) with the recording method set to fixed 10-s intervals. The observer followed approximately 5 m behind the focal animal's position projected onto the ground, moving whenever the animal moved and following along the animal's path. Our study animals were so fully habituated to human presence that they were unbothered by even very close human proximity within 1 m, although we did not intentionally approach the animals to such close distances. Therefore, for the movement paths analyzed here, we are confident that the observer was not "driving" the focal animal's path by triggering avoidance behavior. In very rare cases when the animal appeared to be persistently avoiding the observer, we aborted the sample and discarded the track. This only occurred with males that had recently immigrated and were not as habituated to human presence.

The same observer or a second observer recorded the feeding behavior of the focal animal. We recorded each food item consumed during the 15-min sample, noting the species whenever pos-

sible, as well as the number of separate ingestions required to consume the item. We defined food items as individual food units (e.g., one whole fruit or insect). Invertebrate food items could not be reliably identified beyond broad categories with sufficient regularity. We used four invertebrate categories: “ant/termite” (all tiny, embedded ants and termites that were typically extracted and consumed rapidly from sticks); Lepidoptera larvae; Hymenoptera larvae (typically embedded in the nests of *Polistes* wasps); and “other” (medium- to large-bodied invertebrates such as beetles, crickets, and cockroaches, as well as various arachnids). We kept a continuous record of the focal animal’s activity state and visibility status, which we used to calculate the total time during which the animal was both visible and actively “foraging” (i.e., feeding, searching for food, or moving between feeding sites) during the sample.

NUTRITIONAL CONTENT OF FOOD ITEMS

MLB and several field assistants collected samples of commonly eaten fruits, seeds, flowers, and invertebrates for nutritional analysis. Since capuchins regularly spit out or discard the husk, skin, or seeds of certain foods, the items were carefully separated into eaten and discarded portions based on observations of the monkeys feeding behavior. The nutritional analysis was carried out by Dairy One (Ithaca, New York), and additional details on sample collection, preparation, and analysis can be found in Bergstrom (n.d.). Using only the portions consumed, we calculated estimates of metabolizable energy per g dry matter (E_{gDM}) following Janson (1985):

$$E_{gDM} = \left(0.1674 \times (\%DM_c + \%DM_p) \right) + \left(0.3766 \times \%DM_f \right) \quad (3.1)$$

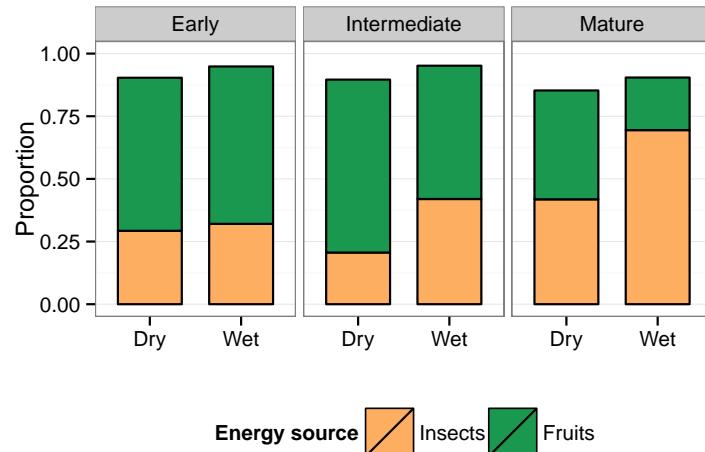
where $\%DM_c$ is the percent dry mass of soluble carbohydrates, $\%DM_p$ is the percent dry mass of protein, and $\%DM_f$ is the percent dry mass of fats. We used these values to calculate total per-item metabolizable energy:

$$E_{item} = E_{gDM} \times m_{DM} \quad (3.2)$$

where m_{DM} is the mean mass (g) of dry matter actually consumed in a single food item.

During focal samples, our study animals consumed 74 identified types of plant food items (primarily fruits and seeds) representing 70 different species. The nutritional analysis, in combination with previously published data for additional food items (McCabe, 2005; Vogel, 2005), enabled us to match 53 of these plant food items with per-item energy values. Twenty-one additional plant food items were eaten and identified during focal samples but were not analyzed for energy content. We estimated per-item energy values for seven of these using the values of analyzed congeners adjusted for mass differences, if any, between the two related species. Two more identified but unanalyzed

(a)



(b)

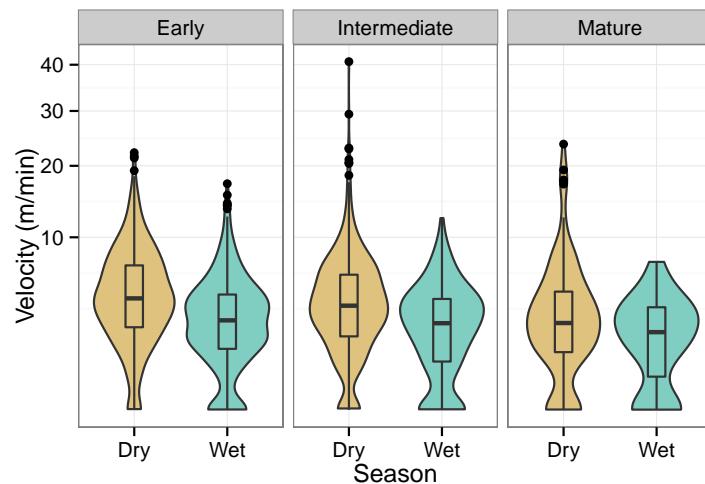


Figure 3.1: Concurrent changes in the energetic resource base and travel velocities, stratified by season and habitat type. (a) Proportion of the total energy ingested from insects and invertebrates. The proportions do not sum to one because of the small contributions of seeds, flowers, and other animal food items. (b) Violin plots and box plots of overall travel velocities during focal samples, each of which contributes one point to the plot.

species consisted of pith, which varied continuously in length and thickness; for these we assigned energy values per bite rather than per item. The remaining 12 unanalyzed plant species and any unidentified plant food items were assigned per-item energy values at the median for all measured fruits, seeds, or flower species, respectively. Food items belonging to these estimated categories contributed about only about 4 % of the total plant-based energy ingested over the course of the study because they were eaten very rarely or, for commonly eaten grass seeds, the energy content was estimated to be very small. All invertebrate food items in the “ant/termite” category were assigned the energy value for the frequently consumed *Pseudomyrmex* ant (McCabe, 2005). Each food item in the other three invertebrate categories was assigned an energy value based on the number of separate bites needed to consume the entire item. We provide justification for the per-bite energy values and miscellaneous other food item categories in Appendix A.

3.2.3 DATA ANALYSIS

TRACK FILTERING AND CHARACTERISTICS

Spatial imprecision is inherent in GPS-derived animal location data, and a variety of methods for identifying unrealistic movement patterns and improving data quality have been developed (reviewed by Frair et al., 2010). Most of these solutions are intended to screen telemetry data that have been collected automatically by GPS collars, the performance of which may be strongly affected by the animal’s behavior and the collar’s orientation (Heard et al., 2008). Because we could verify before and after each 15-min focal sample that the GPS receiver had an adequately good positional fix, our trajectories generally did not have large data gaps and/or extended periods of high positional uncertainty—problems typically associated with GPS collar data. However, our small-scale and temporally dense data had a variety of different challenges that needed to be addressed. Janmaat, Ban, et al. (2013) provide detailed compilation of data-quality issues that arise when an animal’s movement path is recorded by observers following on foot with a recreational-grade GPS receiver. In brief, our principal problems were occasional “outlier” points that suggested unrealistic travel speeds and continuous recording of small movement steps while the receiver was stationary (i.e., pseudorandom noise). We applied a four-stage filtering and smoothing procedure to each 15-min trajectory to remove these likely errors (see Appendix A for details). We intersected each smoothed trajectory with a map of normalized difference vegetation index (NDVI) to extract the NDVI of pixels traversed by each trajectory. The NDVI map was based on a Landsat 5 TM satellite image acquired March 6, 2011, and we use the NDVI values to infer the forest successional stage (Campos, Bergstrom, et al., 2014; Kalacska, Sanchez-Azofeifa, Calvo-Alvarado, et al., 2004; Sorensen and Fedigan, 2000). We calculated distance-weighted mean NDVI based on the length of the trajectory passing through each

traversed cell. This value represents the average habitat conditions traveled through during the sampling period. We also considered a time-weighted mean NDVI (based on point-raster intersections at fixed 10-s intervals along the trajectory), which would represent average habitat conditions occupied during the sample, but the results (not shown) were essentially identical.

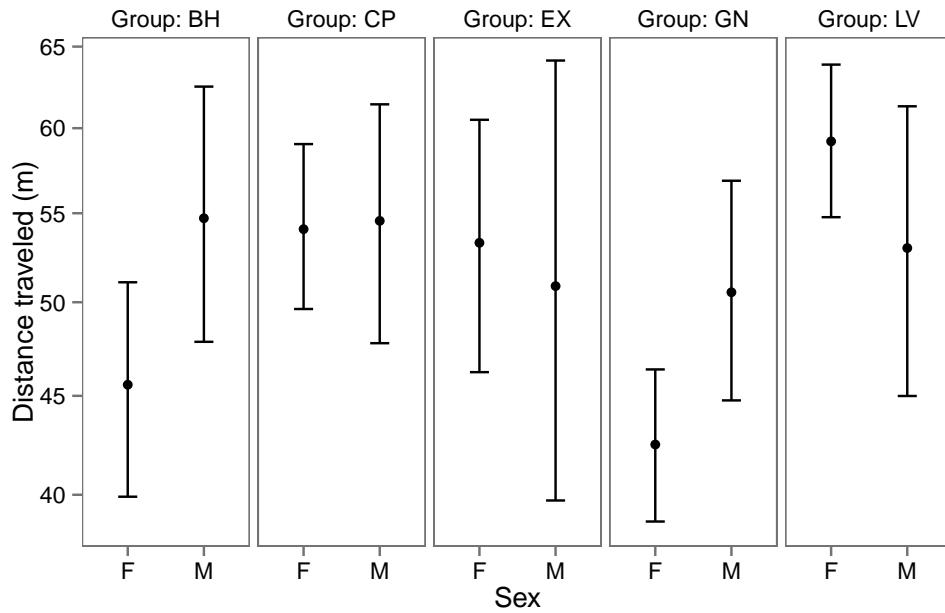


Figure 3.2: Comparison of travel distances during focal samples among groups and sexes. The points and error bars show means and 95 % confidence intervals for the population mean determined by nonparametric bootstrapping.

PREDICTOR VARIABLES: SEASON, HABITAT TYPE, SEX, AND GROUP MASS

We calculated four predictor variables for each focal sample. First, we distinguished two equal-length seasons, wet and dry, based on changes in rainfall, temperature, and relative humidity (Campos, Bergstrom, et al., 2014; Campos and Fedigan, 2013). The wet season spanned May 16 to November 15 and the dry season spanned November 16 to May 15. Second, we determined habitat type by classifying the mean NDVI value for each focal sample trajectory into one of four habitat categories—scrub, early stage forest, intermediate stage forest, and mature forest—based on the NDVI thresholds that maximized classification accuracy in 409 ground control points (see Campos, Bergstrom, et al., 2014, for further details). Due to the rarity and infrequent use of the scrub habitat category, we combined scrub and early-stage forest to a single category for all analyses. Third, we noted the sex of the focal animal. Fourth, we calculated adult group mass on the date of the focal sample. Group compositions were obtained from a continuous record of demographic changes including disappearances

and immigrations. We multiplied the number of sexually mature animals in each of three age/sex classes—adult males, adult females, and subadult males—by their mean body masses: 3.68 kg for adult males and 2.54 kg for adult females (Smith and Jungers, 1997). Following Campos, Bergstrom, et al. (2014), we estimated the body mass of subadult males as equal to that of adult females.

RESPONSE VARIABLES: ENERGY INTAKE RATE, EXPENDITURE RATE, AND NET RETURN

We calculated total energy intake (EI) for each focal sample as the sum of all metabolizable kJ of energy consumed. We make the simplifying assumption that 100 % of every food item was consumed. This assumption is certainly not strictly true, but neither should it introduce any systematic biases between individuals, seasons, or habitat types, and our focus in this study is on relative rather than absolute comparisons. We calculated energy intake rate (EIR) for each focal sample as the total energy intake divided by the minutes of “in-view time” (t_{iv}). To clarify, for calculating all energy-related values analyzed in this study, we excluded any portions of the sample during which poor visibility conditions obscured our view of possible feeding behavior, activity state, or movement. This was intended to account for seasonal or habitat-related differences in observation conditions. We calculated total energy expenditure as follows. First, we determined the basal metabolic rate per minute (BMR_{min}) for males and females separately according to the equation from Kleiber (1932), converted to kJ min⁻¹:

$$BMR_{min} = 0.2034 \times M^{0.75} \quad (3.3)$$

where M is body mass in kg. We used published mean body mass values for adult *C. capucinus* in the wild: 3.68 kg for males and 2.54 kg for females and subadult males (Smith and Jungers, 1997). Second, we calculated the total amount of in-view time (t) in min that the focal animal spent in each of five activity states: resting, vigilant, socializing, feeding/foraging, and traveling. We used “energy-constants” for different activity states from Leonard and Robertson (1997) and the “extrapolated zero speed cost” for locomotion from Taylor, Heglund, et al. (1982) to calculate non-locomotor energy expenditure (EE_{state}), which has units kJ:

$$EE_{state} = BMR_{min} \times \left((1.25 \times t_{rest}) + (1.38 \times t_{vigilant}) + (1.38 \times t_{social}) \right) + \\ \left((t_{forage} + t_{travel}) \times 0.416 \times M^{0.843} \right) \quad (3.4)$$

We justify the assignments of activity states to energetic categories for this equation in Appendix A. Third, we calculated the incremental cost of transport (ICT) (sensu Altmann, 1987), which is the energy cost of locomotion in excess of EE_{state} , using the equation for primates from Taylor, Heglund,

Table 3.1: Overview of variables used in the analysis of foraging energetics.

Acronym	Meaning	Units
EI	Energy intake (total)	kJ
EIR	Energy intake rate	kJ min ⁻¹
t _{iv}	Time in view	min
BMR _{min}	Basal metabolic rate	kJ min ⁻¹
EE _{state}	Energy expenditure due to activity state	kJ
ICT	Incremental cost of transport	kJ m ⁻¹
EE _{travel}	Energy expenditure due to locomotion	kJ
EE	Energy expenditure (total)	kJ
s _{rep}	Scaling constant for reproductive burden	-
EER	Energy expenditure rate	kJ min ⁻¹
NER	Net energy return	kJ min ⁻¹

et al. (1982), converted to units kJ m⁻¹:

$$ICT = 0.0105 \times M^{0.702} \quad (3.5)$$

We derived the energy expenditure for locomotion (EE_{travel}), which has units kJ, as follows:

$$EE_{travel} = 2 \times ICT \times d_{iv} \quad (3.6)$$

where d_{iv} is the distance traveled during in-view observation time. Following Janson (1988), we doubled the estimate of energy expenditure for locomotion to account for the added costs associated with arboreal travel, which should be considerably more costly than travel on flat ground (for which the formula was developed). Total energy expenditure (EE) for the sample, which has units kJ, was calculated as:

$$EE = (EE_{state} + EE_{travel}) \times s_{rep} \quad (3.7)$$

where s_{rep} is a scaling factor based on the animal's reproductive state that accounts for the added costs of lactation and gestation: 1 for males and nonpregnant, nonlactating females; 1.25 for pregnant females; and 1.5 for lactating females (following Key and Ross, 1999). Energy expenditure rate (EER) was thus simply EE divided by t_{iv} . Finally, we calculated net energy return (NER), which has units kJ min⁻¹, for each focal sample:

$$NER = \frac{(EI - EE)}{t_{iv}} \quad (3.8)$$

These variables and their acronyms are recapitulated in table 3.1.

STATISTICAL ANALYSIS

Before undertaking statistical analysis, we excluded all focal samples with less than 10 min of good-quality location data to build the trajectory, as well as all samples that contained less than 60 s of in-view foraging behavior (e.g., cases in which the animal never foraged or with exceptionally bad observation conditions). We further screened the data to require that at least one food item was ingested during the sample. The final data set included 2294 focal samples on 46 animals. Using focal samples as the unit of analysis, we used linear mixed models (LMMs) to examine the effects of our four predictor variables (season, habitat, sex, and group mass) on response variables related to the energetics of foraging behavior: *EER*, *EIR*, and *NER*. We used the R package *lme4* (Bates and Maechler, 2009) to fit the models. We used qq-plots and plots of residuals versus fitted values to check whether the model residuals were homogeneous and normally distributed, and when necessary, we transformed the response variables to meet these assumptions. A log transformation was sufficient to meet the model assumptions for *EER* and *EIR*. *NER* was strongly skewed but ranged from $-3.56 \text{ kJ min}^{-1}$ to 75.9 kJ min^{-1} . To remove the negative values, we added the constant 4.56 to all calculated *NER* values, producing a minimum of value 1, before applying a log transformation.

For each of the three response variables, we first constructed a basic model. The basic models included the focal animal and the focal group as random factors to account for repeated measurements on the same animals and groups. Building on the basic models, we fit full models to each response variable that included the following explanatory variables: sex, group mass, habitat, season, and the habitat-season interaction term. We applied a z-transformation to the continuous variable group mass to make its estimate comparable to those of the categorical predictors. Because our goal was to maximize predictive accuracy and assess variable importance rather than to test specific hypotheses, we used model averaging on complete model subsets with all combinations of the explanatory variables included in the full models. Model averaging involves weighting each model's prediction by its Akaike weight (Burnham and Anderson, 2002). This stabilizes inference when a single model is not clearly superior to all alternative models, as was the case in our study, and is generally a more prudent strategy than basing inference on a single "best" model and discarding the others (Burnham and Anderson, 2002). We used the "dredge" function in the R package *MuMIn* (Barton, 2013) to generate complete model subsets with all combinations of these explanatory variables, and we carried out model averaging based on the sample-size corrected Akaike Information Criterion (AICc) (Burnham and Anderson, 2002).

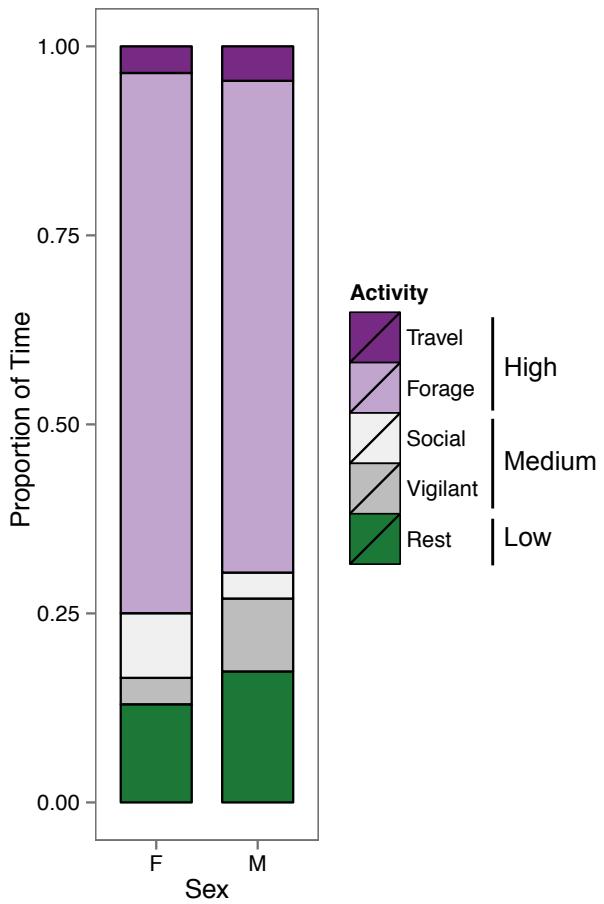


Figure 3.3: Activity budgets of males and females during the focal samples analyzed in this study. High-, medium-, and low-energy states are shown in shades of purple, gray, and green, respectively. Because our data subset was selected to include active foraging behavior, these activity budgets should not be taken as “general” activity budgets.

3.3 RESULTS

3.3.1 GENERAL OBSERVATIONS

A breakdown of the energetic resource base according to season and habitat revealed that capuchins obtained a greater proportion of their energy from invertebrates during the wet season and in more mature habitats (fig. 3.1a). Concurrent with the shift towards greater reliance on insect-energy was a decrease in travel velocity (fig. 3.1b). The sexes did not differ substantially in their distances traveled, although males showed a trend towards longer travel in some groups (fig. 3.2). However, activity budgets differed according to sex (fig. 3.3). Despite devoting 5 % more of their activity budgets to socializing (which we considered a low-energy state), females had a net difference of +5 % devoted to active states such as foraging, traveling, and feeding compared to males. This was due largely to

males' devoting over 10 % more of their activity budgets to low-energy behaviors such as resting and stationary vigilance. It bears repeating here that we excluded focal samples without active foraging behavior; therefore, these activity budgets are biased in favor of active states and do not represent overall time allocation to different behaviors. Females also spent a considerable proportion of time in the costly reproductive states of gestation and lactation (fig. 3.4). The mean time-weighted s_{rep} for all females during the study was 1.30, which corresponds to an average basal energy expenditure rate for females that was 98.7 % that of males (compared to 75.7 % for a nonpregnant, noncycling female).

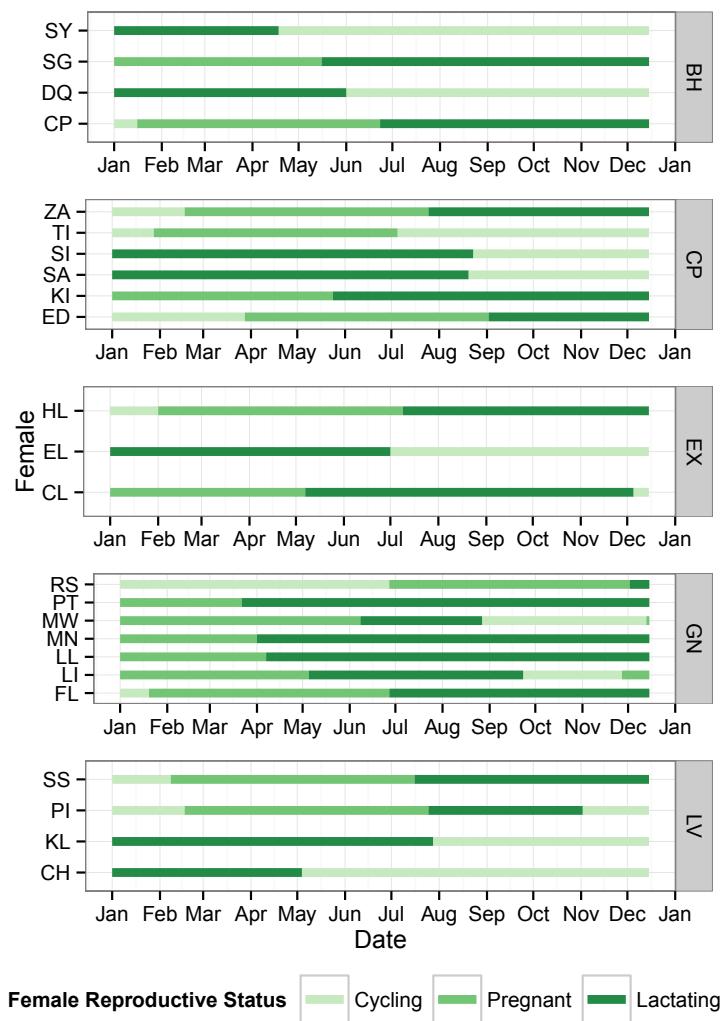


Figure 3.4: Temporal representation of female reproductive status during the study. Unusually short durations for lactation (e.g., female "MW") indicate the death of the infant. Determination of female reproductive status was based on continuous demographic data and is explained fully in Campos and Fedigan (2013).

3.3.2 ENERGY EXPENDITURE RATE

Season, group mass, and habitat type were important influences on energy expenditure rates, with lower *EER* predicted by the wet season, larger group mass, and more mature habitats (fig. 3.5a). A small majority of animals that were observed in both seasons (24/44) had lower median *EER* during the wet season, but the seasonal difference varied in strength and direction across individuals (fig. 3.6a). For females, changes in reproductive status appeared to dominate extrinsic effects on *EER*. For example, five females (SY, DQ, EL, KL, and CL; fig. 3.4) changed from lactating to cycling near the dry-to-wet season transition, and as a consequence they showed large decreases in *EER* (fig. 3.6a). Overall, *EER* did not vary consistently according to sex (fig. 3.5a).

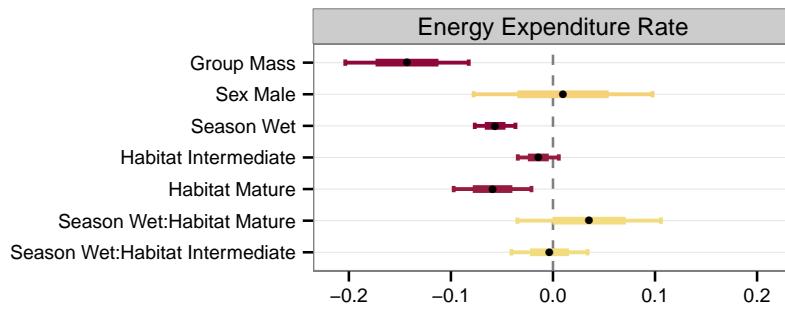
3.3.3 ENERGY INTAKE RATE

The LMMs for *EIR* (fig. 3.5b) provided strong evidence that season, habitat, and the season-habitat interaction term were important determinants of energy intake. The relative influence of season appeared to be most important; indeed, a large majority of animals observed in both seasons (37/44) had higher individual *EIR* in the wet season compared to the dry season (fig. 3.6b). *EIR* did not clearly differ among habitat categories when viewed in isolation, but the LMMs revealed a noteworthy interaction between habitat and season (fig. 3.5b). The relative advantage of the wet season in terms of *EIR* is reduced for animals foraging in intermediate- and mature-stage forest compared to early-stage forest. *EIR* also differed between sexes to a limited extent, with females showing a tendency to ingest energy at a greater rate, although the model-averaged variable importance attributed to sex was smaller. Group mass did not affect *EIR*.

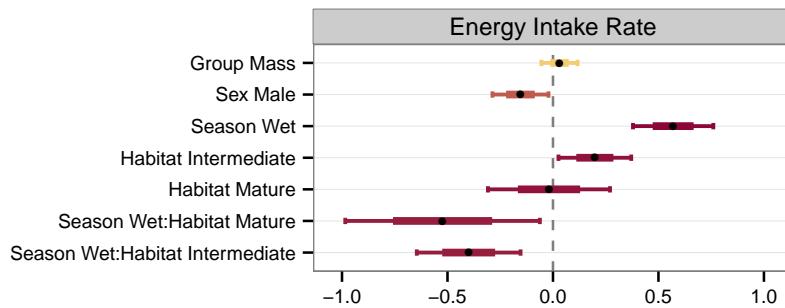
3.3.4 NET ENERGY RETURN

The LMMs for *NER* were nearly identical to those for *EIR*, supporting roles for both season and habitat (fig. 3.5c). Most animals observed in both seasons (37/44) had higher *NER* for foraging bouts during the wet season (fig. 3.6c). Like *EIR*, *NER* was influenced by the interaction between habitat and season: the relative advantage of the wet season in terms of *NER* was less evident in intermediate- and mature-stage forest compared to early-stage forest (fig. 3.5c). The apparent sex-difference that was weakly supported for the *EIR* models was also present in the *NER* models, with males showing a tendency for lower *NER* than females.

(a)



(b)



(c)

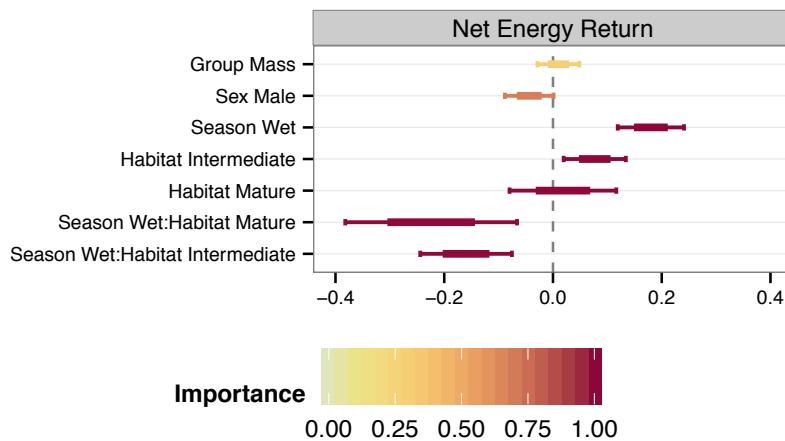


Figure 3.5: Model-averaged regression coefficients and relative variable importance for linear mixed models of (a) energy expenditure rate, (b) energy intake rate, and (c) net energy return. Thick error bars show ± 1 SD and thin bars show 95% confidence intervals. The predictor variables were scaled to facilitate direct comparison of their relative effects. All models included the random effects focal individual and focal group. The relative importance of each predictor variable was calculated as the sum of the Akaike weights for each model in which the variable appeared.

3.4 DISCUSSION

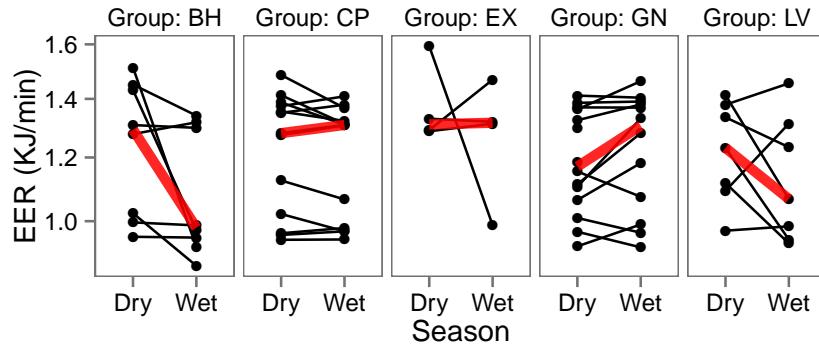
Net energetic returns during a typical bout of foraging varied according to both extrinsic and intrinsic factors. Whereas *EER* was strongly affected by both intrinsic and extrinsic factors, *EIR* was dominated by extrinsic factors such as season and habitat type. *NER* followed a pattern nearly identical to *EIR*, which suggests that variation in food intake explained most of the variation in *NER* whereas variation in expenditure—including both basal metabolic and incremental locomotor costs—was relatively unimportant.

3.4.1 EXTRINSIC EFFECTS ON FORAGING ENERGETICS: SEASON AND HABITAT

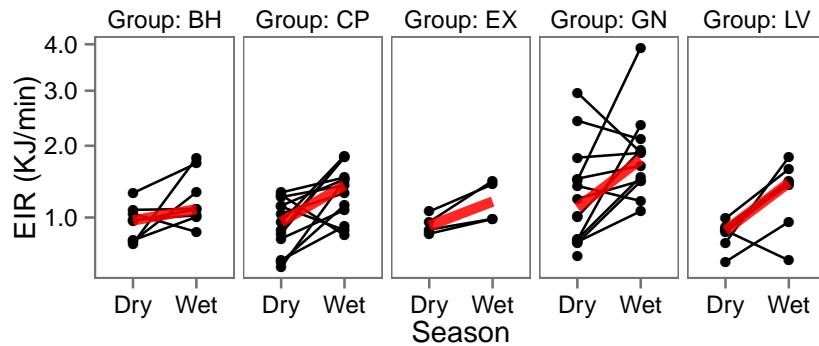
Season and habitat emerged as major extrinsic determinants of small-scale foraging energetics. Multiple lines of evidence suggest that the distribution and abundance of food resources played key roles in mediating this pattern. The wet season is the period of maximum overall fruit abundance in SSR, based on a set of systematically monitored fruit trees (Campos, Bergstrom, et al., 2014; Melin, Young, et al., 2014). This period coincides with the peak of abundance (or at least consumption) for many kinds of invertebrates, particularly those that are gleaned rather than extracted, such as caterpillars and small hemipterans (Melin, Young, et al., 2014). In addition, median fruit biomass per visited fruit tree is greater in all habitat classes during the wet season than during the dry season, and the median fruit biomass of these patches increases with habitat maturity stage (although the difference is slight for the mature habitat category) (fig. 3.7). There are many common, small, and heavily-consumed fruit foods that are available only during the dry season and that are also disproportionately common in younger forest classes, including *Vachellia collinsii*, *Randia monantha*, *Randia thurberi*, *Malvaviscus arboreus*, *Davila kunthii*, *Doliocarpus dentatus*, *Alibertia edulis*, and perhaps most importantly, the terrestrial bromeliads *Bromelia pinguin* and *Bromelia plumieri*. The larger average fruit patches and overall richer food environment (for both fruits and invertebrates) during the wet season and in mature habitats provides straightforward explanations for both reduced *EER* and increased *EIR* and *NER*: capuchins can obtain more energy and afford to spend more time in a typical fruit patch, and they encounter invertebrate food items more frequently. Together, these changes reduce the total number of patches that must be visited as well as total inter-patch travel.

Food resource predictability across space and time is another important consideration. There is now overwhelming evidence that wild primates' movement patterns are informed by spatial memory of food resources (reviewed by Janson and Byrne, 2007 and Zuberbühler and Janmaat, 2010). In tropical forests, locations that offer high payoffs for invertebrate foraging are probably less predictable than locations that offer productive fruit foraging. When spatial memory is less useful (or

(a)



(b)



(c)

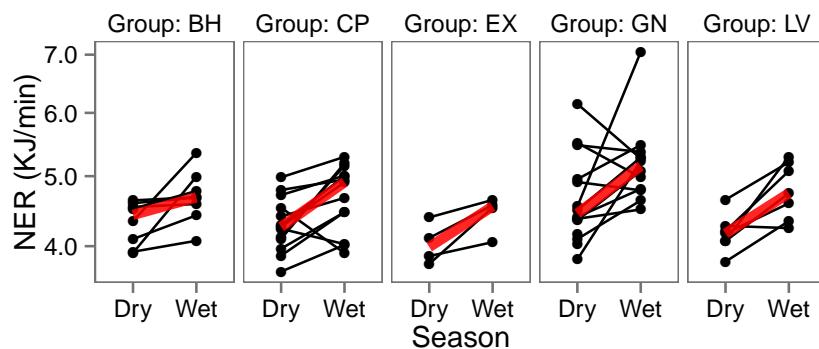


Figure 3.6: Seasonal comparisons of (a) energy expenditure rate, (b) energy intake rate, and (c) net energy return. Each point represents the median value for one individual; each individual's values in the wet and dry seasons are connected by a line segment. The thick red line indicates the seasonal change in the social group's median (the median of individual medians).

less utilized), animals' foraging movements should slow and perhaps lose some degree of directedness (Janson and Byrne, 2007; Pochron, 2001). The widespread abundance of invertebrates during the wet season probably causes an across-the-board increase in the productivity of between-fruit-patch foraging pathways. Although the capuchins continue to visit fruit trees throughout the day during the wet season, we can infer from their trajectories that they move between them more slowly and perhaps with less urgency and single-mindedness, gleaning invertebrates in greater numbers along the way.

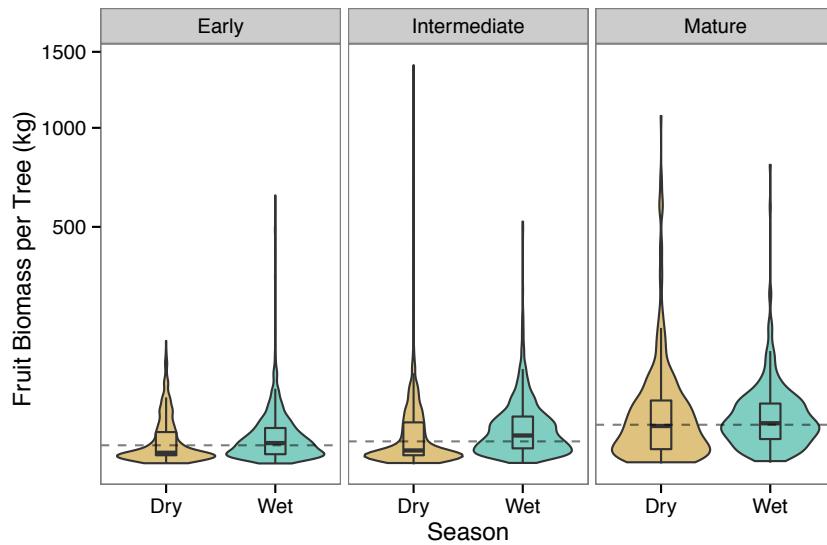


Figure 3.7: Estimated fruit biomass of fruit trees visited during the study period in early, intermediate, and mature habitats during wet and dry season. The biomass calculation for each tree is based on the tree's diameter at breast height and a phenological availability index, following previous studies (Campos, Bergstrom, et al., 2014; Melin, 2011). The dashed horizontal lines show medians for the habitat category with the two seasons combined. The data shown represent 4716 distinct visits to fruit trees of 83 different species.

Finally, differences in the structural environment between seasons and habitat types could have contributed to the changes in capuchins' foraging energetics. First, the changing degree of contrast among habitat types according to season could explain the season-habitat interaction that shaped *EIR* and *NER*. The early and intermediate forest stages are predominantly leafless during the dry season whereas many trees in mature forest patches retain their leaves, providing a shady and relatively cool microhabitat. With the onset of the wet season, deciduous trees quickly put out new leaves and all habitats become fully green. In support of this line of reasoning, we found that the benefits of more mature habitats in terms of *EIR* and *NER* were relatively greater when the degree of contrast among habitats was greatest (i.e., during the dry season). Second, mature habitats have relatively tall, overlapping, and multi-layered canopies that probably offer more continuous canopy-to-canopy linkages for arboreal travel in any direction. Consequently, mature habitats are likely to provide more op-

tions for traveling from one tree to the next and greater overall availability of favorable travel routes, such as those that offer preferred substrates, foliage for concealment, or a more-direct path towards a travel goal. This explanation could also be brought to bear regarding season. Although structural connectivity among adjacent branches in the canopy should be similar across seasons, the absence of green vegetation in many trees during the dry season may motivate the capuchins to be more selective in choosing their routes to avoid exposure to the sun or to predators in completely open areas. Third, an analysis of capuchins' positional behavior during the focal samples included in this study revealed that energy-demanding postures including running, hanging, jumping, clinging, and standing bipedal were overrepresented in younger forest stages whereas lying was overrepresented in mature forest (fig. 3.8). Because positional behavior did not contribute to our *EER* calculation, this provides independent evidence to support our finding that energy expenditure rates are greater in younger forest habitats.

3.4.2 INTRINSIC INFLUENCES ON FORAGING ENERGETICS: SEX AND GROUP MASS

The allometric relationship between body mass and locomotor costs ensured that males, being larger, expended more energy during locomotion than nonpregnant, nonlactating females per unit distance traveled. It may appear surprising, therefore, that we did not find significant sex differences in *EER*. To explore this result further, we quantified sex differences in both distance traveled and activity budgets. While the sexes did not differ in travel distances, we found that males allocated more time to low-energy activity states such as brief resting and stationary vigilance during these focal samples (fig. 3.3), reducing their EE_{state} costs. Moreover, females bore significant added energy costs during gestation and lactation that almost completely compensated for their smaller body size. The combination of these factors apparently nullified sex-differences in *EER*, a finding that accords well with previous research on this topic in nonhuman primates (Key and Ross, 1999).

Although their expenditure rates were similar, we found some evidence that females took in energy at higher rates than males. This finding would seem to contrast with the study by Vogel (2005) on a nearby population of *C. capucinus* in which no sex differences in energy intake rates were found. However, because Vogel's study focused only on the intake of fruits, it overlooked roughly half of the capuchins' total energy base. Moreover, data collection periods in Vogel's study were heavily biased towards the dry season. A different study that focused on insect capture rates found that females devoted more time to insect foraging than males, but that their capture efficiencies were dependent on color vision phenotypes (Melin, Fedigan, Young, et al., 2010). Capuchin females have the potential for color vision trichromacy whereas males do not, but despite their greater ability to discriminate reddish fruits from a green background (Melin, Fedigan, Hiramatsu, Hiwatashi, et al., 2009), there is

no evidence that trichromats have an actual feeding-rate advantage over dichromats (Melin, Fedigan, Hiramatsu, and Kawamura, 2008; Vogel et al., 2007), and in fact, trichromats seem to be disadvantaged for capturing certain kinds of insects (Melin, Fedigan, Young, et al., 2010). We therefore do not believe that color vision phenotypes underlie the small female *EIR* and *NER* advantages that we found in this study. It is possible that females' higher *EIR* and *NER* was simply a product of greater effort and persistence in acquiring food: they rested less and engaged in much less stationary vigilance behavior than males. Sexual selection theory predicts that females are under greater selective constraints regarding the acquisition of food due to their greater reproductive investments (Bateman, 1948; Trivers, 1972). As such, the selective pressure to forage efficiently may act more strongly on females. Although the reasons why females had higher *EIR* and *NER* in this study remain uncertain, the relatively low model-averaged variable importance attributed to sex in these models suggests that sex-related differences were secondary to those of season and habitat.

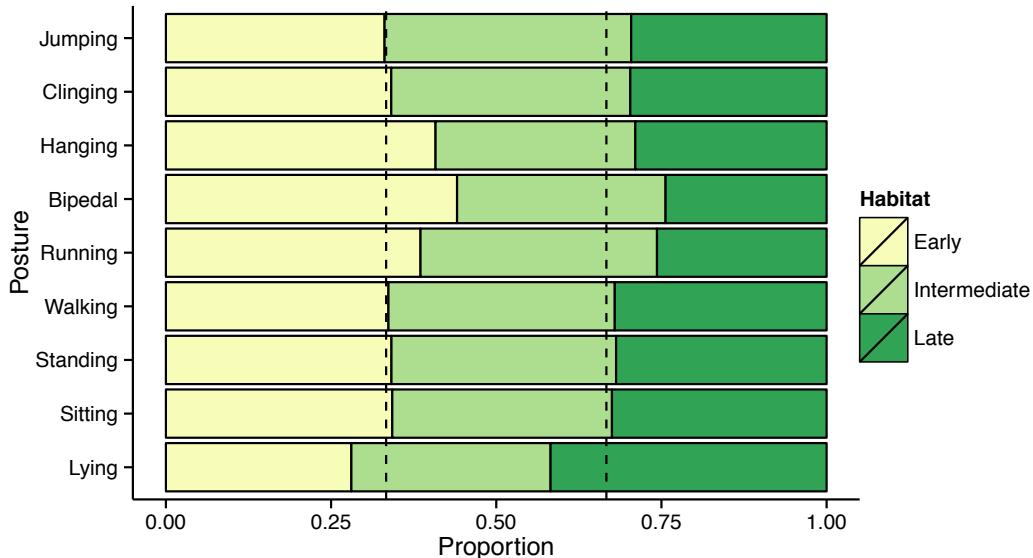


Figure 3.8: Relative differences in the use of specific body postures in early, intermediate, and mature forest habitats. For each posture, the plot shows the deviation from an equalitarian distribution of the posture across the three habitats, adjusted for differences in habitat use and posture occurrence. Expected (equalitarian) values are indicated by dashed gray lines. The postures are sorted roughly from energy-conserving postures at the bottom to energy-demanding postures at the top.

We found that capuchins in larger groups expended energy at lower rates than animals in smaller groups, although *EIR* and *NER* were unaffected by group mass. Given that capuchin home ranges overlap extensively (Campos, Bergstrom, et al., 2014), one possible explanation for the reduced energy expenditure in larger groups is their ability to concentrate their foraging efforts on more productive areas due to their relative dominance over smaller groups in between-group encounters (Childers,

2008). In this way, animals in large groups could maintain adequate *EIR* while expending less energy on food search or inter-patch travel. In addition, both of our large study groups, GN and CP, included a large number of infants and juveniles during the study. Infants and juveniles constrain ranging patterns in chimpanzees (Pontzer and Wrangham, 2006), and it is possible that the presence of many immature animals slowed down our two large groups and reduced overall *EER*.

3.4.3 IMPLICATIONS

This study's unique, fine-grained approach to quantifying the energetics of foraging behavior enables us to draw several important conclusions about the energy landscapes that capuchins navigate over both space and time. First, our findings contribute to our current understanding of the value of landscapes for *C. capucinus* population health and conservation. We found that, from a foraging energetics standpoint, mature habitats were consistently superior to younger habitats, enabling higher *EIR* and lower *EER* for greater overall *NER*. Second, thermoregulatory needs compel capuchins to increase resting time during the dry season (Campos and Fedigan, 2009), but when they do forage, our findings indicate that they must expend greater energy per unit of energy consumed. This finding reinforces the idea that the dry season is a challenging time for capuchins in SSR and that their long-term population dynamics are to some degree contingent on multi-year trends in dry season severity (chapter 5). Third, expected energetic returns on foraging bouts were driven primarily by extrinsic constraints such as seasonality and habitat characteristics rather than by intrinsic constraints such as sex or social group size. This finding underscores the importance of taking spatiotemporal environmental variability into account in studies of wild animals' foraging energetics. Fourth, capuchins' small-scale foraging behavior shifted along with changes in their energetic resource base. We found that their energy expenditure during foraging bouts was inversely proportional to food abundance and that their travel velocities slowed as they incorporated a greater fraction of less-predictable invertebrates in their diet. These findings shed light on the complexities of animal movement ecology and the role of the environment in modulating spatially and temporally variable locomotor costs.

No wild animal roams at random over the country: each has a home region, even if it has not an actual home.

Ernest Thompson Seton, 1909

4

Drivers of home range characteristics across spatiotemporal scales in a Neotropical primate, *Cebus capucinus*

4.1 INTRODUCTION

Recent technological and analytical advances have stimulated a renewed interest in understanding the factors that drive variation in animal home ranges (Börger, Dalziel, et al., 2008; Fryxell et al., 2008; Kie et al., 2010; Smouse et al., 2010). Improvements in GPS technology (Cagnacci et al., 2010; Tomkiewicz et al., 2010) coupled with new home range estimation methods that explicitly account for autocorrelation in temporally dense location data (Benhamou, 2011; Downs et al., 2011; Horne, Garton, Krone, et al., 2007; Kranstauber et al., 2012; Long and Nelson, 2012; Lyons et al., 2013; Steiniger and Hunter, 2013) enable researchers to examine the spatiotemporal dynamics of home ranges with unprecedented precision and detail (Kie et al., 2010). Broad between-species variation in space use patterns are largely explained by body size and trophic level (Harestad and Bunnell, 1979; Jetz et al., 2004; Kelt and Van Vuren, 2001; Lindstedt et al., 1986; Pearce et al., 2013), but the factors that drive within-species variation in space use remain poorly understood and may change de-

pending on the spatial and temporal scales of analysis (Börger, Franconi, et al., 2006). This topic is particularly important for animals living in environments with high spatial and temporal variability because they may face pronounced intra-annual fluctuations in food and water availability, thermal stress, and vegetation characteristics (Morellet et al., 2013; Naidoo et al., 2012; Rivrud et al., 2010). The insights gained from such studies can be used to build a vital knowledge base for predicting how animals will respond behaviorally to a variety of disturbance and climate change scenarios.

Understanding the drivers of variation in home range characteristics remains a fundamental question in behavioral ecology (Börger, Dalziel, et al., 2008). Multi-individual, multiscale approaches have made significant progress toward understanding the spatiotemporal dynamics of home ranges in several ungulate species (Börger, Franconi, et al., 2006; Morellet et al., 2013; Naidoo et al., 2012; Rivrud et al., 2010; van Beest et al., 2011), but this analytical framework has only rarely been applied to other animal taxa. Among nonhuman primates, such approaches have provided insights into the factors that influence home range overlap (Markham et al., 2013) and daily path length (Pebsworth et al., 2012) in African savanna-dwelling baboons (*Papio* spp.) and core areas in Neotropical spider monkeys (*Ateles geoffroyi*) (Asensio, Schaffner, et al., 2012). We use a mixed effects modeling approach to explore space use patterns in an arboreal Neotropical primate living in an acutely seasonal tropical dry forest, which is one of the world's most imperiled ecosystems (Portillo-Quintero and Sánchez-Azofeifa, 2010). We frame our research questions and analytical methods around three prominent ecological processes that characterize the study system: strong climatic seasonality, landscape heterogeneity comprising a wide forest age gradient and temporal fluctuations in food resource availability. Our objectives are to characterize the home ranges of white-faced capuchins, *Cebus capucinus*, and to determine which factors are associated with variance in home range attributes. We focus specifically on home range area and the maturity stage of the forest utilized. By analyzing the same data set from a range of commonly used spatial and temporal scales, we also aimed to determine how varying definitions of the home range may alter biological inferences about space use behavior.

4.1.1 PREDICTIONS

In many primate species, larger groups tend to have larger home ranges than smaller groups (Clutton-Brock and Harvey, 1977; Di Bitetti, 2001; Ganas and Robbins, 2005; Isbell, 1991; Janson and Goldsmith, 1995; van Schaik and van Noordwijk, 1989). This pattern can be understood as an extension of the allometric scaling relationship between home range area and body mass among primates (Pearce et al., 2013). These studies support the hypothesis that, all else being equal, individuals in larger groups will need to travel farther and expend more energy to meet their food requirements because of greater within-group feeding competition (Janson and Goldsmith, 1995). Thus, we pre-

dicted that home range size would increase with group mass, irrespective of spatial or temporal scale. In addition, we predicted that larger groups would occupy home ranges consisting of more mature evergreen forest, which have greater diversity and density of fruit trees (Asensio, Lusseau, et al., 2012) as well as greater overall fruit biomass (Sorensen and Fedigan, 2000), because of the greater resource-holding potential of larger groups and their greater overall success in between-group competition (Childers, 2008; Crofoot and Gilby, 2012; Crofoot, 2008).

Second, weather and other climatic factors are key drivers of home range size and use in many animals (Henzi et al., 1992; Morellet et al., 2013; Rivrud et al., 2010). Capuchins at our study site reduce activity levels and increase their use of areas that contain permanent water sources as the hot dry season intensifies (Campos and Fedigan, 2009). The effects of this behavioral adjustment on home range size are unclear: the animals could maintain smaller home ranges to conserve water or energy, or they could compensate for lost foraging time by moving more quickly over similarly sized areas during cooler times of day. If white-faced capuchins follow the former strategy, we predicted that hotter, dryer conditions would be associated with smaller home range size, and that this effect would be manifested more clearly for high-use zones because of long resting periods. Alternatively, if capuchins follow the latter strategy, with rapid compensatory foraging excursions, then we predicted that total home range size would not be affected by climatic conditions. In either case, we predicted that hotter, dryer conditions would lead to increased use of mature evergreen forest, which provides shade and cooler microhabitats (Chapman, 1988).

Third, many animals adjust their ranging behavior based on temporal variation in available food resources (reviewed by Hemingway and Bynum, 2005, for the order Primates; Asensio, Korstjens, et al., 2009). During seasonal food scarcity, animals may pursue different coping strategies, some of which manifest effects on home range size (Brockman and van Schaik, 2005; van Schaik, Terborgh, et al., 1993). Previous studies have found that capuchin monkeys (*Cebus* and *Sapajus* spp.) use a habitat-shifting strategy to cope with seasonal food scarcity (Di Bitetti, 2001; Peres, 1994; Terborgh, 1983), with concomitant increases in home range size (Peres, 1994). This occurs when the animals increase foraging effort to maintain a high level of food intake, which usually requires moving farther and over a larger area. Thus, we predicted that decreasing food abundance would be associated with larger home range size, and that these effects would be most evident for relatively low-use (noncore) home range zones.

Table 4.1: Data summary and group sizes of white-faced capuchins.

Focal group	Total size	Observation days	Location points
AD	20-22	44	915
BH	17-24	115	2077
CP	17-37	510	9822
EX	8-13	236	4292
GN	20-37	618	12 051
LV	12-23	582	10 645
RM	17-18	45	943
Total		2150	40745

4.2 METHODS

4.2.1 STUDY SITE

We carried out this study in the Área de Conservación Guanacaste (ACG), a UNESCO World Heritage Site in northwestern Costa Rica. Our study was confined to the ACG's Sector Santa Rosa (SSR), which comprises 10 800 ha of tropical dry forest. Although the SSR once consisted of continuous semievergreen forest, a complex history of anthropogenic disturbance has produced a patchwork of regenerating and pristine habitats including mixed deciduous forest, oak forest, mangroves, lightly wooded savannas and open grasslands (Fedigan and Jack, 2012). The SSR experiences a severe, 6-month dry season during which most plants shed their leaves and few sources of surface water remain. The median total yearly rainfall at the site during our study period (2006 to 2013) was 2129 mm (range during study period 1436 mm to 3639 mm).

4.2.2 STUDY SPECIES AND SUBJECTS

White-faced capuchins live in cohesive social groups that are typically composed of one or more adult males, several adult females and numerous immature animals. All members of the group travel in a roughly coordinated fashion, in that each animal usually remains in visual and/or vocal contact with at least some other group members, and it is usually possible to discern the overall direction of group movement. Thus, all animals of a given social group share a home range, and accordingly, we treat the social group as the unit of analysis in our study. The home ranges of neighboring white-faced capuchin groups overlap extensively (Crofoot, 2007; Rose and Fedigan, 1995), with up to 60 % dyadic overlap among our study groups. Intergroup relationships may be best characterized as “xenophobic” rather than territorial, in that groups do not defend well-defined spaces, but their interactions are usually highly agonistic (Crofoot, 2008). Their diet is dominated by fruits and insects, which

are consumed in roughly similar proportions (McCabe and Fedigan, 2007), although fruits are generally preferred and are consumed in proportion to their relative abundance (Melin, Young, et al., 2014). We observed seven neighboring groups of wild white-faced capuchins (AD, BH, CP, EX, GN, LV and RM) in SSR. Two of these groups, AD and RM, formed in late 2012 as fission products of group CP. There is some contiguous forest that extends over the total area traversed by the seven study groups, but the age and structure of the forest varies markedly within each group's range (fig. 4.1). Total group sizes ranged from a minimum of 8 in EX group to a maximum of 37 in GN group (table 4.1).

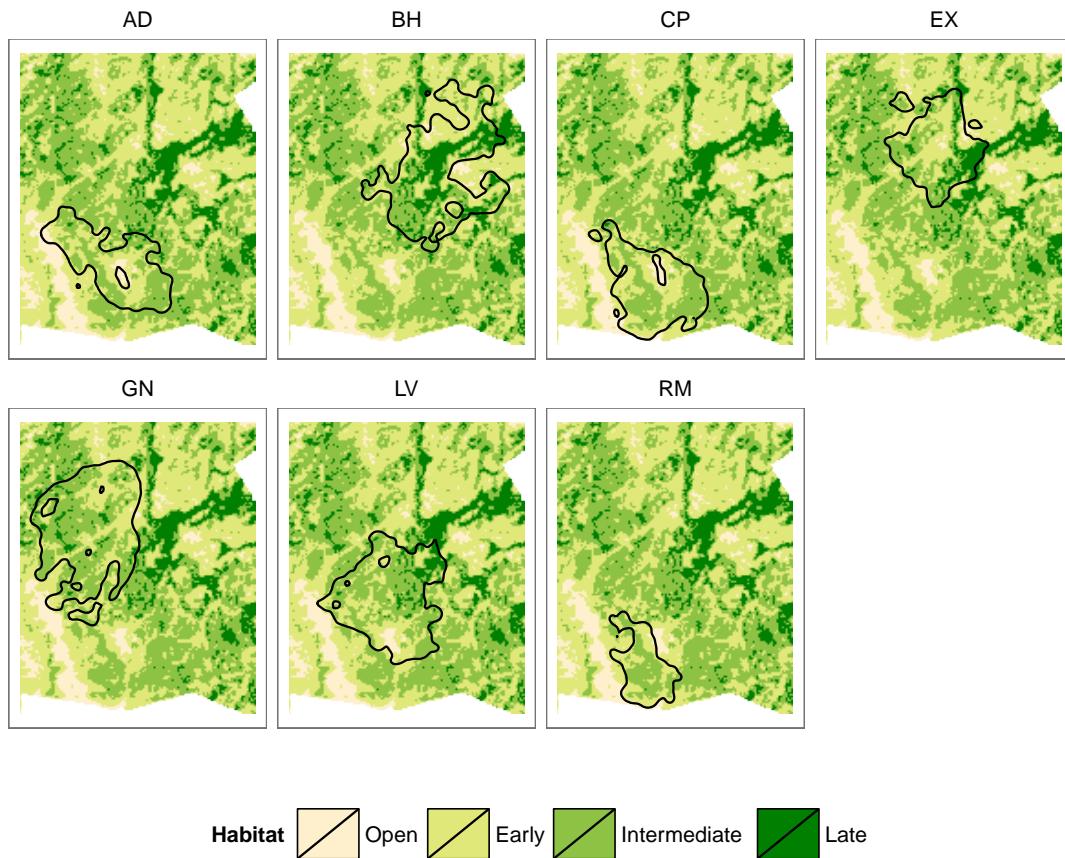


Figure 4.1: Habitat maps of the study area, with a single, multiyear home range for each study group. The multiyear ranges depicted here show the 95 % isopleth based on every available location point for each study group. These ranges were not used for analysis and are presented for illustrative purposes only. Their relative sizes should be treated with caution because they have not been adjusted for sampling effort, which differed greatly among the study groups.

4.2.3 DATA COLLECTION

LOCATION DATA

We collected location data at irregular intervals between May 2006 and August 2013. Each observer's observation schedule and study groups differed to accommodate other data collection requirements, but we used a common methodology to collect location points while observing each group. Observers typically followed a given group from sleep tree to sleep tree (~ 12 h), but shorter data collection days occurred occasionally if observers lost the group or were unable to locate the group quickly in the morning. The group's location was recorded every 30 min on the hour and half-hour using a hand-held GPS receiver (Garmin GPSMAP 62s and 76cx). Whenever possible, we recorded the location point at the group's approximate geometric center. However, other data collection requirements, large group spread and/or poor visibility occasionally prevented observers from confidently identifying the group's geometric center. In these cases, we nevertheless recorded the point as long as some animals were visible directly overhead. If no animals were visible at the half-hour, observers recorded the location point as soon as they re-established visual contact with the focal group, as long as this occurred within 15 min. After settling into a sleep tree shortly after sunset, capuchins remain stationary throughout the night. Thus, roughly half of their time is spent immobile at a sleep tree. As we were concerned only with diurnal use of space, we did not include nocturnal location data. Our final set of location data included 40 745 points, which represented over 20 000 h of observation time on the seven study groups (table 4.1).

ENVIRONMENTAL AND ECOLOGICAL DATA

We used a Kestrel weather meter to record ambient temperature every 30 min on the half-hour. The weather meter was located in a deeply shaded location near the geographic center of the five groups' ranges. Daily total rainfall was recorded using a standard cylindrical rain gauge. To monitor the availability of food, we used both phenological data and tree abundance data on 53 commonly eaten fruit species. The methods involved in collecting these data sets are described in detail elsewhere (Melin, 2011; Melin, Hiramatsu, et al., 2014). The phenology record spans 81 months from February 2007 to October 2013. The data consist of monthly measurements of fruit coverage and maturity on a median of eight individual trees of each species in each month. The tree abundance data were obtained from 151 botanical transects distributed throughout the study site and covering a total area of 3.02 ha (Melin, 2011).

We created maps of land cover (fig. 4.1) and normalized difference vegetation index (NDVI) from a Landsat Surface Reflectance Climate Data Record (LSR-CDR) product (Masek et al., 2006) de-

Table 4.2: Temporal scale definitions and biological interpretations.

Temporal scale	Start	End	Environmental conditions and biological significance
Monthly	First of month	Last of month	Calendar months: no biological significance
Quarterly	16 Feb	15 May	Late dry season: temperatures warm steadily and deciduous trees lose their leaves; green vegetation remains only in mature forest; natural sources of drinking water exhausted
	16 May	15 Aug	Early wet season: arrival of regular rains, high relative humidity and rapid leaf onset in most deciduous plants; temperatures fall immediately after heavy rains begin
	16 Aug	15 Nov	Late wet season: frequent rain and maximum fruit abundance; October typically characterized by prolonged torrential rain
	16 Nov	15 Feb	Early dry season: green vegetation, moderate temperatures and clear skies; dry conditions and frequent high wind in January and February hasten leaf shedding; natural sources of drinking water are abundant
Half-yearly	16 May	15 Nov	Wet season: comprising early and late wet seasons
	16 Nov	15 May	Dry season: comprising early and late dry seasons
Yearly	1 Jan	31 Dec	Complete annual cycle: comprising both wet and dry seasons

rived from a Landsat 5 TM image (scene ID: LT50160532011065CHM00). LSR-CDR data products have been processed to remove artefacts produced by atmospheric conditions, illumination, elevation and viewing geometry. The image was acquired on 6 March 2011, which corresponds to the peak dry season in SSR. Research on the relationship between forest maturity stage and NDVI in the SSR has shown that dry season NDVI values can be used to discriminate maturity stages of forest in this ecosystem (Arroyo-Mora, Sanchez-Azofeifa, Kalacska, et al., 2005; Kalacska, Sanchez-Azofeifa, Calvo-Alvarado, et al., 2004). This is due to the approximately linear relationship between forest stand age and the degree of evergreenness (Sorensen, 1998). To obtain land cover, we classified the image into four habitat categories, as defined in Kalacska, Sanchez-Azofeifa, Calvo-Alvarado, et al. (2004), including open grassland and bare soil, early successional stage forest, intermediate successional stage forest and mature/late successional stage forest. The classification process involved selecting threshold values for NDVI that minimized the number of classification errors in 409 ground control points. We recorded habitat type for each ground control point within about 1 month of the image acquisition date during the peak dry season of 2011 (date range 3 March to 15 May). Based on the ground control points, the overall accuracy of this classification method was 76 %.

4.2.4 DATA ANALYSIS

SPATIOTEMPORAL SCALES AND HOME RANGE ESTIMATION

The commonly cited definition of the home range as the “area traversed by the individual in its normal activities” (Burt, 1943, p. 351) has no inherent temporal or spatial specification. Indeed, home ranges may be continuously dynamic, and their characteristics may therefore vary depending on how they are defined both temporally and spatially. We estimated home ranges for each study group at four nested temporal scales (monthly, quarterly, half-yearly and yearly) and three spatial scales (core zone, primary ranging zone and total home range zone; fig. 4.2). Table 4.2 provides definitions and biological interpretations of the temporal scales, whereas the spatial scales are defined below. Because sampling effort varied considerably over the study period, we excluded time intervals with very few location points (fig. 4.3), and we accounted for sampling effort in our statistical models (see below). After excluding time periods with insufficient data, we were left with 175 monthly ranges, 73 quarterly ranges, 41 half-yearly ranges and 22 yearly ranges (fig. 4.3). To estimate home ranges, we used a recently developed movement-based kernel method that is based on biased random bridges (BRB) (Benhamou, 2011; Benhamou and Cornélis, 2010). Like other movement-based home range methods, the BRB method’s primary advantage over more commonly used location-based methods is that it estimates the utilization distribution from a time-ordered movement path rather than from un-linked points, thereby accounting for autocorrelation and increasing biological realism (Benhamou,

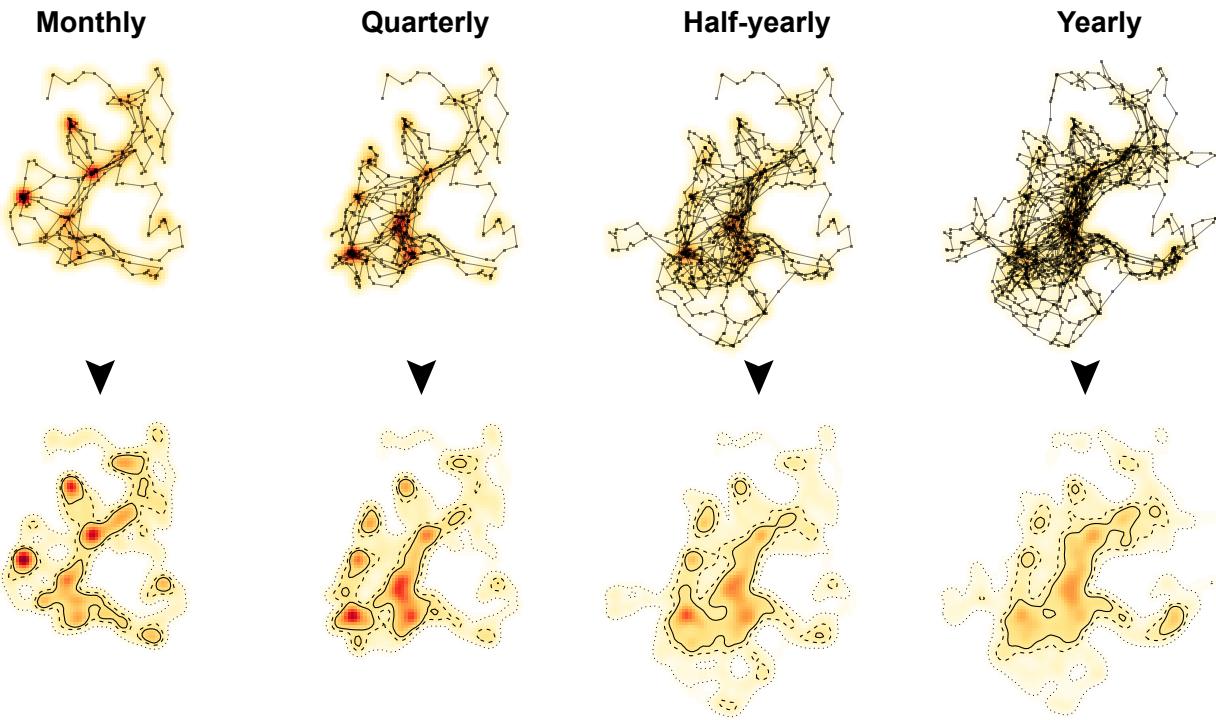


Figure 4.2: Illustration of the movement-based kernel method used for estimating home ranges of white-faced capuchins in this study. Home ranges shown are for group BH at each of four nested temporal scales. The upper panels show the recorded location points (small dots) and the inferred movement paths (black line segments) of BH group during the relevant period. The colored shading represents the utilization distribution. The lower panels show the three home range zones delineated for each home range: core zone (50 % isopleth, solid line); primary ranging zone (70 % isopleth, dashed line); and total home range zone (95 % isopleth; dotted line).

2011; Horne, Garton, Krone, et al., 2007; Kranstauber et al., 2012). We implemented the BRB method using the adehabitat family of packages (Calenge, 2006) for R version 3.0.1 (R Development Core Team, 2014). The parameters that we used for the BRB home range method are detailed and justified in Appendix B.

CALCULATION OF PREDICTOR AND RESPONSE VARIABLES

To account for possible group size and body size effects, we multiplied the number of sexually mature animals by the mean body mass reported for different age/sex classes of this species: 2.54 kg for adult females and 3.68 kg for adult males (Smith and Jungers, 1997). We also used 2.54 kg for subadult males, which have slight build similar to that of adult females. As group compositions fluctuated continuously throughout the study, we calculated a mean group body mass for the time interval that defined each home range based on a continuous daily record of demographic changes such as dispersal events, deaths and disappearances. We excluded immature animals in this calculation because their weights were likely to vary considerably over the time intervals of interest, and because the ex-

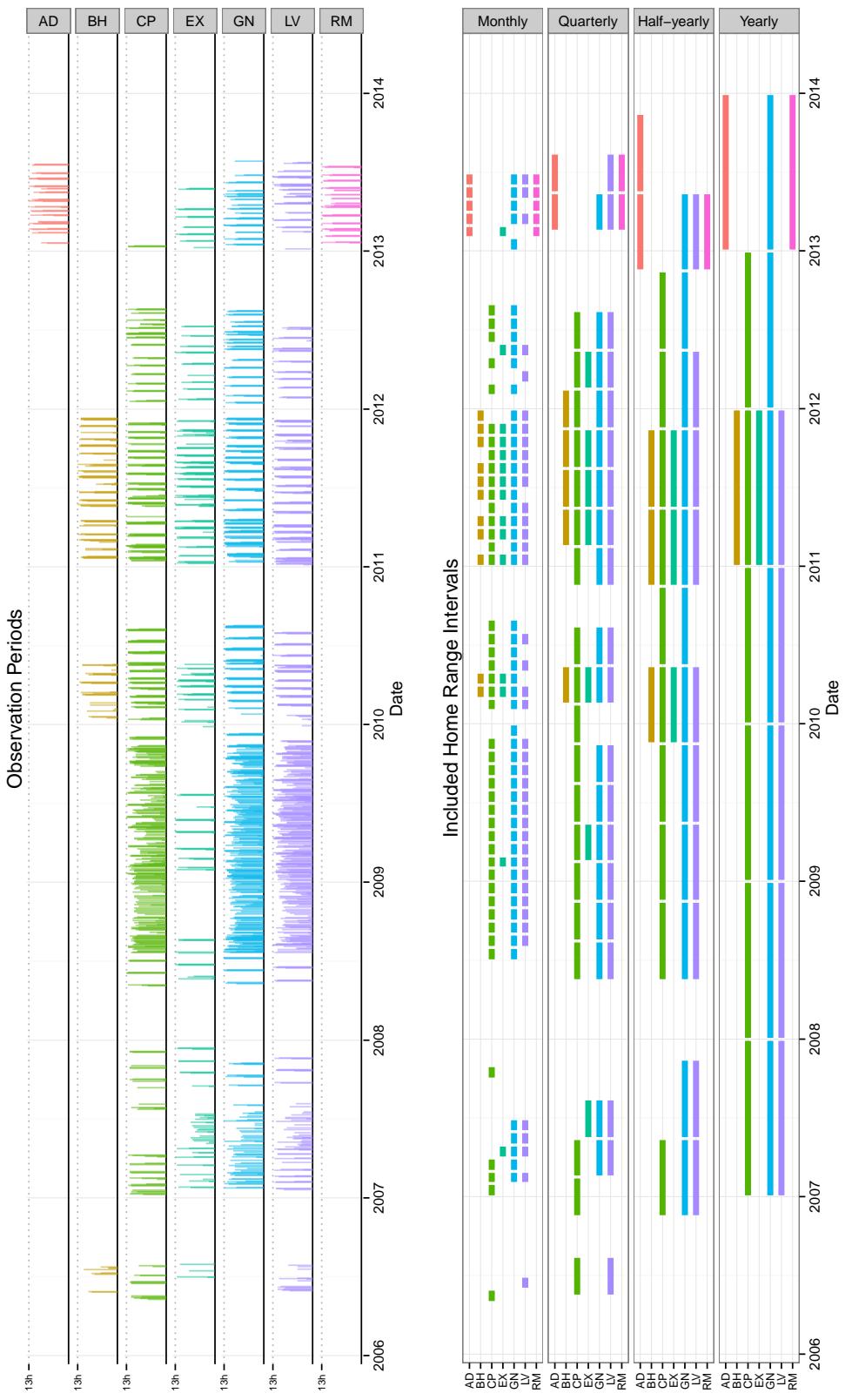


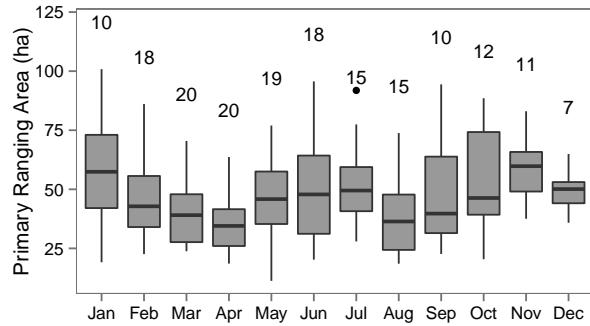
Figure 4.3: Top panel: data coverage, with each day of data collection represented by a thin vertical segment. Contact hours relative to a full 13h day are represented by the segment's height ($N_{\text{days}} = 2150$; $N_{\text{points}} = 40745$). Bottom panel: home range time intervals with sufficient data to be included in the study. Horizontal separation between intervals exaggerated for clarity, but actual intervals were contiguous.

pected allometric scaling relationship between home range area and body mass probably differs for nursing or recently weaned animals. The number of immature animals was strongly correlated with the number of sexually mature animals (Pearson correlation: $r = 0.70$), which suggests that our conclusions are unlikely to be affected strongly by the exclusion of immature animals from the group mass calculation.

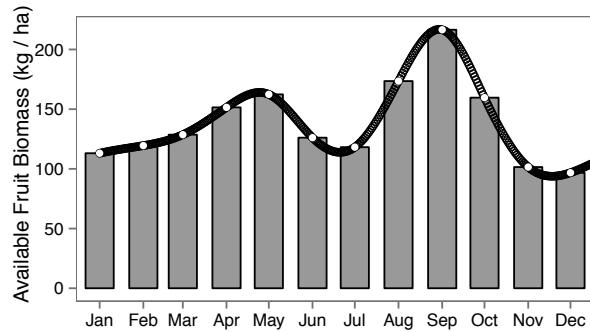
To represent climatic effects in our analyses, we used mean daily maximum temperature, calculated as the mean of each daily maximum temperature for all days contained within the time interval that defined the home range. Because season, temperature and precipitation were strongly correlated at this site, including more than one of these variables in our models would introduce multicollinearity issues, and attempting to disentangle their individual effects on home range size would be problematic. We used maximum temperature because at our study site, temperatures are generally warm throughout the year (Campos and Fedigan, 2013), seasonal variation in maximum daily temperature is much greater than variation in minimum or mean daily temperature (Campos and Fedigan, 2013; Melin, Young, et al., 2014) and previous research has shown that high temperature strongly affects our study animals' activity patterns (Campos and Fedigan, 2009). Thus, of all the climatic variables that we considered, the possible effects of maximum temperature on space use patterns were the most biologically straightforward to interpret.

To represent dietary factors in our analyses, we calculated monthly estimates of available fruit biomass by combining the phenology and tree abundance data sets. We converted each phenology record to an availability index that integrates information about fruit maturity and coverage and is scaled between zero (no mature fruit) and one (full coverage of mature fruit) (see Appendix B for additional detail). For each species separately, we used a generalized additive model to smooth the availability indices over a yearly cycle using a cyclic cubic regression spline smoother, which forces the ends (1 January / 31 December) to match. Following Melin (2011), for each appropriately sized tree in the botanical transects, we used a formula to estimate fruit biomass from the tree's diameter at breast height (DBH) (Peters et al., 1988). We summed these estimates for all individual trees of a given species and divided them by the total transect area to obtain a maximum fruit biomass value per hectare per species. We multiplied these values by the smoothed monthly availability indices for each species, then summed across species to obtain the total available fruit biomass for each month. Finally, because our home range timescales did not correspond to calendar months, we interpolated daily fruit biomass values using a cubic smoothing spline (fig. 4.4b). We used these daily values to calculate the mean available fruit biomass for the time interval that defined the home range. Insects also contribute substantially to the capuchin diet, but we currently lack the data necessary to make objective, realistic estimates of available insect-food biomass.

(a)



(b)



(c)

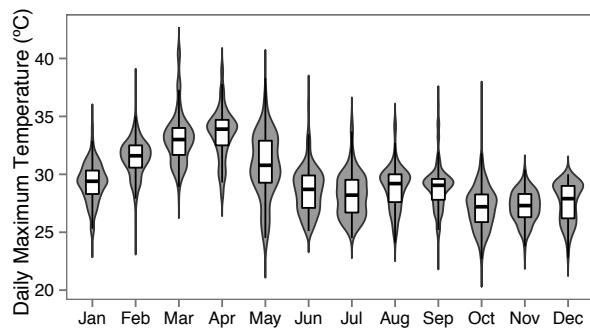


Figure 4.4: (a) Primary ranging area for each month of the year for all study groups. The box plots show medians (thick horizontal lines), first and third quartiles (box hinges), and the data range (whiskers). Numbers above the box plots indicate sample size. Plots were similar for other home range zones at the monthly scale (not shown). (b) Estimated total fruit biomass kg ha^{-1} in the study area for each month of the year (bars). We interpolated between measured values (white dots) for each day of the year (unfilled black dots) using spline smoothing. (c) Box plots and violin plots of daily maximum temperatures for each month of the year during the study period. The box plots are as described above, whereas the violin plots reveal higher-order moments of the temperature distributions, such as skewness and kurtosis.

We were interested in determining how these predictor variables affected home range size and habitat composition within the home range. For home range size, we calculated area at three spatial scales: the core zone, defined as the 50 % isopleth; the primary ranging zone, defined as the 70 % isopleth; and total home range zone, defined as the 95 % isopleth. For home range habitat composition, we calculated an index of forest maturity as the mean NDVI of all pixels contained within the core zone (high use), outside the core zone but within the primary ranging zone (medium use), and outside the primary ranging zone but within the total home range zone (low use). It is important to note that these pixel values are valid measurements of NDVI per se only for the date of image acquisition and not for the time intervals corresponding to each home range. Because peak dry season NDVI is an indicator of forest maturity stage in SSR, we refer to this measurement hereafter as “forest maturity” to avoid confusion.

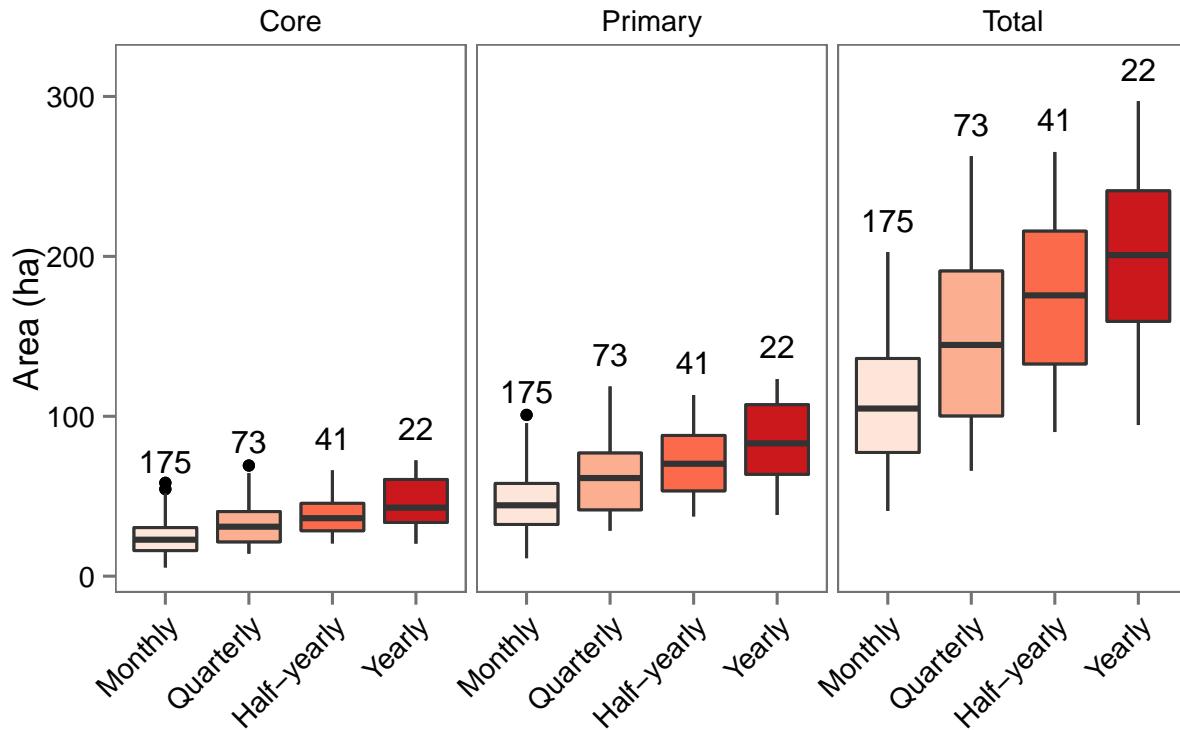


Figure 4.5: Home range area for the seven study groups at three spatial scales and four temporal scales. The components of the box plot are as described in the caption for fig. 5.3. Sample sizes above each box plot indicate the number of distinct home ranges used to construct the box plot (e.g. we calculated a total of 22 yearly ranges, as shown in fig. 4.3).

MODEL FORMULATION AND STATISTICAL ANALYSIS

We used the R package lme4 (Bates and Byrne, 2009) to fit linear mixed effects models (LMM) for each response variable with sets of candidate predictor variables selected a priori based on our predictions. The models described below were applied only at the two smaller temporal scales, monthly ($N = 175$) and quarterly ($N = 73$), because there were relatively few home ranges available for analysis at the larger temporal scales (41 half-yearly ranges and 22 yearly ranges). We carried out model selection and model averaging based on Akaike's Information Criterion values corrected for small sample size, AICc, a procedure advocated by Burnham and Anderson (2002) to reduce the risk of overfitting and to account for model selection uncertainty when sample sizes are relatively small.

We evaluated a set of eight candidate models (tables 4.3 and 4.4) for home range area and habitat composition, with focal group as a random factor to control for repeated observations on the same groups (Börger, Franconi, et al., 2006). We applied a log transformation to the response variables representing area (following Börger, Franconi, et al., 2006; Morellet et al., 2013; Rivrud et al., 2010; van Beest et al., 2011) because the variance of the model residuals increased in proportion to the untransformed response. Following the log transformation, we confirmed that the residuals were well behaved by visual examination of the residuals plotted against fitted values. The basic model for home range area (table 4.3) included the square root of the number of locations as a fixed effect to account for the theoretical scaling relationship between sampling effort and home range area expansion (Gautestad and Mysterud, 1993). Additional predictor variables included mean daily maximum temperature, mean available fruit biomass and group mass (tables 4.3 and 4.4). Prior to running the models, we converted these three predictor variables to unitless Z scores to facilitate direct visual comparison of their relative effects in a coefficient plot (i.e., to remove the influence the different units in which they were measured). We were also interested in determining whether there were systematic differences among the three measures of forest maturity for the different usage zones of each home range. We therefore restructured the data by aggregating the measured forest maturity values in each usage zone (high use, medium use, low use) into a new variable called maturity value, which we grouped by focal group, usage zone and a numerical home range identifier shared by each of the three maturity value measurements obtained from the same home range. We then applied an LMM using maturity value as a response variable, usage zone (high, medium or low) as a fixed effect, and focal group and home range identifier as random effects. For this analysis only, we carried out separate models for each temporal scale. We tested for significant pairwise differences among all linear combinations of levels for that variable (i.e., all combinations of home range zones) using adjusted P values (single-step method) with the R package multcomp (Hothorn et al., 2008).

Table 4.3: Candidate model set and model selection for home range area.

Zone	Model	Fixed effects		Monthly			Quarterly				
				AICc	ΔAICc	w _i	Rank	AICc	ΔAICc	w _i	Rank
Core	1	Basic model		195.285	40.823	1.35×10^{-9}	8	60.027	11.913	1.05×10^{-3}	6
	2	Basic model + T _{max}		178.295	23.833	6.58×10^{-6}	5	60.722	12.608	7.45×10^{-4}	7
	3	Basic model + Fruit		180.444	25.982	2.25×10^{-6}	7	59.540	11.426	1.34×10^{-3}	5
	4	Basic model + Mass		180.406	25.944	2.29×10^{-6}	6	48.114	0.000	0.407	1
	5	Basic model + T _{max} + Fruit		169.385	14.923	5.66×10^{-4}	4	61.239	13.125	5.75×10^{-4}	8
	6	Basic model + T _{max} + Mass		165.173	10.711	0.005	3	49.657	1.543	0.188	3
	7	Basic model + Fruit + Mass		163.720	9.258	0.010	2	48.738	0.624	0.298	2
	8	Basic model + T _{max} + Fruit + Mass		154.462	0.000	0.985	1	50.872	2.758	0.103	4
Primary	1	Basic model		164.925	36.681	9.56×10^{-9}	8	52.273	13.672	5.58×10^{-4}	5
	2	Basic model + T _{max}		154.408	26.164	1.84×10^{-6}	7	53.903	15.302	2.47×10^{-4}	7
	3	Basic model + Fruit		152.264	24.020	5.37×10^{-6}	6	52.937	14.336	4.00×10^{-4}	6
	4	Basic model + Mass		146.989	18.746	7.50×10^{-5}	5	38.600	0.000	0.520	1
	5	Basic model + T _{max} + Fruit		146.457	18.213	9.79×10^{-5}	4	55.094	16.494	1.36×10^{-4}	8
	6	Basic model + T _{max} + Mass		138.173	9.929	0.006	3	40.818	2.217	0.171	3
	7	Basic model + Fruit + Mass		132.388	4.144	0.111	2	40.169	1.568	0.237	2
	8	Basic model + T _{max} + Fruit + Mass		128.244	0.000	0.883	1	42.597	3.997	0.070	4
Total	1	Basic model		100.620	29.615	2.45×10^{-7}	8	27.937	14.641	3.82×10^{-4}	5
	2	Basic model + T _{max}		98.831	27.826	5.99×10^{-7}	7	30.220	16.924	1.22×10^{-4}	7
	3	Basic model + Fruit		92.464	21.459	1.45×10^{-5}	5	29.906	16.610	1.43×10^{-4}	6
	4	Basic model + Mass		80.683	9.678	0.005	4	13.296	0.000	0.578	1
	5	Basic model + T _{max} + Fruit		92.949	21.944	1.13×10^{-5}	6	32.283	18.987	4.35×10^{-5}	8
	6	Basic model + T _{max} + Mass		80.144	9.139	0.007	3	15.550	2.254	0.187	2
	7	Basic model + Fruit + Mass		71.005	0.000	0.661	1	15.652	2.356	0.178	3
	8	Basic model + T _{max} + Fruit + Mass		72.409	1.404	0.327	2	17.933	4.637	0.057	4

The basic model includes the intercept, the square root of the number of location points, and the random effect focal group. The model-averaged coefficients are plotted in fig. 4.7. AICc: Akaike's Information Criterion; ΔAICc : difference in AICc compared to the best model; w_i: Akaike Weight

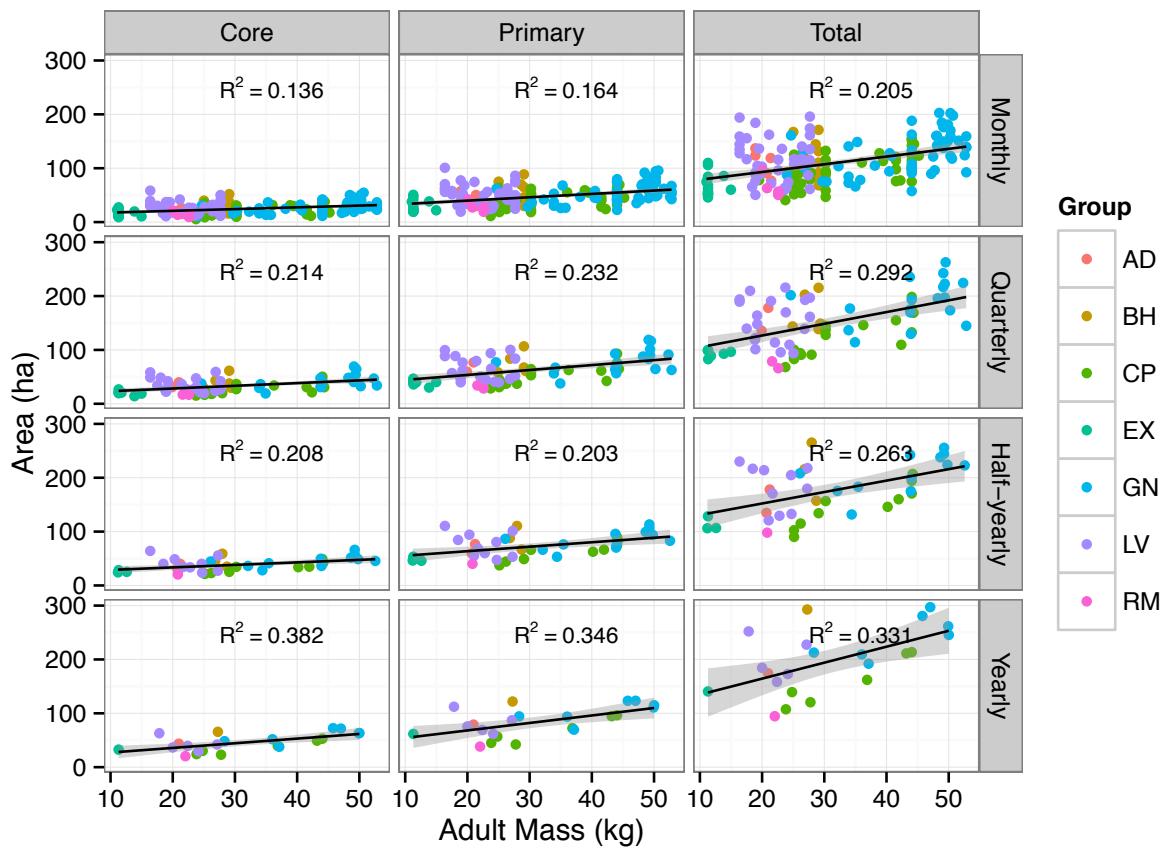


Figure 4.6: Relationship between total body mass of adult animals and home range area measured at three spatial scales (horizontal facets) and four temporal scales (vertical facets). See the main text for definitions of these scales. Linear regression lines with 95 % confidence intervals are shown.

4.3 RESULTS

4.3.1 HOME RANGE SIZE

Descriptive statistics for home ranges and predictor variables at each spatiotemporal scale are presented in tables 4.5 and 4.6, respectively. As expected for an animal that shows seasonal home range shifts, home range size tended to increase with the duration of the temporal scale (fig. 4.5). However, there was extensive overlap across scales both within and between groups. Data exploration revealed that group mass alone explained 13 % to 38 % of the variance in home range size, depending on the spatiotemporal scale of analysis (fig. 4.6), with the caveat that the exploratory regressions did not account for repeated measures on the same groups or differences in sampling effort. After accounting for these and other possible influences in the LMM framework (table 4.3), group mass remained the most important and influential determinant of home range size at all scales analyzed (fig. 4.7). For

example, at the quarterly timescale, group mass and sampling effort, together with the random effect focal group, explained about 66.4 % of the variance in total home range area ($R^2_{GLMM(c)}$: Nakagawa and Schielzeth, 2013). The other two predictor variables that we analyzed, available fruit biomass and mean daily maximum temperature, showed more subtle, scale-dependent effects on home range area. Available fruit biomass had a consistently negative influence on home range area at the smaller monthly timescale but no influence at the larger quarterly timescale (fig. 4.7). The effects of mean daily maximum temperature followed a similar pattern, with higher temperatures predicting smaller areas at the monthly timescale but not the quarterly timescale. Moreover, the effects of maximum temperature on home range area were clearly dependent on spatial scale: temperature had a relatively strong influence on the core zone but essentially no influence on the total home range zone (fig. 4.7).

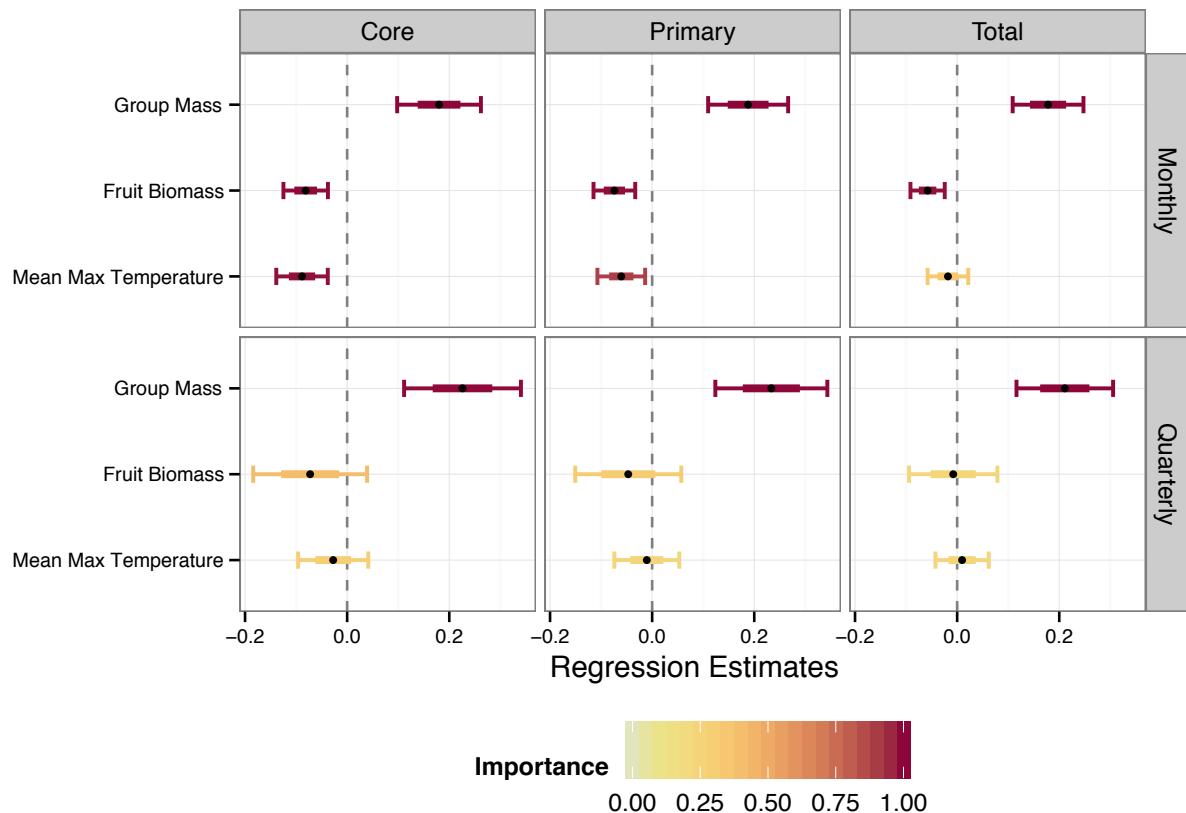


Figure 4.7: Model-averaged regression coefficients and relative variable importance for linear mixed models of home range size. Thin error bars show 95 % confidence intervals, and thick bars show ± 1 SD. The predictor variables were scaled to facilitate direct comparison of their relative effects. All models included the random effect focal group. The relative importance of each predictor variable was calculated as the sum of the Akaike weights for each model in which the variable appeared.

Table 4.4: Candidate model set and model selection for mean forest maturity index within each home range zone.

Zone	Model	Fixed effects		Monthly			Quarterly				
				AICc	ΔAICc	w _i	Rank	AICc	ΔAICc	w _i	Rank
High use	1 Basic model			-541.909	6.868	0.012	6	-242.832	7.195	0.011	8
	2 Basic model + T _{max}			-548.777	0.000	0.369	1	-248.120	1.907	0.151	3
	3 Basic model + Fruit			-541.242	7.535	0.009	8	-243.771	6.257	0.017	7
	4 Basic model + Mass			-542.364	6.413	0.015	5	-245.524	4.503	0.041	6
	5 Basic model + T _{max} + Fruit			-546.976	1.801	0.150	3	-247.107	2.920	0.091	4
	6 Basic model + T _{max} + Mass			-548.399	0.378	0.305	2	-250.027	0.000	0.392	1
	7 Basic model + Fruit + Mass			-541.841	6.936	0.012	7	-246.343	3.685	0.062	5
	8 Basic model + T _{max} + Fruit + Mass			-546.677	2.100	0.129	4	-249.004	1.024	0.235	2
Low use	1 Basic model			-715.331	8.810	0.005	7	-338.399	0.959	0.145	4
	2 Basic model + T _{max}			-723.527	0.614	0.303	2	-339.358	0.000	0.234	1
	3 Basic model + Fruit			-718.425	5.716	0.024	5	-338.832	0.526	0.180	2
	4 Basic model + Mass			-713.278	10.863	0.002	8	-336.800	2.559	0.065	7
	5 Basic model + T _{max} + Fruit			-724.141	0.000	0.411	1	-338.531	0.827	0.155	3
	6 Basic model + T _{max} + Mass			-721.428	2.713	0.106	4	-337.421	1.937	0.089	5
	7 Basic model + Fruit + Mass			-716.391	7.750	0.009	6	-337.096	2.263	0.076	6
	8 Basic model + T _{max} + Fruit + Mass			-721.998	2.143	0.141	3	-336.525	2.833	0.057	8
Medium use	1 Basic model			-618.816	8.737	0.006	5	-276.290	6.564	0.012	8
	2 Basic model + T _{max}			-627.553	0.000	0.493	1	-282.853	0.000	0.327	1
	3 Basic model + Fruit			-618.269	9.284	0.005	6	-277.072	5.781	0.018	6
	4 Basic model + Mass			-617.600	9.953	0.003	7	-276.776	6.077	0.016	7
	5 Basic model + T _{max} + Fruit			-625.737	1.816	0.199	3	-281.623	1.230	0.177	3
	6 Basic model + T _{max} + Mass			-625.811	1.742	0.206	2	-282.552	0.302	0.281	2
	7 Basic model + Fruit + Mass			-617.125	10.429	0.003	8	-277.372	5.482	0.021	5
	8 Basic model + T _{max} + Fruit + Mass			-624.015	3.539	0.084	4	-281.258	1.595	0.147	4

The basic model includes the intercept and the random effect focal group. The model-averaged coefficients are plotted in fig. 4.8. AICc: Akaike's Information Criterion; ΔAICc : difference in AICc compared to the best model; w_i: Akaike Weight

4.3.2 HOME RANGE COMPOSITION

The LMMs for forest maturity that considered the effects of maximum temperature, fruit availability and group body mass showed relatively high consistency across spatial and temporal scales (table 4.4). Model averaging revealed that mean daily maximum temperature was the most important determinant of home range composition at both the monthly and quarterly timescales, with higher temperatures predicting increased use of older, more evergreen forest (fig. 4.8). The home ranges of larger groups (as measured by group mass) were not consistently more mature than those of smaller groups (fig. 4.8). The LMMs that modeled forest maturity as a function of usage intensity (high, medium, low) were also highly consistent at the monthly, quarterly, half-yearly and yearly timescales. Zones of higher use were significantly older, on average, than zones of lesser use (fig. 4.9 and table 4.7). However, the preference for mature forest was not unvarying: for a relatively small number of home ranges, space use was concentrated on younger forest (negatively sloped line segments in fig. 4.10).

4.4 DISCUSSION

4.4.1 DETERMINANTS OF HOME RANGE SIZE

Group mass was consistently the most important predictor of home range size in our models, and its effects were relatively insensitive to spatial or temporal scale. This finding is consistent with the allometric scaling relationship between body mass and space requirements that explains a significant amount of cross-species variation in home range size among primates (Clutton-Brock and Harvey, 1977; Harvey and Clutton-Brock, 1981; Milton and May, 1976). This scaling relationship has also been proposed to explain within-species and within-population variation in home range size (Isbell, 1991; Janson and Goldsmith, 1995). However, given that primate group sizes change relatively slowly, there are few studies on wild primates with a sufficiently large sample of longitudinal home range measurements and/or separate groups to demonstrate this relationship convincingly. Our 8-year longitudinal ranging data set therefore provides valuable and robust evidence that grouping patterns drive within-species and even within-group variation in home range size as group compositions vary over time. This finding also has important implications for theoretical models that examine the costs of group living, because as group size increases, so too does home range size. Further study is needed to determine whether *C. capucinus* individuals in groups with larger home ranges incur metabolic costs by ranging over larger areas, as seems to be the case for most frugivorous primates (Janson and Goldsmith, 1995). Alternatively, larger groups may be able to maintain larger home ranges without increased individual foraging effort if their relative dominance over neighboring groups gives them greater freedom to shift their geographical focus to the most productive areas

Table 4.5: Summary of home range characteristics at four temporal scales.

Variable	Temporal Scale	Zone	Min	Max	Mean	Std Dev
Home Range Size (ha)	Monthly	Core	5.44	58.37	24.42	10.59
		Primary	11.25	100.84	46.67	18.64
		Total	40.81	202.66	108.76	38.43
	Quarterly	Core	14.09	69.19	33.27	13.00
		Primary	28.45	118.67	62.55	22.81
		Total	66.00	262.67	148.17	48.29
	Semiannual	Core	20.48	66.18	38.60	11.97
		Primary	37.36	113.30	72.65	21.51
		Total	90.15	265.30	175.29	48.44
	Yearly	Core	20.37	72.45	45.48	15.92
		Primary	38.28	123.28	83.83	26.91
		Total	94.53	297.07	197.77	58.72
Mean Age Index	Monthly	High use	0.55	0.77	0.68	0.04
		Medium use	0.60	0.77	0.67	0.03
		Low use	0.60	0.73	0.65	0.03
	Quarterly	High use	0.61	0.76	0.68	0.03
		Medium use	0.61	0.74	0.67	0.03
		Low use	0.60	0.69	0.65	0.02
	Half-yearly	High use	0.63	0.76	0.68	0.03
		Medium use	0.61	0.74	0.66	0.03
		Low use	0.61	0.68	0.65	0.02
	Yearly	High use	0.64	0.75	0.68	0.03
		Medium use	0.62	0.69	0.66	0.02
		Low use	0.61	0.67	0.65	0.02

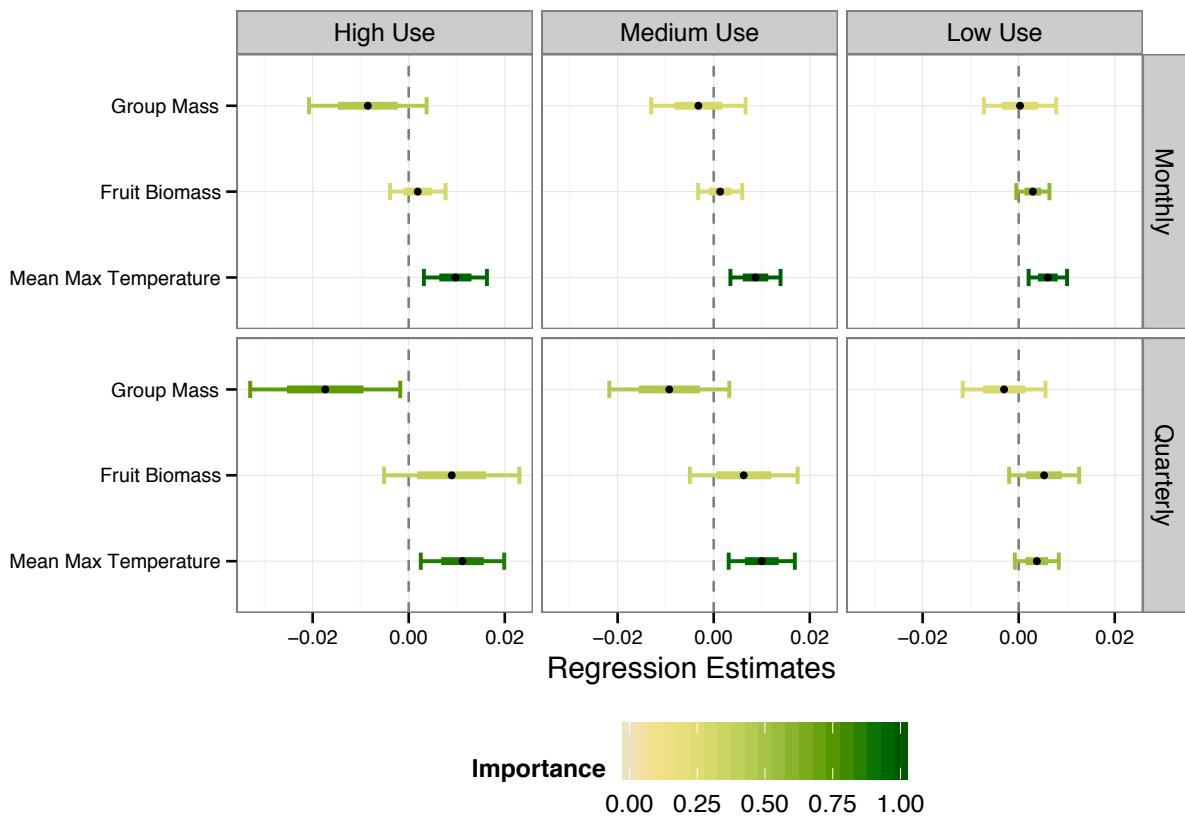


Figure 4.8: Model-averaged regression coefficients and relative variable importance for linear mixed models of mean forest maturity index contained within the home range. Thin error bars show 95 % confidence intervals, and thick bars show ± 1 SD. The predictor variables were scaled to facilitate direct comparison of their relative effects. All models included the random effect focal group. The relative importance of each predictor variable was calculated as the sum of the Akaike weights for each model in which the variable appeared.

(Majolo et al., 2008).

At the monthly timescale, our results demonstrate that seasonal climatic and phenological fluctuations also play important roles in determining home range size. The effect of climate, represented in our models by mean daily maximum temperature, was an important explanatory variable in the monthly home range models. Hotter conditions were associated with smaller monthly ranges, a finding consistent with previous research that found reduced activity levels with increasing temperature (Campos and Fedigan, 2009). As predicted, the temperature-driven reduction of home range size was greatest on high-use core zones. This pattern is consistent with extended resting periods (a behavioral response to hot, dry weather), which produce more uneven utilization distributions and small, dense core zones. The spatial-scale-dependent effects of temperature on different usage zones may suggest some behavioral compensation for lost foraging time during cooler hours of the day, for example, by

Table 4.6: Descriptive statistics of the predictor variables used for modeling home range size and composition.

Variable	Temporal Scale	Min	Max	Mean	Std Dev
T_{max}	Monthly	25.36	36.07	30.22	2.53
	Quarterly	26.16	33.60	29.99	2.35
	Half-yearly	26.41	31.56	29.60	1.64
	Yearly	27.57	31.26	29.39	1.16
Fruit Biomass	Monthly	95.57	202.39	140.87	29.05
	Quarterly	109.78	158.25	140.52	14.78
	Half-yearly	128.13	149.56	137.54	10.69
	Yearly	138.93	138.93	138.93	0.00
Adult Mass	Monthly	11.05	52.82	31.01	12.12
	Quarterly	11.30	52.82	29.85	11.98
	Half-yearly	11.20	52.57	30.87	11.69
	Yearly	11.30	50.02	31.27	11.40
Number of Locations	Monthly	96	470	196.73	81.75
	Quarterly	193	1088	494.70	241.80
	Half-yearly	385	1985	869.37	473.35
	Yearly	773	3636	1615.09	844.12

traveling more quickly and/or traveling longer distances (van Schaik and Brockman, 2005), resulting in only marginal reduction of the total home range area, as was the case in the present study.

Food resource effects on home range size, represented in our models by available fruit biomass, were also consistent with previous research on other capuchin species (Di Bitetti, 2001; Peres, 1994; Terborgh, 1983) in that greater food abundance was associated with smaller home range size at the monthly timescale. A possible explanation for this pattern is movement-related compensation for nutritional shortfalls during seasonal fruit scarcity, which may include area shifting or increased foraging effort (Hemingway and Bynum, 2005; van Schaik and Brockman, 2005; van Schaik, Terborgh, et al., 1993). Future studies will attempt to quantify such behavioral adjustments by examining movement parameters in relation to energy intake rates. There was only minimal evidence of spatial scale dependence for food resource effects on home range size, as the parameter estimates and model-averaged importance attributed to fruit biomass were all strikingly similar for the core, primary and total home range areas.

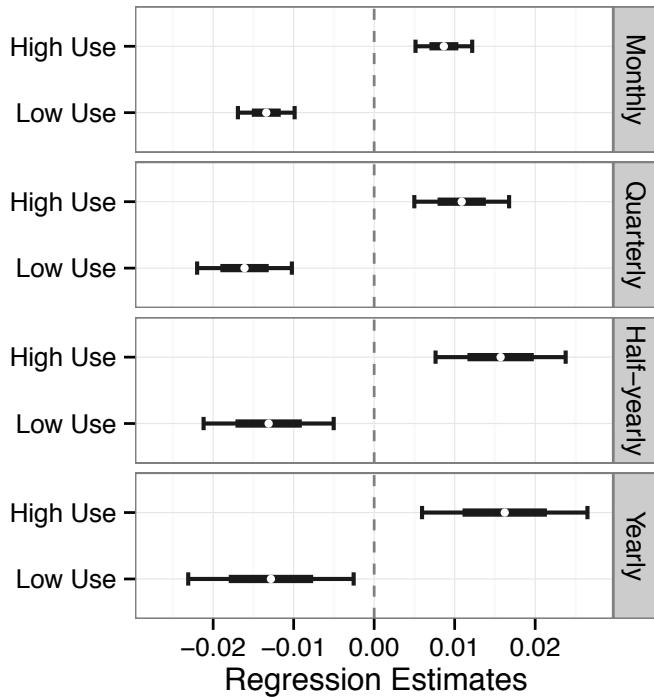


Figure 4.9: Estimated coefficients for linear mixed models of mean forest maturity index as a function of usage zone. All models included the focal group and home range ID number as random effects. The forest maturity index is scaled between 0 and 1, and is based on peak dry season NDVI values. Parameter estimates are relative to the baseline category 'medium use', which is defined as zero. Thin error bars show 95 % confidence intervals, and thick bars show ± 1 SD.

4.4.2 INTENSITY OF USE AND FOREST MATURITY

The forest maturity models that considered the effects of temperature, group mass and food revealed that only temperature had a consistently strong influence on the habitat composition of home ranges. Consistent with our predictions, hotter conditions were associated with more mature evergreen forest contained within the home range. As in the case of home range area, temperature-driven effects on home range forest composition were manifested most clearly on the core zone. Surprisingly, and contrary to our prediction, group mass did not show a consistent positive relationship with home range forest maturity, which suggests that large groups were either not able or not motivated to secure the most mature forest patches, despite their dominance over smaller groups (Childers, 2008). The reasons for this finding are unclear, but we offer three possible explanations. First, our use of forest maturity as a proxy for habitat quality may be a flawed approach because it only considers the greater abundance of fruit in mature forest. Other important food resources, such as seeds, insects and small vertebrates may be more abundant in secondary forest, but their distributions have not been adequately quantified in our study system. Second, the most critically limiting resource in our study is

probably access to water during the dry season (Fedigan et al., 1996). Large groups may gain little from relocating to a slightly more productive (i.e., mature) area if they can meet their basic food requirements while maintaining control over one of the scarce waterholes, none of which are located in mature forest. Third, reliance on long-term spatial memory of specific food resources (Janson, 1998) probably discourages radical shifts to new and unfamiliar areas. This inertia may keep formerly small groups that established themselves in marginal habitat from relocating even if they later grow large enough to displace a smaller group from a more productive area.

We predicted that more intensively used home range zones would consist of older forest, on average, than low-use zones. The prediction was borne out robustly at all temporal scales analyzed (fig. 4.8). Together, these findings suggest a movement strategy in which the capuchins generally avoid using young forest intensively, but they do not exclude such areas entirely from their total home ranges. It is likely that the heterogeneous landscape at SSR forces capuchins to pass through young, regenerating habitats regularly as they move between more highly preferred areas with mature forest. Despite the overall support for our prediction, it is clear from the numerous negatively sloped line segments in fig. 4.10 that more intensively used home range zones were not always older than less intensively used home range zones. This observation provides an interesting basis for comparison with sympatric howler monkeys (*Alouatta palliata*) and spider monkeys (*Ateles geoffroyi*), which also prefer mature forest but appear to be more reliant on access to a mature, high-quality core zone (Asensio, Lusseau, et al., 2012; Sorensen, 1998). Differences in diet provide a possible explanation for the species differences. Our results suggest that the capuchins heavily utilize different types of forest at different times or for different purposes, even if older forests are used more heavily on average. Some fruit-bearing tree species that contribute substantially to the capuchin diet (e.g. *Vachellia collinsii*, *Randia monantha* and *Byrsonima crassifolia*) are relatively abundant in young forest (Kalacska, Sanchez-Azofeifa, Calvo-Alvarado, et al., 2004), and during their fruiting seasons, young forest may become more attractive. Moreover capuchins feed more heavily on insects than do howler or spider monkeys, and previous primate-focused studies at other sites have found that insect-food abundance may be greater in regenerating forest habitats (Parry et al., 2007; Vulinec et al., 2006). The scenario we describe is consistent with capuchins' well-known ability to exploit varied forest types and their willingness to forage in very young regenerating forest (Sorensen and Fedigan, 2000). For example, the yearly home range of group BH was geographically centered on the only large patch of primary forest in the study area, but they made frequent forays into very young regenerating areas, especially during the cooler wet season. In the relatively open conditions of young forest, data indicate that our study animals perceive reduced predation risk from predatory raptors, which are most frequently encountered in mature forest Campos and Fedigan (2014). Thus, capuchins may benefit

Table 4.7: Pairwise comparisons among factor levels for the linear mixed-effects models for forest age as a function of usage intensity.

Temporal Scale	Linear hypothesis	+/-	Z value	Adj. P
Monthly	Low use - Medium use = 0	-	-7.461	<0.001
	High use - Medium use = 0	+	4.818	<0.001
	High use - Low use = 0	+	12.279	<0.001
Quarterly	Low use - Medium use = 0	-	-5.362	<0.001
	High use - Medium use = 0	+	3.620	<0.001
	High use - Low use = 0	+	8.982	<0.001
Half-yearly	Low use - Medium use = 0	-	-3.180	0.004
	High use - Medium use = 0	+	3.810	<0.001
	High use - Low use = 0	+	6.991	<0.001
Yearly	Low use - Medium use = 0	-	-2.446	0.038
	High use - Medium use = 0	+	3.094	0.006
	High use - Low use = 0	+	5.540	<0.001

P-values shown were adjusted using the single-step method.

from maintaining home ranges that include a mix of habitat types.

4.4.3 IMPLICATIONS FOR CAPUCHIN BEHAVIOURAL ECOLOGY AND CONSERVATION

Our study illustrates the complex ecological processes that affect movement behavior in a Neotropical primate across a range of spatial and temporal scales. We found clear evidence that group mass is a fundamental driver of home range size in this species, and that climatic seasonality, food resources and landscape heterogeneity also play important roles in shaping home ranges at relatively short temporal scales. These findings help to contextualize the ecological role of capuchins in Neotropical dry forest ecosystems, which are gravely threatened by climate change and human disturbance (Portillo-Quintero and Sánchez-Azofeifa, 2010). Our findings also have important implications for conservation planning in tropical dry forests. Although mature tropical dry forest is undeniably of high conservation value, our findings suggest that some potential flagship species may benefit from the conservation of a variety of contiguous habitat types, including degraded forest habitats, which may form effective buffer zones or corridors that promote connectivity among remaining mature forest patches.

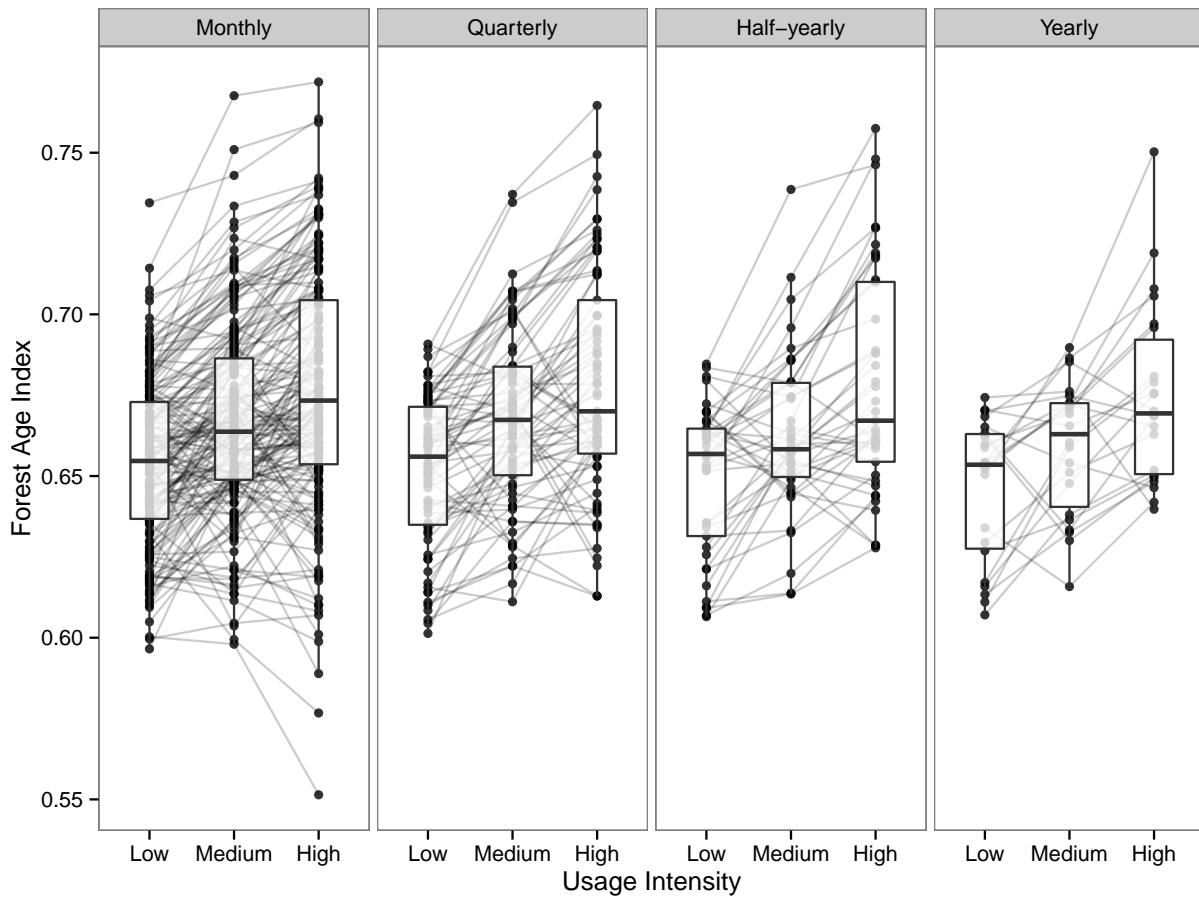


Figure 4.10: Comparison of NDVI-based forest maturity indices at three spatial scales and four temporal scales. Each home range contributes three mean forest maturity measurements, one for each home range use zone (low use, medium use, high use). This trio of points is linked by gray line segments. Most of the line segments were positively sloped, indicating an increase in mean forest maturity from a less intensively used home range zone to a more intensively used zone. The components of the box plots are as described in the caption for fig. 5.3

4.4.4 THE IMPORTANCE OF SCALE

Inferences about sociality and competitive regime are often made based on the relationship between space use variables and environmental factors such as food availability. Our study demonstrates that such inferences are likely to change depending on the scale of analysis. For example, the effects of both temperature and fruit availability on home range size were strong at the monthly timescale but essentially disappeared at the quarterly timescale. One possible explanation for this result is that at relatively long timescales (e.g., several months), important variability in these quickly changing environmental drivers is averaged out as the climate changes and different fruit species come into season. Indeed, when plotted at the monthly timescale, climatic and dietary influences on home range area

were clearly evident: home range area exhibited a strong bimodal pattern with peaks in November–January and June–July, and troughs in April and August–September (fig. 4.4a). This pattern showed a near-perfect inverse relationship with fruit abundance (fig. 4.4b); the trough in April also coincided with the annual peak in maximum temperature (fig. 4.4c). However, as temporal scale increased, these important ecological patterns became increasingly unclear because the longer time intervals spanned both peaks and troughs. The relevance of this finding extends beyond animal home ranges, as it demonstrates that important ecological drivers of animal behavior may go undetected if the scale of analysis is not well matched to the underlying ecological processes. Given the increasing popularity of phylogenetic meta-analyses that require the use of species mean values (e.g., the home ranges analyzed by Pearce et al., 2013), our study provides an important cautionary demonstration that such values may depend critically on somewhat arbitrary decisions regarding temporal scale. The home range sizes reported here at various temporal scales, all of which have been used commonly in the primate literature, almost completely span the range of sizes reported elsewhere for capuchin monkeys in a wide variety of ecosystems (Chapman, 1988; Crofoot, 2007; Defler, 1979, 1982; Di Bitetti, 2001; Izawa, 1980; Matthews, 2009; Terborgh, 1983; Zhang, 1995). We found extensive overlap in home range sizes across temporal scales, an observation that would appear puzzling if important factors such as group mass were not considered. For example, the total area traversed in a typical month by the large group GN was comparable to (and often greater than) the total area traversed by the much smaller groups EX and RM over an entire year. Nevertheless, for a given group, mean home range size increased monotonically with temporal scale up to a full annual cycle. This pattern is consistent with observations that capuchin home ranges shift throughout the year, possibly in response to spatiotemporal variation in food and water availability. As temporal scale increases, more home range shifts, and thus more new areas, are likely to be included in the home range. The tendency for home range size to increase with temporal scale was less pronounced for primary ranging zones and especially core zones. This suggests a lesser degree of shifting among heavily used zones and may indicate frequent reuse of high-value locations throughout the year despite ephemeral shifts in the total home range. Such inferences highlight the power of our longitudinal, multiscale mixed modeling approach to analyzing capuchin movement ecology.

It is the destiny of all conserved wildlands to be anthroecosystems—ecological islands carved out of a much larger anthro-ocean... eventually they will settle into some sort of old-growth status that reflects not only their original composition, but also their particular overlay of climate changes, impeded migrations, altered water regimes, size, introduced species flow, edge effects, industrial contaminants, direct footprints, etc.

Daniel H. Janzen, 2000

5

A multi-decade investigation of primate population dynamics: the effects of climatic oscillations and forest regeneration

5.1 INTRODUCTION

Long-term monitoring is vital for understanding the biological requirements and conservation outlook of threatened animal populations (Clutton-Brock, 2012; Sinclair and Byrom, 2006). A major aim of long-term population monitoring is to describe trends in demographic variables over time (Clutton-Brock and Sheldon, 2010). By documenting such trends, it may be possible to link population fluctuations with changes in climate and habitat (Wright, 2007), thereby improving predictions about how the population will fare in projected disturbance or climate change scenarios (Lawler et al., 2006). The demographic structure of relatively small or isolated populations may be especially sensitive to anomalous events such as human disturbance, natural disasters, prolonged extreme climatic episodes, and disease outbreaks. These dependencies may be impossible to detect without concurrent and systematic data on landscape structure, climate, and population trends over a multi-generational time frame (Clutton-Brock, 2012). Most studies of long-lived nonhuman primates have

not been long enough in duration to investigate these important questions (for some notable exceptions, see Kappeler and Watts, 2012). Consequently, there have been few studies on the long-term dynamics of primate populations in relation to quantitative data on ecosystem change.

With few exceptions (e.g., Strier and Boubli, 2006), our current knowledge about the long-term effects of climate and ecosystem change on primates comes from declining populations of lemurs (Dunham, Erhart, and Wright, 2011; Jolly, 2012; Sussman et al., 2012; Wright, Erhart, et al., 2012) and Old World monkeys (Chapman, Balcomb, et al., 2000; Chapman, Struhsaker, and Lambert, 2005; Chapman, Struhsaker, Skorupa, et al., 2010; Lwanga et al., 2011). Thus, most studies on primates' responses to environmental change have focused on their capacity to cope with diminishing and/or deteriorating ecosystems. This focus pragmatically reflects the dire situation faced by many primate populations around the world (Cowlishaw and Dunbar, 2000). However, it is also important to know how primate populations fare in conservation areas that are "succeeding" (Laurance et al., 2012); that is, areas in which the major anthropogenic detriments to primates—deforestation, logging, live-capture, hunting, and fire (Chapman and Peres, 2001)—have been effectively and lastingly eradicated. Conservation strategies that target large, long-lived animals in profoundly disturbed habitats may be predicated on the belief that dwindling populations will recover over time if their habitats can be adequately restored. There is currently a near-total absence of quantitative information on how climatic fluctuations and landscape structural dynamics affect primate population recovery after the establishment of an effective conservation area. Globally, there are very few study sites that both support primates and meet the reserve-health criteria for investigating these important questions, and even fewer sites with a sufficiently long record of continuous demographic, climatic, and ecological monitoring to draw meaningful conclusions.

Here, we examine the natural recovery process of a population of white-faced capuchins (*Cebus capucinus*) in northwestern Costa Rica over a 42 year period in relation to quantitative information on how the landscape and climate changed over the same period. The study area is situated in the core of a well-studied and thriving endeavor in ecosystem restoration initiated in 1971 (Allen, 2003; Janzen, 1987, 2000; Woodworth, 2013). Our study therefore offers a unique perspective on the factors that promote or limit primate population growth, and it sheds light on their potential for recovery after the elimination of human disturbances. Our objectives are to 1) describe historical trends in our study site's population of capuchins from 1971 to 2013, extending previously published records (Fedigan, 1986; Fedigan, Fedigan, et al., 1985; Fedigan and Jack, 2012; Fedigan and Jack, 2001; Fedigan et al., 1996; Freese, 1976); 2) evaluate the extent to which the capuchin population has been affected by climatic fluctuations, which are known to affect the population dynamics of other mammals, including primates (Dunham, Erhart, Overdorff, et al., 2008; Dunham, Erhart, and Wright,

2011; Hallett et al., 2004; Wiederholt and Post, 2010; Wright, 2007); 3) determine the influence of habitat availability and configuration on capuchin population trends, focusing on the availability of evergreen vegetation, which is an important resource for primates during the severe dry season; and 4) quantify spatial variation in these population and landscape patterns within distinct sub-regions of the study area.

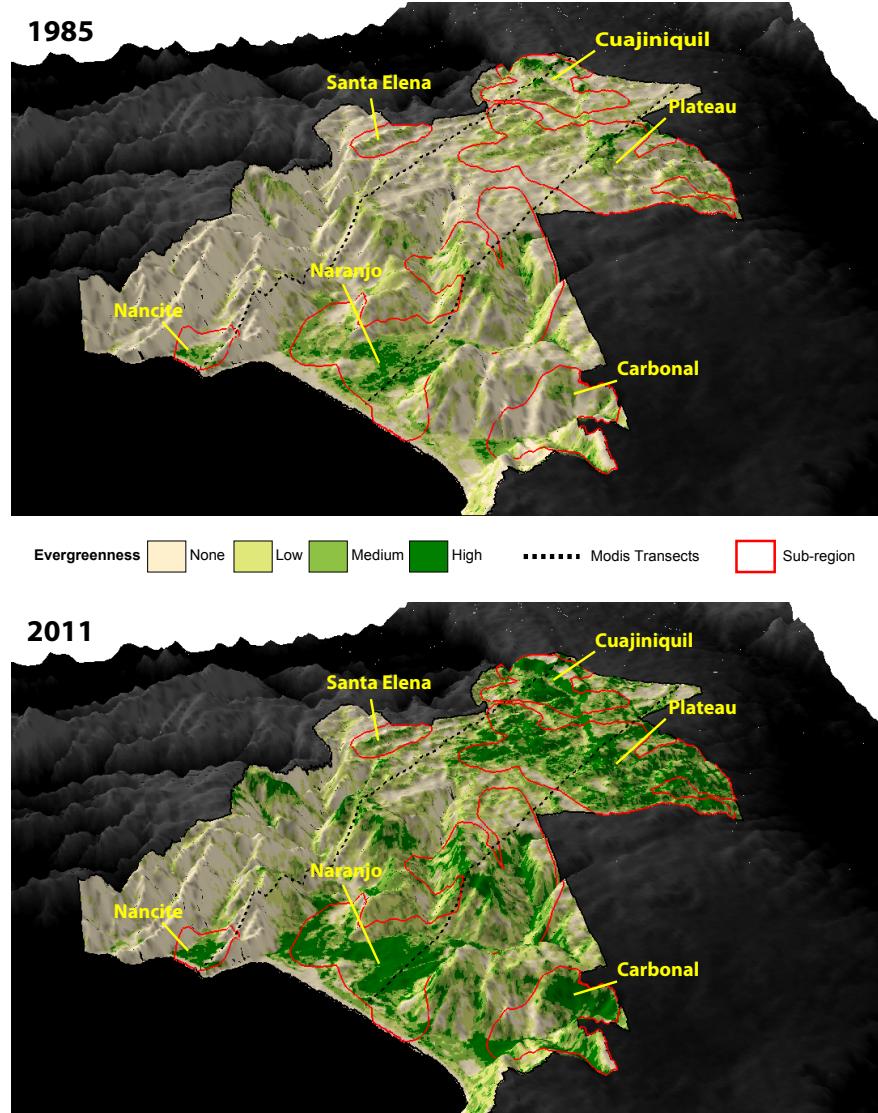


Figure 5.1: Landsat-derived maps of the study area during peak dry season in March 1985 (top) and March 2011 (bottom) showing topography, vegetation greenness, MODIS transects, and sub-regions of relatively high capuchin density. The uniformly dark area in the foreground is the Pacific Ocean. The elevation data are exaggerated by a factor of four, and they come from the ASTER Global Digital Elevation Model, Version 2, a product of METI and NASA.

5.2 MATERIALS AND METHODS

5.2.1 STUDY SYSTEM

Our study area is Sector Santa Rosa (SSR) of the Área de Conservación Guanacaste (ACG) in north-western Costa Rica ($10^{\circ}50'24''\text{N}$ $85^{\circ}37'12''\text{W}$), a UNESCO World Heritage site and a global model of tropical dry forest restoration ecology (Allen, 2003; Janzen, 1987). Janzen (2000) gives a thorough history of the anthropogenic disturbance of this region, the creation and expansion of the ACG, and the ecological recovery that has occurred after decades of active management in the form of aggressive fire suppression. The ACG was classified as “succeeding” in a recent global assessment of 60 representative tropical forest reserves, ranking second in overall reserve-health due in part to its marked improvement over recent decades (Laurance et al., 2012). The geographic boundaries of SSR, which contain 10 800 ha of varied habitat, were formed with the establishment of Santa Rosa National Park in 1971. The National Park has since been enlarged to include neighboring areas, but our research on primate population dynamics remains focused on the groups living within the borders of SSR. The northeastern part of the study area consists of an undulating plateau that is broken by numerous small gullies and sits at an elevation of about 300 m. The plateau is drained to the north and east by many gently sloping, seasonally dry channels (fig. 5.1). To the south, the plateau is drained by several steep-walled ravines, many of which harbor year-round trickles of fresh water and thin strips of evergreen gallery forest. Upon leveling out in the lowlands, these channels pass through pockets of relatively undisturbed dry forest followed by a slender zone of mangrove forest before emptying into the Pacific Ocean. To the west lie dry and geologically ancient hills with sparse vegetation cover. SSR is situated in a dry tropical forest biome that experiences stark rainfall seasonality, with nearly all the annual rain falling between mid-May and late-November. The 6-month-long dry season triggers total leaf shedding in many plant species. The spatially heterogeneous distribution of deciduous and evergreen species produces much local variation in plant communities, from totally deciduous stands of very young woody succession on abandoned pastures to almost entirely evergreen old-growth forest (Janzen, 1988; Klemens et al., 2011). Evergreen forest patches provide important food resources and shade to primates during the hottest and driest months of the year (Campos and Fedigan, 2009; Fedigan and Jack, 2001). SSR supports three primate species, the white-faced capuchin, the mantled howler (*Alouatta palliata*), and the black-handed spider monkey (*Ateles geoffroyi*). This paper focuses on the population of white-faced capuchins. Previous research in SSR has found that whereas the howler and spider monkeys are largely confined to old-growth forest, the capuchins exploit a wide range of regenerating habitats including some as forest as young as 14 years (Sorensen and Fedigan, 2000). Although they venture into very young forest, capuchins nonetheless appear to have limited

opportunities for colonizing new areas because each group must maintain access to scarce and highly localized resources through most of the hot dry season: drinking water, at least some fruit trees in established forest, and shaded (i.e., evergreen) resting areas (Fedigan and Jack, 2001; Fedigan et al., 1996).

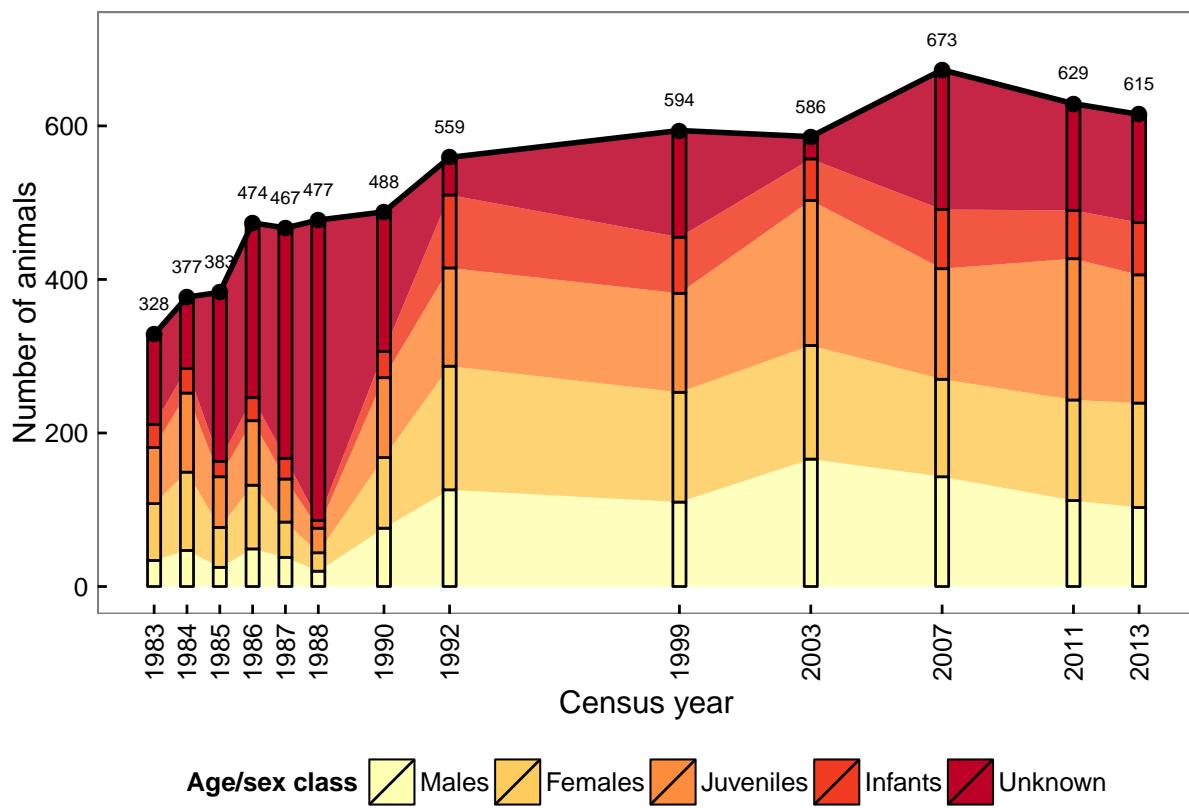


Figure 5.2: Total estimated size of the capuchin population in SSR since intensive monitoring began in 1983, broken up by age/sex class. The “Unknown” category shows supplemental animals added to correct for sampling effort and visibility conditions (see description of “replacement counts” in the main text).

5.2.2 DATA COLLECTION

PARK-WIDE CENSUSES

The population demographic data consist of 14 censuses carried out between 1971 and 2013 (Fedigan, 1986; Fedigan, Fedigan, et al., 1985; Fedigan and Jack, 2012; Fedigan and Jack, 2001; Fedigan et al., 1996; Freese, 1976). Most of the censuses were carried out between late April and June, which corresponds to the dry-to-wet season transition in SSR. Beginning with the 1983 census, teams of

observers employed a “modified quadrat” technique in which separate pairs of searchers walked transects and all trails, roads, fence lines, and stream beds in a chosen sampling area. Any capuchins encountered were followed until multiple observers could agree on a consistent, complete group count and composition, or until the group was lost. Distinctive individuals in each group were described, and these notes were used to avoid repeat counts of the same group. In later years, straight-line transects were discontinued as census-takers became increasingly proficient at relocating known groups and discovering newly-established groups. From 1983 forward, our knowledge of the different capuchin groups living in the park was sufficiently complete that we could calculate true count estimates with reasonably high confidence. Sampling effort varied among censuses, and in some years it was necessary to supplement actual count data with “replacement counts” in cases when particular groups were not found but were known to still exist. All replacement counts were set to the population mean group size for that particular census year. In addition, we replaced a small number of actual counts that were known to be incomplete. Most such cases involved difficult terrain or highly unhabituated animals that fled before a good-quality count could be obtained.

CLIMATE DATA

Daily measurements of accumulated rainfall and minimum and maximum temperature were collected by ACG personnel between July 1979 and February 2007 (Janzen and Hallwachs, unpublished data) and by members of our research team from January 2005 to the present. For the temperature data, we removed extreme outliers (calculated for each day-of-year separately as beyond $Q1/Q3 \pm 4$ times the interquartile range over 1979 to 2013) that were likely sensor errors, and we filled in missing values using day-of-year medians. We did not fill-in any of the infrequent gaps in the rainfall data because any rain that had fallen was included in the accumulated rainfall measured on subsequent days. We obtained standardized historical data for two global climate patterns that are known to affect precipitation in our study region. First, the El Niño-Southern Oscillation (ENSO) is a coupled oceanic-atmospheric oscillation in central Pacific Ocean surface temperatures and air surface pressures, respectively. The extreme “warm” phase of ENSO (El Niño) brings warm and dry conditions to Central America during the normally wet months of June to August, whereas the extreme “cool” phase (La Niña) brings increased rainfall during the same months (Ropelewski and Halpert, 1987). Second, the Pacific Decadal Oscillation (PDO) is a pattern of inter-decadal variability in the ocean surface temperature in the North Pacific. The “warm” and “cool” phases of the PDO have climatic effects similar to those of the corresponding ENSO phases, although they are typically less extreme (Mantua and Hare, 2002). We obtained Southern Oscillation Index (SOI) data from the Australian Government Bureau of Meteorology’s online archive spanning 1876 to the present

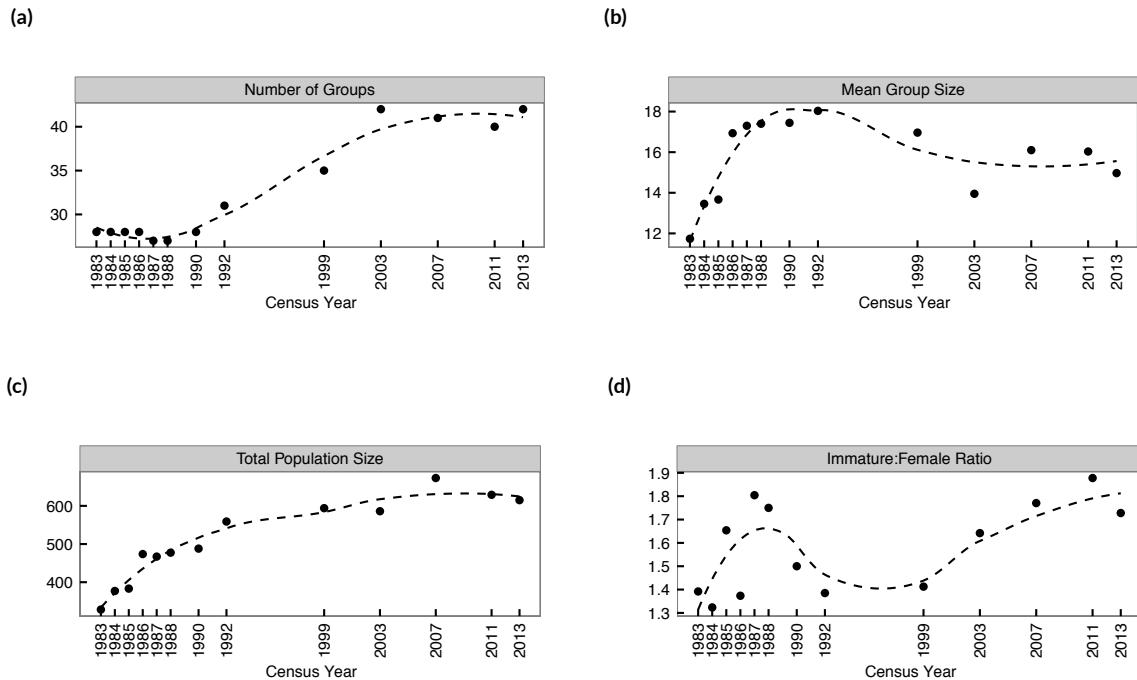


Figure 5.3: Trends in the capuchin population from 1983 to 2013, including (a) the total number of groups, (b) mean group size, (c) total population size, and (d) immature to adult female ratio. Loess smoothers added to aid visual interpretation of the trends.

(<ftp://ftp.bom.gov.au/anon/home/ncc/www/sco/soi/soplaintext.html>, accessed 2014-01-02). We obtained PDO Index (PDOI) data from the University of Washington's Joint Institute for the Study of the Atmosphere and Ocean (<http://jisao.washington.edu/pdo/PDO.latest>, accessed 2014-01-02), which spans 1900 to the present.

SATELLITE DATA

We used two satellite-based sources of Normalized Difference Vegetation Index (NDVI), a commonly used measure of vegetative “greenness”, to make inferences about capuchin habitat characteristics. During peak dry season in SSR (late March), there is marked variation in NDVI as highly deciduous forest stands exhibit low NDVI values and increasingly evergreen forest stands exhibit higher NDVI values. The first set of satellite data comprise a time series of version-5 MODIS Terra Vegetation Indices (MOD13QA3), products from the NASA Land Processes Distributed Active Archive Center (LP DACC), USGS/Earth Resources Observation and Science Center (<https://lpdaac.usgs.gov>). The MODIS data have low spatial resolution (250×250 m pixels), making them unsuitable for analyzing landscape spatial pattern at a scale appropriate for our study, but they have continuous coverage since February 2000 with 16-day granularity. This continuity makes them valuable for

Table 5.1: Landsat surface reflectance Climate Data Record products used for this study.

Scene ID	Acquisition Date	Sensor
LT50160531985073XXX04	1985-03-14	TM
LT50160531986092XXX06	1986-04-02	TM
LT50160531991074AAA04	1991-03-15	TM
LT40160531992085XXX02	1992-03-25	TM
LT40160531993071XXX02	1993-03-12	TM
LT50160521997090XXX02	1997-03-31	TM
LT50160531998077AAA01	1998-03-18	TM
LT50160531999080AAA01	1999-03-21	TM
LE70160532000091EDC00	2000-03-31	ETM
LE70160532001093EDC00	2001-04-03	ETM
LT50160532011065CHM00	2011-03-06	TM

assessing how the NDVI values that we use to make inferences about habitat characteristics are affected by erratic local conditions such as recent rainfall. Using the R package MODISTools (Tuck and Phillips, 2013), we obtained a complete time series of MODIS data for each pixel along two straight-line transects across the study area (315 separate 16-day composites for each of 123 pixels). The transects extend for 28.3 km total (fig. 5.1), and they traverse a representative mix of vegetation with varying degrees of evergreenness. We excluded data for which the pixel reliability assessment indicated reduced quality, which was usually due to persistently cloudy conditions over the 16-day period.

The second set of satellite data consist of Landsat surface reflectance Climate Data Record (CDR) products (Masek et al., 2006), which we obtained courtesy of the U.S. Geological Survey Earth Resources Observation and Science Center (table 5.1). Landsat images have relatively high spatial resolution (30×30 m pixels), but their temporal availability is sparse and irregular. We use the Landsat images to quantify changes in the spatial pattern of vegetation classes over time. All of the Landsat images were acquired within two weeks of the same day-of-year, March 20. We selected this date because March (along with February) is the least variable month of the year in terms of rainfall, other remote sensing studies focused on SSR have used images from March for discriminating dry forest in different stages of regeneration (Campos, Bergstrom, et al., 2014; Castillo et al., 2012; Castillo-Núñez et al., 2011), and more usable CDR products were available for mid- to late-March than for other time periods due to the reliably clear atmospheric conditions during this time. Landsat CDR products are specifically aimed at facilitating the investigation of long-term land surface change, which typically involves comparing satellite images acquired years apart under widely varying atmospheric and illumination conditions (Masek et al., 2006). Each CDR product has undergone

extensive post-processing to increase the comparability of images acquired at different times. This is achieved by applying atmospheric and geometric correction routines to the raw satellite images; the end product provides an approximation of the reflectance values that would be measured by a sensor located just above the canopy. We used the surface reflectance values to create NDVI maps from each image.

5.2.3 DATA ANALYSIS

PARK-WIDE AND SUB-REGIONAL ANALYSES

We examined changes in the monkey population and NDVI-based land cover at two spatial scales. The park-wide scale considers the entire area contained within SSR's boundaries (fig. 5.1). The sub-regional scale examines discrete pockets of relatively high capuchin density to explore if and how the patterns of demographic and land cover change differed spatially among sub-regions of the park. We created sub-regions of interest based on the GPS locations of all capuchin groups found during the 2003, 2007, 2011, and 2013 censuses. GPS locations were not recorded before the 2003 census. We created networks of proximate groups by linking each pair of points separated by less than 1 km with a straight line segment. We then buffered these line segments by 500 m on both sides and dissolved the boundaries among overlapping buffers. After removing small lacunae and bridging trivial gaps, each disjoint set of merged buffers was defined as a sub-region of interest (fig. 5.1). All sub-regions are therefore separated by areas that are evidently used very infrequently, if at all, by capuchin groups.

POPULATION AND SUB-POPULATION TRAJECTORIES

Previous studies have examined a variety of demographic parameters for the capuchin population as a whole. Here, we extend this record by including two additional censuses (2011 and 2013) and by analyzing sub-regional variation. We focus on total number of animals, total number of groups, mean group size, and the ratio of immature animals to adult females (as a measure of reproductive rate). Mean group sizes and immature-to-female ratios are based on high quality counts only (i.e., we excluded the “replacement counts”). For the sub-regional analysis, we assigned the capuchin groups present in each census year to one of the six sub-regions; as the sub-regions themselves were based clusters of group locations, these assignments were unambiguous. We exclude the 1971/1972 census (Freese, 1976) from our analyses because of methodological differences. Judging from the map in Freese's manuscript, the Carbonal sub-region (fig. 5.1) was not searched; moreover, he did not distinguish age/sex categories, and he provided very broad ranges rather than estimates for the number of groups and total population size.

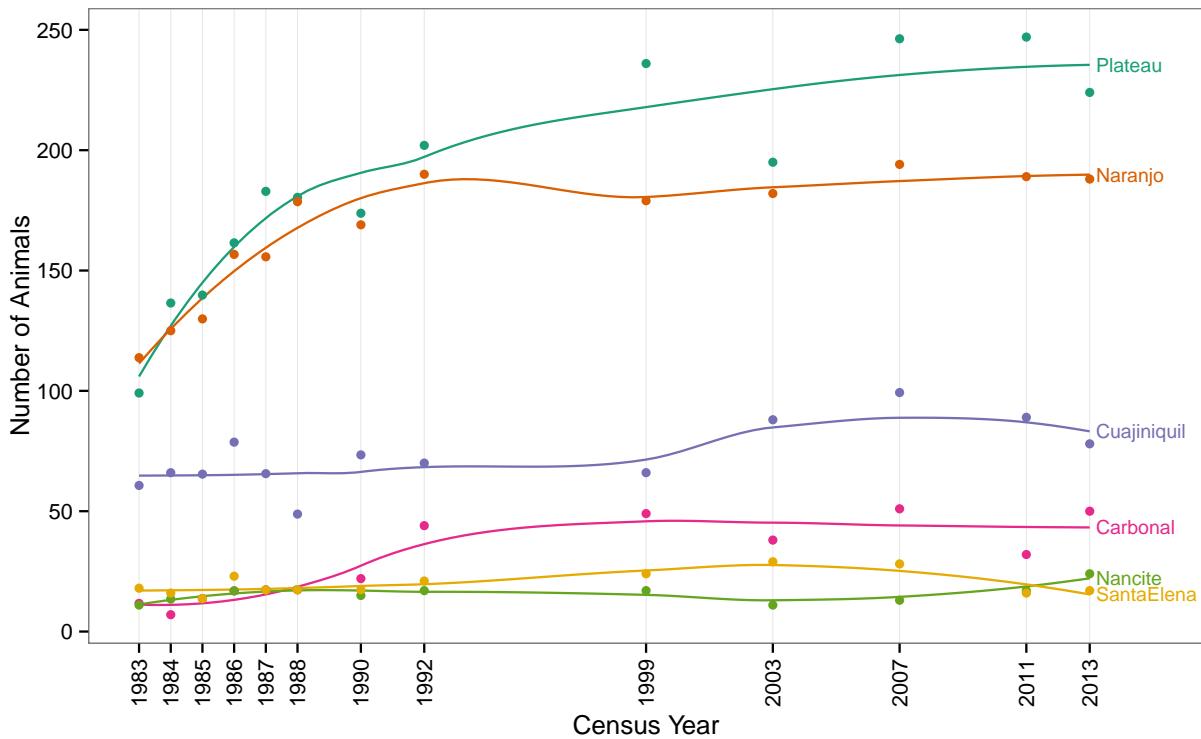


Figure 5.4: Estimated number of animals in each of the six sub-regions of the park for each census year. LOESS smoothers added to aid visual interpretation of the trends.

CLIMATIC TRENDS

To analyze the relationship between standardized SOI values and rainfall, we first performed a seasonal decomposition of the rainfall time series by locally weighted scatterplot smoothing (LOESS) in R (R Development Core Team, 2014). This procedure models the time series as the combination of three different components: a periodic (i.e., annual) seasonal effect, a slowly varying trend, and an irregular remainder (Cleveland et al., 1990). We set the span of the LOESS window for trend extraction to two years. The monthly SOI and PDOI data are already standardized to adjust for seasonal effects. We calculated the cross correlation between monthly SOI values and seasonally-adjusted rainfall (i.e., after subtracting the periodic component), as well as the lag which resulted in maximum correlation. To assess the significance of the cross-correlation, we calculated critical values using a permutation test under the null hypothesis of zero correlation. This involved comparing the actual cross-correlation to the 0.025 and 0.975 quantiles of the empirical distribution obtained by randomly reordering one of the time series, computing the new cross-correlation, and repeating these steps 10 000 times. PDO phases typically extend over multiple decades, and so the time span of our study is inadequate for a formal time series analysis of its relationship with rainfall in SSR. Therefore,

we simply make qualitative observations about possible PDO-related effects on the landscape and capuchin population dynamics.

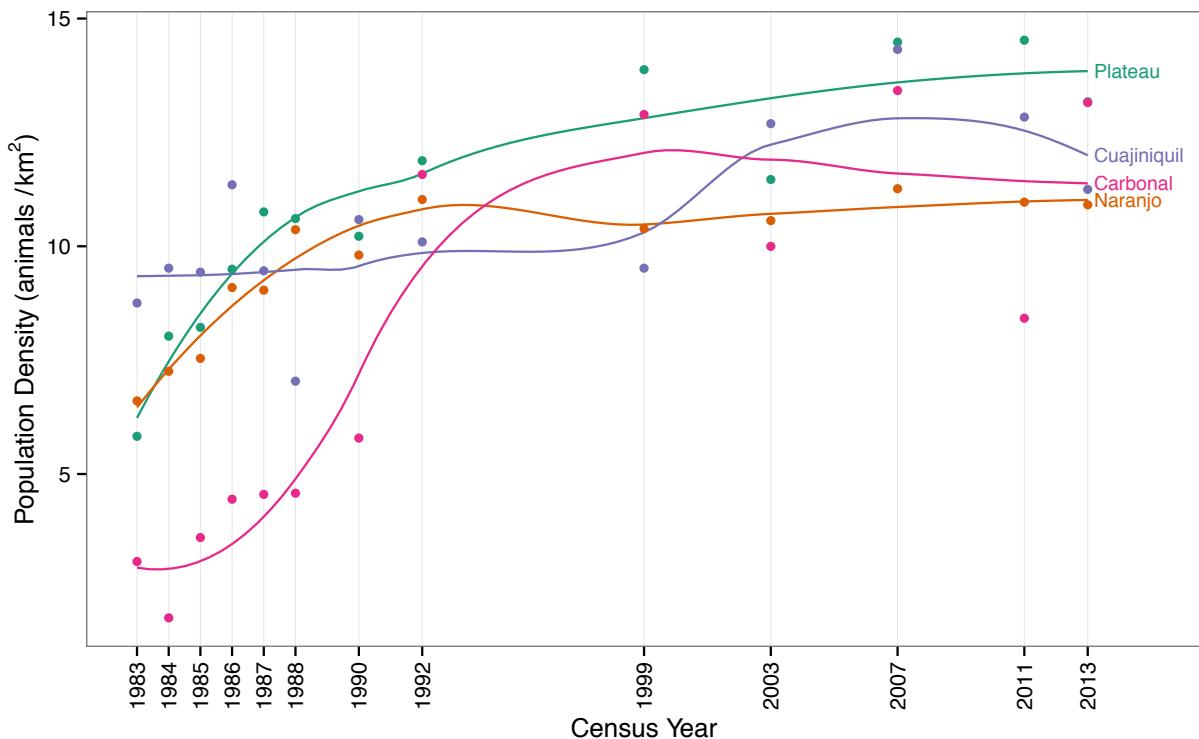


Figure 5.5: Population density in sub-regions of the park for each census year. Two sub-regions, Santa Elena and Nancite, are excluded from this figure because they contained only one group. LOESS smoothers added to aid visual interpretation of the trends.

QUANTIFYING HABITAT CHANGES

We classified the Landsat CDR NDVI maps into vegetation categories using the NDVI threshold values that Arroyo-Mora, Sanchez-Azofeifa, Kalacska, et al. (2005) found to be most accurate for discriminating forest regeneration stages in this ecosystem: <0.43 , 0.43 to 0.58 , 0.58 to 0.7 , and >0.7 . We refer to these classes hereafter by their degree of evergreenness: none, low, medium, and high, respectively. Because these threshold values were derived from a single image acquired January 2000, the categorical maps in our study are unlikely to correspond exactly to the forest stages as defined by Arroyo-Mora, Sanchez-Azofeifa, Kalacska, et al. (2005). Nonetheless, our classes operationalize evergreenness levels exhibited by vegetation during peak dry season so that its spatial pattern can be analyzed quantitatively with landscape metrics and compared across years. We used the MODIS data to investigate how variably intense wet seasons affect the NDVI landscape in the following dry season. We extracted 16-day composites beginning March 21 or March 22 for each pixel of the MODIS

Table 5.2: Class-level metrics of landscape spatial pattern used in this study.

Universal Component ^a	Representative Metric ^b	FRAGSTATS Acronym ^c
Percentage of landscape	Percentage of landscape	PLAND
Edge contrast	Mean edge contrast index	ECON_MN
Patch shape complexity	Mean patch fractal dimension	FRAC_MN
Aggregation	Aggregation index	AI
Nearest neighbor distance	Mean Euclidean nearest neighbor distance	ENN_MN
Patch dispersion	Coefficient of variation in Euclidean nearest neighbor distance	ENN_CV
Large patch dominance	Largest patch index	LPI
Neighborhood similarity	Mean similarity index	SIMI_MN

^a See Cushman et al., 2008, Table 8 for descriptions of these universal components.

^b Metrics with high loadings for the universal components, based on Cushman et al., 2008, Table 3.

^c See McGarigal et al. (2012) for mathematical definitions and descriptions of these metrics.

NDVI data for each year between 2000 and 2013. Because atmospheric conditions are reliably clear during late March, the MODIS data for these composites were generally of high quality (1701/1722 = 98.8 % of late-March pixel values rated reliable and used for analysis). We assessed the relationship using a linear model of mean dry season NDVI values as a function of rainfall of the preceding wet season and as a function of satellite sensor (Landsat or MODIS), including the rainfall × sensor interaction term.

Landscape spatial pattern can be analyzed with landscape metrics: indices that quantify specific spatial characteristics of classes of patches or entire landscape mosaics. We used the program FRAGSTATS version 4.2 (McGarigal et al., 2012) to calculate class-level metrics of land cover spatial pattern for each Landsat CDR image at both the park-wide and sub-regional scales. Class-level metrics describe spatial patterns for a given focal land-cover class (e.g., all patches of high-evergreenness vegetation) (McGarigal et al., 2012). There are dozens of landscape metrics that can be computed by FRAGSTATS, many of which are strongly correlated with each other and essentially redundant. The abundance of interdependent metrics can be a major source of error and confusion in studies of landscape ecology (Cushman et al., 2008; Kupfer, 2012). We followed recommendations by Cushman et al. (2008) by selecting metrics that are representative of the “highly universal and consistent” components of landscape structure identified in that study. Each metric that we selected had a high factor loading in Cushman et al. (2008) for one of these universal components. The metrics are listed and described in table 5.2). Additional detail on parameters that we used to specify variable edge contrast and similarity for pairwise combinations of land cover categories can be found in table 5.3 and table 5.4, respectively.

5.3 RESULTS

5.3.1 DEMOGRAPHIC TRENDS

The estimated number of capuchins in SSR has roughly doubled since the first reliable population estimate in 1983, increasing from 328 animals to over 600 in 2013, although the rate of increase has clearly slowed (fig. 5.2). Since monitoring began, there have been two relatively long periods of stasis in the number of capuchin groups (fig. 5.3a). There were approximately 28 capuchin groups in the park from the first intensive census in 1984 until the early 1990s. There is a gap in monitoring between the 1992 and 1999 censuses, but when monitoring resumed, the total number of groups had increased to 35. Within a few more years, there were approximately 40 capuchin groups in the park, and this number has remained relatively constant since 2003. Mean group size also fluctuated over the study period (fig. 5.3b). From a low of 11.7 animals per group when monitoring began, mean group size increased rapidly and peaked at 17 to 18 in the late 1980s and early 1990s during a time of rapid population growth. Mean group size has since decreased, and in the last decade, appears to have stabilized at about 15 animals. These patterns combine to determine the trajectory for total population size, which exhibits rapid but steadily slowing growth through the 1980s and early 1990s (fig. 5.3c). Total population size for the capuchins appears to have leveled off in the last decade at roughly 620 animals, which gives an overall population density of 5.86 animals km⁻² in SSR. The immature-to-female ratio shows more inter-annual volatility than the other trends, but there appears to have been a trough in reproductive rate through the early and middle 1990s (fig. 5.3d). The sub-regional population analysis revealed two primary foci of capuchin density in the park, which we have labeled “Plateau” and “Naranjo”. These two sub-regions supported remarkably similar population growth until the early 1990s, at which point the Naranjo sub-population appears to have reached its capacity whereas the Plateau sub-population continues to grow (fig. 5.4). Two of the identified sub-populations, Nancite and Santa Elena, contain only one or two capuchin groups that appear to be isolated from other groups in the study area. Densities of the four multi-group sub-populations differed markedly in the early years of the study, but in the last decade all sub-populations appear to be converging to comparable densities of 11 animals km⁻² to 14 animals km⁻² (fig. 5.5).

5.3.2 CLIMATIC TRENDS

Total yearly rainfall was highly variable over the study period (median: 1497 mm, range 818 mm to 3498 mm) (fig. 5.6). Rainfall patterns were strongly coupled with phases and intensity conditions of the ENSO (fig. 5.7). The cross-correlation between the smoothed rainfall and SOI time series trends

Table 5.3: Edge contrast matrix specifying the magnitude of contrast for edges between each pairwise combination of land cover classes. The class labels refer to the relative amounts of green vegetation present during peak dry season.

	High	Medium	Low	None
High	0.00	0.33	0.67	1.00
Medium	0.33	0.00	0.33	0.67
Low	0.67	0.33	0.00	0.33
None	1.00	0.67	0.33	0.00

Table 5.4: Similarity matrix specifying the similarity values between each pairwise combination of land cover classes. The class labels refer to the relative amounts of green vegetation present during peak dry season.

	High	Medium	Low	None
High	1.00	0.67	0.33	0.00
Medium	0.67	1.00	0.67	0.33
Low	0.33	0.67	1.00	0.67
None	0.00	0.33	0.67	1.00

was significantly positive for lags between -4 and +8 months, and the lag which resulted in maximum correlation (0.249) was 5 months (fig. 5.9). This indicates that SOI values and rainfall patterns are positively associated within roughly one half-year in either direction, and changes in SOI precede linked changes in rainfall most congruently by about 5 months. The most severe dry periods, which occurred during 1983, 1987, 1991–1995, and 1997 coincided with unusually intense ENSO activity (i.e., negative SOI values). By increasing the temporal span of the smoother, it is apparent that both SOI and rainfall show an increasing long-term trend since the mid-1990s (fig. 5.7).

5.3.3 LANDSCAPE TRENDS

The MODIS data show that NDVI levels during the peak dry season are noticeably affected by strength of the previous wet season (fig. 5.10). Weak wet seasons with lower than normal rainfall are typically followed by more barren dry seasons, whereas stronger wet seasons lead to relatively greener dry seasons. The regression model of mean dry season NDVI as a function of rainfall during the previous wet season and satellite sensor explained 84.0 % of the variance (adjusted R^2) in year-to-year dry season NDVI ($F_{3,21} = 43.66$, $p = 3.34 \times 10^{-9}$). The model appears to fit the data more poorly for low rainfall years, which suggests that leaf shedding phenology may be more sensitive to other factors that can cause over- or under-prediction by the model following a weak wet season. After separating the MODIS data into weak (defined as at the median or below) vs. strong preceding wet seasons, it is apparent that weak wet seasons shift the dry season NDVI profile both lower and earlier (fig. 5.11).

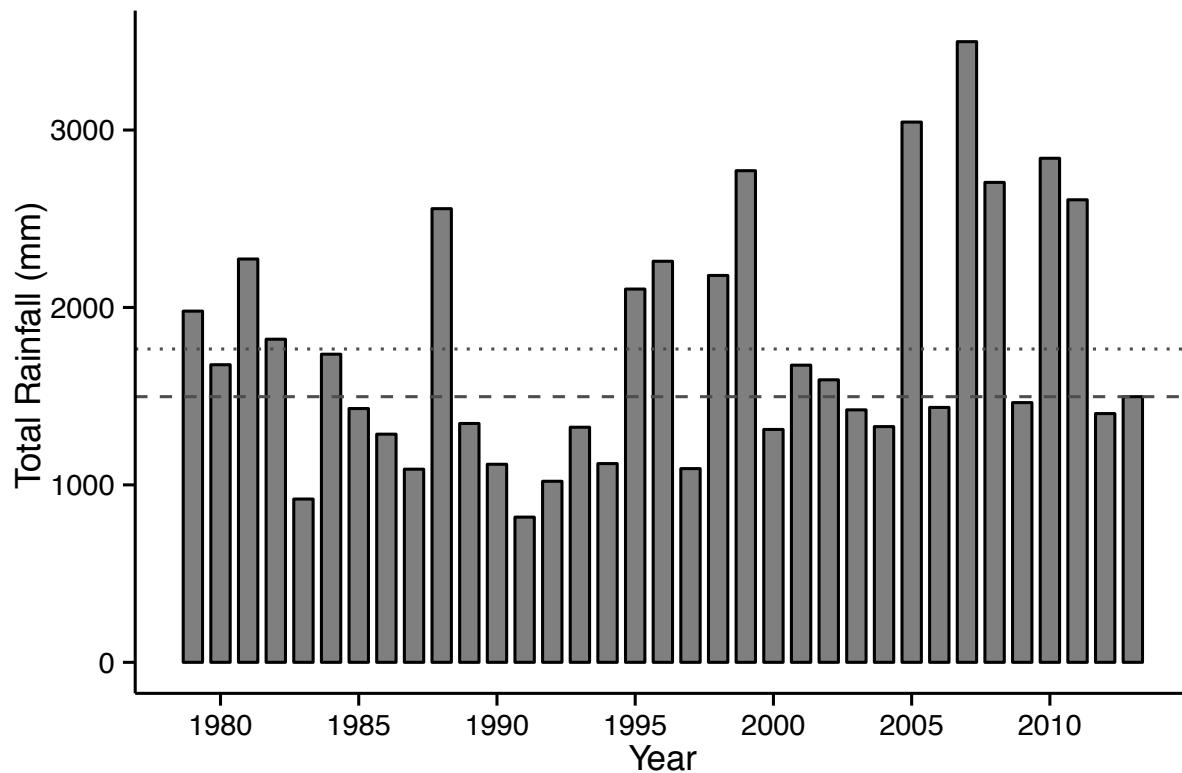


Figure 5.6: Yearly rainfall totals from 1979 to 2013. The dashed line is the annual median and the dotted line is the annual mean.

That is, green vegetation disappears sooner, and although both profiles bottom out in late March and early April, the bottom is “greener” following a strong wet season.

The time series of peak dry-season Landsat CDR images that have been classified to represent categories of vegetation evergreenness are shown in (fig. 5.8). The images exhibit considerable year-to-year variation that may be largely explained by the variable timing or extent of leaf shedding phenology depending on the preceding wet season. The most conspicuously “barren” images (1992, 1993, and 1998) are from dry seasons following the extraordinarily weak wet seasons in 1991, 1992, and 1997. Likewise, greener images (e.g., 1997, 1999, 2000, and 2011) follow strong wet seasons. Despite the phenological variability, the class-level landscape metrics at the park-wide scale suggest an overall “greening” trend, with generally opposing trajectories in most metrics for the highly deciduous and highly evergreen land cover classes (fig. 5.12). We observed marked decreases in the coverage and dominance of large patches of totally deciduous land cover and replacement by habitats containing greater proportions of evergreen vegetation. Additionally, the more evergreen land cover classes showed long-term trends toward greater contiguity, with increasing aggregation and decreasing nearest neighbor distance (fig. 5.12). The six sub-regions comprise less than half of the total area of

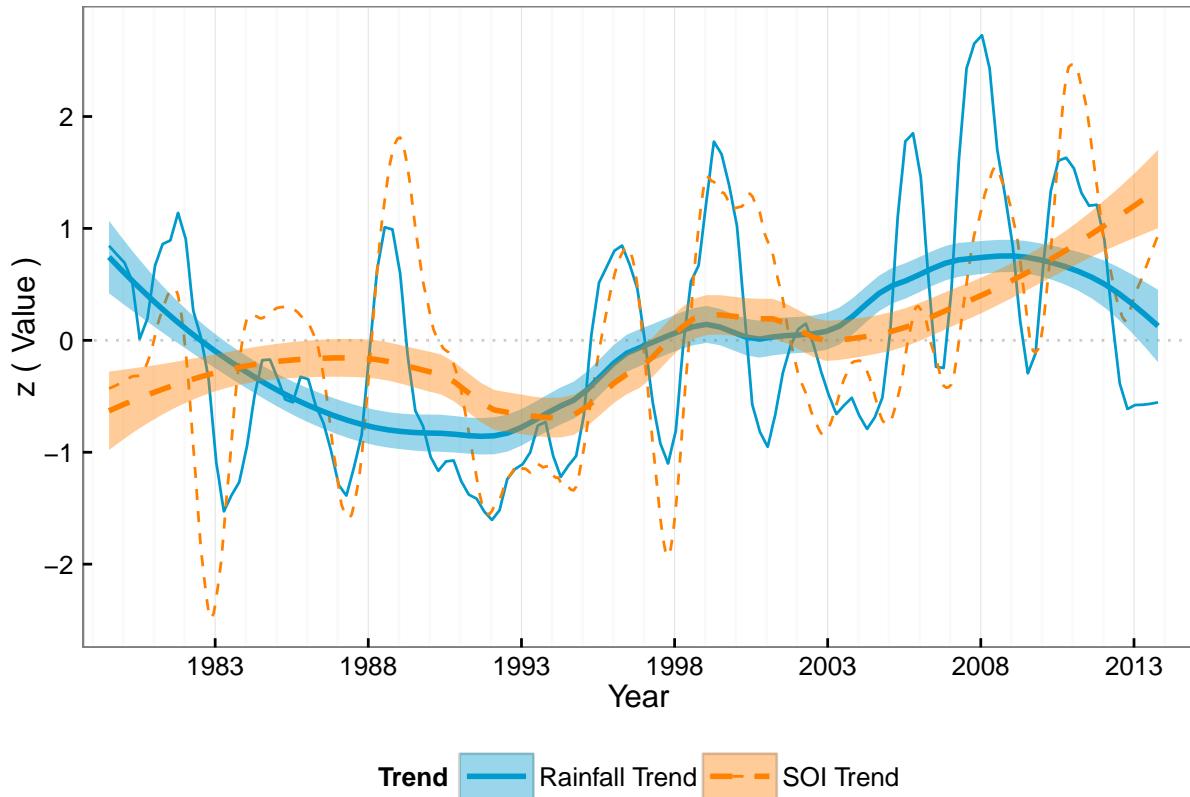


Figure 5.7: Relationship between monthly rainfall totals and Southern Oscillation Index (SOI). The thin lines show loess-smoothed (with 2-year span) and scaled (z-transformed) monthly time series for seasonally adjusted rainfall trend and SOI. The thick line shows a 20-year smooth with 95 % confidence interval.

SSR, but they contain nearly all of the large tracts of forest with medium and high degree of evergreenness. All sub-regions except for Santa Elena exhibited very similar changes in composition over the study period, with steep declines in totally deciduous land cover and simultaneous rapid gains in highly evergreen land cover (fig. 5.13). Changes in the intermediate classes were generally less pronounced, but the Plateau sub-region also experienced large gains in medium-evergreenness land cover.

5.4 DISCUSSION

5.4.1 CHANGES IN CAPUCHIN POPULATION SIZE AND STRUCTURE

Previous studies have documented the growth of this capuchin population since the early 1970s (Fedigan, 1986; Fedigan, Fedigan, et al., 1985; Fedigan and Jack, 2012; Fedigan and Jack, 2001;

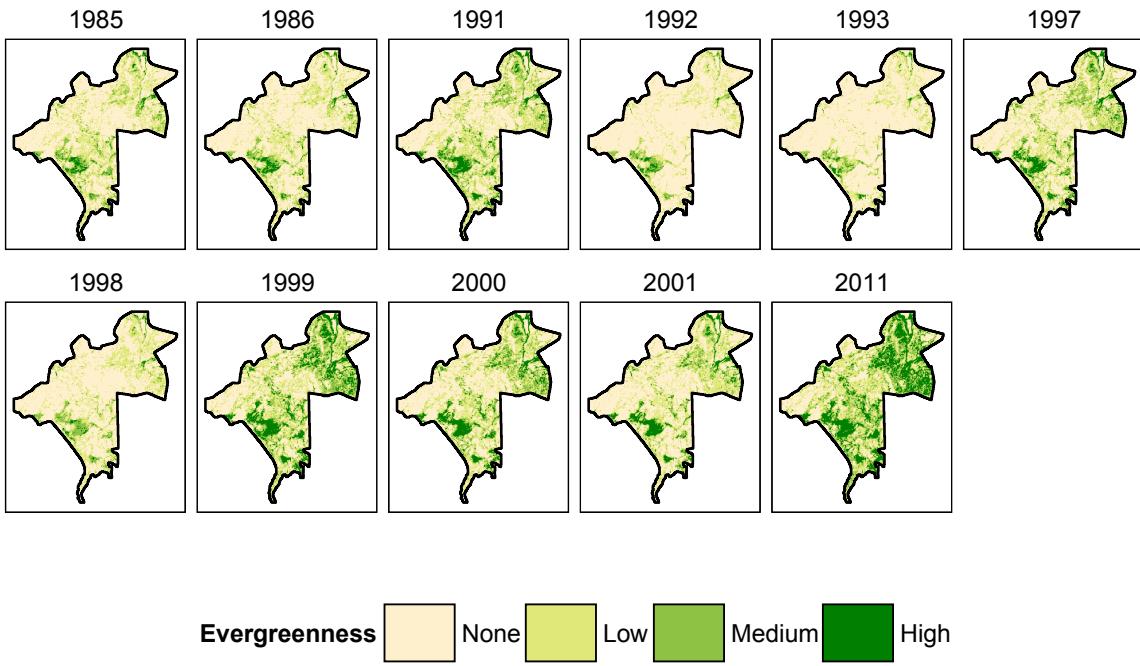


Figure 5.8: Maps of NDVI-based vegetation evergreenness for each Landsat image used in this study. All images were acquired within 2 weeks of March 20, which corresponds to peak dry season.

Fedigan et al., 1996; Freese, 1976), and our new data suggest that in the last decade the population has entered a period of relative stasis with close to zero population growth. The rapid initial population growth suggests that the population was well below its carrying capacity at around the time that the conservation area was established. We lack information on potential causes for the low initial population size, but we believe fire damage to be a likely culprit. Land owners in the Guanacaste province set fires annually to manage overgrown cattle pastures, and throughout the 1970s and early 1980s (and presumably for centuries before), these fires routinely swept into the park with devastating effects (Janzen, 2000). Since the park's founding, there were nascent efforts to limit fire damage, but truly effective fire control was not realized in SSR until 1984 (Janzen, 1988). Some additional management actions taken during these early years may have been immediately beneficial for the capuchin population, including the termination of hunting (completed in 1971) and the removal of free-ranging cattle (completed in 1978) and horses (completed in the early 1990s) (Janzen, 1983, 2000). Previous studies have documented a similar but accelerated trajectory of rapid

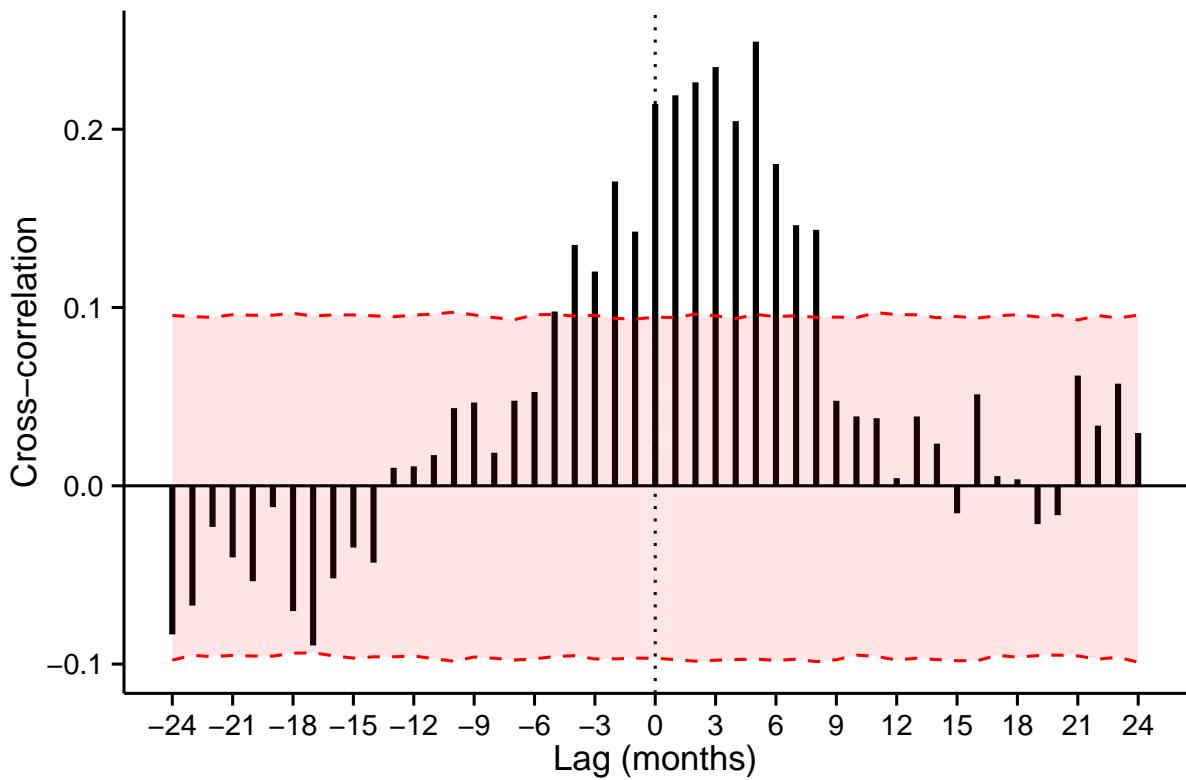


Figure 5.9: Black bars show the cross-correlation between monthly Southern Oscillation Index (SOI) and seasonally-adjusted monthly rainfall time series for lags between -24 and +24 months. Dashed lines show the 0.025 and 0.975 quantiles of the empirical distribution obtained by a permutation test with 10 000 replicates. These values provide a two-tailed test of the null hypothesis that the cross correlation is zero, conditional on the data. Positive values outside this envelope (shaded region) between lags -4 and +8 months indicate a significantly positive relationship between SOI and rainfall, with changes in SOI leading changes in rainfall by several months.

increase and eventual leveling-off among sympatric howler monkeys, but the howler population apparently reached saturation around the late 1980s and has increased little since then (Fedigan and Jack, 2012; Fedigan and Jack, 2001; Fedigan et al., 1998). Long-term research from Kibale National Park, Uganda, provides an interesting contrast. Research in Kibale on the factors that regulate primate populations has focused largely on the effects of recent logging and forest fragmentation. The general picture that emerges from Kibale over several decades of monitoring is that forest recovery has been slow to nonexistent in logged or otherwise disturbed areas (Bonnell et al., 2011; Chapman and Chapman, 1997), and primate populations in disturbed areas have not recovered or are in disequilibrium states (Chapman, Balcomb, et al., 2000; Chapman, Struhsaker, and Lambert, 2005; Chapman, Struhsaker, Skorupa, et al., 2010; Lwanga et al., 2011). The structural recovery of regenerating forest takes at least 95 to 112 years in Kibale (Bonnell et al., 2011) but only 40 to 60 years in SSR (Powers et al., 2009). These differences may stem from the relative abundance of aggressive, wind-

dispersed colonizing tree species in SSR (Janzen, 1988), destructive elephant activity in Kibale (Lawes and Chapman, 2006), the hardiness of dry forest-adapted seedlings to endure the rigors of open pasture (Janzen, 1988), the greater fertility of dry forest soils due to reduced nutrient leaching (Murphy and Lugo, 1986), or different disturbance histories (Chazdon, 2003).

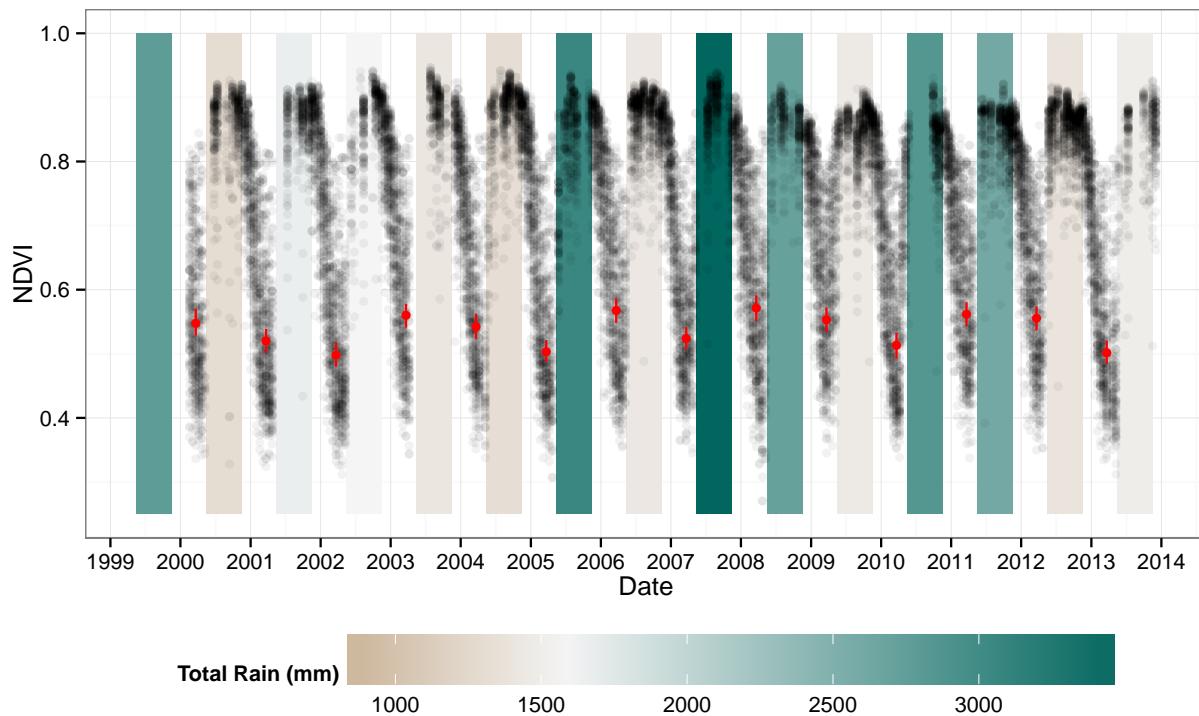


Figure 5.10: Relationship between MODIS NDVI values and total rainfall in the previous wet season. The black points indicate NDVI values for individual pixels along the two transects (123 separate pixels for each of 260 16-day composites with high-quality data). The red dots show mean values with 95 % confidence intervals (obtained via non-parametric bootstrapping with 1000 replicates) for the composites beginning March 21/22. The vertical shaded rectangles indicate the timing and strength of wet seasons (mid-May through mid-November). The neutral whitish hue is the median value for the wet seasons shown (1999–2013). The figure shows that wetter years are followed by higher March NDVI values. The most noticeable outlier, March 2003, follows an exceptionally rare 42 mm of rainfall in mid-March, which is by far the wettest March on record.

5.4.2 EFFECTS OF VARIABLE CLIMATE

A cross-site analysis of annual abundance data from several Neotropical sites has shown that various atelines exhibit immediate or one-year-lagged population declines after strong El Niño events (Wiederholt and Post, 2010). Our irregularly spaced census data do not permit such a year-by-year analysis, but we can infer three major population dynamic events that were coincident with significant climatic events. First, population growth slowed noticeably with the strong El Niño event in

1987, which produced the fourth driest year in our 34-year record (figs. 5.2 and 5.6). Second, an unusually prolonged ENSO episode from 1991–1994 occurred during six consecutive years of below-average rainfall in SSR, including the driest (1991) and third-driest (1992) years on record. During this time, population growth slowed, mean group size decreased, reproductive rate declined, and the total number of groups increased, perhaps as a result of large groups dissolving (figs. 5.3a to 5.3d). In the dry season of 1993, there was unusually high mortality and apparent illness in our study groups that led to the only extinction of a group we have observed in our 30 year study and which may have resulted from, or been exacerbated by, the drought of the previous years. Third, 1998 marked the end of an approximately 22-year long “warm” phase of the PDO (Bond, 2003; Chavez et al., 2003), which is associated with reduced rainfall in Central America (Mantua and Hare, 2002). This coincides with or closely precedes a second inflection point in many of the smoothed population trends which reverses the negative, drought-associated demographic shifts of the early 1990s (figs. 5.3a to 5.3d). Although these observations are obviously not conclusive, they do suggest direct linkages between capuchin population dynamics and rainfall, which in turn is heavily influenced by global climatic and oceanic phenomena. These rainfall-associated effects on capuchin population dynamics in SSR provide an interesting comparison with the capuchin population on Barro Colorado Island (BCI), Panama. The BCI capuchins recently suffered a catastrophic mortality, with greater than 70 % loss of the population, following unprecedeted high rainfall in December 2010 (Milton and Giacalone, 2014). Although relatively near to SSR, BCI is a lowland rainforest ecosystem with very different ecological dynamics. Nonetheless, the combined results from SSR and BCI suggest that rainfall extremes in either direction can have profound negative impacts on capuchin populations.

5.4.3 CHANGES IN THE AVAILABILITY OF CRITICAL CAPUCHIN HABITAT

Our analysis suggests that there has been a gradual greening trend in SSR over recent decades. There are at least two possible explanations for this observation. First, the greening trend coincides with upward-trending annual rainfall totals since the early 1990s. Mean evergreeness levels in late March vary linearly with accumulated rainfall in the previous wet season. It is unclear whether the mechanism driving this relationship involves shifts in the annual timing of leaf-shedding, changes in the degree of leaf-shedding, or both. In support of the former possibility, previous studies have found that the timing of phenological changes in deciduous dry forest trees is strongly dependent on seasonal changes in tree hydration status (Borchert, 1994; Reich and Borchert, 1984), which depends on recent rainfall. Regardless, the linkage suggests that the recent greening trend is, at least in part, a reflection of rainfall patterns. Second, observations on the ground have confirmed that, over the last few decades, there has been a shift in habitat composition across much of SSR as old pastures give

way to young regenerating forest and existing secondary forest continues to mature (Janzen, 1988, 2000). Increasingly mature successional forest stages in SSR support greater proportions of evergreen species (Sorensen, 1998), and so the greening trend could also reflect the gradual maturing of protected land cover across the region (Arroyo-Mora, Sanchez-Azofeifa, Rivard, et al., 2005). These two possibilities are not mutually-exclusive, and both could be contributing to the observed increase in evergreen vegetation cover during peak dry season, although the effects of rainfall probably dominate year-to-year variation.

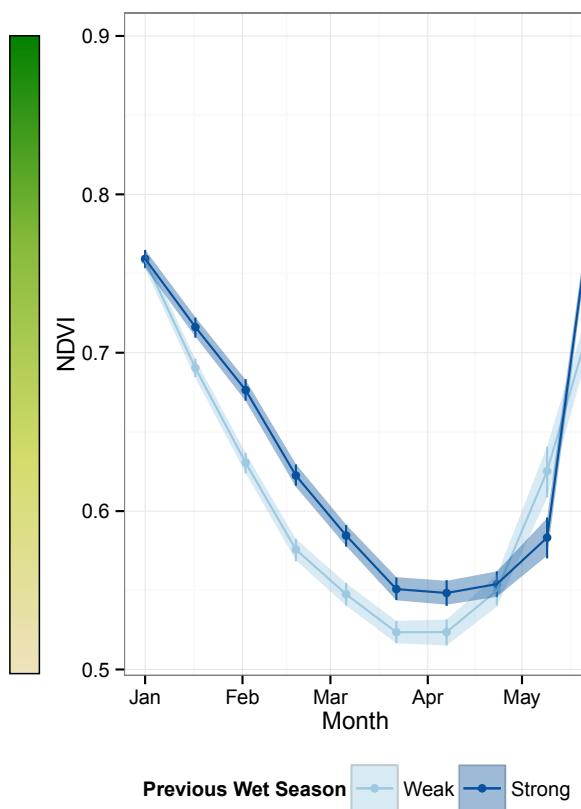


Figure 5.11: Dry season MODIS NDVI profiles for weak (at the median or below, n = 7) vs. strong (greater than the median, n = 7) preceding wet seasons. The dots correspond to 16-day composite start dates. Values shown are means with 95 % confidence intervals determined via non-parametric bootstrapping with 1000 replicates. Weak wet seasons shift the dry season NDVI profile both lower and earlier.

The overall greening trend that we have inferred would seem to contradict the study by Enquist and Enquist (2011), which found that one well-studied patch of mature forest in SSR has become less evergreen over a recent 20-year period. However, our findings and those of Enquist and Enquist (2011) are fully consistent with each other if one considers the timing of the studies in combination with the effects of the PDO on rainfall, and therefore on dry forest evergreenness. The vegeta-

tion surveys by Enquist and Enquist (2011) in 1976 and 1996 correspond almost exactly with major PDO regime shifts: 1976/1977 marks the end of a 30-year cool (i.e. “wet” for SSR) phase and the start of a 22-year warm phase that ended in 1998 (Bond, 2003; Chavez et al., 2003). Thus, the study by Enquist and Enquist succinctly captures the cumulative negative effects of the recent PDO warm phase on mature forest evergreeness, but since these climatic patterns are cyclical and have recently reversed, we find it unsurprising that vegetation patterns have apparently mirrored this shift in rainfall trends. Aside from the general increase in evergreen land cover, landscape metrics indicate that distinct patches of evergreen vegetation are becoming less isolated from one another, with a greater degree of interspersion with less-evergreen patches. Whereas in the early years of the study the total landscape was strongly dominated by expansive patches of totally deciduous vegetation and abandoned pastures, the landscape is growing increasingly diverse and intermixed over time. From the capuchins’ perspective, the major consequence of this change is probably greater continuity among patches of vegetation with high to medium degrees of evergreeness.

5.4.4 DRIVERS OF SPATIAL HETEROGENEITY

The sub-regional analyses revealed spatially heterogeneous trends for SSR’s capuchin population and landscape. Since the first assessment by Freese (1976) in 1971/1972, the Plateau and Naranjo sub-regions have supported a large majority of the capuchin groups as well as the most extensive patches of mature evergreen forest. These two sub-populations experienced rapid increases during the 1980s, which suggests that they were well below saturation, whereas the other sub-regions have experienced only modest or zero population growth over 40 years of monitoring. After its initial rapid growth, the Naranjo sub-population effectively flatlined in the early 1990s (fig. 5.4), which means that most of the population growth over the last 30 years has occurred in the Plateau sub-region. Satellite data indicate that the Plateau sub-region has also experienced the greatest gains in forest cover with medium to high degree of evergreeness (fig. 5.13). Because capuchins depend on forest for food and shelter, the co-occurrence of these increases is not surprising. However, a more fundamental question remains: why has the Plateau sub-region apparently experienced greater proportional gains in forest cover? Our data are inadequate for answering this question, but we offer some speculation in order to guide future studies.

The proportion of deciduous and evergreen species is strongly affected by local variation in the severity of seasonal water deficits, soil characteristics, and disturbance histories (Murphy and Lugo, 1986). LiDAR-based vegetation mapping has indicated that the Plateau and Cuajiniquil sub-regions, situated on generally flat or gently undulating uplands, contain most of the former pastureland in the SSR (Castillo-Núñez et al., 2011). As attractive grazing lands, these upland areas are likely to

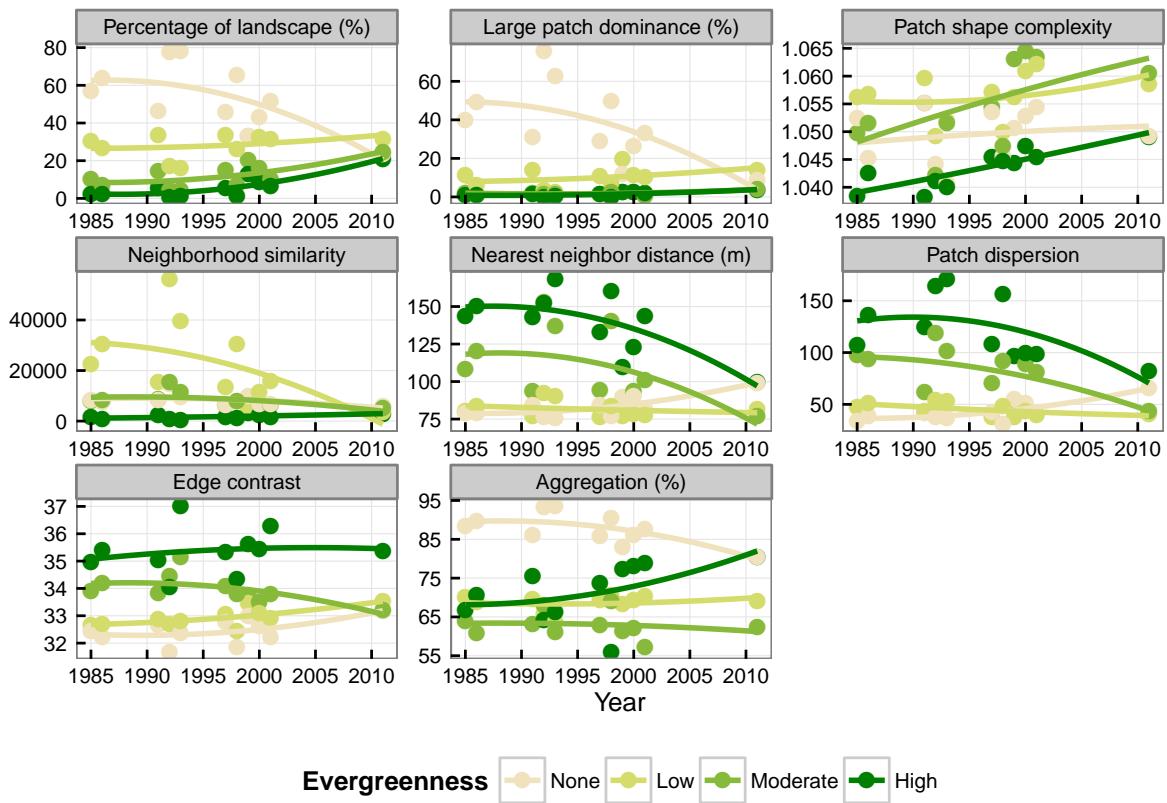


Figure 5.12: Trends in class-level metrics from 1985 to 2011, calculated from Landsat images. See table 5.2 for descriptions of the metrics. Quadratic polynomial smoothers added to aid visual interpretation of the trends.

have suffered the most extensive anthropogenic disturbance in the past (Calvo-Alvarado et al., 2009; Griscom and Ashton, 2011; Murphy and Lugo, 1986), and therefore they also stood to gain most from regenerative forest growth after the park's establishment. The Plateau sub-region in particular contains the greatest concentration of secondary forest stands that are dominated by wind-dispersed species (Castillo-Núñez et al., 2011). These stands develop primarily via wind-borne seed rain falling downwind from established forest onto former pasture (Janzen, 1988). Their concentration in the Plateau sub-region can be attributed to the greater area of former pastureland as well as the fact that some of these former pastures are adjacent to established forest (Janzen, 1983). In contrast, prevailing winds during the dry season would tend to carry wind-borne seed rain from established forest patches in the lowland coastal sub-regions (Carbonal, Naranjo, and Nancite) toward beaches and mangroves fringing the Pacific Ocean. Although generally poor in fruit-bearing trees, young wind-dispersed secondary forest provides benefits to capuchins in the forms of rich insect foraging (Fedigan et al., 1996) and perhaps reduced predation risk (Campos and Fedigan, 2014). Once initiated, the

recolonization of old pastures by woody vegetation may form a positive feedback loop as newly established trees reduce fire fuel loads by shading out invasive grasses, provide new habitat for vertebrate seed-dispersal agents, and supply additional seed sources for the further expansion of wind-dispersed trees (Klemens et al., 2011). In summary, the combined patterns of topography, land-use history, prevailing winds, and the location of established forest relative to receptive pastureland may have favored greater forest regeneration and, in turn, greater population growth by capuchins in the Plateau sub-region.

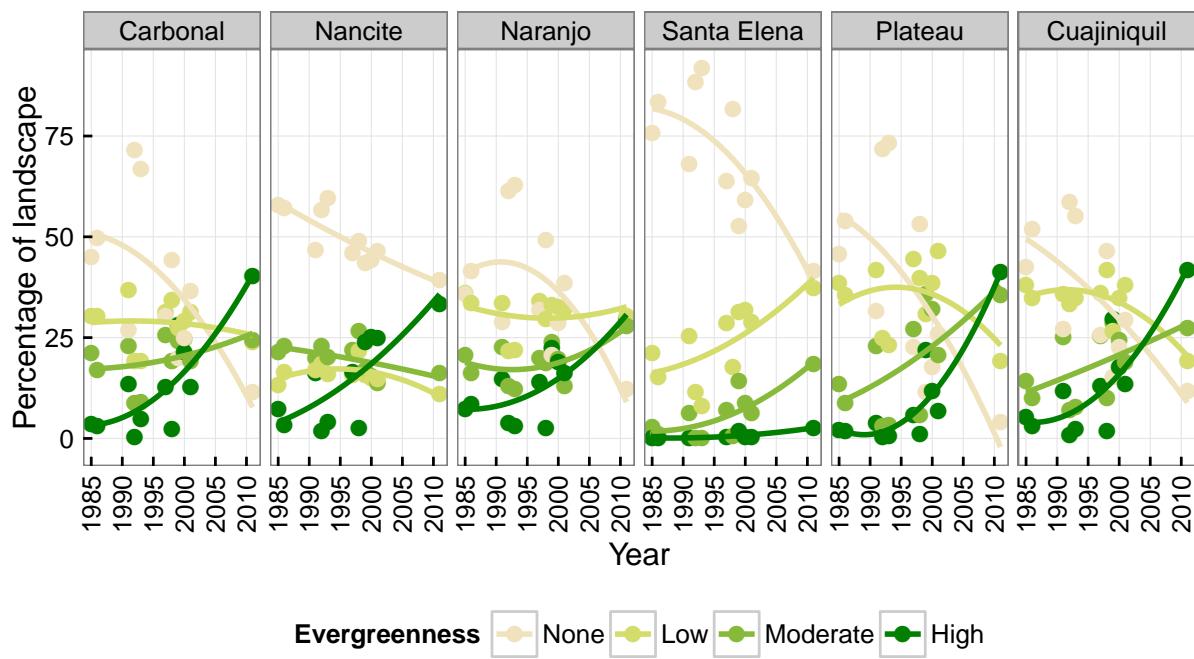


Figure 5.13: Sub-regional trends in percentage of landscape for four habitat categories from 1985 to 2011, calculated from Landsat images. The sub-regions are areas of relatively high capuchin density and are shown in fig. 5.1. Quadratic polynomial smoothers added to aid visual interpretation of the trends.

5.4.5 CONSERVATION AND MANAGEMENT IMPLICATIONS

Several empirical studies have reported a long-term drying trend in Central America (Borchert, 1998; Fleming, 1986; Vargas and Trejos, 1994); climate models bear out these observations and predict continued drying in the future (Christensen et al., 2007; Neelin et al., 2006). Our rainfall data indicate that since the end of the prolonged warm PDO phase in the late-1990s, annual rainfall in SSR has been trending upward, but the recent uptick may be reversed with the next PDO regime shift. Our findings suggest that extreme drought years may challenge small capuchin populations by dis-

rupting tree phenology cycles and reducing the availability of favorable habitat during critical times of year. If drought years become increasingly common as the global climate warms, we expect that many animals in seasonally dry forests will be negatively affected. The long-term growth of the primate populations in SSR represent an encouraging case study of how animals with high public conservation appeal can be nurtured without direct management by focusing on ecological restoration, which has far-reaching ancillary benefits for many other plants and animals. However, one important conclusion from this study is that the effectiveness of such “bottom-up” strategies for promoting primate population growth may be constrained by factors that are impossible to control, such as land-use history, topology, soil fertility, and other complex ecological processes. We hope that these findings will help build predictive models for primate population dynamics in changing habitats to improve future conservation strategies and provide a basis for designing reserves to preserve biodiversity effectively.

6

General discussion

6.1 OVERVIEW

This thesis aimed to provide an integrative look at how environmental change, both in the short term (seasonality and habitat differences) and the long term (changing climate and habitats), has shaped and continues to shape the behavioral ecology of a free-ranging Neotropical primate. I have used a multi-scale approach with the ultimate goal of gaining a more complete understanding of how individual-level selective pressures scale up over space and time to affect group and population dynamics. By framing this research around issues related to ecological restoration, I believe that my findings will make valuable contributions to understanding how natural primate populations may be affected in our increasingly dynamic world. In this concluding chapter, I first summarize and synthesize the main empirical findings from chapters 2 to 5. I return to the specific research questions that I posed in section 1.2, and by drawing links between the different chapters, I attempt to show how the body of work I have presented fits together to advance our understanding of how primates respond to environmental variability. I then discuss the theoretical and policy implications of my work for primate behavioral ecology, biological anthropology, and conservation. Finally, I bring attention to several unresolved questions that I believe to be important areas for future research.

6.2 REVIEW AND SYNTHESIS OF KEY EMPIRICAL RESULTS

6.2.1 PREDATION RISK OVER SPACE AND TIME

Research question 1: How does predation risk for individual *C. capucinus* vary with the spatial and temporal heterogeneity of the current landscape they inhabit, and what behavioral adjustments do they make to mitigate these risks?

The availability and extent of different habitats in SSR were important determinants of perceived predation risk. In chapter 2, I explained how predictive anti-predator behaviors, such as vigilance and avoidance of certain areas, can impart significant fitness costs if they result in the loss of opportunities to secure important resources. The main empirical findings from chapter 2 were:

1. Capuchins perceived greater overall predation risk in more mature forest habitats due to increased encounter frequencies with raptors.
2. Within each habitat type, capuchins were most vigilant near the ground, where the majority of encounters with predatory snakes and terrestrial quadrupeds originated.
3. Incorporating a spatial model of combined risk (i.e., the relative risk of encountering birds, snake, and terrestrial quadrupeds) into a predictive model of vigilance behavior improved prediction relative to models of uniform risk or habitat-specific risk.

The major consequence of these findings with respect to my research question is that, on average, higher perceived predation risk zones tended to be clustered around patches of mature forest habitat, and therefore when using mature forest, capuchins may suffer increased fitness costs associated with this risk (either greater mortality or chronic elevated opportunity costs).

6.2.2 FORAGING EFFICIENCY OVER SPACE AND TIME

Research question 2: What environmental and intrinsic factors are responsible for differences in foraging efficiency over space and time?

In chapter 3, I examined how the capuchins' variable environment affects expected energy returns during foraging, which is another fundamental component of individual fitness. Using brief foraging bouts as the unit of analysis, I quantified energy intake rate using the measured energy content of ingested food items, and I quantified energy expenditure using estimates of basal and locomotor energy costs based on continuous changes in activity and time-matched movement trajectories. The most important findings from chapter 3 were:

1. Net energy returns on foraging bouts were affected more by extrinsic constraints such as seasonality, habitat characteristics, and changes in the resource base than by intrinsic constraints such as sex or social group size.
2. Net energy returns during foraging were consistently higher during the wet season and in mature habitats, which were associated with both higher energy intake rates and lower energy expenditure rates.
3. The relative advantage of foraging in mature forest varied seasonally and was greatest during the dry season, when ecological contrasts between habitat types were most pronounced.

These findings imply that mature habitat provides fitness benefits in the form of increased foraging efficiency, and that energetic stress is likely to be greatest during the dry season. Thus, my findings from chapters 2 and 3 suggest an interesting ecological dynamism in which white-faced capuchins in SSR must balance the counteracting pressures of more productive foraging conditions with greater perceived predation risk when they utilize mature forest habitats.

6.2.3 HOME RANGES OVER SPACE AND TIME

Research question 3: How do groups of *C. capucinus* adjust their use of space to meet the collective and individual challenges of growth, survival, and reproduction? What role does environmental variability play in mediating this response?

Group-living animals continually face the problem of balancing individuals' needs for resource acquisition against the need for group cohesion to maintain critical social bonds. Home ranges are spatial expressions of these compromises borne out over extended time periods; they manifest the group's collective solution to the research question I posed above. The characteristics of a group's home range therefore offer insights into how individual-level selective pressures scale up to the group level. In chapter 4, I examined how seasonal fluctuations in climate, food abundance, and group mass affected variance in home range area and the maturity stage of forest used by capuchins in SSR. The main empirical findings of chapter 4 were:

1. Temperature was an influential factor shaping monthly range area and composition, with hotter weather favoring smaller home range size and increased use of mature evergreen forest.
2. Greater fruit availability was associated with smaller monthly range area.
3. Home range zones of higher use consisted of older, more evergreen forest habitat.
4. Overall, the extrinsic effects on home range area (climate and habitat) were secondary to the effects of group mass, which was consistently the most important predictor of home range size.

These findings demonstrate that environmental variability plays a key role in mediating groups' spatial adjustments to meet the challenges of living in a social group. In view of chapters 2 and 3, my finding that capuchins' high-use home range zones consist of more mature forest habitats suggests that the need to maintain adequate food intake and the need for shaded resting areas outweigh the possible costs of increased predation risk, especially during the dry season. Because the dry season is associated with greater energetic deficits, the capuchins' increased preference for mature forest and more compact use of space during the dry season may be a behavioral adjustment aimed at maximizing the use of the most productive foraging areas and reducing travel, perhaps at the expense of safety.

6.2.4 POPULATION DYNAMICS OVER SPACE AND TIME

Research question 4: How do climate and land cover change in the study area since the park was established relate to concurrent patterns of *C. capucinus* population growth and demography, and what can we infer about ecological recovery processes from this study system?

Knowledge of how capuchin individuals and groups use the landscape provides context for understanding changes in the capuchin population over time. In chapter 5, I investigated how climate fluctuations and landscape changes have affected the dynamics of the capuchin population in SSR after the elimination of most detrimental human disturbances. The most important empirical findings from chapter 5 were:

1. The capuchin population in SSR grew rapidly after the establishment of the conservation area, but growth has slowed in the last decade.
2. Most of the population growth occurred in an upland sub-region of SSR that experienced greater gains in forest cover with medium- to high-degree of evergreenness.
3. The availability of evergreen habitats varied with the strength of the previous wet season, which in turn was strongly coupled with global climatic and oceanic cycles.
4. The landscape of SSR has undergone a gradual greening trend over time that may be related to forest regrowth and upward-trending rainfall.
5. Following extreme drought periods, capuchin population growth slowed, mean group size decreased, and reproductive rate declined.

These results suggest that the major environmental trends in SSR over the last decades—gradual maturation of disturbed forest, overall greening, and (recently) increasing rainfall—have had a net positive effect on the capuchin population. The apparent dependence of population growth on localized increases in the extent of intermediate and mature stage habitat may be due to the importance

of having access to these particular habitats during critical times of year (e.g., the dry season). My findings also suggest that prolonged periods of extreme drought may harm the capuchin population by exacerbating the stresses typically associated with the dry season. For example, extended dry periods reduce the availability of already-scarce drinking water and evergreen habitat. The demographic changes associated with such periods may indicate increased mortality or reduced fertility.

6.3 THEORY AND POLICY IMPLICATIONS

6.3.1 IMPLICATIONS FOR PRIMATE BEHAVIORAL ECOLOGY

Some of the most fundamental aspects of primates' lives show strong variation over time and space that is dependent on changes in climate and/or habitat, including patterns of reproduction (Janson and Verdolin, 2005), mortality (Gogarten et al., 2012), and diet (Hemingway and Bynum, 2005). It has long been suspected that the challenges associated with the dry season may be the ultimate constraints on capuchins in SSR (Fedigan et al., 1996; Freese, 1976; Sorensen, 1998). My research sheds light on some of the mechanisms that underpin these limitations. During the dry season, capuchins must expend more energy per unit of energy ingested; they must contend with an overall food shortage and presumably rely more heavily on spatial memory; they must increase their use of shady evergreen habitats that carry higher predation risk; they must increase resting time during daylight hours to conserve water and avoid overheating; they must extend their home ranges to include potentially unproductive and high-risk areas with surface water; and in the recent past, they had to withstand devastating wildfires. Interestingly, although a majority of the SSR capuchin deaths in the sample analyzed by Gogarten et al. (2012) occurred during the dry season, the seasonal mortality difference did not meet statistical significance. In fact, taking a broader taxonomic perspective, increased seasonal mortality in primates is more commonly associated with wet seasons (perhaps due to disease) and folivorous diets (perhaps due to less dietary flexibility). Primates such as capuchin monkeys—intelligent and omnivorous—may therefore be evolutionarily equipped to cope with large spatiotemporal instability in the fitness landscapes they navigate (e.g., the distributions of energy and predation risk).

6.3.2 IMPLICATIONS FOR BIOLOGICAL ANTHROPOLOGY

Capuchins have exceptionally large, hyper-encephalized brains, with brain to body size ratios comparable to those of apes and far exceeding those of most other platyrhines (Hartwig et al., 2011; Rilling and Insel, 1999). Species with large brains fare better when faced with novel, altered, or changing environments in many birds, mammals, and all major taxonomic radiations of primates (Allman

et al., 1993; Deaner et al., 2003; Sol, 2009; Sol, Bacher, et al., 2008; Sol, Duncan, et al., 2005; van Woerden et al., 2010, 2014; van Woerden, Willems, et al., 2012). The Cognitive Buffer hypothesis posits that this large-brain advantage exists because proportionally larger brains enable greater behavioral flexibility and thereby provide a buffer against new and diverse environmental challenges (Allman et al., 1993; Deaner et al., 2003; Sol, 2009). Essentially similar arguments—the variability selection hypothesis (Potts, 1996, 1998) and the shifting heterogeneity hypothesis (Kingston, 2007)—have been proposed to explain the emergence of key hominin adaptations and the ascendance of *Homo sapiens* during a critical period in hominin evolution 600 ka to 150 ka, a time of rapid environmental change (Potts, 1998). It is reasonable to speculate that the many socioecological convergences shared by *Cebus/Sapajus* and *Homo* can be traced to parallel evolution along this “flexible response” paradigm. Thus, my findings from chapters 2 to 4 illustrate how different forms of behavioral flexibility—the adjustment of anti-predator vigilance to changing levels of risk, dietary shifts, adjustment of foraging effort and travel speed to changing energy conditions, home range shifts, and use of seasonal refugia to withstand difficult periods—might have benefitted human ancestors and enabled them to thrive and diversify in changing landscapes. Furthermore, my findings from chapter 5 provide an example of how extended environmental stresses, such as prolonged droughts, might have affected the growth and demographic makeup of small populations of hominids as they expanded into marginal habitats.

6.3.3 IMPLICATIONS FOR CONSERVATION AND RESTORATION ECOLOGY

If ecological restoration is to provide a realistic solution for conserving living species and sustaining future evolutionary potential, understanding species’ natural recovery processes is of the utmost urgency (Clewell and McDonald, 2009). The main contribution of my thesis research to conservation theory and policy is to provide rare empirical information on primate recovery processes, specifically on the variable selection pressures that a regenerating environment poses. One recurrent theme throughout the thesis is that although mature forest may be essential to many animals in a regenerating mosaic, adaptable animals such as capuchins may not be harmed and may in fact benefit from having access to disturbed secondary habitats. In the capuchins’ case, such habitats can offer reduced predator encounter frequencies and, at certain times of year, a unique set of food resources (e.g., grass seeds during a lean period in November). This is not to discount the value of mature tropical dry forest. Compared to young stages of regenerating forest, mature tropical dry forest is capable of supporting greater botanical (Kalacska, Sanchez-Azofeifa, Calvo-Alvarado, et al., 2004; Kalacska, Sanchez-Azofeifa, Rivard, et al., 2007) and vertebrate (Chazdon et al., 2011) biodiversity; it provides a moist, shady refuge into which animals of all kinds (including primates) migrate during the severe dry sea-

son (Janzen, 1988). Mature tropical dry forest should clearly be a top conservation priority (Miles et al., 2006; Portillo-Quintero and Sánchez-Azofeifa, 2010). However, my findings add to a growing awareness that conservation strategies should not ignore the ecological importance of “matrix” habitats for preserving biodiversity and improving connectivity among mature forest patches (Franklin and Lindenmayer, 2009; Prugh et al., 2008; Watling et al., 2011). The long-term growth of the capuchin population in SSR provides an illuminating case study of how animals with high public conservation appeal can be nurtured without direct management by focusing on ecological restoration. However, the sensitivity of this ecosystem to global climatic phenomena suggests that capuchins (and probably many more animals) will be negatively affected if drought years become increasingly common as the global climate warms.

6.4 UNRESOLVED QUESTIONS, LIMITATIONS, AND DIRECTIONS FOR FUTURE RESEARCH

6.4.1 A MORE SYNTHETIC APPROACH TO STUDYING INDIVIDUAL FITNESS LANDSCAPES

Chapters 2 and 3 dealt separately with two major selective pressures, predation risk and foraging efficiency. However, in most natural systems these two pressures are inextricably linked: animals generally increase foraging effort when they perceive predation risk to be reduced (Abrams, 1993; Kie, 1999; Lima, 1998; Lima and Dill, 1990; Verdolin, 2006). Thus, a logical next step in my research would be to integrate these two research areas to develop a more nuanced and comprehensive understanding of individual fitness landscapes in this study system. Furthermore, I have speculated on how different behavioral responses are likely to influence individual fitness in an ultimate sense. However, the central assumption—that these responses produce meaningful effects on individual survival, health, and/or reproductive success—has not been tested. In future investigations, life history data could provide a powerful test of the relative roles of predation risk and foraging behavior in determining population dynamics (DeCesare et al., 2014).

6.4.2 APPLYING RESOURCE SELECTION ANALYSES TO UNDERSTAND SPACE USE PATTERNS

Resource selection analyses relate the use of resource units to their availability. Although I have calculated some simple use-availability ratios, home range and resource selection analyses can be combined to make stronger inferences about how environmental factors affect use of space (e.g., Horne, Garton, and Rachlow, 2008; Moorcroft and Barnett, 2008). An important source of bias and uncertainty in such analyses is the identification and valuation of unused resource units (Johnson et al., 2006). In the case of this study, an intuitive way to quantify the value of used and unused resource units would be to calculate the available biomass of fruit trees in some defined space (e.g., a pixel). In

an attempt to create spatially explicit maps of landscape productivity, I mapped and measured nearly 11 000 fruit trees used by my capuchin study groups, of which about 4000 I believe to be unique based on their locations and characteristics. However, my exploratory analysis of unique tree visits versus sampling effort revealed that for most fruit tree species, the animals continued to find and feed from new individual trees that I had not recorded, suggesting that my mapped trees were not an exhaustive set and that my valuation of resource units would be spatially biased. Although I abandoned this line of inquiry for my thesis, I believe that it could be a productive avenue for future investigations, either by using average productivity values for different mapped vegetation classes (e.g., Willems, Barton, et al., 2009) or with continued individual tree mapping. Moreover, important ecological insights could be gained by looking at used resource units only (e.g., Shaffer, 2013); for example, how is group movement behavior affected by the value of the resource units traversed during that particular day?

6.4.3 A MORE QUANTITATIVE APPROACH TO LINKING CLIMATE WITH POPULATION DYNAMICS

One of the major limitations that I faced in preparing chapter 5 was the coarse temporal resolution of the census data. With multi-year gaps between many consecutive data points and a small sample size overall, it was not possible to apply statistically rigorous modeling techniques to link changes in population size with changes in the climate and/or landscape. This was particularly true for assessing the impact of single anomalous events, like a particularly severe dry season. One way to strengthen the inferential power of my research on this question would be to use long-term life-history data, and to focus on individual survivorship and birth rates rather than on total population size. Continuous monthly life-history data have been recorded for some capuchin groups in SSR from the 1980s to the present (Fedigan and Jack, 2012). Re-approaching this research question from an individual perspective would allow me to draw on my other completed and planned research on individual fitness and to shed light on the proximate mechanisms that underpin the effects of oscillating environmental conditions on primate individuals, groups, and populations (Ockendon et al., 2014). An important priority moving forward from this thesis will be to combine these data with similar data from other long-term primate research sites (e.g., Strier, Altmann, et al., 2010). In doing so, I hope to gain a deeper understanding of how climate change will affect primate populations and to expand the scope and generality of this research to a global scale.

6.5 CONCLUSION

As habitats change, organisms must adapt to the new conditions, shift their distributions, or go extinct. The importance of ecological variability in directing cebine evolution is evident in their exceptional resourcefulness and behavioral flexibility. It is the cardinal insight of my thesis that these faculties have aided the growth and recovery of this population as their forest gradually regenerates, though their resilience may be tested by the accelerating pace of global change.

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A

Supplement to chapter 3

A.1 SCREENING THE MOVEMENT DATA

We filtered and smoothed each 15-min trajectory in four stages. The first two stages implement the screening methods described by Bjørneraas et al. (2010). Briefly, these methods identify unrealistic travel patterns by analyzing a moving window about each point. The first stage finds unrealistic travel speeds and requires two distance criteria, Δ and μ . The former should be set to an impossible distance for the animal to cover between fixes, while the latter should correspond to a possible but very uncommon travel speed (Bjørneraas et al., 2010). We set Δ to 100 m, a distance that only elite sprinters can cover in 10 s, and we set μ to 19.0 m, which represents the 99.9 % quantile of all recorded movement steps. The second stage removes unrealistic “spikes” from the trajectory formed by two consecutive segments with a very sharp turning angle and substantial ingoing and outgoing speed (Bjørneraas et al., 2010). Here, we set the turning angle criterion $\theta = \cos(\frac{11\pi}{12})$ and the spike speed limit α to 0.6 m s^{-1} , which removes spikes with ingoing and outgoing length greater than 6 m (the median stated GPS error) with a turning angle between 165° and 195° . The third stage was a “stationary bout” filter designed to remove spurious movement steps smaller than the device’s stated accuracy; such steps were continually recorded while the animal was stationary or moving very slowly. We first calculated a threshold distance as the mean of two stated accuracy values (in whole

m) given by the GPS receiver, the first recorded at the trajectory's start and the second recorded at the trajectory's end. A stationary bout began when the current point was displaced less than the threshold distance from the preceding point (if not already in a bout) or from the median location of the current bout (if already in a bout). The stationary bout ended when the focal point was displaced greater than the threshold distance from the running median of all previous points in the same stationary bout, whereupon each point in the bout was replaced by the median location for the entire bout. This filter is similar to the “slow travel” filter used by Janmaat, Ban, et al. (2013), except that we compared each point to the running bout median rather than to the first point of the bout to determine whether movement had occurred. We believe this change is an improvement because it does not impute greater significance to the bout's first point, which may be randomly displaced from the animal's “true” stationary location. In the fourth stage, we filled missing values by rediscertizing the trajectory over a fixed time interval such that the time lag between all consecutive location points was constant (10 s) and missing points were calculated by linear interpolation. Because the location points were recorded at fixed 10-s intervals to begin with, this served primarily to fill data gaps, such as segments marked unreliable by the observer or points removed during previous screening stages. Figure A.1 shows examples of the filtering procedure applied to real trajectories of varying quality.

A.2 ENERGY ESTIMATES FOR PER-BITE FOOD ITEMS

As detailed in the methods, most of the food items consumed in this study were matched to per-item energy values based on their nutritional content, the values of closely-related species adjusted for mass, or median values for that category of food item. The measured values are reported by Bergstrom (n.d.). However, certain food items did not conveniently allow us to assign a per-item energy value, either because the items varied tremendously in size or because there was no straightforward way to define a single item.

Large nests of Hymenoptera larvae: each bite was assumed to contain a single larva, using the value 0.543 kJ from Bergstrom (n.d.) for a single *Polistes* wasp larva.

Lepidoptera larvae: because we did not categorize caterpillars by size in the field, each bite of a caterpillar was assumed to contain 0.5 kJ of energy, which is approximately equal to the energy content of a single small caterpillar that can be consumed in one bite (Bergstrom, n.d.).

“Other” invertebrates: this category spans an enormously diverse range of insects and arachnids, and is the unfortunate consequence of the difficulty of identifying the invertebrate foods eaten by our study animals. We assumed that each bite of an invertebrate in this category contained

1.58 kJ, which is the value reported by McCabe (2005) for a “generic” small insect that can be consumed in a single bite.

Ant larvae inside tender thorns: we assumed that each bite of a tender *Vachellia collinsii* thorn contained two *Pseudomyrmex* ant larvae, and we assumed that each larva contained as much energy as an adult ant, for which the energy value was determined by McCabe (2005).

Vertebrate foods (i.e., meat): our animals periodically consumed vertebrate prey, predominantly small mammals. We assumed that each bite contained 1 g of flesh, and that each gram contained 12.5 kJ of energy, which is the value reported by the USDA for 1 g of raw beef.

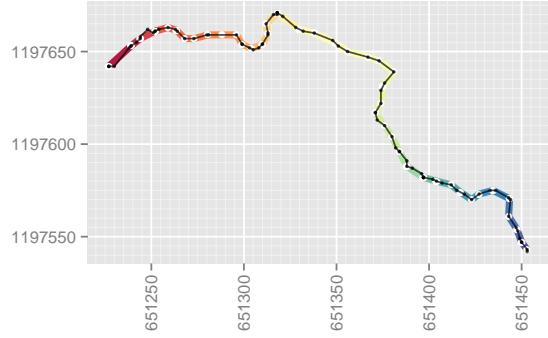
Pith: we lacked reliable information on the nutritional content for the pith of tree branches, for which single items were not easily defined. We assumed that each bite of pith contained 1 kJ of energy.

A.3 DETERMINATION OF ENERGY EXPENDITURE FOR DIFFERENT ACTIVITY STATES

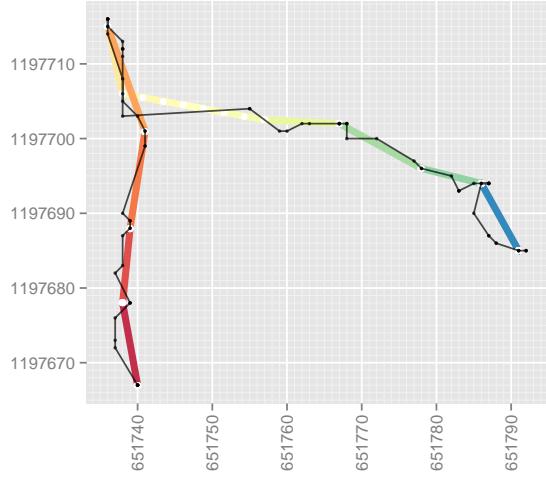
The widely-used energy constants for primate behavior states that are presented in the study by Leonard and Robertson (1997) are adapted from values given by Coelho (1974) and Coelho et al. (1976). These values were in fact adapted from an earlier study by Passmore and Durnin (1955) on human energy expenditure. The primate-specific energy constants are therefore based directly on expenditure measurements “for humans performing actions requiring similar or identical muscular movement” (Coelho, 1974, p. 266). This understanding informed our decisions about how to calculate EE_{state} for different activity states. We assigned the low energy constant (1.25) to the resting state following Leonard and Robertson (1997). The medium energy constant (1.38) that Leonard and Robertson (1997) propose for feeding behavior is based on a human eating while stationary and seated, and is therefore basically the cost of sitting upright while engaged in a low-intensity activity. This accurately describes stationary vigilance and most social behavior in our study animals. Leonard and Robertson (1997) propose a substantially higher energy constant for the socializing state (2.35), which included energy-demanding play behavior. However, the adult animals in our study rarely engaged in play behavior; rather, the socializing state in our study was heavily dominated by social grooming, which was typically undertaken while lying or sitting. We therefore considered the medium energy constant to be more appropriate for the social state. Finally, we considered both food search (“forage”) and non-food-related locomotion (“travel”) as high-energy states. It was often difficult to discriminate forage from travel, but since our definition of foraging typically involved either locomotion or food item extraction (also an energy-demanding behavior), we believed it was appropriate to treat the two states

equally. Here, we obtained EE_{state} for foraging and traveling from the Y-intercept in the equation in Taylor, Heglund, et al. (1982) for primate locomotor costs (also called the “extrapolated zero speed cost”).

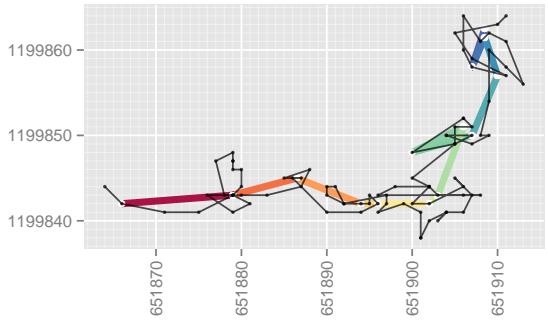
(a)



(b)



(c)



(d)

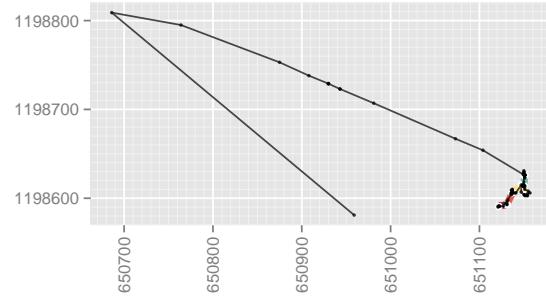


Figure A.1: Examples of raw and filtered trajectories, showing performance of the filtering procedure on the full range of location data quality. Each figure shows the raw location points (tiny black dots) and implied movement steps (thin black segments) as well as the smoothed/filtered location points (white dots) and inferred movement steps (thick colored segments). Time is indicated by the color of the filtered trajectory, increasing from blue (start) to red (end). The axes indicate UTM coordinates (zone 16P, WGS84 ellipsoid), and therefore have meter units. (a) Typical high-quality trajectory with essentially no difference between the raw and filtered track. (b) Typical medium-quality trajectory showing moderate amounts of pseudorandom noise in the location fix. (c) Typical poor-quality trajectory on a very slow-moving animal, showing high-levels of pseudorandom noise that was extensively smoothed by the filtering procedure. (d) Extremely poor-quality trajectory, beginning with impossibly large jumps (>100 m displacement in 10 s) that are removed entirely by the filter and ending with a reasonably accurate fix. Trajectories of such poor quality were very rare.

B

Supplement to chapter 4

B.1 JUSTIFICATION FOR USING THE BIASED RANDOM BRIDGE (BRB) HOME RANGE METHOD

A major theoretical weakness with common location-based kernel methods is the assumption that each recorded location point is independent. However, sequential location points are typically highly autocorrelated in both time and space, especially with high-frequency, GPS-based data sets (Boyce et al., 2010; Fieberg and Kochanny, 2005). This problem is commonly addressed by data filtering (which results in data loss), rationalizing about the value of autocorrelation itself (which violates the assumptions of the statistical model), or ignoring the problem altogether. By treating the location data as a movement process (i.e., an ordered series of track segments) rather than a point process, movement-based kernel methods explicitly account for autocorrelated data to produce a more biologically relevant home range estimate (Benhamou and Cornélis, 2010). In brief, the movement-based kernel method is as follows: (1) each movement step linking pairs of successive location points is divided into subsegments based on a specified time interval, (2) locations are interpolated for the endpoints of each subsegment, and (3) kernel density estimation is applied to each interpolated location, with a smoothing parameter that varies with the uncertainty of the animal's location—that is, the smoothing parameter is minimal at the movement step's endpoints (because this is where the animal's location was recorded) and maximal at the step's midpoint (Benhamou and Cornélis, 2010). Cru-

cially, the BRB method implements this framework by including both a “biased” component (the animal’s tendency to drift in the direction on the next location point) and a “random” component (the animal’s tendency to deviate from a straight path to the next location point) that form a bridge between each pair of successive location points (Benhamou, 2011).

B.2 PARAMETERIZATION OF THE BRB HOME RANGE METHOD

The BRB method requires several parameters that should be based on biological knowledge. First, habitat-specific movement parameters can be used to control the random component of the movement process. Using the habitat map described in the main text, we calculated habitat-specific diffusion coefficients for each group using the BRB.D function in adehabitatHR on the full set of location points for that focal group (Calenge, 2006). These coefficients govern the speed of random drift through each habitat type. Second, it is necessary to specify a maximum time threshold (t_{max}) beyond which pairs of successive location points are not considered linked. Given the discontinuous nature of the location data, with long gaps each night and between different observation blocks, this threshold is necessary to remove these long gaps from the home range calculations. In our data set, time gaps associated with night-time and inter-block intervals were all greater than 8 h. Ignoring these gaps, 99.9 % of the recording intervals were less than 65 min, with 94.7 % falling within 5 min of the scheduled 30-min recording interval. We decided that 90 min would be a reasonable t_{max} , as recording interval gaps of longer duration are likely to represent cases in which the focal group was lost or not observed for a significant amount of time, but shorter intervals are likely to represent location points with a high degree of autocorrelation. Third, we specified a minimum kernel smoothing parameter (b_{min}) of 50 m, a value which accounts for various sources of error in the location data: the group’s centre of mass was not always identifiable, the GPS is not perfectly accurate, and the habitat map is subject to georeferencing errors, classification errors, and geometric distortions due to terrain. Given these sources of error, 50 m seems a reasonable value for b_{min} , as it does not assume unrealistic accuracy for the group’s centre, and it corresponds approximately to a typical group spread in this species. Finally, the parameter L_{min} corresponds to a minimum step length, below which the animal is considered to be stationary. However, even if the group’s centre is stationary, there are usually at least some animals who continue to move around while other group members are resting. We therefore included even very short steps in our home range estimates by setting L_{min} to a small value of 5 m. Steps with a recorded distance less than 5 m occurred rarely (2.26 % of all steps), and in these cases, we set the smoothing parameter to b_{min} for the entire step (i.e., the uncertainty of the group’s location did not vary during the step).

B.3 CALCULATION OF THE FRUIT AVAILABILITY INDEX

The tree crown coverage and fruit ripeness scores are described by (Melin, Young, et al., 2014), but here we provide additional detail and an explanation of the availability index used for this study. The coverage score represents the percentage of fruit (both ripe and unripe) that is present in the tree crown relative to the estimated total that could be produced by the tree if all branches were bearing fruit. The ripeness score represents the percentage of fruit present in the tree crown that is fully ripe. Both of these scores were converted to ranks of 0, 1, 2, 3, or 4, which correspond to the percentage ranges 0 %, 1 % to 25 %, 26 % to 50 %, 51 % to 75 %, and 76 % to 100 %. To calculate the availability index, we took the reciprocal of each rank score then multiplied the two together. Thus, an index value of 1 implies coverage/maturity ranks of 4/4, whereas an index value of 0 could be generated by a 0 in either or both of the coverage/maturity ranks.

C

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