

Copyright
by
Steig Eric Johnson
2002

**The Dissertation Committee for Steig Eric Johnson Certifies that this is the
approved version of the following dissertation:**

**Ecology and Speciation in Brown Lemurs: White-collared
Lemurs (*Eulemur albocollaris*) and Hybrids (*Eulemur albocollaris*
X Eulemur fulvus rufus) in Southeastern Madagascar**

Committee:

Deborah Overdorff, Supervisor

Claud Bramblett

Liza Shapiro

Rob DeSalle

Patricia Wright

**Ecology and Speciation in Brown Lemurs: White-collared
Lemurs (*Eulemur albocollaris*) and Hybrids (*Eulemur albocollaris*
X Eulemur fulvus rufus) in Southeastern Madagascar**

by

Steig Eric Johnson, B.A., M.A.

Dissertation

Presented to the Faculty of the Graduate School of

The University of Texas at Austin

in Partial Fulfillment

of the Requirements

for the Degree of

Doctor of Philosophy

The University of Texas at Austin

August, 2002

Dedication

To Avri

Acknowledgements

I first would like to thank the Association Nationale pour la Gestion des Aires Protégées (ANGAP), the Ministère des Eaux et Forêts (MEF), and the Université de Madagascar for permission to conduct research in Madagascar. I would also like to acknowledge the generous support of the National Science Foundation (BCS-9910257), the Wenner-Gren Foundation for Anthropological Research (Grant No. 6414), and the Institute of International Education Fulbright Program. For funding of preliminary research in Madagascar, I am grateful to Primate Conservation, Inc. (with special thanks to Noel Rowe) and the University of Texas International Education Fee Scholarship program.

Many individuals and non-governmental institutions facilitated my research in Madagascar. I would like to acknowledge the World Wildlife Fund (Antananarivo and Ambalavao) for assistance in research at Parc National d'Andringitra. I would like to express my gratitude to the Institute for the Conservation of Tropical Environments (ICTE) in Stony Brook (especially Rickie van Berkum and Lauren Block). I would also like to thank everyone at Madagascar Institut Pour la Conservation des Environnements Tropicaux (MICET) in Antananarivo: Mandimbihasina Angelo Ramy, Rabenandrasana

Nirimalala Holiarisoa, Rajoharison Liva Miamina, Rakotoarisoa Andriamanampisoa, Rakotoarison Jean Marcel, Rakotomalala François de Borgia, Rakotonirina Dauphin, Rakotonirina Gérard, Ramampandra Nirina, Ramanitrarivelo Narcisse George, Rambonina Bernard Lalao, Randrianambina Benjamin, Randrianantoandro Jean François de Salle, Randrianarimanana Fanja, Randrianarisata Désiré, Randrianarisoa Jean Samuelson, Ranivohariniony Holiniaina, Rasoanaivo Haja Haingovololona, Ratefinjanahary Joelina, Ravelomanantsoa Lalaina, Razananoro Monique, Rinarason Jean Claude, and Tondrasoa Ramahery Laingo. The help of these people made my work possible, and their friendship made life enjoyable in Madagascar. Special thanks are reserved for Andriamihaja Benjamin. His dedication and leadership are inspiring, and I am forever grateful for his officiating of my wedding ceremony at Ranomafana. Which leads me to the good people of the Parc National de Ranomafana (PNR): both administration and research personnel were instrumental in my studies in southeastern Madagascar, especially Razafiarimalala Aimée and Razafindratsita Tiana, and I will never forget those who made my wedding day there so special.

I am indebted to many individuals for their skills and commitment in the trenches of fieldwork. The indefatigable drivers of MICET (especially Anselme, Ranary, Dédé, and Jijy) provided essential logistical support. I am grateful to Yael Wyner for helping out at Andringitra and for her work on brown lemur genetics; her research has been invaluable to this project and it has been a joy to collaborate with her. Thanks to Eddie Louis for assistance with capture. I would

also like to thank my student collaborators from the Université de Madagascar, Andrianjaka Vaniah and Andrianjazalahatra Tantely. I am especially grateful to my research assistants from PNR – particularly Rakotoniaiana Jean-Claude, Solo Justin, and Telo Albert – for their expertise, as well as their enthusiasm and personal sacrifice, working far from their families for so many months. For fieldwork at Vevembe, I greatly appreciate the assistance of Randriatsilanisoa Jean-François and Razafy-Jerome Berthin. For research at Andringitra, I would like to thank Rakotozafy II Joseph and Monja François for their tireless work, companionship, and comic relief. I would also like to acknowledge the special contribution of Razafimandimby Sylvain; I am grateful for his keen insights and his outstanding work as research manager. Finally, I would like to express my appreciation for the assistance and goodwill of the people of Ambalamanenjana and Madiorano.

Closer to home, I would like to acknowledge the many people who have helped me with the dissertation. Thanks to Adam Gordon, Rob Scott, and Dave Raichlen for helpful methodological discussions. Thanks to Mitch Irwin for his work on the maps. I am very grateful to those who gave me access to unpublished data: Summer Arrigo-Nelson, Christina Grassi, Mitch Irwin, Adina Merenlender, Deborah Overdorff, Rebecca Stumpf, and Patricia Wright. I would especially like to acknowledge my committee. I owe the success of my project in large part to Patricia Wright. Her deep commitment, contagious enthusiasm, and boundless energy are an inspiration. I would also like to thank Rob DeSalle for his collaboration on brown lemur genetics and for graciously agreeing to serve on

my committee. As teacher and collaborator, Liza Shapiro has contributed significantly to my training as a scholar. Claud Bramblett has also been a great mentor and I have very much enjoyed his original, provocative views on behavior and evolution. I am especially grateful to my advisor, Deborah Overdorff, for her invaluable professional tutelage and support. Finally, I would like to thank Phyllis Dolhinow for starting me on this path and for her guidance and encouragement throughout my studies.

I would like to express my appreciation to friends and family for helping me through my graduate career. Thanks to the Department of Anthropology staff, especially Pam Becker, Susan Lane, William Sederholm, Celeste Neathery, and Jenni Jones. Thanks to my Austin friends in and out of the university and to many fellow fieldworkers in Madagascar since 1995. Thanks so much to my parents, Nancy and Jim Lange, Bill Johnson and Carol Durantini, and Michael and Melinda Beard, and to my grandparents, Walter and Mary Jane Johnson and Virginia Fleming, for their love and support. Lastly, and most of all, I would like to thank my beautiful wife, Avri Beard – for patience through the constant disruptions of fieldwork, for sharing a tent through the rains at Ambarongy, for being my most insightful critic and staunchest supporter, for wearing leeches on our wedding day, and for everything else she has done to love and support me through this project.

**Ecology and Speciation in Brown Lemurs: White-collared
Lemurs (*Eulemur albocollaris*) and Hybrids (*Eulemur albocollaris*
X Eulemur fulvus rufus) in Southeastern Madagascar**

Publication No. _____

Steig Eric Johnson, Ph.D.

The University of Texas at Austin, 2002

Supervisor: Deborah Overdorff

This dissertation examines the behavioral ecology of hybrids at the species boundary of white-collared lemurs (*Eulemur albocollaris*) and rufous lemurs (*E. fulvus rufus*) at Andringitra National Park, Madagascar. In addition, I present data on an allopatric population of *E. albocollaris* at Vevembe Forest and comparisons to previous studies of allopatric *E. f. rufus*. In particular, I investigate morphometrics, population densities, habitat structure and food availability, feeding ecology, ranging, and social behavior (including social structure and interactions with conspecifics). The goal of these analyses is to evaluate the contribution of ecological mechanisms in determining the directions and limitations of gene flow, in delimiting species boundaries, and in incipient speciation.

The hybrids at Andringitra, *E. albocollaris*, and *E. f. rufus* vary considerably in testes volume and sexual dimorphism in canine height and body size. Resource defense may favor relatively large females in some *E. f. rufus* populations, while sperm competition is most pronounced in fission-fusion *E. albocollaris*. There are also considerable differences in abundance across brown lemur sites in southeastern Madagascar. The contact zone at Andringitra has the highest densities, while populations are most sparse in *E. albocollaris* sites. Population differences are partly explained by habitat quality. Vevembe has the lowest food availability, while the hybrid zone and *E. f. rufus* sites are similarly productive. Variation in habitats may also be reflected in feeding ecology; hybrids consume fruit almost exclusively, while *E. albocollaris* are dietary generalists and may employ fission-fusion to reduce competition. Moreover, *Ficus* species may serve as a keystone resource at Andringitra, allowing for larger hybrid densities. The southeastern brown lemurs also vary in intergroup behavior, with aggression rates in *E. f. rufus* double those of the hybrids or *E. albocollaris*. The highly productive environment at Andringitra may permit overlap of the parental species and highly introgressive hybridization. Dispersal and gene flow out of the contact zone may be limited by poor overall habitat quality and low population density to the south; increased intergroup agonism or, more likely, environmental characteristics (e.g., the lack of keystone resources) may be responsible for lower brown lemur abundance and gene flow in the north. I propose that these behavioral and ecological differences may serve as important mechanisms encouraging speciation in the southeastern brown lemurs.

Table of Contents

List of Tables	xvi
List of Figures	xix
Chapter 1: Introduction	1
Competition and Community Ecology	1
Competition in the Primate Communities of Madagascar	4
Hybrid Zones and Speciation	10
The Brown Lemurs of Southeastern Madagascar	16
Distribution and Ecology	16
Pelage Differences	18
Cytogenetics, Genetics, and Taxonomy	19
Contact Zone at Andringitra National Park	23
Project Goals	29
Hypotheses and Predictions	32
Chapter 2: Sexual Dimorphism and Sperm Competition in Brown Lemurs	41
Introduction	41
Methods	47
Study Animals and Sites	47
Capture and Measurement Procedures	48
Statistical Techniques	49
Results	50
Morphometrics Summary	50
Canine Height-Body Weight Relationship	50
Body Mass	51
Canine Height	51
Sexual Dimorphism	52

Testes Volume.....	53
Discussion.....	53
Chapter 3. Population Structure of Brown Lemurs at Andringitra National Park and Vevembe Forest, Madagascar	70
Introduction	70
Methods	73
Results	77
Mean Population Density	77
Population Densities at Primary Sites	78
Rapid Assessments	79
Discussion.....	79
Chapter 4: Meteorology, Forest Structure, Species Composition, and Phenology at Andringitra National Park and Vevembe Forest	92
Introduction	92
Methods	95
Meteorology	95
Botanical Plot Selection.....	96
Composition and Structure	97
Phenology	98
Synchrony	99
Relationship Between Phenology and Climate	100
Statistics	100
Results	101
Climate.....	101
Forest Structure	103
Diversity	105
Phenology	106
Synchrony	108

Phenology-Climate Relationships	109
Regional Phenology Comparison	110
Discussion.....	111
Climate at Andringitra and Vevembe	111
Forest Structure at Andringitra and Vevembe	113
Diversity at Andringitra and Vevembe.....	115
Phenology and Food Availability at Andringitra and Vevembe	116
Chapter 5: Feeding Ecology of the Brown Lemurs of Andringitra National	
Park and Vevembe Forest.....	145
Introduction	145
Methods	149
Study Groups.....	149
Sampling Procedures	149
Diet Composition	151
Feeding Time and Rates	151
Dietary Diversity	152
Habitat Use.....	153
Sex and Age Differences	153
Statistical Techniques	153
Results	154
Diet Composition	154
Feeding Time and Rates	155
Dietary Diversity	156
Habitat Use.....	157
Sex and Age Differences	157
Feeding and Food Availability	158
Discussion.....	163
Feeding Similarities Among Brown Lemur Groups	163

Feeding Differences Among Brown Lemur Groups	165
Diet and Resource Availability	169
Keystone Resources	172
How Different Are the Brown Lemurs of the Southeast?	176
Chapter 6: Social Structure, Activity Budgets, Habitat Use, Ranging, and	
Intergroup Interactions in the Brown Lemurs of Andringitra National	
Park and Vevembe Forest.....	200
Introduction	200
Methods	204
Study Groups.....	204
Sampling Procedures	204
Group Cohesion	206
Activity Budget	206
Habitat Use.....	206
Intergroup Interactions	207
Daily Path Length and Home Range	208
Statistics	211
Results	211
Group Structure and Cohesion	211
Activity Budget	212
Habitat Use.....	215
Intergroup Interactions	215
Daily Path Length and Home Range	217
Discussion.....	218
Variation in Social Structure.....	218
Activity Budgets Across Study Groups.....	220
Vertical and Horizontal Ranging	223
Intergroup Interactions	225
Summary Patterns	226

Chapter 7: Behavioral Ecology of the Brown Lemurs of Southeastern	
Madagascar: Conclusions and Implications for Speciation	242
Introduction	242
Morphology	242
Population Densities	244
Habitat Quality	246
Feeding Ecology	248
Social Behavior and Ranging	249
Conclusion	253
References	258
Vita.....	288

List of Tables

Table 1.1:	Primate Communities at Andringitra, Veveombe, and Ranomafana .	40
Table 2.1:	Morphometrics for Brown Lemurs at Andringitra and Veveombe (1999-2000 only).....	67
Table 2.2:	Means and Standard Error (SE) for Adult Brown Lemur.....	68
Table 2.3:	Mean Body Weight, Canine Height, Dimorphism Ratios, and Gonadosomatic Index (GI) Across Populations.....	68
Table 2.4:	Relationship of Selected Socioecological Factors with Levels of Dimorphism and Testes Volume.....	69
Table 3.1:	Census Sites in Primary Study Areas.	88
Table 3.2:	Rapid Assessment Sites in Southeastern Region.	88
Table 3.3:	Population Densities (individuals/km ²) at Primary Research Sites..	89
Table 3.4:	Population Densities (individuals/km ²) at Rapid Assessment Sites.....	90
Table 3.5:	Population Densities (individuals/km ²) at Other Southeastern Census Sites....	91
Table 4.1:	Forest Structure from Large Plots.	132
Table 4.2:	Forest Structure from Small Plots.	132
Table 4.3:	Taxonomic Diversity from Large Plots.	133
Table 4.4a:	Tree Species at Andringitra National Park.	134
Table 4.4b:	Tree Species at Veveombe Forest.	136
Table 4.5a:	Species Diversity Indices (H) for the Five Most Common Species in Ambarongy Plots.	138

Table 4.5b: Species Diversity Indices (H) for the Five Most Common Species in Parc Plots.....	139
Table 4.5c: Species Diversity Indices (H) for the Five Most Common Species in Vevembe Plots.....	140
Table 4.6a: Mean Monthly Food Availability (FA/ha).....	141
Table 4.6b: Mean Monthly Food Availability (FA/ha) for May-August 2000.	141
Table 4.7a: Phenological Synchrony at Ambarongy.....	142
Table 4.7b: Phenological Synchrony at Parc.....	143
Table 4.7c: Phenological Synchrony at Vevembe.....	144
Table 5.1: Composition of Study Groups.....	185
Table 5.2: Summary of Feeding Patterns.....	186
Table 5.3a: Diet Across Months in Group AN1, Andringitra.....	187
Table 5.3b: Diet Across Months in Group ANA, Andringitra.....	187
Table 5.3c: Diet Across Months in Group VE1, Vevembe.....	188
Table 5.4a: Plant Species Consumed by Group AN1, Andringitra.....	189
Table 5.4b: Plant Species Consumed by Group ANA, Andringitra.....	191
Table 5.4c: Plant Species Consumed by Group VE1, Vevembe.....	192
Table 5.5: Top Ten Species for All Groups, Including Part Consumed and Percentage of Total Feeding Time.	195
Table 5.6a: Monthly Top Five Food Species for Group AN1, Andringitra, Including Part Consumed and Percentage of Total Feeding Time.	196
Table 5.6b: Monthly Top Five Food Species for Group ANA, Andringitra, Including Part Consumed and Percentage of Total Feeding Time.	197

Table 5.6c: Monthly Top Five Food Species for Group VE1, Vevembe, Including Part Consumed and Percentage of Total Feeding Time.	199
Table 6.1: Subcategories and Behaviors in the Social (S) Category.	238
Table 6.2: Social Spacing Across Groups.	239
Table 6.3: Activity Budgets.	240
Table 6.4: Intergroup Interactions.	241
Table 6.5: Mean Daily Path Length (DPL), Total Home Range (HR), Range Overlap, and Indices of Defensibility (<i>D</i>).	241

List of Figures

Figure 1.1: Brown Lemur Distributions and Study Sites in Southeastern Madagascar.....	38
Figure 1.2: Hybrid and Parental Populations of Brown Lemurs of Southeastern Madagascar	39
Figure 2.1: Brown Lemur Sampling Sites.	62
Figure 2.2: Relationship Between Canine Height and Body Mass.....	63
Figure 2.3: Body Mass (kg) Across Populations.	64
Figure 2.4: Maxillary Canine Height (mm) Across Populations.	64
Figure 2.5: Body Size Dimorphism Across Populations.....	65
Figure 2.6: Canine Height Dimorphism Across Populations.	65
Figure 2.7: Gonadosomatic Index (GI) Across Populations and Seasons.....	66
Figure 2.8: Gonadosomatic Index (GI) in the Lemurids.	66
Figure 3.1: Census Sites.....	84
Figure 3.2a: Frequency of sighting distances using perpendicular animal- transect distance (PD).....	85
Figure 3.2b: Frequency of sighting distances using observer-animal distance (OAD).....	85
Figure 3.3: Population Densities at Primary Research Sites..	86
Figure 3.4: Population Densities at Rapid Assessment Sites..	87
Figure 4.1: Botanical Sampling Locations at Andringitra (A) and Vevembe (B).....	122

Figure 4.2: Mean Monthly Temperature Maxima and Minima ($^{\circ}\text{C}$) with Standard Error at Andringitra and Vevembe.	123
Figure 4.4: Mean Daily Rainfall (mm) and Standard Error at Ambarongy Station, Andringitra National Park and Vevembe Forest.	124
Figure 4.5: Monthly Rainfall (mm) at Andringitra and Vevembe.	124
Figure 4.6: Food Availability (FA/ha) Across Sites.	125
Figure 4.7: Synchrony Across Sites for Fruiting, Leaf Flushing, and Flowering.	126
Figure 4.8: Phenology/Meteorology Relationship at Ambarongy.	127
Figure 4.9: Phenology/Meteorology Relationships at Parc.	128
Figure 4.10: Percentage of Trees Producing Fruit (A), New Leaves (B), and Flowers (C) at Southeastern Sites.	129
Figure 4.11: Mean Temperature Maxima (A) and Minima (B) ($^{\circ}\text{C}$) at Southeastern Madagascar Sites.	130
Figure 4.12: Mean Monthly Rainfall (mm) at Southeastern Madagascar Sites..	131
Figure 5.1: Diet Composition Across Groups.	177
Figure 5.2: Seasonal Variation in Diet Across Groups.	178
Figure 5.3: Total Feeding Time and Feeding Rates.	179
Figure 5.4: Dietary Diversity..	180
Figure 5.5: Mean Height in Canopy (m) During Feeding.	181
Figure 5.6: Sex Differences in Diet Composition.	182
Figure 5.7: Age Differences in Diet Composition.	183
Figure 5.8: Potential Keystone Resources.	184

Figure 6.1: Home Ranges (Method 2) at Andringitra.	228
Figure 6.2: Activity Budgets in Each Study Group Across Months.	229
Figure 6.3: Mean Height in Canopy (m) Across Study Groups.	231
Figure 6.4: Intergroup Encounters.	232
Figure 6.5: Mean Daily Path Length (DPL) Across Study Groups.	233
Figure 6.6: Home Range (Method 2) in Group AN1, Andringitra.	234
Figure 6.7: Home Range (Method 2) in Group ANA, Andringitra.	235
Figure 6.8: Home Range (Method 2) in Group VE1, Vevembe.	236
Figure 6.9: Home Range Overlap.	237

Chapter 1: Introduction

COMPETITION AND COMMUNITY ECOLOGY

One of the organizing principles in ecology is that competition among sympatric species plays a significant role in structuring communities (Lack, 1947; Hutchinson, 1959; MacArthur and Levins, 1964; Diamond, 1975; Roughgarden, 1983; Schoener, 1983). Much of competition and niche theory in community ecology derives from the basic assertion that perfect competitors cannot coexist in nature (Gause, 1934). Competitive exclusion is considered the primary mechanism in maintaining the geographic ranges of close competitors (Gause, 1934). This is evidenced in part by the distribution patterns of related organisms. Species pairs that are similar in size (and often in other morphological or behavioral characters as well) tend to be allopatric or parapatric – the classic "checkerboard" distribution (Hutchinson, 1959). Competitive exclusion may also result in altitudinal or microhabitat segregation among related species (Diamond, 1973; Bergstrom, 1992).

As a corollary, species pairs or sets of related animals that do share habitats tend to demonstrate some form of ecological divergence. Hutchinson (1959) first proposed a minimum size ratio that permits related sympatric species pairs to avoid competition. Differences in gross body size and/or the size of feeding apparatus characters are presumed to correspond with shifts in diet, allowing adjacent species pairs to partition limited resources. This principle of minimum divergence may also apply to other morphological characters,

physiology, and behavioral traits. Particularly as the number of potential competitors increases in a community, species will tend to segregate on multiple niche dimensions (e.g., food type choices, horizontal and vertical habitat preferences, and activity schedule; Schoener, 1974).

Among the more notable instances of niche separation is the phenomenon of character displacement (Brown and Wilson, 1956). Character displacement involves cases where two species are similar when allopatric but diverge in sympatry. Brown and Wilson (1956) propose two functions for character displacement. First, niche separation in sympatric species should mediate interspecific competition for limited resources. Second, character displacement also may reinforce reproductive barriers between closely related parapatric species.

The relationship of morphological shifts to niche partitioning has received considerable attention in the ecological literature (e.g., Grant, 1972; Strong et al., 1979; Strong, 1983; Dayan and Simberloff, 1998). Features directly linked to the trophic apparatus are more likely to demonstrate character displacement, such as the canine teeth of carnivores (Dayan and Simberloff, 1998). Ecological character displacement may arise through the coevolution of sympatric competitors, or through selection against immigrating species with similar feeding adaptations (Strong et al., 1979). The second function of character displacement relates to reproductive or secondary sexual traits (Schoener, 1974). Sexually selected characters may diverge in sympatry to reinforce premating isolation

between related populations, particularly where hybridization results in lower fitness of offspring (Sætre et al., 1997).

The links between ecology and reproductive isolation form the basis of newly revived and productive lines of inquiry (Orr and Smith, 1998; Morrell, 1999; Schluter, 2001). Recent evidence from invertebrates, reptiles, and fish suggests that colonizing species may evolve novel, heritable feeding adaptations extremely rapidly – integrating ecological and evolutionary timescales (Orr and Smith, 1998). For example, among sympatric stickleback fishes in British Columbia, there is evidence for mate selection based on morphological characters important in the ecological divergence of these species (Nagel and Schluter, 1998). Moreover, the fitness (measured by growth rates) of backcrosses varies according to parental habitat type, strongly suggesting that postmating isolation had developed via natural selection (i.e., ecological adaptation to different environments; Rundle, 2002). Thus, in closely related populations distributed sympatrically or parapatrically, ecological adaptation may be a critical factor driving speciation. In these cases, it may be productive to examine the relationship between the two purported functions of character displacement (which can readily be expanded to niche separation in general): mediating competition and reinforcing reproductive isolation. As Barton (2001a) concludes, the speciation process involves both the development of reproductive isolating mechanisms and all forms of phenotypic diversification, including niche separation to permit coexistence.

Acceptance of the importance of interspecific competition has not been universal. Critics have pointed to the myriad factors shaping ecological communities that may override the effects of competition. These include predation, autecology, mutualism, and stochastic events (Wiens, 1977, 1983; Connor and Simberloff, 1979; Connell, 1980, 1983; Strong, 1983). Much of the criticism is based on methodological concerns, charging that competitive effects are often inferred without disproving null hypotheses of chance or random distributions of potentially competing species (Connor and Simberloff, 1979; Strong et al., 1979). To demonstrate positive or negative interactions among species, it is critical to use experimental approaches (Schoener, 1983). This may include direct manipulations of communities or "natural experiments" (i.e., comparative studies of sympatric and allopatric populations of potential competitors). Despite the criticisms, the great majority of field experiments have demonstrated significant interspecific competition (Schoener, 1983; but see Connell, 1983).

COMPETITION IN THE PRIMATE COMMUNITIES OF MADAGASCAR

The community structure and feeding behaviors of primates found in diverse habitats appear to reflect niche partitioning (Africa: Struhsaker and Oates, 1975; Gautier-Hion, 1978; Gonzalez-Kirchner, 1996; Tutin et al., 1997; Neotropics: Mittermeier and van Roosmalen, 1981; Terborgh, 1983; Chapman, 1988; Norconk and Kinzey, 1994; Tomblin and Cranford, 1994; Asia: Rodman, 1973; Raemakers, 1979). While other sympatric animals may exploit similar resources, primate species are generally each other's closest competitors due to

similar morphology, feeding adaptations, and phylogeny (Waser, 1987; Houle, 1997). Primates may respond to competition for limited resources by adopting different diets, ranging patterns, activity schedules, time budgets, and microhabitats (Sussman, 1974; Terborgh, 1983; Waser, 1987). A high degree of dietary overlap among sympatric primates may indicate current competition, and clear niche separation is viewed as evidence for the prevalence of past competition shaping the ecological patterns in the community (Waser, 1987).

The Malagasy strepsirhines also exhibit divergent feeding and foraging strategies in sympatric species (Sussman, 1974, 1977; Ganzhorn, 1988; Wright and Randrimanantena, 1989; Overdorff, 1991, 1993, 1996a; Freed, 1996; Powzyk, 1997; Vasey, 1997, 2000, 2002; Rasmussen, 1999; Tan, 2000), and interspecific competition apparently plays a significant role in structuring lemur communities (but see Richard and Dewar, 1991). According to Fox's assembly rule, communities tend to include a balance of guilds or functional groups (e.g., frugivores, folivores, etc.); if new species are added to the community, they tend to do so in a cycle according to available functional niches (Ganzhorn, 1997). For example, in a community with one omnivore, two folivores, and two frugivores, there is a greater probability that the next community member will be omnivorous. Ganzhorn (1997) tested this rule in twenty-three Malagasy lemur communities and found the predicted assembly pattern in nearly every community, particularly when recently extinct taxa were included in the analysis. Moreover, the likely underlying mechanisms for this structure - including

interspecific competition – have persisted through many climate changes (Ganzhorn, 1997).

The details of dietary niche patterns among sympatric Malagasy primates vary across habitats and taxa. In some cases, dietary differences are marked. For example, at Antserananomby, Sussman (1974, 1977) found *Eulemur fulvus rufus* has a highly restricted, folivorous diet in dry forest habitats, while similar-sized *Lemur catta* pursues a more diverse foraging strategy. Sussman equated these dietary differences with microhabitat preferences: *L. catta* uses the ground frequently, while *E. f. rufus* is restricted to an arboreal environment. As a possible consequence of this spatial separation (and/or competition) with *L. catta*, *E. f. rufus* may be confined to fewer food resources. Sussman (1974) did not find variation in either of these species' diets in areas of allopatry vs. areas of sympatry. Thus, the dietary divergence is not attributed directly to the interaction of the species in their shared environment (i.e., character displacement). Instead, *E. f. rufus* and *L. catta* appear to demonstrate adaptations to dissimilar allopatric environments (*L. catta* being found in drier habitats). Nonetheless, this ecological separation still may minimize direct competition and facilitate sympatry.

In the Masoala Peninsula, another brown lemur population (*Eulemur fulvus albifrons*) is sympatric with larger-bodied *Varecia variegata rubra*. Vasey (1997, 2000) noted these two species also partition their shared environment along numerous niche dimensions. *V. v. rubra* is highly frugivorous, feeds in larger patches, and forages mainly above 15 m in the canopy. Meanwhile, *E. f. albifrons* has a more diverse diet, incorporating greater quantities of flowers,

leaves, and other items, and feeds low in the canopy (Vasey, 1997, 2000). Moreover, niche separation (especially vertical stratification) varies according to seasonal shifts in food abundance, although energy demands for reproductive females also have important effects on both species' diets (Vasey, 2000).

Sympatric lemuroid species within other guilds also demonstrate marked differences in feeding ecology. For example, Powzyk (1997) found that *Indri indri* and *Propithecus diadema diadema*, which coexist at Mantadia National Park, both consume large amounts of foliage. However, the two indrid species diverge in many key dietary components. *Indri* relies more heavily on new leaves and has a much higher content of complex carbohydrates in its diet. In contrast, *Propithecus* feeds more on fruits and flowers, yielding much higher levels of simple sugars and lipids (Powzyk, 1997). These dietary shifts apparently lead to complex differences in behavior, including ranging, activity budgets, and territorial defense strategies (with divergence in vocalizations and scent-marking; Powzyk, 1997).

In other Malagasy lemur communities, separation in feeding niches is more subtle. For instance, the three sympatric species of *Haplemur* at Ranomafana National Park specialize on different parts of the same bamboo species (Wright and Randrimanantena, 1989). During the winter (the period of increased resource scarcity), *H. griseus*, *H. aureus*, and *H. simus* feed on the same three bamboo species. However, *H. griseus* consumes the leaf bases and vine pith of one species, while *H. aureus* and *H. simus* focus on the larger bamboo species. The diet of the latter two is also segregated according to plant part (*H. aureus*

consuming leaves and bases, and *H. simus* feeding on pith). In a longer-term analysis, Tan (2000) found the three *Hapalemur* species feed on bamboo at least 88% of the time. However, *H. griseus* has a much more diverse diet, incorporating fruit and leaves, while *H. simus* is the most obligate bamboo specialist and consumes larger cyanogenic shoots. Variation in ranging and vertical habitat stratification was also recorded. Tan (2000) suggests that divergence in body size – and the concomitant shifts in behavioral ecology – has played a significant role in permitting sympatry in these congeners.

Also in eastern rain forests, *E. f. rufus* co-exists with *E. rubriventer*. Overdorff (1991; 1993; 1996a) found these congeners eat different proportions of the same food species, eat fruit at different stages of ripeness, and have different activity schedules (with *E. f. rufus* frequently active at night; Overdorff, 1996a; Overdorff and Rasmussen, 1995). These differences are manifested primarily during peak food scarcity (Overdorff, 1993; 1996a), further evidence that such divergence may have evolved to reduce feeding competition in the lemur community. Similarly subtle patterns of niche differentiation have been observed in other sympatric *Eulemur* species pairs. For example, Freed (1996) found that *E. coronatus* and *E. fulvus sanfordi* at Mt. d'Ambre have highly convergent overall diets of ripe fruit, but the two taxa differ in daily ranging patterns and forage at different heights; spatial association of the two species also varies according to food availability. In addition, seasonal variability in activity rhythms (i.e., cathemerality) may be associated with reducing competition in other

sympatric *Eulemur* species (Tattersall and Sussman, 1998), including *E. mongoz* and *E. fulvus fulvus* at Ampijoroa (Rasmussen, 1999).

Ganzhorn (1988) has also noted subtle and diverse mechanisms of niche partitioning in both eastern rain forests and western deciduous forests. At Andasibe and Ampijoroa, he found that sympatric lemur species often vary in the chemical composition of their diets (including protein concentrations, condensed tannins, and alkaloids). This variation is sufficient to segregate the communities into species pairs, with each pair significantly different from the others (i.e., pairs of close competitors). Subsequently, the two species within pairs can be distinguished by divergent activity rhythms. These two factors combine to significantly reduce niche overlap (Ganzhorn, 1988).

In contrast to this interest in multi-species communities, no studies have yet directly examined ecological variation *within* a polytypic lemur species. An implicit assumption in much of the research in community ecology is that more closely related taxa must compete more directly, often leading to exclusive, allopatric or parapatric distributions. Houle (1997) tested the assumption that phylogenetic distance is inversely related to competition in 41 primate communities (including 8 in Madagascar). He found that indeed a minimum phylogenetic distance is generally maintained: while congeners (or "kin species") may coexist, sister species will rarely share the same habitat. Moreover, aggression decreases and affiliative behaviors increase with greater phylogenetic distance (Houle, 1997).

HYBRID ZONES AND SPECIATION

In the present study, I investigate ecological divergence in two lemur groups that overlap in the boundary region between their ranges. In this manner, I extend the traditional ecological analysis of sympatric congeners to two taxa of very recent common ancestry (that indeed continue to interbreed). At this fine level of taxonomic distinction, the potential intergradation of these populations through hybridization is a critical factor in the research. Hybrid zones are defined inclusively as “interactions between genetically distinct groups of individuals resulting in at least some offspring of mixed ancestry (Harrison, 1990:72)”. This operational definition is preferred as it minimizes assumptions about historical and evolutionary (selective) processes at work in a given contact zone (Harrison, 1990).

The phenomenon of natural hybridization lies in the gray areas of most species concepts (Godfrey and Marks, 1991). Of particular interest are the differing implications of hybrid zones for two preferred species definitions: (1) the biological species concept (BSC; e.g., Mayr, 1963) and (2) the phylogenetic species concept (PSC; Cracraft, 1983). The BSC, which is based largely on reproductive isolation and espoused by many neontological zoologists, generally regards hybridizing taxa as conspecifics (often subspecies). In contrast, the PSC is favored by paleontologists due its ready application to the fossil record; the PSC uses a more strictly methodical approach to sort taxa into consistently diagnosable clades and tends to retain species-level classification of well-differentiated taxa in the face of hybridization. Vogler and DeSalle (1994)

suggest that the PSC should be used to define conservation units, with diagnosis methodology limiting uncertainties in conservation management decisions. As Jolly (1993, 2001) argues, both concepts are population-based and mainly differ in the relative emphasis placed on probabilities of zygote formation (“zygostructure”) or distribution of characters among populations (“phenostructure”). Accordingly, the undue emphasis placed on assigning hybridizing populations to species or subspecies is a largely semantic exercise that detracts from more important analyses of the underlying evolutionary processes involved in the interface of such taxa (Jolly, 2001).

The precarious position of natural hybridization in species concepts underscores the potential of hybrid zone studies in examining questions of speciation. The role of hybrid zones in limiting or facilitating gene flow between parental populations has significant implications for allopatric, sympatric, and parapatric models of species formation (Hewitt, 1988; Barton and Hewitt, 1989; Harrison, 1990; Bull, 1991; Arnold, 1992; Barton, 2001b). Hybrid zone dynamics may impact the evolution of specific mate recognition systems and other forms of reproductive isolation (Paterson, 1985; Harrison, 1990; Butlin, 1989; Sanderson, 1989; Templeton, 1989), as well as ecological differentiation in parental taxa (Jiggins and Mallet, 2000). Most natural zones of hybridization represent “tension zones”, where narrow clines are maintained through a balance of dispersal by the parental taxa and hybrid inferiority (either through intrinsic genetic or physiological disjunctions, or social or ecological incompatibilities; Barton and Hewitt, 1985, 1989). However, selection pressure against hybrids

may be variable, limiting the extent of reproductive isolation, or hybrids may even be at a competitive advantage in particular ecotones (Arnold, 1992) (i.e., discontinuous environmental transitions or boundary zones) or during fluctuations in climate (Grant and Grant, 1996). Long-term effects of hybridization with extensive introgression (i.e., gene flow between sets of differentiated populations; Reiseberg and Wendel, 1993) may include hybrid speciation or reticulate evolution (Arnold, 1992); these processes are not uncommon in plants (Reiseberg and Wendel, 1993; Nagy, 1997), but may also occur in other organisms, including primates (Jolly, 2001).

The origins of active zones of hybridization (i.e., arising in primary or secondary contact) are often difficult to assess (Harrison, 1990). However, as most researchers agree that most population divergence in nature (including speciation) tends to occur in allopatry, most hybrid zones are likely formed by secondary contact (Barton and Hewitt, 1985). In this model, there is an ancestral taxon existing as a single interbreeding population, wherein all individuals maintain the same “specific-mate recognition system” (i.e., recognize each other as potential mates; Paterson, 1985) and offspring are both viable and fertile. Then, some form of barrier divides the population. This could be a physical barrier, like a shifting river, or perhaps an environmental gradient. For example, forest-dwelling primate species were isolated geographically into smaller refugia habitats as forests shrank and fragmented during Pleistocene glaciation events (e.g., Colyn et al., 1991). In isolation, small genetic differences will begin to accumulate and these smaller populations may develop new adaptations, perhaps

due to divergent selection pressures in the separated habitats. Alternatively, population differences may be present at the initial split, due to genetic drift (e.g., the founder's effect). If and when the physical barrier breaks down, the habitat becomes whole again and the now distinct populations may come into contact. At the population boundary, there may be no overlap whatsoever due, for example, to competitive exclusion (see above). These populations will remain discrete and are easily classified as “good species”. Alternatively, there will be movement by one or both species into the range of the other population. Where reproductive isolation is not yet complete, the two populations will interbreed, forming a hybrid zone.

Contact zones – “natural laboratories” (Hewitt, 1988) for speciation – have spurred a tremendous amount of empirical and theoretical investigation across taxonomic groups (including plants, invertebrates, amphibians and reptiles, birds, and mammals; see reviews in Hewitt, 1988; Barton and Hewitt, 1989; Harrison, 1990; Arnold, 1992). Among nonhuman primates, natural hybridization has been observed across all major groups, including platyrrhines (e.g., callithrichids: Mendes, 1997; Passmani et al., 1997; Melo, 1999; *Cebus*: Torres de Caballero et al., 1976; Sussman and Phillips-Conroy, 1995; *Ateles*: Rossan and Baerg, 1977), cercopithecoids (e.g., *Cercopithecus*: Struhsaker et al., 1988; Butynski, 1990; *Macaca*: Fooden, 1964; Froehlich and Supriatna, 1996; Bynum et al., 1997; Bynum, 2002; Fujita et al., 1997; Evans, 1998; Evans et al., 2001; Gotoh et al., 1999; Tosi et al., 2002; *Papio*: Nagel, 1973; Gabow, 1975; Shotake, 1982; Phillips-Conroy and Jolly, 1986; Hayes et al., 1990; Phillips-Conroy et al.,

1991, 1992; Samuels and Altman, 1986, 1991; Beyene Gebru, 1998; Szmulewicz et al., 1999; Woolley-Barker, 1999; Alberts and Altman, 2001), and hominoids (e.g., *Hylobates*: Brockelman and Gittins, 1984; McConkey et al., 2002); even intergeneric hybrids have been recorded in the wild (e.g., *Theropithecus* X *Papio*: Dunbar and Dunbar, 1974; Jolly et al., 1997).

The best studied primate hybrid zone is the *Papio hamadryas anubis* (olive baboon) X *P. h. hamadryas* (hamadryas baboon) interface at Awash National Park, Ethiopia. Researchers (most notably C. Jolly, J. Phillips-Conroy, and colleagues) have conducted investigations for over 30 years into the morphology, genetics, ecology, and social behavior of the baboons in this contact zone (e.g., Nagel, 1973; Phillips-Conroy and Jolly, 1986; Jolly et al., 1989; Phillips-Conroy et al., 1991, 1992; Jolly, 1993; Beyene Gebru, 1998; Szmulewicz et al., 1999; Woolley-Barker, 1999; Jolly, 2001). In general terms, olive baboons inhabit woodland, forest, or savanna habitats, while hamadryas baboons occupy – and demonstrate behavioral and morphological adaptations to (Jolly, 2001) – semidesert habitats (Nagel, 1973; Phillips-Conroy and Jolly, 1986). Originally described as a narrow hybrid sink occurring at an ecotone, balanced by dispersal and strong selection against hybrids (Nagel, 1973), the Awash zone where these taxa meet came to be viewed as considerably more complex. There is evidence for expansion of the hybrid zone, potentially linked to climatic fluctuations (Phillips-Conroy and Jolly, 1986) and there do not appear to be intrinsic behavioral barriers to interbreeding (Phillips-Conroy et al., 1991). The distinctive social behavior (particularly mating tactics) of the two parental taxa, as well as

differences in dispersal patterns, strongly influence the directions and limitations of gene flow through the Awash hybrid zone (Sugawara, 1979; Phillips-Conroy et al., 1992; Beyene Gebru, 1998; Jolly, 2001). These studies underscore the importance of behavioral and ecological factors in population boundaries, and provide a model for the integration of morphological, behavioral, and genetic techniques in studying the dynamics of primate hybrid zones.

There are presently several studies documenting natural hybridization in lemurs. These cases generally involve closely related *Eulemur* populations (*Eulemur macaco macaco* X *Eulemur macaco flavifrons*: Myers et al., 1989; Rabarivola et al., 1991; *Eulemur fulvus fulvus* X *Eulemur fulvus rufus*: Lehman and Wright, 2000; *Eulemur fulvus fulvus* X *Eulemur mongoz*: Pastorini et al., 2001; *Eulemur fulvus rufus* X *Eulemur albocollaris*: Sterling and Ramarason, 1996; Johnson and Wyner, 2000; Wyner, 2000) but contact zones may also occur in *Varecia* (*Varecia variegata variegata* X *Varecia variegata rubra*: Tattersall, 1982) and *Avahi* (*Avahi laniger* spp: Rumpler, 2000). Despite the growing number of recorded lemur hybrid zones, none has been investigated through in-depth field study of population structure (including population genetics) or behavioral ecology.

The objective of the present study is to examine the behavioral and ecological aspects of a lemur hybrid zone. In particular, I investigate how ecological divergence among the contributing populations may function in the dynamics of the hybrid zone. In this way, I hope to evaluate the contribution of

ecological mechanisms in determining the directions and limitations of gene flow, in delimiting species boundaries, and perhaps in incipient speciation.

THE BROWN LEMURS OF SOUTHEASTERN MADAGASCAR

The subject taxa for the present project are two populations in the brown lemur species complex: the white-collared lemur (*Eulemur albocollaris*) and the rufous lemur (*E. fulvus rufus*) (see below for a discussion of taxonomy). This frugivorous-folivorous brown lemur group demonstrates great flexibility and opportunism, and is found in most lemur communities across Madagascar (Tattersall and Sussman, 1998). These two species are mainly parapatric in southeastern Madagascar (Figure 1.1).

Distribution and Ecology

E. albocollaris has a highly restricted range in southeastern Madagascar (Tattersall, 1982; Figure 1.1). There have been no prior studies on the behavioral ecology of this taxon. Previous research has been restricted to rapid assessments of population density and habitat conditions (Sterling and Ramarason, 1996; Johnson and Overdorff, 1999). The surveys indicated low densities of *E. albocollaris* relative to neighboring populations of *E. f. rufus* and *E. collaris* (Johnson and Overdorff, 1999). Moreover, the *E. albocollaris* forests were relatively small, degraded, and/or showed evidence of hunting. However, of the quantitative botanical variables examined, only high liana density was correlated with higher population densities across sites (Johnson and Overdorff, 1999).

In contrast to *E. albocollaris*, there has been a considerable amount of field research on *E. f. rufus* (e.g., Sussman, 1972, 1974; Overdorff, 1991, 1993,

1996a, 1996b; Ostner and Kappeler, 1999; Gerson, 2000). This taxon has a large and non-contiguous distribution in both western dry forests and eastern rain forest (Tattersall, 1982). In the east, they are primarily frugivores, with seasonally fluctuating supplements of flowers, new leaves, fungi, and, rarely, invertebrates in their diet (Overdorff, 1991, 1993). Like other brown lemurs, *E. f. rufus* are mainly arboreal quadrupeds with variable use of vertical postures and leaping (Dagosto, 1995). Rufous lemurs in the eastern site of Ranomafana have been noted to be sexually monomorphic in both canine height and body weight (Glander et al., 1992). *E. f. rufus* live in multi-male/multi-female groups generally with 6-10 individuals (Overdorff, 1996a). Male-bias in sex ratio has been suggested (Overdorff, 1996a; but see Kappeler, 2000). In terms of activity rhythms, *E. f. rufus* are cathemeral (i.e., active during both day and night for extended periods; Overdorff, 1991; Overdorff and Rasmussen, 1995). Eastern rufous lemurs use home ranges of 85-100 ha, and travel 456-1470 m per day (Overdorff, 1991). Social groups overlap and are not strictly territorial; however, aggressive contests over food resources are not uncommon (Overdorff, 1991). In addition, rufous lemurs have been noted to migrate during times of peak food scarcity (Overdorff, 1993).

Rufous lemurs in the dry forests of the west differ in many respects from their eastern rain forest counterparts. They tend to be smaller (Albrecht et al., 1990; Gerson, 2000) and demonstrate sexual dimorphism in canine height favoring males (Gerson, 1999, 2000). Western *E. f. rufus* are also highly folivorous in western habitats (Sussman 1974, 1977; Gerson, 2000). Moreover,

ranging patterns in these populations also differ from those in the east. Home range size is very small (0.75-1.0 ha) with short daily path lengths (125-150 m) (Sussman, 1977). Intergroup encounters are not generally hostile (Sussman, 1977). Perhaps the most striking characteristic of western *E. f. rufus* is their dramatically high population density: 900-1222 individuals/km² (Sussman, 1974) vs. 13 per km² at Ranomafana (Johnson and Overdorff, 1999).

Pelage Differences

All brown lemur populations are sexually dichromatic (Tattersall, 1982; Figure 1.2). *E. f. rufus* males are characterized by gray bodies with lighter underparts. They have bushy heads with a reddish crown; they also have a black stripe descending from the forehead to the black muzzle, and white or light gray patches above the eyes (Tattersall, 1982). Females have reddish brown bodies also with lighter ventral. They also have a dark stripe down the center of the face to the muzzle with white eye patches, but their heads are smoother than males and lack the reddish crown (Tattersall, 1982).

E. albocollaris males differ from *E. f. rufus* males in numerous coat characters (Tattersall, 1982; Figure 1.2). Their bodies are darker gray to brownish, with variable expression of a dark brown stripe down the center of the dorsum and a dark tail. Their faces are more uniformly dark, but some have slightly lighter patches above the eyes. The head is smoothly haired. Their most distinctive (and namesake) feature is their bushy white collar or beard. *E. albocollaris* differ from closely related *E. collaris* (see Figure 1.1) mainly in beard color: *E. collaris* have reddish-orange collars. As in most brown lemurs,

pelage differences in females of *E. albocollaris* and *E. f. rufus* are less striking. Most notably, they lack the distinctive facial masking pattern of *E. f. rufus*. Instead, their faces are uniformly gray. *E. albocollaris* females are virtually indistinguishable from *E. collaris* females (Tattersall, 1982; Mittermeier et al., 1994).

Cytogenetics, Genetics, and Taxonomy

Eulemur fulvus is traditionally considered to contain seven subspecies (Tattersall, 1982). These include: the common brown lemur (*E. f. fulvus*), the white-fronted lemur (*E. f. albifrons*), Sanford's lemur (*E. f. sanfordi*), the Mayotte lemur (*E. f. mayottensis*), the red-fronted or rufous lemur (*E. f. rufus*), the collared lemur (*E. f. collaris*), and the white-collared lemur (*E. f. albocollaris*). The Mayotte lemur, however, is likely not a valid taxon as it represents an introduced population of common brown lemurs (Mittermeier et al., 1994).

The remaining six subspecies can be separated based on karyotypes. *E. f. fulvus*, *E. f. rufus*, *E. f. albifrons*, and *E. f. sanfordi* share a common diploid number ($2N = 60$) and have similar chromosome morphology in G-, Q-, and R-banding patterns (Rumpler, 1975, Hamilton and Buettner-Janusch, 1977). In contrast, *E. f. collaris* is polymorphic in karyotype ($2N = 50, 51, 52$) (Buettner-Janusch and Hamilton, 1979), although $2N = 50$ is normative for this taxon (Rumpler, 1990; in Wyner, 2000). Meanwhile, *E. f. albocollaris* – only formally separated from closely related *E. f. collaris* in 1975 (Rumpler, 1975; see Tattersall, 1982) – maintains a diploid number of 48.

However, similarity in chromosome complements in these groups does not necessarily translate into reproductive compatibility. As expected, all four $2N = 60$ subspecies are fully interfertile in captivity. Moreover, both *E. f. collaris* and *E. f. albocollaris* produce fertile hybrids when each is crossed with *E. f. fulvus* (a $2N = 60$ subspecies) (Rumpler, 1975, 1990, in Tattersall, 1993; Buettner-Janusch and Hamilton, 1979). However, captive hybrids of *E. f. albocollaris* X *E. f. collaris* are sterile (Dutrillaux and Rumpler, 1977), with meiotic chromosomes arranged in long chains of six (Rumpler, 1990, in Tattersall, 1993). More recently, Djlelati et al. (1997) noted severe reproductive breakdown in *E. f. albocollaris* X *E. f. collaris* hybrids, citing autosomal-sex chromosomal associations as a cause for impairment of spermatogenesis. These authors also support the more recent common ancestry of these two taxa, their karyotypes having developed through different rearrangements of the chromosomes found in an intermediary ancestor (Djlelati et al., 1997). However, with reproductive isolation apparent in these groups, Djlelati et al. (1997) propose elevating these taxa to full species: *E. albocollaris* and *E. collaris*. Tattersall (1993) takes a more circumspect view, suggesting that the chromosomal innovations within the brown lemur complex have not yet resulted in complete speciation.

Recent studies in molecular genetics have also examined the brown lemur speciation problem (Wyner et al., 1998; Wyner, 2000; Pastorini, 2000). Wyner et al. (1999) investigated evolutionary relationships among the six brown lemur taxa by sequencing mitochondrial DNA (including d-loop, 12S rRNA, and cytochrome *b*) and nuclear DNA (casein kinase II) regions. These authors used population

aggregate analysis to segregate the brown lemurs into three distinct evolutionary units: a *E. f. collaris* unit (supported by three diagnostic sites), a *E. f. albocollaris* unit (with six diagnostic sites), and a group comprised of the other four subspecies (supported by two diagnostic sites, but with no diagnostic sites for the subspecies within this group). Based mainly on phylogenetic species concept principles, Wyner et al. (1999) support the proposal by Djlelati et al. (1997) to elevate the two southeastern-most brown lemur populations to full species (*E. albocollaris* and *E. collaris*).

Pastorini et al. (2000), however, arrived at opposite conclusions in their study of brown lemur phylogeny. These authors sequenced part of the COIII gene, and all of ND3, ND4L, and ND4 and five tRNA genes. *E. f. collaris* and *E. f. albocollaris* did indeed form a clade: pair-wise distances for these two taxa were among the lowest of subspecies comparisons, and distances were large between each of these groups and any other distinguished *E. fulvus* population. However, because pair-wise distances were much greater between *E. fulvus* and the outgroup *E. macaco*, combined with the evidence for continued interfertility (see above), Pastorini et al. (2000) opted to retain collared and white-collared lemurs as *E. fulvus* subspecies. However, there are some potential limitations in this study. Only two individuals each were sampled for *E. f. collaris* and *E. f. albocollaris*, and precise localities were not available for any of them (Pastorini et al., 2000). Moreover, while six brown lemur clades were identified, they did not segregate the traditionally recognized subspecies. *E. f. rufus* was sorted into two separate clades (not based on the recent east-west split) while *E. f. fulvus* also

appeared in two groups (one of which also included *E. f. sanfordi* and *E. f. albifrons*). Thus, the potentially polyphyletic nature of these groupings casts some doubt on the validity of these clades – which, regardless, maintain the separation of *E. f. collaris* and *E. f. albocollaris*.

Given these lines of evidence, ascertaining whether white-collared and collared lemurs “really” represent species distinct from *Eulemur fulvus* is probably a semantic exercise, wherein a biological continuum is arbitrarily separated into categories. Following Jolly (2001), it is more appropriate perhaps to adopt the term “allotaxa” (Grubb, 1999) for such populations that are distinct and diagnosable but may not be completely reproductively isolated. Nonetheless, I have chosen herein to refer to *Eulemur albocollaris* and *E. collaris* by their binomial, species-level designations (cf. Djlelati et al., 1997), while other brown lemur taxa are retained as subspecies of *Eulemur fulvus*. However, to emphasize the close relationships of the taxa within this group, I will refer to the *E. fulvus* subspecies, *E. albocollaris*, and *E. collaris* collectively as “brown lemurs”. Separating *E. albocollaris* and *E. collaris* as different species is based largely on population aggregate analysis and the phylogenetic species concept (Wyner et al., 1999; but see Pastorini et al., 2000). The biological species concept is difficult to apply to the brown lemur group, as not all populations are interfertile but reproductive isolation is independent of the degree of relatedness. The phylogenetic species concept also has great utility in conservation biology (Vogler and DeSalle, 1994). This method helps underscore the biological significance and dire conservation status of critically endangered lemur taxa such

as the white-collared lemur (e.g., Harcourt and Thornback, 1990; Mittermeier et al., 1992).

Contact Zone at Andringitra National Park

Recent census research (Sterling and Ramarason, 1996; Johnson and Wyner, 2000) has identified a boundary region between *Eulemur albocollaris* and *E. f. rufus* at Andringitra National Park (Figure 1.1). This reserve is located in the Andringitra Massif in Fianarantsoa Province, between 22° 7' and 22° 21' S and between 46° 47' and 47° 2' E (Goodman, 1996a). The mountainous region is the source for many major river systems, including the Manampatrana River (noted erroneously by some to represent the *E. albocollaris*-*E. f. rufus* boundary; see Mittermeier et al., 1994; Johnson and Wyner, 2000) and the Mananara River (the division between *E. albocollaris* and *E. collaris*; Tattersall, 1982; Mittermeier et al., 1994). The 31,160-ha protected area incorporates numerous floristic zones corresponding to variation in altitude; Andringitra has an elevation range of 650-2658 m and includes several of the highest peaks in Madagascar (Goodman, 1996a). Moreover, there is a clear contrast between plant communities of the eastern and western slopes of the Andringitra Massif. The western slope marks the transition to more arid habitats of central and western Madagascar, while the eastern slope contains three distinct zones: lowland rain forest, mid-altitude moist forest, and dwarf montane flora and heathlands (Goodman and Lewis, 1996).

The diversity of animal communities – including lemurs – is also dependent on elevational zone, with generally greater species numbers at lower altitudes (Goodman and Rasolonandrasana, 2001). Overall, the Andringitra

National Park maintains one of the richest primate communities in Madagascar. Eleven species have been recorded on the eastern rain forest slope, including five nocturnal species and six day-active species (Sterling and Ramarason, 1996; Table 1.1). In addition, a disjunct population of *Lemur catta* has been noted at high elevations and in western areas of the reserve (Goodman and Langrand, 1996).

Among these numerous lemur taxa is the unusual brown lemur population. During population surveys in 1993, Sterling and Ramarason (1996) identified individuals with phenotypes of *Eulemur fulvus rufus* primarily on the western slope, but also at higher elevations on the eastern slope. In addition, they observed some orange-bearded males and suspected the presence of *Eulemur collaris* in this brown lemur population as well. However, the majority of males (the more diagnostic sex) had the white beards typical of *Eulemur albocollaris*.

These observations prompted genetic sampling of the brown lemur population on the eastern slope of Andringitra, conducted simultaneously with the initiation of the present study. Wyner and colleagues analyzed sequences of mtDNA (d-loop) and nuclear (hemopexin intron 5, microsatellite 26, malic enzyme intron 8, and ceruplasmin intron 16) markers to determine if *E. f. rufus*, *E. collaris*, and/or *E. albocollaris* diagnostic haplotypes were present in the Andringitra brown lemurs, along with a broader comparison to pure parental populations sampled elsewhere (Wyner, 2000; Wyner et al., 2002). Wyner (2000) found low mitochondrial nucleotide diversity in *E. albocollaris*, suggesting a relatively recent origin for this taxon and historically small populations – results

that agree with the small range (Figure 1.1) and presently low densities (Johnson and Overdorff, 1999).

Wyner (2000) also determined that the Andringitra contact zone was nearly entirely composed of *E. albocollaris* X *E. f. rufus* hybrids (18 of 21 individuals sampled). No *E. collaris* markers were found in the Andringitra population, a result that concurs with the apparent lack of viable migration routes for this taxon into the region. The three individuals lacking hybrid haplotypes demonstrated only *E. albocollaris* markers, but were phenotypically indistinguishable from other individuals in their area (with males, in particular, displaying a variety of pelage features, including the bushy white beards of *E. albocollaris* and the reddish crowns and facial stripe of *E. f. rufus*; see Figure 1.2). Moreover, as the number of homozygotes or heterozygotes was not skewed in this population (i.e., no deviation from Hardy-Weinberg equilibrium), the hybrids represented multiple generations of intergradation (Wyner, 2000). Perhaps most strikingly, the hybrids of Andringitra maintained private sites (mostly in ceruloplasmin intron 16) *not* found in either pure populations of *E. albocollaris* or *E. f. rufus*. These results denote extensive introgressive hybridization in the Andringitra region; furthermore, as indicated by the apparent localized sequence evolution, the hybrid zone likely has been stable for many generations and is at least partially isolated from parental source populations (Wyner, 2000; Wyner et al., 2002).

The hybrids were sampled in three locations at roughly 3.5 km intervals. The central site, Korokoto, lies at the northeast boundary of the park. (S 22° 11'

44.2", E 47° 1' 55.6"). This location is situated near the headwaters of the Manampatrana River. Two small rivers (the Korokoto and the Iantara) converge at Korokoto to form an effective barrier to lemur dispersal downstream. Thus, Korokoto lies at the hypothetical center of migration for populations from the east and west banks of the Manampatrana (known locally as the Iantara River). One likely source of *E. f. rufus* is along the Iantara River from the western portions of the reserve, as well as from the Ivohibe region to the southwest (Sterling and Ramarason, 1996; Rasoloarison and Rasolonandrasana, 1999; personal observation; Figure 1.1). *E. albocollaris* derives from the southeast and should arrive at Korokoto from along the eastern bank of the Iantara (Figure 1.1). The two remaining sampling sites – and the locations of focal groups for the present study – are located across the Iantara River from one another at approximately 725 m altitude. Accordingly, they are equidistant from Korokoto, the theoretical meeting point of *E. f. rufus* and *E. albocollaris* populations. These sites are Ambarongy, on the eastern bank, and Parc, on the eastern bank.

The distance between Parc and Ambarongy (approximately 7 km) represents the minimum possible width of the hybrid zone. While the only potentially pure *E. albocollaris* were sampled at Ambarongy (Wyner, 2000) and the individuals from Parc somewhat more closely resemble *E. f. rufus* in phenotype (personal observation), it is highly unlikely that these sites represent the endpoints of the contact zone. As noted, nearly all of the individuals at both locations are hybrids. Moreover, individuals from both Parc and Ambarongy share alleles unique to the hybrid zone, strongly suggesting they are more similar

to each other than to either of the pure parental types. Indeed, intermediate phenotypes have been noted as far as Ivohibe, 32 km SSW of Korokoto. On the other side, the limit may lie close to Evendra (34 km SE of Korokoto); at this site, phenotypes are not dissimilar to some of the hybrids at Ambarongy (personal observation) but no hybrid haplotypes were detected in limited sampling here (Wyner et al., 1999). Accordingly, I propose that that Andringitra hybrid zone may be 60-70 km in width. These dimensions are very large, particularly in relation to home ranges (a surrogate measure for dispersal) recorded for individual social groups of eastern brown lemurs (13-100 ha; Overdorff, 1991; Vasey, 1997). More strikingly, these estimates for the hybrid zone are equivalent to more than half the length of the probable range of pure *E. albocollaris* (approximately 100-120 km; Figure 1.1)

The origins of the Andringitra hybrid zone are not yet established. Crucial information is lacking for brown lemur population genetics, as well as the history of the local Andringitra environment (including climate change and shifts in river systems). It is perhaps most likely that *E. albocollaris* and *E. f. rufus* originally diverged in allopatry, as with most speciation events (e.g., Mayr, 1963; Ayala et al., 1974; but see Futuyma and Mayer, 1980) – including in lemurs (Tattersall, 1982). Paleoenvironmental studies of the late Pleistocene and Holocene indicate fluctuating periods of increased aridity in Madagascar (Gasse and van Campo, 1998, 2001), associated with forests contracting into isolated refugia (Tattersall, 1982; Richard and Dewar, 1991; Ganzhorn, 1998). Particularly with migration routes through the central plateau limited, rivers could have served (and continue

to serve) to subdivide eastern rain forests and their lemur communities. While it appears that these rivers were barriers for already differentiated species (Tattersall, 1982; Richard and Dewar, 1991; Ganzhorn, 1998), it is possible that such closely related populations as *E. f. rufus* and the ancestor to the *E. collaris*-*E. albocollaris* group may have diverged during these more recent drying cycles. Subfossil and extant lemur species assemblages suggest that, while major biogeographic regional distinctions (e.g., between the dry west and humid east and north-south gradients) have long existed, there were formerly numerous routes for faunal exchange among regions prior to the arrival of humans (Ganzhorn, 1998; Godfrey et al., 1999). Present-day parapatry of brown lemur taxa may then have arisen during forest expansion subsequent to the last major period of aridity (e.g., Tattersall, 1982; Richard and Dewar, 1991).

A closer look at the modern biogeography of *E. albocollaris* and *E. f. rufus* in southeastern Madagascar suggests a final event must have taken place to explain the origin of the Andringitra contact zone. Modern populations of *E. collaris* and *E. albocollaris* appear to be entirely allopatric, with the Indian Ocean to the east, uninhabitable, degraded habitats to the west, and the wide Mananara River between the two taxa eliminating any points of contact (Figure 1.1). It has been implied in recent range limit descriptions for *E. albocollaris* (e.g., Mittermeier et al., 1994) that the Manampatrana River constitutes this taxon's northern limit (and thus the southern limit for *E. f. rufus*). This river does indeed represent a biogeographic barrier for lemurs in this region, forming the southern limit for *E. rubriventer*, *Haplemur simus*, *H. aureus*, and *Propithecus diadema*

(Mittermeier et al., 1994; personal observation). However, the assertion that the Manampatrana divides *E. f. rufus* and *E. albocollaris* has been refuted by the existence of putatively pure *E. albocollaris* north of the river (Johnson and Wyner, 2000), as well as the contact zone at Andringitra (Sterling and Ramarason, 1996; Wyner et al., 2002; Figure 1.1). Moreover, it appears that *E. albocollaris* populations do not enter the hybrid zone primarily by following the Manampatrana/Iantara River along its southern bank to the headwaters at Korokoto, as phenotypically pure *E. f. rufus* populations are found just southwest of this point (e.g., at Ivohibe, Rasoloarison and Rasolonandrasana, 1999; personal observation; Figure 1.1; see also Figure 3.1 inset). I suggest that the *E. albocollaris* populations north of the Manampatrana River may have arrived there via a sweepstakes crossing of this large river (e.g., during a change in the course of the river). Once the Manampatrana was traversed, the white-collared lemurs dispersed north to make contact with *E. f. rufus*, forming the present-day Andringitra brown lemur contact zone.

PROJECT GOALS

The principle objective of the present study is to examine the behavioral ecology of brown lemurs in the border region of *E. albocollaris* and *E. f. rufus* at Andringitra National Park. Because there are no previous studies of the behavioral ecology of *E. albocollaris*, an allopatric population of this species at Vevembe Forest is also included in this investigation. Vevembe (base camp: 22° 47' 3.9"S 47° 11' 6.6"E) is an unclassified forest located south of the Manampatrana River, approximately 14 km from the town of Vondrozo (Figure

1.1). The habitat is lowland rain forest and the elevation is approximately 500 m. While part of the continuous eastern corridor, forests in the Vevembe region are generally more fragmented (Figure 1.1). The lemur community at Vevembe is comprised of the same five nocturnal species present at Andringitra, along with the diurnal *Haplemur griseus griseus* (Table 1.1); thus, lemur species richness is lower relative to Andringitra and to allopatric *E. f. rufus* sites further north (e.g., Ranomafana; Table 1.1).

The original intent of this investigation was to examine sympatric populations of *E. albocollaris* and *E. f. rufus*. However, due to the unexpected composition of the brown lemur population at Andringitra (described above), it was not possible to examine these parental taxa in direct sympatry. The large – and likely old, stable, and isolated – population consisting entirely of hybrids (or at least, nearly so) presented new opportunities to examine ecological divergence and speciation in brown lemurs. Accordingly, two social groups of hybrids were selected for intensive study at Andringitra: one at the Ambarongy site, closer to the *E. albocollaris* source population, and another at Parc, closer to the potentially pure *E. f. rufus* population located further to the southwest (Ivohibe); the groups were effectively 7 km apart, but situated directly across the Iantara River from one another. While the two groups more closely resembled the respective parental taxa in phenotype, there is limited evidence for underlying genetic differences. A “*E. albocollaris*-like” group did have two individuals in which no *E. f. rufus* markers were detected; yet, as noted, the same ceruloplasmin intron 16 private sites unique to the Andringitra hybrid zone were found in individuals of

both study groups, suggesting the two groups were more similar to each other than either was to pure parentals.

To interpret the ecological, behavioral and genetic relationships among these brown lemur populations, the following major questions are addressed:

- Do ecological and behavioral factors permit *E. albocollaris* and *E. f. rufus* to overlap?
- Do ecological and behavioral variables inhibit further expansion of the area of overlap?
- How do ecological and behavioral variables contribute to the limitations of hybridization and gene flow between parental populations?

To answer these questions, the following specific variables affecting the interaction of the two populations are examined. As a corollary to genetic evidence indicating diagnosable population differences in these taxa, I examine morphological variation across several southeastern brown lemur populations, with particular emphasis on characters linked to mating systems (including sexual dimorphism and testes size). Furthermore, population densities are quantified in both allopatric and contact zone sites to determine how population structure relates to the interactions of parental species. In addition, environmental conditions (including climate, forest structure, and food availability) are monitored across sites to determine if the species (and hybrid zone) are associated with particular habitat types. Moreover, feeding behavior is recorded to examine population-specific ecological adaptations, as well as the influence of habitat characteristics on diet. Finally, other aspects of behavioral ecology are also

compared in these populations, including activity budgets, social structure, ranging, and patterns of intergroup interactions (including territoriality); these data are used to assess relationships with diet and, ultimately, dispersal and gene flow.

HYPOTHESES AND PREDICTIONS

To examine the ecological parameters of the *E. albocollaris*/*E. f. rufus* species boundary, the following series of hypotheses are tested. These hypotheses are interrelated and build upon each other, resulting in an array of alternate predictions. Falsifying individual hypotheses will greatly restrict the predictions derived from others. Thus, evaluating these hypotheses leads to the identification of a discrete range of ecological and behavioral variables impacting the *E. albocollaris*/*E. f. rufus* interface in the Andringitra region. The dramatic results from genetic surveys indicate a fully introgressed and at least partially distinct hybrid population; this population serves as a buffer to direct interaction between the parental taxa. Incorporating this new information on the genetics of the Andringitra hybrid zone, these hypotheses have been modified to represent comparisons of niche dimensions within and between related populations (in lieu of investigating the direct interactions of sympatric species).

Null Hypothesis 1: Population densities are similar in allopatric and contact zone regions. Population structure then would not be a factor contributing to range limits or hybridization.

Alternative Hypothesis 1: Population densities vary between isolated and overlapping areas for one or both parental species. If the contact zone at

Andringitra is characterized by low brown lemur density, the habitat there may be limiting, decreasing the potential for interface and hybridization beyond the boundary. However, if there are high densities in the contact zone, then the habitat here may have a relatively high carrying capacity. The inability of one or both species to extend beyond this zone suggests that the adjacent regions may be limited in their extent to support the feeding or other behavioral specializations of the other parental species. Alternatively, these habitats may be of poor quality for all brown lemur groups.

Predictions: Previous survey work indicates high densities at the contact zone relative to other brown lemur populations in southeastern Madagascar, and high densities in *E. f. rufus* relative to *E. albocollaris* (Sterling and Ramarason, 1996; Johnson and Wyner, 2000). I predict more long-term surveys will corroborate these results. Most individuals observed during previous surveys at Andringitra were likely hybrids, but their greater phenotypic (and perhaps genetic) resemblance to *E. albocollaris* suggests a larger influx of this parental species. In addition *E. f. rufus*' migration into the contact zone is reportedly periodic (P. Schachenman, pers. comm.), suggesting a lower genetic contribution for this taxon in the zone and perhaps lower densities in surrounding areas. This population structure may have a significant impact on direct and indirect interactions between the two species, including on the direction and extent of gene flow.

Null Hypothesis 2: There are no major differences in habitat (including structure of plant communities and food availability) in areas of overlap and

allopatric populations. Accordingly, any limits on distribution in the two species will not be the result of major habitat distinctions.

Alternative Hypothesis 2: The contact zone and allopatric regions correspond to habitat shifts. The species may be adapted to specific environmental conditions, leading to boundaries based on specific habitat types.

Predictions: Based on available evidence on the biogeography of brown lemurs throughout Madagascar, it is unlikely that both species are limited to particular habitats. The species complex is the most widespread in Madagascar and occupies many environments, from the western dry forests to eastern rain forest (Tattersall and Sussman, 1998); moreover, *E. f. rufus* inhabits both extremes in its disjunct range (Tattersall, 1982). Moreover, all study sites are located within the southeastern rain forest corridor. However, preliminary observations have suggested that the two species appear to be segregated by habitat type in the Andringitra region (Sterling and Ramarason, 1996) and *E. albocollaris* is confined to rain forests throughout its limited distribution (Johnson and Overdorff, 1999). Despite the diverse habitat types present at Andringitra, I predict similarity in forest type and resource abundance across the rain forest study sites.

Null Hypothesis 3: There are no significant differences in feeding ecology among parental and hybrid groups.

Alternative Hypothesis 3: Populations demonstrate quantitative differences in feeding behavior. Such differences may either be species-specific

dietary adaptations of the parental (or hybrid) groups or plastic responses to habitat shifts.

Predictions: While discussion continues regarding the taxonomic identity of *E. albocollaris*, *E. f. rufus* and *E. albocollaris* are clearly very closely related (Djlelati et al., 1997; Wyner et al., 1999; Pastorini et al., 2000). This would argue against significant divergence in feeding adaptations. *E. f. rufus* has shown great flexibility in diet, ranging from largely folivorous (Sussman, 1974) to almost exclusively frugivorous (Overdorff 1991, 1993). There are no previous studies of the feeding behavior of *E. albocollaris*. However, as brown lemurs appear to be generalists, I predict similar feeding ecology in similar habitats, while differences in diet will be linked to peculiarities of specific environments.

Null Hypothesis 4: Other aspects of behavioral ecology do not vary across populations. These variables include activity patterns, social structure, ranging, and intergroup interactions.

Alternative Hypothesis 4: There are important differences in these behavioral variables across populations. Activity patterns reflect other niche dimensions beyond feeding activities, and variation in group structure, ranging, and intergroup behavior may impact mating behavior and/or dispersal across populations. Again, any differences that do appear among the study populations here could be species-specific adaptations or flexible responses to ecotonal shifts. Ranging behavior (perhaps coupled with levels of aggression among conspecifics groups) may be of particular interest; low dispersal rates may maintain the border zone between populations and facilitate local genetic divergence, even speciation.

Such divergence may occur in the absence of geographic barriers or habitat specialization. This process has been suggested to account for the origin of the numerous, yet ecologically similar gibbon species (Brockelman and Gittins, 1984).

Predictions: As in feeding ecology, *E. f. rufus* has demonstrated marked flexibility in some of these behaviors. Ranging, for instance, varies dramatically between eastern and western populations (Sussman, 1974; Overdorff, 1996a). Levels of hostility in intergroup encounters, perhaps related to differences in resource defense, may also vary among populations of this taxon (Sussman, 1977; Overdorff, 1991). However, overall group composition and cohesion – factors with important influence on ecology – appear to be more stable across *E. f. rufus* groups. Because the study habitats are expected to be similar, I predict greater similarity in these behavioral ecological variables among the eastern rain forest brown lemurs.

In summary, due to the wide geographic range and the ecological flexibility demonstrated by this species complex, coupled with the predicted similarity in the rain forest habitats studied, I expect brown lemurs in the contact zone and in allopatric populations to be broadly similar in behavioral ecology. In essence, the null hypothesis is that differences in ecology and behavior will be minimal and thus will have little impact on speciation processes in these populations. Current distribution patterns (including the hybrid zone) may be artifacts of history; we may simply be observing these groups at an early stage of

secondary contact after initial divergence in allopatry. However, the evidence for introgressive hybridization suggests that these populations are not reproductively isolated and that the contact zone is not maintained simply by a balance between parental dispersal and hybrid inferiority. The development of novel alleles within the hybrid zone also attests to some degree of population isolation and distinctiveness. Accordingly, falsifying combinations of the above hypotheses may illuminate behavioral and ecological mechanisms operating to minimize gene flow and promote speciation.

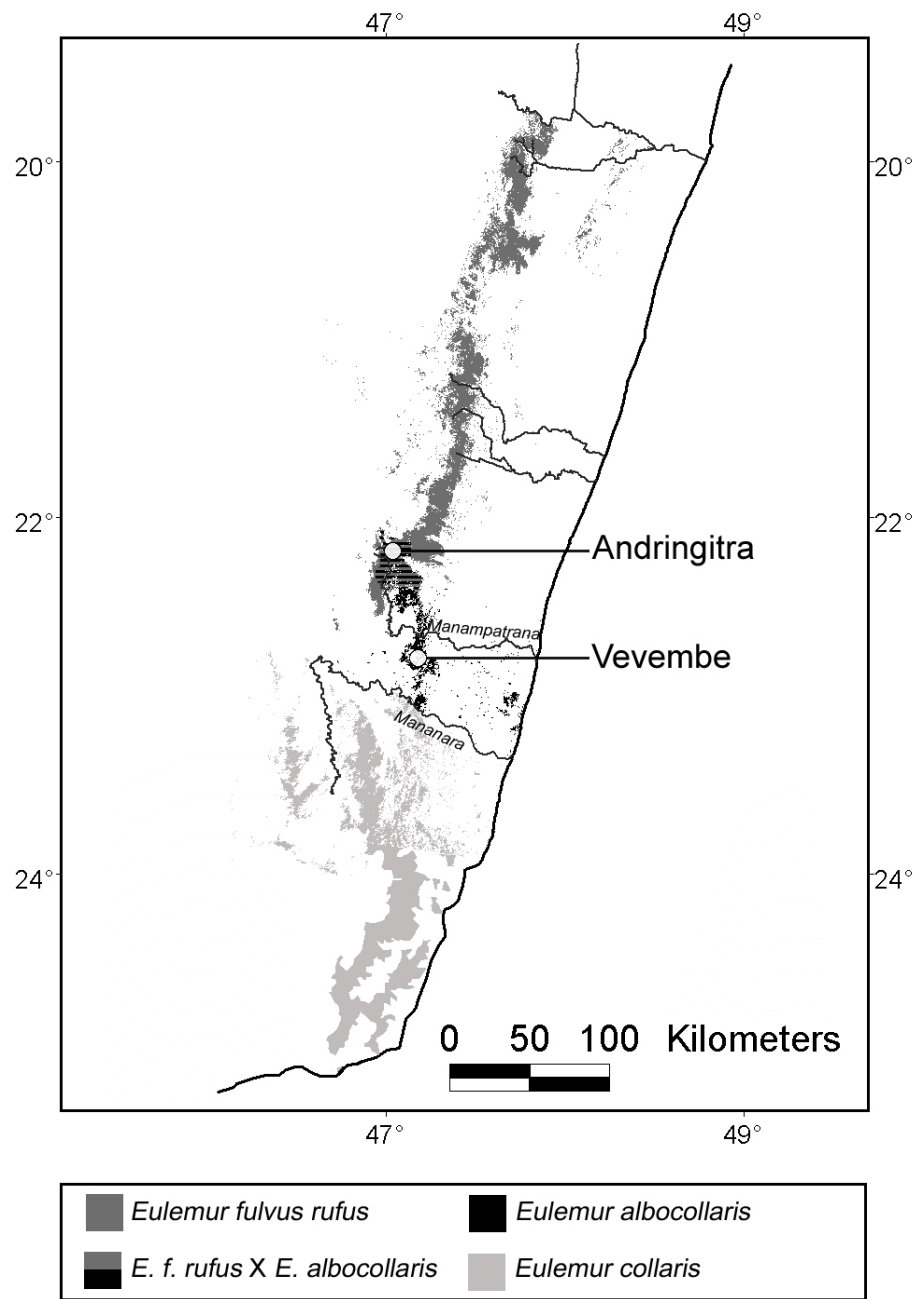


Figure 1.1: Brown Lemur Distributions and Study Sites in Southeastern Madagascar. Shaded areas represent remaining forest habitats. Major rivers near study locations are indicated in italics.



Eulemur albocollaris Female



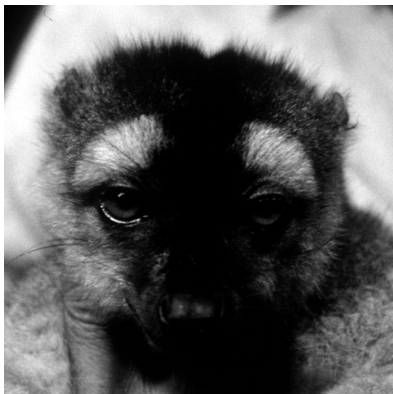
Eulemur albocollaris Male



Hybrid Female



Hybrid Male



Eulemur fulvus rufus Female



Eulemur fulvus rufus Male

Figure 1.2: Hybrid and Parental Populations of Brown Lemurs of Southeastern Madagascar. *E.f. rufus* male photo by D.J. Overdorff.

Table 1.1: Primate Communities at Andringitra, Veveombe, and Ranomafana¹

	Taxon	Ranomafana	Andringitra	Veveombe
Day-active	<i>Eulemur albocollaris</i> ²		X	X
	<i>Eulemur fulvus rufus</i> ²	X	X	
	<i>Eulemur rubriventer</i>	X	X	
	<i>Hapalemur aureus</i>	X	X	
	<i>Hapalemur griseus griseus</i>	X	X	X
	<i>Hapalemur simus</i>	X	X	
	<i>Lemur catta</i> ³		X	
	<i>Propithecus diadema edwardsi</i>	X	X	
	<i>Varecia variegata variegata</i>	X		
Nocturnal	<i>Avahi laniger</i>	X	X	X
	<i>Cheirogaleus major</i>	X	X	X
	<i>Daubentonia madagascariensis</i>	X	X	X
	<i>Lepilemur</i> sp. / <i>L. microdon</i>	X	X	X
	<i>Microcebus rufus</i>	X	X	X
Total Number of Taxa		12	13	7

¹ Ranomafana: Mittermeier et al. (1994), P. Wright (personal communication); Andringitra: Sterling and Ramarason (1996); Veveombe: personal observation.

² Note that nearly all brown lemurs sampled on the eastern slope of Andringitra are hybrids, with a few individuals showing only *E. albocollaris* markers (Wyner et al., 2002); western slope brown lemurs have been identified as *E. f. rufus* (Sterling and Ramarason, 1996).

³ *Lemur catta* is found on the arid western slope of Andringitra and is not found in the hybrid zone (Goodman and Langrand, 1996; personal observation).

Chapter 2: Sexual Dimorphism and Sperm Competition in Brown Lemurs

INTRODUCTION

Understanding the causes and socioecological implications of sexual dimorphism has been the source of extensive inquiry in primatology (e.g., Crook, 1972; Clutton-Brock et al., 1977; Leutenegger and Kelly, 1977; Leutenegger and Cheverud, 1982; Cheverud et al., 1985; Oxnard, 1987; Kay et al., 1988; Kappeler, 1990, 1991; Plavcan and van Schaik, 1992, 1994, 1997; Martin et al., 1994; Leigh, 1995; Mitani et al., 1996; Lindenfors and Tullberg, 1998; Plavcan, 1999, 2001). Morphological differences between males and females may take many forms, but shifts in body mass and canine tooth height have been the central focus of theoretical and empirical research on primates (Plavcan, 1999, 2001).

The most common explanation for sexual dimorphism is sexual selection, particularly male-male competition (Crook, 1972; Kay et al., 1988; Mitani et al., 1996; Plavcan and van Schaik, 1992, 1997; Lindenfors and Tullberg, 1998; Plavcan, 1999, 2001). It is generally perceived that primate males' fitness is limited chiefly by the ability to gain mating access to females; females are limited instead by food resources (e.g., Darwin, 1871; Emlen and Oring, 1977; Plavcan and van Schaik, 1994; Plavcan, 2001). Therefore, it is more likely that males will compete over mates, leading to the development of larger body size and canines as means of winning fights with other males over females.

Sexual dimorphism should be particularly pronounced in mating systems where males can compete directly and gain exclusive access to estrous females. Accordingly, sex differences in body size or canines should be more prevalent in mating systems with multiple females (Mitani et al., 1996; Lindenfors and Tullberg, 1998; Plavcan, 2001). There is general empirical support for this assertion, at least among haplorhines (Crook, 1972; Plavcan, 2001). The relationship is stronger when operational sex ratios (Emlen and Oring, 1977; Mitani et al., 1996) or more refined categories of competition levels are used (Kay et al., 1988; Plavcan and van Schaik, 1992, 1997).

Comparative studies of primates have identified many other potentially important causes and constraints on sexual dimorphism. These include: predation pressure and defense (DeVore and Washburn, 1963; Leutenegger and Kelly, 1977; Rowell and Chism, 1986; Plavcan and van Schaik, 1992, 1997), body size (allometry) (Clutton-Brock et al., 1977; Leutenegger and Cheverud, 1982; Cheverud et al., 1985; Plavcan and van Schaik, 1992, 1994, 1997), variance dimorphism (Leutenegger and Cheverud, 1982; Cheverud et al., 1985), correlated response (Lande, 1980), substrate use (Clutton-Brock et al., 1977; Leutenegger and Kelly, 1977), feeding ecology (Clutton-Brock et al., 1977; Milton, 1985), tendency to form agonistic coalitions (Plavcan et al., 1995), and phylogenetic inertia (Cheverud et al., 1985). Although the significance of these factors varies (and is often contested), there may be multiple variables leading to the expression of sexual dimorphism (Oxnard, 1987; Plavcan, 2001).

Canine size dimorphism is not necessarily linked allometrically with body size dimorphism (Plavcan and van Schaik, 1992, 1994). In some cases, canine size may be less constrained than body size by ecological influences (e.g., colobines; Plavcan and van Schaik, 1997; Plavcan, 2001), while in other primates, canine size and shape is constrained by dietary (e.g., pitheciines; Greenfield, 1992; Plavcan and Kelley, 1996) or other specializations (e.g., strepsirrhines; Plavcan and van Schaik, 1994).

Variation in relative testes size across primate species is indicative of another form of male-male competition: sperm competition (Short, 1979; Harcourt et al., 1981; Harvey and Harcourt, 1984; Møller, 1988; Harcourt and Gardiner, 1994; Harcourt, 1991, 1995; but see Brown, et al., 1995). When females mate with several males, the male with the most sperm may have the greatest probability of fertilization (Harcourt et al., 1981; Møller, 1988; Harcourt, 1991, 1994). Thus, under conditions where multiple partners are likely, males should be under selection pressure to increase sperm output (with testes size being a corollary) (Møller, 1988; Harcourt, 1994).

As in sexual dimorphism, the mating system most conducive to this form of male-male competition would involve multiple males and multiple females (Harcourt et al., 1981; Møller, 1988; Harcourt, 1991, 1994). Indeed, while constraints of breeding seasonality may be important, mating system better explains variation in primate sperm weight (Harcourt et al, 1995). Unlike sexual dimorphism in canines or body size, sperm competition should be more intense when precopulatory competition is insufficient for males to monopolize access to

estrous females (Harcourt et al., 1981; Krebs and Davies, 1993; Kappeler, 1997). Mating will be more promiscuous, achieved through more dispersed spacing of females, strongly bonded males (e.g. *Pan*), or other means (Harcourt et al., 1995). The expectation, then, is that increased size or canines in males and increased testes size represent alternative strategies. Therefore, the prediction is that there is an inverse relationship between dimorphism and sperm competition.

While these patterns in sexual dimorphism and levels of sperm competition have been mostly consistent in haplorhines (Harcourt et al., 1981; Harcourt, 1994; Harcourt et al., 1995; Plavcan and van Schaik, 1992, 1997; Plavcan, 1999, 2001), strepsirhine primates are a different story (Kappeler, 1990, 1991, 1996, 1997; Godfrey et al., 1993). There is a general lack of dimorphism, particularly in Malagasy strepsirhines (Kappeler, 1990, 1991, 1996; Glander et al., 1992; Plavcan and van Schaik, 1997). This includes the large-bodied subfossil lemurs (Godfrey et al., 1993). There have been some indications of “reverse” body size dimorphism (i.e., females being larger than males) (Kappeler, 1990, 1991) and canine size dimorphism (Kappeler, 1996). Slight canine dimorphism favoring males also occurs rarely in the lemurid and lepilemurid lineages (Kappeler, 1996).

Despite the presence of multi-female groups and potentially intense male-male competition, there are no consistent correlations between mating systems and dimorphism patterns in lemurs (Kappeler, 1996; van Schaik and Kappeler, 1996; Wright, 1999). Explanations for this deviation from typical haplorhine patterns include Madagascar’s extreme seasonality, hypometabolism, female

dominance, pair-bonding within multi-male groups, activity patterns, narrow birth seasonality, or combinations thereof (Richard, 1992; Godfrey et al., 1993; van Schaik and Kappeler, 1993; Wright, 1999). In addition, Kappeler (1996) suggests that speed and agility may be more important than size and weaponry in male competition. There may also be powerful developmental constraints on sexual dimorphism. According to Leigh and Terranova (1998), the expression of dimorphism may be constrained by selection for extremely rapid growth rates, giving males less time to grow to larger sizes.

More in accord with haplorhines, lemurs generally demonstrate the expected relationships between sperm competition and mating systems (Glander et al., 1992; Kappeler, 1996; Pochran et al., 2002; Pochran and Wright, 2002). Those species with multi-male/multi-female social groups tend to show evidence of sperm competition, with larger testes size relative to pair-living strepsirhines (although not relative to solitaries) (Kappeler, 1997). Thus, with constraints on dimorphism, postcopulatory competition may be more prevalent in group-living lemurs (Kappeler, 1997; Pochran and Wright, 2002).

In this chapter, I will examine patterns of sexual dimorphism and sperm competition in populations of brown lemurs. Brown lemurs generally maintain characteristics consistent with relatively strong male-male competition. They are sexually dichromatic (Tattersall, 1982), suggesting that sexual selection (female choice, at least) is operating. Group structure is multi-female and breeding is highly seasonal (Overdorff, 1998; Overdorff et al., 1999; Gerson, 2000). Unlike many Malagasy primates, brown lemurs are not female dominant (Pereira et al.,

1990) and evidence is lacking for monogamous breeding pairs within social groups (Overdorff, 1998; Ostner and Kappeler, 1999; Gerson, 2000). Their diet is generally frugivorous, although folivory is more prevalent in some populations (Sussman, 1977; Overdorff, 1993; Freed, 1996; Vasey, 2000). Moreover, some instances of significant canine dimorphism (favoring males) have been noted in this diverse group, including *Eulemur fulvus albifrons* (Kappeler, 1996) and *E. f. rufus* (Gerson, 1999, 2000; but see Glander et al., 1992).

Relatively little is known about the morphology of *Eulemur albocollaris*, a brown lemur group now considered to be a distinct species (Djlelati et al., 1997; Wyner et al., 1999). However, preliminary research indicates potential canine dimorphism in this taxon (Bradley and Stumpf, 1997). Accordingly, I will further investigate this relatively rare trait by comparing *E. albocollaris* to other closely related brown lemur populations. The comparative sample includes populations of *E. fulvus rufus* (Overdorff, unpublished data; Merenlender, unpublished data), as well as *E. albocollaris* X *E. fulvus rufus* hybrids. The closely related set of populations has the particular advantage of controlling for phylogenetic effects that may impact dimorphism (e.g., Cheverud et al., 1985). The goal of this analysis is to compare levels of dimorphism and testes size and to investigate the relationship between these morphological characters to variation in mating systems and ecology.

METHODS

Study Animals and Sites

I collected morphometrics data on brown lemur populations at Andringitra National Park and Vevembe Forest (Figure 2.1). At Vevembe, I sampled white-collared lemurs (*Eulemur albocollaris*). Andringitra study animals were hybrids of *E. albocollaris* and red-fronted lemurs (*E. fulvus rufus*) (Johnson and Wyner, 2000; Wyner et al., 2002). Capture and measurement at Andringitra was conducted from March-August 1999. At Vevembe, animals were captured in April 2000 (Table 2.1). Only adults and sub-adults were captured (Andringitra: N = 16; Vevembe: N = 11); not all measurements were all collected for all individuals (Table 2.1).

For a more effective regional and taxonomic comparison, additional datasets were used in most analyses. These included data from the eastern rain forest site of Ranomafana National Park (Figure 2.1) on *E. f. rufus* (A Merenlender, unpublished data; D Overdorff, unpublished data; N = 38 individuals). Some individuals within these samples are included in the Glander et al. (1992) study. However, I selected the unpublished datasets because they included additional characters (i.e., maxillary canine height) necessary for this study; moreover, Glander et al. (1992) include some results (i.e., inflated testes volume scores) that make cross-population comparisons difficult. Finally, to increase sample sizes, I included data collected by B Bradley, R Stumpf, and P Wright in 1996 on *E. albocollaris* at Vevembe (N = 12) (Bradley and Stumpf,

1997) and by R Stumpf and R Kitko in 1997 on *E. albocollaris* at Vevembe (N = 6) and hybrids at Korokoto, Andringitra (N = 5).

Capture and Measurement Procedures

Capture and morphometrics procedures followed K Glander and colleagues (Glander et al., 1992; Glander, 1993). The animals were darted with a Pneu-Dart™ (Pneu-Dart, Inc., Williamsport, PA 17701) CO₂ powered rifle using disposable non-barbed 9 mm darts. The anesthetic/tranquilizer Telazol™ (equal parts tiletamine hydrochloride and zolazepam hydrochloride; A. H. Robbins, Richmond, VA 23220) was used to immobilize the animals. The dosage was set at 20 mg/kg (i.e., 50 mg for adult brown lemurs).

During immobilization, each animal was measured using techniques modified from Glander et al. (1992). The measurements included:

- 1) body weight (kg);
- 2) body length (mm);
- 3) tail length (mm);
- 4) hindlimb length (mm);
- 5) foot length (mm);
- 6) forelimb length (mm);
- 7) hand length (mm);
- 8) testicle width and length (mm);
- 9) maxillary canine height (C) (mm); and
- 10) mandibular second (caniniform) premolar height (p2) (mm).

For the present analysis, the only characters considered in depth are: body weight, maxillary canine height, and (for males) testes measurements. However, a summary of other morphometrics is also included for the Andringitra and Vevembe data collected in 1999 and 2000, respectively. For all characters except testes morphometrics, left side measurements were taken only when right side equivalents were unavailable (e.g., in the case of a broken right canine).

For both right and left sides, testes length (L) and width (W) were converted to volume (V) using the following formula:

$$V = \frac{4}{3}\pi\left(\frac{1}{2}L\right)\left(\frac{1}{2}W^2\right)$$

The mean volume (cm^3) for left and right testes was then divided by body weight (kg) to yield the gonadosomatic index (GI) (Pochran and Wright, 2002; Pochran et al., 2002). To examine variation according to reproductive period, I sorted testes volume and GI measures into two seasons: mating season (April-June, centered on the short mid-May breeding season; Overdorff, 1998) and non-mating season (July-March). The mating season data were used for comparison with previous research on strepsirhine testes volume (Kappeler, 1997).

Statistical Techniques

For comparisons within and between populations, I used nonparametric statistics, including Kruskal-Wallis and Mann-Whitney U tests. To determine the independence of body size and canine height, I calculated least-squares regressions using all samples (including those from other studies). Separate correlations were tested for all individuals, for males only, and for females only. In addition, I analyzed differences in sexual dimorphism in body weight and

maxillary canine height across populations, as well as significant departure from monomorphism. For these tests, I used a nonparametric bootstrapping technique, producing 9,999 pseudo-samples with replacement for dimorphism ratios (expressed as male values divided by female values). I then determined 95% confidence limits for dimorphism ratios from this generated sample. For all statistical tests, significance was set at $\alpha = .05$.

RESULTS

Morphometrics Summary

General morphometrics data collected for the present study from Andringitra (1999) and Vevembe (2000) are presented in Tables 2.1-2.2. These samples were too small to compare statistically and, thus, are only presented as summaries. Body weight, canine height, and testes volume are discussed in more detail below.

Canine Height-Body Weight Relationship

Maxillary canine height and body mass were not closely linked in the total sample of brown lemurs from Andringitra, Vevembe (present study; Bradley and Stumpf, 1997; R Stumpf and R Kitko, unpublished data), and Ranomafana (A Merenlender, unpublished data; D Overdorff, unpublished data) (Figure 2.2). The correlations are not significant for the combined sample ($R^2 = .0126$; $P = .3735$ NS), for males ($R^2 = .0516$; $P = .1644$ NS), or for females ($R^2 = .0019$; $P = .8335$ NS). Based on these results, canine height measures were compared without body size correction.

Body Mass

There were shifts in body weight across sexes and populations (Figure 2.3). Within populations, there were no significant differences between the sexes in *E. albocollaris* ($Z = - .420$; $P = .6743$ NS) or the *E. albocollaris* X *E. f. rufus* hybrids ($Z = - .133$; $P = .8943$ NS). There are, however, significant differences between males and females in the *E. f. rufus* population ($Z = - 2.232$; $P = .0256$) with females (2.32 kg) outweighing males (2.16 kg) (Table 2.3). There was also variation among populations in body mass in females ($H = 6.779$; $P = .0337$), but not in males ($H = 1.311$; $P = .5192$ NS). *E. f. rufus* females were significantly larger (2.29 kg) than either of the other populations (Table 2.3). To control for variation in body weight due to reproductive state, the three sites were compared using only female capture data collected during the likely period of pregnancy (June-September; Overdorff et al., 1999; Overdorff, personal communication). Variation among sites remained significant ($H = 5.926$; $P = .05$), again with Ranomafana females (mean = 2.289 kg) outweighing those at Andringitra (2.05 kg) and Vevembe (2.217 kg). However, the differences between Ranomafana and Vevembe females during the pregnancy period were not significant ($Z = -1.658$; $P = .0974$ NS).

Canine Height

There were different patterns for maxillary canine height across populations (Figure 2.4). Within populations, there were significantly larger canines in males in *E. albocollaris* ($Z = -3.046$; $P = .0023$). The hybrids at Andringitra followed this trend, but were excluded from statistical tests due to

sample size ($N = 4$ for this character). By contrast, *E. f. rufus* showed no sex differences in canine height ($Z = -.636$; $P = .525$ NS). Females of *E. albocollaris* and *E. f. rufus* did not differ ($Z = -.483$; $P = .6292$ NS). In males, there was significant variation between groups ($Z = -4.365$; $P < .0001$). This was due to the large canines of *E. albocollaris* males (10.9 mm) (Table 2.3).

Sexual Dimorphism

Another means of examining the variation in mean dimorphism across groups is to compare dimorphism ratios (expressed as male means divided by female means). Figure 2.5 depicts mean body mass dimorphism, including 95% confidence limits generated by bootstrapping techniques. The confidence limits are also shown to determine significant deviation from monomorphism and significant differences in dimorphism ratios across groups. Most populations in this analysis were monomorphic and there were no major differences among populations (Figure 2.5). However, *E. f. rufus* demonstrated significant body size dimorphism favoring females (Figure 2.5). Reproductive state again may confound these results. There are insufficient data to test for the effects of pregnancy in this population as all captures were conducted during June-September. However, Ranomafana females sampled during the first month of pregnancy (June) were actually heavier than those from subsequent months ($Z = -2.534$; $P = .0098$), suggesting that pregnancy alone may not be driving the sex differences in body weight in this taxon. Canine height dimorphism also varied across groups (Figure 2.6). *E. albocollaris* showed significant dimorphism

favoring males (with hybrids following this trend), while *E. f. rufus* were monomorphic for canines (Figure 2.6).

There are indications of common trends when the patterns for body mass and canine height dimorphism are examined together. There appeared to be a link between the degree of body size dimorphism and the extent of canine dimorphism. In examining Figures 5-6, all populations appeared to shift in tandem. For example, *E. f. rufus* demonstrated a shift favoring females (i.e., to the left) relative to the other populations in both body mass and canine height – resulting in female-biased dimorphism in body size and monomorphism in canines.

Testes Volume

There was evidence for temporal variation across populations in testes volume, represented by the gonadosomatic index (GI) (Figure 2.7). Testes volume was significantly larger during the breeding season in *E. f. rufus* males ($Z = -2.030$; $P = .0423$). Seasonal variation fell short of significance in hybrids ($Z = -1.757$; $P = .0790$ NS) and *E. albocollaris* ($Z = -1.135$; $P = .2566$ NS). While there were no statistical differences across populations in either the mating ($H = 1.362$; $P = .5061$ NS) or non-mating seasons ($H = 2.201$; $P = .3328$ NS), *E. albocollaris* had the largest overall relative and absolute testes size (Table 2.3).

DISCUSSION

Despite the close taxonomic affinities among the brown lemur groups considered in this study, there was notable variation in body size, canine height, and the extent of sex differences in these characters. The existence of significant

canine size dimorphism favoring males in *E. albocollaris* (and likely the hybrids as well) is remarkable considering the rarity of this trait in the Lemuriformes (Kappeler, 1996). Larger canines in males are most commonly associated with sexual selection (i.e., male-male competition over mates; e.g., Crook, 1972; Leutenegger and Kelley, 1977; Kay et al., 1988; Greenfield, 1992; Plavcan and van Schaik, 1992). Also noteworthy is the significant body size dimorphism favoring females recorded in *E. f. rufus*, a very unusual characteristic for lemurs (Kappeler, 1991) and for primates in general (e.g., Clutton-Brock et al, 1977; Cheverud et al., 1985; Crook, 1972; Plavcan and van Schaik, 1997). There was also variation in testes volume among these brown lemur groups – but all populations exhibited large testes size compared to other lemurs (Kappeler, 1997), consistent with high levels of sperm competition.

The dimorphism trends among the brown lemur taxa in this study are particularly striking when compared to closely related populations from western Madagascar (Gerson, 1999, 2000). At Anjamena, Gerson (1999, 2000) found that both male (1.78 kg) and female (1.84 kg) *E. f. rufus* were smaller than their eastern counterparts. The larger body weights for eastern brown lemurs in this study (see Table 2.3) corroborate Gerson's (1999, 2000) findings. Previous studies on ecogeographic variation in Madagascar have also demonstrated that eastern rain forest lemurs are larger than those from drier habitats in western Madagascar (Albrecht, et al., 1990; Godfrey et al., 1990). Gerson (1999, 2000) also found significant sex differences in canine height, with larger canines in males, while body size dimorphism was absent. These trends mirror those in *E.*

albocollaris and the hybrids in the present study but *not* those in eastern *E. f. rufus*. Thus, dimorphism patterns in brown lemurs do not appear to be related to allometric scaling (similar levels of dimorphism occur in large- and small-bodied populations) or phylogeny (similar trends occur in more distantly related groups).

As noted, while most groups in this study were monomorphic in body weight, *E. f. rufus* females from Ranomafana were significantly larger than males (and females of other populations) apparently independent of the effects of reproductive state. The differences in both sexes across populations stress the point that sexual dimorphism is often the result of variation in both males and females (Leigh, 1995; Plavcan et al., 1995; Plavcan, 2001). Size dimorphism favoring females is extremely rare, even among female-dominant lemuroids (Kappeler, 1990, 1991). However, significant sex differences in body mass favoring females have been recorded in *Microcebus murinus* (Kappeler, 1991), and non-significant tendencies for larger females have been recorded in *Propithecus diadema* (Kappeler, 1991; Glander et al., 1992), *Indri indri* (Powzick, 1997), and in a slightly smaller (yet overlapping) sample of *E. f. rufus* from Ranomafana (Glander et al., 1992). The differences between the latter study and the present one in statistical significance underscore potential problems due to sampling issues, including sample size (Kappeler, 1991) and age structure of sample populations (Godfrey et al., 2002).

Different yet complementary patterns were observed in canine height across brown lemur populations. Both *E. albocollaris* and the hybrids demonstrated slight dimorphism favoring males. These results concur with

previous studies indicating a relatively high frequency of canine dimorphism in the Lemnridae, including *E. f. albifrons*, *E. mongoz*, *Lemur catta* (Kappeler, 1996), and western *E. f. rufus* (Gerson, 1999, 2000). It should be pointed out that dental measures are particularly vulnerable to error due to biases in age structure (due to pronounced wear in older individuals) (Godfrey, et al., 2002). Yet, there was no indication of age bias according to sex in these populations. Interestingly, levels of canine dimorphism appeared to shift in conjunction with body size dimorphism: Ranomafana *E. f. rufus* was the only population lacking canine dimorphism favoring males and the only group maintaining body size dimorphism favoring females (see Figures 5-6).

There were also some indications of seasonal differences in testes volume across populations. Gonadosomatic index increased during the breeding season across groups, significantly in *E. f. rufus* males from Ranomafana. *E. albocollaris* had the largest absolute and relative testes volume of these groups. These results accord well with analyses across strepsirhines (Kappeler, 1997). Figure 2.8 demonstrates gonadosomatic indices in lemurids, calculated from Kappeler (1997). Kappeler used different methods to measure relative testes size and, thus, results are not identical. However, the brown lemur populations from this study fall in with other multi-male/multi-female lemurids where sperm competition is expected to be stronger (Harcourt et al., 1981; Møller, 1988; Harcourt, 1991, 1994; Kappeler, 1997). For example, *Lemur catta* is known to mate promiscuously (Sauther, 1991; Sussman, 1992). *Eulemur macaco* has a dispersed, fission-fusion social system wherein access to females may be difficult

for males to control directly (Colquhoun, 1997). These species maintain the highest GI among lemurids (Kappeler, 1997), and it is noteworthy that *E. albocollaris* falls in just behind these taxa (Figure 2.8; see below).

These observations of sexual dimorphism in canines, as well as the high testes size values, may have important implications for the behavioral ecology of these populations. These findings corroborate other analyses suggesting the brown lemur group as a whole exhibits male-biased canine dimorphism (see also Kappeler, 1996; Gerson, 1999, 2000), with the sole known exception being *E. f. rufus* at Ranomafana. While many factors may be involved in producing or constraining sex differences in morphology (Plavcan, 2001), sexual dimorphism is typically associated with elevated levels of male intrasexual competition, generally over access to estrous females (Darwin, 1871; Crook, 1972; Emlen and Oring, 1977). Such expressions of dimorphism and potential intrasexual competition are extremely rare in Malagasy primates (Kappeler, 1990, 1991, 1996; Wright, 1999). As noted, selection for rapid growth rates may inhibit the development of body size dimorphism in lemurs (Leigh and Terranova, 1998), which may help explain the lack of size differences in brown lemurs (again, excepting eastern *E. f. rufus*).

Yet, the larger canines in brown lemur males imply strong male-male competition relative to other lemurs. The multi-male social structure common in brown lemurs is generally an important precondition for more intense intrasexual competition (Crook, 1972; Emlen and Oring, 1977; Mitani et al., 1996). Moreover, unlike many lemur species, brown lemurs are not female dominant

(Pereira et al., 1990; Overdorff and Johnson, in press); the absence of female dominance in these taxa may release important constraints on sexual dimorphism in canine weaponry (but see Kappeler, 1996 for male-biased canine dimorphism in female-dominant *Lemur catta*). Although intragroup aggression among males (or females) is uncommon in the study populations of brown lemurs (e.g., only .03 fights/hour in *E. albocollaris*; unpublished data), these findings of significant canine dimorphism in the brown lemur species group warrant more direct observation of the use of canines in male interactions in these taxa (e.g., bluffs and displays; see also Pereira and Kappeler, 1997).

While the above patterns may apply to brown lemurs as a group, it is also important to take into account the variation observed *within* this group. Does the variation in body size dimorphism, canine dimorphism, and testes volume, correlate with shifts in behavior or ecology? As the study populations are closely related, they may be expected to be broadly similar in socioecology (see Overdorff, 1991, 1993, 1996a, 1996b; Overdorff, et al., 1999; Chapters 5-6). Therefore, I have isolated three factors that are known to vary across populations of *E. albocollaris*, hybrids (Chapters 5-6), and eastern *E. f. rufus* (Overdorff, 1991, 1993), as well as western *E. f. rufus* (Sussman, 1974, 1977; Gerson, 2000) (Table 2.4). These include aspects of diet, levels of intergroup agonism, and social organization (Sussman, 1974; 1977; Overdorff, 1991, 1993; Gerson, 2000).

The first factor considered is the degree of folivory. In some small-bodied folivores, sexual dimorphism in body size may be minimized (Plavcan, 1999). For example, in colobines, there may be a balance of selection pressures acting on

body size: selection to maximize body size for increased digestion efficiency, but with limits imposed by locomotor constraints (Leutenegger and Kelley, 1977; Plavcan, 1999). These pressures may restrict the expression of body size dimorphism, but canine dimorphism may still be strong (Plavcan, 1999). While several of the brown lemur groups fit this pattern of canine dimorphism and body size monomorphism, folivory does not appear to be associated with dimorphism in the brown lemurs considered here. The highly folivorous and small-bodied western *E. f. rufus* (Sussman, 1974, 1977) lack body size dimorphism and do demonstrate canine dimorphism (Gerson, 1999, 2000). Yet, similar patterns of dimorphism are evident in the hybrids and *E. albocollaris*, both of which rarely consume leaves (Chapter 5).

The next variable is the nature of intergroup interactions within populations. None of these populations is territorial in the strictest sense (cf. Mitani and Rodman, 1979; Lawes and Henzi, 1995; see Sussman, 1974; Overdorff, 1991; Chapter 6). However, *E. f. rufus* at Ranomafana are known to engage in agonistic encounters with rival groups, including over food resources (Overdorff, unpublished data). Moreover, rates of aggression in intergroup encounters are twice those in *Eulemur albocollaris* at Vevembe or in hybrid groups at Andringitra (Chapter 6). As feeding resources are likely more important for females, groups with a high incidence of intergroup conflict may be expected to have larger females with larger canines relative to groups where fighting over resources may be less intense. This indeed appears to be the case for eastern *E. f. rufus*. However, it is also plausible that western *E. f. rufus*

populations only differ from those in the humid eastern forests because females are disproportionately affected by the stressful ecological conditions in western Madagascar that tend to reduce body size (Albrecht et al., 1990; Godfrey et al., 1990, Gerson, 1999, 2000).

Finally, these brown lemur populations differ in cohesiveness and spatial proximity (i.e., the presence of fission-fusion social structure) (Sussman, 1974; Overdorff, 1991; Chapter 6). *E. albocollaris* is one of the few lemurs known to be regularly fission-fusion (Overdorff and Johnson, in press; Chapter 6). This would imply less potential for direct male-male competition (producing dimorphism) and greater impetus for sperm competition. Thus, the relatively high degree of canine dimorphism in this population may not be related to fission-fusion structure. However, the results showing large relative testes volume fit well with the possibility of sperm competition operating in this species. Again, the only lemurid species with higher GI scores, *Lemur catta* and *E. macaco* (Kappeler, 1997), are promiscuous breeders or maintain fission-fusion social structure, respectively (Sauther, 1991; Sussman, 1992; Colquhoun, 1997). Kappeler (1997) found *Varecia variegata* (another fission-fusion species; e.g., Morland, 1991; Vasey, 1997) also has large testes volume. It is noteworthy that the other populations in this study also show relatively large and seasonally variable testes, suggesting sperm competition may be strong in all of these brown lemurs.

In conclusion, there is clear variation among closely related populations of brown lemurs in sexual dimorphism and testes volume, unrelated to allometry or

phylogeny. In addition, there were indications of a link between trends in body size dimorphism and canine size dimorphism. As in previous studies of lemurs (e.g., Kappeler, 1996), variability in dimorphism trends within this brown lemur group are difficult to associate clearly with socioecology – except perhaps the association between larger females and resource defense. However, the presence of significant, male-biased canine dimorphism in nearly all brown lemur populations suggests generally high levels of male-male competition in this species complex. Finally, there is also evidence for sperm competition acting in all of these populations – especially the fission-fusion *E. albocollaris* – indicating postcopulatory competition is important across brown lemur groups, as in many other multi-male/multi-female lemuroids (Kappeler, 1997; Pochran et al., 2002; Pochran and Wright, 2002).

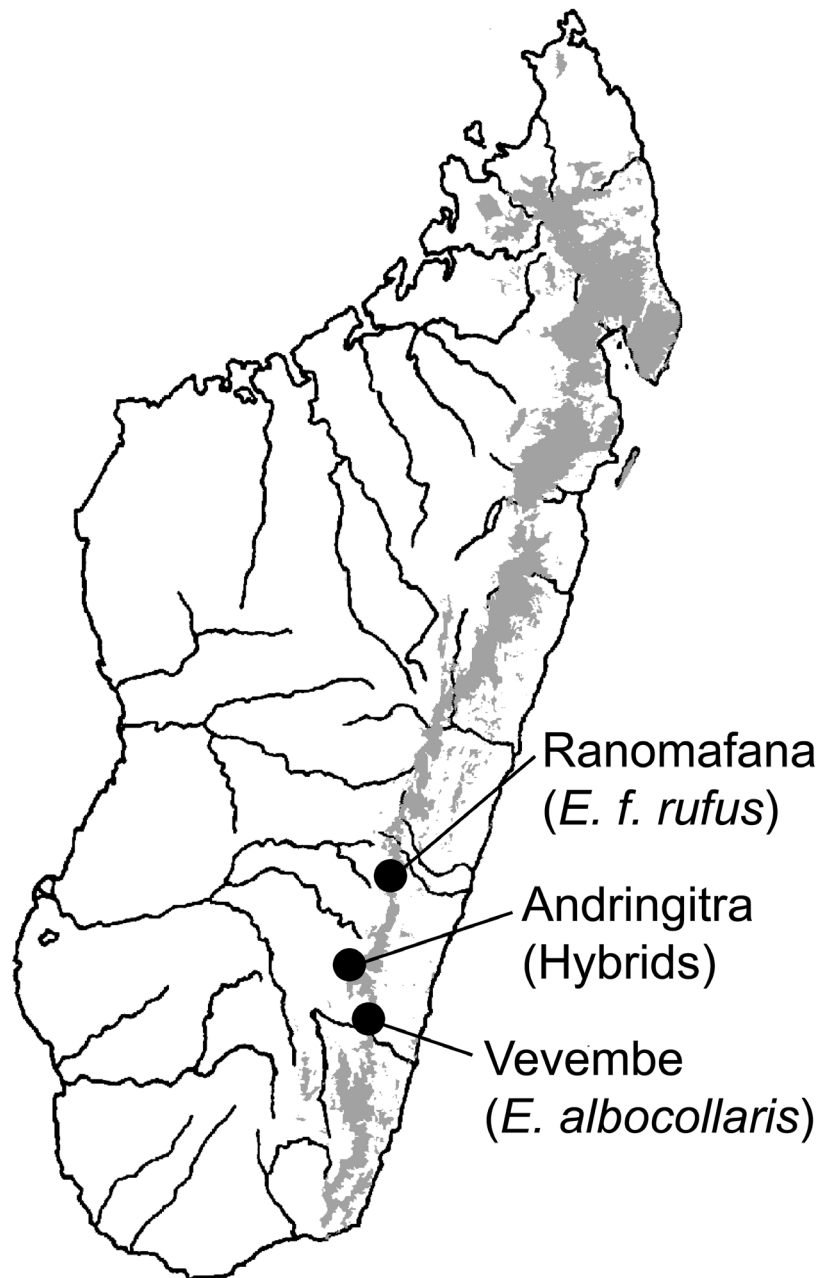


Figure 2.1: Brown Lemur Sampling Sites. Shaded regions represent remaining rain forest habitats of the north and east.

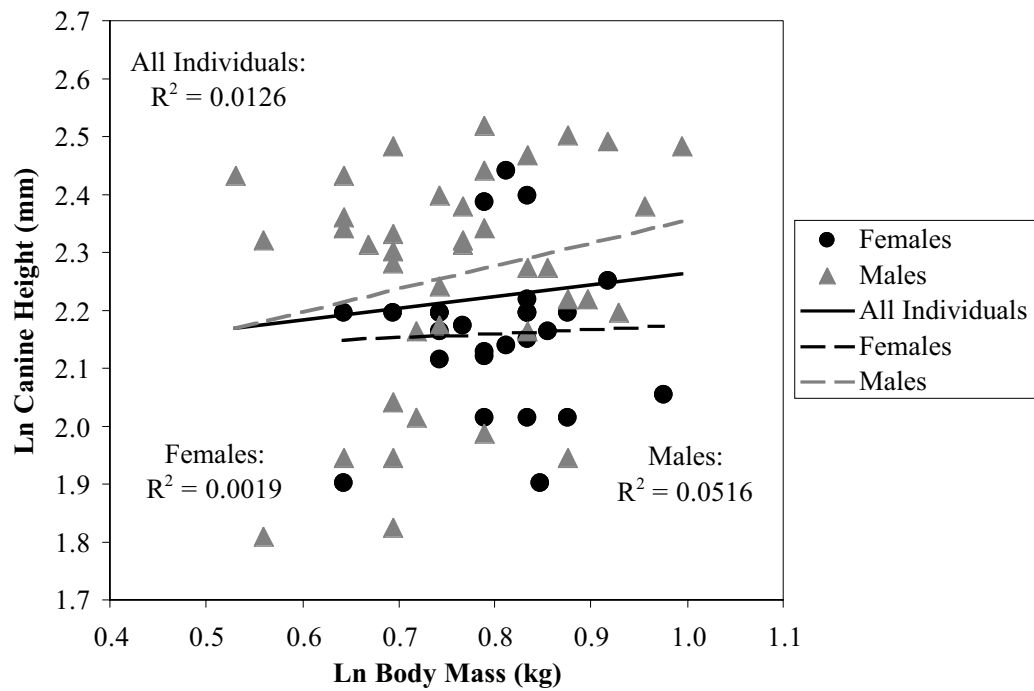


Figure 2.2: Relationship Between Canine Height and Body Mass. Dashed lines are the regression lines for females (black) and males (gray).

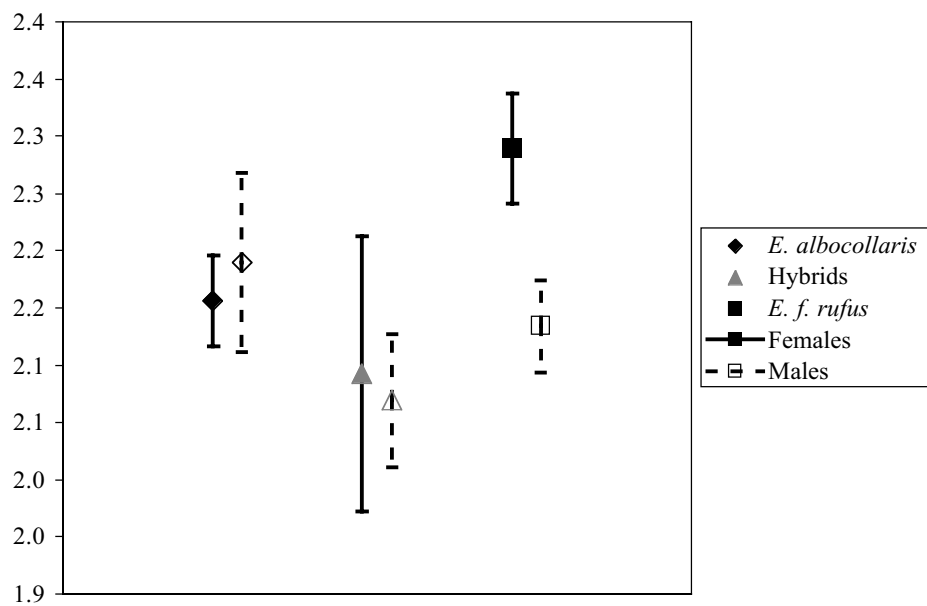


Figure 2.3: Body Mass (kg) Across Populations.

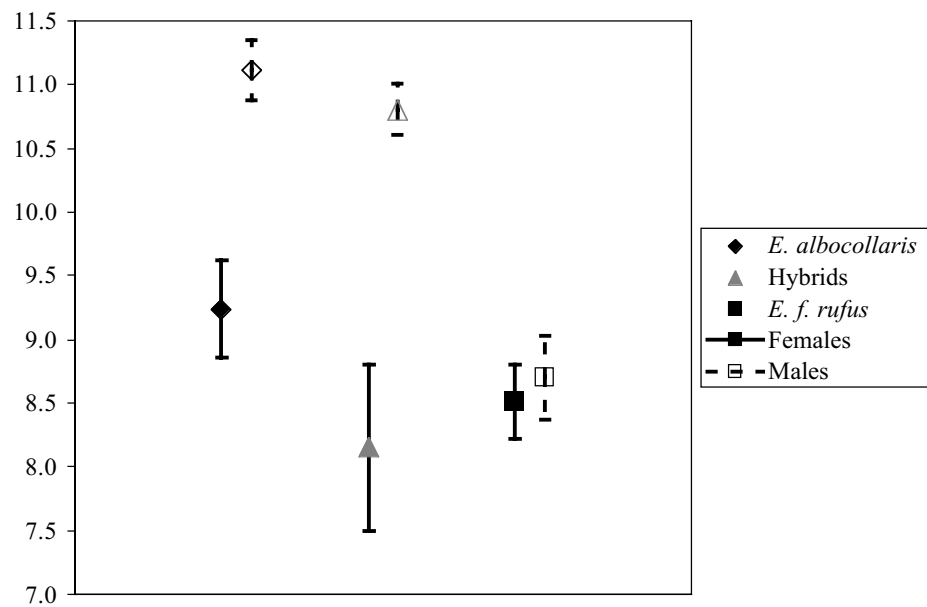


Figure 2.4: Maxillary Canine Height (mm) Across Populations.

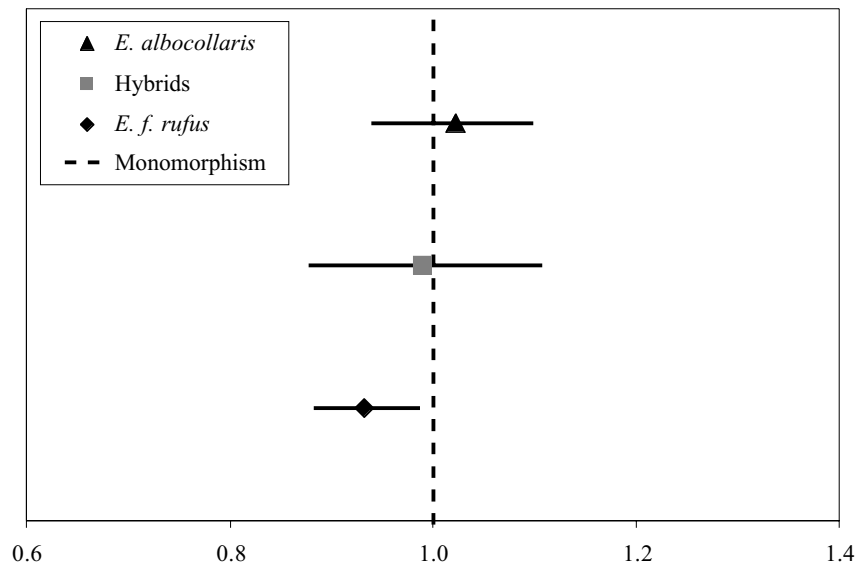


Figure 2.5: Body Size Dimorphism Across Populations. Horizontal lines indicate 95% confidence limits.

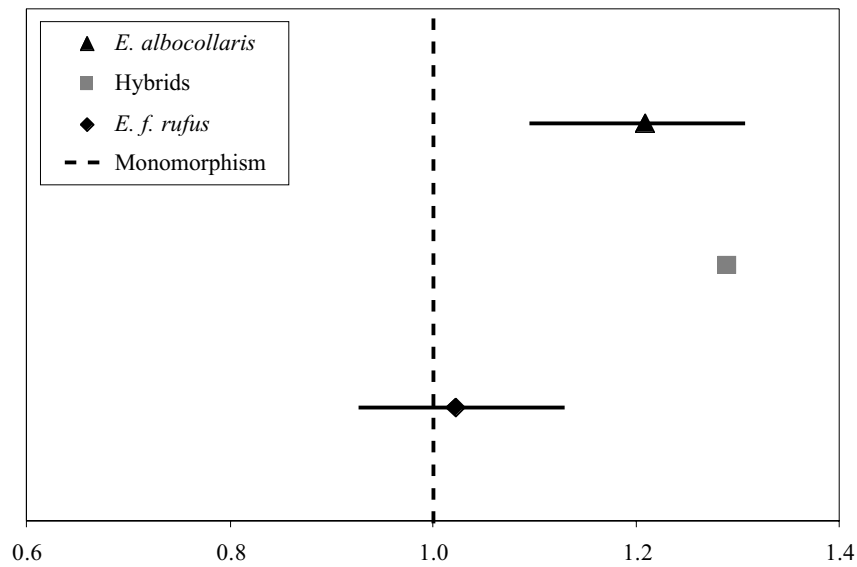


Figure 2.6: Canine Height Dimorphism Across Populations. Horizontal lines indicate 95% confidence limits. Hybrid limits are excluded.

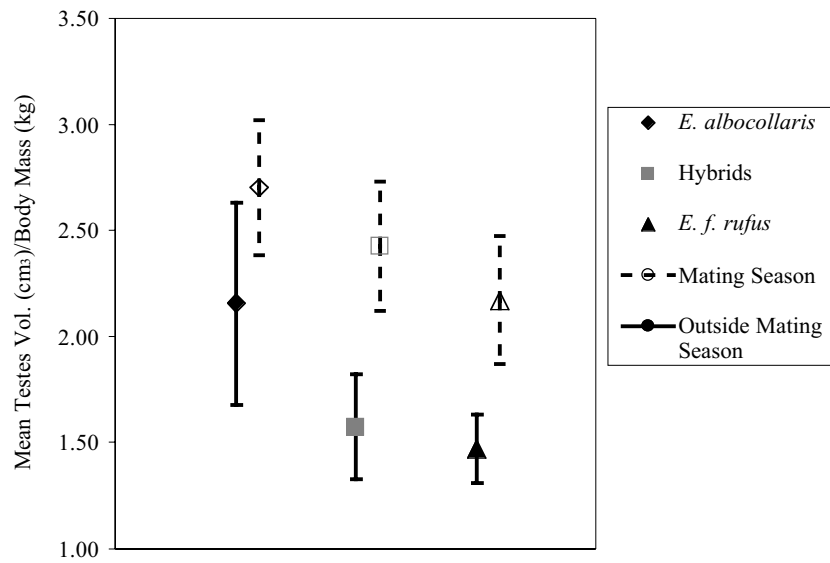


Figure 2.7: Gonadosomatic Index (GI) Across Populations and Seasons. Mating season category includes animals captured April-June.

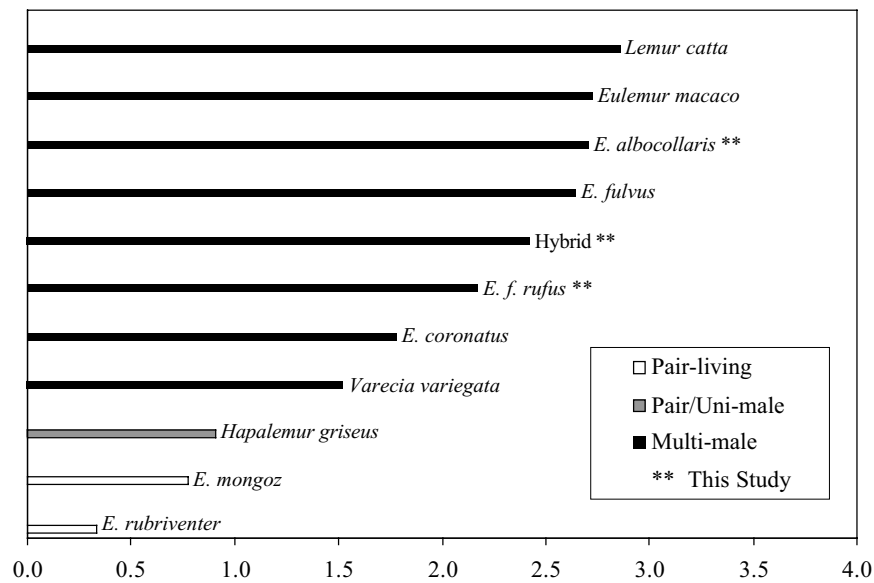


Figure 2.8: Gonadosomatic Index (GI) in the Lemurids. Data are from mating seasons only. Unless indicated by the double asterisk (**), data are from Kappeler (1997).

Table 2.1: Morphometrics for Brown Lemurs at Andringitra and Vevembe (1999-2000 only).

ID	Species	Sex	Age ¹	Date	Weight (kg)	Body (mm)	Tail (mm)	Hind Limb (mm)	Foot (mm)	Fore Limb (mm)	Hand (mm)	Testes (mm ³)	Maxil. Canine (mm)	Mand. p2 (mm)
Am-01	Hybrid	F	A	3/99	2.60	330	570	360	95	251	75	--	--	--
Am-03	Hybrid	F	A	3/99	1.90	417	540	342	92	211	71	--	--	--
Am-04	Hybrid	F	A	3/99	1.90	368	572	282	94	191	60	--	--	--
Pa-01	Hybrid	F	A	8/99	1.80	401	605	307	75	256	61	--	--	--
Am-05	Hybrid	M	A	3/99	2.20	360	490	320	93	240	72	9,534	--	--
Am-06	Hybrid	M	A	3/99	2.30	391	642	372	98	330	76	8,021	--	--
Am-07	Hybrid	M	A	3/99	2.40	382	570	333	96	221	70	15,237	--	--
Am-09	Hybrid	M	A	3/99	2.20	429	541	350	72	232	64	7,083	--	--
Am-10	Hybrid	M	A	5/99	1.80	370	570	320	91	230	68	8,252	--	--
Am-11	Hybrid	M	A	5/99	2.10	371	590	333	99	232	61	8,333	--	--
Am-12	Hybrid	M	A	5/99	2.20	390	550	341	94	204	72	13,258	--	--
Pa-02	Hybrid	M	A	8/99	1.90	400	550	251	100	155	68	6,035	--	--
Pa-03	Hybrid	M	A	8/99	2.00	430	542	221	79	141	71	3,041	--	--
Pa-04	Hybrid	M	A	8/99	1.65	440	570	260	71	171	63	2,566	--	--
Am-02	Hybrid	F	SA	3/99	1.55	490	480	290	83	203	58	--	--	--
Ve-11	<i>E. albocollaris</i>	F	A	4/00	2.10	342	500	270	101	214	70	--	8.3	5.5
Ve-1	<i>E. albocollaris</i>	M	A	4/00	2.15	334	498	271	98	193	74	18,393	10.8	5.5
Ve-3	<i>E. albocollaris</i>	M	A	4/00	2.70	351	403	293	104	200	75	15,866	12	6.7
Ve-5	<i>E. albocollaris</i>	M	A	4/00	2.20	--	--	--	--	--	--	--	--	--
Ve-6	<i>E. albocollaris</i>	M	A	4/00	2.40	366	545	271	107	225	72	15,782	9.2	4.9
Ve-7	<i>E. albocollaris</i>	M	A	4/00	2.15	--	--	--	--	--	--	--	--	--
Ve-8	<i>E. albocollaris</i>	M	A	4/00	2.60	362	590	269	107	219	77	--	10.8	5.1
Ve-10	<i>E. albocollaris</i>	M	A	4/00	2.50	361	532	281	107	218	71	13,839	12.1	5.2
Ve-4	<i>E. albocollaris</i>	F	SA	4/00	1.70	335	567	295	104	219	75	--	6.5	4.9
Ve-9	<i>E. albocollaris</i>	M	SA	4/00	1.75	310	493	277	105	200	73	1,386	6	5.1

¹ A = adult; SA = sub-adult.

Table 2.2: Means and Standard Error (SE) for Adult Brown Lemur¹.

Species	Sex	N		Weight (kg)	Body (mm)	Tail (mm)	Hind Limb (mm)	Foot (mm)	Fore Limb (mm)	Hand (mm)	Maxil. Canine Height (mm)	Mand. p2 (mm)	Testes (mm ³)
<i>E. albocollaris</i>	F	1	Mean	2.10	342	500	270	101	214	70	8.3	5.5	--
			SE	--	--	--	--	--	--	--	--	--	--
<i>E. albocollaris</i>	M	6	Mean	2.42	355	514	277	105	211	74	11.0	5.5	15,971
			SE	0.09	5.8	31.3	4.5	1.7	6.1	1.1	0.5	0.3	933.6
Hybrids	F	4	Mean	2.05	379	572	323	89	227	67	--	--	--
			SE	0.18	19.3	13.3	17.5	4.7	15.7	3.7	--	--	--
Hybrids	M	10	Mean	2.07	396	562	310	89	216	69	--	--	8,136
			SE	0.07	8.9	12.3	15.5	3.5	16.9	1.5	--	--	1,252.5

¹ Morphometrics at Andringitra and Vevembe (1999-2000 only).

Table 2.3: Mean Body Weight, Canine Height, Dimorphism Ratios, and Gonadosomatic Index (GI) Across Populations.

Species	Site		N	Body Weight (kg)	Body Wt. Dimorph. (M:F)	Canine Height (mm)	Canine Dimorph. (M:F)	GI Mating Season	GI Non-mating Season
<i>E. albocollaris</i>	Vevembe ^{1,2,3}	Males	15	2.19	1.02	10.9	1.21	2.70	2.16
		Females	9	2.14		9.1		--	--
Hybrids	Andringitra ^{1,3}	Males	13	2.07	0.99	10.6	1.29	2.43	1.58
		Females	6	2.09		8.2		--	--
<i>E. f. rufus</i>	Ranomafana ^{4,5}	Males	23	2.13	0.93	8.7	1.02	2.18	1.47
		Females	15	2.29		8.5		--	--

Data from ¹ present study, ²Bradley and Stumpf (1997), ³R Stumpf and R Kitko (unpublished data), ⁴A Merenlender (unpublished data), and ⁵D Overdorff (unpublished data).

Table 2.4: Relationship of Selected Socioecological Factors with Levels of Dimorphism and Testes Volume.

Population	Folivory	Resource Defense	Fission-Fusion	Body Size Dimorphism ¹	Canine Dimorphism ¹	Mating Season GI
<i>E. albocollaris</i>	Low	Low	Yes	None	Yes (Males)	2.71
Hybrids	Low	Low	No	None	Yes (Males)	2.43
<i>E. f. rufus</i> (East)	Low ²	High ²	No ²	Yes (Females)	None	2.18
<i>E. f. rufus</i> (West)	High ³	Low ³	No ³	None ⁴	Yes (Males) ⁴	n/a

¹ Larger sex in parentheses.

² Overdorff (1991, 1993, unpublished data); ³ Sussman (1974, 1977); ⁴ Gerson (1999, 2000).

Chapter 3. Population Structure of Brown Lemurs at Andringitra National Park and Vevembe Forest, Madagascar

INTRODUCTION

Population density plays a pivotal role in the interactions of primate communities. Many forces are involved in shaping primate population structure, including forest structure and diversity, soil fertility, levels of degradation and fragmentation, and predation (including hunting by humans) (Oates et al., 1990; Lawes, 1992; Pinto et al., 1993; Decker, 1994; Oates, 1996; Stoner, 1996; Peres, 1997; Rosenbaum et al., 1998; Wallace et al., 1998; Pontes, 1999; Peres and Dolman, 1999; Strier, 2000; Gonzalez-Solis et al., 2001). In turn, population dynamics influence variation in many aspects of behavioral ecology, such as ranging, feeding ecology, activity budgets, group interactions, social structure, dispersal, and gene flow (Decker, 1994; Rodrigues de Moraes et al., 1998; Strier, 2000; Ostro et al., 2001).

Population densities have also been noted as potentially critical factors in the origin and maintenance of primate hybrid zones (Struhsaker et al., 1988). For example, hybridization between blue monkeys (*Cercopithecus mitis*) and redbellied monkeys (*C. ascanius*) appears to be density-dependent (Butynski, 1990). In areas of very low population density (and a high incidence of solitary males), blue monkey males will mate with redbellied females; hybridization does not occur elsewhere despite widespread sympatry (Butynski, 1990). In the olive-hamadryas (*Papio hamadryas anubis* X *P. h. hamadryas*) baboon contact zone, population

pressure may cause olive baboons to expand into hamadryas territory (Nagel, 1973; although hamadryas may also migrate into “pure” anubis range; see Phillips-Conroy and Jolly, 1986). Parental population densities also vary considerably in the *Hylobates lar* X *H. pileatus* contact zone in Thailand (Brockelman and Gittins, 1984).

The brown lemurs (*Eulemur fulvus* complex) are among the most widespread primates of Madagascar (Jolly, 1986; Mittermeier et al., 1994). Their ranges include every lemur habitat with the exception of the arid south (Tattersall, 1982). However, this diverse group includes several rare and vulnerable taxa (Harcourt and Thornback, 1990). Like all lemurs, these populations are threatened primarily by the conversion of suitable habitats into agricultural land (Jolly, 1986; Harcourt and Thornback, 1990), exacerbated in local areas by selective logging and hunting practices (Harcourt and Thornback, 1990; Johnson and Overdorff, 1999). Thus, despite the apparent adaptability of the brown lemur group as a whole, there is notable variation in abundance across populations.

The white-collared lemur (*Eulemur albocollaris*) may be the most critically endangered of the brown lemur group. They occupy a highly restricted and fragmented range in the rain forest of southeastern Madagascar (Tattersall, 1982; Figure 3.1). Previous census research in the southeastern region indicates low population densities relative to neighboring brown lemur populations (Johnson and Overdorff, 1999). In contrast, red-fronted lemurs (*Eulemur fulvus rufus*) are the most widespread of the brown lemurs, with a large (but disjunctive) range in both eastern and western Madagascar (Tattersall, 1982). This subspecies

occupies a large range of habitat types from the dry deciduous forests of the west to eastern humid forests (Tattersall, 1982). Population densities of *E. f. rufus* are higher than those of *E. albocollaris* in the east (Johnson and Overdorff, 1999); moreover, *E. f. rufus* densities in western dry forest areas (Sussman, 1974; Müller et al., 2000) are orders of magnitude higher than those recorded in the eastern rain forest.

The apparent disparity in population structure may have significant effects on the border area between closely related *E. f. rufus* and *E. albocollaris*. Accordingly, in this chapter, I present data on population densities of *E. fulvus rufus*, *E. albocollaris*, and their hybrids in the southeastern rain forest region of Madagascar. The objective of these analyses is to determine how shifts in population structure may interact with ecological factors to effect parental species' introgression in the contact zone, gene flow across the southeastern region, and, ultimately, potential speciation (see Chapter 7). If brown lemur population density is low in the contact zone, the habitat here may be limiting, decreasing the potential for hybridization beyond the boundary. Alternatively, if densities are high in the contact zone, then the habitat may have a relatively high carrying capacity and encourage gene flow, at least locally. Lower densities in allopatric areas suggest that the habitat in regions adjacent to the contact zone may not support the encroaching hybrids (although behavioral interactions or ecological specializations may also be important; Chapters 5-6). Hybridization would be effectively reduced beyond the contact zone.

Based on rapid assessment censuses in the southeastern region (Sterling and Ramarason, 1996; Johnson and Overdorff, 1999; Johnson and Wyner, 2000), I predict variation in brown lemur population densities across study sites. As noted, previous survey work indicates high densities of *E. f. rufus* relative to *E. albocollaris* (Johnson and Overdorff, 1999). Accordingly, there may be a north-south decrease in brown lemur abundance, perhaps with *E. f. rufus* more common than *E. albocollaris* in the boundary region. However, there is evidence that *E. albocollaris* may contribute disproportionately to the hybrid zone at Andringitra. All twenty-one individuals sampled at Andringitra contained either hybrid or pure *E. albocollaris* nuclear DNA markers (although there were only three pure individuals; Wyner et al., 2002). Furthermore, particularly high densities have been recorded in the Andringitra region during short surveys in the Andringitra region (Sterling and Ramarason, 1996; Johnson and Wyner, 2000), with estimates exceeding those in *E. f. rufus* sites further north (Johnson and Overdorff, 1999). Prior research suggests very low densities throughout the range of *E. albocollaris* (Johnson and Overdorff, 1999; Johnson and Wyner, 2000). Therefore, the transition to low brown lemur abundance may occur abruptly south of the Andringitra contact zone.

METHODS

I conducted censuses of lemur populations at Andringitra National Park from May 1999-August 2000 and at Vevembe Forest from May-September 2000 (Table 3.1). Rapid assessment surveys at other brown lemur sites in the region were conducted in May-August 1995 (see Johnson and Overdorff, 1999) and

June-July 1997 (Table 3.2). These include the following locations: Ranomafana National Park (Vatoharanana site: S 21° 30' E 47° 21'), Manombo Special Reserve (S 22° 59' 51.0 E 47° 45' 6.4), Evendra Forest (S 22° 26' 6.6", E 47° 13' 46.3"), Imitso Forest (on the western slope of Andringitra National Park: S 22° 08' E 46° 56') and Korokoto Forest (near the northeastern limit of Andringitra National Park: S 22° 11' 44.2", E 47° 1' 55.6"). Ranomafana is located at the center of *E. f. rufus*' eastern distribution. Korokoto lies at the likely center of the Andringitra hybrid zone, while Evendra and Manombo are in *E. albocollaris*' range (although the forest is not continuous between these sites; Figure 3.1).

Populations densities were estimated using standard line transect methods (Cant, 1978; Struhsaker, 1981; Brockelman and Ali, 1987; Whitesides et al., 1988). At each site, sampling was conducted 1-5 days per week, with 1-3 transect repetitions per day during daylight hours. At Andringitra National Park in 1999-2000, transects were established in four locations (Table 3.1): three at the Ambarongy site on the eastern bank of the Iantara (in the home range of groups A1 and A2) and one on the western bank (the Parc site, including the range of group AA). These transects varied in length from .8-2.5 km and were surveyed 20-27 times (Table 3.1). At Vevembe in 2000, one 3.5 km was censused 25 times (Table 3.1). During rapid assessments at Andringitra, Vevembe, and other southeastern locations, 1-2 transects were surveyed 3-12 times at each site (Table 3.1). While these brief censuses are not ideal, test transects using identical methods obtained accurate estimates for brown lemurs at Ranomafana National Park (Johnson and Overdorff, 1999).

The following information was obtained during lemur sightings on transect walks:

1. Lemur species (or hybrids);
2. Number of individuals;
3. Time of day;
4. Perpendicular distance between the first animal sighted and the transect;
5. Distance between the observer and the first animal sighted;
6. Angle of observation (relative to the transect);
7. Location on transect;
8. Height in canopy;
9. Age-sex composition of the social group;
10. Method of detection (visual or auditory);
11. Behavior of social group (rest, travel, feed, social);
12. Group spread (the largest distance between two individuals in the social group);
13. Subjective quality of group size estimate;
14. Distance to other groups sighted previously on the transect; and
15. Compass bearing and distance from a transect meter marker and/or GPS coordinates.

Density estimates were obtained by calculating the total number of individuals per total transect area for each transect at each site. For easier comparison across studies, we include area calculations based on both perpendicular animal-transect distance (PD) and observer-animal distance (OAD).

Transect area was calculated according to the histogram-inspection technique (Whitesides et al., 1988; see Plumptre, 2000, for some associated limitations). In this method, observations are placed into observer-animal and perpendicular distance categories (e.g., 0-4 m, 5-9 m, etc.). The distance at which observation frequencies drop to $\leq 50\%$ of the previous interval is the fall-off distance (Figure 3.2a-b). This distance is used to calculate the effective sighting distance and, ultimately, transect width. Theoretically, observations at distances greater than the effective distance should equal the number of sightings missed at distances closer than this point (Struhsaker, 1981).

Effective distance is calculated according to the following formula:

$$E = \frac{N_t}{N_f} FD$$

Where E is the effective sighting distance, N_t is the total number of sightings, N_f is the number of sightings at less than the fall-off distance, and FD is the fall-off distance for a given species (Whitesides et al., 1988).

Effective distance (to the first individual sighted within each group) is used in conjunction with species-specific group spread to estimate strip width. This calculation is then used with the total length of each transect (transect length X number of repetitions) to generate transect area. Transect area is based on the following formula:

$$A = 2(\frac{1}{2}S + E)L_t$$

Where A =transect area, S =mean group spread (km), E =effective distance (km), and L_t =total transect length (Whitesides et al., 1988).

Sample sizes were often too small to calculate effective distances for each location and/or each taxon. Accordingly, I have pooled observations from multiple southeastern censuses to calculate transect width for all brown lemur populations. These include all sites reported here, as well as those listed in Table 3.5. By pooling data, transect width is standardized across sites and brown lemur taxa. Moreover, comparing widths derived separately for each taxon reveals no significant differences (PD: $X^2 = .0005$, $P > .99$; OAD: $X^2 = .009$, $P > .99$). The total PD sample was 150 groups; the OAD sample was 229 groups. Reflecting larger distribution and/or density, sample size was largest for *Eulemur fulvus rufus* (PD: $N = 117$; OAD: $N = 30$), followed by the Andringitra region hybrids (PD and OAD: $N = 85$), and *E. albocollaris* (PD: $N = 19$; OAD: $N = 18$). Observations of *E. collaris* were also included in width calculations (PD: $N = 16$; OAD: $N = 9$). Nonparametric statistical tests were used, with $P = .05$.

RESULTS

Mean Population Density

The mean density for each taxon from sites represented in this study varied greatly. Hybrids of *E.f. rufus* X *E. albocollaris* in the Andringitra region were the most abundant (PD = 44.44 ± 11.25 individuals/km²; OAD = 45.57 ± 11.53 individuals/km²). *E.f. rufus* populations were much less dense (PD = 19.88 ± 5.28 individuals/km²; OAD = 20.38 ± 5.43 individuals/km²) and *E. albocollaris* at Vevembe was by far the least abundant of all study taxa (PD = 7.06 ± 1.81 individuals/km²; OAD = 7.24 ± 1.85 individuals/km²).

Population Densities at Primary Sites

There was also considerable variation in brown lemur population density estimates across species and sites (Tables 3.3-3.4, Figures 3.3-3.4). There were significant differences in densities among taxa (*E. fulvus rufus*, *E. albocollaris*, and hybrids; Kruskal-Wallis: $H = 11.661$, $P = .0029$) and across primary sites ($H = 12.434$, $P = .0060$).

While hybrids were the most abundant overall, there were significant differences among sites within the hybrid zone ($H = 13.564$, $P = .0036$) and within the Ambarongy site ($H = 9.459$, $P = .0088$). Paired comparisons show that the AA transect had significantly larger brown lemur populations, both relative to other Ambarongy trails (Mann-Whitney U: AA vs. AB: $Z = -2.305$, $P = .0212$; AA vs. AC: $Z = -2.732$, $P = .0063$) and to the Parc transect (AA vs. APC: $Z = -3.389$, $P = .0007$). There were no significant differences in other paired comparisons of hybrid zone transects.

There was less variation across transects in the *E. fulvus rufus* population at Andringitra-Imaitso ($H = 2.110$; $P = .3482$ NS). Furthermore, population estimates at the three transects at this site differed little from those in the hybrid zone on the eastern slope of the park. Again, abundance from AA was significantly greater (or nearly so) than at the three Imaitso transects (AA vs. AIA: $Z = -3.134$, $P = .0017$; AA vs. AIR: $Z = -1.925$, $P = .0543$ NS; AA vs. AIT: $Z = -3.425$, $P = .0006$). Only one other paired comparison showed significant variation (APC vs. AIT: $Z = -2.092$, $P = .0364$).

Rapid Assessments

Results from rapid surveys were consistent with those from more long-term censuses (Table 3.4, Figure 3.4). Population estimates among rapid assessment sites were highest at Korokoto, the likely center of the *E. f. rufus* X *E. albocollaris* hybrid zone in the Andringitra region. Densities were within the range of those derived from other transects in the contact zone (PD: 27.26-83.41 individuals/km², OAD: 27.95-85.53 individuals/km²; Table 3.3). Densities from the Vatoharanana site at Ranomafana were lower; these estimates were also somewhat lower than those from *E. f. rufus* populations from the Andringitra region (PD: 17.86-42.10, OAD 18.31-43.18; Table 3.3). Population densities of *E. albocollaris* were generally lower across their limited geographic range. At some sites (Evendra, Lambohazo), no animals were detected during transect surveys despite confirmed sightings of this species in these locations. At Vevembe, rapid assessments yielded very different results in 1995 and 1997. The 1997 estimates were much higher than those from 1995, possibly due to the cessation of commercial logging in nearby areas (and the concomitant reduction in hunting pressure). However, findings from the 1995 survey were consistent with more long-term censuses conducted in 2000 (when logging was still absent and hunting presumably rare). Results at Manombo varied by transect, but were similar to those at Vevembe.

DISCUSSION

These results indicate great variability in brown lemur abundance across the southeastern region. As predicted, *E. albocollaris* tends to have the lowest

densities of all southeastern brown lemurs, often with few or no sightings during brief censuses. The rarity of *E. albocollaris* is exacerbated by severe habitat fragmentation throughout much of its highly restricted geographic distribution (see Figure 3.1; Johnson and Overdorff, 1999; Irwin et al., 2001). Hunting pressure also appears to be strong for this taxon (Johnson and Overdorff, 1999; personal observation). Also as expected, densities of *E. f. rufus* at Andringitra National Park (Imaitso) and Ranomafana National Park are generally higher than those recorded in *E. albocollaris* sites. These results are even more striking when considering the lemur communities at these sites. Red-fronted lemurs in the humid eastern forests are part of some of the richest primate communities in the world (up to 12 species, including 6 other day-active lemurs; Mittermeier et al., 1994). In contrast, *E. albocollaris* is sympatric with only 6-7 lemur species in much of its range (with generally only 1-2 other diurnal species present; Tattersall, 1982; Mittermeier et al., 1994; see Table 1.1).

The density estimates of *E. f. rufus* accord broadly with results from other surveys in the region (Table 3.5). These densities were also similar to those of *Eulemur collaris*, the southernmost brown lemur species (Figure 3.1; Table 3.5); Banks (2002), however, found higher densities of *E. collaris* (45.7 individuals/km²) in the southeastern littoral forest. It should be noted that, with a much larger range than other southeastern brown lemurs, *E. f. rufus* encounters much more heterogeneity in habitat types. Likely as a result, there is great variation in abundance estimates from sites in the Ranomafana region down through the Andringitra region (a distance of 150 km; Tables 3.3-3.5). However,

overall densities were highest near the Andringitra region, at the southern limit of the species. Within the contact zone at Andringitra, population densities were generally higher than those from most other *E. f. rufus* sites in the southeast, and strikingly higher than in any *E. albocollaris* site. This is consistent with the possibility of high carrying capacity in the Andringitra hybrid zone and the presence of ecotones (abrupt habitat shifts) at the species boundary (see Chapter 4). Yet there is little evidence that *E. f. rufus* populations are particularly limited at other sites near the border region. Populations at Imitso – a drier, western-type habitat isolated from the hybrid zone by the high Andringitra Massif – are not significantly less dense than those at most eastern slope (i.e., hybrid) sites. Moreover, populations of *E. f. rufus* at nearby Ikongo Forest are among the highest for any brown lemur in the southeast (Table 3.5). By contrast, *E. albocollaris* densities were consistently low, with no indication of population increase toward the north – again, suggestive of an abrupt habitat shift in the Andringitra hybrid zone region.

Despite the high overall brown lemur density, there is some indication of variation in abundance among sites within Andringitra. Ambarongy, on the eastern bank of the Iantara River, had the highest densities of any Andringitra site. There was also significant variation in transects *within* Ambarongy, suggesting microhabitat differences (see Chapter 4). Somewhat unexpected from the low abundance of *E. albocollaris* throughout their range, the hybrid population at Andringitra presumably has a greater concentration of *E. albocollaris*; Ambarongy is closer geographically to pure source populations in the southeast

(Figure 3.1) and the three pure *E. albocollaris* individuals were caught here (Wyner et al., 2002). Densities were generally lower at the other hybrid sites (Parc), as well as the *E. f. rufus* site at Imitso. Brown lemurs at these sites are either pure *E. f. rufus* or hybrids that more closely resemble *E. f. rufus* phenotypically (in accordance with the presumed vectors of migration into the contact zone; Figure 3.1). Brown lemurs at the suspected center of the hybrid zone (Korokoto) also appear to be less abundant.

It is possible that the differences in density among sampling sites at Andringitra and across the southeast reflect variation in the intrinsic adaptive capabilities of *E. albocollaris*, hybrids, and *E. f. rufus*. The generally higher densities at the Andringitra sites (especially within the contact zone) suggest potential hybrid vigor – i.e., that hybrids are more fit than the parental species, at least within the contact zone habitats. However, this possibility is unlikely for a variety of reasons. First, *E. f. rufus* is a highly adaptable taxon, with an enormous geographic range containing a wide range of habitat types (Tattersall, 1982). Moreover, as noted, *E. f. rufus* population densities in areas close to the hybrid zone (e.g., Andringitra-Imaitso and Ikongo) are much higher than in sites further north. Differences in habitat quality across the region (and microhabitat shifts within sites) are more likely responsible for the observed variation in brown lemur densities. Elevation gradients in the mountainous Andringitra region may also affect lemur densities. Sterling and Ramarason (1996) found no brown lemurs above 1210 m. However, below this point, different estimate methods produced conflicting results for the correlation between brown lemur density and elevation

(Sterling and Ramarason, 1996). In the present study, brown lemur density at Andringitra did not vary consistently with elevation (e.g., Parc and Ambarongy are at the same elevation, while Korokoto, with intermediate densities, is higher in elevation). As mentioned above, lemur community composition may also play a role. Unlike many *E. f. rufus* sites to the north, the Andringitra hybrids are not sympatric with *Varecia variegata*, a highly frugivorous species (Morland, 1991; White, 1991; Vasey, 1997, see Table 1.1). However, competition from sympatric lemurs is not a factor in the very low densities in *E. albocollaris* sites (e.g., Vevembe, where the only other day-active lemur is the bamboo specialist *Hap Alemur griseus*; Table 1.1).

In summary, the Andringitra region supports a relatively large brown lemur population. Areas with apparently greater concentrations of *E. albocollaris* have the highest population densities in the contact zone. In contrast, *E. f. rufus* are more abundant than *E. albocollaris* in allopatric areas. In terms of gene flow in and out of the contact zone, it appears that the high carrying capacity of the Andringitra habitat would encourage introgression into this region. However, in adjacent regions, lower densities suggest more restricted gene flow into these areas and beyond into the parental ranges, effectively reducing the extension of the hybrid zone. This effect may be more dramatic in the transition to pure *E. albocollaris*' range, a region with extensive fragmentation and very low population densities.

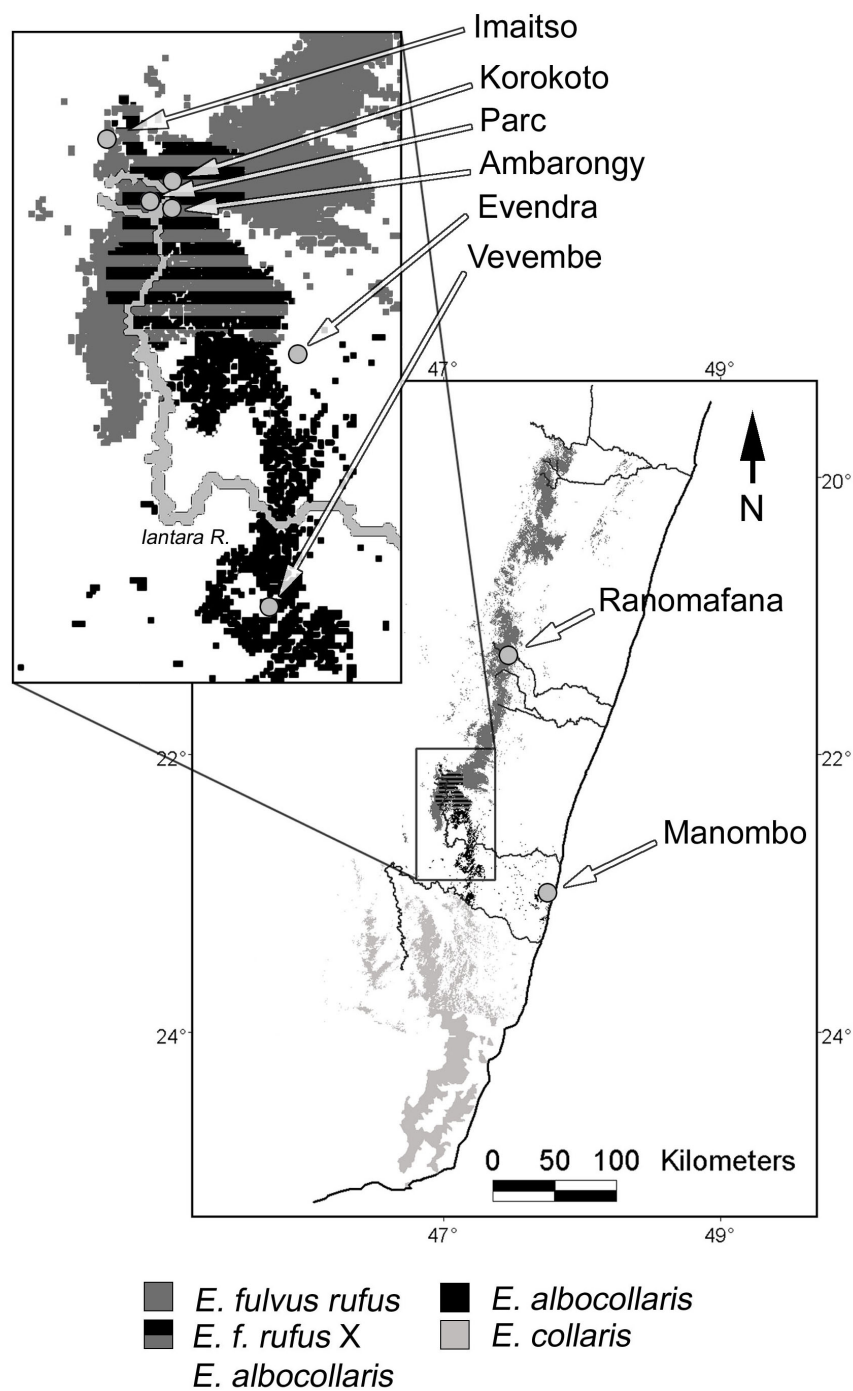


Figure 3.1: Census Sites. Shaded areas indicate forest habitats.

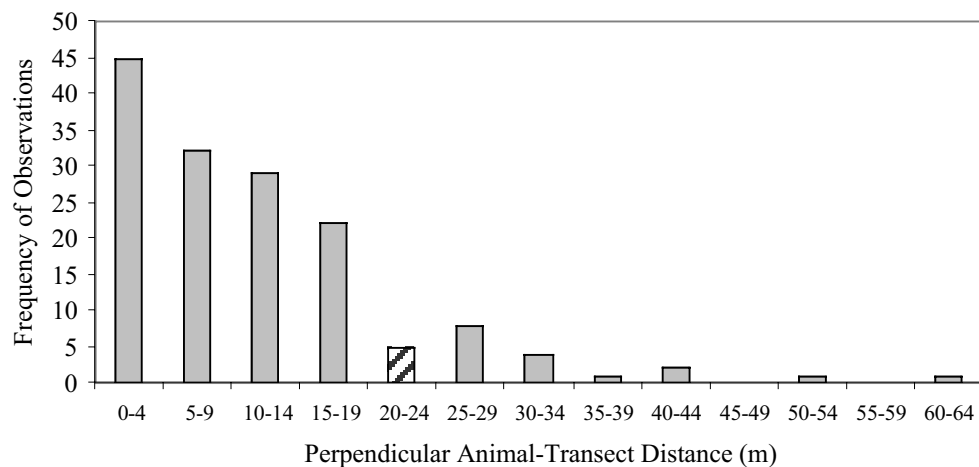


Figure 3.2a: Frequency of sighting distances using perpendicular animal-transect distance (PD). Cross-hatching indicates the interval at the 50% drop-off distance.

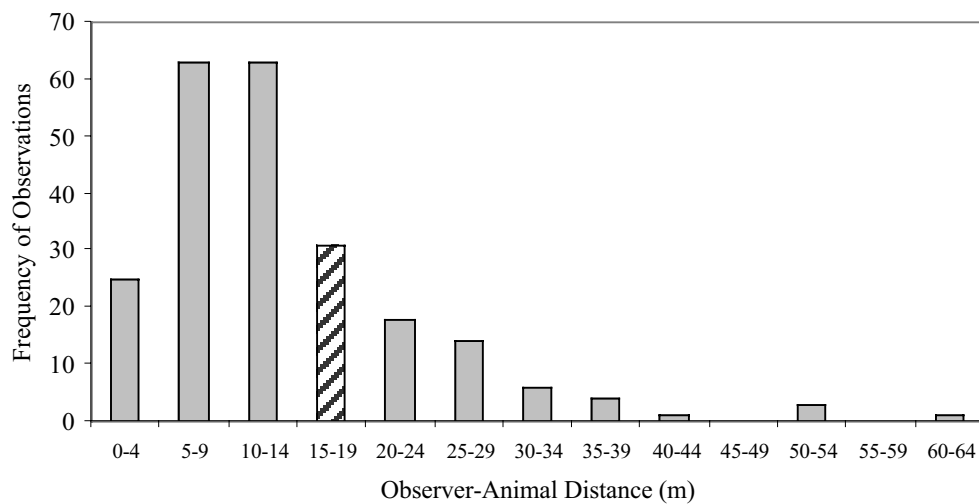


Figure 3.2b: Frequency of sighting distances using observer-animal distance (OAD). Cross-hatching indicates the interval at the 50% drop-off distance.

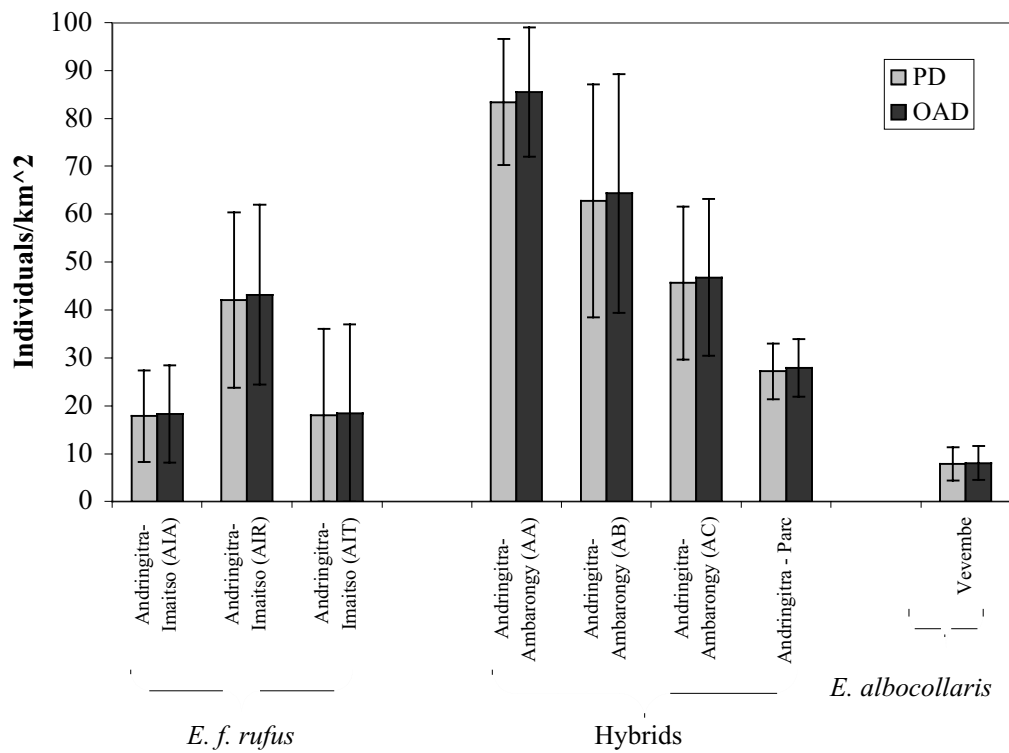


Figure 3.3: Population Densities at Primary Research Sites. PD = perpendicular distance; OAD = observer-animal distance.

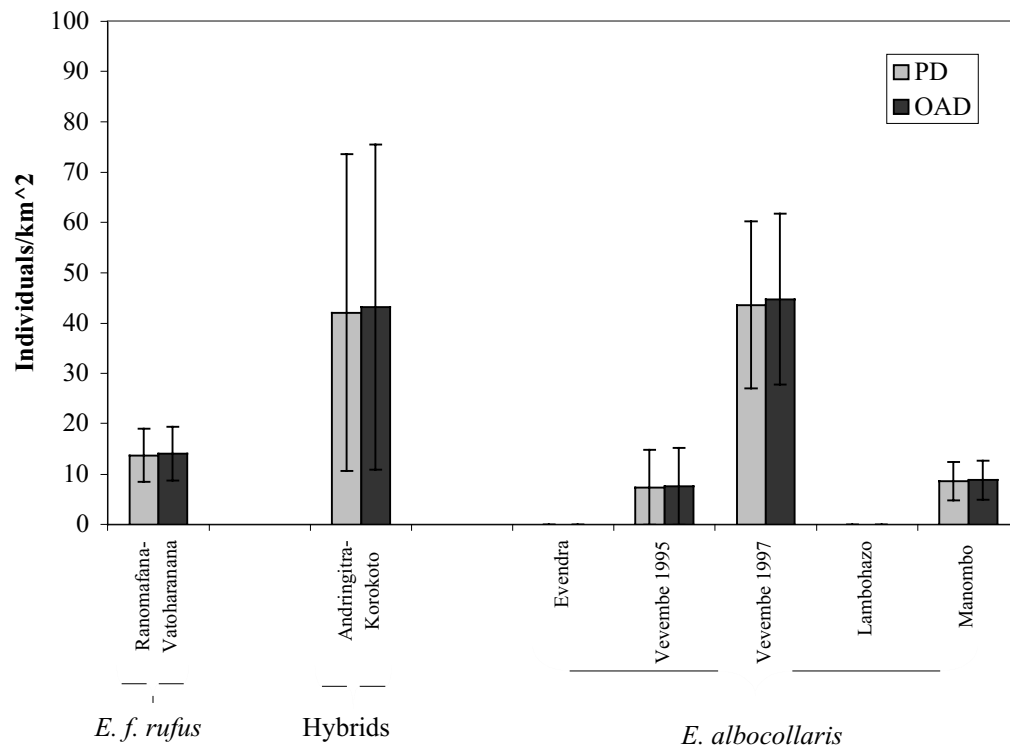


Figure 3.4: Population Densities at Rapid Assessment Sites. PD = perpendicular distance; OAD = observer-animal distance.

Table 3.1: Census Sites in Primary Study Areas. Sites are listed from north to south in descending order.

Site	Taxon	Transect	Date	Length (km)	# Surveys	Total Length (km)
Andringitra - Imitso	<i>E. f. rufus</i>	AIA	8-9/00	1.60	12	19.20
Andringitra - Imitso	<i>E. f. rufus</i>	AIR	8-9/00	1.75	12	21.00
Andringitra - Imitso	<i>E. f. rufus</i>	AIT	8-9/00	1.00	12	12.00
Andringitra - Ambarongy	Hybrids	AA	4-7/99	2.50	27	67.50
Andringitra - Ambarongy	Hybrids	AB	4-5/99	0.88	22	19.25
Andringitra - Ambarongy	Hybrids	AC	4-5/99	0.78	25	19.38
Andringitra - Parc	Hybrids	APC	6/99-8/00	2.35	20	47.00
Veveombe	<i>E. albocollaris</i>	VE00	7-9/00	3.49	25	87.23

Table 3.2: Rapid Assessment Sites in Southeastern Region. Sites are listed from north to south in descending order.

Site	Species	Transect	Date	Length (km)	# Surveys	Total Length (km)
Ranomafana - Vatoharanana	<i>E. f. rufus</i>	VA95	7/95	3.5	6	21.00
Andringitra - Korokoto	Hybrids	AK	7/97	3.00	5	15.00
Evendra	<i>E. albocollaris</i>	EA	6/97	1.4	5	6.80
Evendra	<i>E. albocollaris</i>	EB	6/97	1.0	5	5.00
Veveombe	<i>E. albocollaris</i>	VE95	6/95	1.62	3	4.86
Veveombe	<i>E. albocollaris</i>	VE97	6/97	3.00	4	12.00
Lambohazo	<i>E. albocollaris</i>	L	6/95	1.0	3	3.00
Manombo	<i>E. albocollaris</i>	MAA	6/95	1.5	7	10.50
Manombo	<i>E. albocollaris</i>	MAB	7/95	3.5	6	21.00

Table 3.3: Population Densities (individuals/km²) at Primary Research Sites. Perpendicular (PD) and observer-animal (OAD) distances were used to estimate transect width. SE = standard error. Site means are in bold.

Site	Transect	Species	PD		OAD	
			Density	SE	Density	SE
Andringitra - Imitso	Mean	<i>E.f. rufus</i>	26.00	9.15	26.67	9.42
Andringitra - Imitso	AIA	<i>E.f. rufus</i>	17.86	9.56	18.31	10.14
Andringitra - Imitso	AIR	<i>E.f. rufus</i>	42.10	18.33	43.18	18.79
Andringitra - Imitso	AIT	<i>E.f. rufus</i>	18.04	18.04	18.51	18.51
Andringitra - Ambarongy	Mean	Hybrid	63.95	10.65	65.58	10.92
Andringitra - Ambarongy	AA	Hybrid	83.41	13.16	85.53	13.49
Andringitra - Ambarongy	AB	Hybrid	62.81	24.33	64.41	24.95
Andringitra - Ambarongy	AC	Hybrid	45.64	15.99	46.80	16.40
Andringitra - Parc	APC	Hybrid	27.26	5.82	27.95	5.97
Vevembe	VE00	<i>E. albocollaris</i>	7.86	3.47	8.06	3.56

Table 3.4: Population Densities (individuals/km²) at Rapid Assessment Sites. Perpendicular (PD) and observer-animal (OAD) distances were used to estimate transect width. Sites are listed in descending order from north to south. Site means are in bold.

Site	Trail	Species	PD		OA	
			Density	SE	Density	SE
Ranomafana - Vatoharanana	VA95	<i>E. f. rufus</i>	13.75	5.27	14.10	5.40
Andringitra - Korokoto	AK	Hybrid	42.10	31.49	43.18	32.29
Evendra	Mean	<i>E. albocollaris</i>	0.00	0.00	0.00	0.00
Vevembe	Mean	<i>E. albocollaris</i>	25.52	9.07	26.17	9.30
Vevembe	VE95	<i>E. albocollaris</i>	7.43	7.43	7.62	7.62
Vevembe	VE97	<i>E. albocollaris</i>	43.61	16.54	44.72	16.96
Lambohazo	L	<i>E. albocollaris</i>	0.00	0.00	0.00	0.00
Manombo	Mean	<i>E. albocollaris</i>	8.59	3.78	8.81	3.88
Manombo	MAA	<i>E. albocollaris</i>	3.44	3.44	3.52	3.52
Manombo	MAB	<i>E. albocollaris</i>	13.75	6.74	14.10	6.92

Table 3.5: Population Densities (individuals/km²) at Other Southeastern Census Sites.

Site	Species	PD		OA		Source*
		Density	SE	Density	SE	
Kirisiasy	<i>E.f. rufus</i>	0.00	0.00	0.00	0.00	¹
Marofotsy	<i>E.f. rufus</i>	10.06	3.73	10.32	3.83	¹
Ranomafana - Bevoahazo	<i>E.f. rufus</i>	23.01	--	23.59	--	²
Ranomafana - Manidika	<i>E.f. rufus</i>	16.54	--	16.96	--	³
Ranomafana - Miaranony	<i>E.f. rufus</i>	19.77	--	20.28	--	³
Ranomafana - Namahoaka	<i>E.f. rufus</i>	1.76	1.23	1.80	1.26	¹
Ranomafana - Vatoharanana 1996	<i>E.f. rufus</i>	2.44	1.67	2.50	1.71	⁴
Ranomafana - Vatoharanana 2000	<i>E.f. rufus</i>	24.81	7.93	25.44	8.13	²
Ambantofotsy	<i>E.f. rufus</i>	27.07	--	27.76	--	²
Tolongoina	<i>E.f. rufus</i>	0.38	--	0.39	--	²
Ikongo	<i>E.f. rufus</i>	75.19	--	77.10	--	²
Kalambatritra	<i>E. collaris</i>	37.78	--	38.75	--	⁵
Midongy-Sud 1995	<i>E. collaris</i>	12.89	5.92	13.22	6.07	⁶
Midongy-Sud 2000	<i>E. collaris</i>	22.99	8.46	23.57	8.68	²

* Modified from ¹ Irwin, et al., 2000, ² P. Wright, ³ S. Arrigo-Nelson, and ⁴ C. Grassi, ⁵ M. Irwin, unpublished data, and ⁶ Johnson and Overdorff, 1999.

Chapter 4: Meteorology, Forest Structure, Species Composition, and Phenology at Andringitra National Park and Vevembe Forest

INTRODUCTION

The structure, diversity and phenology of tropical forests are key components in the study of primate community ecology and diversity (van Schaik et al., 1993; Tutin and Fernandez, 1993; Chapman et al., 1994; White, 1994; Reed and Fleagle, 1995; Ganzhorn et al., 1997; Chapman, et al., 1999). Many studies in tropical botany have examined adaptive systems in tree communities, including proximate mechanisms for the timing of phenological stages, dispersal, and reproduction, as well as their evolutionary consequences (Frankie et al., 1974; Rathke and Lacey, 1985; van Schaik et al., 1993). As predators, dispersers, or pollinators, animal consumers may serve pivotal coevolutionary roles in these adaptive systems (Smythe, 1970; Frankie et al., 1974; Sussman and Raven, 1978; Janson et al., 1981; Terborgh, 1986; Estrada and Coates-Estrada, 1991; Rowell and Mitchell, 1991; Tutin et al., 1991; van Schaik et al., 1993; Gautier-Hion and Maisels, 1994; Wrangham et al., 1994; Chapman and Chapman, 1996; Juillot, 1996; Chapman and Onderdonk, 1998; Dew and Wright, 1998; Lambert and Garber, 1998; Overdorff and Strait, 1998). In addition, documenting phenological processes and resource availability in tropical forests provides the basis for understanding the behavioral ecology of primary consumers, including primates (Terborgh, 1983; Leighton and Leighton, 1983; van Schaik et al., 1993). In conjunction with the activities of animal consumers, seasonality in abiotic factors

(such as temperature, irradiance, and rainfall) may impose important constraints on phenological stages (Hilty, 1980; Rathke and Lacey, 1985; van Schaik et al., 1993; Chapman et al., 1999).

In this chapter, I examine the structure and phenology of the tree communities at Andringitra National Park (Ambarongy and Parc stations) and Vevembe Forest based on data collected from April 1999-September 2000. The primary objective is to quantify resource availability across seasons for the lemur communities at these sites. In addition, I examine variation in structural characteristics of the these forests (e.g., tree size and density), as well as the relationships between phenology and climate variables. The structure and productivity of forest habitats are critical factors for assessing the distribution of and interactions among brown lemur populations across the southeastern region. Moreover, variation in habitats may explain shifts in feeding ecology or social behavior across brown lemur populations.

Forest communities and meteorological patterns are expected to be generally similar at Andringitra and Vevembe. The sites are located 66 km apart in Madagascar's eastern lowland rain forests (White, 1983). The eastern rain forest follows a general pattern of a warm, rainy period (October-March) followed by a cool, drier season (April-September) (Donque, 1972; Goodman and Andrianarimisa, 1996; Overdorff and Wright, unpublished ms). However, weather patterns are not uniform across the region or through time. There is a trend of decreasing temperatures from north to south, and variation in relief and altitude can impact rainfall (Donque, 1972). Moreover, this region is affected by

stochastic events such as drought, frequent cyclones, occasional frost in high altitude forests, and the ongoing desiccating effects of deforestation (Wright, 1999). Furthermore, previous studies in the Andringitra and Vevembe regions demonstrate variation within and between sites. In the Andringitra Massif region, there are marked differences in both temperature and rainfall across sites, following altitude gradients and/or east-west position (Paulian et al., 1971, in Goodman and Andrianarimisa, 1996). Vondrozo (14 km east of Vevembe) generally has more precipitation, although annual totals are similar to the wetter eastern Andringitra sites (Donque, 1972; Paulian et al., 1971, in Goodman and Andrianarimisa, 1996).

It is difficult to derive firm predictions about comparative forest structure and diversity at Andringitra and Vevembe. Ganzhorn et al. (1997) report variation across and within eastern Malagasy forests in tree density, structural diversity, total basal area, and species diversity. These authors found a general relationship between annual rainfall and tree size and species diversity; these measures were also correlated with lemur species richness across Madagascar (Ganzhorn et al., 1997), mirroring trends throughout the tropics (Reed and Fleagle, 1995). Mild disturbance may also increase tree productivity and lemur diversity (Ganzhorn et al., 1997). However, Lewis et al. (1996) found tree communities were less diverse and there were fewer and smaller trees in areas of slight disturbance at Andringitra. There were also fewer lemur species in the disturbed area (Sterling and Ramarason, 1996). Similarly, at Ranomafana National Park, the ruffed lemur (a large bodied frugivorous lemur) is absent from

more disturbed areas (White et al., 1995; Balko, 1998). Vevembe is likely more affected by human activities (personal observation) and may be wetter (see above) than Andringitra. The lemur community is also much less diverse at Vevembe (7 species) than at Andringitra (13 species on the eastern rain forest slope) (Sterling and Ramarason, 1996).

In addition to variable climate and forest structure, eastern Madagascar has been characterized as unpredictable over time in resource availability (Wright, 1999; Overdorff, 1996; Overdorff and Wright, unpublished ms). At Ranomafana National Park (115 km NNE of Andringitra), fruiting is most frequent in October, while flowering has three distinct peaks (February, June, and October) and leaf flushing is most common in February (Overdorff and Wright, unpublished ms). However, there was considerable variation in the timing and abundance of resources across years (Overdorff and Wright, unpublished ms) and across studies (Overdorff, 1993; Hemingway and Overdorff, 1999). Moreover, the relationships between phenophases and temperature or rainfall were not consistent over time (Overdorff and Wright, unpublished ms). Therefore, the phenological data presented herein may not capture long-term temporal variation and are best considered as supporting evidence for more stable measures of habitat structure, such as tree height, diameter, crown size, and density.

METHODS

Meteorology

Rainfall was recorded from April 1999-August 2000 at Ambarongy station, Andringitra National Park and April-September 2000 at Vevembe Forest.

Precipitation was collected with Tru-Chek ® rain gauges on 241 non-consecutive days at Ambarongy and 137 days at Vevembe. The total quantity measured each month was divided by the number of days sampled to yield average daily rainfall per month. For comparison with other published data, estimated monthly rainfall totals were computed using the daily average rainfall and the number of days in each month.

Maximum and minimum temperatures were recorded with Taylor thermometers at Andringitra from April 1999-August 2000 (N = 246 sampling days). Temperature data were only recorded for parts of April and May 2000 at Vevembe (N = 27 sampling days).

Botanical Plot Selection

Data on floristic composition, forest structure, and resource availability were collected at Ambarongy and Parc stations, Andringitra National Park, and at Vevembe Forest. While there are no standard techniques for evaluating tropical forest plant communities (Lewis et al., 1996), the plot-based methods employed here accord generally with previous studies in southeastern Madagascar (e.g., Ganzhorn, et al., 1997; Lewis et al., 1996). At each site, 625 m² (25 m x 25 m) botanical plots were established. Plots were positioned on primary research trails at intervals of at least 300 m. At Ambarongy, plots were located at A 300 (A1), A 600 (A2), B 300 (A3), and C 300 (A4) (Figure 4.1a); these plots were between 700-900 m elevation. Additional plots were situated at PC 300 (P1) and PC 600 (P2) at the Parc site (Figure 4.1a), at approximately 800 m elevation. The two sites – located within the home range of the two main study groups – were

analyzed separately to detect microhabitat differences that may influence the behavior of the focal animals. At Vevembe, plots were placed at AN 300 (V1), M 300 (V2), M 600 (V3), and CN 600 (V4) (Figure 4.1b). Elevation at Vevembe is 600 m.

Composition and Structure

For plant community structure, trees ≥ 10 cm dbh (diameter at breast height) were selected for analysis. This size category has been used in previous research at Andringitra (Lewis et al., 1996) and elsewhere in Madagascar (Ganzhorn et al., 1997; Overdorff and Wright, unpublished ms). Within each botanical plot, the following information was recorded for all trees ≥ 10 cm dbh: (1) species identification; (2) dbh (cm); (3) height (m); (4) tree crown height (m), diameter (m), and shape (triangular, rectangular, or circular); and (5) continuity of tree canopy with neighboring trees. For species identification, Malagasy vernacular names were recorded in the field. Subsequently, scientific nomenclature was applied using Turk (1995) as the primary key and Overdorff (1991; unpublished data) as a secondary resource. For comparison with previous research (Lewis et al., 1996; Ganzhorn et al., 1997; Overdorff and Wright, unpublished ms), basal area was also included, using the following formula for calculation:

$$\text{basal area (m}^2\text{)} = \pi \left(\frac{\text{dbh(cm)}}{2 \times 100} \right)^2$$

Species and structural diversity were measured using the relative abundance and the Shannon Index (Overdorff, 1991; Ganzhorn et al., 1997):

$$\text{Relative abundance: } p_i = N_i/N_t$$

where p_i is the relative abundance of a tree species or size category, N_s is the number of individuals of the species or category, and N_t is the number of individuals of all species or categories in the plot.

$$\text{Shannon Index: } H = -\sum_{i=1}^s (p_i)(\log p_i)$$

Where H = diversity index, s = number of species or size categories, and p_i is the relative abundance of each i th species or category. For taxonomic diversity, the index was calculated separately for each plot at all sites, using trees ≥ 10 cm dbh. Trees that could not be identified taxonomically (max = 2 per plot) were treated as separate species, resulting in slightly higher diversity scores than if unknowns were grouped as a single species. For structural diversity, trees ≥ 10 cm dbh were divided into size categories at increments of 5 cm dbh up to ≥ 30 cm dbh (Ganzhorn et al., 1997).

Within each plot, a 5 x 5 m subsection was established. In these subplots, the same information as in the larger plots was collected for all trees ≥ 2.5 cm dbh. In addition, the following data were recorded: (1) estimated percentage of ground cover; (2) number of bamboo stems (including bamboo lianas); (3) number of epiphytes; (4) number of ground ferns; (5) number of lianas; and (6) number of small stems (< 2.5 cm dbh and ≥ 25 cm height). Within these subplots, a 1 m x 1 m section was used to count the number of herb stems (and taxonomic identification).

Phenology

To calculate resource availability, phenological data were collected bi-weekly or monthly at each site. For standardization across sites, only one

sampling period per month is presented here. At Ambarongy, data were collected at A1-A4 from April-August 1999. Only plots A1-A3 were subsequently examined from September 1999-August 2000. Plots P1-P2 were monitored from June 1999-August 2000. At Vevembe, data were collected for all plots from May-September 2000. Monitoring was completed in 1-2 days in each data collection cycle. A total of 373 trees were monitored at Andringitra and 267 trees at Vevembe (Table 4.5). For each tree, it was noted if the tree contained new leaves, flower buds or flowers (grouped as “flowers” for this analysis), or unripe fruit or ripe fruit (combined as “fruit” herein). Moreover, the quantity of food items was estimated using an ordinal scale (1-5) corresponding to the estimated percentage of maximum coverage (20-100%) for that particular food category. Resource availability was then calculated according to the formula:

$$FA = \sum_{i=0}^i CV \times (A/5)$$

where FA = availability of the selected resource, i = number of trees with the selected resource (ripe or unripe fruit, etc.), CV = crown volume, and A= amplitude score (1-5) (Overdorff, 1991). These analyses were conducted on all trees as well as a sub-sample consisting of species known to be consumed by brown lemurs at these sites (Chapter 5). In addition, analysis of only percentage of trees with fruit, flowers, or new leaves is presented for comparison with previous studies in the region (Overdorff and Wright, unpublished ms).

Synchrony

To assess synchrony in fruiting, leaf flushing, and flowering events, the coefficient of dispersion (CD = sample variance/mean) was calculated for all

identified trees at each site (Chapman et al., 1999). When CD is greater than one, the distribution of phenological events is clumped, suggesting seasonality. When CD is less than one, phenological events occur regularly throughout the time period examined. Finally, when CD approximates one, the pattern is random (Sokal and Rolf, 1995). The index of dispersion (I_D ; sample variance $\times$ degrees of freedom/mean) was used to determine significant departure from a Poisson distribution (Southwood, 1978). In addition, species-specific synchrony patterns were examined for all identified morphospecies with more than one individual at a site.

Relationship Between Phenology and Climate

Regression analyses were used to examine the potential effects of seasonal climate changes on food production. The correlation coefficients (r) from least-squares regressions were used to examine the strength of relationships between food availability (FA/ha) and meteorological patterns (rainfall and temperature) for equivalent months and for each month up to 11 months prior (Chapman et al., 1999). In this manner, I examined how food availability may have been influenced by weather patterns that occurred earlier, throughout an entire 12-month annual cycle. However, due to limited sampling at Vevembe, it was only possible to examine the relationships for the concurrent months and one month prior for this site.

Statistics

Primarily nonparametric analyses were used to compare meteorology, botanical structure, diversity, and phenology within and between sites. Kruskal-

Wallis, Mann Whitney U, and chi-square tests were used to examine differences in botanical structure variables and diversity, floristic diversity, and seasonal variation in food production.

RESULTS

Climate

In general, Andringitra and Vevembe demonstrated similar trends in meteorological variables during the study period. Vevembe was somewhat wetter during overlapping sampling months, while Andringitra showed some inter-annual variation in both temperature and rainfall.

There was significant variation in both maximum and minimum temperatures across all months sampled at Andringitra (max: $H = 179.578$; $P < .0001$; min: $H = 197.867$; $P < .0001$; Figure 4.2). Temperatures also became significantly lower from April to May at Vevembe (max: $Z = -2.858$; $P = .0043$; min: $Z = -2.941$; $P = .0033$; Figure 4.2). At Andringitra, temperatures were higher between November-February with a peak in December; the lowest mean temperatures occurred in July (Figure 4.3).

Though the data were restricted to two months, Vevembe showed a similar trend in the transition to cooler temperatures in April-May (Figures 2-3). There were no significant differences between Andringitra and Vevembe in April 2000 (max: $Z = -1.163$; $P = .2449$ NS; min: $Z = -1.884$; $P = .0596$ NS). However, in May 2000, temperature maxima were higher at Andringitra ($Z = -3.652$ $P = .0003$), while minima were higher at Vevembe ($Z = -3.332$; $P = .0009$; Table 4.1).

Comparing April-August, there was also evidence for inter-annual variation at Andringitra. August was the only month sampled in which there were no significant differences between 1999 and 2000 in both temperature maxima ($Z = -.707$; $P = .4795$ NS) and minima ($Z = -.967$; $P = .3337$ NS). Minimum temperatures also did not vary for the month of May ($Z = -1.400$; $P = .1614$ NS). However, in general, temperatures were warmer in 2000. Maximum temperatures were higher in 2000 for April ($Z = -3.667$; $P = .0002$), May ($Z = -4.332$; $P < .0001$), June ($Z = -4.074$; $P < .0001$), and July ($Z = -4.141$; $P < .0001$). Minima were also higher in 2000 for the months of April ($Z = -2.709$; $P = .0068$) and June ($Z = -4.142$; $P < .0001$). Only in July were minimum temperatures significantly higher in 1999 than in 2000 ($Z = -3.871$; $P = .0001$). However, it should be noted that all months in 2000 were more poorly sampled ($N = 7-8$ days per month), thus less variation is possible and comparisons may be affected.

There was significant variation in rainfall across months at each site (Andringitra: $H = 91.033$; $P < .0001$; Vevembe: $H = 22.674$; $P = .0004$; Figure 4.4). At Andringitra, the wettest months were December-February, with a peak in February (Figure 4.5). The drier months were March-November, particularly the winter months of June and August (Figure 4.5). There was a mid-winter spike in precipitation during July 1999, though no rain fell at Andringitra during the 8 days sampled in July 2000 (Figure 4.4).

Vevembe followed a similar pattern in April-September 2000 (i.e., all months were relatively dry except for July; Figure 4.5). In 2000, there were no differences between the sites for April ($Z = -.410$; $P = .6204$ NS) or May ($Z = -$

1.329; $P = .1838$ NS). There were significant differences for June ($Z = -2.822$; $P = .0048$), July ($Z = -2.491$; $P = .0128$), and August ($Z = -2.726$; $P = .0064$). However, no rainfall was recorded during these winter months at Andringitra, an unusual result that may be due to poor sampling or an anomalously dry year at this site.

There was little inter-annual variation for April-August at Andringitra. There were no differences between 1999 and 2000 for April ($Z = -.751$; $P = .4529$ NS), June ($Z = -1.729$; $P = .0838$ NS), and August ($Z = -1.512$; $P = .1306$ NS). However, there were differences for the months of May ($Z = -2.496$; $P = .0126$) and July ($Z = -3.166$; $P = .0015$). In both cases, there was more rainfall in 1999 as, again, Andringitra was conspicuously dry during the winter of 2000 (Figure 4.4).

Forest Structure

The two Andringitra National Park sites (Ambarongy and Parc) and Vevembe Forest varied substantially in several forest structure variables (Table 4.1). Comparing the three locations, there was significant variation in tree height ($H = 183.256$; $P < .001$) and crown volume ($H = 136.282$; $P < .0001$). The mean values were highest at Ambarongy (height = 20.6 m; crown volume = 618.2 m²); mean tree height was lowest at Parc (13.2 m), while crown volume was lowest at Vevembe (51.1 m²). In contrast, dbh ($H = 5.193$; $P = .0745$ NS) and the number of trees ≥ 10 cm dbh ($H = 2.045$; $P = .3596$ NS) did not vary across the three sites. Moreover, basal area did vary across sites, in either the mean ($H = 5.193$; $P = .0745$ NS) or the total area per hectare ($H = 4.009$; $P = .1347$ NS). Comparing

Veveembe to Andringitra as a single site yields identical results (height: $Z = -10.756$; $P < .0001$; crown volume: $Z = -10.475$; dbh: $Z = -.987$; $P = .3235$ NS; number of trees: $Z = 0.000$; $P > .9999$ NS; mean basal area: $Z = -.987$; $P = .3235$ NS; total basal area: $Z = 0.000$; $P > .9999$ NS). Analyses of structural diversity (a variable related to dbh) produced no significant differences across sites or regions (all sites: $H = 4.4404$; $P = .1106$; Andringitra v. Veveembe: $Z = -.962$; $P = .3359$; Table 4.1).

In smaller plots (25 m^2 and 1 m^2), there were few differences among sites or between regions (Table 4.2). There was no significant variation among sites in the percentage of ground cover or the number of stems of bamboo, epiphytes, herbs, saplings ($\geq 25 \text{ cm}$ height), ground ferns, or lianas. Comparing Andringitra and Veveembe, only ground ferns varied by region ($H = -1.922$; $P = .0547$), as they were absent from the Veveembe plots. However, these analyses of variation are hampered by the fact that these variables yield only a single data point per plot. Accordingly, I also performed chi-square analyses using site means. These tests yielded significant differences in mean stem counts of bamboo ($\chi^2 = 9.000$; $P = .0111$), herbs ($\chi^2 = 85.822$; $P < .0001$), and saplings ($\chi^2 = 15.106$; $P = .0005$).

To test for microhabitat differences within regions and sites, I compared structural characteristics at Ambarongy and Parc, as well as among plots at each site. Between the Andringitra sites, there were significant differences for dbh ($Z = -1.928$; $P = .0538$), tree height ($Z = -9.585$; $P < .0001$), and crown volume ($Z = -5.525$; $P < .0001$). Again, Ambarongy had the higher mean for each of these characteristics. Within the Ambarongy site, there was also significant variation in

dbh ($H = 7.917$; $P = .0478$) and crown volume ($H = 27.102$; $P < .0001$), but not in height ($H = 2.682$; $P = .4434$ NS). There were no differences between the two plots in the Parc site (dbh: $Z = -.025$; $P = .9801$ NS; height: $Z = -.804$; $P = .4213$ NS; crown volume: $Z = -1.302$; $P = .1928$ NS). Within Vevembe, height and crown volume were significantly different across plots ($H = 59.214$; $P < .0001$; $H = 53.093$; $P < .0001$, respectively), but dbh did not vary ($H = 6.821$; $P = .0778$ NS).

Diversity

A total of 64 morphospecies from 29 families were identified in the ≥ 10 cm dbh sample at Andringitra National Park (Tables 4.3-4.4). At Vevembe, 60 morphospecies from 31 families were recorded. However, a larger area was sampled (6 vs. 4 plots) and taxonomic identification was more complete at Andringitra: at Vevembe, there were 11 morphospecies for which the genus was unknown, while at Andringitra, there were only 5 (plus 6 entirely unidentified individual trees).

Only 19 identified tree species were common to both Andringitra and Vevembe (Table 4.4a-b). There were also substantial differences in species composition between the sites within Andringitra. There were 42 species present at Andringitra and 41 at Parc. Only 19 species were common to both sites. As there were only 2 plots at Parc and 4 at Ambarongy, there were approximately twice the species per unit area at Parc. While certainly not all tree species present at these sites have been detected in this study, this result indicates that sampling at the Parc site was likely sufficient to be comparable to Ambarongy and Vevembe.

There was significant variation in the number of plant families across sites ($H = 7.509$; $P = .0234$) and regions ($Z = -2.598$; $P = .0094$). Vevembe had the highest number of families per plot (17.25), followed by Parc (14.50) and Ambarongy (12.00) (Table 4.3). However, there were no differences in the number of species or genera either across sites or regions. Furthermore, there were no significant differences between the two Andringitra sites or within Vevembe, Ambarongy, or Parc (among plots) in the number of families, genera, or species. There was also no significant variation in Shannon Index values (H ; indicators of species diversity) across sites, regions, or between sites within Andringitra (Tables 4.3, 4.5).

Phenology

There was great variation in phenology and food production across sites, regions, and seasons. Across all sites, there was significant variation for the overlapping sampling period (May-August 2000) for overall fruiting ($H = 8.769$; $P = .0125$), leaf flushing ($H = 9.846$; $P = .0073$), and flowering ($H = 8.142$; $P = .0171$). Results are similar for the phenological patterns of tree species exploited for food by brown lemurs (fruit: $H = 9.269$; $P = .0097$; new leaves: $H = 9.269$; $P = .0097$; flowers: $H = 6.240$; $P = .0442$). In general, the availability of fruit, new leaves, and flowers was much greater at Andringitra than at Vevembe (Table 4.6a-b). The two sites at Andringitra also varied in food availability in overlapping months (June 1999-August 2000). There were differences between Ambarongy and Parc in productivity for all trees (fruit: $Z = -3.422$; $P = .0006$; new leaves: $Z = -2.924$; $P = .0035$; flowers: $Z = -3.924$; $P < .0001$) and brown

lemur food trees (fruit: $Z = -3.505$; $P = .0005$; new leaves: $Z = -3.090$; $P = .0020$; flowers: $Z = -2.915$; $P = .0036$). Ambarongy had more fruit and new leaves, while Parc had more flowers available (Table 4.6a-b).

In addition to inter-site differences in overall productivity, there was some evidence for seasonal differences in the availability of resources (Figure 4.6). At Ambarongy, there was significant variation across months in food availability (FA/ha) for new leaves ($H = 33.897$; $P = .0056$) and flowers ($H = 28.478$; $P = .0277$), but not for fruit ($H = 4.922$; $P = .9961$ NS). Similar variation was found in these resources when restricting the sample to only known brown lemur food sources (fruit: $H = 5.531$; $P = .9924$ NS; new leaves: $H = 35.876$; $P = .0030$; flowers: $H = 29.949$; $P = .0183$). There were three separate peaks in fruit production: in April, August, and the summer (December-February) (Figure 4.6). Leafing tended to be high from November-March, while flowering showed a clear peak in October (Figure 4.6).

There were no significant differences across months in the production of these resources at Parc or Vevembe (including within the food species-only sample). However, these analyses of variation were hampered by the small number of plots at Parc (2) and the short sampling period at Vevembe (5 months). Results from one group chi-square tests on total FA/ha showed significant variation in fruiting, leafing, and flowering across months at each site (including for the food-only samples). Parc had the highest fruit availability in February and June, the highest leaf flushing in October, and the largest flower availability in

November-April (Figure 4.6). Vevembe was characterized by very low production in all resources for all study months (May-September) (Figure 4.6).

Synchrony

Another means of determining seasonality in resources is to examine the synchrony of phenological events. The number of trees participating in fruiting, leaf flushing, and flowering varied across sites (Tables 4.7a-c; Figure 4.7). Across tree species, Ambarongy demonstrated a significantly clumped distribution ($CD > 1$) for the number of trees with new leaves ($CD = 7.00$) and flowers ($CD = 4.91$), but not for fruit ($CD = 0.74$ NS; Table 4.7a). Parc also demonstrated high overall synchrony, with significantly clumped distributions of fruit ($CD = 1.85$), new leaves ($CD = 2.96$), and flowers ($CD = 2.58$). Vevembe did not show significant synchrony in any phenological event. However, this site was sampled for only five months, a sampling period wherein synchrony would be more difficult to demonstrate. The results indicating higher productivity at Parc relative to Ambarongy contradict the above data on food availability (FA/ha) in the Andringitra sites. This is due to the lack of information on crown size or crop size in these synchrony measures.

The timing of peaks in the number of trees with resources was generally similar across sites (Figure 4.7). Both Ambarongy and Parc showed a summer (December-February) spike in fruiting trees, with a variable secondary peak in April-June (Figure 4.7a). The number of trees with new leaves peaked in November at both Andringitra sites (Figure 4.7b), while flowering synchrony was highest in October-November (Figure 4.7c). Although the sampling period for

Vevevembe is limited, this site does appear to follow loosely the timing of the Andringitra trends (Figure 4.7a-c).

Phenology-Climate Relationships

Regression analyses were used to assess the relationship of phenology and climate. In these tests, the correlation coefficients (r) were used to determine the strength of the association between seasonal shifts in food availability (FA/ha) and climatic factors (temperature and rainfall) – including seasonal climate changes over previous months in an annual cycle (Figures 8-9).

At Ambarongy, fruit production did not appear to be related to maximum or minimum temperature (Figure 4.8). The strongest relationship was a negative correlation ($r = -.963$; $P = .0020$) between fruit availability and rainfall 11 months prior; there was no significant positive correlation (Figure 4.8). Leaf flushing was positively correlated with rainfall and temperature in the concurrent month and in the 1-3 months prior (Figure 4.8b). Leaf production was also negatively correlated precipitation and temperatures 6-8 months prior (Figure 4.8b). The strongest relationship was the positive correlation of leafing with mean maximum temperature in the previous month ($r = .775$; $P = .0004$). Finally, flower production at Ambarongy was only significantly (negatively) correlated with minimum temperature 4 months prior ($r = -.699$; $P = .0078$); there was no significant positive correlation (Figure 4.8c).

At Parc, fruit availability was positively correlated with temperatures in the 2-4 months prior, with the strongest relationship with maximum temperature two months prior ($r = .813$; $P = .0007$; Figure 4.9a). New leaf production was

negatively correlated with minimum temperature four months prior ($r = -.730$; $P = .0107$), with no significant positive associations (Figure 4.9b). Flower availability was positively correlated with rainfall and temperature in the 0-2 months prior and negatively associated with these variables in the 5-7 months prior (Figure 4.9c). The strongest association was the negative correlation between flowering and mean maximum temperature seven months prior (Figure 4.9c). The strongest positive correlation for flowering was with mean minimum temperature in the current (0 prior) month ($r = .730$; $P = .0020$; Figure 4.9c).

Annual cycle analyses were not possible for Vevembe. Due to sample period constraints and the absence of temperature data, only the relationship between phenological events and rainfall was examined for 0-1 months prior. There were no significant correlations between fruit, new leaf, or flower production and precipitation in 0-1 months prior.

Regional Phenology Comparison

In this section, the phenological data are expressed as percentages of trees sampled to facilitate comparison with data from long-term studies at Ranomafana National Park (Overdorff and Wright, unpublished ms). The mean monthly percentages of trees (all species) containing fruit, flowers, or new leaves are shown for both sites at Andringitra, for Vevembe, and for Ranomafana (Figure 4.10). Like the measures for synchrony above, these results do not provide data on tree size or crop size. The most notable difference in these comparisons is the difference in the timing and magnitude of the fruiting peak at Ranomafana (Figure 4.10a). While the Andringitra sites had their highest fruiting percentages in the

summer months, Ranomafana is characterized by a striking peak in October and a dramatic decline in the summer (Figure 4.10a). Leafing patterns are broadly similar, although Ranomafana consistently maintains higher percentages across the annual cycle (Figure 4.10b). Trends in flowering are very consistent across southeastern sites, with peaks in October-November (Figure 4.10c).

DISCUSSION

Climate at Andringitra and Vevembe

The meteorological data collected during this study indicate similar seasonal weather trends at Andringitra and Vevembe. In April 1999-August 2000, Andringitra was characterized by warm, very wet summers with peaks in mean maximum and minimum temperatures in December and rainfall in February. This site also had cool, dry winters with the lowest temperatures in July and the least rainfall in June (but with a variable spike in rainfall in July). Though the data from Vevembe were limited, this site showed a similar cooling trend from April-May 2000, as well as low rainfall totals during April-September 2000 (but with an increase in July). Although no full year comparisons are possible, there was a tendency for Vevembe to be warmer and wetter than Andringitra.

These results accord broadly with long-term meteorological studies of southeastern Madagascar (Figure 4.11). Mean temperatures are highest in January and lowest in July-August in the eastern escarpment (Donque, 1972), including at Antanifotsy in the Andringitra region (Goodman and Andrianarimisa, 1996). In the present study, temperatures at the Ambarongy station followed a similar

seasonal pattern but were higher, reflecting the lower elevation (Paulian et al., 1971, in Goodman and Andrianarimisa, 1996). Earlier research at Vevembe indicates less extreme seasonality, with cooler maximum and warmer minimum temperatures (F. Mananasy, unpublished data from 1998-1999), although there are no data in the present study to corroborate this. At Ranomafana National Park (115 km NNE of Ambarongy), mean temperatures were lower than at Ambarongy, with the most extreme months occurring later in the seasons (Overdorff and Wright, unpublished ms). These results contradict a general trend of slightly decreasing mean temperatures from north to the south (Donque, 1972), again likely a sign of altitude differences across sites.

Seasonal patterns in precipitation at Ambarongy and Vevembe are also similar to those from previous long-term studies (Figure 4.12). In the Malagasy eastern escarpment, rainfall peaks occur from January-March, while the driest months tend to be September-October (with peaks occurring earlier in the north) (Donque, 1972). At Andringitra, precipitation levels are also highest in January but the driest month occurs earlier (June); there is also a marked increase in rainfall from west to east in the region (1,057-2,625 mm) (Goodman and Andrianarimisa, 1996, and sources cited therein). In this study, the eastern Andringitra site of Ambarongy followed the seasonality trends but had higher estimated annual rainfall (5,449.6 mm). However, the dramatic increase may be an aberration caused by unusually high rainfall during a single wet season. In the Vevembe region, annual totals are comparable (2,465.1 mm at nearby Vondrozo), with the most precipitation in February and the least in September (Donque,

1972). At Vevembe in 1998-1999 (F. Mananasy, unpublished data), rainfall was somewhat higher during a comparable period. Moreover, the peak in rainfall apparently occurred slightly later (although November-December data are missing); like Andringitra, the driest period immediately preceded the coolest months. While limited to April-September, the Vevembe data here exhibit similar trends (and even higher totals than those from Andringitra in 2000). Finally, Ranomafana National Park also demonstrates similar seasonal rainfall patterns, with a zenith in February and a nadir in September; annual totals at Ranomafana (2,838.3 mm) are relatively high for the southeast (Overdorff and Wright, unpublished ms).

Forest Structure at Andringitra and Vevembe

Forest structure varied in key aspects at Vevembe and Andringitra (including between the Ambarongy and Parc stations). Ambarongy was conspicuous for its tall trees with large crowns, while Parc had very short trees and Vevembe very small crowns. Crown volume may be considered a measure of food patch size (Janson, 1988; Overdorff, 1996), thus Ambarongy represents a potentially more productive habitat (see phenology discussion below). However, the values for both tree height and crown diameter are higher than those from previous research at Andringitra (Lewis et al., 1996), suggesting there may be high variability in microhabitats (or variability across time; see below). Inter-observer reliability may also be a question, as crown dimensions were estimated visually. Microhabitat variation is supported by significant differences in several structural attributes across plots both at Andringitra and Vevembe. Like

Ranomafana, but unlike other tropical regions (Ganzhorn et al., 1999; Wright, 1999; Overdorff and Wright, unpublished ms), Andringitra and Vevembe lacked any trees with crown diameters exceeding 30 m; the distribution of crown diameters suggests Ambarongy trees also may have larger crowns than those at Ranomafana (with 13% *vs.* 7% exceeding 10 m; Overdorff and Wright, unpublished ms). The generally smaller tree crowns (particularly those of lemur feeding trees) are seen as evidence for the relative poverty of Malagasy rain forests for primate frugivores (Ganzhorn et al., 1999; Wright, 1999).

Although some forest characteristics clearly varied across sites, there were no differences in dbh, tree density, or structural diversity, leading to an overall similarity in total basal area (a measure of forest biomass). Moreover, the values for these features were very similar to those reported previously at Andringitra (Lewis et al., 1996), as well as at other forests across eastern Madagascar (Ganzhorn et al., 1997, and sources therein; Overdorff and Wright, unpublished ms) and other tropical regions (Gentry, 1993). However, consistent with previous studies at Ranomafana (Schatz and Malcomber, in Overdorff and Wright, unpublished ms), Andringitra and Vevembe both appear to have smaller tree diameters compared to African and South American forests (Gentry, 1993; Wright, 1999), with no trees exceeding 100 cm dbh. These results (as well as those for height and crown size above) contradict the assertion that Ambarongy, on the periphery of the national park, is particularly degraded (Lewis et al., 1996); this suggests bias between studies in plot selection or substantial forest regeneration since 1993. Although formerly agricultural areas on the margins of

study sites have recovered dramatically in that period (personal observation), it is difficult to assess regeneration in interior forest where these studies were carried out.

Diversity at Andringitra and Vevembe

Despite differences in species composition, the Andringitra sites and Vevembe did not differ in the levels of species diversity in tree communities. Only the number of families varied significantly across sites, with Vevembe showing the highest diversity. Comparisons across the eastern rain forest region are hindered greatly by a lack of concordance in sampling area (see variation in plot size in Overdorff, 1991; Lewis et al., 1996; Ganzhorn et al., 1997; Overdorff and Wright, unpublished ms). Clearly, there is less chance of encountering new species with increasing sample area. Thus, studies with smaller cumulative plot sizes are subject to overestimation in diversity per unit area. Despite these comparison pitfalls, the results here suggest that both Andringitra and Vevembe may be relatively species-poor forest communities. Forty-two species were detected in a 0.25 ha area at Ambarongy, while 41 were identified in 0.125 ha at Parc (with 64 total species at Andringitra); at Vevembe, 60 tree species were recorded in a 0.25 ha sampling area. These values are low relative to other eastern Malagasy rain forests (76-80 per 0.1 ha) but still higher than mainland African rain forests (33 per 0.1 ha) (Gentry, 1993). In addition, species diversity indices were lower than elsewhere in the east (Overdorff, 1991; Abraham et al., in Ganzhorn et al., 1997).

Interestingly, Lewis et al. (1996) recorded much higher species diversity at Andringitra (74 per 0.1 ha across sampling areas). This result again raises the possibility of bias from plot selection or changes in species composition since 1993. Additionally, Lewis et al. (1996) may have made finer distinctions in species classification. Indeed, at the family level, the differences between studies in diversity are less striking: 20-26 families per locality in 1993 (Lewis et al., 1996) *vs.* 19-23 in the present analysis. Thus, on balance, the sites in this study have equivalent, somewhat low diversity in tree species composition, but fall in with other Malagasy sites in being more diverse than mainland African forests (Gentry, 1993; but see Sussman and Rakotozafy, 1994, for dry forest and Overdorff and Wright, unpublished ms, for rain forest).

Phenology and Food Availability at Andringitra and Vevembe

There were clear differences in the production of fruit, flowers, and leaves across study sites. Although not all seasons were considered at Vevembe, total resource availability of fruit and new leaves (including that of brown lemur food species) at Ambarongy greatly exceeded the productivity at Parc and, especially, at Vevembe. Flowers were most prevalent at Parc. As noted, the Malagasy eastern rain forest is highly variable from year to year in the timing and magnitude of resource production (Overdorff, 1996; Wright, 1999; Overdorff and Wright, unpublished ms). Accordingly, these analyses are conditional pending long-term research at these sites. However, the phenological measures used in this study are based in part on tree crown size, so presumably stable structural factors play a significant role in determining resource availability (but see

Chapman et al., 1992, for a discussion of the reliability of these estimators). The highest availability scores at Ambarongy are then partly linked to the high mean crown volume discussed earlier.

There were clear changes in forest productivity across seasons. Synchrony in the number of individual trees participating in phenophases was apparent at both Andringitra sites (more data are needed to evaluate synchrony at Vevembe). However, the timing of phenological peaks was not tightly constrained between sites at Andringitra. Despite similar synchrony patterns, maxima in fruiting, flowering, and leaf flushing were staggered differently at Ambarongy and Parc. Mid-summer represented a fruiting peak at both sites, but additional distinct peaks occurred in June (Parc), April and August (Ambarongy). Leafing and flowering were similarly out of phase at the two sites, with leaf flushing peaking earlier Parc and flowering occurring earlier at Ambarongy. Again, while annual data are unavailable, Vevembe exhibited very low productivity throughout the sampling period.

This variation in phenology within Andringitra may be an artifact of limited sampling, particularly in light of the high inter-annual variability observed elsewhere in Madagascar (Overdorff, 1996) and in other tropical regions (Newstrom et al., 1994; Chapman et al., 1999). Alternatively, Parc and Ambarongy may represent distinct microhabitats both structurally (see above) and temporally despite their close proximity (Figure 4.1a). This may entail differences in soil fertility (Ganzhorn et al., 1999; Wright, 1999) or differences in local terrestrial animal communities involved in significant plant-animal

interactions. The sites are effectively 7 km apart by land (i.e., each is 3.5 km from the narrow headwaters of the Iantara River) and the lemur communities appear to vary in species composition and density (Chapters 1, 3).

Regardless of the possible causes, the variation in the timing of resource production has clear repercussions for any observed linkage with temperature and rainfall. Accordingly, Ambarongy demonstrated relatively strong associations between new leaf flushing and meteorological factors in concurrent and immediately preceding months, while at Parc there were stronger correlations between fruiting and flowering and climate variables. These results agree with a lack of consistent associations between phenology and climatic factors reported by Overdorff and Wright (unpublished ms) for Ranomafana (although these authors only compared phenophases with climate data from concurrent months). Solar radiation (a variable not examined here) may be a more important factor than precipitation or rainfall (van Schaik et al., 1993). However, irradiance levels should be constant across sites at Andringitra and thus would not explain the observed variation in phenology at Ambarongy and Parc.

Unfortunately, the food availability scores used in this study are not directly comparable to other descriptions of seasonal phenology in Madagascar (e.g., Hladik, 1980; Overdorff, 1991; Meyers and Wright, 1993; Hemingway and Overdorff, 1999; Overdorff and Wright, unpublished ms). Consequently, percentages of trees participating in phenological stages were also calculated (Figure 4.10). These analyses yielded somewhat different results, notably Parc became comparable to Ambarongy in fruit and new leaf availability scores, and

the two sites were far more similar in the timing of resource production across seasons. Vevembe remained the least productive for all measures. The inclusion of long-term data from Ranomafana (1988-1994; Overdorff and Wright, unpublished ms) in these comparisons yields striking results. Ranomafana had much higher overall availability of leaves and somewhat greater fruit production (although flowering was less prevalent) (Overdorff and Wright, unpublished ms).

Perhaps more remarkable is the near reversal in food production across seasons (see Figure 4.10): at Ranomafana, fruit availability is highest from July-December with a definitive peak in October (Overdorff and Wright, unpublished ms); by contrast, fruit production at Andringitra increased from December-May (when fruit availability declines dramatically at Ranomafana). This is particularly compelling when considering that seasonal shifts in climatic variables were similar across the southeastern rain forest region (see above). Again, it must be noted that there is great variation in the seasonality of resources at Ranomafana across years and studies (Overdorff, 1996; Hemingway and Overdorff, 1999; Overdorff and Wright, unpublished ms) and this surprising result must await confirmation from long-term studies at Andringitra. Provisionally, however, the timing of scarce and abundance seasons for animal consumers appears to vary dramatically across southeastern Madagascar. Nevertheless, in terms of total annual food availability, these sites are similar to (or somewhat less productive than) other Malagasy rain forests – which in turn have been described as resource poor relative to other tropical regions (Wright, 1999).

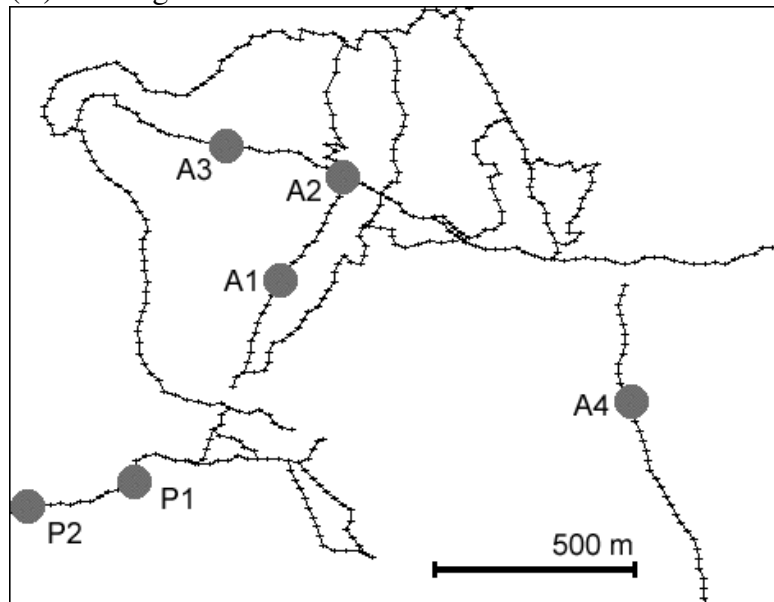
Clear effects of disturbance on forest structure, diversity, productivity, and, ultimately, lemur communities are lacking in this study. Ambarongy, Parc, and Vevembe have all sustained low levels of human encroachment, with the Vevembe region probably most affected (although not by human settlement). There is certainly great variation in some structural variables (e.g., crown volume) and resource availability across these sites. However, other characteristics such as tree biomass and species diversity are comparable across sites. Moreover, with similar levels of human disturbance, the difference within Andringitra may be more reflective of microhabitat variation.

The relationships among climate, habitat quality, and lemur communities at Andringitra and Vevembe does not strongly support the expectations from comparative studies of primate habitats across Madagascar (Ganzhorn et al., 1997) or the tropics (Reed and Fleagle, 1995). These include the correlation between rainfall and/or forest productivity and primate species richness (Reed and Fleagle, 1995; Ganzhorn et al., 1997; Kay et al., 1997); climate and tree diversity being equal, mild disturbance may also increase resource output and lemur diversity (Ganzhorn et al., 1997). Despite similarities in climate, there was tremendous variation in food production among and within sites, as well as in lemur diversity (although tree diversity was constant, as expected). Resource availability was higher at Andringitra, and this site does support a much richer and more populous lemur community (Chapter 3). Results for Vevembe indicating relatively low forest productivity, small tree crown size, and a small, species-poor lemur population accord with previous studies demonstrating a

negative impact of disturbance on frugivorous lemurs (Sussman and Rakotazafy, 1994; White et al., 1995). However, Andringitra and Vevembe are distant enough and forest species composition distinct enough to require that these sites be compared on a larger biogeographic scale. As Ganzhorn et al. (1997) point out, on a large scale, lemur species diversity will likely decrease with habitat disturbance.

In conclusion, despite many similarities in climate, forest structure, and forest diversity, there were important differences across study sites in resource availability. The Andringitra sites – particularly Ambarongy – had the highest production of resources for primary consumers, comparable to other rain forests sites in southeastern Madagascar. By contrast, Vevembe had much lower resource availability. It is important to note also that there was marked seasonality in phenology across the region, and that the timing of seasonal booms and busts in food production varied dramatically among and even within sites. Thus, while some locations may be more productive overall, lemur communities in all of these sites are challenged by a high degree of unpredictability of food resources across time and space.

(A) Andringitra



(B) Vevembe

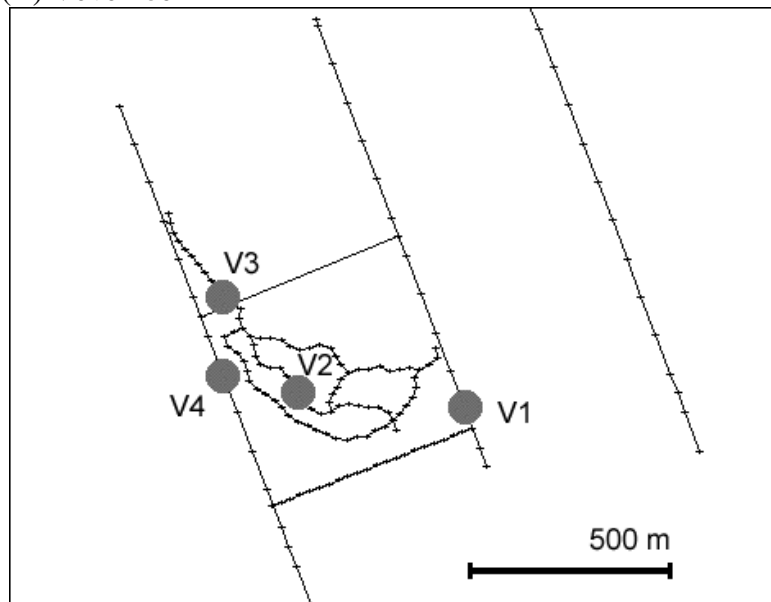


Figure 4.1: Botanical Sampling Locations at Andringitra (A) and Vevembe (B).
Within Andringitra, A1-A4 are in the Ambarongy site and P1-P2 in the Parc site.

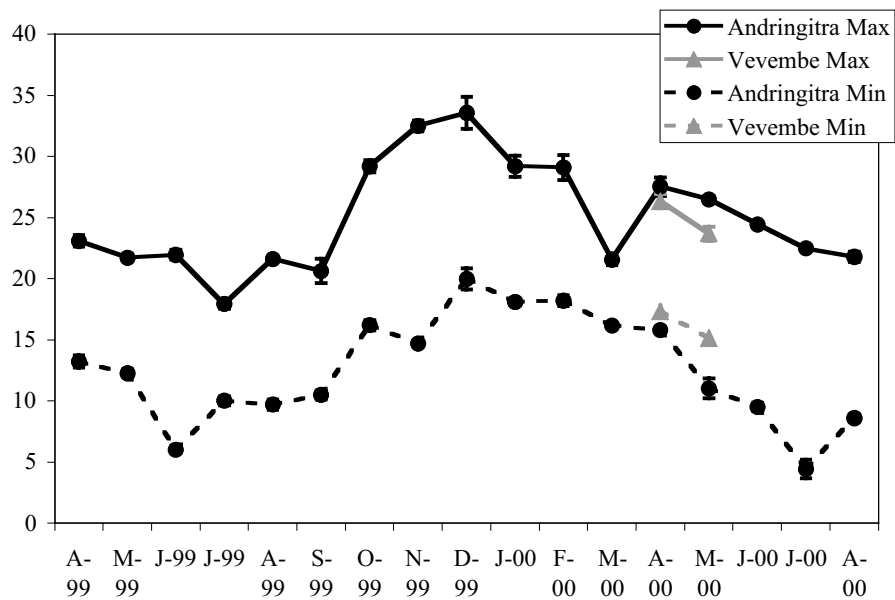


Figure 4.2: Mean Monthly Temperature Maxima and Minima ($^{\circ}\text{C}$) with Standard Error at Andringitra and Vevembe.

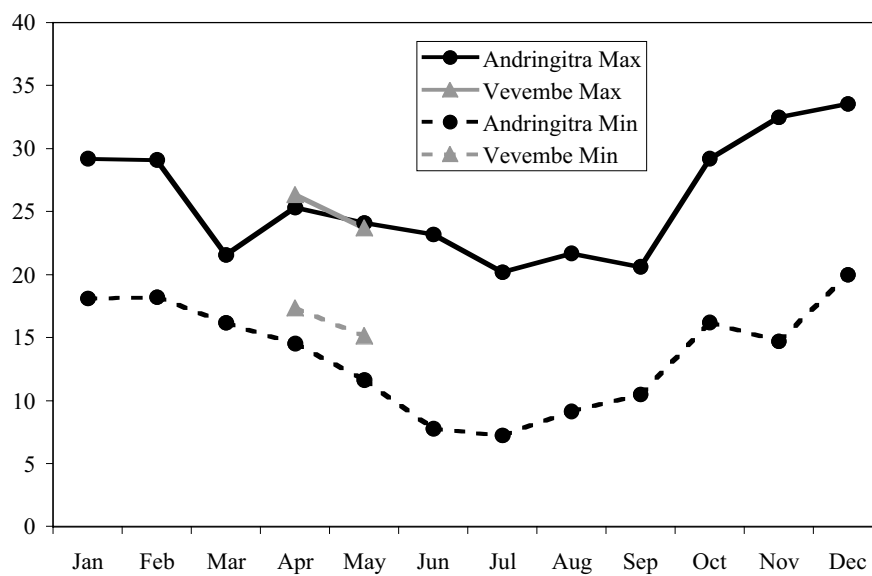


Figure 4.3: Mean Monthly Temperatures ($^{\circ}\text{C}$) at Andringitra and Vevembe.

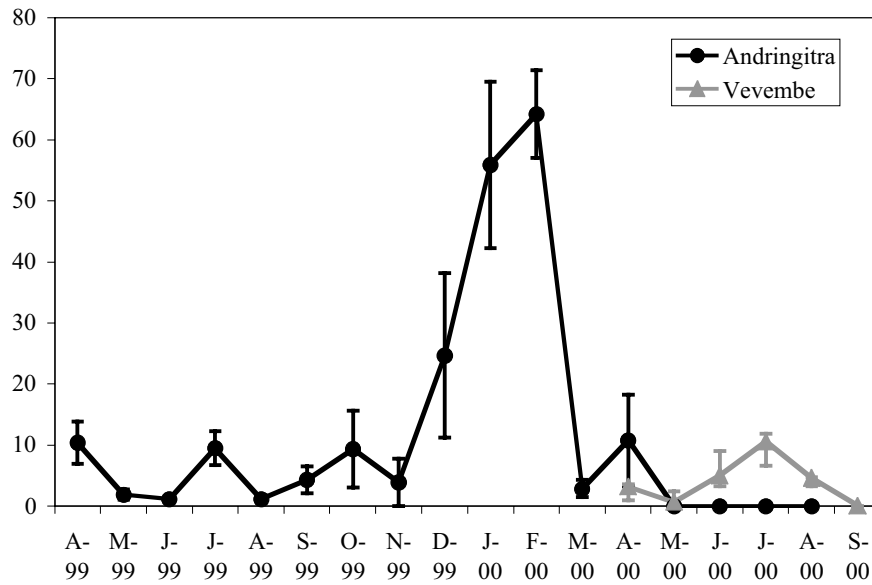


Figure 4.4: Mean Daily Rainfall (mm) and Standard Error at Ambarongy Station, Andringitra National Park and Vevembe Forest.

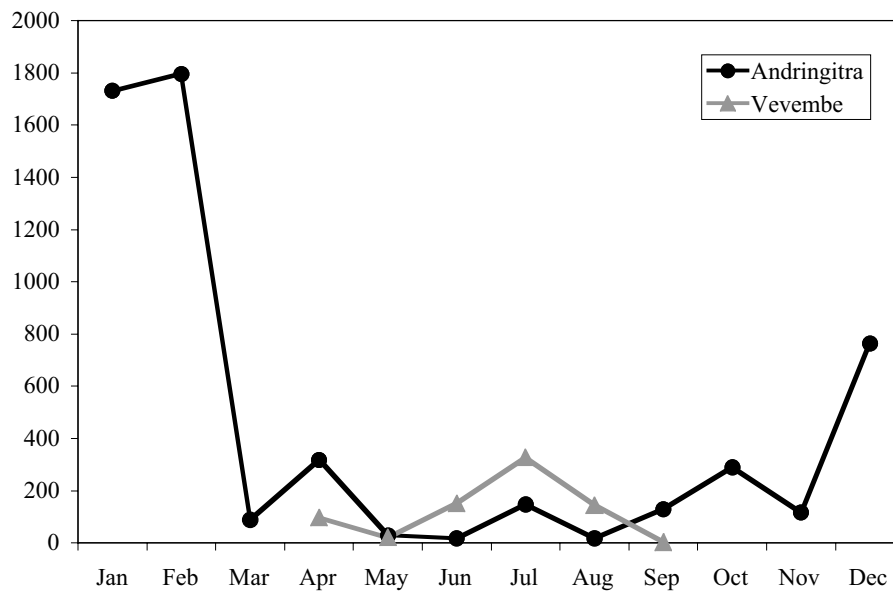
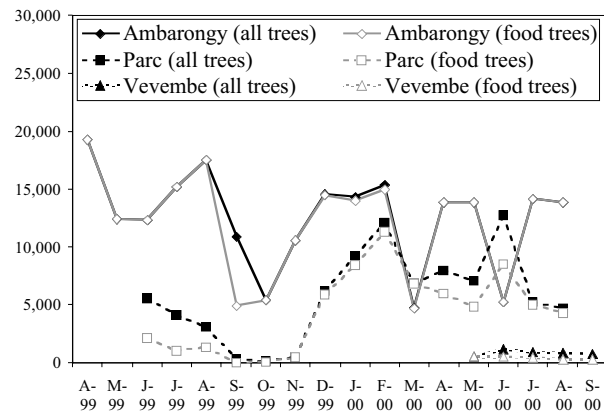
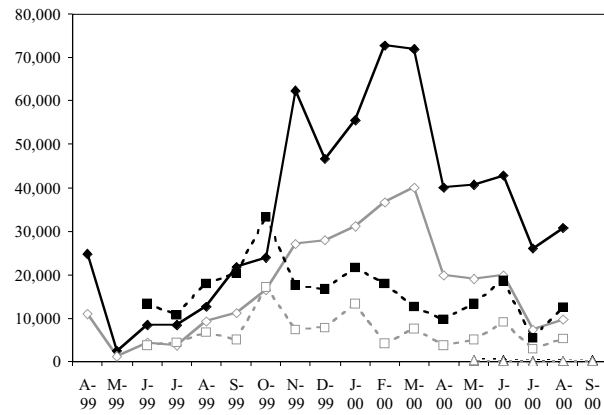


Figure 4.5: Monthly Rainfall (mm) at Andringitra and Vevembe.

(A) Fruit



(B) New Leaves



(C) Flowers

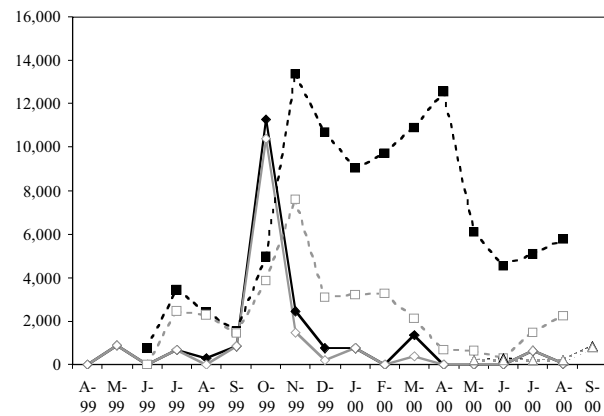
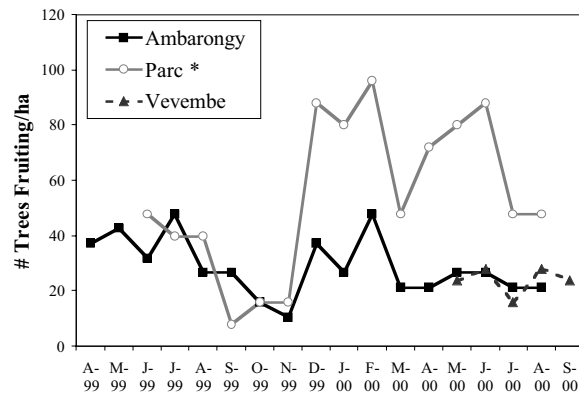
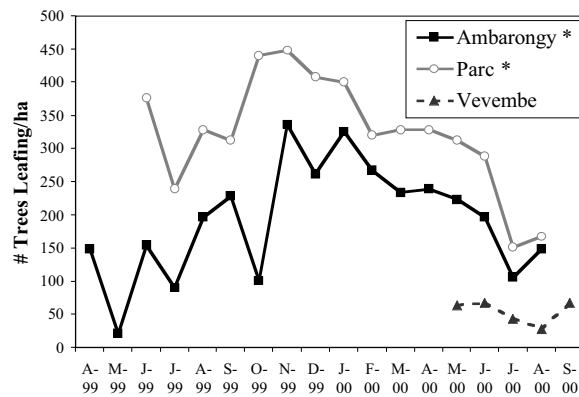


Figure 4.6: Food Availability (FA/ha) Across Sites.

(A) Fruit



(B) New Leaves



(C) Flowers

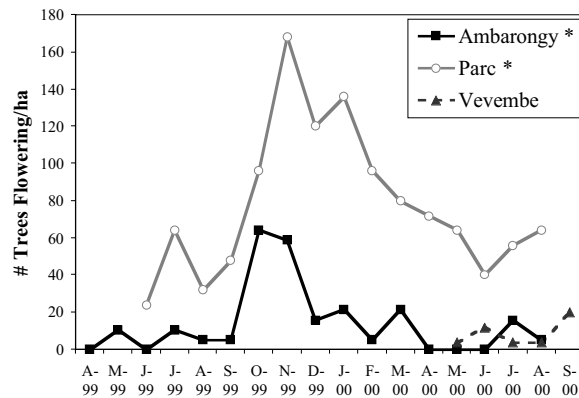
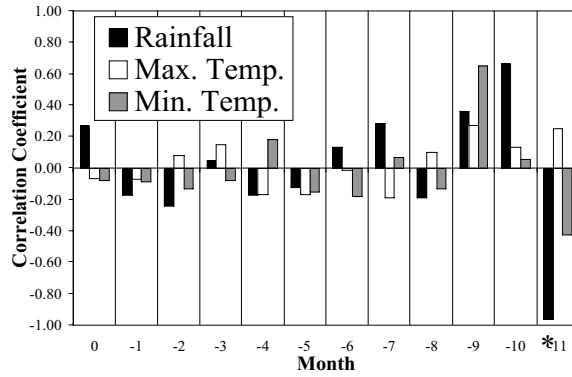
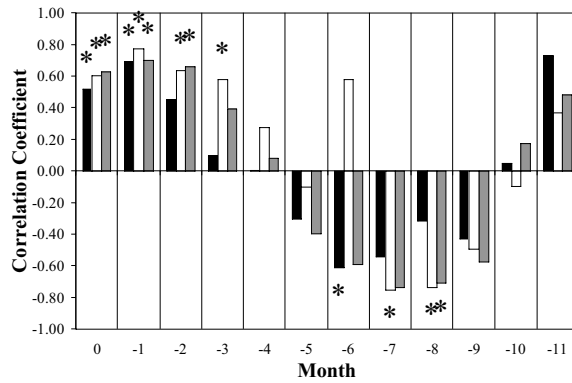


Figure 4.7: Synchrony Across Sites for Fruiting, Leaf Flushing, and Flowering. Significantly clumped distributions are indicated by asterix (*).

(A) Fruit



(B) New Leaves



(C) Flowers

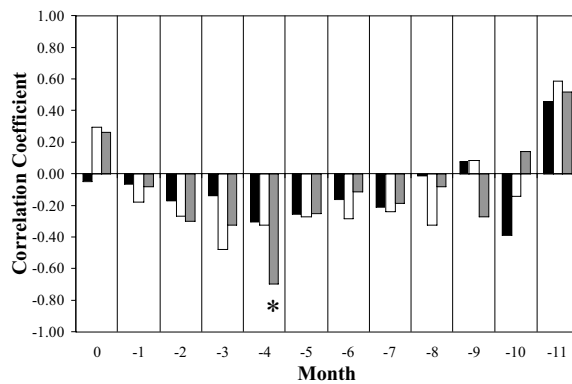
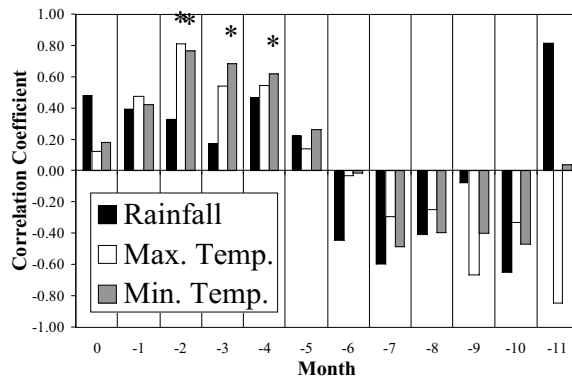
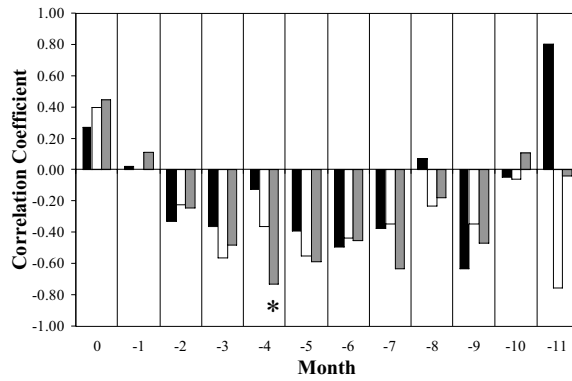


Figure 4.8: Phenology/Meteorology Relationship at Ambarony. Coefficients (r) represent the relationship between food availability (FA/ha) of fruit, new leaves, and flowers and climate variables for concurrent months and previous months within an annual cycle. Asterisk (*) denotes a significant correlation.

(A) Fruit



(B) New Leaves



(C) Flowers

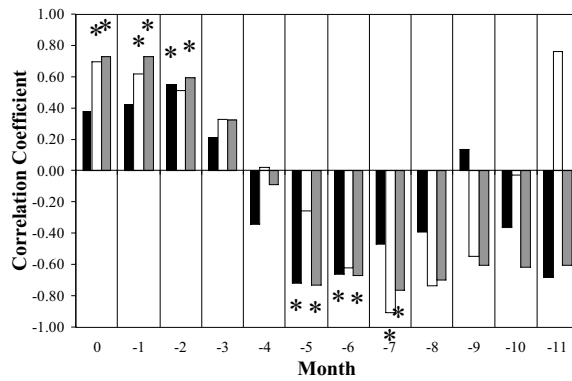
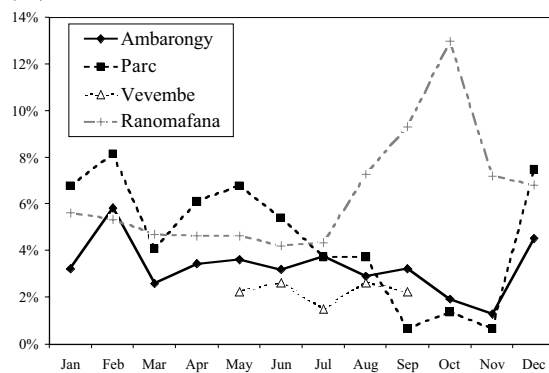
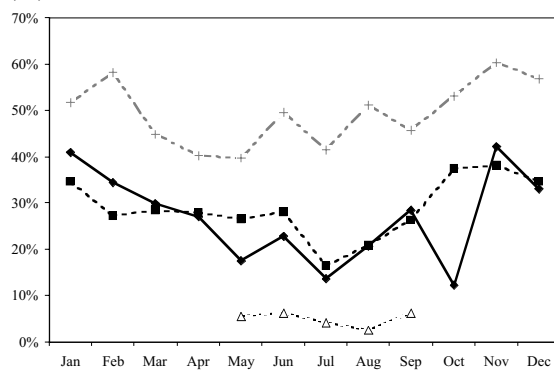


Figure 4.9: Phenology/Meteorology Relationships at Parc. See Figure 4.8 for description.

(A) Fruit



(B) New Leaves



(C) Flowers

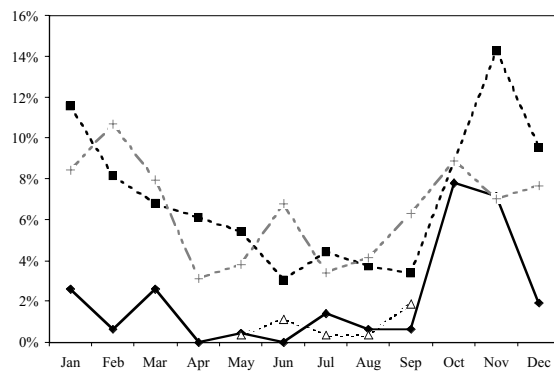


Figure 4.10: Percentage of Trees Producing Fruit (A), New Leaves (B), and Flowers (C) at Southeastern Sites. Ranomafana data from Overdorff and Wright (unpublished ms).

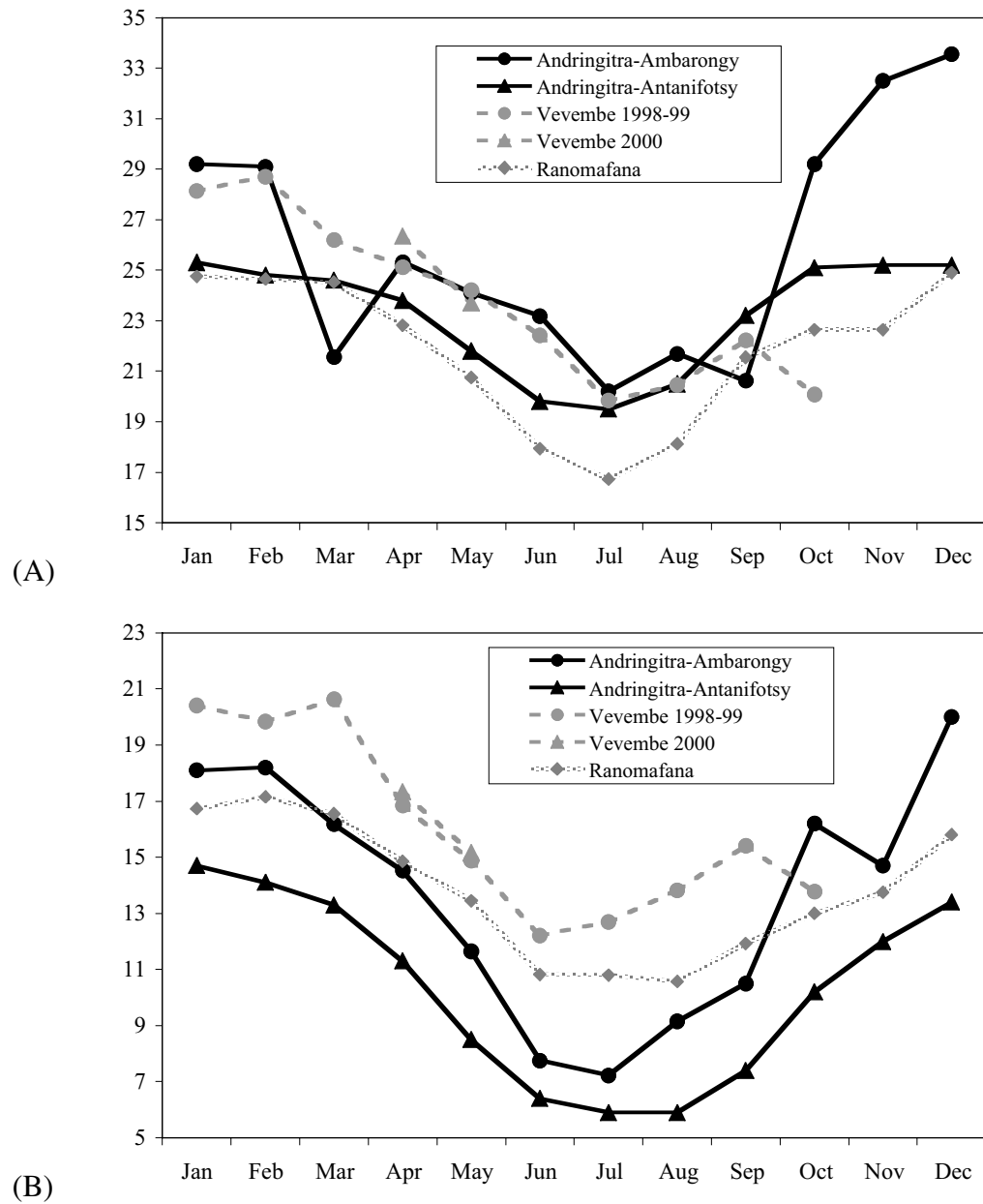


Figure 4.11: Mean Temperature Maxima (A) and Minima (B) ($^{\circ}\text{C}$) at Southeastern Madagascar Sites. Sources for additional sites are: Antanifotsy (Goodman and Andrianarimisa, 1996), Vevebe 1998-9 (F. Mananasy, unpublished data), and Ranomafana (Overdorff and Wright, unpublished ms).

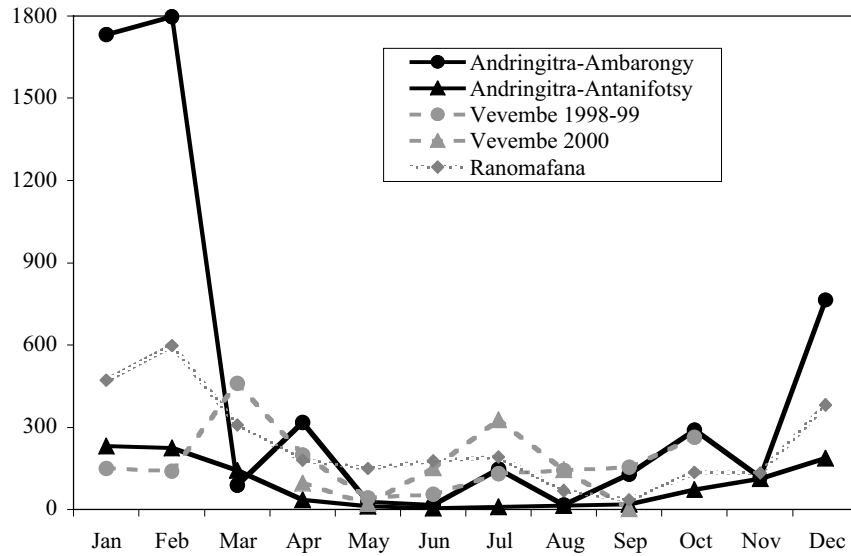


Figure 4.12a: Mean Monthly Rainfall (mm) at Southeastern Madagascar Sites.
See Figure 4.11 for sources.

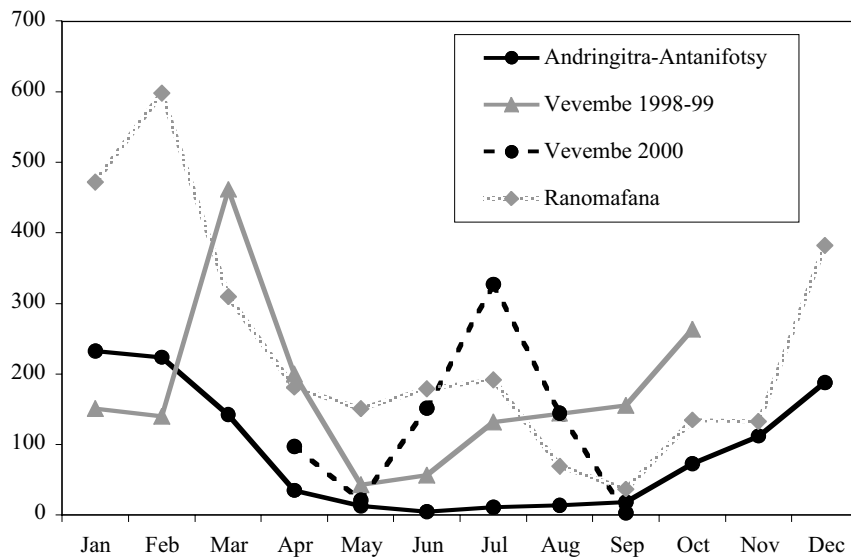


Figure 4.12b: Mean Monthly Rainfall (mm) at Southeastern Madagascar Sites.
Ambarongy is excluded. See Figure 4.11 for sources.

Table 4.1: Forest Structure from Large Plots¹.

Site	Plot	N	DBH (cm)	Height (m)	Crown Volume (m ³)	Basal Area (m ² /ha)	Structural Diversity (H)
Andringitra - Ambarongy	A1	65	16.8	20.0	191.4	28.5	0.519
Andringitra - Ambarongy	A2	30	27.6	20.7	692.9	44.3	0.619
Andringitra - Ambarongy	A3	59	18.9	19.6	505.8	34.2	0.533
Andringitra - Ambarongy	A4	71	21.6	21.9	1082.7	56.9	0.625
Andringitra - Parc	P1	79	15.5	13.2	115.5	25.7	0.470
Andringitra - Parc	P2	69	15.8	13.2	178.6	23.9	0.503
Vevebe	V1	78	20.5	20.5	102.1	51.0	0.649
Vevebe	V2	57	17.2	17.2	40.5	24.4	0.564
Vevebe	V3	62	19.1	19.1	18.2	40.5	0.574
Vevebe	V4	70	16.4	16.4	43.4	27.2	0.519

¹ Values are means for dbh, height, and crown volume. Basal area is the sum area of all trees in each plot (m²)per hectare. Structural diversity (H) is the Shannon Index value for dbh.

Table 4.2: Forest Structure from Small Plots.

Site	Plot	Ground Cover	Bamboo /ha.	Epiphytes /ha.	Herbs /ha.	Saplings /ha.	Ground Ferns/ha.	Lianas /ha.
Andringitra - Ambarongy	A1	40%	3,200	800	0	30,000	3,600	3,600
Andringitra - Ambarongy	A2	30%	2,800	0	400	13,600	2,000	3,600
Andringitra - Ambarongy	A3	50%	1,200	800	0	27,600	5,600	2,000
Andringitra - Ambarongy	A4	50%	800	0	400	32,800	0	4,800
Andringitra - Parc	P1	40%	1,600	400	2,000	18,800	0	5,600
Andringitra - Parc	P2	20%	0	2,000	400	10,000	800	4,800
Vevebe	V1	80%	0	400	27,200	26,800	0	3,600
Vevebe	V2	40%	0	2,800	26,800	60,000	0	2,400
Vevebe	V3	70%	20,000	2,000	24,800	32,800	0	11,600
Vevebe	V4	5%	0	0	0	4,000	0	62,800

Table 4.3: Taxonomic Diversity from Large Plots.

Site	Plot	Families	Genera	Species	Species Diversity (H) ¹
Andringitra - Ambarongy	A1	9	12	18	1.055
Andringitra - Ambarongy	A2	11	13	16	1.172
Andringitra - Ambarongy	A3	14	18	23	1.122
Andringitra - Ambarongy	A4	14	15	19	1.188
Andringitra - Parc	P1	14	22	27	1.250
Andringitra - Parc	P2	15	23	26	1.252
Vevembe	V1	19	20	28	1.264
Vevembe	V2	16	15	23	1.207
Vevembe	V3	17	18	22	1.072
Vevembe	V4	17	17	25	1.269

¹ Species diversity (H) is the mean Shannon Index value.

Table 4.4a: Tree Species at Andringitra National Park.

Family	Species	Vernacular	Food ¹
Anacardiaceae	<i>Rhus taratana</i> (Baker) H. Perrier	tarantana	
Annonaceae	<i>Xylopia</i> sp. "ramiavona"	ramiavona	
Apocynaceae	<i>Cabucala</i> sp. "kaboka"	kaboka	
Apocynaceae	<i>Mascarenhasia arborescens</i> A. DC.	herodrano	
Aquifoliaceae	<i>Ilex mitis</i> (L.) Radlk.	hazondrano	
Araliaceae	<i>Polyscias</i> sp. "maniny"	maniny	
Araliaceae	<i>Polyscias</i> sp. "vatsilana ravimboanjo"	vatsilana ravimboanjo	
Araliaceae	<i>Schefflera vatsilana</i>	vatsilambato	
Araliaceae	spec. indet. "vatsilana"	vatsilana	
Burseraceae	<i>Canarium madagascariense</i> Engler	ramy	x
Canellaceae	<i>Cinnamosma madagascariensis</i> Danguy	fanalamangidy	
Clusiaceae	<i>Calophyllum</i> aff. <i>paniculatum</i> P. Stevens	vitanona	x
Clusiaceae	<i>Rheedia</i> sp. "voamalambotaholahy"	voamalambotaholahy	x
Compositae	<i>Brachylaena ramiflora</i> (DC.) Humbert	kotolahy	
Cunoniaceae	<i>Weinmannia rutenbergii</i> Engl.	lalona	
Ebenaceae	<i>Diospyros gracilipes</i> Hiern	mandravaianonana	
Elaeocarpaceae	<i>Sloanea rhodantha</i>	vanana	
Erythroxylaceae	<i>Erythroxylum</i> sp. "malambovony"	malambovony	x
Euphorbiaceae	<i>Antidesma petiolare</i>	hazonovy	
Euphorbiaceae	<i>Bridelia tulasneana</i> Baillon	harina	
Euphorbiaceae	<i>Macaranga myriolepidea</i> Baker	karambitona	
Euphorbiaceae	<i>Macaranga</i> sp. "mokaranana"	mokaranana	
Flacourtiaceae	spec. indet. "faritraty"	faritraty	
Icacinaceae	<i>Cassinopsis madagascariensis</i> Baillon	hazomafaika	
Lauraceae	<i>Beilschmiedia velutina</i> Kosterm.	sarivanga (sarivanana)	
Lauraceae	<i>Cryptocarya</i> "acuminata"	tavolo malady	
Lauraceae	<i>Cryptocarya</i> cf. "flavescens"	tavolo maintso	x
Lauraceae	<i>Cryptocarya</i> cf. <i>crassifolia</i> Baker	tavolo zahana	
Lauraceae	<i>Cryptocarya</i> sp. "tavolo molaliambo"	tavolo molaliambo	
Lauraceae	<i>Cryptocarya</i> sp. "tavolo pina"	tavolo pina	x
Lauraceae	<i>Ocotea auriculiformis</i> Kosterm.	varongy ravinamotana	x
Lauraceae	<i>Ocotea</i> cf. <i>racemosa</i> (Danguy) Kosterm.	varongy fotsy	x
Lauraceae	<i>Ocotea longipes</i> Kosterm.	varongy ravinbakoka	x
Lauraceae	<i>Ocotea</i> sp. "varongy"	varongy	x
Lauraceae	<i>Potameia</i> sp. "saritovokaromay"	saritovokiaromay	
Leguminosae	<i>Albizia gummifera</i> (J.F. Gmelin) C.A. Smith	volomborona	
Leguminosae	<i>Calliandra alternans</i>	ambilazona	

¹ Parts of these tree species (fruit, flowers, leaves) were consumed by brown lemurs at Andringitra during this study.

Table 4.4a: Tree Species at Andringitra National Park (cont.).

Family	Species	Vernacular	Food ¹
Leguminosae	<i>Dalbergia baroni</i> Baker	voamboana	x
Loganiaceae	<i>Anthocleista</i> sp. "dendemy"	dendemy	
Melastomataceae	<i>Dechaetanthra cordifolia</i> Baker	tsitrotroka (tsingotroka)	x
Monimiaceae	<i>Tambourissa</i> sp. "ambora"	ambora	x
Monimiaceae	<i>Tambourissa</i> sp. "tambonetra tambalakoko"	tambonetra tambalakoko	
Monimiaceae	<i>Tambourissa</i> sp. "tambonetra"	tambonetra	
Myrsinaceae	<i>Oncostemon botryoides</i> Baker	kalafana	x
Myrtaceae	<i>Eugenia</i> sp. "robe"	robe	
Myrtaceae	<i>Syzygium</i> "emirnsensis"	robary	x
Myrtaceae	<i>Syzygium</i> sp. "rotrafotsy"	rotrafotsy	
Myrtaceae	<i>Syzygium</i> sp. "rotramena"	rotramena	x
Rubiaceae	<i>Canthium micrantha</i> Baker	fatsikahitra	x
Rubiaceae	<i>Gaertnera</i> sp. "hazotoho"	hazotoho	x
Rubiaceae	<i>Psychotria</i> sp. "fohaninasity"	fohaminatsity	x
Rubiaceae	<i>Schismatoclada farahimpensis</i> Homolle	hazomporetaka	
Sapindaceae	<i>Allophylus cobbe</i>	dikana	x
Sapindaceae	<i>Plagioscyphus louvelii</i> Danguy & Choux	lanary mainty	
Sapindaceae	<i>Tina striata</i> Radlk.	lanary	
Sapotaceae	<i>Chrysophyllum boivinianum</i> (Pierre) Baehni	rahiaka	x
Sapotaceae	<i>Lambramia louvelii</i> Capuron ex Aubreville	nato	
Sterculiaceae	<i>Dombeya</i> sp. "hafodahy"	hafodahy	x
Tiliaceae	<i>Grewia</i> sp. "hafipotsy"	hafipotsy	x
Verbenaceae	<i>Premna corymbosa</i> (Burm. f.) Rottler & Willd.	odimamo	
	spec. indet. "fatsy"	fatsy	
	spec. indet. "hazomena"	hazo mena	x
	spec. indet. "ramanjavona"	ramanjavona grande feuille	
	spec. indet. "tarambito"	tarambito	

¹ Parts of these tree species (fruit, flowers, leaves) were consumed by brown lemurs at Andringitra during this study.

Table 4.4b: Tree Species at Vevembe Forest.

Family	Species	Vernacular	Food ¹
Agavaceae	<i>Dracaena</i> sp. "hasina"	mangary	x
Anacardiaceae	spec. indet. "sandramy"	sandramy	x
Annonaceae	<i>Ambavia capuronii</i> (Cavaco and Keraudren) Le Thomas	rombavy	
Annonaceae	<i>Xylopia</i> sp. "ramiavona"	fotsivavo	x
Apocynaceae	<i>Cabucala cryptophlebia</i> (Baker) Pichon	kabokala	
Apocynaceae	<i>Cabucala madagascariensis</i>	tandrokosy	
Apocynaceae	<i>Mascarenhasia arborescens</i> A. DC.	herodrano	
Aquifoliaceae	<i>Ilex mitis</i> (L.) Radlk.	hazondrano	
Araliaceae	spec. indet. "vatsilana"	vatsilana	
Asteraceae	<i>Vernonia</i> sp. "tavilona"	vilona	x
Burseraceae	<i>Canarium madagascariense</i> Engler	ramy	
Clusiaceae	<i>Calophyllum</i> aff. <i>paniculatum</i> P. Stevens	vitanona	
Clusiaceae	<i>Garcinia</i> sp. "kimbaletaka"	kimbaletaka	x
Clusiaceae	<i>Mammea</i> "angustifolia var. <i>pseudoprotorhus</i> "	zambo	x
Combretaceae	<i>Combretum madagascariensis</i>	tamenaka	
Combretaceae	<i>Terminalia tetranora</i>	veso	x
Cunoniaceae	<i>Weinmannia rutenbergii</i> Engl.	lalona	
Ebenaceae	<i>Diospyros gracilipes</i> Hiern	hazomainty	x
Elaeocarpaceae	<i>Sloanea rhodantha</i>	vanana	
Erythroxylaceae	<i>Erythroxylum</i> sp. "malambovony"	malambovony	x
Euphorbiaceae	<i>Uapaka louvelii</i> M. Denis	voapaka	x
Flacoutaceae	<i>Homalium</i> sp. "hazoambato"	hazoambato	x
Icacinales	<i>Apodytes thouvenotii</i> Danguy	malanimata	x
Lauraceae	<i>Ocotea</i> cf. <i>racemosa</i> (Danguy) Kosterm.	varongy fotsy	x
Lauraceae	<i>Ocotea</i> sp. "varongy mena"	varongy mena	x
Leguminosae	<i>Albizia gummifera</i> (J.F. Gmelin) C.A. Smith	sambalahy	x
Loganiaceae	<i>Anthocleista</i> sp. "dendemy"	dendemy	x
Moraceae	<i>Streblus dimeptate</i> (Bureau) C.C. Berg	andromena	
Myrsinaceae	<i>Oncostemum</i> sp. "kalafambakaka gf"	sitohitohy	x
Myrtaceae	<i>Syzygium</i> sp. "rotrafotsy"	rotrafotsy	
Myrtaceae	<i>Syzygium</i> sp. "rotramainty"	rotramainty	
Myrtaceae	<i>Syzygium</i> sp. "rotramena"	rotramena	x
Ochnaceae	<i>Diporidium</i> sp. "menahy"	menahy	
Oleaceae	<i>Noronhia</i> sp. "solaitra fotsy"	solaitra fotsy	x
Oleaceae	<i>Noronhia</i> sp. "solaitra"	hazombary	x

¹ Parts of these tree species (fruit, flowers, leaves) were consumed by brown lemurs at Vevembe during this study.

Table 4.4b: Tree Species at Vevembe Forest (cont.).

Family	Species	Vernacular	Food ¹
Palmae	<i>Dyopsis nodifera</i>	sira hazo	x
Palmae	<i>Ravanea</i> sp. "lafa gf"	lafa gf	x
Palmae	<i>Ravanea</i> sp. "lafa pf"	lafa pf	x
Pandanaceae	<i>Pandanus</i> sp. "tsirika gf"	tsirika gf	x
Pandanaceae	<i>Pandanus</i> sp. "tsirika mf"	tsirika mf	x
Pandanaceae	<i>Pandanus</i> sp. "tsirika pf"	tsirika pf	x
Rubiaceae	<i>Canthium micrantha</i> Baker	fatsikahitra	x
Rubiaceae	<i>Gyrostipula foveolata</i> (Capuron) Leroy	valotra	x
Rubiaceae	<i>Mussaenda erectiloba</i> Wernham	malimiravina	x
Rubiaceae	<i>Psychotria</i> sp. "fohaninasity gf"	fohaninasity gf	x
Sapindaceae	<i>Neotina coursii</i> Capuron	sangira	
Sapindaceae	spec. indet. "lanary fotsy"	lanary fotsy	
Sapotaceae	<i>Lambramia louvelii</i> Capuron ex Aubreville	nato	
Tiliaceae	<i>Grewia repanda</i>	sely	
Tiliaceae	<i>Grewia</i> sp. "hafipotsy"	hafipotsy	
	spec. indet. "babona"	babona	x
	spec. indet. "bararaka"	bararaka	
	spec. indet. "bernono"	bernono	
	spec. indet. "disaka"	disaka	
	spec. indet. "fonty"	fonty	x
	spec. indet. "hazombahy"	hazombahy	
	spec. indet. "ramy hafahafa"	ramy, spiky	x
	spec. indet. "rara"	rara	
	spec. indet. "revandra"	revandra	
	spec. indet. "tavia"	tavia	

¹ Parts of these tree species (fruit, flowers, leaves) were consumed by brown lemurs at Vevembe during this study.

Table 4.5a: Species Diversity Indices (H) for the Five Most Common Species in Ambarongy Plots¹.

Plot	Species	N	H
A1	<i>Cryptocarya</i> cf. " <i>flavescens</i> "*	14	0.144
A1	<i>Antidesma petiolare</i>	13	0.140
A1	<i>Syzygium</i> sp. " <i>rotramena</i> "*	7	0.104
A1	<i>Ocotea longipes</i> Kosterm. *	6	0.096
A1	<i>Syzygium</i> sp. " <i>rotrafotsy</i> "	5	0.086
A2	<i>Antidesma petiolare</i>	5	0.130
A2	<i>Chrysophyllum boivinianum</i> (Pierre) Baehni*	4	0.117
A2	<i>Syzygium</i> sp. " <i>rotramena</i> "*	3	0.100
A2	<i>Dombeya</i> sp. " <i>hafodahy</i> "*	2	0.078
A2	<i>Macaranga</i> sp. " <i>mokaranana</i> "*	2	0.078
A2	<i>Sloanea rhodantha</i>	2	0.078
A3	<i>Antidesma petiolare</i>	19	0.158
A3	<i>Syzygium</i> sp. " <i>rotramena</i> "*	8	0.118
A3	<i>Chrysophyllum boivinianum</i> (Pierre) Baehni*	5	0.091
A3	<i>Cryptocarya</i> cf. " <i>flavescens</i> "*	3	0.066
A3	<i>Dalbergia baroni</i> Baker*	2	0.050
A3	<i>Ocotea auriculiformis</i> Kosterm. *	2	0.050
A3	<i>Ocotea</i> cf. <i>racemosa</i> (Danguy) Kosterm. *	2	0.050
A4	<i>Rheedia</i> sp. " <i>voamalambotaholahy</i> "*	11	0.125
A4	<i>Antidesma petiolare</i>	9	0.114
A4	<i>Cryptocarya</i> cf. " <i>flavescens</i> "*	8	0.107
A4	<i>Cryptocarya</i> sp. " <i>tavolo pina</i> "*	7	0.099
A4	<i>Cabucala</i> sp. " <i>kaboka</i> "	4	0.070
A4	<i>Sloanea rhodantha</i>	4	0.070
A4	<i>Syzygium</i> sp. " <i>rotrafotsy</i> "	4	0.070

¹ Asterix (*) indicates brown lemur food species.

Table 4.5b: Species Diversity Indices (H) for the Five Most Common Species in Parc Plots¹.

Plot	Species	N	H
P1	<i>Syzygium</i> sp. "rotramena"*	11	0.119
P1	<i>Weinmannia rutenbergii</i> Engl.	11	0.119
P1	<i>Antidesma petiolare</i>	10	0.114
P1	spec. indet. "vatsilana"	6	0.085
P1	<i>Syzygium</i> "emirnensis"*	5	0.076
P1	spec. indet. "tarambito"	5	0.076
P2	<i>Syzygium</i> sp. "rotramena"*	16	0.147
P2	<i>Syzygium</i> "emirnensis"*	6	0.092
P2	<i>Canthium micrantha</i> Baker*	4	0.072
P2	<i>Dalbergia baroni</i> Baker*	4	0.072
P2	<i>Eugenia</i> sp. "robe"	4	0.072

¹ Asterix (*) indicates brown lemur food species.

Table 4.5c: Species Diversity Indices (H) for the Five Most Common Species in Vevembe Plots¹.

Plot	Species	N	H
V1	<i>Noronhia</i> sp. "solaitra"*	13	0.130
V1	spec. indet. "rara"	7	0.094
V1	<i>Syzygium</i> sp. "rotrafotsy"	7	0.094
V1	spec. indet. "babona"*	6	0.086
V1	<i>Ambavia capuronii</i> (Cavaco and Keraudren) Le Thomas	5	0.076
V1	<i>Syzygium</i> sp. "rotramena"*	5	0.076
V2	<i>Garcinia</i> sp. "kimbaletaka"*	12	0.142
V2	<i>Apodytes thouvenotii</i> Danguy*	6	0.103
V2	<i>Ravanea</i> sp. "lafa pf #2"*	5	0.093
V2	<i>Syzygium</i> sp. "rotramena"*	5	0.093
V2	spec. indet. "fonty"*	3	0.067
V2	<i>Uapaka louvelii</i> M. Denis*	3	0.067
V2	<i>Xylopi</i> sp. "ramiavona"*	3	0.067
V3	spec. indet. "babona"*	17	0.154
V3	spec. indet. "sandramy"*	9	0.122
V3	<i>Erythroxylum</i> sp. "malambovony"*	8	0.115
V3	<i>Noronhia</i> sp. "solaitra fotsy"*	7	0.107
V3	<i>Syzygium</i> sp. "rotramena"*	3	0.064
V4	<i>Pandanus</i> sp. "tsirika pf"*	9	0.115
V4	spec. indet. "bararaka"	7	0.100
V4	<i>Pandanus</i> sp. "tsirika mf"*	6	0.091
V4	<i>Syzygium</i> sp. "rotramena"*	6	0.091
V4	<i>Ilex mitis</i> (L.) Radlk.	5	0.082
V4	spec. indet. "vatsilana"	5	0.082

¹ Asterix (*) indicates brown lemur food species.

Table 4.6a: Mean Monthly Food Availability (FA/ha)¹.

	Fruit	New Leaves	Flowers/Buds
<i>All Trees</i>			
Ambarongy	12,562.2	34,895.9	1,181.9
Parc	5,722.7	16,168.4	6,726.6
Vevey	881.7	294.8	356.8
<i>Food Trees</i>			
Ambarongy	12,162.7	17,492.3	960.6
Parc	4,409.8	6,959.7	2,308.7
Vevey	430.0	195.3	321.5

¹ Data collection periods: Ambarongy (April 1999-August 2000), Parc (June 1999-August 2000), Vevey (May-September 2000).

Table 4.6b: Mean Monthly Food Availability (FA/ha) for May-August 2000.

	Fruit	New Leaves	Flowers/Buds
<i>All Trees</i>			
Ambarongy	11,775.5	35,157.3	175.0
Parc	7,426.6	12,508.8	5,376.4
Vevey	901.5	287.8	230.0
<i>Food Trees</i>			
Ambarongy	11,775.5	14,077.9	175.0
Parc	5,659.7	5,607.7	1,156.7
Vevey	464.9	195.7	204.8

Table 4.7a: Phenological Synchrony at Ambarongy¹.

Species	N	Fruit		Leaves		Flowers	
		# Events	CD	# Events	CD	# Events	CD
<i>Antidesma petiolare</i>	37	3	0.88	98	2.79*	11	2.31*
<i>Syzygium</i> sp. "rotramena"	18	2	0.94	71	1.05	1	1.00
<i>Cryptocarya</i> cf. "flavescens"	17	11	1.15	61	1.05	0	
<i>Chrysophyllum boivinianum</i> (Pierre) Baehni	9	0		44	3.82*	1	1.00
<i>Ocotea longipes</i> Kosterm.	7	0		52	1.16	2	0.94
<i>Syzygium</i> sp. "rotrafotsy"	7	3	1.58	25	1.12	1	1.00
<i>Ocotea auriculiformis</i> Kosterm.	5	0		23	1.29	0	
<i>Dalbergia baroni</i> Baker	4	0		26	0.66	0	
<i>Dombeya</i> sp. "hafodahy"	4	1	1.00	22	1.33	8	1.36
<i>Gaertnera</i> sp. "hazotoho"	4	25	0.95	17	1.38	10	2.56*
<i>Ocotea</i> cf. <i>racemosa</i> (Danguy) Kosterm.	4	0		9	1.21	0	
<i>Oncostemon botryoides</i> Baker	3	2	0.94	11	0.38*	0	
<i>Psychotria</i> sp. "fohaninasity"	3	24	0.89	5	1.18	8	1.63
<i>Cryptocarya</i> sp. "tavolo molaliambo"	2	0		17	0.50	0	
<i>Macaranga</i> sp. "mokaranana"	2	0		14	0.95	1	1.00
<i>Sloanea rhodantha</i>	2	0		12	0.67	0	
<i>Tambourissa</i> sp. "tambonetra tambalakoko"	2	0		11	0.95	0	
<i>Tambourissa</i> sp. "tambonetra"	2	0		6	1.04	0	
<i>Tina striata</i> Radlk.	2	0		5	1.18	0	
Total	150	92	0.74	616	7.00*	45	4.91*

¹ Coefficient of dispersion (CD) demonstrates degree of clumping (>1), uniformity (<1), or randomness (=1) in phenological events. Asterix (*) indicates significant departure from a Poisson distribution.

Table 4.7b: Phenological Synchrony at Parc¹.

Species	N	Fruit		Leaves		Flowers	
		# Events	CD	# Events	CD	# Events	CD
<i>Syzygium</i> sp. "rotramena"	27	7	0.88	137	1.97*	13	0.97
<i>Weinmannia rutenbergii</i> Engl.	13	0		106	4.27*	42	8.48*
<i>Antidesma petiolare</i>	11	3	0.86	11	1.26	2	0.93
<i>Syzygium</i> "emirnenensis"	11	10	0.79	45	1.10	8	1.57
<i>Canthium micrantha</i> Baker	8	1	1.00	41	1.02	0	
spec. indet. "vatsilana"	6	13	1.13	14	2.21*	11	1.45
<i>Tina striata</i> Radlk.	6	4	0.79	14	1.14	5	0.71
<i>Dalbergia baroni</i> Baker	5	0		14	2.21*	0	
<i>Gaertnera</i> sp. "hazotoho"	5	32	1.73*	13	2.29*	8	2.91*
spec. indet. "tarambito"	5	2	0.93	14	1.45	5	0.71
<i>Eugenia</i> sp. "robe"	4	2	0.93	22	0.57	1	1.00
<i>Tambourissa</i> sp. "tambonetra"	4	0		15	2.14*	1	1.00
<i>Dombeya</i> sp. "hafodahy"	3	0		6	1.00	13	1.63
<i>Tambourissa</i> sp. "ambora"	3	0		11	0.87	0	
<i>Allophylus cobbe</i>	2	3	0.86	6	0.64	3	0.86
<i>Grewia</i> sp. "hafipotsy"	2	0		11	1.06	2	0.93
<i>Ocotea</i> cf. <i>racemosa</i> (Danguy) Kosterm.	2	3	0.86	2	0.93	0	
<i>Plagioscyphus louvelii</i> Danguy & Choux	2	1	1.00	3	0.86	1	1.00
<i>Polyscias</i> sp. "maniny"	2	0		2	0.93	0	
<i>Polyscias</i> sp. "vatsilana ravimboanjo"	2	0		21	0.29*	8	0.50
<i>Psychotria</i> sp. "fohaninasity"	2	13	0.47	3	0.86	5	0.71
spec. indet. "ramanjavona"	2	0		6	1.36	0	
<i>Syzygium</i> sp. "rotrafotsy"	2	0		6	1.36	0	
Total	147	102	1.85*	606	2.96*	145	2.58*

¹ Coefficient of dispersion (CD) demonstrates degree of clumping (>1), uniformity (<1), or randomness (=1) in phenological events. Asterix (*) indicates significant departure from a Poisson distribution.

Table 4.7c: Phenological Synchrony at Vevembe¹.

Species	N	Fruit		Leaves		Flowers	
		# Events	CD	# Events	CD	# Events	CD
spec. indet. "babona"	23	0		2	0.75	0	
<i>Syzygium</i> sp. "rotramena"	19	0		3	1.33	0	
<i>Garcinia</i> sp. "kimbaletaka"	13	0		1	1.00	0	
<i>Noronhia</i> sp. "solaitra"	13	0		0		0	
spec. indet. "sandramy"	13	1	1.00	4	0.88	0	
<i>Pandanus</i> sp. "tsirika mf"	11	0		0		0	
<i>Pandanus</i> sp. "tsirika pf"	11	1	1.00	1	1.00	0	
<i>Erythroxylum</i> sp. "malambovony"	10	0		3	1.33	0	
<i>Syzygium</i> sp. "rotrafotsy"	10	1	1.00	2	0.75	0	
<i>Cabucala cryptophlebia</i> (Baker) Pichon	7	2	0.75	1	1.00	2	2.00
<i>Noronhia</i> sp. "solaitra fotsy"	7	0		0		0	
spec. indet. "bararaka"	7	0		0		0	
spec. indet. "rara"	7	4	0.25	0		0	
<i>Xylopi</i> sp. "ramiavona"	7	0		2	0.75	1	1.00
<i>Apodytes thouvenotii</i> Danguy	6	1	1.00	6	2.25	1	1.00
<i>Diospyros gracilipes</i> Hiern	6	1	1.00	3	0.50	0	
<i>Ilex mitis</i> (L.) Radlk.	6	0		3	3.00*	0	
<i>Ravanea</i> sp. "lafa pf #2"	6	0		1	1.00	0	
spec. indet. "vatsilana"	6	0		0		0	
<i>Ambavia capuronii</i>	5	0		7	0.21	1	1.00
<i>Combretum madagascariensis</i>	5	0		2	0.75	0	
<i>Uapaka louvelii</i> M. Denis	5	6	0.17	1	1.00	0	
<i>Mussaenda erectiloba</i> Wernham	4	0		7	0.21	0	
<i>Ocotea</i> cf. <i>racemosa</i> (Danguy) Kosterm.	4	0		2	2.00	1	1.00
<i>Anthocleista</i> sp. "dendemy"	3	2	0.75	1	1.00	0	
<i>Canarium madagascariense</i> Engler	3	0		0		0	
<i>Pandanus</i> sp. "tsirika gf"	3	0		0		5	0.00*
<i>Ravanea</i> sp. "lafa gf"	3	0		0		0	
spec. indet. "fonty"	3	0		0		0	
<i>Cabucala madagascariensis</i>	2	0		6	0.58	0	
<i>Homalium</i> sp. "hazoambato"	2	0		0		0	
<i>Lambramia louvelii</i> Capuron ex Aubreville	2	0		3	0.50	0	
<i>Mammea</i> "angustifolia var. <i>pseudoprotorhus</i> "	2	0		1	1.00	0	
<i>Mascarenhasia arborescens</i> A. DC.	2	0		1	1.00	0	
spec. indet. "tavia"	2	0		0		0	
<i>Streblus dimeptate</i> (Bureau) C.C. Berg	2	0		0		0	
<i>Syzygium</i> sp. "rotramainty"	2	0		0		0	
<i>Vernonia</i> sp. "tavilona"	2	0		1	1.00	0	
<i>Weinmannia rutenbergii</i> Engl.	2	0		0		0	
Total	267	30	0.25	68	1.46	11	1.45

¹ Coefficient of dispersion (CD) demonstrates degree of clumping (>1), uniformity (<1), or randomness (=1) in phenological events. Asterix (*) indicates significant departure from a Poisson distribution.

Chapter 5: Feeding Ecology of the Brown Lemurs of Andringitra National Park and Vevembe Forest

INTRODUCTION

The niche concept has long been central to evolutionary ecology (Gause, 1934; Lack, 1947). The ecological niche has been described inclusively as the sum of all adaptations an organism uses to fit its environment (Pianka, 1994). More particularly, niche characteristics are typically seen to vary along three principal axes: food, space, and time (Schoener, 1974, 1989). Variation among sympatric species across niche dimensions serves to alleviate competition for limited resources and facilitate coexistence in shared environments (Schoener, 1983; but see Wiens, 1977; Connell, 1983). Ecomorphic specialization – including in types of food exploited, levels of dietary diversity, and vertical stratification – is often viewed as important in shaping ecological adaptations in primate communities across diverse habitats and taxonomic groups (e.g., Rodman, 1973; Struhsaker and Oates, 1975; Gautier-Hion, 1978; Raemakers, 1979; Mittermeier and van Roosmalen, 1981; Terborgh, 1983; Chapman, 1988; Wright, 1989; Norconk and Kinzey, 1994; Tomblin and Cranford, 1994; Gonzalez-Kirchner, 1995; Tutin et al., 1997; Porter, 2001), including among Malagasy strepsirrhines (e.g., Sussman, 1974, 1977; Ganzhorn, 1988; Overdorff, 1991, 1993, 1996a; Freed, 1996; Powzyk, 1997; Vasey, 1997, 2000, 2002; Tan, 1999, 2000). The development of distinctive ecological niches to permit sympatry is also

considered a significant phase in the formation of distinct species, often as integral to the speciation process as reproductive isolation (Orr and Smith, 1998; Barton, 2001a; Schluter, 2001). Thus, evaluating differences in feeding ecology may help to ascertain distinct evolutionary trajectories in related populations.

The feeding ecology of other brown lemur populations has been documented in diverse localities in Madagascar (e.g., Sussman, 1974; Overdorff, 1993; Freed, 1996; Vasey, 1997; Rasmussen, 1999). The brown lemur complex has been characterized as highly flexible ecologically with relatively high dietary diversity (Tattersall and Sussman, 1998), demonstrating niche contraction and expansion in response to community structure (Vasey, 2000). Most populations are primarily frugivorous (i.e., > 50% of feeding time is devoted to fruit), but often consume (especially in particular seasons) substantial quantities of leaves, flowers, and miscellaneous food items (fungi, invertebrates, etc.) (e.g., *E. f. rufus* at Ranomafana: Overdorff, 1991, 1993; *E. f. sanfordi* at Montagne d'Ambre: Freed, 1996; *E. f. albifrons* at Andranobe: Vasey, 1997, 2000, 2002; *E. f. fulvus* at Andasibe: Ganzhorn, 1988; *E. f. fulvus* at Ampijoroa: Rasmussen, 1999; naturalized *E. f. fulvus* on Mayotte: Tattersall, 1977). However, western dry forest populations of *E. f. rufus* at Antserananomby and Tongobato are highly folivorous (Sussman, 1974, 1977).

In many of the previous studies, researchers have investigated the behavioral ecology of brown lemurs in conjunction with a sympatric lemur species (*Lemur catta*: Sussman, 1974, 1977; *Eulemur rubriventer*: Overdorff, 1991, 1993; *E. coronatus*: Freed, 1996; *Varecia variegata rubra*: Vasey, 1997,

2000, 2002; *E. mongoz*: Rasmussen, 1999). Many mechanisms have been proposed to allow brown lemurs to share their habitats with these potential competitors. These include: having greater dietary diversity (Vasey, 2000), utilizing higher (Sussman, 1974; Freed, 1996) or lower (Vasey, 2000) vertical microhabitats, feeding in smaller patches (Vasey, 2000), and/or consuming lower quality food items (leaves: Sussman, 1974; mature leaves, unripe fruit, and flowers: Overdorff, 1993; higher levels of toxic compounds: Ganzhorn, 1988).

In this chapter, I examine feeding niche characteristics across study populations of brown lemurs. The pure parental types of the study taxa – white-collared lemurs (*Eulemur albocollaris*) and red-fronted lemurs (*E. fulvus rufus*) – are buffered by the large hybrid zone centered at Andringitra National Park, wherein nearly all individuals are hybrids (Johnson and Wyner, 2000; Wyner, 2000; Wyner et al., 2002; see Chapter 1). As a consequence, direct examination of niche differences in shared habitats is likely not feasible in these species. The objective of the present analysis then is to assess levels of variation in feeding ecology within and between study populations. Diet profiles may then be compared to other brown lemur localities, including where niche separation with sympatric competitors has been recorded (e.g., Overdorff, 1991, 1993; Vasey, 1997). The degree of divergence between the Andringitra and Vevembe populations (as well as adjacent *E. f. rufus*; Overdorff, 1993) may be evaluated in part relative to the diet separation observed between brown lemurs and their sympatric competitors. Moreover, I will investigate proximate environmental influences on diet, such as the relationship between shifts in feeding preferences

and food availability. Seasonal scarcity in resource production may impose greater diet restrictions and increase niche separation (e.g., Gautier-Hion, 1980, 1989; Terborgh, 1983, 1986).

Predictions regarding the feeding ecology of white-collared lemurs at Vevembe and the hybrids at Andringitra are complicated by the great diet variability observed in previous studies of other brown lemur populations (including their varied responses to sympatric competitors). While early research on western brown lemurs suggested a relatively narrow econiche, largely unchanged by potential competition from sympatric lemurs (Sussman, 1974), subsequent investigations have revealed brown lemurs to be highly plastic in response to habitat shifts and lemur community structure (Tattersall and Sussman, 1998; Vasey, 2000). Consequently, I expect differences among the study populations to be clear responses to local environmental characteristics and/or community ecology. In general, like other eastern rain forest brown lemurs, I expect both Vevembe and Andringitra groups to be primarily frugivorous but with some variation in quantities of fruit, as well as secondary resources, in response to seasonal resource base. Free from competition from the highly frugivorous *Varecia* (e.g., Vasey, 2000; see Table 1.1), both populations may have higher fruit consumption than other eastern brown lemurs. In the absence of congener *E. rubriventer* (e.g., Overdorff, 1993; see Table 1.1), competitive release (again, potentially expressed as increased frugivory) may be even more evident in the *E. albocollaris* population at Vevembe. However, the greater scarcity of food resources at Vevembe (Chapter 4) may impose constraints on the diet of *E.*

albocollaris, necessitating increased consumption of alternative resources (e.g., leaves, flowers, or invertebrates; Overdorff, 1993).

METHODS

Study Groups

Feeding behavior data were collected for two social groups of hybrids (*Eulemur fulvus rufus* X *E. albocollaris*) at Andringitra National Park (groups AN1 and ANA) and one *E. albocollaris* group at Vevembe Forest (group VE1). The AN1 group was located at the Ambarongy site and the ANA group was located across the Iantara River at the Parc site (see Figure 3.1). Age and sex composition of each group is indicated in Table 5.1. There was a slight male bias in the sex ratio of all study groups (*contra* Kappeler, 2000), although there are insufficient data herein to test this bias statistically.

Sampling Procedures

Feeding activities were recorded using all-occurrence and focal animals (Altman, 1974). Focal animals were selected according to a regular rotation of all adult and juvenile group members (infants were excluded). Each animal was followed from when the group was first located (generally 06:30-07:30) until 16:30. Terrain and distance of focal groups from camp prevented nocturnal sampling and longer follows during daylight hours.

Data were collected on the AN1 group during 84 non-consecutive days (May-December 1999) for a total of 591 hours of continuous observation. ANA was followed on 44 days (January-August 1999) for total of 329 hours of

observation. Finally, I observed VE1 on 83 days (May-August 2000), collecting 691 observation hours.

Feeding bouts were considered to begin when the focal animal bit into a food item or placed a food item in its mouth; bouts were deemed finished after swallowing or dropping a food item. However, bouts were only considered independent if the interval between swallowing and placing a new food item in the mouth exceeded 15 seconds. For each feeding session initiated by the focal animal, the following information was recorded:

1. Date
2. Time begin (hh:mm:ss)
3. Time end (hh:mm:ss)
4. Height in canopy (m)
5. Plant species (Malagasy vernacular)
6. Plan part consumed: ripe fruit (RF), unripe fruit (UF), mature leaves (ML), new leaves (NL), leaf bases (LB), flowers (FL), flower buds (BU), and other (OT: mushrooms, moss, and soil)
7. Nearest neighbor
8. Distance to neighbor
9. Presence and identity of another social group or lemur species < 30 m
10. Weather (clear, overcast, or rain)
11. Location (relative to trail system or GPS waypoint).

As in phenological analyses (Chapter 4), Malagasy vernacular names were recorded in the field for all plant species consumed by the focal animals.

Subsequently, taxonomic identification was applied using Turk (1995) as the primary key and Overdorff (1991; unpublished data) as a secondary resource.

Diet Composition

Feeding profiles were constructed using the relative contribution of plant parts to the overall diet. Plant part categories included fruit, leaves, flowers, and other; subcategories consisted of ripe fruit, unripe fruit, mature leaves, new leaves, leaf bases, flowers, flower buds, and other. For most analyses herein, only the major categories are considered. The miscellaneous, or “other”, category included mushrooms or other fungi, moss, and soil.

I classified diet according to both the proportion of bouts for each food item relative to the total number of feeding bouts and the percentage of total feeding time spent feeding on each food part. The two measures of diet composition were highly correlated across populations for each category (fruit: $r_s = .962$; $Z = 4.304$; $P < .0001$; leaves: $r_s = .869$; $Z = 3.884$; $P = .0001$; flowers: $r_s = 1$; $Z = 4.472$; $P < .0001$; other: $r_s = .957$; $Z = 4.237$; $P < .0001$). Accordingly, only percentages of total feeding time results are presented for some tests. Variation in dietary profiles among study groups was investigated by comparing monthly percentages of each food item category.

Feeding Time and Rates

Feeding time was calculated as the percentage of total observation time spent feeding in each food item category. Feeding rates were calculated as the number of feeding bouts initiated per hour of observation. Monthly percentages

and rates were compared across study groups. In addition, I compared mean bout length for all feeding bouts and categories among focal groups.

Dietary Diversity

Diversity in diet was measured using the relative proportion in the diet of each food item subcategory (both percentage of bouts and proportion of feeding time). The following formula was used to obtain diversity scores:

$$D = \left(\sum_{i=0}^n p_i^2 \right)^{-1}$$

where D is dietary diversity and p_i is the proportion of feeding bouts or time spent feeding in food item category i for each category within the total sample (Gautier-Hion, 1980; Overdorff, 1993). Because of potential biases from unequal sampling of study groups, I did not include Shannon Index (H) values of dietary diversity of plant parts or species consumed (e.g., Struhsaker and Oates, 1975; Guillotin et al., 1994; Fashing, 2001b). Instead, I used an alternative measure of dietary breadth: the number of different plant species consumed per hour of observation. While avoiding the difficulties from the unequal observation time, this measure is not necessarily a good indicator of total plant species diversity over time. I compared monthly D and species/hour values across study groups. Finally, for each study group, I tallied all plant species consumed, the top ten food species (as percentage of total feeding time), and the five most commonly eaten plant species for each month (also assessed by percentage of feeding time).

Habitat Use

To analyze vertical habitat use, I measured the feeding height of study animals. Height was estimated visually and recorded at the initiation of the feeding bout. Study groups were compared using height measures from all bouts.

Sex and Age Differences

Within-group comparisons were conducted to examine differences between sexes (of all ages) and between age classes (i.e., adults and juveniles). I tested variation in: monthly percentages of feeding time for each category, monthly percentage of observation time spent feeding, mean feeding bout length, monthly dietary breadth (*D*) based on feeding time, and mean feeding height.

Statistical Techniques

I used distribution-free nonparametric tests for all comparisons. These included Kruskal-Wallis tests for variation among focal groups in monthly diet composition categories, monthly feeding time and rates, bout duration, feeding height, and monthly diversity measures (*D* and species consumed/hour). Differences between pairs of study groups and within-group sex and age differences were evaluated using Mann-Whitney U and Wilcoxon signed ranks tests (the former test was used for these comparisons unless otherwise noted). Finally, I conducted Spearman rank correlation tests to assess the relationships between seasonal fluctuation in feeding ecology measures and food availability (FA) scores (see Chapter 4). Significance for all tests was set at $\alpha = .05$.

RESULTS

Diet Composition

A summary of feeding patterns in the three study groups is presented in Table 5.2. There was substantial variation in the proportions of plant part categories in the diets of the three groups (Figures 5.1-5.2). There were significant differences in all categories for monthly proportions of feeding time (FR: $H = 10.086$; $P = .0065$; LV: $H = 6.092$; $P = .0476$; FL: $H = 14.907$; $P = .0006$; OT: $H = 10.443$; $P = .0054$). Analyses of feeding bouts yielded identical statistical results. Feeding profiles also diverged when the comparisons were restricted to May-August (i.e., the months in which all groups were sampled in 1999 and/or 2000); only time spent feeding on leaves did not vary significantly (time: FR: $H = 7.295$; $H = .0261$; LV: $H = 4.902$; $P = .0862$ NS; FL: $H = 9.116$; $P = .0105$; OT: $H = 7.758$; $P = .0207$); leaves as proportion of feeding bouts did differ significantly ($H = 8.028$; $P = .0181$). Variation across months for each group is depicted in Figure 5.2.

Differences in diet composition are also evident in paired comparisons of study groups. Between AN1 and ANA, fruit ($Z = -2.033$; $P = .0421$) and miscellaneous ($Z = -2.46$; $P = .0139$) feeding differed, but proportions of time spent feeding on leaves or flowers were similar ($Z = -1.512$; $P = .1306$ NS). AN1 and VE1 only differed in flower feeding ($Z = -2.323$; $P = .0202$). ANA and VE1 were the least similar pair, with significant differences in all food item categories (FR: $Z = -2.323$; $P = .0202$; LV: $Z = -2.033$; $P = .0421$; FL: $Z = -1.984$; $P = .0472$; OT: $Z = -1.984$; $P = .0472$).

ANA was nearly exclusively frugivorous (95% of feeding time), while AN1 had high levels of fruit feeding (87%) and some reliance on leaves (11%; Table 5.2). The Vevembe group VE1, while mostly frugivorous (66%), had the most diverse diet, with significant proportions of leaves (13%) and especially flowers (20%; Table 5.2); seasonal reliance on flowers was even more striking (Figure 5.2; Table 5.3; see below). VE1 also had the only demonstrable use of miscellaneous resources (for this group, this category consisted solely of fungi).

Feeding Time and Rates

Variability across groups in feeding time and rates are shown in Figure 5.3. There were no significant differences in the monthly proportion of observation time spent feeding ($H = 3.5$; $P = .1738$ NS) (Figure 5.3a; Table 5.2). There were, however, differences in the total time spent feeding on fruit ($H = 9.726$; $P = .0077$), flowers ($H = 14.411$; $P = .0007$), and other ($H = 5.917$; $P = .0519$), reflecting the diet composition differences described above. For overlapping months (May-August), the groups differed in minutes spent feeding on leaves ($H = 6.038$; $P = .0478$) and flowers ($H = 10.455$; $P = .0054$).

Feeding rates (bouts/hour) varied across brown lemur groups for the entire sampling period ($H = 11.293$; $P = .0035$) and May-August ($H = 8$; $P = .0183$) (Figure 5.3b). These differences were also evident for each food item category (FR: $H = 8.213$; $P = .0165$; LV: $H = 10.934$; $P = .0042$; FL: $H = 15.451$; $P = .0004$; OT: $H = 8.56$; $P = .0138$); results were statistically identical for May-August. VE1 initiated the greatest number of bouts (3.4 per hour), followed closely by ANA at Andringitra (2.7 per hour); AN1 had substantially fewer

feeding bouts (1.8 per hour). As a corollary to these differences and to the similarities in time spent feeding, there were significant differences in mean feeding bout length ($H = 440.997$; $P < .0001$). AN1 had the longest feeding bouts (4.5 minutes; Table 5.2; Figure 5.3c). In sum, study groups varied in the length and frequency of feeding, but overall feeding time remained similar.

Dietary Diversity

Measures of dietary diversity varied consistently across study groups (Figure 5.4). Monthly diversity scores (D) were significantly different for the proportions of bouts ($H = 10.131$; $P = .0063$) and feeding time ($H = 10.947$; $P = .0042$). This variation was also present in May-August comparisons (bouts: $H = 8.8$; $P = .0123$; time: $H = 9.302$; $P = .0096$). However, dietary diversity in plant species (species consumed per hour) did not differ among groups ($H = 3.094$; $P = .2129$ NS; May-August: $H = 3.5$; $P = .1738$ NS); however, as noted, while compensating for unequal sampling periods, this measure does not capture total plant species diversity in the diet of these groups.

Paired comparisons of study groups also revealed some divergence in dietary diversity. There were no differences between the Andringitra groups in D values or plant species diversity, excepting D scores from percentage of feeding time for May-August ($Z = -2.033$; $P = .0421$). Similarly, comparisons between the Andringitra groups and the Vevembe study group also demonstrated differences only in D values from proportions of time (AN1-VE1: $Z = -2.489$; $P = .0128$; May-August: $Z = -2.309$; $P = .0209$; ANA-VE1: $Z = -2.785$; $P = .0054$; May-August: $Z = -2.323$; $P = .0202$).

As a reflection of the greater balance in feeding scores for leaves, miscellaneous items, and especially flowers, the Vevembe study group showed the highest dietary diversity ($D = 3.7\text{-}3.9$; Table 5.2). VE1 was followed by AN1 (1.9-2.2) and finally ANA (1.2-1.4), with its highly monotonous diet of fruit. VE1 also consumed the largest number plant species during the study period (96, vs. 27 in ANA and 69 in AN1), and ate the most species per hour of observation (although plant species rates were not significantly different among study groups). Lists of all plant species consumed by each group are included in Table 5.4. As further indications of diet breadth in common food items, the top ten overall food species are included in Table 5.5 and the top five plant species for each month are shown in Table 5.6.

Habitat Use

There were substantial differences in vertical foraging among study groups (Figure 5.5). There was significant variation in mean feeding height ($H = 272.041$; $P < .0001$), including during overlapping study months (May-August: $H = 175.676$; $P < .0001$). Group AN1 foraged the highest in the canopy (11.5 m), followed by VE1 (11.1 m) and ANA (8.7 m; Table 5.2).

Sex and Age Differences

Within-group comparisons indicated very little divergence in feeding ecology between sexes (Figure 5.6). In group AN1, there were no sex differences in monthly percentage of time spent feeding in any category (Wilcoxon signed ranks test: FR: $Z = -.42$; $P = .6744$ NS; LV: $Z = -.28$; $P = .7794$ NS; FL: $Z = -.365$; $P = .715$ NS; OT: $Z = -1.095$; $P = .2733$ NS). There were also no

differences between the sexes in monthly percentage of observation time spent feeding (Wilcoxon signed ranks test: $Z = -1.54$; $P = .1235$ NS), mean feeding bout duration (Mann-Whitney U: $Z = -.064$; $P = .9486$ NS), feeding height (Mann-Whitney U: $Z = -.152$; $P = .8792$ NS), or monthly dietary diversity (D ; Wilcoxon signed ranks test: $Z = -.28$; $P = .7794$ NS). Groups ANA and VE1 showed identical patterns, with no significant sex differences in any feeding category, proportion of time spent feeding, bout duration, feeding height, or dietary diversity.

Similarly, there was little divergence between age classes (Figure 5.7). In group ANA, only mean duration of feeding bouts differed between juveniles and adults (Mann-Whitney U: $Z = -2.37$; $P = .0178$); the juvenile ED had longer feeding bouts (4.3 minutes) than adults (4.0 minutes). In group VE1 at Vevembe, there was significant variation in the proportion of observation time spent feeding, as well as the percentage of feeding time spent consuming flowers and miscellaneous items (Wilcoxon signed ranks test: $Z = -2.023$; $P = .0431$). Total feeding time was higher in juveniles (17.6%) than adults (12.0%), while feeding proportions were higher in adults than in juveniles for flowers (22.2% vs. 15.4%) and miscellaneous items (1.8% vs. 0.6%). Age differences in AN1 were not assessed because there were no juveniles in this group during the study period.

Feeding and Food Availability

Overall, there were few consistent relationships between feeding ecology and seasonal shifts in resource availability across focal groups. In group AN1, there was a significant positive relationship between mean feeding bout duration

and new leaf flushing ($r_s = .81$; $Z = 2.142$; $P = .0322$) and a negative correlation between mean feeding height and new leaf flushing ($r_s = -.785$; $Z = -2.079$; $P = .0376$). The same two significant relationships were apparent when considering only the productivity of tree species consumed by the Andringitra brown lemurs. Although not statistically significant ($P > .05$), some tests showed high enough correlation coefficients (absolute $r_s > .6$) to indicate potentially biologically meaningful trends. These included positive relationships between fruit feeding (percentage of feeding bouts) and fruit availability, feeding rates and fruit availability, dietary diversity (D) and new leaf flushing, and total feeding time and leaf flushing. There were also non-significant (but possibly important) negative relationships between miscellaneous food items in the diet (percentage of feeding time) and new leaf production. However, when considering only food tree species productivity, fewer non-significant trends were present in AN1. There were trends for positive relationships between diversity (bouts) and leaf flushing, between total feeding time and leaf flushing, and for a negative correlation between miscellaneous food items (time) and leaf flushing.

In the Andringitra group ANA, different relationships emerged between feeding behavior variables and food availability. There were positive correlations between folivory (bouts) and fruit availability, and between dietary diversity (bouts) and flower production ($r_s = .732$; $Z = 1.933$; $P = .0533$). There was a significant negative relationship between fruit feeding (bouts) and fruit productivity ($r_s = -.72$; $Z = -1.933$; $P = .0533$). There were no significant correlations when only food tree species were considered for food production

scores. Non-significant (but, again, possibly meaningful) positive relationships were suggested for: folivory (bouts and time) and new leaf availability, folivory (time) and fruit availability, diversity (bouts and time) and fruit availability, and diversity (time) and flower production; non-significant negative relationships were present for frugivory (bouts and time) and leaf flushing, and frugivory (time) and fruit availability. When food availability is confined to food species, there were trends for positive associations between folivory (bouts and time) and fruit production, diversity (bouts and time) and fruit production, total feeding time and flower production, and mean feeding bout duration and flower production.

In the Vevembe group VE1, again, different associations were present. The only significant correlations were negative relationships between miscellaneous food item in the diet (proportions of bouts and time) and new leaf production ($r_s = -1$; $Z = -2$; $P = .0455$). However, it should be noted that sample size for this group ($N = 5$ months) was limiting for these tests. Non-significant relationships with relatively high correlation coefficients include: positive associations between frugivory (bouts and time) and leaf flushing, number of species consumed per hour and flower production, feeding rates and flower production, and feeding height and leaf flushing; non-significant negative correlations occurred between folivory (bouts) and flower production, folivory (bouts) and leaf flushing, flower feeding (bouts and time) and fruit production, and diversity (bouts and time) and leaf flushing. In tests involving food tree species productivity, there were non-significant positive associations between frugivory (bouts and time) and fruit availability, and frugivory (bouts and time)

and leaf flushing; there were negative non-significant relationships in these tests between folivory (time) and fruit availability, folivory (time) and leaf flushing, flower feeding (bouts and time) and fruit availability, and miscellaneous item feeding (bouts and time) and leaf flushing.

In summary, the patterns of association between feeding variables and resource abundance varied greatly across study groups, often in unpredictable ways. For example, there were no consistent correlations between the availability of particular food items and the proportion of the diet committed to these resources, even for highly preferred food items like fruit. In addition, with lower availability of important food items, there was no concomitant switch to alternative food types or to increased diet breadth (e.g., folivory, flower-feeding, and/or dietary diversity did not necessarily increase during fruit shortages). Furthermore, the few strong relationships that did emerge did not necessarily indicate biologically relevant patterns. For example, the significant correlation in VE1 between feeding on miscellaneous food items and new leaf productivity is of unclear ecological meaning. Moreover, the inverse relationship between frugivory and fruit availability in ANA contradicts the expected pattern.

A final set of correlation tests was conducted to determine the relationship between dependence on key food items and seasonal shifts in resource availability. I recorded a dramatic seasonal shift to fruits of fig (*Ficus*) species (especially *F. lutea*) during particular months in the Andringitra brown lemurs (Table 5.6). Fig species have been noted to serve as keystone resources during periods of food scarcity in primate frugivore communities elsewhere in the tropics

(Terborgh, 1986). Accordingly, I examined the associations between monthly *Ficus* spp. (including *F. lutea* in particular) feeding and food availability in the Andringitra groups. In group VE1 at Vevembe, it was clear that flowers of *Pandanus* were the most important food items seasonally. Flowers (or nectar) have also been noted to serve as potential keystone resources (Terborgh, 1986). Therefore, I tested the associations between *Pandanus* feeding and food availability in VE1.

In these tests of critical resources, AN1 did not follow the expected patterns. There were no relationships between high levels of *Ficus* or *F. lutea* feeding and low overall production or fruit, flowers, or leaves – despite monthly reliance on *Ficus* reaching 79.4% of feeding time in July 1999 and *F. lutea* alone reaching 66.1% in August 1999 (Figure 5.8). However, in group ANA, there was a significant negative correlation between the proportion of *Ficus lutea* in the diet (both bouts and time) and overall fruit production ($r_s = -.764$; $Z = -2.021$; $P = .0433$). The ANA group fed on this one species 58.5% of feeding time in August 2000 when fruit production was lowest (Figure 5.8). Similar patterns occurred for the relationship between *F. lutea* feeding and fruit availability in known food species – but this association did not reach statistical significance ($r_s = -.655$; $Z = -1.732$; $P = .0833$ NS). There was also an inverse relationship between feeding on all *Ficus* spp. and flower availability (bouts: $r_s = -.88$; $Z = -2.327$; $P = .02$; time: $r_s = -.766$; $Z = -2.028$; $P = .0426$). This result, however, is of doubtful importance, as ANA never fed on flowers (Table 5.2) and thus would not likely need *Ficus* as a seasonal substitute. In the Vevembe group VE1, there was a negative

relationship, albeit statistically non-significant, between *Pandanus* flower feeding and fruit availability in food tree species (bouts: $r_s = -.8$; $Z = -1.6$; $P = .1096$ NS; time: $r_s = -.9$; $Z = -1.8$; $P = .0719$ NS). Again, limited sampling ($N = 5$ months) hampers statistical tests for this site. There were also some indications of negative associations between *Pandanus* flower consumption and new leaf flushing (bouts: $r_s = -.7$; $Z = -1.4$; $P = .1615$ NS; time: $r_s = -.6$; $Z = -1.2$; $P = .2301$ NS). However, like flowers for ANA, new leaves represented a very minor part of VE1's diet (Table 5.3c) and VE1 would not likely need a seasonal alternative when new leaves were less available. In sum, there is some support for *Ficus lutea* fruit acting as a keystone resource in the Andringitra brown lemurs, while *Pandanus* sp. flowers may serve this function at Vevembe.

DISCUSSION

Feeding Similarities Among Brown Lemur Groups

The brown lemur groups at Andringitra and Vevembe demonstrated many similarities in feeding ecology. Fruit (particularly ripe fruit) represented the most important component of the diet for *E. albocollaris* and for both hybrid groups. Despite some variation in feeding rates and time for individual food items (see below), all three focal groups spent similar proportions of time feeding. The number of different plant species consumed (per observation time) was also roughly consistent across the hybrid and white-collared lemur groups. However, this apparent lack of taxonomic diversity appears to belie other measures of dietary diversity, including total numbers of species consumed by each group (see below).

The degree of frugivory in the Andringitra and Vevembe groups fell close to the range observed in other brown lemur populations across Madagascar. Except in *E.f. rufus* groups studied by Sussman (1974, 1977), fruit is the primary resource among brown lemurs, encompassing 67-89% of feeding records (Tattersall, 1977; Overdorff, 1991, 1993; Freed, 1996; Vasey, 1997, 2000; Rasmussen, 1999). The VE1 group of *E. albocollaris* was just below this range (66% of feeding time), while the ANA hybrid group at Andringitra exceeded levels of frugivory found in other brown lemurs (95% of feeding time). Indeed, both of the hybrid groups consumed fruit in quantities equal to or greater than those observed in lemur species considered to be more strictly frugivorous than brown lemurs (e.g., *Eulemur rubriventer*: 81%; Overdorff, 1993; *Varecia variegata*: 71-90%; Morland, 1991; White, 1991; Balko, 1998; Vasey, 2000) and more than the brown lemur groups in those communities (67-69%; Overdorff, 1993; Vasey, 2000).

In addition to the dietary similarities among groups, the Andringitra and Vevembe brown lemurs exhibited a conspicuous absence of within-group variation. A few age class feeding differences were noted; the juvenile and adults in ANA had different feeding bout durations, while the VE1 juveniles spent more time feeding and consumed flowers and miscellaneous food items less frequently than adults. These differences may reflect developmental differences in feeding efficiency or age-specific dietary requirements. Alternatively, these differences may be of little functional consequence for development or general feeding ecology. For example, despite the differences in flower and miscellaneous

feeding, the ranking of food classes remained identical for adults and juveniles in VE1 (see Figure 5.7). In respect to sex differences, males and females in all study groups were remarkably uniform in all measures of feeding behavior, including diet composition, diversity, rates, and canopy use during feeding.

Sex and age differences in diet have not been investigated extensively among brown lemurs. Sex differences in feeding ecology (e.g., time spent feeding and feeding priority) have been explored more thoroughly in female dominant lemur species (e.g., Jolly, 1984; Richard and Nicoll, 1987; Sauther, 1993; Wright, 1995). Vasey (2000, 2002) examined variation between the sexes in *E.f. albifrons* in relation to degrees of niche separation with sympatric *Varecia variegata rubra*. Sex differences in diet were not as pronounced in *E.f. albifrons* as in *Varecia*, which Vasey (2002) attributes to reduced costs of reproduction in the former species. Only slight differences were present in *E.f. albifrons*, with females seasonally consuming more flowers and males more invertebrates (though neither of these were primary food items; Vasey, 2002). Thus, the lack of sex differences in the present study is generally replicated in other brown lemurs.

Feeding Differences Among Brown Lemur Groups

While there is broad similarity in dietary profiles, there are many differences in feeding ecology across focal groups. While frugivory was prominent in all groups, there were significant differences in the monthly number of bouts and the percentage of feeding time devoted to fruit. As noted above, the Andringitra hybrids were far more frugivorous than the white-collared lemurs at Veveve. As a consequence, there were also substantial differences in the

amount of supplementary food items in the diet, including leaves (4-13% of feeding time) and especially flowers (0-20%) (with the highest percentages observed in Vevembe brown lemurs). Not surprisingly, the *E. albocollaris* also had the highest dietary diversity, while the two hybrid groups were similarly monotonous. Moreover, the Vevembe brown lemurs fed from the largest number of plant species: 96 vs. 69 in AN1 and only 27 in ANA. Compensating for differences in observation time, white-collared lemurs consumed the greatest number of plant species, though the differences among groups were not significant.

Comparison to other populations suggest that *E. albocollaris* is closer to the norm in diet for brown lemurs. Again, frugivory is prominent everywhere, but at levels more like those in the Vevembe group (Tattersall, 1977; Overdorff, 1991, 1993; Freed, 1996; Vasey, 1997, 2000; Rasmussen, 1999). Except in the folivorous western *E. f. rufus* (Sussman, 1977), secondary food categories for brown lemurs generally include leaves (2-26% of feeding records) and flowers (4-13%) (Tattersall, 1977; Overdorff, 1991, 1993; Freed, 1996; Vasey, 1997, 2000; Rasmussen, 1999). While these levels are equivalent to those recorded across groups in the present study, the combined contribution of leaves and flowers in most brown lemurs (25-32%) is comparable to that in *E. albocollaris* (34%) and exceeds those in the hybrids (4-13%) (Tattersall, 1977; Overdorff, 1991, 1993; Vasey, 1997, 2000; Rasmussen, 1999). Only the highly frugivorous *E. f. sanfordi* relies so little on these supplemental resources (9%; Freed, 1996). In addition, the greater number of plant species exploited by *E. albocollaris* more closely

approximates that in other brown lemur populations. For example, Overdorff (1993) reports 104 total species in the diet of *E. f. rufus* at Ranomafana, while Ampijoroa *E. f. fulvus* consumed 281 “potential” species (although this is almost certainly an overestimate; Rasmussen, 1999). Moreover, using comparable techniques, *E. albocollaris* at Vevembe had virtually identical values of dietary diversity (*D*) as *E. f. rufus* at Ranomafana (Overdorff, 1993). In contrast, red-fronted lemurs in western Madagascar exploited far fewer species (8-11; Sussman, 1977), fewer even than group ANA at Andringitra.

In some brown lemur communities, the ability to exploit a more diverse array of food sources may contribute to niche separation with sympatric competitors (e.g., the more generalist *E. f. albifrons* and the highly frugivorous *Varecia variegata rubra* in the Masoala Peninsula; Vasey, 2000; *E. f. fulvus* and *E. mongoz* at Ampijoroa: Rasmussen, 1999). In other sites, brown lemurs and sympatric congeners have similar dietary diversity (e.g., *E. f. rufus* and *E. rubriventer*, in some measures, at Ranomafana; Overdorff, 1993; *E. f. sanfordi* and *E. coronatus* at Mt. d'Ambre; Freed, 1996). Meanwhile in western Madagascar, *E. f. rufus* has a highly monotonous, folivorous diet compared to sympatric *Lemur catta*, a more diverse frugivore (Sussman, 1974, 1977); also, *E. f. rufus* does not shift its diet in nearby localities where *Lemur catta* is absent (i.e., there is no character displacement; Sussman, 1974, 1977). Clearly, many different dietary strategies (or other behavioral mechanisms; see Chapter 6) may serve to mitigate competition between brown lemurs and sympatric species, depending on the local environment and the other lemur species involved. While

no data are available on sympatric lemur species at Andringitra or Vevembe, it does not appear likely that differences between these populations in dietary diversity are related to niche separation in their respective habitats. Release from competition due to the absence of other sympatric frugivores could permit greater fruit feeding in brown lemurs. However, Andringitra maintains a richer lemur community, including the congeneric frugivore *E. rubriventer* (Sterling and Ramarason, 1996), while Vevembe brown lemurs coexist with only one day-active lemur (the bamboo specialist *Hapalemur griseus*). Alternatively, a more diverse diet may be preferable for brown lemurs and occur more frequently in the absence of competition. For example, naturalized *E.f. fulvus* on Mayotte have no lemur competitors yet resemble more closely the generalist *E. albocollaris* at Vevembe (see Tattersall, 1977). These questions may be illuminated by further studies on the behavioral ecology of sympatric *E. rubriventer* in the Andringitra hybrid zone and by comparison of *E. albocollaris* to *Varecia variegata variegata* where these species overlap. Of course, additional factors, such as habitat quality, may also be important determinants of diet in brown lemurs (see below).

While similar in time devoted to feeding, the Andringitra and Vevembe brown lemurs differed in feeding rates and bout duration. Vevembe white-collared lemurs initiated more, shorter feeding bouts than the hybrids at Andringitra. A similar pattern was observed in *E. rubriventer* and *E.f. rufus* at Ranomafana, the latter having shorter and more frequent bouts (Overdorff, 1993). Overdorff (1993) attributed these differences to group size, with larger groups of red-fronted lemurs likely exhausting food patches more quickly. However, this

association between group size and feeding rates was not apparent in the present study: all groups were similar in size and did not follow the predicted relationship. The differences in feeding rates may instead be related to the types of food exploited and patch size.

In addition to food item preferences and feeding rates, the brown lemurs of Andringitra and Vevembe varied in habitat use (i.e., vertical stratification) during feeding. The hybrid group AN1 fed highest in the canopy, followed by the white-collared lemurs at Vevembe; the ANA hybrids had the lowest feeding heights. Vertical stratification has been seen as a critical factor in niche separation in other brown lemur communities, with brown lemurs using higher (Sussman, 1974, 1977; Freed, 1996) or lower (Vasey, 2000) levels of the canopy than potential competitors. Others have found no difference in vertical foraging between brown lemurs and sympatric congeners (Overdorff, 1996a). The variation observed in the present study is more likely linked to microhabitat structure than to niche divergence. The Parc site at Andringitra, where ANA ranges, is characterized by relatively short trees, while Ambarongy (the AN1 site) has the tallest trees; Vevembe has an intermediate canopy height (see Chapter 4).

Diet and Resource Availability

Given the differences observed in feeding ecology, as well as the variation in food availability among sites (see Chapter 4), it may be instructive to examine seasonal influences on diet among the brown lemur groups. However, there were remarkably few correlations between feeding behavior and fluctuations in resource base. For example, among the significant (or nearly so) relationships,

there were indications of a positive relationship between frugivory and fruit availability in groups AN1 and VE1, but an inverse association was indicated in group ANA despite this group's near total reliance on fruit. Similarly contradictory trends were present for secondary resources. Nor did the focal groups necessarily increase dietary diversity or the use of alternative food sources when fruit production decreased. These results suggest that the brown lemurs at Andringitra and Vevembe did not track resources (at least broad categories of food items) in predictable ways. It is also possible that broad measures of resource availability (such as the phenological analyses herein) do not adequately reflect shortages or abundance of particular crucial or preferred food items. The one-month interval for food availability measures may be either too fine or too coarse; that is, brown lemurs may track resources on a daily or weekly basis or they may only respond to broader seasonal fluctuations (e.g., three months of reduced food availability during or following the cold winter). To test for the latter case, it would be instructive to examine multi-month blocks (but more annual cycles would be required for adequate sample size, especially at Vevembe).

Surprisingly, it is often difficult to link diet choices in other brown lemurs to shifts in food availability. In *E.f. fulvus* at Ampijoroa, there was no correlation between seasonal variation in frugivory and fruit production, nor between secondary resources (leaves and flowers) and their availability (Rasmussen, 1999); however, these brown lemurs did feed more on preferred individual species according to availability (Rasmussen, 1999). Similar trends were

observed in sympatric *E. mongoz* (Rasmussen, 1999). At Ranomafana, *E. f. rufus* had greater dietary diversity when fruit was most available *and* least available (Overdorff, 1993). They also increased feeding time when fruit was scarce. However, the most dramatic behavioral response during peak scarcity was migration: red-fronted lemur groups moved 4-5 km from their normal home ranges to more productive microhabitats (Merenlender, 1993; Overdorff, 1993); this ranging pattern never observed in the study populations at Andringitra and Vevembe. In addition, niche separation between *E. f. rufus* and sympatric *E. rubriventer* fluctuated according to seasonality in resource base. During peak fruit scarcity, dietary overlap was lowest and the two species varied greatly in time spent exploiting coinciding plant species (Overdorff, 1993). Nevertheless, frugivory remained high for both species in periods of low fruit availability (Overdorff, 1993). This pattern is similar to the year-round obligate frugivory seen in the Andringitra hybrids, but not to the seasonal flower dependence of *E. albocollaris*. In the Masoala Peninsula, *E. f. albifrons* and sympatric *Varecia* also remained highly frugivorous during seasonal food scarcity (Vasey, 2000). Vertical stratification and direct contest competition likely served to minimize niche overlap between these species during these periods. Again, dietary demands of reproductive females in both species likely mitigated seasonal diet separation (Vasey, 2000).

Thus it appears that seasonal shifts in resource availability do not directly control food choice in brown lemurs. However, year-round food production may have a substantial impact on diet in the Vevembe and Andringitra brown lemurs.

Availability of all food resources (fruit, flowers, and leaves) is much higher at Andringitra than at Vevembe (Chapter 4). This higher overall productivity may permit both the very high population density and the greater degree of frugivory recorded in the Andringitra hybrid populations – despite the richer lemur community at this site. Yet, overall resource production may be even higher at Ranomafana (Overdorff and Wright, unpublished ms; Chapter 4), while diet breadth in *E. f. rufus* there is more like that observed in *E. albocollaris* at resource-poor Vevembe. Therefore, the abundant brown lemur population at Andringitra may be better explained by more specific characteristics of the habitat, such as the availability of critical resources.

Keystone Resources

Despite the lack of predictable relationships between fluctuations in food availability and general resource use, particular plant species may serve as crucial seasonal food sources for the brown lemur groups in this study. At Andringitra, both hybrid groups exhibited a striking dietary shift to fruits of fig species (notably the hemi-epiphytic *Ficus lutea*) especially in August-September. In AN1, the emphasis on figs corresponded with peak fruit scarcity. However, this association was not evident in AN1. In *E. albocollaris* at Vevembe, flowers of *Pandanus* species appear to serve as the critical resource during fruit scarcity (although more data are necessary from a complete annual cycle to confirm this). Unfortunately, there are no independent measures of the availability of these plant species during these periods. *Ficus* species did not appear in the Andringitra botanical plots, and at Vevembe, flowering occurred too rarely to adequately

assess seasonality in individual species (Chapter 4). Nevertheless, *Pandanus* species are a prominent feature in the Vevembe habitat. It should be noted that it was not always clear in what way *E. albocollaris* fed on the large flowers of *Pandanus* (i.e., specifically on pollen, nectar, and/or destructively on the whole flower). It appeared that these brown lemurs fed preferentially on petals, with incidental consumption of nectar or pollen. However, I did not observe the study animals to consume the flowers entirely. Therefore, *E. albocollaris* may serve as a pollinator for these plant species (e.g., see Sussman and Raven, 1978).

The use of specific resources during scarce seasons is important in primate communities elsewhere. Keystone resources – particularly asynchronously fruiting *Ficus* species, but also flowers – likely sustain the primates of Cocha Cashu, Peru during the dry season (Terborgh, 1986b). Indeed, Terborgh (1986b) asserts that the absence of figs would be catastrophic for this frugivore community. However, the universality of *Ficus* as a keystone resource has been questioned. In Gabon, figs are rare and individual trees tend to ripen too rapidly to provide a sustained resource (Gautier-Hion and Michaloud, 1989). As a result, primates rarely feed on them. Gautier-Hion and Michaloud (1989) suggest that high-volume terrestrial fig trees may only be prevalent in second-growth forests.

The rarity of *Ficus* has been cited as an important factor contributing to the paucity of frugivorous vertebrates in Madagascar (Goodman and Ganzhorn, 1997). The historical isolation of the island has limited dispersal and given rise to distinct evolutionary trajectories relative to continental landmasses. An example is the dearth of *Ficus* species; only 24 total species have been recorded, and only

12 in individual forests – less than half than in other Old World tropical forests (Goodman and Ganzhorn, 1997). Furthermore, the density of individual *Ficus* trees tends to be low in Malagasy forests (Goodman and Ganzhorn, 1997), and thus, rarely consumed by frugivores (Goodman et al., 1997). Overall fruit availability is also lower in Madagascar, and there is evidence that seasonality is less predictable and more extreme (Goodman and Ganzhorn, 1997; Wright, 1999). Therefore, the lack of an important keystone resource like *Ficus* may contribute significantly to the rarity of frugivorous mammals and birds. Overdorff (1993) found that *Ficus* feeding was relatively prominent in the diet of *E. f. rufus*. However, these brown lemurs fed on figs year-round, and reliance was generally lower than at Andringitra (11% of feeding time; Johnson and Overdorff, 2002). There was an increase in fig feeding immediately preceding scarce seasons, but the migrations seen in these groups suggest that *Ficus* cannot sustain the brown lemurs during peak scarcity at Ranomafana (Johnson and Overdorff, 2002).

The seasonal reliance of Andringitra hybrids on figs suggests there may be variation in this pattern within the eastern rain forest region. The evidence is equivocal, however: while both groups consumed large quantities of *Ficus* fruits during similar months, this period only corresponded to overall fruit scarcity in group ANA. Accordingly, the hybrids may have a preference for *Ficus* regardless of season or resource base. Alternatively, the fruit availability measures here failed to capture seasonal shortages within the range of AN1. The relatively high availability at Ambarongy during July-August 1999 is perhaps an aberration; fruit

productivity is generally low in these winter months across southeastern Malagasy forests (see Chapter 4) and perhaps many specific foods necessary or preferred by brown lemurs were not available at this time (regardless of the indication of overall fruit abundance). Despite the somewhat equivocal results, the striking dependence on *Ficus* during two winters in two study groups indicates that this resource has great significance for the brown lemurs at Andringitra, certainly more than has been suggested for elsewhere in Madagascar. An independent phenological assessment of *Ficus* species at Andringitra would be helpful in resolving these issues. However, Malagasy figs are generally asynchronous in their reproductive stages (Dalecky et al., in press); thus fruit availability across the *Ficus* population is not expected to fluctuate seasonally.

Flower feeding as a keystone resource has received less attention. There are many lemur species that may consume significant quantities of flowers and/or nectar (Sussman and Raven, 1978). For example, Rasmussen (1999) describes heavy reliance by *E. mongoz* on *Hura crepitans* nectar during the dry months of May-June; however, these months do not correspond to peak scarcity in fruit (or flowers). Similarly, flower consumption increases in female *E. f. albifrons* (27%) during the resource-rich hot dry season, likely reflecting particular nutritional needs during late gestation-early lactation (Vasey, 2002). Thus, *E. albocollaris* at Vevembe may be unusual in their use of *Pandanus* flowers as a potential keystone resource. Yet, given the species-poor lemur community and low brown lemur densities at Vevembe, this resource may not be as effective as figs at Andringitra in sustaining frugivores through scarce seasons.

How Different Are the Brown Lemurs of the Southeast?

Assessing the similarities and differences described above begs questions about the degree of ecological divergence in these populations. Are differences among the southeastern brown lemurs considered here – *E. albocollaris* at Vevembe and the hybrids at Andringitra, as well as *E. f. rufus* at Ranomafana – equivalent to species-level distinctions? Based on the comparisons to other communities of brown lemurs and their sympatric competitors, the answer appears to be “yes”. There is clear variation among the hybrid and parental populations in general feeding profiles (e.g., differences in frugivory and secondary food categories), dietary diversity, and diet switching during resource scarcity. These differences are almost certainly related to particular habitat characteristics at Andringitra, Vevembe, and Ranomafana, including animal community structure and seasonal and year-round variation in resource availability. The inter-population differences in feeding observed here rival those between more distantly related sympatric competitors, underscoring the distinctiveness of the southeastern brown lemur populations or, more likely, the high degree of adaptability of the brown lemur complex.

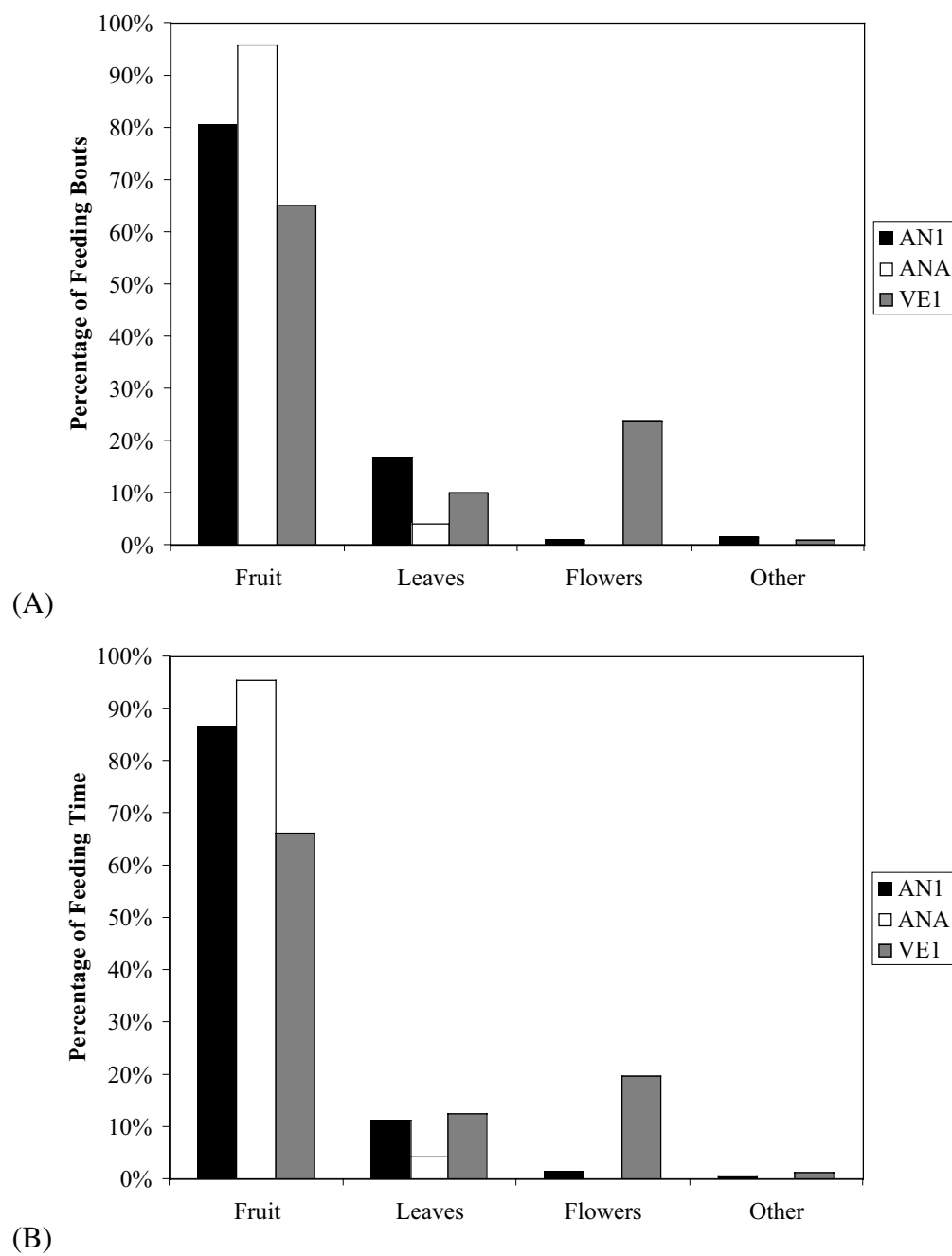


Figure 5.1: Diet Composition Across Groups.

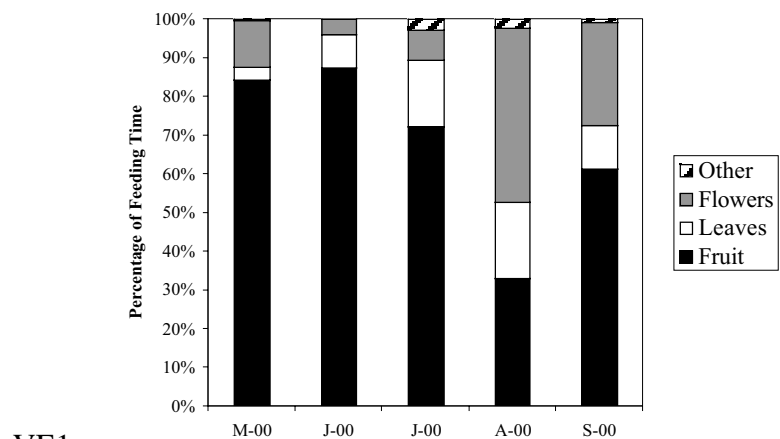
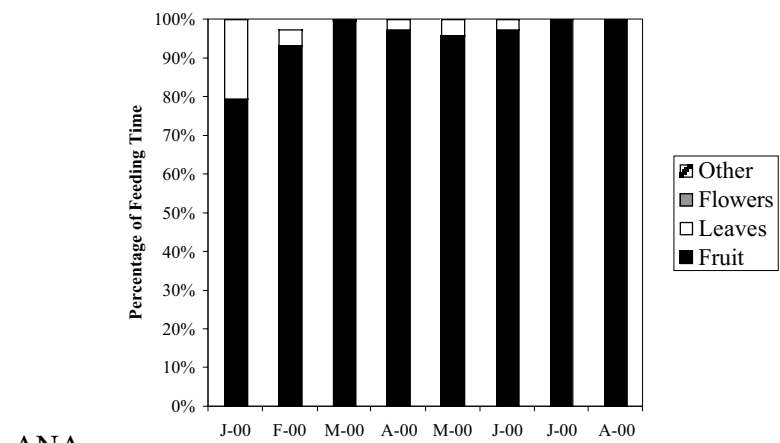
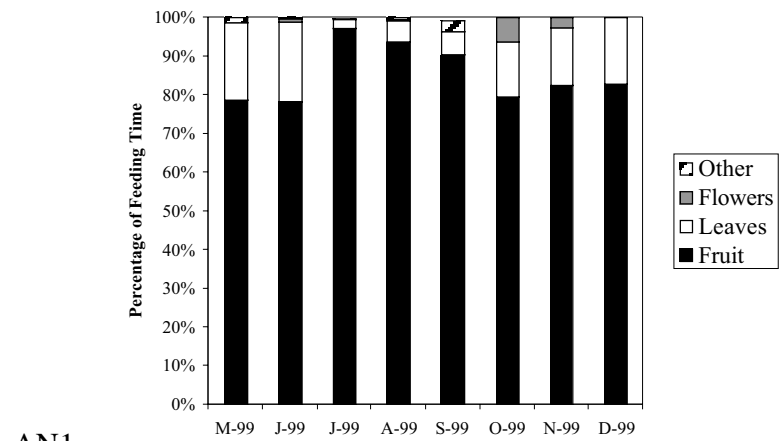


Figure 5.2: Seasonal Variation in Diet Across Groups.

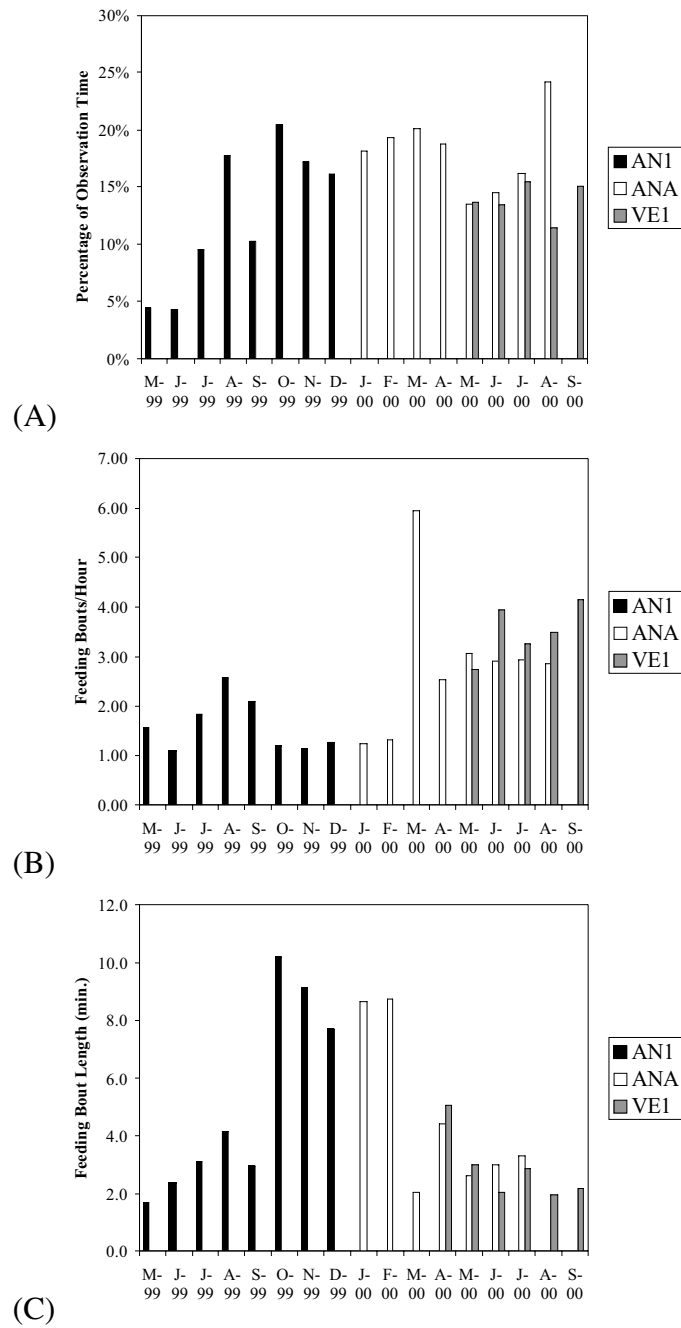


Figure 5.3: Total Feeding Time and Feeding Rates. (A) Percentage of overall feeding time spent feeding. (B) Feeding bouts per hour of observation. (C) Mean feeding bout length (minutes).

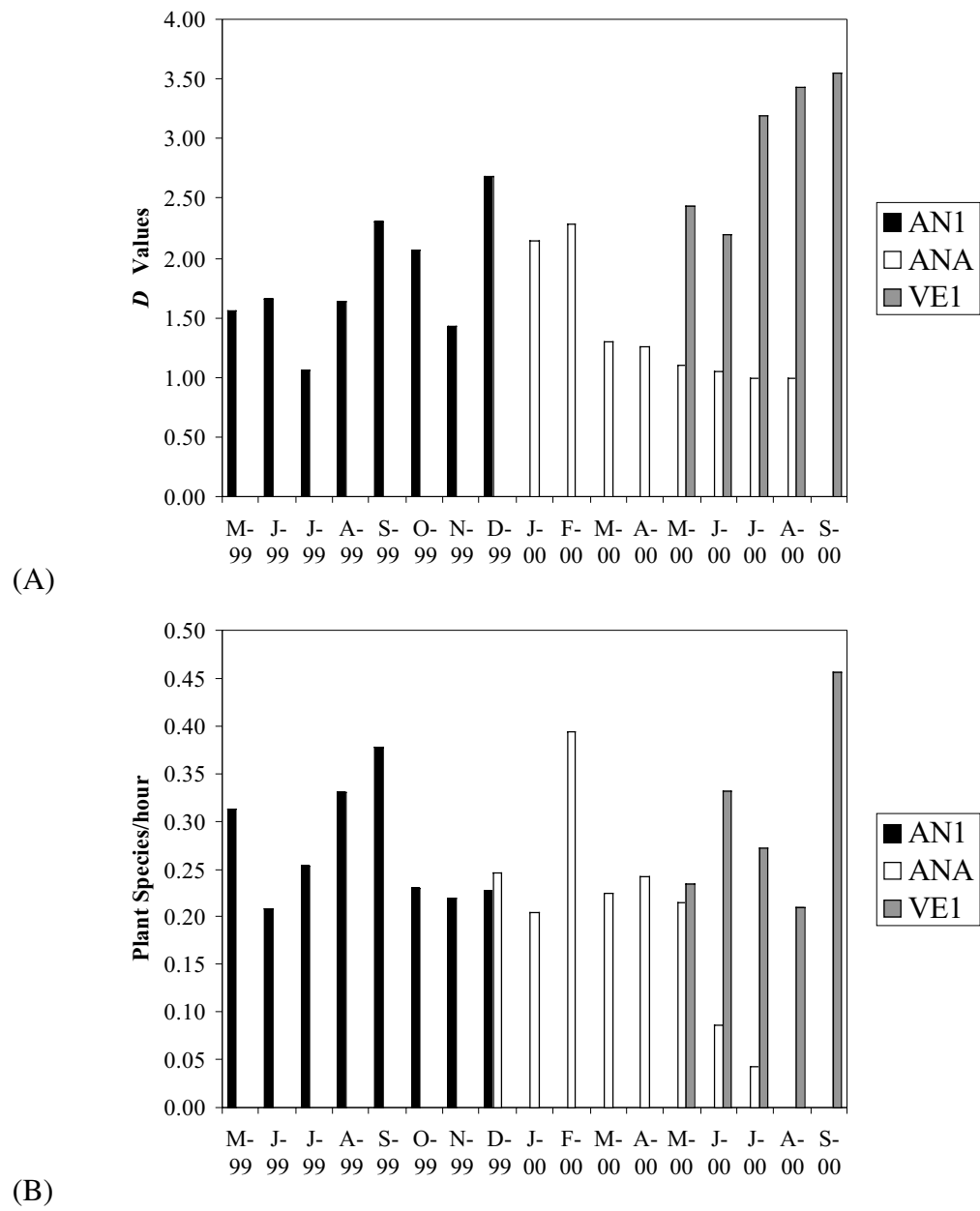


Figure 5.4: Dietary Diversity. (A) D values for food plant part subcategories (see Table 5.1). (B) Plant species consumed per hour of observation.

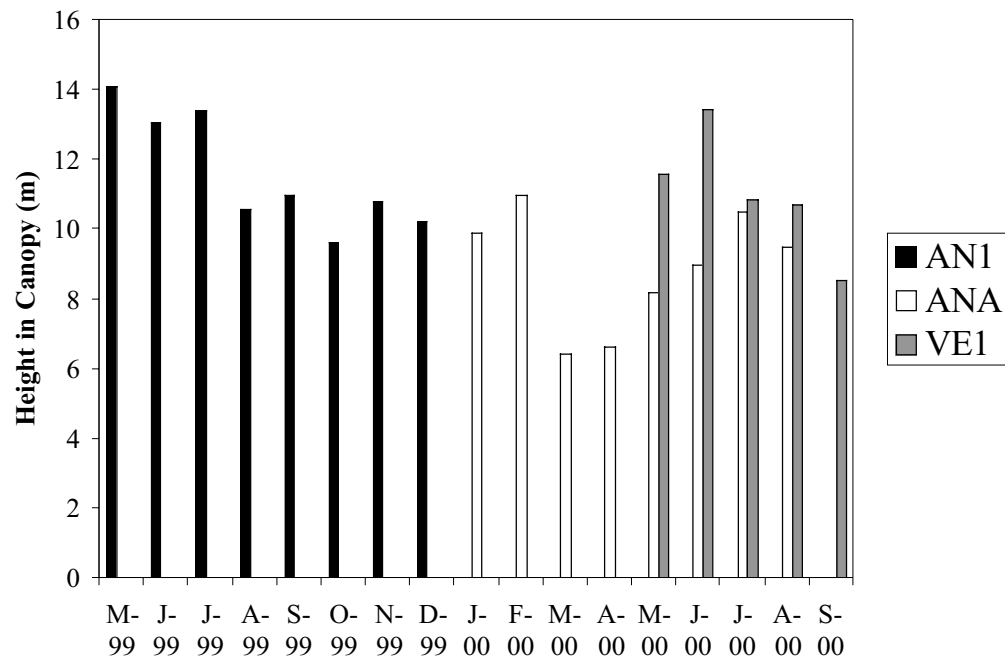


Figure 5.5: Mean Height in Canopy (m) During Feeding.

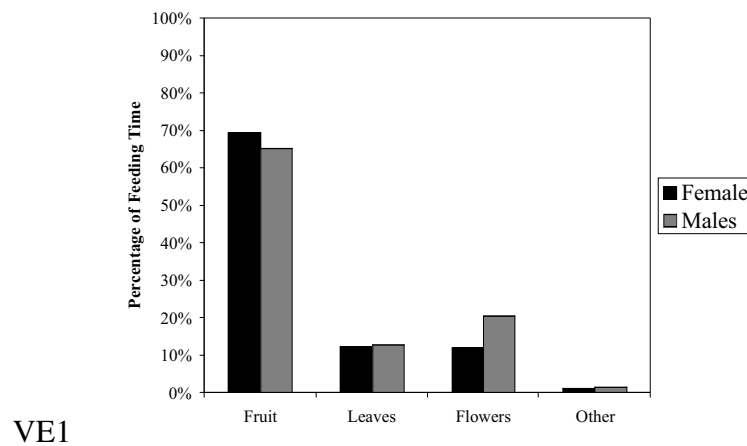
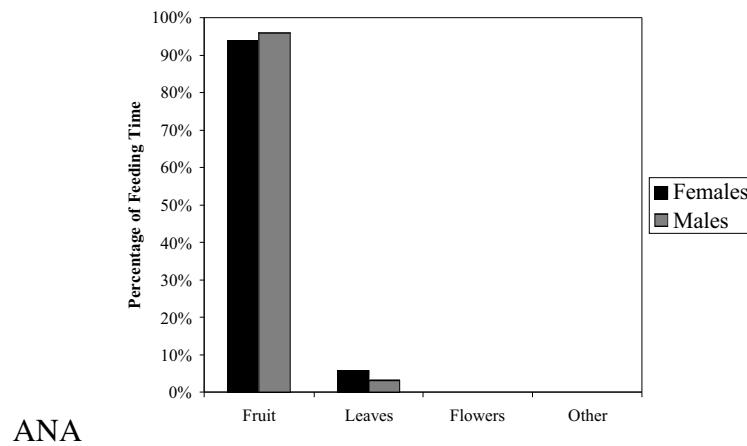
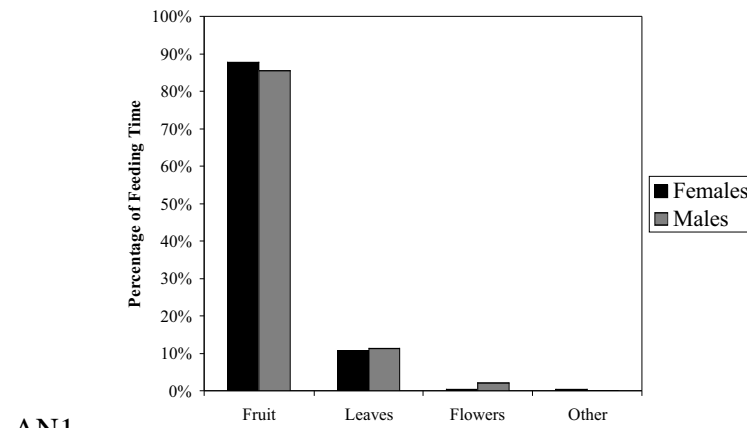


Figure 5.6: Sex Differences in Diet Composition. Group VE1 had only one female during the study period.

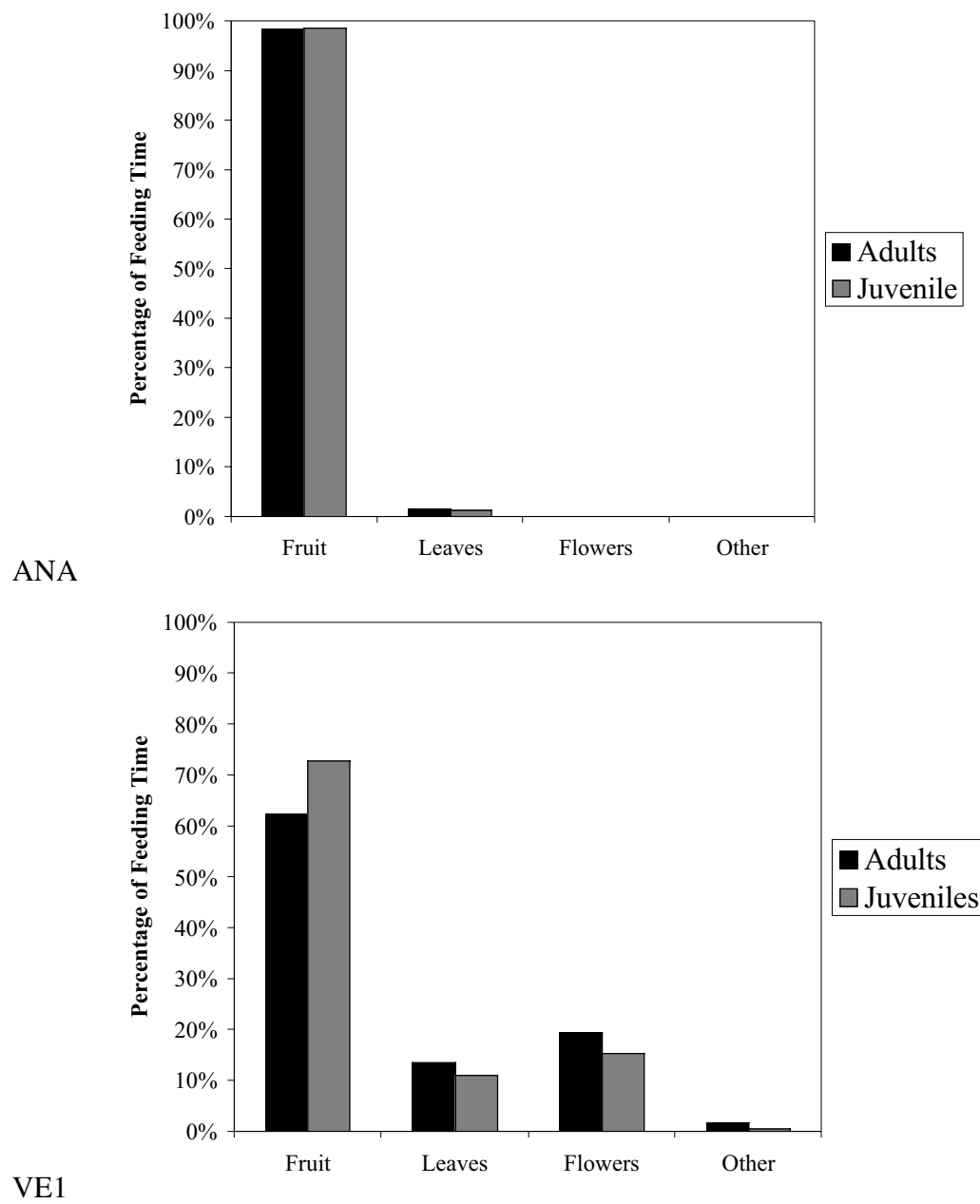


Figure 5.7: Age Differences in Diet Composition. There was one juvenile in group ANA and no juveniles in group AN1 during the study.

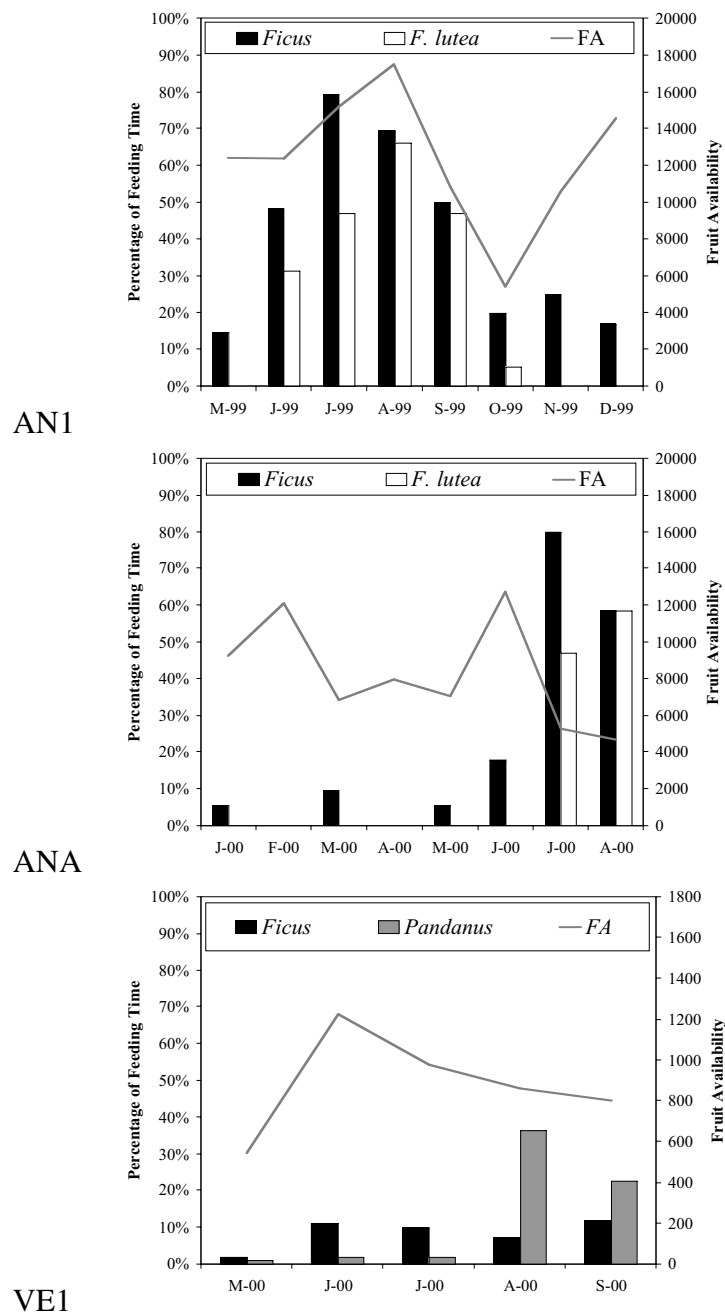


Figure 5.8: Potential Keystone Resources. Fruit availability (FA) is shown on the secondary axis. The values for *Ficus* represent fruit. *Pandanus* = flowers.

Table 5.1: Composition of Study Groups.

Site	Group	Name	Age Class	Sex
Andringitra-Ambarongy	AN1	RA	Adult	F
		RE	Adult	F
		YE	Adult	F
		GR	Adult	M
		YB	Adult	M
		PB	Adult	M
		RG	Adult	M
Andringitra-Parc	ANA	RF	Adult	F
		CF	Adult	F
		GG	Adult	M
		BB	Adult	M
		BT	Adult	M
		ED	Juvenile	M
Veveembe	VE1	VF	Adult	F
		NC	Adult	M
		YG	Adult	M
		RB	Adult	M
		JA	Juvenile	M
		JB	Juvenile	M

Table 5.2: Summary of Feeding Patterns.

		Andringitra AN1	ANA	Veveve VE1
Diet Composition	<u>% Feeding Bouts</u>			
	Fruit	80.4%	95.9%	65.1%
	Leaves	16.8%	4.0%	10.0%
	Flowers	0.9%	0.0%	23.7%
	Other	1.5%	0.0%	0.9%
	<u>% Feeding Time</u>			
	Fruit	86.8%	95.4%	66.2%
	Leaves	11.2%	4.3%	12.7%
	Flowers	1.5%	0.0%	19.7%
	Other	0.5%	0.0%	1.4%
Feeding Rates	% Observation Time Spent Feeding	12.6%	17.9%	13.6%
	Feeding Bouts/hour	1.8	2.7	3.4
	Mean Bout Duration (min.)	4.5	4.0	2.4
Diet Diversity ¹	<i>D</i> (% Feeding Bouts)	2.2	1.2	3.7
	<i>D</i> (% Feeding Time)	1.9	1.4	3.9
	Total Plant Species	69	27	96
	Plant Species/hour	0.117	0.082	0.139
Habitat Use	Feeding Height (m)	11.5	8.7	11.1

¹ *D* values are based on contribution to overall diet of plant part subcategories: ripe fruit (RF), unripe fruit (UF), mature leaves (ML), new leaves (NL), leaf bases (LB), flowers (FL), flower buds (BU), and other (OT).

Table 5.3a: Diet Across Months in Group AN1, Andringitra¹.

Month	Fruit			Leaves				Flowers			Other			
	RF	UF	Unspec. Fruit	ML	NL	LB	Unspec. Leaves	FL	BU	NE	Moss	Fungus	Soil	Unk.
May-99	78.6	0.0	0.0	11.1	8.9	0.0	0.0	0.0	0.0	0.0	1.3	0.0	0.0	0.0
Jun-99	75.9	2.2	0.0	5.2	15.5	0.0	0.0	0.8	0.0	0.0	0.3	0.0	0.0	0.0
Jul-99	96.8	0.0	0.4	0.8	1.3	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.2	0.2
Aug-99	75.8	17.9	0.0	1.4	4.2	0.0	0.0	0.1	0.0	0.0	0.0	0.6	0.0	0.0
Sep-99	54.9	35.8	0.0	0.0	5.7	0.0	0.0	0.0	0.0	0.0	2.9	0.0	0.1	0.7
Oct-99	66.4	13.2	0.0	0.0	14.3	0.0	0.0	6.1	0.0	0.0	0.0	0.0	0.0	0.0
Nov-99	82.5	0.0	0.0	0.4	13.4	0.0	1.1	2.6	0.0	0.0	0.0	0.0	0.0	0.0
Dec-99	37.8	45.1	0.0	0.0	16.0	0.0	1.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Total	70.4%	16.4%	0.0%	1.3%	9.6%	0.0%	0.3%	1.5%	0.0%	0.0%	0.3%	0.2%	0.0%	0.1%

¹ Diet in subcategories calculated by percentage of total feeding time. Subcategory codes are: RF = ripe fruit, UF = unripe fruit, "Unspec." = unspecified maturation stage, ML = mature leaves, NL = new leaves, LB = leaf bases, FL = flowers, BU = flower buds, NE = nectar, "unk." = unidentified part.

Table 5.3b: Diet Across Months in Group ANA, Andringitra¹.

Month	Fruit			Leaves				Flowers			Other			
	RF	UF	Unspec. Fruit	ML	NL	LB	Unspec. Leaves	FL	BU	NE	Moss	Fungus	Soil	Unk.
Jan-00	63.0	16.4	0.0	0.0	20.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Feb-00	47.9	45.3	0.0	0.0	4.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.5
Mar-00	86.7	13.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Apr-00	88.6	8.8	0.0	1.0	1.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
May-00	94.8	1.0	0.0	0.8	3.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Jun-00	97.5	0.0	0.0	0.4	2.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Jul-00	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Aug-00	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Total	85.4%	10.0%	0.0%	0.3%	4.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.3%

¹ See Table 5.2a for explanation.

Table 5.3c: Diet Across Months in Group VE1, Vevembe¹.

Month	Fruit			Leaves				Flowers			Other			
	RF	UF	Unspec. Fruit	ML	NL	LB	Unspec. Leaves	FL	BU	NE	Moss	Fungus	Soil	Unk.
May-00	56.8	27.5	0.1	2.6	0.4	0.4	0.0	1.0	10.9	0.0	0.0	0.3	0.0	0.1
Jun-00	63.2	21.7	2.4	8.1	0.7	0.0	0.0	2.6	1.2	0.0	0.0	0.0	0.0	0.0
Jul-00	26.7	45.6	0.1	16.6	0.6	0.0	0.0	7.7	0.0	0.0	0.0	2.7	0.0	0.1
Aug-00	18.9	13.4	0.7	19.0	0.9	0.0	0.0	44.8	0.0	0.0	0.0	2.3	0.0	0.1
Sep-00	13.3	42.8	5.1	11.2	0.0	0.0	0.0	25.5	1.4	0.0	0.0	0.7	0.0	0.0
Total	35.5%	29.5%	1.2%	12.0%	0.6%	0.1%	0.0%	16.8%	2.9%	0.0%	0.0%	1.4%	0.0%	0.1%

¹ See Table 5.2a for explanation.

Table 5.4a: Plant Species Consumed by Group AN1, Andringitra¹.

Vernacular	Family	Species	RF	UF	ML	NL	FL	BU	Unk.
velatra	Acanthaceae	<i>Ruellia</i> sp. "velatra"				X			
voatakaboka	Apocynaceae	<i>Landolphia</i> sp. "voatakaboka"		X					
ramy	Burseraceae	<i>Canarium madagascariense</i> Engler	X	X					
kimbaletaka	Clusiaceae	<i>Garcinia</i> sp. "kimbaletaka"	X	X					
voamalambotaholahy	Clusiaceae	<i>Rheedia</i> sp. "voamalambotaholahy"			X				
kimba	Clusiaceae	<i>Symphonia</i> sp. "kimba"		X					
malambovony	Erythroxylaceae	<i>Erythroxylum</i> sp. "malambovony"				X			
mongina	Euphorbiaceae	<i>Croton mongue</i> Baillon		X					
vahimboamena	Fabaceae	<i>Arbrus precatorius</i>			X	X			
fandramana	Flacourtiaceae	<i>Aphloia theaeformis</i> Bennett	X				X		
tavolo maitso	Lauraceae	<i>Cryptocarya</i> cf. "flavescens"	X	X					
tavolo pina	Lauraceae	<i>Cryptocarya</i> sp. "tavolo pina"		X					
varongy	Lauraceae	<i>Ocotea</i> sp. "varongy"	X	X					
voamboana	Leguminosae	<i>Dalbergia baroni</i> Baker				X			
tongolahy	Loranthaceae	<i>Bakerella</i> sp. "tongolahy"		X	X	X			
kalamasimbarika	Melastomataceae	<i>Medinilla</i> sp. "kalamasimbarika"	X						
kitonda	Melastomataceae	<i>Medinilla</i> sp. "kitonda"	X						
vahy zezika, vahivoraka	Mendonciaceae	<i>Mendoncia couvanii</i> Vell ex Vand		X		X			
ambora pf	Monimiaceae	<i>Tambourissa</i> sp. "ambora pf"	X						
ambora	Monimiaceae	<i>Tambourissa</i> sp. "ambora"			X				
amboralahy	Monimiaceae	<i>Tambourissa</i> sp. "amboralahy"	X		X	X			
amboravavy	Monimiaceae	<i>Tambourissa</i> sp. "amboravavy"	X						
amotana	Moraceae	<i>Ficus lutea</i> Baker	X						
apana	Moraceae	<i>Ficus pachyclada</i>		X					
nonoka	Moraceae	<i>Ficus rubra</i> Vahl	X						
fopohona	Moraceae	<i>Ficus</i> sp. "fopohona"	X						
ara	Moraceae	<i>Ficus tiliifolia</i> Baker	X						
apaly nala	Moraceae	<i>Treculia africana</i> Decaisne ssp. <i>madagascariense</i> (N.E. Brown)	X						
kalamasina	Myrsinaceae	<i>Embelia madagascariensis</i> A. DC.			X	X			X
kalafana	Myrsinaceae	<i>Oncostemon botryoides</i> Baker	X	X		X			
kalafambakaka	Myrsinaceae	<i>Oncostemon</i> sp. "kalafambakaka"	X		X	X			X
robary	Myrtaceae	<i>Syzygium</i> "emirnensis"	X	X					
rotra	Myrtaceae	<i>Syzygium</i> sp. "rotra"		X					
rotrabe	Myrtaceae	<i>Syzygium</i> sp. "rotrabe"	X	X					
rotramadinika	Myrtaceae	<i>Syzygium</i> sp. "rotramadinika"		X					
rotramena	Myrtaceae	<i>Syzygium</i> sp. "rotramena"	X	X					
fatsikahitra	Rubiaceae	<i>Canthium micrantha</i> Baker	X	X		X			
hazotoho	Rubiaceae	<i>Gaertnera</i> sp. "hazotoho"	X						
fatora	Rubiaceae	<i>Mussaenda erectiloba</i> Wernham	X	X					
valotra pangady	Rubiaceae	<i>Neobreonia decaryana</i>	X						
fohaninasy gf	Rubiaceae	<i>Psychotria</i> sp. "fohaninasy gf"	X						

Table 5.4a: Plant Species Consumed by Group AN1, Andringitra¹ (cont.).

Vernacular	Family	Species	RF	UF	ML	NL	FL	BU	Unk.
fohaninacity pf	Rubiaceae	<i>Psychotria</i> sp. "fohaninacity pf"	X						
fohaninacity	Rubiaceae	<i>Psychotria</i> sp. "fohaninacity"	X	X					
ranjopody	Rubiaceae	<i>Psychotria</i> sp. "ranjopody"	X						
dikana	Sapindaceae	<i>Allophylus cobbe</i>	X						
rahiaka	Sapotaceae	<i>Chrysophyllum boivinianum</i> (Pierre) Baehni	X						
roindambo	Smilacaceae	<i>Smilax anceps</i> Wildenow	X	X	X				
hafodahy	Sterculiaceae	<i>Dombeya</i> sp. "hafodahy"					X		
sele	Tiliaceae	<i>Grewia repanda</i>	X						
hafipotsy	Tiliaceae	<i>Grewia</i> sp. "hafipotsy"		X					
vahirano	Vitaceae	<i>Cissus</i> sp. "vahirano"					X		
vahimavo		sp. indet. "vahimavo"				X	X		
hazomena		spec. indet. "hazomena"		X					
hazotana		spec. indet. "hazotana"					X		
tsivoka		spec. indet. "tsivoka"	X	X					
vahiambaniakondro		spec. indet. "vahiambaniakondro"					X		
voakirepoka		spec. indet. "voakirepoka"	X	X					
voanananala		spec. indet. "voanananala"	X						
voadavena		spec. indet. "voandavenona"		X					
moss									
mushroom									
soil									
unknown #1						X			
unknown #2			X						
unknown #3			X						
unknown #4			X						
unknown #5						X			
unknown #6									X
unknown #7			X						

¹ Plant part categories are: RF = ripe fruit, UF = unripe fruit, ML = mature leaves, NL = new leaves, FL = flowers, BU = flower buds, "unk." = unidentified.

Table 5.4b: Plant Species Consumed by Group ANA, Andringitra¹.

Vernacular	Family	Species	RF	UF	ML	YL	FL	BU	Unk.
mananasy	Bromeliaceae	<i>Ananas comosus</i> Merr.	X						
ramy	Burseraceae	<i>Canarium madagascariense</i> Engler	X	X					
vitanona	Clusiaceae	<i>Calophyllum</i> sp. "vitanona"		X					
kimbaletaka	Clusiaceae	<i>Garcinia</i> sp. "kimbaletaka"	X	X					
harongana	Clusiaceae	<i>Harungana madagascariensis</i> Lam. Ex Poirét	X	X					
vahimboamena	Fabaceae	<i>Arbrus precatorius</i>	X		X	X			
tavolo maitso	Lauraceae	<i>Cryptocarya</i> cf. "flavescens"				X			
varongy	Lauraceae	<i>Ocotea</i> sp. "varongy"	X						
kitonda	Melastomataceae	<i>Medinilla</i> sp. "kitonda"	X						
tsitrotroka	Melastomataceae	spec. indet. "tsitrotroka"	X						
ambora pf	Monimiaceae	<i>Tambourissa</i> sp. "ambora pf"	X						
ambora	Monimiaceae	<i>Tambourissa</i> sp. "ambora"	X						
amboralahy	Monimiaceae	<i>Tambourissa</i> sp. "amboralahy"	X						
amotana	Moraceae	<i>Ficus lutea</i> Baker	X						
nonoka	Moraceae	<i>Ficus rubra</i> Vahl	X	X					
ara	Moraceae	<i>Ficus tiliifolia</i> Baker	X						
kalamasina, vahikisina	Myrsinaceae	<i>Embelia madagascariensis</i> A. DC.			X	X			X
faripandoa	Myrsinaceae	<i>Oncostemon</i> sp. "faripandoa"	X	X					
kalafambakaka	Myrsinaceae	<i>Oncostemon</i> sp. "kalafambakaka"			X				
goavy	Myrtaceae	<i>Psidium guajava</i> L.		X					
menahy	Ochnaceae	<i>Diporidium</i> sp. "menahy"	X						
hova, sihara, voanova	Palmae	<i>Dypsis decipiens</i> (Becc.) Beentje & J. Dransf.	X	X		X			
hazotoho	Rubiaceae	<i>Gaertnera</i> sp. "hazotoho"	X						
fohaninasity	Rubiaceae	<i>Psychotria</i> sp. "fohaninasity"	X	X					
rahiaka	Sapotaceae	<i>Chrysophyllum boivinianum</i> (Pierre) Baehni	X						
roindambo	Smilacaceae	<i>Smilax anceps</i> Willdenow		X					
voanananala		spec. indet. "voanananala"	X						

¹ Plant part categories are: RF = ripe fruit, UF = unripe fruit, ML = mature leaves, NL = new leaves, FL = flowers, BU = flower buds, "unk." = unidentified.

Table 5.4c: Plant Species Consumed by Group VE1, Vevembe¹.

Vernacular	Family	Species	RF	UF	ML	YL	LB	FL	BU	NE	Unk.
hasina	Agavaceae	<i>Dracaena</i> sp. "hasina"			X						
sandramy	Anacardiaceae	spec. indet. "sandramy"	X	X							
ramiavona	Annonaceae	<i>Xylophia</i> sp. "ramiavona"	X								
vahiherotra gf	Apocynaceae	<i>Landolphia</i> sp. "vahiherotra gf"			X	X					
vahiherotra	Apocynaceae	<i>Landolphia</i> sp. "vahiherotra"	X	X	X	X					
vahia, vahimbahia	Asteraceae	<i>Mikania scandens</i>			X	X					
tavilona	Asteraceae	<i>Vernonia</i> sp. "tavilona"		X							
kimbaletaka gf	Clusiaceae	<i>Garcinia</i> sp. "kimbaletaka gf"			X						
kimbaletaka mf	Clusiaceae	<i>Garcinia</i> sp. "kimbaletaka mf"			X						
kimbaletaka pf #1	Clusiaceae	<i>Garcinia</i> sp. "kimbaletaka pf #1"			X						
kimbaletaka pf #2	Clusiaceae	<i>Garcinia</i> sp. "kimbaletaka pf #2"			X						
kimbaletaka	Clusiaceae	<i>Garcinia</i> sp. "kimbaletaka"			X			X			
harongana	Clusiaceae	<i>Harungana madagascariensis</i> Lam. Ex Poiret	X								
nato voraka	Clusiaceae	<i>Mammea "angustifolia" var. "pseudoprotorhus"</i>	X								
kimba special pf	Clusiaceae	<i>Symphonia</i> sp. "kimba special pf"				X			X		
kimba	Clusiaceae	<i>Symphonia</i> sp. "kimba"			X						
veso	Combretaceae	<i>Terminalia tetranora</i>	X	X		X					
hazomainty	Ebenaceae	<i>Diospyros gracilipes</i> Hiern			X						
malambovony gf	Erythroxylaceae	<i>Erythroxylum</i> sp. "malambovony gf"							X		
malambovony pf	Erythroxylaceae	<i>Erythroxylum</i> sp. "malambovony pf"									X
malambovony	Erythroxylaceae	<i>Erythroxylum</i> sp. "malambovony"		X	X						
mokaranana	Euphorbiaceae	<i>Macaranga</i> sp. "mokaranana"	X	X	X	X		X			
voapaka	Euphorbiaceae	<i>Uapaka louvelii</i> M. Denis		X							
vahimboamena	Fabaceae	<i>Arbrus precatorius</i>	X		X						
hazoambato mena pf	Flacoutaceae	<i>Homalium</i> sp. "hazoambato mena pf"									X
hazoambato	Flacoutaceae	<i>Homalium</i> sp. "hazoambato"	X	X							
malanimata	Icacinaceae	<i>Apodytes thouvenotii</i> Danguy	X	X	X						
tavolo fotsy	Lauraceae	<i>Cryptocarya</i> sp. "tavolo fotsy"		X							
tavolo	Lauraceae	<i>Cryptocarya</i> sp. "tavolo"		X							
varongy	Lauraceae	<i>Ocotea</i> sp. "varongy"				X					
sary	Lauraceae	<i>Potameia chartacea</i> Kosterm.	X	X		X					
sambalahy	Leguminosae	<i>Albizia gummifera</i> (J.F. Gmelin) C.A. Smith		X							
demdemy	Loganiaceae	<i>Anthocleista</i> sp. "dendemy"	X								
lambinanala	Loganiaceae	<i>Nuxia</i> sp. "lambinanala"		X							

Table 5.4c: Plant Species Consumed by Group VE1, Vevembe¹ (cont.).

Vernacular	Family	Species	RF	UF	ML	YL	LB	FL	BU	NE	Unk.
ambora pf	Monimiaceae	<i>Tambourissa</i> sp. "ambora pf"	X								
amotana	Moraceae	<i>Ficus lutea</i> Baker	X								
mandresy	Moraceae	<i>Ficus polita</i>	X								
famakilela	Moraceae	<i>Ficus politoria</i> Lam.		X							
nonoka	Moraceae	<i>Ficus rubra</i> Vahl	X	X							
ara	Moraceae	<i>Ficus tiliifolia</i> Baker	X								
kalamasina	Myrsinaceae	<i>Embelia madagascariensis</i> A. DC.			X						
kalafana gf	Myrsinaceae	<i>Oncostemon botryoides</i> Baker		X							
kalafambakaka pf	Myrsinaceae	<i>Oncostemon</i> sp. "kalafambakaka"	X								
kalafana pf	Myrsinaceae	<i>Oncostemon</i> sp. "kalafana pf"		X							
robary	Myrtaceae	<i>Syzygium</i> "emirnenensis"	X	X							
rotramena mf	Myrtaceae	<i>Syzygium</i> sp. "rotramena mf"	X	X							
rotramena	Myrtaceae	<i>Syzygium</i> sp. "rotramena"	X	X							
rotramena	Myrtaceae	<i>Syzygium</i> sp. "rotramena"		X							
solaitra fotsy	Oleaceae	<i>Noronia</i> sp. "solaitra fotsy"	X		X			X			
solaitra, hazombary	Oleaceae	<i>Noronia</i> sp. "solaitra"	X		X						
sira	Palmae	<i>Dypsis</i> sp. "sira"	X	X							
lafa pf #1	Palmae	<i>Ravanea</i> sp. "lafa pf #1"	X	X							
lafa pf #2	Palmae	<i>Ravanea</i> sp. "lafa pf #2"						X			
lafa	Palmae	<i>Ravanea</i> sp. "lafa"	X					X			
vakoana, tsirika mf	Pandanaceae	<i>Pandanus</i> sp. "tsirika mf #1"	X					X			
vakoana mf escalier	Pandanaceae	<i>Pandanus</i> sp. "tsirika mf escalier"	X								
vakoana, tsirika pf #1	Pandanaceae	<i>Pandanus</i> sp. "tsirika pf #1"	X				X	X			X
vakoana, tsirika pf #2	Pandanaceae	<i>Pandanus</i> sp. "tsirika pf #2"					X	X			
vakoana, tsirika	Pandanaceae	<i>Pandanus</i> sp. "tsirika"	X					X			
vilonala	Poaceae	spec. indet. "vilonala"			X						
fatsikahitra	Rubiaceae	<i>Canthium micrantha</i> Baker		X	X	X		X	X		
fatsikahitra mf	Rubiaceae	<i>Canthium</i> sp. "fatsikahitra mf"						X			
fatsikahitra pf	Rubiaceae	<i>Canthium</i> sp. "fatsikahitra pf"						X			
valotra, valotra mainty	Rubiaceae	<i>Gyrostipula foveolata</i> (Capuron) Leroy	X	X							
fatora, malemiravina	Rubiaceae	<i>Mussaenda erectiloba</i> Wernham	X	X							
fohaninasity gf	Rubiaceae	<i>Psychotria</i> sp. "fohaninasity gf"	X								
fohaninasity mf	Rubiaceae	<i>Psychotria</i> sp. "fohaninasity mf"	X								
fohaninasity pf	Rubiaceae	<i>Psychotria</i> sp. "fohaninasity pf"	X								

Table 5.4c: Plant Species Consumed by Group VE1, Vevembe¹ (cont.).

Vernacular	Family	Species	RF	UF	ML	YL	LB	FL	BU	NE	Unk.
valotra fotsy	Rubiaceae	sp. indet. "valotra fotsy" (tribe Naucleae)	X	X							
lanary special	Sapindaceae	<i>Glenniea pervillei</i> (Baill.) Leenh.					X				
lanary madinka	Sapindaceae	<i>Neotina coursii</i> Capuron		X	X	X					
lanary	Sapindaceae	<i>Tina striata</i> Radlk.			X						
roindambo	Smilacaceae	<i>Smilax anceps</i> Willdenow	X								
hafodahy pf	Sterculiaceae	<i>Dombeya</i> sp. "hafodahy pf"						X			
ravinala	Sterlitziaceae	<i>Ravenala madagascariensis</i> Sonn.						X			
apanga		spec. indet. "apanga"									X
raloto		spec. indet. "babona"			X						
fatsy		spec. indet. "fatsy"		X							
fonty		spec. indet. "fonty"	X	X	X	X					
mushroom		spec. indet. "fungus"									
mazambody		spec. indet. "mazambody"	X								
spiky ramy		spec. indet. "ramy hafahafa"	X								
tendrikazo		spec. indet. "tendrikazo"		X							
tongely		spec. indet. "tongely"	X								
tsoihy		spec. indet. "tsoihy"							X		
vahiakondro		spec. indet. "vahiakondro"			X	X					
vahignena		spec. indet. "vahignena"						X			
voanananala		spec. indet. "voanananala"	X								
unknown #1			X								
unknown #2					X						
unknown #3					X						
unknown #4				X							
unknown #5										X	
unknown #6					X						
unknown #7											X

¹ Plant part categories are: RF = ripe fruit, UF = unripe fruit, ML = mature leaves, NL = new leaves, LB = leaf base, FL = flowers, BU = flower buds, "unk." = unidentified.

Table 5.5: Top Ten Species for All Groups, Including Part Consumed and Percentage of Total Feeding Time¹.

Group	Family	Species	Part Consumed	% Feeding Time
AN1	Moraceae	<i>Ficus lutea</i> Baker	RF	29.7%
	Myrtaceae	<i>Syzygium</i> sp. "rotramena"	RF, UF	9.1%
	Moraceae	<i>Ficus rubra</i> Vahl	RF	7.1%
	Acanthaceae	<i>Ruellia</i> sp. "velatra"	YL	6.5%
	Moraceae	<i>Ficus tiliifolia</i> Baker	RF	6.2%
		spec. indet. "tsivoka"	RF, UF	5.6%
	Burseraceae	<i>Canarium madagascariense</i> Engler	RF, UF	5.1%
	Sapotaceae	<i>Chrysophyllum boivinianum</i> (Pierre) Baehni	RF	3.3%
	Myrtaceae	<i>Syzygium</i> "emirnenensis"	RF, UF	3.2%
	Lauraceae	<i>Ocotea</i> sp. "varongy"	RF, UF	2.7%
ANA	Moraceae	<i>Ficus lutea</i> Baker	RF	17.0%
	Rubiaceae	<i>Gaertnera</i> sp. "hazotoho"	RF	16.7%
	Rubiaceae	<i>Psychotria</i> sp. "fohaninasity"	RF, UF	10.4%
	Burseraceae	<i>Canarium madagascariense</i> Engler	RF, UF	10.0%
	Palmae	<i>Dypsis decipiens</i> (Becc.) Beentje & J. Dransf.	RF, UF, YL	8.8%
	Ochnaceae	<i>Diporidium</i> sp. "menahy"	RF	7.8%
	Moraceae	<i>Ficus rubra</i> Vahl	RF, UF	7.2%
	Myrsinaceae	<i>Oncostemon</i> sp. "faripandoa"	RF, UF	4.9%
	Clusiaceae	<i>Harungana madagascariensis</i> Lam. Ex Poiret		4.3%
	Fabaceae	<i>Arbrus precatorius</i>	RF, ML, YL	2.8%
VE1	Pandanaceae	<i>Pandanus</i> sp. "sirika pf #2"	LB, FL	11.1%
	Combretaceae	<i>Terminalia tetranora</i>	RF, UF, YL	9.1%
	Burseraceae ?	spec. indet. "ramy hafahafa"	RF	7.9%
	Flacoutaceae	<i>Homalium</i> sp. "hazoambato"	RF, UF	7.0%
	Moraceae	<i>Ficus rubra</i> Vahl	RF, UF	6.6%
	Rubiaceae	<i>Psychotria</i> sp. "fohaninasity mf"	RF	5.9%
		spec. indet. "fonty"	RF, UF, ML, YL	3.1%
	Rubiaceae	<i>Canthium micrantha</i> Baker	RF, UF, ML, FL, BU	2.8%
	Clusiaceae	<i>Symphonia</i> sp. "kimba special"	YL, BU	2.8%
	Pandanaceae	<i>Pandanus</i> sp. "sirika mf #1"	RF, FL	2.8%

¹ See Table 5.4 for plant part categories.

Table 5.6a: Monthly Top Five Food Species for Group AN1, Andringitra,
Including Part Consumed and Percentage of Total Feeding Time.

Month	Family	Species	Part Consumed	% Feeding Time
May-99	Sapotaceae	<i>Chrysophyllum boivinianum</i> (Pierre) Baehni	RF	41.6%
	Moraceae	<i>Ficus rubra</i> Vahl	RF	14.6%
	Loranthaceae	<i>Bakerella</i> sp. “tongoalahy”	RF, UF	8.6%
		spec. indet. “voanananala”	RF	7.0%
	Myrtaceae	<i>Syzygium</i> sp. “rotramena”	RF	6.1%
Jun-99	Moraceae	<i>Ficus lutea</i> Baker	RF	31.4%
	Sapotaceae	<i>Chrysophyllum boivinianum</i> (Pierre) Baehni	RF	20.5%
	Moraceae	<i>Ficus rubra</i> Vahl	RF	16.9%
	Myrsinaceae	<i>Oncostemon</i> sp. “kalafambakaka”	RF, ML, NL	7.0%
	Erythroxylaceae	<i>Erythroxylum</i> sp. “malambovony”	RF	6.1%
Jul-99	Moraceae	<i>Ficus lutea</i> Baker	RF	46.9%
	Moraceae	<i>Ficus rubra</i> Vahl	RF	32.5%
	Burseraceae	<i>Canarium madagascariense</i> Engler	RF	5.9%
	Sapotaceae	<i>Chrysophyllum boivinianum</i> (Pierre) Baehni	RF	5.3%
	Lauraceae	<i>Cryptocarya</i> cf. “flavescens”	RF	3.1%
Aug-99	Moraceae	<i>Ficus lutea</i> Baker	RF	66.1%
	Tiliaceae	<i>Grewia</i> sp. “hafipotsy”	UF	6.7%
	Rubiaceae	<i>Psychotria</i> sp. “fohaninasity pf”	RF	3.0%
	Moraceae	<i>Ficus rubra</i> Vahl	RF	2.9%
	Rubiaceae	<i>Canthium micrantha</i> Baker	RF, UF	2.5%
Sep-99	Moraceae	<i>Ficus lutea</i> Baker	RF	47.0%
		spec. indet. “voakirepoka”	RF	12.5%
	Myrtaceae	<i>Syzygium</i> sp. “rotramena”	RF, UF	8.1%
	Lauraceae	<i>Cryptocarya</i> cf. “flavescens”	UF	5.5%
	Acanthaceae	<i>Ruellia</i> sp. “velatra”	UF	4.5%
Oct-99		spec. indet. “tsivoka”	RF, UF	21.8%
	Myrtaceae	<i>Syzygium</i> sp. “rotramena”	RF	20.5%
	Acanthaceae	<i>Ruellia</i> sp. “velatra”	NL	12.5%
	Moraceae	<i>Ficus tiliifolia</i> Baker	RF	12.0%
	Myrtaceae	<i>Syzygium</i> “emirnensis”	RF	11.8%

Table 5.6a: Monthly Top Five Food Species for Group AN1, Andringitra, Including Part Consumed and Percentage of Total Feeding Time (cont.).

Month	Family	Species	Part Consumed	% Feeding Time
Nov-99	Myrtaceae	<i>Syzygium</i> sp. "rotramena"	RF	30.9%
	Moraceae	<i>Ficus tiliifolia</i> Baker	RF	15.6%
		spec. indet. "tsivoka"	RF	13.4%
	Moraceae	<i>Ficus rubra</i> Vahl	RF	9.4%
	Acanthaceae	<i>Ruellia</i> sp. "velatra"	NL	9.3%
Dec-99	Burseraceae	<i>Canarium madagascariense</i> Engler	RF, UF	33.5%
	Lauraceae	<i>Ocotea</i> sp. "varongy"	RF, UF	20.3%
	Moraceae	<i>Ficus tiliifolia</i> Baker	RF	13.6%
	Acanthaceae	<i>Ruellia</i> sp. "velatra"	NL	10.9%
	Flacourtiaceae	<i>Aphloia theaeformis</i> Bennett	RF	6.6%

Table 5.6b: Monthly Top Five Food Species for Group ANA, Andringitra, Including Part Consumed and Percentage of Total Feeding Time.

Month	Family	Species	Part Consumed	% Feeding Time
Jan-00	Palmae	<i>Dypsis decipiens</i> (Becc.) Beentje & J. Dransf.	RF, NL	36.6%
	Burseraceae	<i>Canarium madagascariense</i> Engler	UF	16.4%
	Melastomataceae	<i>Medinilla</i> sp. "kitonda"	RF	11.9%
	Fabaceae	<i>Arbrus precatorius</i>	NL	11.7%
	Myrsinaceae	<i>Embelia madagascariensis</i> A. DC.	NL	7.4%
Feb-00	Burseraceae	<i>Canarium madagascariense</i> Engler	UF	43.6%
	Palmae	<i>Dypsis decipiens</i> (Becc.) Beentje & J. Dransf.	RF	28.7%
	Lauraceae	<i>Ocotea</i> sp. "varongy"	RF	9.2%
	Melastomataceae	<i>Medinilla</i> sp. "kitonda"	RF	5.2%
	Clusiaceae	<i>Garcinia</i> sp. "kimbaletaka"	RF, UF	5.0%
Mar-00	Rubiaceae	<i>Gaertnera</i> sp. "hazotoho"	RF	79.0%
	Palmae	<i>Dypsis decipiens</i> (Becc.) Beentje & J. Dransf.	UF	8.0%
	Moraceae	<i>Ficus tiliifolia</i> Baker	RF	7.5%
	Clusiaceae	<i>Calophyllum</i> sp. "vitanona"	UF	3.1%
	Moraceae	<i>Ficus rubra</i> Vahl	UF	1.9%

Table 5.6b: Monthly Top Five Food Species for Group ANA, Andringitra,
Including Part Consumed and Percentage of Total Feeding Time
(cont.).

Month	Family	Species	Part Consumed	% Feeding Time
Apr-00	Rubiaceae	<i>Gaertnera</i> sp. "hazotoho"	RF	83.1%
	Rubiaceae	<i>Psychotria</i> sp. "fohaninasity"	UF	4.4%
	Bromeliaceae	<i>Ananas comosus</i> Merr.	RF	4.0%
	Myrsinaceae	<i>Oncostemon</i> sp. "faripandoa"	UF	3.7%
	Myrsinaceae	<i>Embelia madagascariensis</i> A. DC.	ML, NL	1.6%
May-00	Rubiaceae	<i>Psychotria</i> sp. "fohaninasity"	RF	55.7%
	Clusiaceae	<i>Harungana madagascariensis</i> Lam. Ex Poiret	RF	17.2%
	Sapotaceae	<i>Chrysophyllum boivinianum</i> (Pierre) Baehni	RF	7.7%
	Myrsinaceae	<i>Oncostemon</i> sp. "faripandoa"	RF, UF	5.9%
	Moraceae	<i>Ficus rubra</i> Vahl	RF	4.0%
Jun-00	Rubiaceae	<i>Psychotria</i> sp. "fohaninasity"	RF	27.8%
	Burseraceae	<i>Canarium madagascariense</i> Engler	RF	19.6%
	Moraceae	<i>Ficus rubra</i> Vahl	RF	17.9%
	Clusiaceae	<i>Harungana madagascariensis</i> Lam. Ex Poiret	RF	13.3%
	Myrsinaceae	<i>Oncostemon</i> sp. "faripandoa"	RF	12.4%
Jul-00	Moraceae	<i>Ficus lutea</i> Baker	RF	47.1%
	Moraceae	<i>Ficus rubra</i> Vahl	RF	32.9%
	Myrsinaceae	<i>Oncostemon</i> sp. "faripandoa"	RF	17.9%
	Rubiaceae	<i>Psychotria</i> sp. "fohaninasity"	RF	2.2%
Aug-00	Moraceae	<i>Ficus lutea</i> Baker	RF	58.5%
	Ochnaceae	<i>Diporidium</i> sp. "menahy"	RF	41.5%

Table 5.6c: Monthly Top Five Food Species for Group VE1, Vevembe,
Including Part Consumed and Percentage of Total Feeding Time.

Month	Family	Species	Part Consumed	% Feeding Time
May-00	Burseraceae (?)	spec. indet. "ramy hafahafa"	RF	17.4%
	Flacoutaceae	<i>Homalium</i> sp. "hazoambato"	UF	17.2%
	Clusiaceae	<i>Symphonia</i> sp. "kimba special"	BU	10.9%
	Anacardiaceae	spec. indet. "sandramy"	RF	9.0%
	Palmae	<i>Ravanea</i> sp. "lafa pf"	UF	6.6%
Jun-00	Burseraceae (?)	spec. indet. "ramy hafahafa"	RF	23.8%
	Flacoutaceae	<i>Homalium</i> sp. "hazoambato"	RF	16.8%
	Moraceae	<i>Ficus rubra</i> Vahl	RF, UF	10.2%
	Combretaceae	<i>Terminalia tetranora</i>	UF	6.9%
	Euphorbiaceae	<i>Macaranga</i> sp. "mokaranana"	ML	6.8%
Jul-00	Combretaceae	<i>Terminalia tetranora</i>	UF	30.1%
	Moraceae	<i>Ficus rubra</i> Vahl	RF	9.2%
		spec. indet. "fatsy"	UF	8.5%
	Rubiaceae	<i>Psychotria</i> sp. "fohaninasity mf"	RF	8.0%
	Rubiaceae	<i>Canthium micrantha</i> Baker	ML, NL, FL	6.7%
Aug-00	Pandanaceae	<i>Pandanus</i> sp. "tsirika pf #2"	FL	35.6%
	Clusiaceae	<i>Garcinia</i> sp. "kimbaletaka gf"	ML	9.7%
	Clusiaceae	<i>Garcinia</i> sp. "kimbaletaka pf"	ML	6.6%
	Euphorbiaceae	<i>Uapaka louvelii</i> M. Denis	UF	5.8%
	Rubiaceae	<i>Psychotria</i> sp. "fohaninasity mf"	RF	5.6%
Sep-00	Lauraceae	<i>Potameia chartacea</i> Kosterm.	UF	16.3%
		spec. indet. "fonty"	UF	13.3%
	Pandanaceae	<i>Pandanus</i> sp. "tsirika pf #2"	FL	12.0%
	Pandanaceae	<i>Pandanus</i> sp. "tsirika mf #1"	FL	10.6%
	Moraceae	<i>Ficus rubra</i> Vahl	RF, UF	9.5%

Chapter 6: Social Structure, Activity Budgets, Habitat Use, Ranging, and Intergroup Interactions in the Brown Lemurs of Andringitra National Park and Vevembe Forest

INTRODUCTION

Ecological niche dimensions are not limited to feeding behaviors. Space and time are also critical factors affecting the behavioral ecology of primate species (cf. Schoener, 1974), manifested in ranging patterns (both horizontal and vertical habitat use) and activity schedules. In addition, the nature of competition with other conspecific groups may have significant effects on feeding and foraging decisions (Struhsaker, 1974; Mitani and Rodman, 1979; Isbell, 1983). None of these variables exists in a behavioral vacuum – these factors are often part of interconnected adaptive strategies. For example, among primates, variation in diet and ranging behavior is related in complex ways to body weight, biomass, community structure, resource abundance and distribution, rainfall, group size and cohesion, predation, disease, reproductive events, and a variety of social factors (e.g., Milton and May, 1976; Clutton-Brock and Harvey, 1977; Mitani and Rodman, 1979; Freeland, 1980; Gautier-Hion et al., 1981; Isbell, 1983; Terborgh, 1983; van Schaik et al., 1983; Boinski, 1987; Janson, 1988; Symington, 1988; Barton et al., 1992; Overdorff, 1996a; Wright, 1998).

In this chapter, I analyze several behavioral factors in the brown lemurs of Andringitra and Vevembe to explore niche characteristics beyond feeding ecology (Chapter 5). I examine social organization (including group composition and cohesiveness), activity budgets, ranging behavior (home range size, daily travel,

and vertical ranging), and intergroup encounters in one social group of white-collared lemurs and two hybrid groups. Variation in these characteristics may be related to differences in habitat (Chapter 4) and diet composition (Chapter 5). Accordingly, I examine potential associations between seasonal fluctuation in feeding and resource base and shifts in activity, ranging, and intergroup behaviors. Despite habitat and feeding differences, comparisons among the Andringitra and Vevembe brown lemurs control for variation in potentially strong influences on activity and ranging: both group size (Chapter 5) and body weight (Chapter 2) are similar across study populations.

Differences in ranging patterns, social organization, and activity budgets have been suggested to minimize interspecific competition between brown lemurs and other sympatric lemurs (Sussman, 1974, 1977; Overdorff, 1991, 1996a; Vasey, 1997). Intrinsic habitat characteristics such as spatio-temporal variation in resources may also affect these behaviors in brown lemurs (e.g., Vasey, 1997; Overdorff, 1996a). Therefore, examining variation in these activities will assist in gauging the levels of ecological divergence among the brown lemurs of Vevembe and Andringitra, including habitat effects.

The activity, ranging, and social structure variables examined herein have been studied in many brown lemur taxa and localities (e.g., Sussman, 1974, 1977; Harrington, 1975; Tattersall, 1977; Overdorff, 1991, 1996a; Freed, 1996; Vasey, 1997; Rasmussen, 1999; Gerson, 2000). In some respects, brown lemurs demonstrate great consistency across populations. For instance, brown lemurs are generally found in cohesive, multi-male social groups (Vasey, 1997; Overdorff

and Johnson, in press). However, *E. f. fulvus* on Mayotte maintain loose, fission-fusion communities (Tattersall, 1977). In addition, *E. f. rufus* groups may undergo a fission-fusion period during permanent group division events (Overdorff et al., 1999). Brown lemurs are also similar in intergroup behavior. Social groups are generally described as non-territorial and home ranges overlap extensively (Sussman, 1974; Harrington, 1975; Overdorff, 1991; Vasey, 1997; Gerson, 2000).

In contrast, brown lemurs across Madagascar exhibit great variability in activity budgets. While the most common overall activity among study populations is resting, the frequency varies greatly across groups (47-77%; Sussman, 1974; Overdorff, 1991; Vasey, 1997; Rasmussen, 1999; Gerson, 2000). Brown lemurs also exhibit marked variation in time devoted to feeding (10-26%), travel (6-30%), and social or other activities (1-28%) (Sussman, 1974; Overdorff, 1991; Vasey, 1997; Rasmussen, 1999; Gerson, 2000).

Ranging patterns also differ dramatically across Madagascar. In western dry forests, home ranges are very restricted (0.75-1.0 ha in *E. f. rufus*; Sussman, 1974; 7-16 ha in *E. f. fulvus*; Harrington, 1975; Rasmussen, 1999). Eastern rain forest brown lemurs tend to have larger ranges, but there is tremendous variation (e.g., 13 ha in *E. f. albifrons* at Andranobe; Vasey, 1997; 85-100 ha in *E. f. rufus* at Ranomafana; Overdorff, 1991). Partly in conjunction with home range differences, daily travel also differs considerably among populations. Again, western brown lemurs have shorter daily path lengths (*E. f. rufus*: 125-150 m at Anteranannomby; Sussman, 1974; 213-368 m at Anjamena; Gerson, 2000; *E. f.*

fulvus: 447 m in the wet season at Ampijoroa; Rasmussen, 1999). In the eastern forests, *E. f. albifrons* and *E. f. rufus* both have much longer daily path length (978 m and 962 m, respectively; Vasey, 1997; Overdorff, 1996a), despite clear differences in total home range area.

Based on previous research on brown lemurs and data from previous chapters, as well as theoretical considerations, I anticipate some differences among the focal groups. Like other eastern populations, these groups should have relatively long day ranges (see Overdorff, 1991; Vasey, 1997). As noted, variation in group size is minimal and thus should not produce differences in intragroup feeding competition and ranges (Janson, 1988; Isbell, 1991). Increased frugivory may also be associated with larger ranges (Milton and May, 1976). Accordingly, the Andringitra hybrids may maintain larger home ranges with longer daily travel. However, poor habitat quality at Vevembe may also increase travel (e.g., Dunbar, 1992). I predict seasonal effects on activity and ranging due to fluctuations in food availability. Food shortages may lead to reductions in resting and travel but increases in feeding (Overdorff, 1996a) – although scarcity may impose complex strategies of either energy maximization or minimization (Vasey, 1997). Release from competition with *E. rubriventer* (e.g., Overdorff, 1996a) may allow use of lower parts of the canopy for *E. albocollaris* at Vevembe (i.e., apart from feeding height only; Chapter 5). Finally, based on prior brown lemur studies, I expect little variation in social organization, with cohesive, non-territorial groups (e.g., Vasey, 2000).

METHODS

Study Groups

Data on social organization, activity, ranging, and intergroup encounters were collected for two social groups of hybrids (*Eulemur fulvus rufus* X *E. albocollaris*) at Andringitra National Park (AN1 and ANA) and one *E. albocollaris* group at Vevembe Forest (VE1). The AN1 group was located at the Ambarongy site and the ANA group was located across the Iantara River at the Parc site (Figure 6.1). Age and sex composition of each group is indicated in Chapter 5 (Table 6.1).

Sampling Procedures

Data on social organization, activity, and ranging were collected using instantaneous focal animal sampling (Altman, 1974). Focal animals were selected according to a regular rotation of all adult and juvenile group members (infants were excluded). Each animal was followed from when the group was first located (generally 06:30-07:30) until 16:30. Terrain and distance of focal groups from camp prevented nocturnal sampling and longer follows during daylight hours.

Data were collected on the AN1 group during 84 non-consecutive days (May-December 1999) for a total of 591 hours of continuous observation and 7165 point time samples. ANA was followed on 44 days (January-August 1999) for total of 329 hours of observation and 4007 point time samples. I observed VE1 on 83 days (May-August 2000), obtaining 691 observation hours and 8374 point time samples.

Point time samples were collected at 5-minute intervals. During each sample the following information was recorded:

1. Date
2. Focal animal
3. Time
4. Group behavior
5. Individual behavior
6. Height in canopy
7. Food species (if any)
8. Plant part consumed
9. Nearest neighbor (< 5 m)
10. Distance to nearest neighbor
11. Presence and identity of another group or lemur species (< 30 m)
12. Distance to other group
13. Weather
14. Location

Group behavior was defined as the behavior of > 50% of group members. Group behavior categories included: Rest (R), Social (S), Feed (F), and Travel (T). Individual behavior included the same categories, as well as Rest in Contact (C). Description of affiliative, agonistic, marking, and vocalization behaviors was further elaborated within the Social (S) individual behavior category. Subcategories and specific social behaviors are listed in Table 6.1. Actors and recipients for social behaviors were also recorded.

Group Cohesion

To quantify differences in the spacing of group members, I examined the presence of group members within 5 m of the focal animal, as well as mean distances to nearest group members (“nearest neighbor”). For presence/absence, mean monthly frequencies were compared across sites. For distance to nearest neighbor, data from all point time samples with a neighbor present (< 5 m from the focal) were analyzed.

Activity Budget

Individual behaviors were used to construct activity budgets for each study group. Each category recorded in point time samples (R, C, S, F, and T) was summed for each day of observation to generate daily frequencies of behaviors. A separate calculation was also performed for total resting samples (i.e., Rest and Rest in Contact combined). The day was chosen as the time unit for comparison to obtain sufficient variation within a monthly period for an examination of seasonality. Shifts in activity within a 24-hour period were not analyzed here (see, for example, Overdorff, 1996a). Variation in mean daily frequencies of each behavior category was compared across groups. Within each social group, mean daily frequencies were compared across individuals, age classes, and sexes. In addition, variation in frequencies was analyzed across months to examine seasonal shifts.

Habitat Use

Habitat use was compared across brown lemur populations. Variation in mean height of focal animals in the tree canopy was used to assess differences

among study groups in microhabitat use. Vertical stratification has been noted to be a critical factor in brown lemur ecological niches elsewhere (e.g., Freed, 1996; Vasey, 1997). Seasonal variation (i.e., monthly) was also examined within study groups.

Intergroup Interactions

All-occurrence sampling was used to record encounters with other lemur groups. Only interactions with conspecifics are considered here. For each approach of another group within 30 m, the following information was obtained:

1. Time
2. Duration
3. Identity of other group
4. Number of individuals in other group
5. Group behavior of focal group
6. Approaching and departing group
7. Nature of interaction
8. Winner of agonistic encounter
9. Location
10. *Ad libitum* recording of specific interactions (number of chases, bouts of grunt vocalizations, etc.)

The nature of intergroup encounters was recorded on a 1-5 scale. This was assessed as follows:

1. Hostile – multiple and/or intense agonistic encounters (e.g., chases)
2. Neutral/Hostile – mild agonism, usually grunt vocalizations

3. Neutral – no evident interactions
4. Neutral/Affiliative – some positive social interaction (social approaches, etc.)
5. Affiliative – extensive positive social interaction (grooming, mating)

Mean duration of intergroup encounters was compared across focal groups. In addition, I examined variation in monthly frequency (proportion of observation time) and rate of intergroup interactions (bouts/hour of observation) across groups. The nature of intergroup interactions was compared by compiling monthly percentages of hostile (categories 1-2), and neutral (3), and affiliative (4-5) encounters. The month was used as the unit of analysis due to the rarity of encounters on a daily basis; indeed, interactions did not occur in all months. Intergroup encounters were also plotted on maps of each focal group's home range (see below) to assess whether interactions occurred in the center or periphery of the groups' ranges.

Daily Path Length and Home Range

Distances traveled by focal individuals during one day of observation were used to estimate mean daily path length (DPL) of the group. Distances were calculated by plotting location data from 5-minute point time samples to the nearest 25 m interval trail marker using the mapping software package Pathfinder 1.5© (Michael Winslett, Austin, TX). Locations were connected and distances between then summed to yield total path length. Only observation days when the focal was followed from at latest 08:30 until at least 15:00 were considered for analysis (AN1: N = 63; ANA: N = 40; VE1: N = 73). Groups would

occasionally move well beyond the established trail systems. In these cases, coordinates were obtained with a global positioning system (GPS) device whenever possible and the points plotted on the site maps. When GPS readings were unavailable due to rapid group movement or forest cover (see Phillips et al., 1998), distance and direction to the nearest trail were estimated. However, due to the large potential error in these estimates, I discarded all location samples > 25 m from a trail or GPS waypoint. Thus, DPL values likely underestimate ranging somewhat. Variation in mean DPL was compared across groups, as well as within groups by month to test for seasonal shifts in ranging.

Home ranges were estimated using two methods. For both techniques a .25-ha quadrat (50 m X 50 m) grid was superimposed on maps of the trail systems and daily paths of focal groups. In method 1, I used the cumulative DPL to determine the total number of quadrats entered during these observation days. This method does not attain total home range size due to the restricted sampling period (i.e., not all sampling days are included and the study duration may not have been adequate to capture total home range) and to the limitations of the daily path length calculation described above. For example, some intergroup encounters occurred outside of the home range estimated in method 1. In method 2, I included all observed points of travel from DPL (method 1), as well as GPS points obtained during other sampling days (i.e., follows too short to be included in DPL analyses) and the locations of intergroup encounters. I fitted a minimum convex polygon to these points and then summed the quadrats incorporated in the polygon. The use of minimum convex polygon is common in primate ranging

studies, but may overestimate home range size (Ostro et al., 1999). However, considering the underestimating tendency of DPL-based techniques, method 2 is likely a better representation of total ranging.

Areas of overlap with other brown lemur social groups were calculated in three ways. The lowest estimate was obtained by summing the quadrats where intergroup interactions occurred. An intermediate method added the minimum quadrats needed to connect the intergroup encounter quadrats to the boundaries of the home range (method 2 above). Finally, a maximum area of overlap was calculated by adding quadrats to connect the areas of encounters with other groups (i.e., connecting the areas obtained in the intermediate method).

To understand the potential relationship between ranging patterns and interspecific agonism, I also determined the index of defensibility (D ; Mitani and Rodman, 1979) for all study groups. This index expresses the relative mobility of the group by examining the relationship of day range to total home range (represented as a circle with an area equal to observed home range). The assumption is that more mobile groups can more easily patrol their home ranges and potentially exclude conspecifics competitors (Mitani and Rodman, 1979; Lawes and Henzi, 1995). Separate analyses were conducted for methods 1 and 2 for home range estimation. The index was calculated as follows:

$$D = d / (4A/\pi)^{1/2}$$

where d = mean daily path length and A = home range.

Statistics

I used nonparametric tests for all comparisons among focal groups. These included Kruskal-Wallis and Mann-Whitney U tests for: distance to neighbors, frequencies of presence/absence of neighbors, frequencies of activity profiles (including within-group comparisons between individuals, ages, and sexes), height in canopy, daily path length (including within groups by month), and intergroup encounters (including mean duration, mean monthly proportion of observation time, monthly rates, and monthly frequencies of nature of interaction categories). I used Spearman rank correlations to test associations between monthly activity budgets, ranging, and intergroup encounters with food availability, dietary profiles, and/or rainfall. Food availability included monthly FA values for fruit, new leaves, and flowers (see Chapter 4). Diet was recorded as monthly percentage of overall feeding time dedicated to fruit, leaves, and flowers (Chapter 5). Rainfall data included mean daily rainfall across months for each site (Chapter 4). Significance for all tests was set at $\alpha = .05$.

RESULTS

Group Structure and Cohesion

The three study groups differed somewhat in composition (Chapter 5, Table 6.1). Group AN1 at Andringitra was the largest, with seven adults. In addition, three infants were born to the group's females during September-October 1999 (although they were not included as focal individuals). AN1 was smaller, with five adults and one juvenile (the offspring of RF, born in the 1999 birth season). At Vevembe, the focal group VE1 also had six individuals (4

adults, 2 juveniles). However, the group consisted of individuals from a larger group (11 adults) that had fissioned permanently immediately prior to the study period. These group sizes were consistent with observations of other groups during censuses (Chapter 2) at these sites and there was little variation among sites (Ambarongy: mean = 6.2, max = 16; Parc: mean = 5.9; max = 9; Vevembe: mean = 4.9; max = 11). There was an apparent male bias in the sex ratios of all groups but sample sizes were too small to test these differences.

There were indications of group differences in spacing (Table 6.2). The *E. albocollaris* group VE1 was the only study group that separated regularly into subgroups for long periods (up to several days); similar patterns were observed in neighboring groups at Vevembe. Hybrids at Andringitra did not display a similar fission-fusion social structure – all group members generally remained within visual or auditory contact (< 20-30 m). Accordingly, there were small differences in the frequencies of the presence of another group member within 5 m of the focal, with the lowest mean frequency in VE1 (76.7%), followed by AN1 (79.4%) and ANA (88.4%). However, this variation fell short of statistical significance ($H = 5.782$; $P = .0555$). Despite the lower frequency of group members in proximity, VE1 had the shortest mean distance to a neighbor (0.81 m), followed by ANA (1.04 m) and AN1 (1.05 m); these differences were significant ($H = 417.497$; $P < .0001$).

Activity Budget

There was variation across study groups in activity profiles (Table 6.3). There were significant differences among groups in mean daily frequencies of

Rest in Contact ($H = 18.329$; $P = .0001$), Social ($H = 33.22$; $P < .0001$), Forage ($H = 30.905$; $P < .0001$), and Travel ($H = 79.92$; $P < .0001$). Rest was the only category that did not vary across social groups ($H = 3.428$; $P = .1802$ NS). Individuals in group VE1 had the highest percentage of resting in contact. Group AN1 had the greatest frequency of social behaviors, while ANA had the highest percentages of feeding and moving.

There were fewer indications of variation within groups (Table 6.3). There were no significant differences between sexes in any behavioral category for either of the Andringitra hybrid groups, while sexes in *E. albocollaris* only differed in the frequency of social behavior ($Z = -3.624$; $P = .0003$) – a rare activity for both males and females. Moreover, there was no significant variation according to age class in group ANA. Age categories in the *E. albocollaris* group VE1 only differed in the frequency of resting ($Z = -1.974$; $P = .0484$) and feeding ($Z = -3.688$; $P = .0002$). AN1 was not compared because it contained no juveniles.

There were significant shifts in activity budgets across seasons (Figure 6.2). In group AN1 at Andringitra, there were significant differences across months in the frequencies of resting ($H = 17.527$; $P = 0.0143$), resting in contact ($H = 27.166$; $P = 0.0003$), social activities ($H = 37.467$; $P < .0001$), feeding ($H = 57.539$; $P < .0001$), and moving ($H = 33.85$; $P < .0001$). In ANA, there was seasonal variation in rest ($H = 18.134$; $P = .0114$), social ($H = 13.989$; $P = .0514$), feed ($H = 30.396$; $P < .0001$), and travel ($H = 28.34$; $P = .0002$) categories, but not in rest in contact ($H = 13.151$; $P = .0685$ NS). Group VE1 at Vevembe varied

across months in rest ($H = 9.331$; $P = .0533$), rest in contact ($H = 12.445$; $P = .0143$), and travel ($H = 19.178$; $P = .0007$), but not in social behavior ($H = 3.615$; $P = .4606$ NS) or feeding ($H = 5.757$; $P = .2181$ NS).

Despite evidence for seasonal changes in activity, there were few correlations with seasonal shifts in food availability, rainfall, or feeding profiles. There was a significant negative relationship between frequency of resting and percentage of leaves in the diet in the hybrid group AN1 ($r_s = -.743$; $Z = -1.965$; $P = .0495$). There was also a negative correlation between the frequency of social behavior and the availability of new leaves in this group ($r_s = -.762$; $Z = -2.016$; $P = .0438$). In ANA, there was a positive relationship between travel and young leaf flushing ($r_s = .738$; $Z = 1.953$; $P = .0508$). Because sample size for correlation analyses was smaller for Vevembe ($N = 5$ months), it was difficult to reach statistical significance. However, many relationships had relatively high absolute r_s values ($\geq .70$). These included negative relationships between resting and rainfall, resting and the percentage of leaves in the diet, and travel and the percentage of leaves in the diet ($r_s = -.7$; $Z = -1.4$; $P = .1615$ NS). There were positive (non-significant) associations between the frequency of resting in contact and rainfall ($r_s = .7$; $Z = 1.4$; $P = .1615$ NS), and between travel and the availability of new leaves ($r_s = .8$; $Z = 1.6$; $P = .1096$ NS), flowers production ($r_s = .783$; $Z = 1.565$; $P = .1175$ NS), and the percentage of fruit in the diet ($r_s = .7$; $Z = 1.4$; $P = .1615$ NS).

Habitat Use

There was substantial variation in habitat use as defined by the height in the canopy of focal animals. There were significant differences across study groups, driven by the low mean height of group ANA ($H = 2974.56$; $P < .0001$), as well as seasonal variation within sites (AN1: $H = 916.188$; $P < .0001$; ANA: $H = 158.953$; $P < .0001$; VE1: $H = 1534.835$; $P < .0001$; Figure 6.3). Individuals in group VE1 at Vevembe were found highest in the canopy (12.3 m), followed closely by group AN1 at Andringitra (12.2 m); as noted, ANA had the lowest mean height in canopy values (8.9 m).

There were few significant relationships between monthly habitat use and variation in food availability, climate, or feeding behavior. However, in group AN1, height in canopy was negatively correlated with new leaf flushing ($r_s = -.762$; $Z = -2.016$; $P = .0438$). There were positive (but non-significant) relationships between height and fruit availability ($r_s = .8$; $Z = 1.6$; $P = .1096$) and height and rainfall ($r_s = .7$; $Z = 1.4$; $P = .1615$) in group VE1.

Intergroup Interactions

Encounters with other conspecifics varied in some respects across study groups (Table 6.4; Figure 6.4). Although differences among groups were not significant ($H = 2.138$; $P = .3433$ NS), mean duration of intergroup interactions was lowest in group ANA (5.2 min.) and comparably higher in AN1 and VE1 (16.5 and 16.8 min., respectively). There was no significant variation in encounter duration across months (AN1: 1.019; $P = .907$ NS; VE1: $H = 5.300$; $P = .2579$ NS); monthly variation could not be tested for ANA because all

intergroup encounters occurred during March. Despite some similarity in the encounters, both frequency and rate of encounters varied across study groups (percentage of observation time: $H = 7.448$; $P = .0241$; bouts/hour: $H = 6.514$; $P = .0385$). Again, both measures were lowest in ANA and similar in AN1 and VE1 (Table 6.4).

The types of intergroup interactions were also compared across social groups (Table 6.4). There were no differences in mean monthly frequencies of hostile (categories 1-2: $H = 1.222$; $P = .5427$ NS), neutral (category 3: $H = .852$; $P = .6532$ NS), or affiliative (categories 4-5: $H = 2.64$; $P = .2671$ NS) interactions (although the latter categories never occurred in AN1 or VE1). Because in group ANA intergroup encounters occurred very rarely and only during one month, groups AN1 and VE were also compared directly, but with identical results (1-2: $Z = -1.048$; $P = .2948$ NS; 3: $Z = -.838$; $P = .402$; 4-5: $Z = -1.491$; $P = .136$). In all groups, the majority of encounters were neutral, followed in frequency by agonistic encounters, while affiliative interactions were nearly absent (Table 6.4).

There were no strong relationships between either intergroup encounter monthly frequency (percentage of observation time) or rate (bouts/hour) and seasonal shifts in food availability or diet. Group ANA showed tendencies for increased encounter time and rate to be associated with a greater percentage of flowers in the diet (for both tests: $r_s = .833$; $Z = 2.205$; $P = .0275$). However, with all encounters occurring in one month (March), the utility of these tests is suspect.

Daily Path Length and Home Range

There were substantial differences in ranging patterns across focal groups (Table 6.5). Mean daily path length (DPL) varied significantly among groups ($H = 35.466$; $P < .0001$; Figure 6.5). These differences remained when the analysis was restricted to months in which all groups were studied (i.e., June-August; $H = 13.55$; $P = .0011$). These differences were due to the very low mean DPL in group ANA at Andringitra (Table 6.5). There were also seasonal differences in DPL across study groups (AN1: $H = 27.823$; $P = .0001$; ANA: $H = 22.636$; $P = .0009$; VE1: $H = 12.597$; $P = .0134$).

Despite the seasonal variation in DPL across groups, there were no significant correlations between ranging patterns and food availability, climate, or rainfall. In AN1, only relationships between DPL and new leaf and flower production approached significance (for both tests: $r_s = .679$; $Z = -1.662$; $P = .0965$ NS). VE1, again with a smaller sample size ($N = 5$ months), had relatively strong positive relationships between monthly DPL and new leaf flushing ($r_s = .8$; $Z = 1.6$; $P = .1096$ NS), flowering ($r_s = .783$; $Z = 1.565$; $P = .1175$ NS), as well as DPL and the percentage of fruit in the diet ($r_s = .7$; $Z = 1.4$; $P = .1615$ NS); there was also a negative, non-significant association between ranging and the percentage of leaves in the diet ($r_s = -.7$; $Z = -1.4$; $P = .1615$ NS).

Home range area also varied considerably across focal groups. Minimum home range (method 1; based on quadrats entered with DPL analyses) was smallest in group ANA and largest in AN1 (Table 6.5). Comparison of maximum home range (method 2; derived from the quadrats incorporated in minimum

convex polygons) yielded identical order among groups (Table 6.5; Figures 6.6-6.8). However, method 2 increased home estimates by nearly two-fold (Table 6.5).

The study groups also differed in the extent of home range overlap with neighboring conspecifics (Table 6.5; Figure 6.9). Based on the minimum method (i.e., only the quadrats where intergroup encounter occurred plus the minimum number of quadrats required to reach the edge of the home range), the groups varied from 8.3 % (ANA) to 15.2% (VE1) overlap (Table 6.5). With the highest estimate techniques, range overlap reached 100% in VE1, but were still only 25% in ANA. Group AN1 was intermediate in all measures (8.7%-84.7%).

In conjunction with differences in daily ranging and home range area, the study groups varied in indices of defensibility (*D*; Table 6.5). Group AN1 had the highest *D* values for both methods of calculating home range area, followed by VE1 for method 1 or ANA for method 2 (Table 6.5). AN1 maintained the highest relative group mobility despite its large home range area. Thus, AN1 had the highest theoretical potential to defend access to its home range.

DISCUSSION

Variation in Social Structure

Contrary to expectations, there were important differences in group structure across study sites. The Andringitra hybrids demonstrated the typical brown lemur pattern: cohesive multi-male/multi-female social units (Overdorff, 1991; Vasey, 1997, 2000). In contrast, group VE1 had only one adult female and frequently formed subgroups for up to several days. The polyandrous state of the

group was likely anomalous, however. Neighboring social groups at Vevembe had several females. Moreover, the VE1 group originally contained two adult females and one sub-adult female, but had split permanently prior to the study period. It is possible that the flexible composition throughout the study was an artifact of this permanent group fission event, similar to *E. f. rufus* at Ranomafana (Overdorff et al., 1999, personal communication). However, fission-fusion structure was seen in other groups at Vevembe (personal observation), as well as at Manombo Special Reserve (J. Ratsimbazafy, personal communication), and thus appears to be a consistent characteristic of white-collared lemur social structure.

Fission-fusion social structure is rare among brown lemurs, having been recorded previously only in introduced *E. f. fulvus* in Mayotte (Tattersall, 1977). However, it has been documented in other lemur taxa, including *E. macaco* (Calquhoun, 1997) and *Varecia* (e.g., Morland, 1991; Vasey, 1997). This form of group structure may mitigate intragroup competition for scarce resources (Symington, 1988). However, smaller sub-groups are often at greater risk of predation than large, cohesive social units (van Schaik, 1983; van Schaik and van Hoof; Terborgh and Janson, 1986; Janson, 1992). While detailed data on the abundance and behavior of predators at the study sites are not available, potential raptor (e.g., *Buteo brachypterus*) and carnivore (e.g., *Cryptoprocta ferox*) predators are present at both locations (Goodman and Putnam, 1996; Goodman, 1996b; F. Mananasy, personal communication; personal observation). As predation pressure on brown lemurs in general is not trivial (Goodman et al.,

1993), white-collared lemurs may adopt this flexible group structure to adapt to acute resource scarcity (see Chapter 4). Despite having social group members nearby less often than the more cohesive Andringitra hybrids, white-collared lemurs maintained closer spatial proximity when a neighbor was present. This spacing behavior may mitigate increased predation pressure by facilitating communication when predators are detected or by enabling the smaller subgroups to move more cryptically (Wright, 1998).

Activity Budgets Across Study Groups

The brown lemurs of Andringitra and Vevembe demonstrated great variability in activity patterns. Resting alone was the only behavior with similar frequencies across study groups. Vevembe white-collared lemurs participated in more huddling behavior (despite generally higher ambient temperature; Chapter 4), while the Andringitra hybrids traveled more often. Frequency of moving did not necessarily relate to distances traveled, as the ANA hybrid group had the lowest daily path length (see below). Feeding and social activities did not vary according to population. Feeding was most frequent in the Andringitra group ANA, followed by VE1 at Vevembe, and finally AN1 – replicating almost exactly the percentages of feeding time recorded during continuous sampling (Chapter 5). Social activities (usually grooming) were rare in all study groups, but somewhat more common in AN1 and VE1.

Activity budgets in the study groups also varied significantly by season. However, these seasonal shifts were not clearly associated with changes in resource base, rainfall, or diet. Of the few apparent correlations, most were likely

of little functional consequence. For example, shifts in activity according to new leaf flushing or folivory in the Andringitra hybrids were probably not ecologically significant, as leaves were not a very important food item and leaves were relatively ubiquitous in the environment. In contrast, some of the seasonal trends in the Vevembe white-collared lemurs may have been meaningful. For instance, the increase in resting in contact with higher rainfall may have been a thermoregulatory response. In addition, the increased movement associated with flower availability and frugivory suggests that increased travel may be necessary to exploit these relatively patchy resources (e.g., Clutton-Brock and Harvey, 1977; Terborgh, 1983). Thus, the relatively poor habitat at Vevembe may compel brown lemurs to shift their activities according to resource base and feeding requirements, while the Andringitra hybrids are less constrained.

The overall activity budgets in the Andringitra and Vevembe groups are broadly comparable to brown lemurs studied elsewhere (Sussman, 1974; Tattersall, 1977; Overdorff, 1996a; Vasey, 1997; Rasmussen, 1999; Gerson, 2000). What appears to distinguish the Andringitra and Vevembe lemurs is their relative inactivity. Resting (including resting in contact) accounted for 65-77% of all activity records, a level of lassitude only reached by western brown lemurs (*E. f. rufus* at Anjamena: 76-77%; Gerson, 2000). In contrast, travel only made up 7-16% of activity budgets in the present study, considerably less than in other eastern brown lemurs (22-30%; Overdorff, 1996a; Vasey, 1997) with more or less similar daily travel distances and home ranges (see below). This suggests that

travel was more rapid and/or directed in the Andringitra hybrids and Vevembe *E. albocollaris* than in other eastern brown lemurs.

Other important differences between the study groups and neighboring eastern populations are the associations between activity and resource availability. During food scarcity at Ranomafana, *E. f. rufus* increase feeding while reducing travel and rest (Overdorff, 1996a). In some scarce periods, *E. f. albifrons* minimize energy expenditure by increasing rest and feeding and traveling less; but in other seasons of low resource availability, this population adopts the opposite strategy due to the patchiness of resources and increased direct interspecific competition for particular food items (Vasey, 1997). There are some indications that the Vevembe white-collared lemurs exhibit the latter approach (although without competition from other lemurs), while the associations between activity and the availability of important food items are not clear in the Andringitra brown lemurs.

In contrast to the variation across seasons and among groups, intragroup sex differences in activity (as in feeding behavior; Chapter 5) were absent or very slight in the Andringitra and Vevembe brown lemurs. These results parallel trends in *E. f. albifrons* in the Masoala Peninsula (Vasey, 1997, 2002). Similarity between the sexes in diet and activity across seasons implies that brown lemur females may not be subject to acute reproductive stresses, at least relative to other lemur species (Vasey, 1997, 2002).

Vertical and Horizontal Ranging

There was substantial variation in ranging patterns among the Andringitra hybrids and Vevembe white-collared lemurs. In terms of vertical canopy use, the Vevembe group ranged higher (12.3 m) than either Andringitra group (8.9 m and 12.2 m). These results contradicted predictions that white-collared lemurs may use lower portions of the canopy due to the absence of *E. rubriventer* at Vevembe. Ranomafana *E. f. rufus* typically range higher than any of the focal groups, perhaps as a means of niche separation with *E. rubriventer* (Overdorff, 1996a). However, study groups were similar to brown lemurs at Andranobe; *E. f. albifrons* generally ranges below 15 m to lessen competition with *Varecia* (Vasey, 1997, 2000). Despite the variation among groups, there were few meaningful associations between height and diet, resource base, or precipitation, the most likely possibility being the correlation between height and fruit availability in *E. albocollaris*. I suspect that the differences in general vertical ranging – like feeding height (Chapter 5) – are purely a reflection of the height of the forest canopy in the microhabitats occupied by the study groups.

The brown lemurs at Andringitra and Vevembe also differed considerably in horizontal ranging, including daily path length and home range area. As expected, groups AN1 at Andringitra and VE1 at Vevembe traveled relatively long distances during the day (637 m and 744 m), nearly as far as other rain forest brown lemurs (800-978 m; Tattersall, 1977; Overdorff, 1996a; Vasey, 1997). Given the potential for underestimating daily ranging in this study, ANA and VE1 probably have day ranges typical for the eastern region. In contrast, the hybrid

group ANA moved only 286 m daily, more comparable to the restricted ranges of dry forest brown lemurs (125-368 m; Sussman, 1974; Gerson, 2000; but see Rasmussen, 1999, for higher values at Ampijoroa).

Mirroring the trends for travel in the activity budgets, there were few clear associations between daily path length and seasonal oscillation in resources, rainfall, or diet. Again, *E. albocollaris* appeared to increase travel in relation to increased flower availability and greater frugivory (as expected; Clutton-Brock and Harvey, 1977; Terborgh, 1983). However, the more frugivorous Andringitra hybrids had very different path lengths (both lower and higher than at Vevembe). The ambiguity in results also casts doubt on the relationship between dietary diversity and ranging among these groups – although the two more generalist groups (see Chapter 5) did have the longest mean path lengths (cf. Clutton-Brock and Harvey, 1977). It is important to note, however, that the cathemeral activity rhythms of these brown lemurs (and others) complicate analyses of daily ranging; night travel (not recorded here) can substantially add to total 24-hour path length (e.g., Rasmussen, 1999).

Home ranges also varied in the brown lemurs of Andringitra and Vevembe, following the patterns for daily travel. Again, the areas for the AN1 and VE1 groups fell within the wide range recorded for other eastern brown lemurs. Yet home ranges for both groups (34-72 ha, depending on estimate methods) were considerably larger than in *E. f. albifrons* at Andranobe (16 ha; Vasey, 1997) and smaller than in *E. f. rufus* at nearby Ranomafana (85-100 ha; Overdorff, 1991). Conversely, the ANA hybrids had a range area (9-12 ha)

comparable to those of western brown lemurs (.75-16 ha; Sussman, 1974; Harrington, 1975; Rasmussen, 1999). It is difficult to link these striking differences among the focal groups to particular ecological constraints or strategies. The Andringitra hybrids ANA and AN1 – the most similar in density (Chapter 3), resource availability (Chapter 4), and diet (Chapter 5) – are the most divergent in home range area among the study groups.

As in other brown lemurs, overlap with other conspecific groups was extensive in the hybrid group AN1 and the *E. albocollaris* group VE1 (see also Sussman, 1974; Overdorff, 1991; Vasey, 1997). The ANA hybrid is once again the outlier: at most only 25% of its range was shared with other groups during the study period, compared to 85-100% in the other focal groups. However, despite its small range and limited overlap, ANA theoretically had very little capacity for territorial defense, with a defensibility index score well within the range of other non-territorial primate species (Mitani and Rodman, 1979). By contrast, AN1 had a defensibility score near the hypothetical threshold for territoriality (Mitani and Rodman, 1979; see below).

Intergroup Interactions

Does this variation in ranging and capacity for territoriality influence intergroup behavior in these groups? Analysis of intergroup encounters does not suggest a relationship between territorial behavior and the ability to patrol the home range (i.e., in group AN1). As Mitani and Rodman (1979) point out, simply because a primate group can defend its range does not obligate it to do so. While some encounters engendered conflict, the brown lemurs of Andringitra and

Vevembe had mostly relaxed interactions with conspecifics – far more tranquil, perhaps, than in other brown lemurs. In *E. f. fulvus* at Ampijoroa, for example, 50% of intergroup encounters were negative (i.e., involved aggression; Rasmussen, 1999). More strikingly, in closely related *E. f. rufus* at nearby Ranomafana, 65% of associations with conspecifics were hostile (nearly twice the rate in the hybrids and *E. albocollaris*), with contests arising frequently over food resources (Overdorff, 1991, unpublished data). Brown lemurs are not considered territorial (e.g., Vasey, 2000) in the sense of obligate home range defense (cf. Mitani and Rodman, 1979). However, agonism among conspecific primate groups is not limited to range defense – it may often be a facultative response to particular social or ecological conditions (Dunbar, 1988; Lawes and Henzi, 1995). The results in this study suggest that, despite the absence of strict territorial defense, there are important differences in the frequency and nature of intergroup encounters among southeastern brown lemur populations. As most fights appear to involve food resources, the population differences imply different strategies based on the distribution of preferred food items (although this variation was not clear from the defensibility index above). Moreover, differences in intergroup interactions may entail variable costs associated with increased ranging and perhaps dispersal (i.e., group transfers; see Chapter 7).

Summary Patterns

The brown lemurs of Andringitra and Vevembe exhibit some divergence in social structure, activity, ranging, and intergroup behavior. These populations differ from other brown lemurs in the conspicuous lack of clear seasonal

relationships between ecological factors – including resource base, rainfall, and feeding behavior – and activity and ranging. One of the salient results from this analysis is the variation in group cohesion, with *E. albocollaris* demonstrating a fission-fusion social structure never before recorded in a Malagasy brown lemur population. Also of note are the markedly diminished levels of intergroup aggression in the hybrids of Andringitra and in the white-collared lemurs of Vevembe. In all, these results corroborate the findings from previous chapters that suggest important flexibility and adaptability in the behavioral ecology of brown lemurs across southeastern Madagascar. The magnitude of differences in the region is comparable to the range of variation observed across the disparate populations of this diverse species group; indeed, the divergence in social structure alone is equivalent to species-level distinctions among lemur taxa.

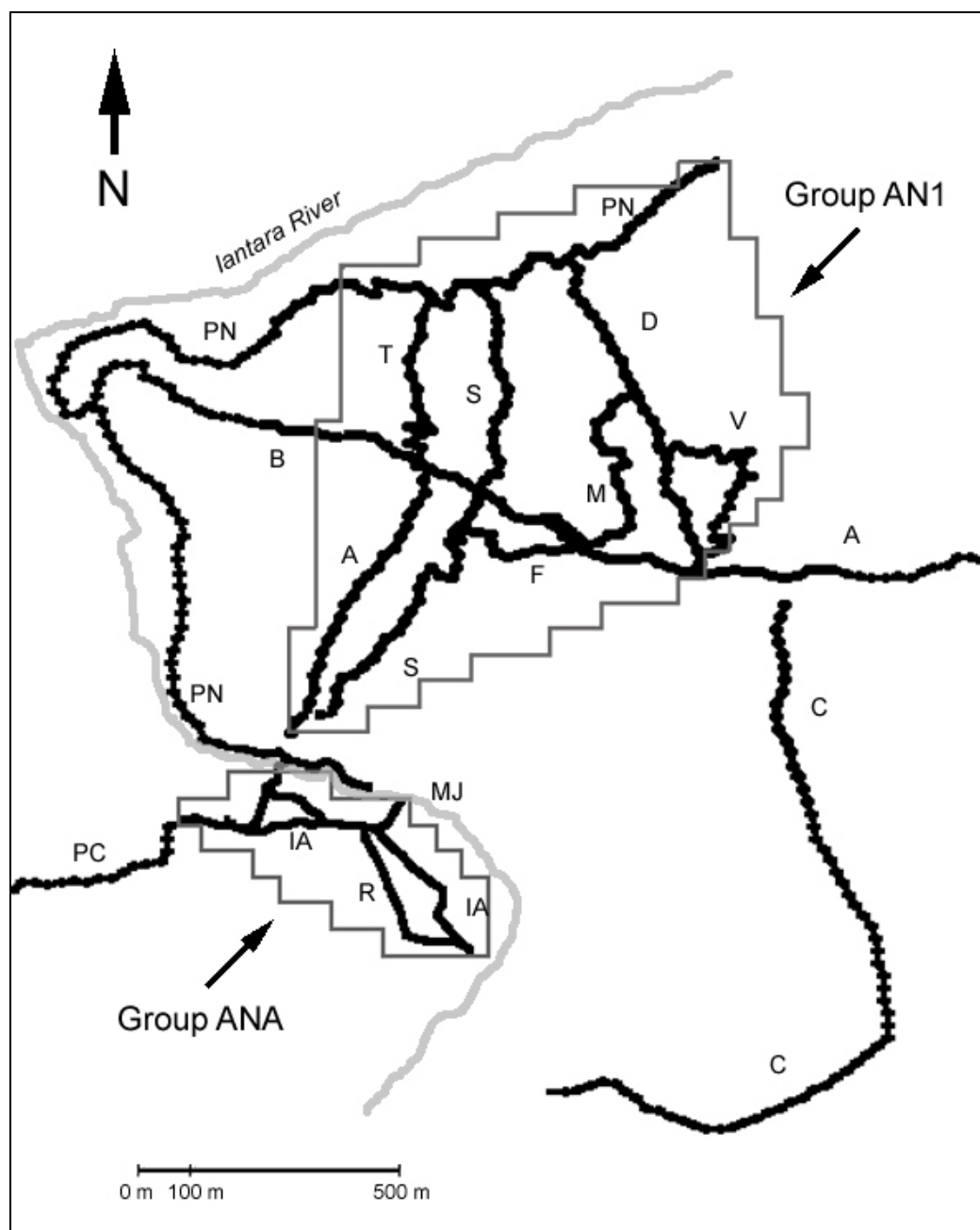
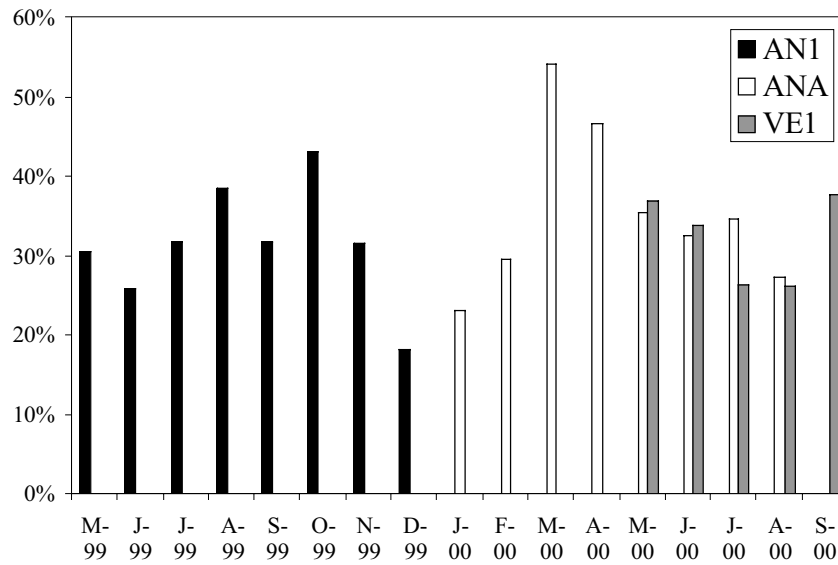


Figure 6.1: Home Ranges (Method 2) at Andringitra. Letters indicate trail names.

Rest



Rest in Contact

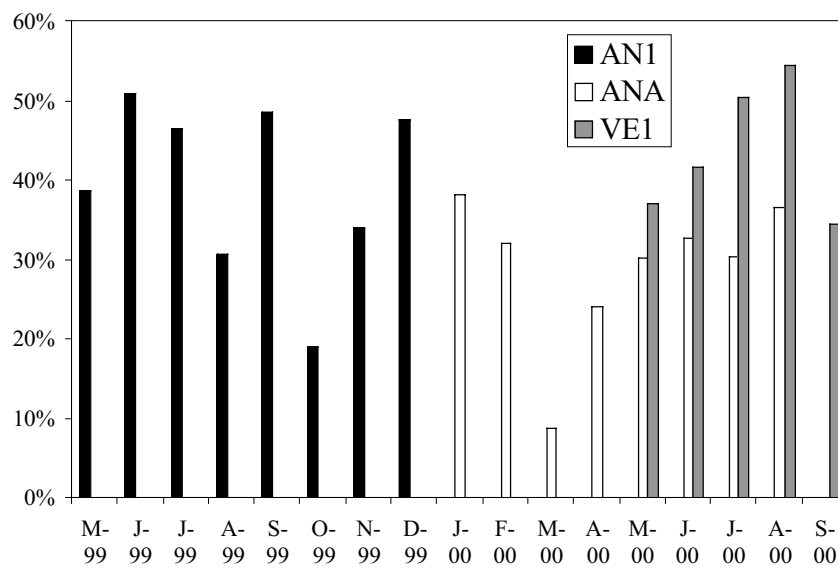
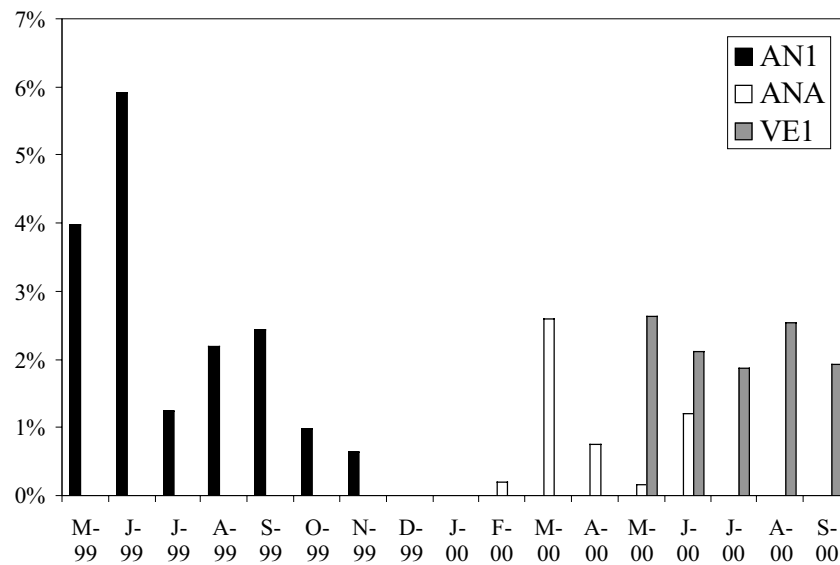


Figure 6.2: Activity Budgets in Each Study Group Across Months.

Social



Feed

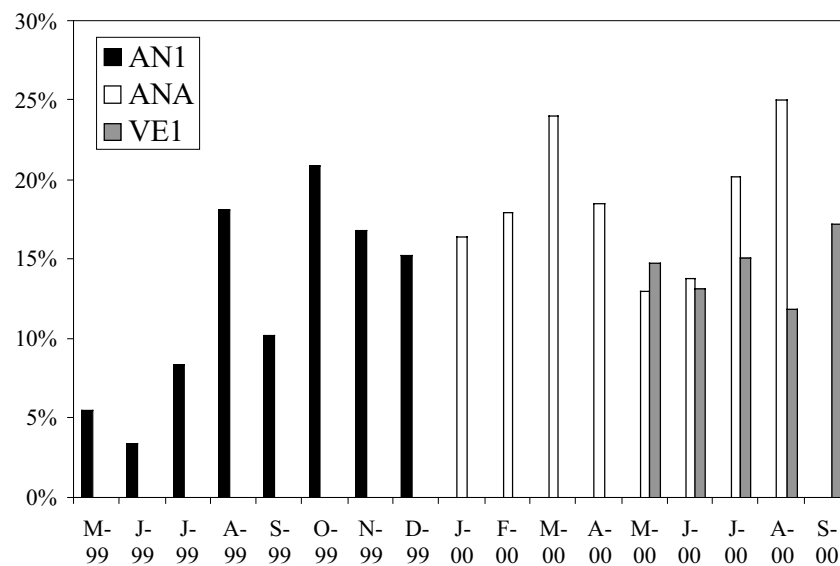


Figure 6.2: Activity Budgets in Each Study Group Across Months (cont.)

Travel

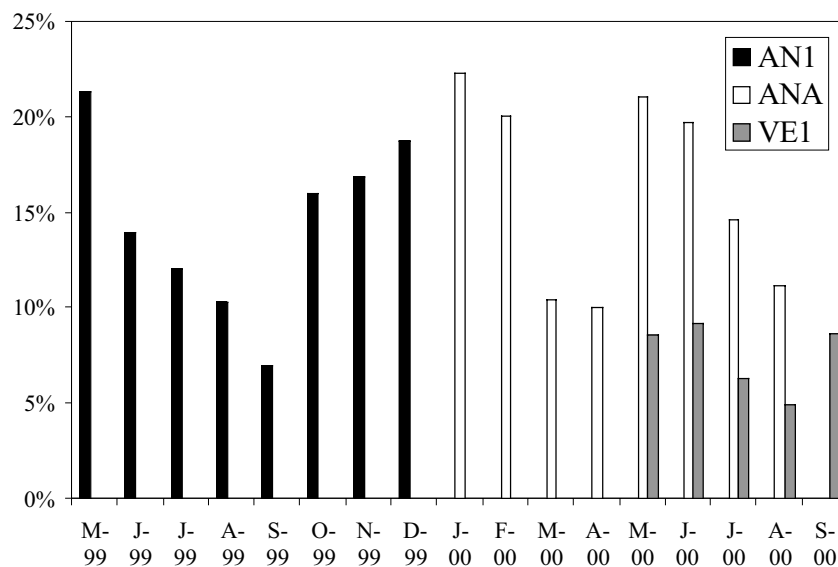


Figure 6.2: Activity Budgets in Each Study Group Across Months (cont.).

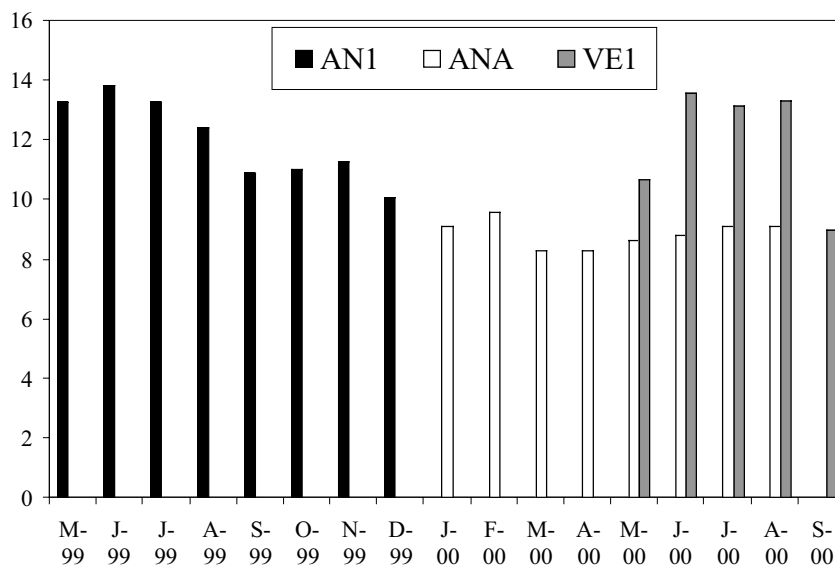


Figure 6.3: Mean Height in Canopy (m) Across Study Groups.

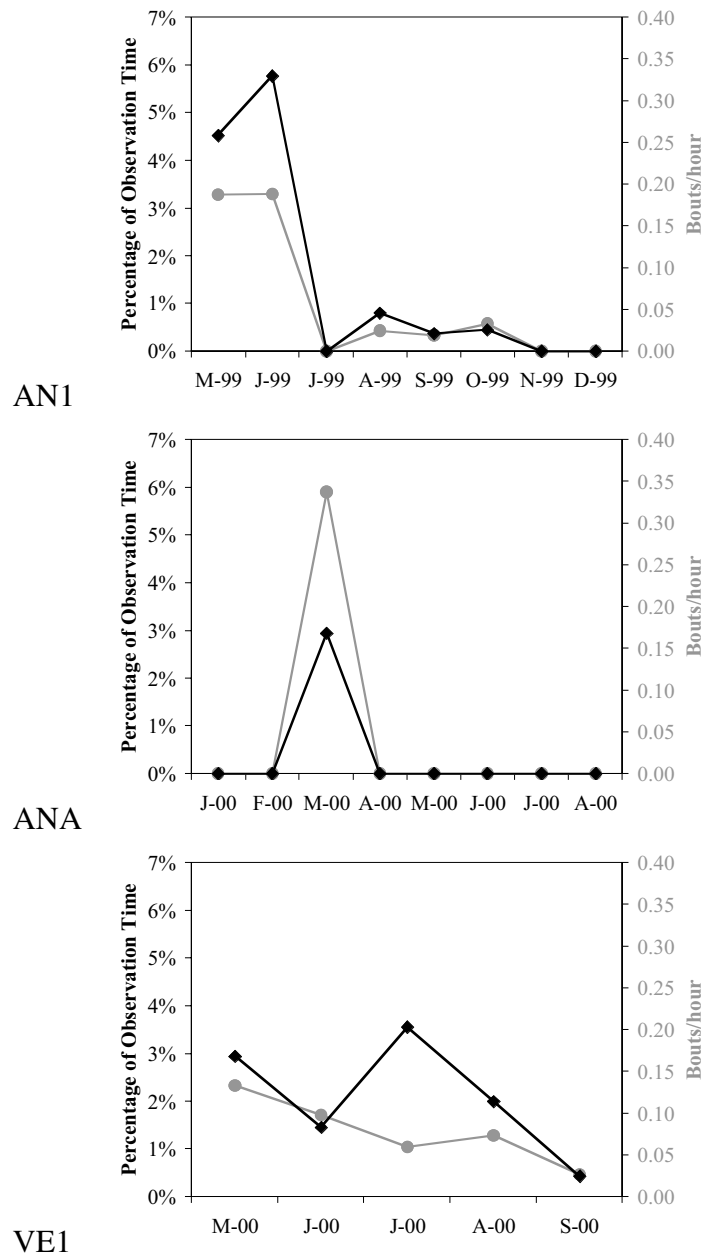


Figure 6.4: Intergroup Encounters. Frequency of encounters (percentage of observation time) is shown on the primary axis (black) and the rate of encounters (bouts/hour) is on the secondary axis (gray).

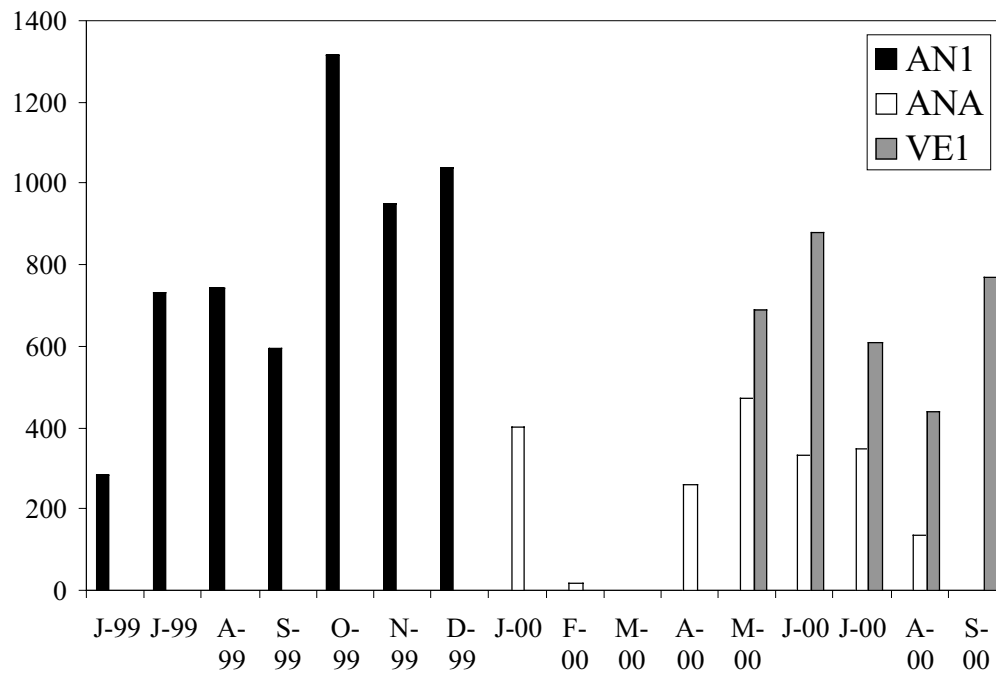


Figure 6.5: Mean Daily Path Length (DPL) Across Study Groups. No data are available for March 2000.

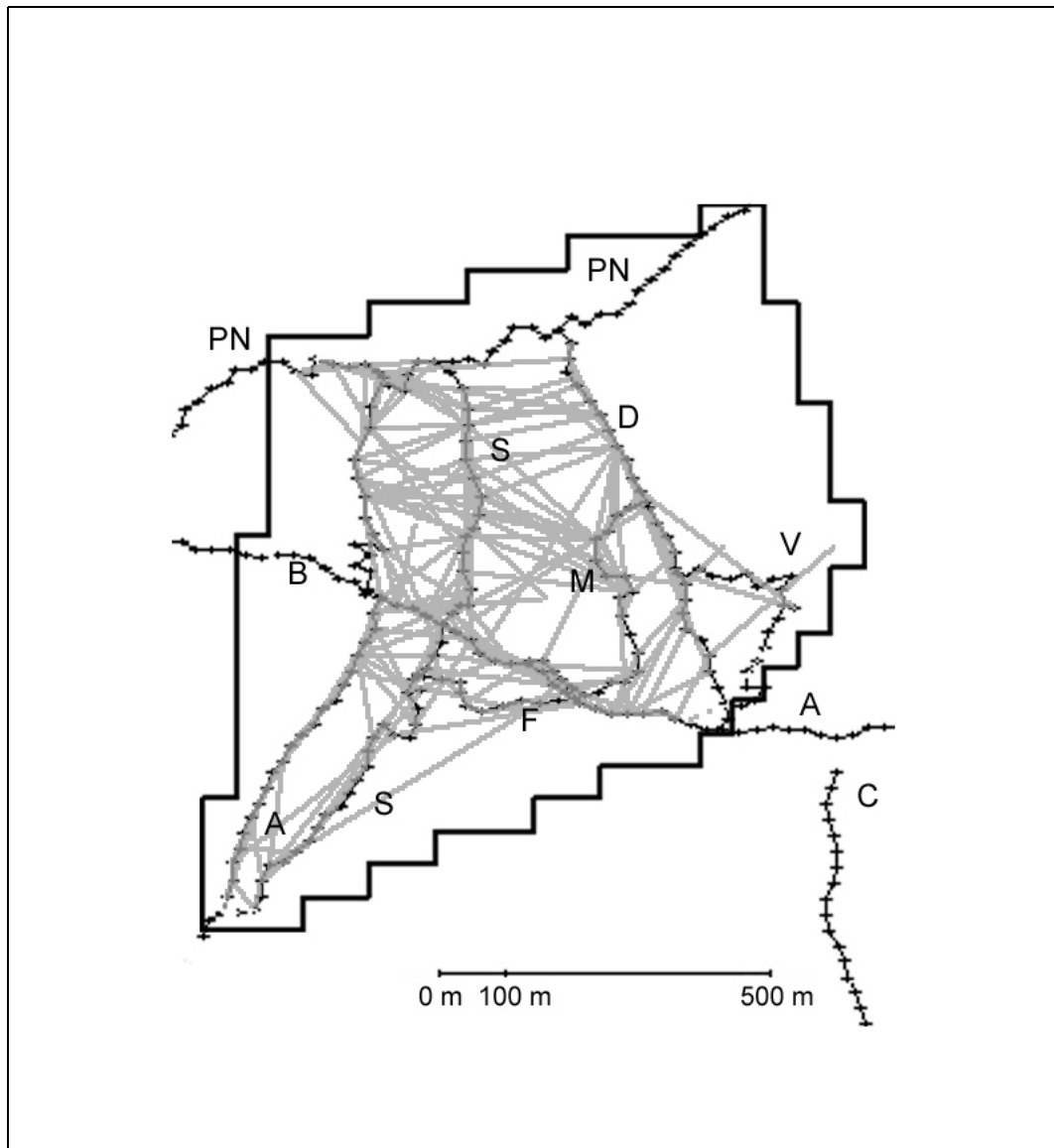


Figure 6.6: Home Range (Method 2) in Group AN1, Andringitra. Cumulative daily path lengths (DPL) demonstrate areas of concentrated use.

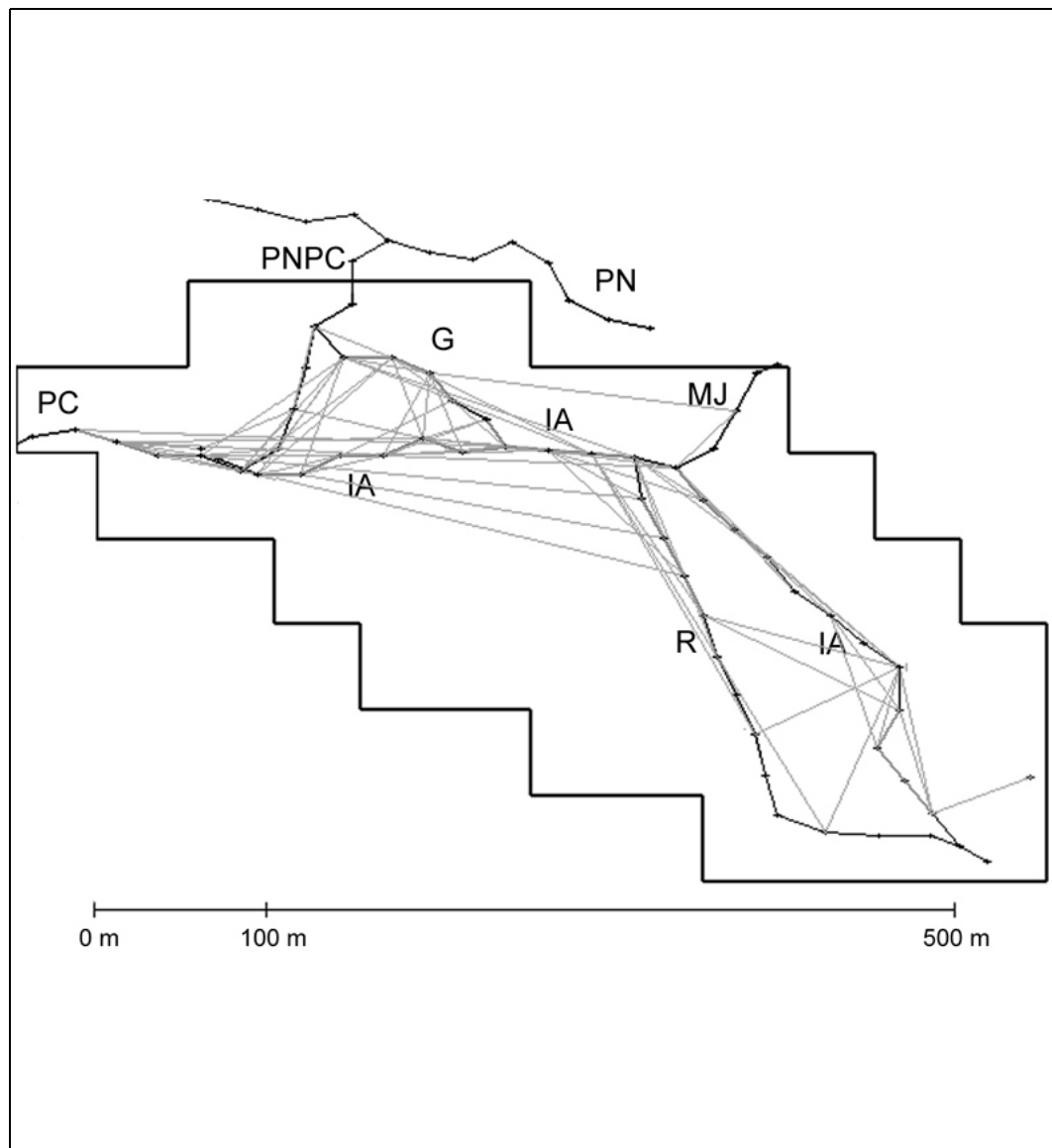


Figure 6.7: Home Range (Method 2) in Group ANA, Andringitra. Cumulative daily path lengths (DPL) demonstrate areas of concentrated use. Note larger scale.

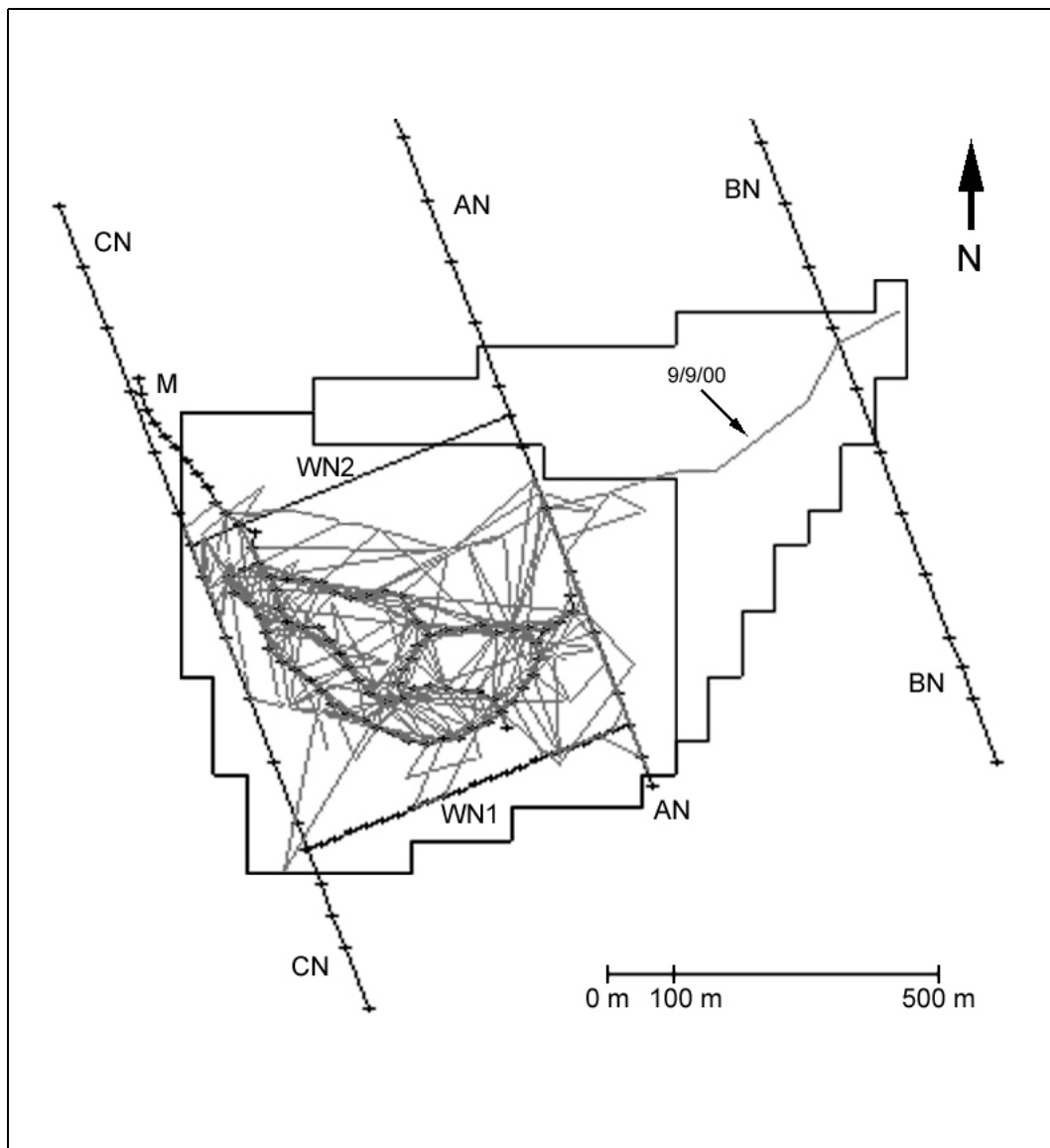


Figure 6.8: Home Range (Method 2) in Group VE1, Vevembe. Cumulative daily path lengths (DPL) demonstrate areas of concentrated use. Smaller area indicates home range estimate excluding travel on 9/9/00.

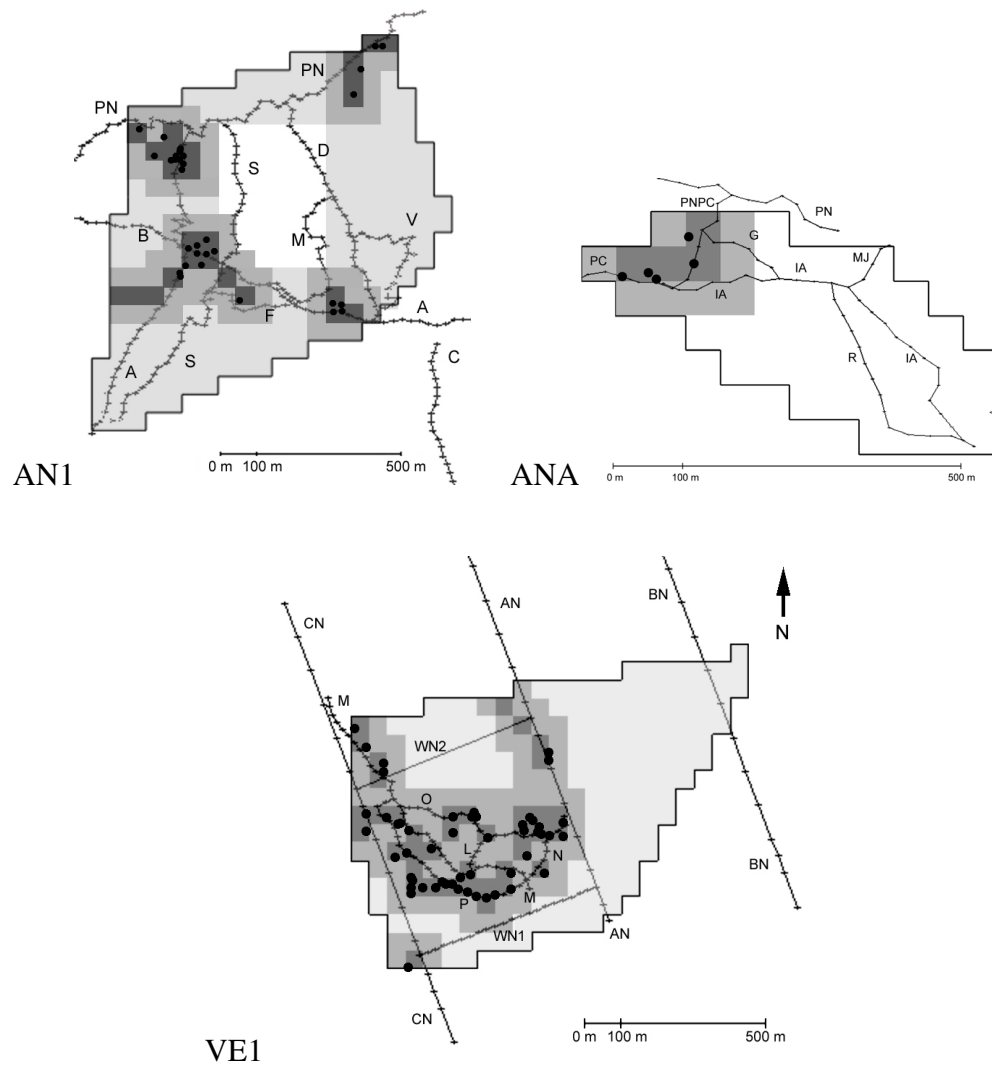


Figure 6.9: Home Range Overlap. Points indicate locations of intergroup encounters. Overlap estimates include: minimum (darkest shading), medium (medium shading), and maximum (lightest shading). See text for explanation of methods.

Table 6.1: Subcategories and Behaviors in the Social (S) Category.

Subcategory	Code	Behavior
Affiliative	GR	Groom
	RG	Reciprocal Groom
	AP	Social Approach (<1 m)
	DE	Depart
	PL	Play
Sexual	MT	Mount
	EJ	Ejaculate
Agonistic	CH	Chatter
	GT	Grunt
	SA	Submissive Approach
	TH	Threat
	SW	Submissive Withdrawal
	CW	Cower
	HI	Hit
	BI	Bite
	CS	Chase
Vocalization	CG	Contact Grunt
	LC	Lost Call
Other	SM	Scent-Mark
	VI	Vigilance
	SG	Self Groom

Table 6.2: Social Spacing Across Groups¹.

Group	Frequency of Neighbor Present (< 5 m)	Distance to Neighbor (m)*
AN1	79.4%	1.05
ANA	88.4%	1.04
VE1	76.7%	0.81

¹ Asterix (*) denotes significant variation (Kruskal-Wallis test).

Table 6.3: Activity Budgets¹.

Group		R	C	S	F	T
AN1	All	31.6%	40.3%*	2.6%*	11.4%*	14.2%*
	Males	33.0%	39.4%	2.2%	10.5%	14.9%
	Females	29.7%	41.4%	3.1%	12.6%	13.1%
	Adults	31.6%	40.3%	2.6%	11.4%	14.2%
	Juveniles	--	--	--	--	--
ANA	All	35.0%	29.8%*	0.6%*	18.5%*	16.2%*
	Males	34.6%	29.4%	0.4%	19.0%	16.6%
	Females	35.8%	30.4%	0.8%	17.5%	15.5%
	Adults	35.8%	29.2%	0.6%	17.8%	16.7%
	Juvenile	30.2%	33.6%	0.0%	22.8%	13.4%
VE1	All	31.2%	45.4%*	2.3%*	14.0%*	7.2%*
	Males	31.8%	46.2%	1.9%*	13.4%	6.7%
	Female	28.7%	42.5%	3.8%*	16.1%	8.8%
	Adults	33.4%*	44.9%	2.5%	12.4%*	6.8%
	Juveniles	25.3%*	46.6%	1.8%	18.1%*	8.2%

¹ Behavior categories include: Rest (R), Rest in Contact (C), Social (S), Feed (F), and Travel (T). Asterix (*) indicates significant variation among groups (Kruskal-Wallis test) or between age or sex classes within groups (Mann-Whitney U test).

Table 6.4: Intergroup Interactions.

Group	% Observation		Nature of Interactions ¹		
	Time	Bouts/hour	1-2 (Hostile)	3 (Neutral)	4-5 (Affiliative)
AN1	1.7%	0.063	37.8%	62.2%	0.0%
ANA	0.2%	0.018	33.3%	66.7%	0.0%
VE1	2.3%	0.082	39.2%	56.9%	3.9%

¹ See text for explanation of categories of interactions.

Table 6.5: Mean Daily Path Length (DPL), Total Home Range (HR), Range Overlap, and Indices of Defensibility (*D*)¹.

Group	DPL (m)	HR	HR	HR Overlap			<i>D</i>	<i>D</i>
		(Method 1)	(Method 2)	Min.	Med.	Max.	(Method 1)	(Method 2)
AN1	743.5	42.5	71.8	8.7%	32.4%	84.7%	1.01	0.78
ANA	285.9	8.8	12.0	8.3%	25.0%	25.0%	0.86	0.73
VE1	637.4	33.5	64.3	15.2%	46.7%	100.0%	0.98	0.70

¹ See text for explanation of methods for determining home range and overlap.

Chapter 7: Behavioral Ecology of the Brown Lemurs of Southeastern Madagascar: Conclusions and Implications for Speciation

INTRODUCTION

In the preceding chapters, I have documented population differences in the white-collared lemurs (*Eulemur albocollaris*) of Vevembe and white-collared X rufous lemur hybrids (*E. albocollaris* X *E. fulvus rufus*) at Andringitra National Park. In particular, I have examined morphometrics, population densities, habitat structure and food availability, feeding ecology, ranging, and social behavior (including social structure and interactions with conspecifics). Where possible, I have made direct comparisons with a third key population in this complex: the parental species *Eulemur fulvus rufus* at Ranomafana National Park (e.g., Overdorff, 1991, 1993, 1996a-b). In this chapter, I use these data to evaluate the original hypotheses posed in Chapter 1. I construct a synthesis of the behavioral and ecological trends observed in present-day populations and discuss how these patterns may signal population divergence in the past and impact future separation. In short, I examine the role of behavioral ecology in speciation in the southeastern brown lemurs.

MORPHOLOGY

While not addressed in the initial set of hypotheses, differences in morphology may certainly be related to population divergence in behavior and

ecology. While sample sizes from Andringitra and Vevembe alone were too small to investigate most measures (summarized in Chapter 2), I have used additional sources to examine characters of particular socioecological significance. Specifically, I compare testes volume and sexual dimorphism in canine height and body weight in *E. albocollaris*, hybrids, and neighboring *E. f. rufus* from Ranomafana (Overdorff, unpublished data; Merenlender, unpublished data).

The results of these analyses are striking. There are clear differences in levels of sexual dimorphism in both body weight and maxillary canines across brown lemur populations, unrelated to allometric scaling or phylogeny. Males have larger canines in most groups, while *E. f. rufus* females at Ranomafana are larger in body size. Moreover, dimorphism in size and canines appear to shift in tandem across populations. The large canines in the males of most brown lemur populations suggest intense intrasexual competition relative to most lemur species. The multi-male group structure and lack of female dominance in brown lemurs are conducive to the development of this rare characteristic. However, *E. f. rufus* at Ranomafana do not follow the same morphological trends; females in this population are larger than males and there are no sex differences in canine height. A possible explanation for this deviation from the general brown lemur pattern is that high levels of agonism over food resources at Ranomafana may favor relatively larger females with larger canines.

Sperm competition is likely mitigating the effects of dimorphism on mating systems and intrasexual competition in these groups. All brown lemurs

examined here have large testes relative to body weight compared to other lemurid primates (see Kappeler, 1997). In addition, testes volume increases sharply during the mating season, underscoring the importance of greater sperm output during this critical period. Finally, white-collared lemurs have the largest relative and absolute testicle size, falling close to other lemur species with fission-fusion social structure and to lemurs with highly promiscuous mating (Kappeler, 1997). Due to their flexible grouping pattern, *E. albocollaris* males may have more difficulty in gaining exclusive access to estrous females, favoring the development of additional indirect means of intrasexual competition – sperm competition – in this species.

POPULATION DENSITIES

The first formal hypothesis pertains to population densities across the study populations. The null hypothesis is that there are no differences among allopatric, parental groups and the hybrids at Andringitra. However, as expected from prior rapid assessments, the study populations vary considerably in abundance. The magnitude of these differences is remarkable: densities in the hybrid zone are up to eight times higher than those in pure parental sites. Also as predicted, *E. albocollaris* populations at Vevembe are the sparsest among the southeastern brown lemurs, despite having the lowest species richness (i.e., the fewest potential competitors). These results imply that white-collared lemurs are found in sub-optimal environments, while the hybrid zone is likely associated with higher quality habitats – findings corroborated by analyses of forest structure and food availability (see below).

Due to the combination of high population density and large area, the brown lemur contact zone of the Andringitra Massif has enormous potential for gene flow. These factors may have led to the strikingly introgressive hybrid zone – a “hybrid swarm” (Mayr, 1963) – wherein 86% of individuals sampled are hybrids (Wyner, 2000). There are no indications of severely reduced fitness in the hybrids, as backcrosses appear to abound in the zone (Wyner, 2000). Therefore, intrinsic factors in the allopatric environments or populations may ultimately limit expansion of the zone. The very low densities in white-collared lemurs (coupled with poor habitats, discussed below) are almost certainly important factors in inhibiting gene flow to the south.

It is less clear what factors may be responsible for the somewhat reduced densities in *E.f. rufus* (e.g., Ranomafana), or for the limitations of gene flow and the contact zone to the north. Community ecology is probably not a significant factor, as the hybrid zone contains nearly the same number of lemur species as, for example, Ranomafana. However, *Varecia variegata*, a frugivorous lemur species (e.g., White, 1991; Morland, 1991; Vasey, 1997), is present in the Ranomafana community, but absent from Andringitra. Release from competition with *Varecia* may permit higher population densities, as well as increased frugivory (see below), in the Andringitra hybrids. The importance of *Varecia* as a potential competitor is evidenced by relatively frequent interference competition, with *Varecia* excluding *E. fulvus* from particular resources during scarce seasons (Vasey, 2000). Nevertheless, *Varecia* has a disjunct geographic range and is very sensitive to shifts in microhabitat quality (While et al., 1995). Thus, it is unlikely

that such a rare and patchily distributed species will have an important impact on brown lemur abundance across the entire southeastern region. It is also unlikely that overall habitat quality accounts for the lower densities in most *E. f. rufus* sites relative to the hybrid zone. Ranomafana appears to have higher annual food availability than even Andringitra (see below). The roles of keystone resources and territoriality are two additional possibilities that will be discussed in more detail.

HABITAT QUALITY

There is great variation in habitat structure and resource base among the southeastern rain forest sites, falsifying the second original null hypothesis predicting consistency across the region. The forest at Andringitra is highly variable, but with much greater overall food availability than at Vevembe. Andringitra appears to be somewhat less productive than Ranomafana over an annual cycle and the timing of resource peaks differs among the eastern rain forests (Overdorff and Wright, unpublished ms). As indicated in the preceding discussion, the impact of these differences may be very important for the population structure of the southeastern brown lemur groups, as well as for their feeding ecology. The hybrid zone does appear to coincide with an ecotone – a transition to more resource-poor habitats to the south. In addition, the contact zone is located at the more obvious junction between the dry west, the high mountains, and the eastern lowland rain forest (Goodman and Lewis, 1996). While there is probably pure *E. f. rufus* in the more arid western slopes of Andringitra, the hybrid zone bisects more closely the *E. f. rufus* population *within*

the eastern rain forest corridor. Therefore, the habitat transitions within this corridor likely have greater significance for gene exchange between *E. f. rufus* and *E. albocollaris*. Such environmental boundaries frequently characterize hybrid zones between ecologically distinct primate taxa (e.g., the Awash baboon contact zone; Nagel, 1973; Phillips-Conroy and Jolly, 1986; Jolly, 2001).

Again, the critical environmental difference appears to be the scarcity of food resources at Vevembe. However, seasonal productivity of Malagasy forests is notoriously unpredictable (Wright, 1999). Long-term phenological studies are required to confirm differences in food availability at Andringitra and Vevembe (although examining the study sites simultaneously in 2000 helped to control for inter-annual irregularities). Another potentially crucial habitat difference between Andringitra and Vevembe (as well as Ranomafana) is the presence of keystone resources during food scarcity. Unfortunately, no independent phenological data are available for the possible critical resources suggested by behavioral observations: *Ficus* fruits at Andringitra and *Pandanus* flowers at Vevembe. While the asynchronous nature of the phenology of most fig species suggests this may be an ideal candidate for a keystone resource, the relative abundance of *Ficus* trees and hemi-epiphytes must be established at Andringitra. Considering the large hybrid population at this site, as well as the intensive seasonal exploitation of figs (see below), the distribution of *Ficus* species may have a substantial impact on the biogeography of southeastern brown lemurs.

FEEDING ECOLOGY

The third null hypothesis states that there are no significant differences in feeding ecology among parental and hybrid groups. This hypothesis is falsified by behavioral observations of Andringitra hybrids and Vevembe white-collared lemurs. The former population has relatively low dietary diversity and consumes a very high proportion of fruit, more akin to obligate frugivore lemurs than to other brown lemur groups. In contrast, the *E. albocollaris* population follows the more typical brown lemur dietary regime; it is mainly frugivorous, but with substantial reliance on secondary resources (in this case, flowers, flower buds, and/or nectar). In fact, the two parental species, *E. albocollaris* and *E. f. rufus*, are more similar in their diet than either is to the hybrids of Andringitra (see Overdorff, 1993).

The dearth of food resources at Vevembe may help to explain the more generalist feeding ecology of white-collared lemurs. However, rufous lemurs at Ranomafana do not suffer from comparatively low resource availability; as noted, annual food production at this site appears to be even higher than at Andringitra. Again, particular seasonal resources may be important in determining the feeding ecology and abundance of brown lemurs. The near-exclusive reliance on *Ficus* fruits during July and August attests to the potential impact of this food resource for the hybrids at Andringitra (e.g., Terborgh, 1986b; although results are equivocal from tests of the association between fig-feeding and overall scarcity). The apparent abundance of *Ficus* at Andringitra may be exceptional for Madagascar (Goodman and Ganzhorn, 1997). In the sparsely populated *E.*

albocollaris community at Veveombe, figs are seldom consumed and may be rare; the *Pandanus* flowers so prevalent in the diet during July and August may be a less reliable or suitable keystone resource. Similarly, at Ranomafana, *E. f. rufus* groups do consume *Ficus* variably, but are forced to migrate to more productive habitats during peak fruit scarcity (Overdorff, 1993). Further research (especially long-term phenology that includes *Ficus* species) is clearly necessary to better understand this critical dietary divergence among southeastern brown lemurs. However, based on preliminary evidence, I suggest that *Ficus* may be responsible for maintaining the dense hybrid population at Andringitra.

SOCIAL BEHAVIOR AND RANGING

Other aspects of behavioral ecology also vary across southeastern brown populations, at least partially falsifying the final null hypothesis. There are substantial differences among the study groups in activity budgets and ranging patterns. However, there is little association with seasonal shifts in diet or resource base and there is greater variation within populations than between them. Perhaps the most consistent pattern that emerges is that, relative to rufous lemurs at Ranomafana, both the hybrids and white-collared lemurs employ an energy minimization strategy, with increased resting and reduced travel.

Comparison of social structure reveals more notable differences among southeastern brown lemurs. In contrast to the cohesive grouping pattern typical of most brown lemurs, *E. albocollaris* has fission-fusion groups. This flexible social structure is very rare in Malagasy primates, having been recorded only in *Varecia variegata* (e.g., Morland, 1991; Vasey, 1997) and *Eulemur macaco* (e.g.,

Calquhoun, 1997). Fission-fusion is potentially a response to increased intragroup feeding competition over limited resources (Symington, 1988). Like increased dietary diversity, this behavioral shift may be imposed by resource scarcity at Vevembe. Despite these likely proximate ecological cues, fission-fusion group structure appears to be consistent across white-collared lemur sites. Conversely, other Malagasy brown lemurs have highly cohesive groups, with more flexible group structure occurring only during permanent group splitting (e.g., Overdorff et al., 1999; Vasey, 2000). Therefore, this divergence in social structure may reflect underlying genetic differences between *E. albocollaris* and other brown lemur taxa. Fission-fusion social structure could then be an adaptation to chronically poor habitat quality throughout the limited distribution of white-collared lemurs.

Variation in other aspects of brown lemur social behavior may have important repercussions for gene flow across southeastern brown lemurs. Highly relaxed relations among conspecific groups characterize both *E. albocollaris* and the hybrids. In contrast, rufous lemurs to the north have high frequencies of aggression during intergroup encounters (double those of the Andringitra and Vevembe groups; Overdorff, 1991). There is extensive home range overlap among Ranomafana *E. f. rufus* groups, thus intergroup agonism does not lead to the formation of strictly defended territories (Overdorff, 1991). Ecological conditions and ranging behavior may inhibit invariant spatial defense (e.g., Mitani and Rodman, 1979; Dunbar, 1988). However, variable expressions of intergroup agonism in species without defended territories, often in response to habitat

conditions or food resources (e.g., Kavanagh, 1981; Lawes and Henzi, 1992), suggest that such aggression may be an important facultative response in some species or environments.

Territoriality (or other forms of intergroup aggression) may have significant impacts on dispersal patterns and thus, ultimately, on genetic exchange among populations. The most territorial primates have exceptionally low dispersal distances; in the most extreme examples, offspring will only occupy adjacent ranges or even remain within the parental territory (e.g., hylobatids; Brockelman et al., 1998). Animals dispersing beyond home territories or adjoining areas may incur higher costs (e.g., greater agonism from unfamiliar groups or increased chance for aggression as distances traveled increase). Moreover, greater intensity of territorial behavior may drastically alter population structure. Mathematical models – supported empirically in domestic cat communities – indicate that substantially lower population densities are obtained with increased levels of conspecific aggression (Auger and Pontier, 1998). Such low dispersal rates and population density may significantly reduce gene flow among contiguous populations, maintaining overall regional population differences in the face of hybridization. This should be the case even if, as in the gibbon example (Brockelman and Gittins, 1984), contact zones are more likely to be the result of secondary contact rather than sympatric or parapatric speciation.

It is possible that *E. f. rufus* dispersal into the Andringitra region may be inhibited by increased intergroup conflict in this taxon. Evaluating this hypothesis will require more data on comparative brown lemur life history in the

southeastern Madagascar. Long-term analyses at Ranomafana have provided some of this information, such as ages of dispersing males and the social and reproductive dynamics of immigrant males (Overdorff et al., 1999). Moreover, there are suggestions that *E.f. rufus* males may migrate in pairs (perhaps reducing extra-group agonism and facilitating dispersal). In addition, males do not appear to migrate multiple times during their lifetimes (Overdorff, et al., 1999) – again potentially reducing aggression received, but in this case, reducing gene flow among groups. However, direct observations on dispersing males are still lacking. To assess the impact of intergroup aggression on dispersal, it will be necessary to examine dispersal distances, genetic relatedness of migrants and their new groups, and rates of aggression incurred (and other possible selective factors) by migrants.

Observations of ranging differences among southeastern brown lemurs cast some doubt on the importance of intergroup agonism in limiting rufous lemur dispersal. Despite the high rates of aggression in this population, Ranomafana *E.f. rufus* groups have the largest home ranges and longest day ranges of any brown lemur (Overdorff, 1991; see Chapter 6). Moreover, these groups move long distances (4-5 km) in search of food during peak resource scarcity (Merenlender, 1993; Overdorff, 1993), a behavior that was never observed in the Andringitra hybrids or *E. albocollaris*. Therefore, it is possible that increased intergroup aggression in *E.f. rufus* is simply a by-product of more extensive ranging. It may be, for example, that aggression increases due to a lack of familiarity with other social groups in more distant portions of the home range. Accordingly, it is

perhaps more likely that crucial environmental conditions – such as the lack of keystone resources discussed above – have a greater impact in reducing *E. f. rufus* abundance and, thus, gene flow.

CONCLUSION

I would like to conclude by returning to the original three major questions of the project to assess whether there are now some satisfactory answers. Without straying too far into speculation, I will tie together the proximate ecological processes that I have discussed herein with their potential evolutionary consequences. In addition, I address the concerns these analyses raise for brown lemur conservation.

The first question of this study is, do ecological and behavioral factors permit *E. albocollaris* and *E. f. rufus* to overlap? With evidence for a highly introgressive hybrid zone at Andringitra, the answer is an unreserved “yes”. The obvious follow-up question is, which factors are important? I think there is clear indication that the Andringitra contact zone coincides with a broad ecotone, an exceptional habitat that allows not only for overlap, but also for one of the most dense brown lemur populations in eastern Madagascar. I propose that the availability of *Ficus* (particularly *Ficus lutea*) may be a critical environmental factor, supporting this large frugivorous lemur population through seasonal shortages and, thus, allowing for a high degree of genetic exchange and introgressive hybridization. Other behavioral differences probably play more minor roles in encouraging overlap and interbreeding. The one notable exception is perhaps the variation in intergroup aggression – as discussed above, this

behavioral difference may lead to differential population sizes and dispersal patterns among southeastern brown lemurs.

The next, complementary question is, do ecological and behavioral variables inhibit further expansion of the area of overlap? This is an extremely difficult question to answer definitively. The null scenario is that the location and extent of the hybrid zone are simply artifacts of history. With little indication for reduced fitness in the hybrids, their present distribution is possibly only an expression of how long ago and where the original point of contact occurred. This contact would have involved two populations of an ancestral southeastern brown lemur species that had diverged in allopatry (perhaps in forest refugia during Pleistocene cooling events).

Nevertheless, results from this study suggest potential mechanisms for limiting the expansion hybrid zone beyond the highly productive and densely populated Andringitra region. Several lines of evidence suggest that population movement to the south may be curtailed by the poor quality habitats found there. *E. albocollaris* is found in low density throughout its range. This may be caused by the paucity of food resources (as indicated by phenology at Vevembe) – which is also reflected in the feeding ecology and fission-fusion social structure of white-collared lemurs. To the north, it is possible that increasing intergroup aggression among conspecifics, like that in *E. f. rufus* at Ranomafana, may hinder both population growth and dispersal; however, it is more likely that habitat characteristics, such as the lack of keystone resources, limits rufous lemur abundance and gene flow in this region.

How, then, might these variables contribute to the limitations of hybridization and gene flow between parental populations? The habitat conditions and behavioral responses potentially limiting the contact zone may be variable over time and space. Furthermore, there is no clear evidence yet to imply that the Andringitra Massif is the original location for the *E. f. rufus* X *E. albocollaris* contact zone. For example, this region does not represent the boundary for other lemur species (e.g., Tattersall, 1982; Mittermeier et al., 1994). However, genetic studies of the brown lemur population reveal extensive introgression, suggesting multiple generations of backcrossing. More dramatically, novel alleles are present in the contact zone. Such genetic innovation indicates that the hybrid zone may be at least partially isolated from the original parental populations. Based on the genetic and ecological evidence from this region, it is likely that the hybrid zone has “settled” in this location long enough for stable population differences to have developed – differences that distinguish not only the two parental taxa from each other, but also the hybrids from either ancestral group.

The hybrid zone as a partially bounded population has major long-term implications for gene flow and speciation in the brown lemurs southeastern Madagascar. Due to possible behavioral and ecological restrictions on dispersal to the north and south within the eastern rain forest corridor, the hybrid zone may have little genetic exchange with the central portions of the parental species’ ranges. *E. albocollaris* and *E. f. rufus* may then go on evolving on separate trajectories, continuing to diverge in their socioecology and, eventually,

developing reproductive barriers as well. Perhaps more remarkably, in light of the evidence for novel genetic diversity, the hybrid zone could ultimately be an example of the processes of reticulate speciation – a distinct taxon arising from the complex interactions of parental species. Reticulate evolution, although rare in animals (Arnold, 1992), appears to occur in other primate groups with extensive hybridization (e.g., baboons; Jolly, 2001).

Pending more research on population genetics, biogeography, and life history across the southeastern brown lemurs, the speciation scenarios outlined above remain highly speculative. However, there is reason to believe that the population differences observed here could reflect evolutionary trends, with continued divergence likely. With persistent human encroachment, lemur populations and suitable habitats are dwindling rapidly (Harcourt and Thornback, 1990; Mittermeier et al., 1992). What remains of the fragmented rain forests inhabited by these brown lemur groups increasingly resemble island habitats. Perhaps as in insular environments, dispersal and genetic exchange among populations are diminished, creating greater potential for divergence within much more confined areas (e.g., Blondel, 2000). Certainly if migration corridors through the Andringitra boundary region are eliminated by habitat destruction, the divergence of the southeastern brown lemurs will be permanent.

The myriad conservation implications of this project will not be explored in detail here. However, it should be pointed out that this study does provide support for those who prefer to distinguish *Eulemur albocollaris* from other brown lemur taxa based on diagnostic methods of species and conservation units

(e.g., Wyner, 2000). There are important differences among the southeastern brown lemur populations, including density, diet, intergroup interactions, and social structure. Moreover, many of these differences may be critical factors in processes inhibiting genetic exchange among these groups – processes that may indeed be linked to speciation. Such distinctions are reflected in the genetic diagnosis of *E. albocollaris* (as separate from other brown lemurs). Acceptance of species-level designation for this taxon highlights its dire prospects; with a highly restricted range, dramatically low population densities, ongoing habitat destruction, and hunting pressure (e.g., Tattersall, 1982; Mittermeier et al., 1994; Johnson and Overdorff, 1999), *E. albocollaris* as a species surely ranks among the most endangered of the Malagasy primates. Results from this study also underscore the significance of the Andringitra contact zone. There are many unique aspects of this region and population, not least of which is its role as a potential source for new genetic variation. Moreover, the dynamics of this boundary region clearly serve important functions in the divergence of white-collared and rufous lemurs. Accordingly, to maintain biodiversity in this group, as well as to better understand lemur speciation processes, it is imperative to preserve both the Andringitra contact zone and the adjoining forest corridors that allow dispersal among southeastern brown lemurs.

References

- Alberts SC, Altmann J. 2001. Immigration and hybridization patterns of yellow and anubis baboons in and around Amboseli, Kenya. *American Journal of Primatology* 53:139-154.
- Albrecht GH, Jenkins PD, Godfrey LR. 1990. Ecogeographic size variation among the living and subfossil prosimians of Madagascar. *American Journal of Primatology* 22:1-50.
- Altmann J. 1974. Observational study of behavior: Sampling methods. *Behaviour* 49:227-265.
- Arnold ML. 1992. Natural hybridization as an evolutionary process. *Annual Review of Ecology and Systematics* 12: 237-261.
- Auger P, Pontier D. 1998. Fast game theory coupled to slow population dynamics: The case of domestic cat populations. *Mathematical Biosciences* 148:65-82.
- Ayala FJ, Tracey ML, Hedgecock D, Richmond RC. 1974. Genetic differentiation during the speciation process in *Drosophila*. *Evolution* 28:45-58.
- Balko EA. 1998. A behaviorally plastic response to forest composition and logging disturbance by *Varecia variegata variegata* in Ranomafana National Park, Madagascar. Ph.D. dissertation, State University of New York-Syracuse, Syracuse, NY.
- Banks M. 2002. Littoral forest primate fauna in the Tolagnaro (Fort Dauphin) region of southeastern Madagascar. *American Society of Primatologists Bulletin* 26:8.
- Barton NH, Hewitt GM. 1985. Analysis of hybrid zones. *Annual Review of Ecology and Systematics* 16:113-148.
- Barton NH, Hewitt GM. 1989. Adaptation, speciation and hybrid zones. *Nature* 341:497-503.

- Barton RA, Whiten A, Strum S, Byrne RW, Simpson AJ. 1992. Habitat use and resource availability in baboons. *Animal Behaviour* 43:831-844.
- Barton NH. 2001a. Speciation. *Trends in Ecology and Evolution* 16:325.
- Barton NH. 2001b. The role of hybridization in evolution. *Molecular Ecology* 10:551-568.
- Bergstrom BJ. 1992. Parapatry and encounter competition between chipmunk (*Tamias*) species and the hypothesized role of parasitism. *American Midland Naturalist* 128:168-179.
- Beyene Gebru S. 1998. The role of female mating behavior in hybridization between anubis and hamadryas baboons in Awash, Ethiopia. Ph.D. dissertation, Washington University, St. Louis, MO.
- Blondel J. 2000. Evolution and ecology of birds on islands: Trends and prospects. *Vie et Milieu* 50:205-220.
- Boinski S. 1987. Habitat use by squirrel monkeys (*Saimiri oerstedii*) in Costa Rica. *Folia Primatologica* 49:151-167.
- Bradley B, Stumpf RM. 1997. Morphometrics of *Eulemur fulvus albocollaris* in Vevev Forest, Madagascar. *American Journal of Physical Anthropology Supplement* 24:79-80.
- Brockelman WY, Gittins SP. 1984. Natural hybridization in the *Hylobates lar* species group: Implications for speciation in gibbons. In: Preuschoft H, Chivers DJ, Brockelman WY, Creel N, editors. *The lesser apes: Evolutionary and behavioural biology*. Edinburgh: Edinburgh University Press. p 498-532.
- Brockelman WY, Ali R. 1987. Methods of surveying and sampling forest primate populations. In: Marsh CW, Mittermeier RA, editors. *Primate conservation in the tropical rain forest*. New York: Alan R. Liss, Inc. p 23-62.
- Brockelman WY, Reichard U, Treesucon U, Raemaekers JJ. 1998. Dispersal, pair formation and social structure in gibbons (*Hylobates lar*). *Behavioral Ecology and Sociobiology* 42:329-339.

- Brown WL, Wilson EO. 1956. Character displacement. *Systematic Zoology* 5:49-64.
- Brown L, Shumaker RW, Downhower JF. 1995. Do primates experience sperm competition? *American Naturalist* 146:302-306.
- Buettner-Janusch J, Hamilton AE. 1979. Chromosomes of Lemuriformes part IV: Karyotype evolution in *Lemur fulvus collaris*. *American Journal of Physical Anthropology* 50:363-365.
- Bull CM. 1991. Ecology of parapatric populations. *Annual Review of Ecology and Systematics* 22:19-36.
- Burney DA, MacPhee RDE. 1988. Mysterious island: What killed Madagascar's large native animals? *Natural History* 97:46-55.
- Burney DA. 1993. Late Holocene environmental change in arid southwestern Madagascar. *Quaternary Research* 40:98-106.
- Butlin RK. 1989. Reinforcement of premating isolation. In: Otte D, Endler JA, editors. *Speciation and its consequences*. Sunderland, Mass.: Sinauer Associates, Inc. p 158-179.
- Butynski TM. 1990. Comparative ecology of blue monkeys (*Cercopithecus mitis*) in high-density and low-density subpopulations. *Ecological Monographs* 60:1-26.
- Bynum EL, Bynam DZ, Supriatna J. 1997. Confirmation and location of the hybrid zone between wild populations of *Macaca tonkeana* and *Macaca hecki* in central Sulawesi, Indonesia. *American Journal of Primatology* 43:181-209.
- Bynum N. 2002. Morphological variation within a macaque hybrid zone. *American Journal of Physical Anthropology* 118:45-49.
- Calquhoun IC. 1997. A predictive socioecological study of the black lemur (*Eulemur macaco macaco*) in northwestern Madagascar. Ph.D. dissertation, Washington University, St. Louis, MO.
- Cant JGH. 1978. Population survey of the spider monkey, *Ateles geoffroyi* at Tikal, Guatemala. *Primates* 19:525-535.

- Chapman CA. 1988. Patterns of foraging and range use by three species of neotropical primates. *Primates* 29:177-194.
- Chapman CA, Chapman LJ, Wrangham RW, Hunt K, Gebo D, Gardner L. 1992. Estimators of fruit abundance of tropical trees. *Biotropica* 24:527-531.
- Chapman CA, Wrangham RW, Chapman LJ, Kennard DK, Zanne AE. 1999. Fruit and flower phenology at two sites in Kibale National Park, Uganda. *Journal of Tropical Ecology* 15:189-211.
- Cheverud JM, Dow MM, Leutenegger W. 1985. The quantitative assessment of phylogenetic constraints in comparative analysis: Sexual dimorphism in body weight among primates. *Evolution* 39:1335-1351.
- Clutton-Brock TH, Harvey PH, Rudder B. 1977. Sexual dimorphism, socionomic sex ratio and body weight in primates. *Nature* 269:797-800.
- Clutton-Brock TH, Harvey PH. 1977. Species differences in feeding and ranging behaviour in primates. In: Clutton-Brock TH, editor. *Primate ecology*. London: Academic Press. p 557-584.
- Colquhoun I. 1997. A Predictive socioecological study of the black lemur (*Eulemur macaco macaco*) in Northwestern Madagascar. Ph.D. dissertation, Washington University, St. Louis, MO.
- Colyn M, Gautier-Hion A, Verheyen W. 1991. A re-appraisal of the palaeoenvironmental history in Central Africa: Evidence for a major fluvial refuge in the Zaire Basin. *Journal of Biogeography* 18:403-407.
- Connell JH. 1980. Diversity and the coevolution of competitors, or the ghost of competition past. *Oikos* 35.
- Connell JH. 1983. On the prevalence and relative importance of interspecific competition: evidence from field experiments. *American Naturalist* 122:661-696.
- Connor EF, Simberloff D. 1979. The assembly of species communities: Chance or competition? *Ecology* 60:1132-1140.
- Cracraft J. 1983. Species concepts and speciation analysis. *Current Ornithology* 1:159-187.

- Crook JH. 1972. Sexual selection, dimorphism, and social organization. In: Campbell B, editor. Sexual selection and the descent of man 1871-1971. Chicago: Aldine. p 231-281.
- Dagosto M. 1995. Seasonal variation in positional behavior of Malagasy lemurs. *International Journal of Primatology* 16:807-833.
- Dalecky A, Kerdelhué C, Johnson S, Razafindratsita VR, Grassi C, Razafiarimalala AC, Overdorff D, Rasplus J-Y. in press. Malagasy *Ficus* (Moraceae) and associated fauna. In: Goodman SM, Benstead J, editors. The Natural History of Madagascar. Chicago: University of Chicago Press.
- Darwin C. 1871. The descent of man, and selection in relation to sex. New York: Appleton.
- Dayan T, Simberloff D. 1998. Size patterns among competitors: Ecological character displacement and character release in mammals, with special reference to island populations. *Mammal Review* 28.
- Decker BS. 1994. Effects of habitat disturbance on the behavioral ecology and demographics of the tana river red colobus (*Colobus badius rufomitratus*). *International Journal of Primatology* 15:703-737.
- DeVore I, Washburn SL. 1963. Baboon ecology and human evolution. In: Howell FC, Bourlière F, editors. African ecology and human evolution. Chicago: Aldine. p 335-367.
- Dew JL, Wright PC. 1998. Frugivory and seed dispersal by four species of primates in Madagascar's eastern rainforest. *Biotropica* 30:425-437.
- Diamond JM. 1973. Distribution ecology of New Guinea birds. *Science* 179:759-769.
- Diamond JM. 1975. Assembly of species communities. In: Cody ML, Diamond JM, editors. Ecology and evolution of communities. Cambridge: Harvard University Press. p 342-444.
- Djlelati R, Brun B, Rumpler Y. 1997. Meiotic study of hybrids in the genus *Eulemur* and taxonomic considerations. *American Journal of Primatology* 42:235-245.

- Donque G. 1972. The climatology of Madagascar. In: Battistini R, Richard-Vindard G, editors. Biogeography and ecology in Madagascar. The Hague: Dr. W. Junk B.V. p 87-144.
- Dunbar RIM, Dunbar P. 1974. On hybridization between *Theropithecus gelada* and *Papio anubis* in the wild. *Journal of Human Evolution* 3:187-192.
- Dunbar RIM. 1988. Primate social systems. New York: Cornell University Press.
- Dunbar RIM. 1992. Time: a hidden constraint on the behavioural ecology of baboons. *Behavioral Ecology and Sociobiology* :35-49.
- Dutrillaux B, Rumpler Y. 1977. Chromosomal evolution in Malagasy lemurs. II. Meiosis in intra- and interspecific hybrids in the genus *Lemur*. *Cytogenetics and Cell Genetics* 18:197-211.
- Emlen ST, Oring LW. 1977. Ecology, sexual selection, and the evolution of mating systems. *Science* 197:215-223.
- Estrada A, Coates-Estrada R. 1991. Howler monkeys (*Alouatta palliata*), dung beetles (Scarabaeidae) and seed dispersal: Ecological interactions in the tropical rain forest of Los Tuxtlas, Mexico. *Journal of Tropical Ecology* 7:459-474.
- Evans BJ. 1998. Hybridization, molecular phylogeography, and population structure: Case studies of clawed frogs and macaque monkeys. Ph.D. dissertation, Columbia, New York, NY.
- Evans BJ, Supriatna J, Melnick DJ. 2001. Hybridization and population genetics of two macaque species in Sulawesi, Indonesia. *Evolution* 55:1686-1702.
- Fashing PJ. 2001b. Feeding ecology of guerezas in the Kakamega Forest, Kenya: The importance of Moraceae fruit in their diet. *International Journal of Primatology* 22:579-610.
- Fooden J. 1964. Rhesus and crab-eating macaques: Intergradation in Thailand. *Science* 143:363-365.
- Frankie GW, Baker HG, Opler PA. 1974. Comparative phenological studies of trees in tropical wet and dry forests in the lowlands of Costa Rica. *Journal of Ecology* 62:881-919.

- Freed BZ. 1996. Co-occurrence among crowned lemurs (*Lemur coronatus*) and Sanford's lemurs (*Lemur fulvus sanfordi*) of Madagascar. Ph.D. dissertation, Washington University, St. Louis, MO.
- Freeland WJ. 1980. Mangabey (*Cercocebus albigena*) movement patterns in relation to food availability and faecal contamination. *Ecology* 61:1297-1303.
- Froehlich JW, Supriatna J. 1996. Secondary intergradation between *Macaca maurus* and *M. tonkeana* in South Sulawesi, and the species status of *M. togeanus*. In: Fa JE, Lindberg DG, editors. *Evolution and ecology of macaque societies*. Cambridge: Cambridge University Press. p 43-70.
- Fujita K, Watanabe F, Widarto TH, Suryobroto B. 1997. Discrimination of macaques by macaques: The case of Sulawesi species. *Primates* 38:233-245.
- Futuyma DJ, Mayer GC. 1980. Non-allopatric speciation in animals. *Systematic Zoology* 29:254-271.
- Gabow SA. 1975. Behavioral stabilization of a baboon hybrid zone. *American Naturalist* 109:701-712.
- Ganzhorn JU. 1988. Food partitioning among Malagasy primates. *Oecologia* 74:436-450.
- Ganzhorn JU. 1997. Test of Fox's assembly rule for functional groups of lemur communities in Madagascar. *Journal of Zoology (London)* 241:533-542.
- Ganzhorn JU, Malcomber S, Andrianatoanina O, Goodman SM. 1997. Habitat characteristics and lemur species richness in Madagascar. *Biotropica* 29:331-343.
- Ganzhorn JU. 1998. Nested patterns of species composition and their implications for lemur biogeography in Madagascar. *Folia Primatologica* 69 (Suppl. 1):332-341.
- Ganzhorn JU, Wright PC, Ratzimbazafy J. 1999. Primate communities: Madagascar. In: Fleagle JG, Janson CH, Reed KE, editors. *Primate communities*. Cambridge: Cambridge University Press. p 75-89.

- Gasse F, van Campo E. 1998. A 40,000-yr pollen and diatom record from Lake Tritrivakely, Madagascar, in the southern tropics. *Quaternary Research* 49:299–311.
- Gasse F, van Campo E. 2001. Late Quaternary environmental changes from a pollen and diatom record in the southern tropics (Lake Tritrivakely, Madagascar). *Palaeogeography, Palaeoclimatology, Palaeoecology* 167:287-308.
- Gause GF. 1934. *The struggle for existence*. Baltimore: Williams and Wilkins.
- Gautier-Hion A. 1978. Food niches and coexistence in sympatric primates in Gabon. In: Chivers DJ, Herbert J, editors. *Recent advances in primatology*. New York: Academic Press. p 269-286.
- Gautier-Hion A. 1980. Seasonal variations of diet related to species and sex in a community of *Cercopithecus* monkeys. *Journal of Animal Ecology* 49:237-269.
- Gautier-Hion A, Gautier J-P, Quris R. 1981. Forest structure and fruit availability as complementary factors influencing habitat use by a troop of monkeys (*Cercopithecus cephus*). *Revue Ecologie (Terre et Vie)* 35:511-536.
- Gautier-Hion A, Michaloud G. 1989. Are figs always keystone resources for tropical frugivorous vertebrates? A test in Gabon. *Ecology* 70:1826-1833.
- Gautier-Hion A, Maisels F. 1994. Mutualism between a leguminous tree and large African Monkeys as pollinators. *Behavioral Ecology and Sociobiology* 34:203-210.
- Gentry AH. 1993. Diversity and Floristic composition of lowland tropical forest in Africa and South America. In: Goldblatt P, editor. *Biological Relationships between Africa and South America*. New Haven: Yale University. p 500-547.
- Gerson JS. 1999. Size in *Eulemur fulvus rufus* from western Madagascar: Sexual dimorphism and ecogeographic variation. *American Journal of Physical Anthropology Supplement* 28:134.
- Gerson JS. 2000. Social relationships in wild red-fronted brown lemurs (*Eulemur fulvus rufus*). Ph.D. dissertation, Duke University, Durham, NC.

- Glander KE, Wright PC, Daniels PS, Merenlender AM. 1992. Morphometrics and testicle size of rain forest lemur species from southeastern Madagascar. *Journal of Human Evolution* 22:1-17.
- Glander KE. 1993. Capture and marking techniques for arboreal primates. In: Estrada A, Rodriguez-Luna E, Lopez-Wilchis R, Coates-Estrada R, editors. *Estudios primatologicos en Mexico*. Veracruz: Universidad Veracruzana. p 299-304.
- Godfrey LR, Sutherland MR, Petto AJ, Boy DS. 1990. Size, space, and adaptation in some subfossil lemurs from Madagascar. *American Journal of Physical Anthropology* 81:45-66.
- Godfrey LR, Marks J. 1991. The nature and origins of primate species. *Yearbook of Physical Anthropology* 34:39-68.
- Godfrey LR, Lyon SK, Sutherland MR. 1993. Sexual dimorphism in large-bodied primates: The case of the subfossil lemurs. *American Journal of Physical Anthropology* 90.
- Godfrey LR, Jungers WL, Simons EL, Chatrath PS, Rakorosamimanana B. 1999. Past and present distributions of lemurs in Madagascar. In: Rakotosamimanana B, Rasamimanana H, Ganzhorn JU, Goodman SM, editors. *New directions in lemur studies*. New York: Kluwer Academic / Plenum Publishers. p 19-53.
- Godfrey LR, Razafimahzo JC, Schwartz M. 2002. Dental monorphism in a wild population of *Propithecus verreauxi* from Beza Mahafaly, Southwestern Madagascar. *American Journal of Physical Anthropology Supplement* 34:76.
- Gonzalez-Kirchner JP. 1995. The diet of sympatric prosimians in equatorial Guinea. *Folia Zoologica* 44:13-18.
- Gonzalez-Kirchner JP. 1996. Habitat preference of two lowland sympatric guenons on Bioko Island, Equatorial Guinea. *Folia Zoologica* 45:201-208.
- Gonzalez-Solis J, Guix JC, Mateos E, Llorens L. 2001. Population density of primates in a large fragment of the Brazilian Atlantic rainforest. *Biodiversity and Conservation* 10:1267-1282.

- Goodman SM, O'Connor S, Langrand O. 1993. A review of predation on lemurs: Implications for the evolution of social behavior in small, nocturnal primates. In: Kappeler PM, Ganzhorn JU, editors. Lemur social systems and their ecological basis. New York: Plenum Press. p 51-66.
- Goodman SM, Langrand O. 1996. A high mountain population of the ring-tailed lemur *Lemur catta* on the Andringitra Massif, Madagascar. *Oryx* 30:259-268.
- Goodman SM, Putnam MS. 1996. The birds of the eastern slope of the Réserve Naturelle Intégrale d'Andringitra, Madagascar. *Fieldiana: Zoology* 85:171-190.
- Goodman SM, Lewis BA. 1996. Description of the Réserve Naturelle Intégrale d'Andringitra, Madagascar. *Fieldiana: Zoology* 85:7-19.
- Goodman SM. 1996a. Description of the 1993 biological inventory of the Réserve Naturelle Intégrale d'Andringitra, Madagascar. *Fieldiana: Zoology* 85:1-6.
- Goodman SM. 1996b. The carnivores of the Réserve Naturelle Intégrale d'Andringitra, Madagascar. *Fieldiana: Zoology* 85:289-292.
- Goodman SM, Ganzhorn JU. 1997. Rarity of figs (*Ficus*) on Madagascar and its relationship to a depauperate frugivore community. *Review of Ecology* 52:321-329.
- Goodman SM, Ganzhorn JU, Wilmé L. 1997. Observations at a *Ficus* tree in Malagasy humid forest. *Biotropica* 29:480-488.
- Goodman SM, Rasolonandrasana BPN. 2001. Elevational zonation of birds, insectivores, rodents and primates on the slopes of the Andringitra Massif, Madagascar. *Journal of Natural History* 35:285-305.
- Gotoh S, O. T, Watanabe K, Hamada Y, Kawamoto Y, Watanabe T, Suryobroto B, Sajuthi D. 2001. Hematological values and parasite fauna in free-ranging *Macaca hecki* and the *M. hecki*/*M. tonkeana* hybrid group of Sulawesi Island, Indonesia. *Primates* 42:27-34.
- Grant PR. 1972. Convergent and divergent character displacement. *Biological Journal of the Linnean Society* 4:39-68.

- Grant BR, Grant PR. 1996. High survival of Darwin's finch hybrids: Effects of beak morphology and diets. *Ecology* 77:500-509.
- Grassi C. 2002. Sex differences in feeding, height, and space use in *Hapalemur griseus*. *International Journal of Primatology* 23:677-693.
- Greenfield LO. 1992. Relative canine size, behavior, and diet in male ceboids. *Journal of Human Evolution* 23:469-480.
- Grubb P. 1999. Evolutionary processes implicit in distribution patterns of modern African mammals. In: Bromage TG, Schrenk F, editors. *African biogeography, climate change, and human evolution*. New York: Oxford University Press. p 150-164.
- Guillotin M, Dubost G, Sabatier D. 1994. Food choice and food competition among the three major primate species of French Guiana. *Journal of Zoology (London)* 233:551-579.
- Hamilton AE, Buettner-Janusch J. 1977. Chromosomes of Lemuriformes, III. The genus *Lemur*: Karyotypes of species, subspecies and hybrids. *Annals of the New York Academy of Sciences* 239:125-159.
- Harcourt AH, Harvey PH, Larson SG, Short RV. 1981. Testis weight, body weight, and breeding system in primates. *Nature* 293:55-57.
- Harcourt C, Thornback J. 1990. *Lemurs of Madagascar and the Comoros*. The IUCN Red Data Book. Switzerland and Cambridge: IUCN, Gland.
- Harcourt AH. 1991. Sperm competition and the evolution of nonfertilizing sperm in mammals. *Evolution* 45:314-328.
- Harcourt AH, Gardiner J. 1994. Sexual selection and genital anatomy of male primates. *Proceedings of the Royal Society London [Biological Sciences]* 255:47-53.
- Harcourt AH. 1995. Sexual selection and sperm competition in primates: What are male genitalia good for? *Evolutionary Anthropology* 4:121-129.
- Harcourt AH, Purvis A, Liles L. 1995. Sperm competition: Mating system, not breeding season, affects testes size of primates. *Functional Ecology* 9:468-476.

- Harrington JE. 1975. Field observations of social behavior of *Lemur fulvus fulvus* E. Geoffroy 1812. In: Tattersall I, Sussman RW, editors. Lemur biology. New York: Plenum Press. p 259-279.
- Harrison RG. 1990. Hybrid zones: Windows on evolutionary process. In: Futuyma D, Antonovics J, editors. Oxford Surveys in Evolutionary Biology. Oxford: Oxford University Press. p 69-128.
- Harvey PH, Harcourt AH. 1984. Sperm competition, testes size, and breeding systems in primates. In: Smith RL, editor. Sperm competition and the evolution of animal mating systems. San Diego, CA: Academic Press. p 589-599.
- Hayes VJ, Feedman L, Oxnard CE. 1990. The taxonomy of savannah baboons: An odontomorphometric analysis. American Journal of Primatology 22:171-190.
- Hemingway CA, Overdorff DJ. 1999. Sampling effects on food availability estimates: Phenological method, sample size, and species composition. Biotropica 31:354-364.
- Hewitt GM. 1988. Hybrid zones - natural laboratories for evolutionary studies. Trends in Ecology and Evolution 3:158-167.
- Hilty SL. 1980. Flowering and fruiting periodicity in a premontane rainforest in Pacific Columbia. Biotropica 12:292-306.
- Houle A. 1997. The role of phylogeny and behavioral competition in the evolution of coexistence among primates. Canadian Journal of Zoology 75:827-846.
- Hutchinson GE. 1959. Homage to Santa Rosalia or why are there so many kinds of animals? American Naturalist 93.
- Irwin MT, Johnson SE, Wright PC. 2001. Lemur conservation In southeastern Madagascar: Population assessments using surveys, satellite Imagery and G.I.S. Society for Conservation Biology Annual Meeting.
- Isbell LA. 1983. Daily ranging behavior of red colobus (*Colobus badius tephrosceles*) in Kibale Forest, Uganda. Folia Primatologica 41:34-48.

- Isbell LA. 1991. Contest and scramble competition: Patterns of female aggression and ranging behavior among primates. *Behavioral Ecology* 2:143-155.
- Janson CH. 1988. Intra-specific food competition and primate social structure: A synthesis. *Behaviour* 105:1-17.
- Janson CH. 1992. Evolutionary ecology of primate social structure. In: Smith EA, Winterhalder B, editors. *Evolutionary ecology and human behavior*. New York: Aldine de Gruyter. p 95-130.
- Jiggins CD, Mallet J. 2000. Bimodal hybrid zones and speciation. *Trends in Ecology and Speciation* 15:250-255.
- Johnson SE, Overdorff DJ. 1999. A census of brown lemurs (*Eulemur fulvus* spp.) in southeastern Madagascar: methods-testing and conservation implications. *American Journal of Primatology* 47:51-60.
- Johnson SE, Wyner Y. 2000. Notes on the biogeography of *E. f. albocollaris*. *Lemur News* 5:25-28.
- Johnson SE, Overdorff DJ. 2002. Scarce season diet and keystone resources in three brown lemur (*Eulemur fulvus* spp.) populations. *American Journal of Primatology* 56:65-66.
- Jolly A. 1984. The puzzle of female feeding priority. In: Small M, editor. *Female primates: Studies by women primatologists*. New York: Alan R. Liss. p 197-215.
- Jolly A. 1986. Lemur survival. In: Benirschke K, editor. *Primates, the Road to Self-Sustaining Populations*. New York: Springer-Verlag. p 71-99.
- Jolly CJ, Rogers J, Phillips-Conroy JE. 1989. DNA polymorphisms in the Awash baboon hybrid zones. *American Journal of Physical Anthropology* 78:248.
- Jolly CJ. 1993. Species, subspecies, and baboon systematics. In: Kimbel WH, Martin LB, editors. *Species, species concepts, and primate evolution*. New York: Plenum Press. p 67-107.
- Jolly CJ, Woolley-Barker T, Beyene S, Disotell TR, Phillips-Conroy JE. 1997. Intergeneric hybrid baboons. *International Journal of Primatology* 18:597-627.

- Jolly CJ. 2001. A proper study for mankind: Analogies from the papionin monkeys and their implications for human evolution. *Yearbook of Physical Anthropology* 44:177-204.
- Julliot C. 1996. Seed dispersal by red howling monkeys (*Alouatta seniculus*) in the Tropical rain forest of French Guiana. *International Journal of Primatology* 17:239-258.
- Kappeler PM. 1990. The evolution of sexual size dimorphism in Prosimian primates. *American Journal of Primatology* 21:201-214.
- Kappeler PM. 1991. Patterns of sexual dimorphism in body weight among prosimian primates. *Folia Primatologica* 57:132-146.
- Kappeler PM. 1996. Intrasexual selection and phylogenetic constraints in the evolution of sexual canine dimorphism in strepsirhine primates. *Journal of Evolutionary Biology* 9:43-65.
- Kappeler PM. 1997. Intrasexual selection and testis size in strepsirhine primates. *Behavioral Ecology* 8:10-19.
- Kappeler PM. 2000. Causes and consequences of unusual sex ratios among lemurs. In: Kappeler PM, editor. *Primate males*. Cambridge: Cambridge University Press. p 55-63.
- Kavanagh M. 1981. Variable territoriality among tantalus monkeys in Cameroon. *Folia Primatologica* 36:76-98.
- Kay RF, Plavcan JM, Glander KE, Wright PC. 1988. Sexual selection and canine dimorphism in New World monkeys. *American Journal of Physical Anthropology* 77:385-397.
- Kay RF, Madden RH, van Schaik C, Higdon D. 1997. Primate species richness is determined by plant productivity: Implications for conservation. *Proceedings of the National Academy of Sciences* 94:13023–13027.
- Krebs JR, Davies NB. 1993. *Behavioural ecology*. Oxford: Blackwell.
- Lack D. 1947. *Darwin's finches: An essay on the general biological theory of evolution*. Cambridge: Cambridge University Press.

- Lambert JE, Garber PA. 1998. Evolutionary and ecological implications of primate seed dispersal. *American Journal of Primatology* 45:9–28.
- Lande R. 1980. Sexual dimorphism, sexual selection, and adaptation in polygenic characters. *Evolution* 33:292-305.
- Lawes MJ. 1992. Estimates of population-density and correlates of the status of the Samango monkey *Cercopithecus mitis* in Natal, South Africa. *Biological Conservation* 60:197-210.
- Lawes MJ, Henzi SP. 1995. Inter-group encounters in blue monkeys: How territorial must a territorial species be? *Animal Behaviour* 49:240-243.
- Lehman SM, Wright PC. 2000. Preliminary study of the conservation status of lemur communities Betsakafandrika region of eastern Madagascar. *Lemur News* 5:23-25.
- Leigh SR. 1995. Socioecology and the ontogeny of sexual size dimorphism in anthropoid primates. *American Journal of Physical Anthropology* 97:339-356.
- Leigh SR, Terranova CJ. 1998. Comparative perspectives in bimaturism, ontogeny, and dimorphism in lemurid primates. *International Journal of Primatology* 19:723-750.
- Leighton M, Leighton DR. 1983. Vertebrate responses to fruiting seasonality within a Bornean rain forest. In: Sutton SL, Whitmore TC, Chadwick AC, editors. *Tropical rainforest: Ecology and management*. Oxford: Blackwell press. p 181-196.
- Leutenegger W, Kelly JT. 1977. Relationship of sexual dimorphism in canine size and body size to social, behavioral and ecological correlates in anthropoid primates. *Primates* 18:117-136.
- Leutenegger W, Cheverud JM. 1982. Correlates of sexual dimorphism in primates: Ecological and size variables. *International Journal of Primatology* 3:387-402.
- Lewis BA, Phillipson PB, Andrianarisata M, Rahajaso G, Rakotomalaza PJ, Randriambololona M, McDonagh JF. 1996. A study of the botanical structure, composition, and diversity of the eastern slopes of the Réserve Intégrale d'Andringitra, Madagascar. *Fieldiana: Zoology* 85:24-82.

- Lindenfors P, Tullberg BS. 1998. Phylogenetic analysis of primate size evolution: The consequences of sexual selection. *Biological Journal of the Linnean Society* 64:413-447.
- MacArthur RH, Levins R. 1964. Competition, habitat selection, and character displacement in a patchy environment. *Proceedings of the National Academy of Sciences* 51:1207-1210.
- Martin RD, Willner LA, Dettling A. 1994. The evolution of sexual size dimorphism in primates. In: Short RV, Balaban E, editors. *The differences between the sexes*. Cambridge: Cambridge University Press. p 159-200.
- Mayr E. 1963. *Animal species and evolution*. Cambridge: Harvard University Press.
- McConkey KR, Aldy F, Ario A, Chivers DJ. 2002. Selection of fruit by gibbons (*Hylobates muelleri* x *agilis*) in the rain forests of central Borneo. *International Journal of Primatology* 23:23-145.
- Melo FR. 1999. Atlantic forest marmosets - species and hybrids. *Neotropical Primates* 7:58-59.
- Mendes SL. 1997. Hybridization in free-ranging *Callithrix flaviceps* and the taxonomy of the Atlantic forest marmosets. *Neotropical Primates* 5:6-8.
- Merenlender AM. 1993. The effects of sociality on the demography and genetic structure of *Lemur fulvus rufus* (polygamous) and *Lemur rubriventer* (monogamous) and the conservation implications. Ph.D. dissertation, University of Rochester, Rochester, NY.
- Meyers DM, Rabarivola C, Rumpler Y. 1989. Distribution and conservation of Sclater's lemur: Implications of a morphological cline. *Primate Conservation* 10:77-81.
- Milton K, May ML. 1976. Body weight, diet and home range area in primates. *Nature* 259:459-462.
- Milton K. 1985. Multimale mating and absence of canine tooth dimorphism in wooly spider monkeys (*Brachyteles arachnoides*). *American Journal of Physical Anthropology* 68:519-523.

- Mitani JC, Rodman PS. 1979. Territoriality: The relation of ranging patterns and home range size to defendability, with an analysis of territoriality among primate species. *Behavioral Ecology and Sociobiology* 5:241-251.
- Mitani JC, Gros-Louis J, Richards AF. 1996. Sexual dimorphism, the operational sex ratio, and the intensity of male competition in polygynous primates. *American Naturalist* 147:966-980.
- Mittermeier RA, van Roosmalen MGM. 1981. Preliminary observations on habitat utilization and diet in eight Surinam monkeys. *Folia Primatologica* 36:1-39.
- Mittermeier RA, Konstant WR, Nicoll ME, Langrand O. 1992. Lemurs of Madagascar: An action plan for their survival 1993-1999. Gland, Switzerland: IUCN Species Survival Commission.
- Mittermeier RA, Tattersall I, Konstant WR, Meyers DM, Mast RB. 1994. Lemurs of Madagascar. Washington, DC: Conservation International.
- Morell V. 1999. Ecology returns to speciation studies. *Science* 284:2106-2108.
- Morland HS. 1991. Social organization and ecology of the black and white ruffed lemurs (*Varecia variegata*) in lowland rain forest, Nosy Mangabe, Madagascar. Ph.D. dissertation, Yale University, New Haven, CT.
- Møller AP. 1988. Ejaculate quality, testes size and sperm competition in primates. *Journal of Human Evolution* 17:479-488.
- Müller P, Velo A, Raheliarisoa EO, Zaramody A, Curtis DJ. 2000. Surveys of sympatric lemurs at Anjamena, north-west Madagascar. *African Journal of Ecology* 38:248-257.
- Myers DM, Wright PC. 1993. Resource tracking: Food availability and *Propithecus* seasonal reproduction. In: Kappeler PM, Ganzhorn JU, editors. *Lemur social systems and their ecological basis*. New York: Plenum Press. p 179-192.
- Nagel U. 1973. A comparison of anubis baboons, hamadryas baboons and their hybrids at a species border in Ethiopia. *Folia Primatologica* 19:104-165.
- Nagel L, Schluter D. 1998. Body size, natural selection, and speciation in sticklebacks. *Evolution* 52:210-218.

- Nagy ES. 1997. Frequency-dependent seed production and hybridization rates: Implications for gene flow between locally adapted plant populations. *Evolution* 51:703-714.
- Newstrom LE, Frankie GW, Baker HG. 1994. A new classification for plant phenology based on flowering patterns in lowland tropical rain forest trees at La Selva, Costa Rica. *Biotropica* 26:141-159.
- Norconk MA, Kinzey WG. 1994. Challenge of neotropical frugivory: Travel patterns of spider monkeys and bearded sakis. *American Journal of Primatology* 34:171-183.
- Oates JF, Whitesides GH, Davies AG, Waterman PG, Green SM, Davsilva GL, Mole S. 1990. Determinants of variation in tropical forest primate biomass: New evidence from West Africa. *Ecology* 71:328-343.
- Oates JF. 1996. Habitat alteration, hunting and the conservation of folivorous primates in African forests. *Australian Journal of Ecology* 21:1-9.
- Orr MR, Smith TB. 1998. Ecology and speciation. *Trends in Ecology and Evolution* 13:502-506.
- Ostner J, Kappeler PM. 1999. Central males instead of multiple pairs of redfronted lemurs, *Eulemur fulvus rufus* (Primates, Lemnridae)? *Animal Behaviour* 58:1069-1078.
- Ostro LET, Silver SC, Koontz FW, Horwich RH, Brockett R. 2001. Shifts in social structure of black howler (*Alouatta pigra*) groups associated with natural and experimental variation in population density. *International Journal of Primatology* 22:733-748.
- Overdorff DJ. 1991. Ecological correlates to social structure in two prosimian primates: *Eulemur fulvus rufus* and *Eulemur rubriventer* in Madagascar. Ph.D. dissertation, Duke University, Durham, NC.
- Overdorff DJ. 1993. Similarities, differences, and seasonal patterns in the diets of *Eulemur rubriventer* and *Eulemur fulvus rufus* in the Ranomafana National Park, Madagascar. *International Journal of Primatology* 14:721-753.
- Overdorff DJ, Rasmussen MA. 1995. Determinants of nighttime activity in "diurnal" lemurid primates. In: Alterman L, Doyle GA, Izard MK,

- editors. *Creatures of the dark: The nocturnal prosimians*. New York: Plenum Press. p 61-74.
- Overdorff DJ. 1996a. Ecological correlates to activity and habitat use of two prosimian primates: *Eulemur rubriventer* and *Eulemur fulvus rufus* in Madagascar. *American Journal of Primatology* 40:327-342.
- Overdorff DJ. 1996b. Ecological correlates to social structure in two lemur species in Madagascar. *American Journal of Physical Anthropology* 100:487-506.
- Overdorff DJ. 1998. Are *Eulemur* species pair-bonded? Social organization and mating strategies in *Eulemur fulvus rufus* from 1988-1995 in southeast Madagascar. *American Journal of Physical Anthropology* 105:153-166.
- Overdorff DJ, Strait SG. 1998. Seed handling by three prosimian primates in southeastern Madagascar: Implications for seed dispersal. *American Journal of Primatology* 45:69-82.
- Overdorff DJ, Merenlender AM, Talata P, Telo A, Forward ZA. 1999. Life history of *Eulemur fulvus rufus* from 1988-1998 in southeastern Madagascar. *American Journal of Physical Anthropology* 108:295-310.
- Overdorff DJ, Johnson SE. in press. *Eulemur*. In: Goodman SM, Benstead J, editors. *The Natural History of Madagascar*. Chicago: University of Chicago Press.
- Oxnard CE. 1987. *Fossils, teeth and sex: New perspectives on human evolution*. Seattle: University of Washington Press.
- Passamani M, Aguiar LMS, Machado RB, Figueiredo E. 1997. Hybridization between *Callithrix geoffroyi* and *C. penicillata* in southeastern Minas Gerais, Brazil. *Neotropical Primates* 5:9-10.
- Pastorini J, Forstner MRJ, Martin RD. 2000. Relationships among brown lemurs (*Eulemur fulvus*) based on mitochondrial DNA sequences. *Molecular Phylogenetics and Evolution* 16:418-429.
- Pastorini J, Zaramody A, Curtis DJ, Martin RD, Forstner MRJ. 2001. Sympatric hybridisation between *Eulemur fulvus* and *E. mongoz*. *Folia Primatologica* 72:176.

- Paterson HEH. 1985. The recognition concept of species. In: Vrba ES, editor. Species and speciation. Pretoria: Transvaal Museum. p 21-29.
- Pereira ME, Kaufman R, Kappeler PM, Overdorff DJ. 1990. Female dominance does not characterize all of the Lemuridae. *Folia Primatologica* 55:96-103.
- Pereira ME, Kappeler PM. 1997. Divergent systems of agonistic behaviour in lemurid primates. *Behaviour* 134:225-274.
- Peres CA. 1997. Primate community structure at twenty western Amazonian flooded and unflooded forests. *Journal of Tropical Ecology* 13:381-405.
- Peres CA, Dolman PM. 2000. Density compensation in neotropical primate communities: evidence from 56 hunted and nonhunted Amazonian forests of varying productivity. *Oecologia* 122:175-189.
- Phillips KA, Elvey CR, Abercrombie CL. 1998. Applying GPS to the study of primate ecology: A useful tool? *American Journal of Primatology* 46:167-172.
- Phillips-Conroy JE, Jolly CJ. 1986. Changes in the structure of the baboon hybrid zone in the Awash National Park, Ethiopia. *American Journal of Physical Anthropology* 71:337-350.
- Phillips-Conroy JE, Jolly CJ, Brett FL. 1991. Characteristics of hamadryas-like male baboons living in anubis baboon troops in the Awash hybrid zone, Ethiopia. *American Journal of Physical Anthropology* 86:353-368.
- Phillips-Conroy JE, Jolly CJ, Nystrom P, Hemmalin HA. 1992. Migration of male hamadryas baboons into anubis groups in the Awash National Park, Ethiopia. *International Journal of Primatology* 13:455-476.
- Pianka ER. 1994. *Evolutionary ecology*. New York: HarperCollins College Publishers.
- Pinto LPS, Costa CMR, Strier KB, Dafonseca GAB. 1993. Habitat, density and group-size of primates in a Brazilian tropical forest. *Folia Primatologica* 61:135-143.
- Plavcan JM, van Schaik CP. 1992. Intrasexual competition and canine dimorphism in anthropoid primates. *American Journal of Physical Anthropology* 87:461-477.

- Plavcan JM, van Schaik CP. 1994. Canine dimorphism. *Evolutionary Anthropology* 2:208-214.
- Plavcan JM, van Schaik CP, Kappeler PM. 1995. Competition, coalitions and canine size in primates. *Journal of Human Evolution* 28:245-276.
- Plavcan JM, Kelley J. 1996. Evaluating the "dual selection" hypothesis of canine reduction. *American Journal of Physical Anthropology* 99:379-387.
- Plavcan JM, van Schaik CP. 1997. Intrasexual competition and body weight dimorphism in anthropoid primates. *American Journal of Physical Anthropology* 103:37-68.
- Plavcan JM. 1999. Mating systems, intrasexual competition and sexual dimorphism in primates. In: Lee PC, editor. *Comparative primate socioecology*. Cambridge: Cambridge University Press. p 241-269.
- Plavcan JM. 2001. Sexual dimorphism in primate evolution. *Yearbook of Physical Anthropology* 44:25-53.
- Plumptre AJ. 2000. Monitoring mammal populations with line transect techniques in African forests. *Journal of Applied Ecology* 37:356-368.
- Pochran ST, Wright PC. 2002. Dynamics of testes size compensates for variation in male body size. *Evolutionary Ecology Research* 4:577-585.
- Pochran ST, Wright PC, Schaentzler E, Ippolito M, Rakotonirina G, Ratsimbazafy R, Rakotosoa R. 2002. Effect of season and age on the gonadosomatic index of Milne-Edward's sifakas (*Propithecus diadema edwardsi*) in Ranomafana National Park, Madagascar. *International Journal of Primatology* 23:355-364.
- Pontes ARM. 1999. Environmental determinants of primate abundance in Maraca Island, Roraima, Brazilian Amazonia. *Journal of Zoology* 247:189-199.
- Porter LM. 2001. Dietary differences among sympatric Callithrichinae in northern Bolivia: *Callimico goeldii*, *Saguinus fuscicollis* and *S. labiatus*. *International Journal of Primatology* 22:961-992.
- Powzyk JA. 1997. The socio-ecology of two sympatric indriids: *Propithecus diadema diadema* and *Indri indri*, a comparison of feeding strategies and

their possible repercussions on species-specific behaviors. Ph.D. dissertation, Duke University, Durham, NC.

Rabarivola C, Meyers DM, Rumpler Y. 1991. Distribution and morphological characters of intermediate forms between the black lemur (*Eulemur macaco macaco*) and the Sclater's lemur (*E. m. flavifrons*). *Primates* 32:269-273.

Raemakers J. 1979. Ecology of sympatric gibbons. *Folia Primatologica* 31:227-245.

Rasmussen MA. 1999. Ecological influences on activity cycle in two cathemeral primates, the mongoose lemur (*Eulemur mongoz*) and the common brown lemur (*Eulemur fulvus fulvus*). Ph.D. dissertation, Duke University, Durham, NC.

Rathcke B, Lacey EP. 1985. Phenological patterns of terrestrial plants. *Annual Review of Ecology and Systematics* 16:179-214.

Reed KE, Fleagle JG. 1995. Geographic and climatic control of primate diversity. *Proceedings of the National Academy of Sciences* 92:7874-7876.

Reiseberg L, Wendel JF. 1993. Introgression and its consequences in plants. In: Harrison RG, editor. *Hybrid zones and the evolutionary process*. New York: Oxford University Press. p 70-109.

Richard AF, Nicoll ME. 1987. Female social dominance and basal metabolism in a Malagasy primate, *Propithecus verreauxi*. *American Journal of Primatology* 12:309-314.

Richard AF, Dewar RE. 1991. Lemur ecology. *Annual Review of Ecology and Systematics* 22:145-175.

Richard AF. 1992. Aggressive competition between males, female-controlled polygyny and sexual monomorphism in a Malagasy primate, *Propithecus verreauxi*. *Journal of Human Evolution* 22:395-406.

Rodman PS. 1973. Synecology of Bornean primates I. A test for interspecific interactions in spatial distribution of five species. *American Journal of Physical Anthropology* 38:655-660.

- Rodrigues de Moraes PL, de Carvalho O, Strier KB. 1998. Population variation in patch and party size in muriquis (*Brachyteles arachnoides*). *International Journal of Primatology* 19:325-337.
- Rosenbaum B, O'Brien TG, Kinnaird M, Supriatna J. 1998. Population densities of Sulawesi crested black macaques (*Macaca nigra*) on Bacan and Sulawesi, Indonesia: Effects of habitat disturbance and hunting. *American Journal of Primatology* 44:89-106.
- Rossan RN, Baerg DC. 1977. Laboratory and feral hybridization of *Ateles geoffroyi panamensis* Kellogg and Goldman 1944 and *A. fusciceps robustus* Allen 1914 in Panama. *Primates* 18:235-237.
- Roughgarden J. 1983. Competition and theory in community ecology. *American Naturalist* 122:583-601.
- Rowell TE, Chism J. 1986. Sexual dimorphism and mating systems: Jumping to conclusions. In: Pickford M, Chiarelli B, editors. *Sexual dimorphism in living and fossil primates*. Florence: Il Sedicesimo. p 107-111.
- Rowell TE, Mitchell BJ. 1991. Comparison of seed dispersal of guenons in Kenya and capuchins in Panama. *Journal of Tropical Ecology* 7:269-274.
- Rumpler Y. 1975. The significance of chromosomal studies in the systematics of the Malagasy lemurs. In: Tattersall I, Sussman RW, editors. *Lemur biology*. New York: Plenum Press. p 25-40.
- Rumpler Y. 2000. What cytogenetic studies may tell us about species diversity and speciation of lemurs. *International Journal of Primatology* 21:865-881.
- Rundle HD. 2002. A test of ecologically dependent postmating isolation between sympatric sticklebacks. *Evolution* 56:322-329.
- Samuels A, Altmann J. 1986. Immigration of a *Papio anubis* male into a group of cynocephalus baboons and evidence for an anubis-cynocephalus hybrid zone in Amboseli, Kenya. *International Journal of Primatology* 7:131-138.
- Samuels A, Altmann J. 1991. Baboons of the Amboseli Basin: Demographic stability and change. *International Journal of Primatology* 12:1-19.

- Sanderson N. 1989. Can gene flow prevent reinforcement? *Evolution* 43:1223-1235.
- Sauther ML. 1991. Reproductive behavior of free-ranging *Lemur catta* at Beza Mahafaly Special Reserve, Madagascar. *American Journal of Physical Anthropology* 84:463-477.
- Sauther ML. 1993. Resource competition in wild populations of ringtailed lemurs (*Lemur catta*): Implications for female dominance. In: Kappeler P, Ganzhorn JU, editors. *Lemur social systems and their ecological basis*. New York: Plenum Press. p 135-152.
- Sætre G-P, Moum T, Bures S, Král M, Adamjan M, Moreno J. 1997. A sexually selected character displacement in flycatchers reinforces premating isolation. *Nature* 387:589-592.
- van Schaik CP, van Hooff JARAM. 1983. On the ultimate causes of primate social systems. *Behaviour* 85:91-116.
- van Schaik CP, van Noordwijk MA, de Boer RJ, den Tonkelaar I. 1983. The effect of group size on time budgets and social behaviour in wild long-tailed macaques (*Macaca fascicularis*). *Behavioral Ecology and Sociobiology* 13:173-181.
- van Schaik CP. 1983. Why are diurnal primates living in groups? *Behaviour* 87:120-143.
- van Schaik CP. 1986. Phenological changes in a Sumatran rain forest. *Journal of Tropical Ecology* 2:327-347.
- van Schaik CP, Kappeler PM. 1993. Life history, activity period, and lemur social systems. In: Kappeler PM, Ganzhorn JU, editors. *Lemur social systems and their ecological basis*. New York: Plenum. p 241-260.
- van Schaik CP, Terborgh JW, Wright SJ. 1993. The phenology of tropical forests: Adaptive significance and consequences for primary consumers. *Annual Review of Ecology and Systematics* 24:353-377.
- van Schaik CP, Kappeler PM. 1996. The social systems of gregarious lemurs: Lack of convergence with anthropoids due to evolutionary disequilibrium? *Ethology* 102:915-941.

- Schluter D. 2001. Ecology and the origin of species. *Trends in Ecology and Evolution* 18:372-380.
- Schoener TW. 1974. Research partitioning in ecological communities. *Science* 185:27-39.
- Schoener TW. 1983. Field experiments on interspecific competition. *American Naturalist* 122:240-285.
- Schoener TW. 1989. The ecological niche. In: Cherrett JM, editor. *Ecological concepts. The contribution of ecology to an understanding of the natural world*. Oxford: Blackwell Scientific Publications. p 467-479.
- Short RV. 1979. Sexual selection and its component parts, somatic and genital selection, as illustrated by man and the great apes. *Advances in the Study of Behavior* 9:131-158.
- Shotake T. 1982. Population genetical study of natural hybridization between *Papio anubis* and *Papio hamadryas*. *Primates* 23:285-308.
- Smythe N. 1970. Relationships between fruiting seasons and seed dispersal methods in a Neotropical forest. *American Naturalist* 104:25-35.
- Sokal RR, Rohlf FJ. 1995. *Biometry: The principles and practice of statistics in biological research*. New York: W. H. Freeman and Company.
- Sterling EJ, Ramarason MG. 1996. Rapid assessment of the primate fauna of the eastern slope of the Réserve Naturelle Intégrale d'Andringitra, Madagascar. *Fieldiana: Zoology* 85:293-305.
- Stoner KE. 1996. Habitat selection and seasonal patterns of activity and foraging of mantled howling monkeys (*Alouatta palliata*) in northeastern Costa Rica. *International Journal of Primatology* 17:1-30.
- Strier KB. 2000. Population viabilities and conservation implications for muriquis (*Brachyteles arachnoides*) in Brazil's Atlantic Forest. *Biotropica* 32:903-913.
- Strong DR, Szyska LA, Simberloff DS. 1979. Tests of community-wide character displacement against null hypotheses. *Evolution* 33:897-913.

- Strong DR. 1983. Natural variability and the manifold mechanisms of ecological communities. *American Naturalist* 122:636-660.
- Struhsaker TT. 1974. Correlates of ranging behavior in a group of red colobus monkeys (*Colobus badius tephrosceles*). *American Zoologist* 14:177-184.
- Struhsaker TT, Oates JF. 1975. Comparison of the behavior and ecology of red colobus and black-and-white colobus monkeys in Uganda: A summary. In: Tuttle RH, editor. *Socioecology and psychology of primates*. The Hague: Mouton. p 103-124.
- Struhsaker TT. 1981. Census methods for estimating densities. In: Subcommittee on Conservation of Natural Populations, editor. *Techniques for the study of primate population ecology*: National Academy Press. p 36-80.
- Struhsaker TT, Butynski TM, Lwanga JS. 1988. Hybridization between redbellied (*Cercopithecus ascanius schmidt*) and blue (*C. mitis stuhlmanni*) monkeys in the Kibale Forest, Uganda. In: Gautier-Hion A, Bourlière F, J-P G, editors. *A primate radiation: Evolutionary biology of the African guenons*. Cambridge: Cambridge University Press. p 477-497.
- Sugawara K. 1979. Sociological study of a wild group of hybrid baboons between *Papio anubis* and *Papio hamadryas* in the Awash Valley, Ethiopia. *Primates* 20:21-56.
- Sussman RW. 1974. Ecological distinctions in sympatric species of *Lemur*. In: Martin RD, Doyle GA, Walker AC, editors. *Prosimian biology*. Pittsburgh: University of Pittsburgh Press. p 74-108.
- Sussman RW. 1977. Feeding behavior of *Lemur catta* and *Lemur fulvus*. In: Clutton-Brock TH, editor. *Primate ecology*. London: Academic Press. p 1-36.
- Sussman RW, Raven PH. 1978. Pollination by lemurs and marsupials: an archaic coevolutionary system. *Science* 200:731-736.
- Sussman RW. 1991. Demography and social organization of free-ranging *Lemur catta* in the Beza Mahafaly Reserve, Madagascar. *American Journal of Physical Anthropology* 84:43-58.
- Sussman RW. 1992. Male life history and intergroup mobility among ringtailed lemurs (*Lemur catta*). *International Journal of Primatology* 13:395-413.

- Sussman RW, Rakotozafy A. 1994. Plant diversity and structural analysis of a tropical dry forest in southwestern Madagascar. *Biotropica* 26:241-254.
- Sussman RW, Phillips-Conroy JE. 1995. A survey of the distribution and density of primates of Guyana. *International Journal of Primatology* 16:761-791.
- Symington MM. 1988. Food competition and foraging party size in the black spider monkey (*Ateles paniscus chamek*). *Behaviour* 105:117-134.
- Szmulewicz MN, Andino LM, Reategui EP, Woolley-Barker T, Jolly CJ, Disotell TR, Herrera RJ. 1999. An *Alu* insertion polymorphism in a baboon hybrid zone. *American Journal of Physical Anthropology* 109:1-8.
- Tan CL. 1999. Group composition, home range size, and diet of three sympatric bamboo lemur species (genus *Hapalemur*) in Ranomafana National Park, Madagascar. *International Journal of Primatology* 20:547-566.
- Tan CL. 2000. Behavior and ecology of three sympatric bamboo lemur species (genus *Hapalemur*) in Ranomafana National Park, Madagascar. Ph.D. dissertation, State University of New York at Stony Brook, Stony Brook, NY.
- Tattersall I. 1977. Ecology and behavior of *Lemur fulvus mayottensis* (Primates, Lemuriformes). *Anthropological Papers of the American Museum of Natural History* 54:421-482.
- Tattersall I. 1982. *The primates of Madagascar*. New York: Columbia University Press.
- Tattersall I. 1993. Speciation and morphological differentiation in the genus *Lemur*. In: Kimbel WH, Martin LB, editors. *Species, species concepts, and primate evolution*. New York: Plenum Press. p 163-176.
- Tattersall I, Sussman RW. 1998. 'Little brown lemurs' of northern Madagascar. *Folia Primatologica* 69 (suppl. 1):379-388.
- Templeton AR. 1989. The meaning of species and speciation. In: Otte D, Endler JA, editors. *Speciation and its consequences*. Sunderland, Mass: Sinauer Associates, Inc. p 3-27.
- Terborgh J. 1983. *Five New World Primates*. Princeton: Princeton University Press.

- Terborgh J, Janson CH. 1986. Socioecology of primate groups. *Annual Review of Ecology and Systematics* 17:111-135.
- Terborgh J. 1986a. Community aspects of frugivory in tropical forests. In: Estrada A, Fleming TH, editors. *Frugivores and seed dispersal*. Dordrecht: Dr. W. Junk Publishers. p 371-384.
- Terborgh J. 1986b. Keystone plant resources in the tropical forest. In: Soule M, editor. *Conservation Biology: The Science of Scarcity and Diversity*. Sunderland: Sinauer Associate Press. p 330-344.
- Tomblin DC, Cranford JA. 1994. Ecological niche differences between *Alouatta palliata* and *Cebus capucinus* comparing feeding modes, branch use, and diet. *Primates* 35:265-274.
- Torres de Caballero OM, Ramirez C, Yunis E. 1976. Genus *Cebus* Q- and G-band karyotypes and natural hybrids. *Folia Primatologica* 26:310-321.
- Tosi AJ, Morales JC, Melnick DJ. 2002. Y-chromosome and mitochondrial markers in *Macaca fascicularis* indicate introgression with Indochinese *M. mulatta* and a biogeographic barrier in the Isthmus of Kra. *International Journal of Primatology* 23:161-178.
- Turk D. 1995. A guide to the trees of Ranomafana National Park and central eastern Madagascar: USAID.
- Tutin CEG, Williamson EA, Rodgers ME, Fernandez M. 1991. A case study of a plant-animal relationship: *Colia lizae* and lowland gorillas in the Lopes Reserve, Gabon. *Journal of Tropical Ecology* 7:181-199.
- Tutin CEG, Fernandez M. 1993. Relationships between minimum temperature and fruit production in some tropical forest trees in Gabon. *Journal of Tropical Ecology* 9:241-248.
- Tutin CEG, Ham RM, White LJT, Harrison MJS. 1997. The primate community of the Lope Reserve, Gabon: Diets, responses to fruit scarcity, and effects on biomass. *American Journal of Primatology* 42:1-24.
- Vasey N. 1997. Community ecology and behavior of *Varecia variegata rubra* and *Lemur fulvus albifrons*, on the Masoala Peninsula, Madagascar. Ph.D. dissertation, Washington University, St. Louis, MO.

- Vasey N. 2000. Niche separation in *Varecia variegata rubra* and *Eulemur fulvus albifrons*: I. Interspecific Patterns. *American Journal of Physical Anthropology* 112:411-432.
- Vasey N. 2002. Niche separation in *Varecia variegata rubra* and *Eulemur fulvus albifrons*: II. Intraspecific patterns. *American Journal of Physical Anthropology* 118:169-183.
- Vogler AP, DeSalle R. 1994. Diagnosing units of conservation management. *Conservation Biology* 8:354-363.
- Wallace RB, Painter RLE, Taber AB. 1998. Primate diversity, habitat preferences, and population density estimates in Noel Kempff Mercado National Park Santa Cruz Department, Bolivia. *American Journal of Primatology* 46:197-211.
- Waser PM. 1987. Interactions among primate species. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT, editors. *Primate societies*. Chicago: University of Chicago Press. p 210-226.
- White F. 1983. *The vegetation of Africa*. Paris: UNESCO.
- White FJ. 1991. Social organization, feeding ecology, and reproductive strategy of ruffed lemurs, *Varecia variegata*. In: Ehara A, Kimura T, Takenaka O, Iwamoto M, editors. *Primate Today*. Amsterdam: Elsevier Science Publishers. p 81-84.
- White LJT. 1994. Patterns of fruit-fall phenology in the Lopé Reserve, Gabon. *Journal of Tropical Ecology* 10:289-312.
- White FJ, Overdorff DJ, Balko EA, Wright PC. 1995. Ecological determinants of the distribution of *Varecia variegata* in Ranomafana National Park, Madagascar. *Folia Primatologica* 64:124-131.
- Whitesides GH, Oates JF, Green SM, Kluberanz RP. 1988. Estimating primate densities from transects in a West African rain forest: A comparison of techniques. *Journal of Animal Ecology* 57:345-367.
- Wiens JA. 1977. On competition and variable environments. *American Scientist* 65:590-597.

- Wiens JA. 1983. Avian community ecology: An iconoclastic view. In: Brush AH, Clark GA, editors. Perspectives in Ornithology. Cambridge: Cambridge University Press. p 355-403.
- Woolley-Barker T. 1999. Social organization and genetic structure in a baboon hybrid zone. Ph.D. dissertation, New York University, New York, NY.
- Wrangham RW, Chapman CA, Chapman LJ. 1994. Seed dispersal by forest chimpanzees in Uganda. *Journal of Tropical Ecology* 2:355-368.
- Wright PC. 1989. The nocturnal primate niche in the New World. *Journal of Human Evolution* 18:635-658.
- Wright PC, Randrimanantena M. 1989. Comparative ecology of three sympatric bamboo lemurs in Madagascar. *American Journal of Physical Anthropology* 78:327.
- Wright PC. 1995. Demography and life history of free-ranging *Propithecus diadema edwardsi* in Ranomafana National Park, Madagascar. *International Journal of Primatology* 16:835-854.
- Wright PC. 1998. Impact of predation risk on the behaviour of *Propithecus diadema edwardsi* in the rain forest of Madagascar. *Behaviour* 135:483-512.
- Wright PC. 1999. Lemur traits and Madagascar ecology: Coping with an island environment. *Yearbook of Physical Anthropology* 42:31-72.
- Wyner Y, Absher R, Amato G, Sterling E, Stumpf R, Rumpler Y, DeSalle R. 1999. Species concepts and the determination of historic gene flow patterns in the *Eulemur fulvus* (brown lemur) complex. *Biological Journal of the Linnean Society* 65:39-56.
- Wyner YM. 2000. Species boundaries and conservation units in two species in the family Lemnidae. Ph.D. dissertation, New York University, New York, NY.
- Wyner YM, Johnson SE, Stumpf RM, DeSalle R. 2002. Genetic assessment of a white-collared X red-fronted lemur hybrid zone at Andringitra, Madagascar. *American Journal of Primatology* 57:51-66.

Vita

Steig Eric Johnson was born July 12, 1968 in Sacramento, California. His parents are Nancy Lange and William Johnson. After graduating from Tamalpais High School in Mill Valley, California, he attended the University of California at Berkeley, receiving a B.A. in Anthropology in 1990. He enrolled at the University of Texas at Austin in 1993 and received an M.A. in Anthropology in 1995. He held teaching assistantships for two and a half years and received three University Fellowships at the University of Texas. He has published articles in *American Journal of Physical Anthropology* (105:333-354), *American Journal of Primatology* (57:51-66, 47:51-60), *Lemur News* (5:25-28), and *Laboratory Primate Newsletter* (31:18), and has contributed papers to annual meetings of the American Association of Physical Anthropology, the American Primatological Society, and the Society for Conservation Biology.

Permanent address: 273 Cypress Dr., Fairfax, California 94930

This dissertation was typed by the author.