Diet and Behavior of Adult *Propithecus verreauxi* in Southern Madagascar During the Birth Season

By

Katherine Markham
BSc, The George Washington University, 2011

A Thesis Submitted in Partial Fulfillment of the Requirements for the Degree of

MASTER OF ARTS

In the Department of Anthropology

Supervisory Committee

Diet and Behavior of Adult *Propithecus verreauxi* in Southern Madagascar During the Birth Season

By

Katherine Markham
BSc, The George Washington University, 2011

Supervisory Committee

Dr. Lisa Gould, (Department of Anthropology)
Supervisor

Dr. Helen Kurki, (Department of Anthropology)
Departmental Member

ABSTRACT

Supervisory Committee
Dr. Lisa Gould, (Department of Anthropology)
Supervisor
Dr. Helen Kurki, (Department of Anthropology)
Departmental Member

The environment in which *Propithecus verreauxi* (common name: Verreaux's sifaka) is found is highly seasonal, arid and frequently undergoes periods of drought. *P. verreauxi* compounds these challenges by giving birth during the dry season when resources are scarce. Considering lactation is the most energetically expensive reproductive stage, understanding how *P. verreauxi* females meet energetic requirements during periods of low resource availability is important. This study examines the behavior and diet of adult male and lactating female *P. verreauxi* to identify intersex differences. Continuous focal observations were completed at Berenty Private Reserve, Madagascar, over six weeks early in the birth season. The number of bites an individual consumed of an item was recorded along with the plant part and species. Intersex differences were largely nonexistent. Males and females did not differ significantly in regards to intake rate, the amount of total food consumed, and water intake. Females devoted a greater portion of time to feeding than did males but both sexes allocated similar amounts of time to resting. There were also no essential differences in amount of feeding time allocated to specific plant species and food types. Findings may suggest that *P. verreauxi* is a capital breeder, storing energy year-round.

Table of Contents

SUPERVISORY COMMITTEE ii

ABSTRACT iii

LIST OF TABLES vi

LIST OF FIGURES vii

ACKNOWLEDGEMENTS viii

CHAPTER ONE: INTRODUCTION 1

1.0 PRIMATE DIETARY ECOLOGY 1
1.1 OVERVIEW OF SEX-BASED FEEDING DIFFERENCES IN PRIMATES 2
1.2 BACKGROUND 6
I. ISLAND HISTORY 6
II. ISLAND GEOGRAPHY AND GENERAL ECOLOGY 7
III. GENERAL SPECIES INFORMATION AND DISTRIBUTION 7
1.3 ECOLOGY 12
I. HABITAT 12
II. DIET 13
1.4 BEHAVIOR 17
I. SOCIAL STRUCTURE 17
II. FEMALE DOMINANCE 18
1.5 LIFE HISTORY 20
1.6 THE LEMUR SYNDROME AND REPRODUCTION 22
I. REPRODUCTION 24
1.6 SIGNIFICANCE OF STUDY 27

CHAPTER TWO: HYPOTHESES 29

CHAPTER THREE: MATERIALS AND METHODS 31

3.0 STUDY SITE 31
3.1 STUDY POPULATIONS 35
I. ANKOBA 1 TROOP (A1) 37
II. ANKOBA 2 TROOP (A2) 37
III. MALAZA TROOP (M) 37
3.2 DATA COLLECTION 39
CALCULATION OF ACTIVITY BUDGET DATA 40
GPS DATA COLLECTION AND HOME RANGE CALCULATIONS 40
3.3 DATA COLLECTION-FEEDING SPECIFIC 42
CALCULATION OF FEEDING INGESTION RATES 43
CALCULATION OF WATER CONTENT FOR PLANT SPECIES AND FOOD TYPE 44
3.4 PHENOLOGY 46
3.5 DATA ANALYSIS 48

CHAPTER FOUR: RESULTS 50

4.0 HOME RANGE **50**
4.1 FOREST TREE PHENOLOGY **51**
4.2 INTAKE RATES OF MALES AND FEMALES: ALL FOOD TYPES **55**
4.3 INTAKE RATES OF MALES AND FEMALES: BY FOOD TYPE **56**
FLOWERS 56
4.4 PROPORTION OF TIME DEVOTED TO FEEDING ON SPECIFIC FOOD TYPES **58**
4.5 PROPORTION OF TIME DEVOTED TO SPECIFIC BEHAVIORS **59**
4.6 AMOUNT OF FOOD CONSUMED **61**
4.7 ANALYSIS OF PLANT SPECIES CONSUMED **62**
MOST FREQUENTLY CONSUMED PLANT SPECIES AS DETERMINED BY NUMBER OF FEEDING BOUTS 62
AMOUNT OF TIME DEVOTED TO SPECIFIC PLANT SPECIES AS A PERCENTAGE OF TOTAL FEEDING TIME 64
4.8 WATER CONTENT ANALYSIS **67**
AVERAGE OBSERVED WATER INTAKE OF MALES AND FEMALES 68
4.9 POST-HOC POWER ANALYSIS **70**

CHAPTER FIVE: DISCUSSION **71**

5.0 KEY FINDINGS **71**
5.1 FEEDING DIFFERENCES **72**
INTAKE RATE 72
FOOD TYPE CONSUMED 73
PLANT SPECIES CONSUMED 76
5.2 DIFFERENCES IN TOTAL FOOD CONSUMED **77**
5.3 BEHAVIORAL DIFFERENCES **78**
5.4 WATER INTAKE DIFFERENCES **81**
5.5 HOME RANGE **83**
5.6 THE ENERGY CONSERVATION HYPOTHESIS AND REPRODUCTIVE STRATEGIES **85**
5.7 LIMITATIONS OF STUDY **95**
5.8 CONSERVATION IMPLICATIONS **98**
5.9 CONCLUSIONS **101**

LITERATURE CITED **103**

APPENDIX I-ETHOGRAM **123**

APPENDIX II-DATA COLLECTION SHEETS **124**

APPENDIX III-INDEX OF KNOWN PLANTS CONSUMED AT BERENTY **126**

APPENDIX IV-FOOD AVAILABILITY RATINGS FOR DURATION OF STUDY **128**

List of Tables

Table 3.0 Composition of the three *P. verreauxi* groups studied……………………………36
Table 3.1 Focal sessions and troop composition of study animals………………………38
Table 4.0 Species consumed along with plant parts consumed, percentage of total feeding time allocated to species, and number of feeding bouts allocated to species. ………62
Table 4.1 Percentage of feeding time and average water content of each plant species and part……………………………………………………………………………………………67
Table 4.2 Linear model used to determine relationship between water content and plant species and food type……………………………………………………………………………68
Table 5.0 Home ranges reported for *P. verreauxi* across forest types and research sites. ……………………………………………………………………………………………………83
Table 5.1 Sex-based differences in feeding behavior. …………………………………………91

List of Figures

Figure 1.0 Propithecus verreauxi current range………………………………………………9
Figure 1.1 Sites at which *P. verreauxi* can presently be found…………………………10
Figure 3.0 Satellite Image of Berenty Private Reserve alongside the Mandrare River………………………………………………………………………………………………….34
Figure 4.0 Home ranges of troops studied……………………………………………………51
Figure 4.1 Flower availability over course of study………………………………………52
Figure 4.2 Young leaf availability over course of study…………………………………..53
Figure 4.3 Mature leaf availability over course of study………………………………….54
Figure 4.4 Kernel density plot showing the distribution of average intake rate values of both sexes of all food types consumed……………………………………………………55
Figure 4.5 Average hourly intake rates regardless of food type consumed………….56
Figure 4.6 Average hourly intake rates by food type consumed…………………………..57
Figure 4.7 Average proportion of total feeding time devoted to specific food type..58
Figure 4.8 Average proportion of total time observed allocated to behaviors……….60
Figure 4.9 Total amount of food each individual consumed over course of study…61
Figure 4.10 Most frequently consumed plant species determined by number of feeding bouts………………………………………………………………………………………………64
Figure 4.11 Average proportion of total feeding time allocated to species…………….65
Figure 4.12 Total observed water intake of males and females…………………………69

Acknowledgements

I must first thank Dr. Lisa Gould, my academic supervisor, for holding me to her high standards these past two years. I learned how to be a better scholar and academic through your examples. I am also thankful to Dr. Helen Kurki, my departmental committee member, for all of her insightful and thorough comments and edits. You always made time to answer my questions and I appreciate that. I am grateful Dr. Brian Starzomski acted as my outside external examiner, as his questions and comments substantially strengthened this thesis. Allan Roberts helped me create graphs that are considerably improved from my originals. Dr. Yin Lam, the department graduate advisor, guided me through this degree and taught me a lot about human primates and, although he may not know it, how to be a better one. Finally, thank you to Dr. Paul Constantino, my "unofficial advisor," for encouraging me to study primates, for continuing to support me, and for always having a kind word when I needed it. I can't thank you enough.

Most importantly, words cannot express the gratitude I have for my parents, Dorothy and Edward Markham, for not once balking when their daughter said she wanted to run around after monkeys for a living. I count myself as one of the luckiest people alive because, "I found something I (truly) love and (sort-of) figured out a way to get paid for it." Thank you both for making sure I still laughed at myself and finished this degree strong. I owe you too much.

I appreciatively thank Sigma Xi and the University of Victoria for funding my research. I must again thank Dr. Gould for partially funding my fieldwork through her grant from the Natural Sciences and Engineering Research Council of Canada. I also thank the Département des Eaux et Forêts Madagascar and the De Heaulme family for granting me permission to study at Berenty Private Reserve. My research was made possible due to an Accord between Dr.s Gould and Hantanirina Rasamimanana of University of Victoria's Anthropology Department and the Université d'Antananarivo's École Normale Supérieure respectively. I am proud to have conducted my fieldwork with the aid of Saotra Rakotonomenjanahary, from the Ecole Normale Supérieure department at the Université d'Antananarivo. Saotra you taught me so much about Madagascar and were such a great friend to have in the field. I couldn't have done it without you.

CHAPTER ONE: INTRODUCTION

1.0 PRIMATE DIETARY ECOLOGY

Primates require energy for growth, reproduction, basic life processes, and for behaviors such as travel, vigilance against predators, and social interactions (Lambert, 2011). It is perhaps unsurprising that, in the history of primate studies, foraging and diet research have played a key role (Lambert, 2011). Primate feeding ecology examines how primates navigate their environment through feeding behaviors with respect to the primates' morphology and physiology (Robbins and Hohmann, 2006). Researchers in this field ask questions about how, when, where, and what primates eat in specific environments (Nakagawa, 2009). Understanding why primates feed on certain items requires studying the relationships among multiple variables such as development, morphology, ecology, and social factors, such as group size and composition (Chalk and Vogel, 2012).

Primate feeding ecology has traditionally been studied through observational or laboratory work, although there is an increasing interest in assimilating laboratory and field methodology (for review, see Chalk and Vogel, 2012). Regardless of the study type, understanding how a primate solves feeding challenges can provide insight into the ecology and evolution of that species (Lambert, 2011).

1.1 OVERVIEW OF SEX-BASED FEEDING DIFFERENCES IN PRIMATES

Sex-based differences in diet may occur due to: 1) differing diets as a strategy to reduce feeding competition between males and females, 2) distinct energetic requirements caused by different body size, and 3) dissimilar nutritional requirements due to different energetic investment in reproduction (Clutton-Brock, 1977). When resources are limited, it is to be expected that individuals will avoid feeding competition with their mates and selection will favor those individuals (Clutton-Brock, 1977). In reference to reason two (sex-based differences are due to sexual dimorphism in body size), males that are substantially larger than females of their species require more energy to maintain their increased body size (Key and Ross, 1999). Larger animals have higher absolute but lower relative energetic requirements for maintenance compared to smaller animals (Bell, 1971), thus males would need to consume more in total or higher quality foods than females. Larger males may also be able to displace females from optimal foods (Young et al., 1990). For example, silverback gorillas (*Gorilla gorilla gorilla)* at Bai Hokou consume termites more frequently than both juvenile males and adult females, and displacement rates surrounding termite mounds are higher than expected (Cipolletta et al., 2007), which may support the hypothesis that differences in body size cause distinct energetic requirements.

Finally, intersex differences in diet may be caused by the differing energetic investment in reproduction of males and females, which results in nutritional requirements specific to each sex (Clutton-Brock, 1977). ~~Finally,~~ while males may incur increased energetic costs associated with mating efforts, females must cope with energetic costs of gestation and lactation, which may result in seasonal dietary differences corresponding with these reproductive stages (Key and Ross, 1999). Costs incurred during gestation are due to production of fetal, uterine, placental and mammary tissue and corresponding costs of maintaining these tissues (Gittleman and Thompson, 1988) in addition to the obvious cost of embryonic development (Kunz and Orrell, 2004). Milk production and corresponding increased rates of maternal maintenance are energetically costly and may be met through increased consumption or reliance on fat stores (Gittleman and Thompson, 1988). Lactation also places demands on a mother's water balance (Gittleman and Thompson, 1988). The energetic cost of milk production increases as the infant grows and thus requires more energy (Kunz and Orrell, 2004). It is the increased costs due to lactation and resulting potential sex-based differences in diet and behavior that is the focus of my study.

Lactation is thought to be especially energetically demanding to the extent that females of some primate species lose weight while nursing (Altman, 1980; Bercovitch, 1987; Pereira, 1993). Females may meet higher energetic demands by increasing food consumption, using any available stored energy, or reducing time devoted to specific activities (Lappan, 2009). Captive female *Galago senegalensis braccatus* increase energy and protein intake while lactating by increasing food consumption and choosing foods high in protein (Sauther and Nash, 1987). Lactating female titi monkeys (*Callicebus cupreus* and *C. moloch*) consume more protein-rich insects when compared to males and females without infants (Wright, 1984; Tirado Herrera and Heymann, 2004). Female *Varecia variegata rubra* and *Eulemur fulvus albifrons* consume a more diverse diet higher in low-fiber protein during gestation and lactation in comparison to males (Vasey, 2002). Serio-Silva and colleagues (1999) found gestating and lactating female *Alouatta palliata* consume more fat and protein than non-lactating females, but there was no significant difference in ingestion when comparing gestating and lactating females.

Behavioral changes during lactation have also been recorded in female primates. Lactating female baboons (*Papio hamadryas ursinus*) reduce social activities and increase time spent resting when infant feeding demand is high (Barrett et al., 2006). While it may seem counterintuitive initially, primate females may respond to the demands of lactation by decreasing feeding time. For example, lactating female green monkeys (*Cercopithecus sabaeus)* allocate less time to feeding than non-lactating females, possibly to conserve bodily resources and minimize energy expenditure (Harrison, 1983). Female siamangs (*Symphalangus syndactylus)* spend significantly less time feeding when lactating in comparison to non-lactating stages of infant care (Lappan, 2009). Rose (1994) observed lactating female white-faced capuchins (*Cebus capucinus)* devote less time to foraging in comparison to non-lactating females, but more recent findings report lactating females consume more food items per hour and have higher energy intake rates compared to non-lactating females, despite feeding for the same amount of time (McCabe and Fedigan, 2007).

Conversely, sex-based differences in diet do not always exist. It was recently reported that *Lemur catta* females in a spiny forest habitat do not differ significantly from males in food intake rate or in average energy and crude protein intake of the five most frequently consumed foods (Gould et al., 2011). *L. catta* females also do not differ from males in the percent of time allocated to feeding or time devoted to specific food types in early through mid-lactation (Gould et al., 2011). The lack of differences may be because the high energetic costs males sustain during the mating period result in males requiring a recovery (Gould et al., 2011). An absence of sex-based differences in diet and behavior during gestation and lactation has also been reported for *P. edwardsi* (Hemingway, 1999). Hemmingway (1999) attributed a lack of sex-based differences to a combination of physiological storage of energy in the females and that the costs of reproduction for *P. edwardsi* are not great enough to necessitate significant variation from males in feeding and resting time.

Given that *P. verreauxi* is not a sexually dimorphic species (Kappeler, 1991; Kappeler and Schaffler, 2008) and primarily feeds on widely available leaves, thus making it unlikely feeding competition is prevalent, any feeding variations between males and females during the early lactation period are likely due to differing reproductive costs.

1.2 BACKGROUND

I. Island History

Madagascar likely reached its current location relative to the African continent approximately 130 mya (Dewar and Richard, 2012). Having passed through the Arid Belt, in which desert-like conditions prevailed and only drought-adapted plants would have survived, Madagascar then lay to the Arid Belt's south (Dewar and Richard, 2012). Africa and Madagascar both began moving north and reached their current location relative to latitude by approximately 30 mya (Dewar and Richard, 2012). Madagascar split from India between 100-88 mya and from Australia and Antarctica between 130-80 mya (de Witt, 2003; Dewar and Richard, 2012), and has been completely isolated from other landmasses by water since at least 80 mya (Ali and Krause, 2011).

Malagasy lemurs colonized Madagascar in one event, as indicated by genetic findings showing all extant lemurs are descended from a single common ancestor (Dene et al., 1976; Yoder et al., 1996a,b; Porter et al., 1997; Goodman et al., 1998; Pastorini, 2000). The fossil record after 65 mya, around the time ancestral lemurs would have arrived on the island, is very sparse, thus it is uncertain what types of fauna ancestral lemurs would have encountered (Dewar and Richard, 2012). However, recent constructions of the primate phylogenetic tree using genetic data indicate the ancestral lemurs underwent a rapid adaptive radiation upon reaching Madagascar (Perelman et al., 2011).

Lemuriformes, an infraorder within primates including lemurs, lorises, and galagos, are thought to have diverged from ancestral lemurs in two events: the first divergence occurred ~62 mya during a period of geological havoc and rapid change in fauna now known as the Cretaceous/Paleogene boundary but previously referred to as the Cretaceous/Tertiary or K/T boundary (Yoder and Yang, 2004). The second event took place around ~ 43 mya, indicating there were two lemuriform lineages in existence for approximately 20 million years (Yoder and Yang, 2004).

II. Island Geography and General Ecology

The island of Madagascar is approximately 400km off the coast of Africa, east of Mozambique (Dewar and Richard, 2012). It has a land area of 581,540 sq. km and is the fourth largest island in the world (World Factbook, 2012).

Madagascar's climate is greatly affected by the southeastern trade winds, cyclones, and the Southern Indian Drift, all of which move from the Indian Ocean westward to Madagascar and bring rain to the eastern part of the island (Wells, 2003). The tropical ocean, the geographic location and relief of the island, and the monsoon winds from the northwest are the primary causes of Madagascar's variable climatic conditions (Jury, 2003). The island is characterized by exceptionally unpredictable amounts and patterns of rainfall (Dewar and Wallis, 1999) that are suggested to have resulted in the high variance in mammalian life histories found on Madagascar (Dewar and Richard, 2007). Much of the flora and fauna of Madagascar is endemic, displaying an extremely high amount of diversity in the number of species present.

III. General Species Information and Distribution

Propithecus verreauxi, a strepsirhine primate (a suborder of primates including lemurs, galagos, pottos, and lorises), is a member of the Indriidae family (Petter, 1972). There are currently nine recognized members of the genus *Propithecus*: *P. verreauxi, P. deckeni, P. coronatus, P. coquereli, P. tattersalli, P. diadema, P. edwardsi, P. candidus*, and *P. perrieri* (Mittermeier et al., 2006). *P. verreauxi* is a folivorous, diurnal primate (Dewar and Richard, 2007) generally characterized as having a white body with a brown crown (Jolly, 1966). This species is not sexually dimorphic with average mass of 3.637 kg for females and 3.696 kg for males reported in a free-ranging captive population (Kappeler, 1991). A significant difference between males and females in mass exists only during the late dry season (July-October) at Beza Mahafaly with females and males measuring on average 2.54 and 2.73 kg respectively (Richard et al., 2000).

P. verreauxi is found in the south and southwestern part of Madagascar (Figure 1.0) in western dry deciduous and spiny forests (Richard, 1976; Richard et al., 2002). Home range size has been reported to vary from 2.5 to 8.5 ha (Richard, 1977) and 1.6 ha (Prew, 2005) at Berenty Private Reserve, from 4 to 6 ha at Beza Mahafaly (Richard et al., 1991), and approximately from 1.5 to 4.5 (Norscia et al., 2006) and 5.7 and 10.1 ha at Kirindy (Benadi et al., 2008).

Figure 1.0 *Propithecus verreauxi* current range in grey. Image from IUCN Redlist.

Much of what is known about *P. verreauxi* is the result of research conducted at three primary field sites: Berenty Private Reserve, Kirindy Private Reserve, and Beza Mahafaly Reserve. See Figure 1.1 for a map detailing the location of all three sites. Kirindy is the furthest north of these three sites and is located approximately 20km from the eastern coast of Madagascar. Kirindy forest is primary, dry deciduous (Sorg et al., 2003). The forest grows on slightly acidic sandy soils, which have a very low capacity to retain water (Sorg et al., 2003). The forest contains mostly deciduous trees at the canopy level and lacks a herbaceous level (Sorg et al., 2003). Beza Mahafaly Reserve is a national wildlife reserve composed of two forest parcels 10km apart (Ratsirarson, 2003). One of these parcels is composed of spiny forest and one of gallery forest containing deciduous and semi-deciduous vegetation (Ratsirarson, 2003). The 100-hectare gallery forest at Beza Mahafaly is composed of a small strip of riverine forest dominated by *Tamarindus indica* which transitions to xerophytic further from the river (Sussman and Rakotozafy, 1994; Richard et al., 1991; Gould et al., 2003). The spiny forest is 520 hectares and characterized by species adapted for a long dry season (Ratsirarson, 2003). Berenty Private Reserve is the furthest south of these research sites. More information about Berenty can be found in the section "Study Site" in Chapter Three.

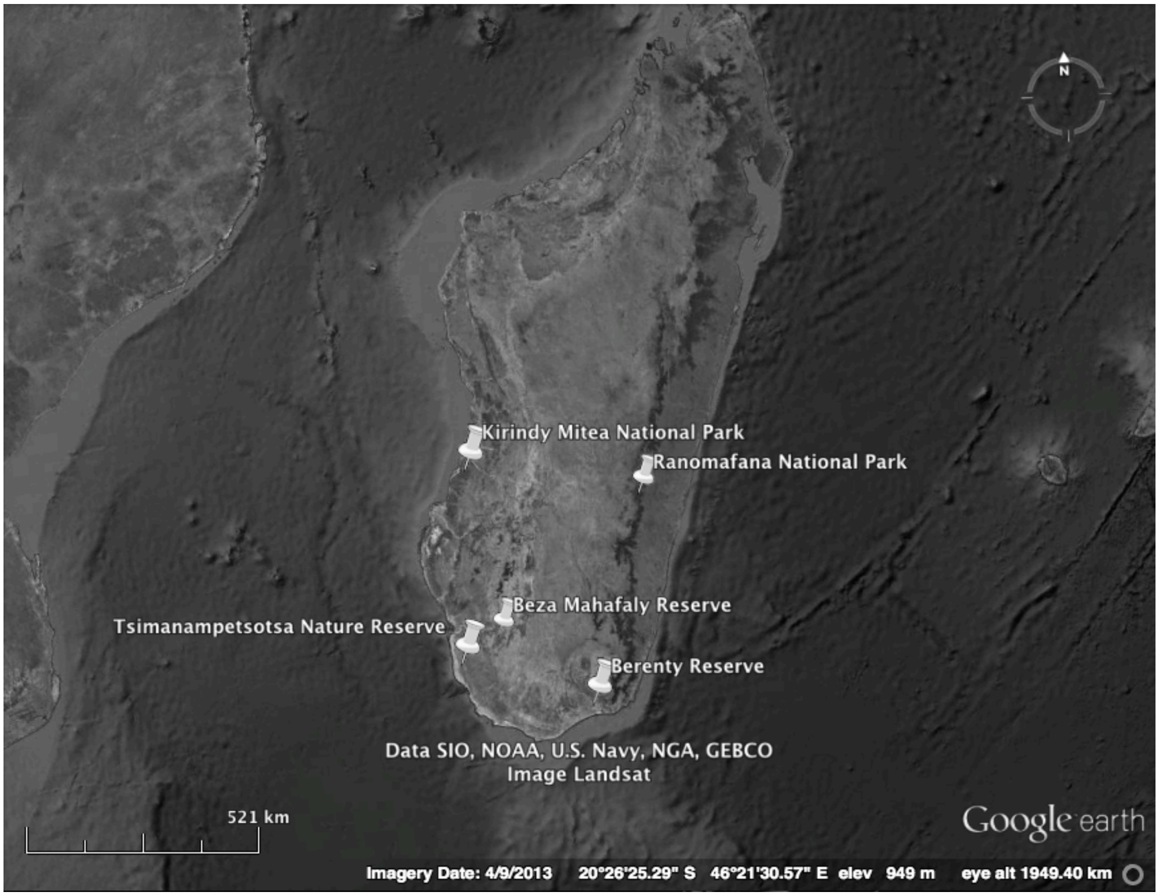


Figure 1.1. Sites at which *P. verreauxi* can presently be found. Google Earth 7.1 Accessed on June 5, 2014.

P. verreauxi is classified as “endangered” and is threatened by habitat loss, forest degradation, and hunting for consumption (Schwitzer et al., 2013). Models suggest extinctions occur generations from the original habitat destruction, creating a time lag from when a species loses its habitat to its extinction (Tilman et al., 1994; Colishaw, 1999), thus *P. verreauxi* may be one of the many species in Madagascar thought to be living on “borrowed time” (Harper et al., 2007: 331).

1.3 ECOLOGY

I. Habitat

P. verreauxi live in a challenging, highly seasonal environment that experiences variable amounts of rainfall, droughts, and cyclones (Wright, 1999; Richard et al., 2002). The phenological cycles in Madagascar are thought to be especially challenging for frugivores: fruiting is distinctly seasonal and confined to a very narrow time of the year whereas leafing is continuous (Terborgh and van Schaik, 1987).

In southern Madagascar, summers (October-March) are hot and wet with temperatures above 40 °C at midday, and winters (April-September) are cool and dry with temperatures falling below 10°C at night and varying amounts of rainfall (Jolly et al., 2006). Temperatures have been known to drop as low as 5°C during the winter (Gould, personal communication).

P. verreauxi employs several behavioral strategies to cope with Madagascar's seasonality, such reducing home range, core area, and daily path length in the dry season (Richard, 1978). In Kirindy, *P. verreauxi* contracts home range, balances activity patterns, focuses on consuming adult leaves, and potentially searches for nutritious foods during the dry season (Norscia et al., 2006). *P. verreauxi* clearly differentiates its folivorous niche from other lemur species temporally and either spatially or through diet composition (Dammhahn and Kappeler. 2014). Dammhahn and Kappeler (2014) suggest this distinct niche separation is possibly due to the harsh, seasonal environment *P. verreauxi* inhabits.

P. verreauxi travel by a method known as vertical clinging and leaping (Napier and Walker, 1967), propelling themselves up to 10m in one leap using their strong hind limb muscles (Jolly, 1966). *P. verreauxi*'s location within the forest structure (canopy, forest floor, etc.) is typically determined by corresponding foliage availability (Jolly, 1966). *P. verreauxi* at Berenty have been found to forage on the ground anywhere from <1-10% of the time (Prew, 2008).

In Berenty Private Reserve, *P. verreauxi* can be found in both gallery and spiny forest. *P. verreauxi* in gallery forest occur in higher densities and have smaller home ranges than those inhabiting spiny forest (Norscia and Palagi, 2008). *P. verreauxi* habitat is under acute threat. Southern gallery forests are one of the most threatened types of forest in Madagascar (Sussman et al., 2006). The patchy quality of these forests is known to affect vital services, such as seed dispersal by *Lemur catta* (Bodin et al., 2006). *L. catta* is a major seed disperser whose movement is greatly affected by the arrangement of forest patches, thus seed dispersal is also affected (Bodin et al., 2006). At the site for this project, Berenty Private Reserve, I studied *P. verreauxi* in gallery forest.

II. Diet

P. verreauxi is considered a folivore, foraging for 24-37% of the day and consuming mainly leaves (Richard, 1978; Charrier et al., 2007). The extent of folivory can vary dependent on season, with *P. verreauxi* at Kirindy consuming mature leaves for as much of 80% of its diet during the dry season (Norscia et al., 2006). *P. verreauxi* at Beza Mahafaly devoted anywhere from 0-70% of foraging time to mature leaves depending on the month (Yamashita, 2008). Other species of the genus *Propithecus* devote varying amounts of time to foraging on leaves. *Propithecus diadema* and *Propithecus tattersalli* both allocate less than 50% of foraging time to leaves, whereas *P. edwardsi* devotes anywhere from 11-78% of feeding time (Meyers, 1993; Hemingway 1995, 1996; Powzyk and Mowry, 2003; Richard, 2003).

The diet of a folivore is higher in fiber than that of frugivores and thus is high in cellulose, hemicellulose, and lignin (Parra, 1978). Requiring fermentation by symbiotic microbes, fiber is typically thought to be an antifeedant (McNab, 2002). Cellulose, hemicellulose, and lignin are only partially digestible by microbes (McNab, 2002). Given these digestive difficulties, folivores often have to consume large amounts of food to meet energetic needs (Richard, 1978). *P. verreauxi* has the morphological and physiological adaptations expected for folivores, including large salivary glands, a capacious stomach, and a long, convoluted caeca (Hill, 1953). However, *P. verreauxi* lacks a sacculated stomach found in colobine monkeys, which are also heavily folivorous (Hill, 1953).

It has been suggested that food requirements of folivorous lemurs living in deciduous forests in Madagascar may exceed availability during the dry season because of food shortages (Charles-Dominiques and Hladik, 1971). However, it is important to remember that food quality, the amount and mix of nutrients present in a food item can be more important than food availability (Norscia et al., 2006). *Lemur catta* at Berenty are known to consume Tamarind leaves higher in protein and water content during the lean season (Mertl-Millhollen et al., 2003) and lactating females residing in spiny forest prefer foods high in protein and water content (Gould et al., 2011). *P. diadema* at Kirindy show no difference in the average macronutrient and energy composition of flowers and leaves consumed during the lean season in comparison to the fruits consumed during the abundant season (Irwin et al., 2013). *P. verreauxi* inhabiting tropical dry forests at Beza Mahafaly, Madagascar are not nutrient-starved during the dry season (Yamashita, 2008).

Even though they are folivores, *P. verreauxi*'s diet is not composed entirely of leaves: they consume 60-70% flowers, less than 20% leaves, and less than 20% bark during the wet season (Richard, 1978). During the dry season, 70% of their diet is composed of leaves, less than 20% of flowers, and 5% of dead wood at Berenty Private Reserve (Richard, 1978). Simmen and colleagues (2003), examined *P. verreauxi*'s diet at Berenty by middle dry season, late dry season, and late wet season and found unripe fruit accounted for 2, 61, 1%, ripe fruit accounted for 6, 0, and 1%, mature leaf 45, 4, and 22%, and young leaf for 16,7, and 46% of diet for each season respectively. Appendix III lists plant species *P. verreauxi* is known to consume at Berenty. Despite differences in forest types, all *Propithecus* sp. appear to feed on 75-100 plant species total (Richard, 2003). All *Propithecus* sp. seem to spend 60-80% of feeding time on a narrow 10% of the species making up their diet (Richard, 2003).

P. verreauxi at Kirindy was found to consume the highest amount of protein during the late dry season and higher amounts of carbohydrates when fruit production was at its peak in March and when flowers were consumed August through October (Norscia et al., 2006). Lipid consumption was shown to remain low throughout all seasons (Norscia et al., 2006). Mature leaves are always available, but fruit, flowers, and young leaves of a higher sugar and protein content (Waterman, 1984), and *P. verreauxi* preferentially feed on these items when available (Norscia et al., 2006). These results indicate that *P. verreauxi* exhibits preference for specific food items based on nutritional quality (Norscia et al., 2006).

1.4 BEHAVIOR

I. Social Structure

P. verreauxi social structure is quite fluid, with multimale/multifemale groups fissioning to form smaller foraging parties (Jolly, 1966; Richard, 1978). A combination of pre-reproductive age mortality and slow and late reproduction is thought to be the reason for the fluid social structure (Pochron et al., 2004). Males in particular are known to visit neighboring groups and also frequently transfer to other groups entirely (Jolly, 1966; Richard, 1978; and Richard *et al.*, 1993). *P. verreauxi* can also be found in single-male single-female family groups (Richard, 1979; Norscia and Palagi, 2008). Average group size ranges from two to fourteen members at Beza Mahafaly (Richard et al., 2002) compared to a range of 1-10 individuals at Berenty (Norscia and Palagi, 2008). Group size at Kirindy across multiple years averages 6.1 individuals per group (Kappeler and Fichtel, 2012).

The sex ratio of males to females has been found skewed in favor of more males (Richard, 1985; Norscia and Palagi, 2008), which is common in lemurs such as *L. catta, L. fulvus,* and *P. verreauxi* (Richard and Dewar, 1991; Wright, 1999; Kappeler, 2000). While the sex ratio for *P. verreauxi* at Beza Mahafaly is not skewed at 1:1 (Richard et al., 1991), at Kirindy male: female ratios of 1:1, 2:1, 1:2, 3:2 have all been observed (Lewis and van Schaik, 2007). At Berenty specifically, Norscia and Palagi (2008) found an average of one female per group in both gallery and scrub forests and sex ratios exceptionally biased in favor of males across forest types.

Both female and male *P. verreauxi* disperse from their natal group at Beza Mahafaly Special Reserve (Richard et al., 1993; Richard et al., 2002) and at Kirindy

(Lewis, 2008), as do *Propithecus edwardsi* and *P. diadema* in Ranomafana National Park (Wright, 1995; Irwin, 2007; Morelli et al., 2009). Data on *P. verreauxi* dispersal in Berenty has yet to be published.

P. verreauxi is territorial (Jolly, 1966) with scent-marking usually occurring during intergroup encounters (Lewis, 2005). Intergroup aggression in *P. verreauxi* has been classified as moderate in comparison to other primates (Benadi et al., 2008). The possibility of encountering a neighboring group does not strongly influence behavior or resource use (Benadi et al., 2008). Both sexes scent mark their territory using urine, fecal matter, and anogenitally, but males also have an additional scent gland on their throat (Jolly, 1966). Scent marking is done almost entirely by adults and can serve many purposes in addition to its occurrence during inter-group encounters, such as attracting a mate and advertising an identity (Lewis, 2006). *P. verreauxi* in the Kirindy Forest of western Madagascar scent mark more in the perimeter of their territory as opposed to the core area (Lewis, 2006). Males at Kirindy Forest and Beza Mahafaly scent mark more frequently than females, possibly to guard their mates (Brockman, 1999; Lewis, 2005). At Berenty, those scent-marking more have mating priority (Norscia et al., 2009).

II. Female Dominance

In most polygynous primate species, or primate species in which males mate with more than one female, males are dominant over females during feeding competition (Hrdy, 1981; Jolly, 1984). The larger body size of males allows them to displace females and access preferred foods (Young et al., 1990). When males and females do not differ significantly in body size, male dominance, codominance, and female dominance may all occur (Smuts, 1987). Female dominance, the system in which males consistently submit to and are displaced by females, is exhibited by most lemur species (Jolly, 1984), though it is rare in the mammalian class (Ralls, 1976; Kappeler, 1993). Female dominance in primates typically occurs when females form coalitions against males (Smuts, 1987), but female *Lemuroidea* are the exception in that they consistently dominate males. Jolly (1966) was the first researcher to note female dominance in *P. verreauxi*. Hypotheses explaining female dominance will be addressed in “The Lemur Syndrome” later in this thesis.

1.5 LIFE HISTORY

Female *P. verreauxi* exhibit asynchronous receptivity related to age and rank within a distinct, seasonal mating period (Brockman et al., 1998). Both males and females typically mate with multiple individuals both within and outside of their group (Brockman et al., 1998). The gestation period is between 150-162 days and females typically give birth to one offspring (Petter-Rousseaux, 1962; Eaglen and Boskoff, 1978; Richard et al., 1991). The youngest age a female has been observed to give birth is three years old, however infant mortality is high until females are six years old (Richard et al., 2002). Males are sexually active by at least age four (Richard et al., 2002).

Richard and colleagues (2002) argue that *P. verreauxi* employs a reproductive strategy known as "bet-hedging" that occurs when a species lives in a fluctuating environment (Stearns, 1976; Richard et al., 2002). Bet-hedging occurs when it pays for a species to reduce reproductive effort in order to live longer and produce more offspring over an extended period of time, increasing the number of offspring born into good conditions (Stearns, 1992). Richard and colleagues (2002) suggest that *P. verreauxi* reproduce later in life and for a longer period given their body size in comparison to data available for other primate species.

Infant *P. verreauxi* cling transversely across their mother's torso until about three months of age when they switch to their mother's back (Jolly, 1966). Infant mortality for *P. verreauxi* at Berenty ranges from 53-70% (Richard et al., 1991). At Kirindy, 62% of infants die within the first two years (Kappeler and Fichtel, 2012) and 53% of infants die at Beza Mahafaly (Richard et al., 2002). Infants are weaned between 6-9 months of age during the wet season (Richard, 2003). Age of maturity is reached more quickly under favorable ecological conditions, and *P. verreauxi* in the harsh spiny forest may take up to five years to reach full size (Richard et al., 2002; Richard, 2003). Less than half of these females give birth before the age of six (Richard et al., 2002).

1.6 THE LEMUR SYNDROME AND REPRODUCTION

The major traits that distinguish lemurs from haplorhines (tarsiers, new and old world moneys, and apes) and other strepsirhines (lorises, pottos, and galagoes) include female dominance, lack of sexual dimorphism regardless of social system, sperm competition combined with male-male aggression, high infant mortality, cathemerality in certain species, low basal metabolic rate, and strict breeding season determined by photoperiods (Wright, 1999). Primatologists commonly refer to this unique combination of traits as the "lemur syndrome." The first hypothesis proposed to explain the lemur syndrome was the energy conservation hypothesis (Jolly, 1984) followed by the energy frugality hypothesis (Wright, 1999).

The energy conservation hypothesis (ECH) states that female dominance arose in response to energetic stress caused by ecological challenges and strong seasonality effects (Jolly, 1984). Every animal experiences stress, (Moberg, 2000). First defined as the general response of the body to any harmful stimulus (Selye, 1950), this definition was refined to state that stress is the biological response an individual identifies as a threat to homeostasis (Moberg, 2000). Once stress is perceived, a combination of the behavioral, autonomic nervous system, neuroendocrine, or the immune response is elicited by the central nervous system (Moberg, 2000). Stress in reproductive animals is linked to decreased reproductive function/output (see Foley et al., 2001 for elephants, *Loxodonta africana*; Cry and Romero, 2003 for starlings, *Sturnus vulgaris*; and Foerster et al., 2012 for blue monkeys, *Cercopithecus mitis*). Generally speaking, mammalian female reproduction is typically suppressed by stress through… "(i) disruption of ovulation; (ii) impairment of the uterine maturation needed for implantation; and (iii) inhibition of proceptive and receptive behaviours." (Wingfield and Sapolsky, 2003: 714).

More specifically, the ECH states that females responded to increased reproductive stress due to Madagascar's ecology by adapting priority in feeding situations (Jolly, 1984; Young et al., 1990). The ECH addresses the lemur syndrome in terms of the climatic conditions of Madagascar, hypothesizing that the harsh and unpredictable climate is energetically stressful for reproductive females, who reacted to the stress with female dominance (Wright, 1999). Yet not all traits of the lemur syndrome conserve energy (Wright, 1999). Cathemerality, meaning the organism is active intermittently over twenty-four hours, (Tattersall, 1987; Overdorff and Rasmussen, 1995; van Schaik and Kappeler, 1996; Rasmussen, 1999), high rates of infant mortality (Wright, 1993), and male aggression and sperm competition (van Schaik and Kappeler, 1996) do not fit this hypothesis.

Because not all lemur syndrome traits fit the ECH, Wright (1999) suggests another hypothesis, the energy frugality hypothesis (EFH), which states that the majority of lemur traits are adaptations either to conserve energy (low basal metabolic rate, torpor, sperm competition, small group size, and seasonal breeding) or to maximize usage of scarce resources (cathemerality, territoriality, and female dominance) (Wright, 1999). In support of this hypothesis, *P. verreauxi* has been shown to decrease home range, core area, and daily path length during the dry season to reduce energy expenditure in the deciduous dry forest at Kirindy, Madagascar (Norscia et al., 2006), and to employ a feeding strategy in which food is selected based on nutritional quality dependent upon the season (Norscia et al. 2006).

Many traits of the lemur syndrome are interlinked with reproduction (strict breeding season, high infant mortality, among others). If the lemur syndrome is thought to conserve energy and maximize resource usage as per the EFH (Wright, 1999), the effects of this strategy should be especially evident in regards to reproduction.

I. Reproduction

P. verreauxi exhibit seasonal reproduction (Richard et al., 2000), giving birth typically in July and August during the dry season (Richard et al., 2002; Erkert and Kappeler, 2004; Lewis and Kappeler, 2005). The timing of reproductive cycles varies within and between lemur species, but interspecies birth asynchrony is thought to occur in preference to weaning during periods when fruit, new leaves, and insects are abundant (Wright, 1999). *P. verreauxi* times mid/late lactation with periods of increasing food availability (November and December at Kirindy Forest) (Lewis and Kappeler, 2005), suggesting this species follows the so-called "classic" reproductive strategy in which a species conceives during period of high or declining food supply so that the most energetically demanding phase of reproduction (mid/late lactation) coincides with a peak in food supply (Jolly, 1984; van Schaik and van Noordwijk, 1985; Wright, 1999). At both Kirindy and Beza Mahafaly, *P. verreauxi* populations have been found to employ this strategy (Richard et al., 2002; Lewis and Kappeler, 2005).

Female lemurs face notably high physiological stress during reproduction (Young, 1990; Sauther, 1994; Gould et al., 2011). Lactation specifically is the most costly reproductive period of the mammalian female life cycle (Hanwell and Peaker 1977; Robbins, 1983; Gittleman and Thompson 1988; Clutton-Brock et al. 1989). Female *P. verreauxi* at Beza Mahafaly lose more mass than males do in the dry season when gestating and lactating (Richard et al., 2000). Energy management during lactation crucially influences infant health and the length of interbirth interval (Emery Thompson et al., 2012). *P. verreauxi* infant mortality is notably high during the first year of life, with 48% of individuals failing to survive the first year (Richard et al., 2002). Body mass of *P. verreauxi* females at the commencement of the mating season is significantly related to her likelihood of giving birth (Richard et al., 2000, 2002). In Richard and colleagues' study (2000), females with a mass of 2.99 ± 0.23 kg gave birth whereas females measuring 2.69 ± 0.31 kg did not. Given the increased energetic challenges during lactation and the difficult environment *P. verreauxi* inhabits, this species likely exhibits strategies to cope with giving birth during a period of low food availability. Energetic condition has previously been shown to affect conception of *P. verreauxi*: their window of conception broadens when energetic condition improves (Brockman and Whitten, 1996; 2003; Brockman et al., 1998; Brockman and van Schaik, 2005).

The extent to which diet affects lactating female *P. verreauxi* during the birth season in Berenty Private Reserve is unknown. Reproductive female *P. verreauxi* in Beza Mahafaly lose more body mass than males and non-reproductive females during the birth season (Richard et al., 2000), but this site is decidedly different than

Berenty. Sex differences in the activity budgets of a species closely related to *P. verreauxi, Propithecus edwardsi,* in Ranomafana National Park were absent, but significant differences in dietary composition of both sexes were found for the months of August, September, and October (Hemingway, 1999). Ranomafana is a markedly different site than Berenty, as it is composed of evergreen vegetation and lacks a true dry season (Hemingway, 1999).

1.6 SIGNIFICANCE OF STUDY

Timing a crucial reproductive stage with optimal ecological conditions is a strategy that maximizes fitness and can be especially beneficial in seasonal environments (Negus and Berger, 1972). Due to the energetic costs of gestating and rearing an infant, nutrition is likely to affect the timing of reproductive events (Lee and Bowman, 1995). Heat stress, resource availability, and droughts significantly affect a female baboon's chance of cycling, conceiving, and successfully giving birth (Beehner et al., 2006). When lactation costs are highest, food availability is also highest for *Cercopithecus aethiops* females (Lee, 1987).

P. verreauxi birth and lactation fall during a suboptimal ecological period, the dry season (Richard et al., 2002; Erkert and Kappeler, 2004; Lewis and Kappeler, 2005). Weaning occurs during a period of high food availability (Lewis and Kappeler, 2005). In accordance with the energy frugality hypothesis (Wright, 1999), *P. verreauxi* should have adaptations that either decrease energy expenditure and/or maximize energy intake to endure the dry season. My study will test aspects of the energy frugality hypothesis as it applies to *P. verreauxi* by identifying behavioral and diet adaptations females employ to manage increased energetic costs. Specifically, results will indicate if lactating females increase time spent foraging, increase food intake rate, or engage in other behaviors that reduce energy expenditure and/or maximize energy intake in comparison to males.

Results from my study will also have implications for conservation. Studying *P. verreauxi* at Berenty is especially important given that the ecology and distribution patterns of dry forest of southern Madagascar are not well documented nor understood (Ganzhorn et al., 2003). Models created by Bodin and colleagues (2006) predict that the dry forest ecosystem is highly vulnerable to habitat loss. Analysis of deforestation in Madagascar from 1953-2000 found that dry forests were the most fragmented forest type (Harper et al., 2007). Small forest fragments can have great importance in terms of species biodiversity (Bodin et al., 2006), yet very few forest areas are under conservation in southern Madagascar (Fenn, 2003). By detailing the feeding behavior of *P. verreauxi* during early lactation, we can better understand how this species copes with the burdens of lactation in a dry forest. Of the dry forest ecosystems, *P. verreauxi* has only been thoroughly studied at Berenty and Beza Mahafaly both of which are protected (Schwitzer et al., 2013). Little research has been done on *P. verreauxi* populations in forested areas outside of these sites (Axel and Maurer, 2011).

P. verreauxi populations at Berenty already display signs of stress (Norscia and Palagi, 2008). Results of my study will show how lactating *P. verreauxi* obtain adequate energy during the birth season and what plant species are most important during this crucial time. With better comprehension of what plants sustain *P. verreauxi*, we can then begin to protect them. Given rates of deforestation and habitat fragmentation, knowing what plant species are needed for lactating mothers to successfully raise their offspring may help declining population numbers.

CHAPTER TWO: HYPOTHESES

Females have higher metabolic requirements while nursing infants (Hanwell and Peaker 1977; Robbins, 1983; Gittleman and Thompson 1988; Clutton-Brock et al. 1989). Lactation may be an even greater challenge for *P. verreauxi* because the birth season falls within the dry season, when food availability is low. Given the costs of lactation, I tested the following hypotheses:

Null hypothesis 1: There is no difference in intake rate between males and lactating females.

Alternative hypothesis 1: There is a difference in intake rates of males and lactating females.

I predict that females will feed at a greater rate when compared to males due to the expense of lactation (Hanwell and Peaker 1977; Robbins, 1983; Gittleman and Thompson 1988; Clutton-Brock et al. 1989). Because male and female *P. verreauxi* are not sexually dimorphic in body size (Kappeler, 1991; Kappeler and Schaffler, 2008), I assume possible increases in intake rate of females compared to males will be due to energy needs during lactation, provided there is no significant difference in the amount of time each sex allocates to active behaviors such as locomoting.

Null hypothesis 2: There is no difference in average time spent feeding between males and females.

Alternative hypothesis 2: There is a difference between males and females in the average time spent feeding.

Given that lactation is energetically costly for females (Hanwell and Peaker 1977; Robbins, 1983; Gittleman and Thompson 1988; Clutton-Brock et al. 1989) and that male *P. verreauxi* are not involved in parental care (Jolly, 1966; Richard, 1978), I predict lactating females will devote an increased amount of time to feeding when compared to males.

Null hypothesis 3: No difference exists in the water intake rates of males and females.

Alternative hypothesis 3: There is a difference in water intake rates of males and females.

I predict females will have higher water intake rates than do males, as primate infants nurse on demand and milk is largely composed of water and therefore, lactating females need a greater water intake to produce milk (Kunz and Orrell, 2004).

Null hypothesis 4: Males and females do not differ in the amount of time spent resting on average.

Alternative hypothesis 4: A difference exists between the amount of time males and females spend resting on average.

I predict females will allocate more time of their day to resting than males do, as reducing time spent in social activities and allocating more time to resting has been observed for other lactating female primates (Barrett et al., 2006) and resting during lactation may conserve energy (Rose, 1994).

CHAPTER THREE: MATERIALS AND METHODS

3.0 STUDY SITE

I collected data from August 8th to September 15th, 2014 at Berenty Private Reserve in the Toliara Province of southern Madagascar (S 25° 0.5' latitude, E 46° 18.5' longitude; See Figure 1.1 for map and major lemur research sites). Berenty Private Reserve is part of the Berenty Estate, which was established in 1936 by the French colonial de Heaulme family in agreement with the local Malagasy Tandroy clans (Jolly, 2004). Noted as the easiest place in Madagascar to study and film wild lemurs (Jolly, 2004: 10), both tourists and researchers travel to Berenty.

Berenty Reserve is approximately 240ha in size flanked by sisal plantation at the south and the Mandrare River at the north (Soma, 2006). The area is extremely diverse in terms of habitat types, with spiny, scrub, and gallery forest (both open-canopy and closed-canopy) all naturally occurring in this area (Figure 3.0). In the tourist area or "front", gardens of exotic species were planted and lemurs feed on *Azadirachta indica, Cordia sinensis, Melia azedarah* and others (Jolly, 2006; Soma, 2006).

Data collection occurred in gallery forest dominated by *Tamarindus indica*, the tamarind tree or "kily" to the Malagasy people (Jolly, 2004, 2006; Soma, 2006). The gallery portion of Berenty is divided into a strict gallery forest with a closed-canopy called "Malaza" and a second-growth, open-canopy forest named "Ankoba".Malaza gallery forest exists along the river and is dominated by

Tamarindus and *Acacia* (Jolly, 2004; Jolly et al., 2006). Canopy coverage becomes increasingly open as one moves further from the Mandrare River, grading into forest dominated by *Neotina isoneura* (Jolly et al., 2006). Ankoba forest was cleared originally to grow crops, but the attempt was eventually abandoned (Jolly et al., 2006). The de Heaulmes planted *Pithecellobium dulce* in this second-growth forest, providing a source of protein-rich flowers and pods for the lemurs (Jolly et al., 2006). Introduced plant species include *Leucaena leucocephala* and *Azadirachta indica* (Soma, 2006). Density of sifakas, ring-tailed lemurs, and brown lemurs is higher in Ankoba forest in comparison to Malaza (Jolly et al., 2006).

The climate in this area fluctuates between a hot, wet season that runs from November to April and a cool, dry season that runs from May to September (Jolly, 1966; Jolly et al., 2006). Rainfall is seasonal with 70% of the annual rainfall occurring between November and February (Jolly et al., 2002). Average yearly rainfall at Berenty is 500mm (Koyama et al., 2002). Droughts are more common in the southern region of the island and they are occurring at a greater frequency due to climate change (Climate risk and adaptation country profile for Madagascar, 2011). Climate change is greatly affected by the deforestation of tropical forests, and Madagascar’s forests are notably reduced in size and quality (Harper et al., 2007). Deforestation itself releases carbon into the atmosphere and additional greenhouse gases may also be introduced if the cleared area is converted for agriculture (Houghton, 2005). Thus, animals inhabiting southern Madagascar must cope with a difficult dry season and an increasing number of droughts. During data collection for this research, it rained briefly (no longer than ten minutes) once (personal observation). Temperatures at Berenty from July-September range between 14-31.5 ºC (Richard, 1977).

While researchers have traveled to Berenty since the early 1960s (Jolly, 1966), tourism was not introduced until 1983 (Simmen et al., 2003) and the site remains a popular tourist destination today (Jolly, 2004; Jolly, 2006). Tourism at Berenty has multiple effects on the ecology of the site. Lemurs are not obstructed from feeding on non-native plant species found in the decorative gardens. *L. catta* also frequently steals food from tourists at the on-site restaurant.

Lemurs at Berenty are unintentionally supplemented with water from multiple sources. Previously, it was common practice to supplement the wild lemurs with freestanding water to ease stress during the dry season (Jolly, 2006). This practice has ceased, yet the stone basins remain, creating pools of standing water during rainfall and thus unintentionally supplying the wildlife with water (personal observation). All three species of diurnal lemurs (ring-tailed, sifaka, and the hybrid brown lemur) were observed drinking from a well at "Naturaliste," although sifakas were observed drinking from this source far less than the ring-tailed and brown lemurs.

Crops have been grown in certain parts of Berenty Reserve in the past and non-native plant species remain (Jolly et al., 2006). The de Heaulme family has also recently planted flora of the native spiny forest in plots spread out through the property in attempts to return portions of the property to the original state (flora in these plots is replanted adjacent to present spiny forest). Because of these reforestation attempts, lemur troops inhabiting the gallery forest may feed in these plots on spiny forest plant species (personal observation).

Figure 3.0. Satellite Image of Berenty Private Reserve alongside the Mandrare River. Google Earth 7.1 Accessed on August 2, 2014.

3.1 STUDY POPULATIONS

P. verreauxi at Berenty are highly habituated to human presence, as they have been studied since the 1960s, and a considerable body of literature has been published on this species (see for example: Jolly, 1966; Jolly, 1972; Jolly et al., 1982; Oda, 1998, 1992; Simmen et al., 2003; Jolly et al., 2006; Norscia and Palagi, 2008,). *P. verreauxi* population density at Berenty is notably high (Richard, 2003). *P. verreauxi* are sympatric with *Lemur catta*, *Microcebus griseorufus*, *M. murinus*, *Lepilemur leucopus*, and an introduced hybrid population of *Eulemur fulvus rufus* X *E. collaris* (Sussman, 1972; Simmen et al., 2003; Pinkus, 2004; Norscia and Palagi, 2008). The average group size of *P. verreauxi* at Berenty regardless of forest type is 4.22 individuals per group with a range of 1-10 member(s) (Norscia and Palagi, 2008).

Three study groups were chosen: two groups in Ankoba forest (A1 and A2) and one group in Malaza forest (M). Spiny forest troops were not studied because sample size was far too small (only one lactating female was found) and because troops typically ranged outside of the boundaries of Berenty (personal observation). Table 3.0 details group composition and Table 3.1 specifies amount of data collected per individual. In total, data were collected on ten individuals: five lactating females and five adult males (see Table 3.0 for further information). No group with more than two lactating females was found out of approximately ten groups surveyed. Study troops and focal individuals were chosen in order to maximize data collection on lactating females. For each lactating female studied, data were collected on one adult male. Non-lactating adult females were not studied because they were absent in study troops: the only other females present were sub-adults. Many troops surveyed during this time contained one lactating female with two-three males (personal observation).

Individuals were identified based on fur patterns and unique markings, such as a cut ear, facial scarring, cap color, cap shape. No individual from any study group was ever observed drinking water from either the stone basins present in the forest or from the well at Naturaliste. No individual from any study group was ever observed feeding on human foods.

Table 3.0 Composition of the three *P. verreauxi* groups studied. A1=Ankoba 1, A2=Ankoba 2, M=Malaza. Note: focal animals are named and individuals on which data were not collected are unnamed.

Individual	**Sex**	**Maturity**	**Group**
Blackspot	F	Adult	A1
Katrina	F	Adult	A1
Bob	M	Adult	A1
Fred	M	Adult	A1
Unnamed	F	Sub-adult	A1
Unnamed	M	Sub-adult	A1
Blondie	F	Adult	A2
Jenny	F	Adult	A2
Sofina	M	Adult	A2
Ted	M	Adult	A2
Unnamed	M	Sub-adult	A2
Unnamed	M	Sub-adult	A2
Sarah-Louise	F	Adult	M
Dido	M	Adult	M
Unnamed	M	Adult	M
Unnamed	F	Sub-adult	M
Unnamed	M	Sub-adult	M
Unnamed	M	Sub-adult	M

I. Ankoba 1 Troop (A1)

Over the course of six weeks, daily follows on this troop totaling forty-three hours and forty-four minutes show that A1's range spanned from the Mandrare River to a large road that runs along the edge of the forest. A1's habitat was not immediately adjacent to the tourist bungalows or Naturaliste and thus was not afforded the opportunity to feed on/drink from additional sources.

II. Ankoba 2 Troop (A2)

Daily follows totaling roughly forty-six hours reveal that the home range of A2 at times overlapped spatially with that of A1. This troop also ranged from the river up to the main road at the edge of the forest, although A2 traveled up to the road less often than A1. A2's habitat was not immediately adjacent to the tourist bungalows or Naturaliste and thus was not afforded the opportunity to feed on/drink from additional sources.

III. Malaza Troop (M)

Over the study period, twenty-one hours and forty-three minutes of focal observations completed in half-day increments show Malaza troop ranged closest to the tourist bungalows but they were never observed leaving the forest to explore the bungalows. M troop typically ranged closer to the river than to the bungalows.

Table 3.1 Focal sessions and troop composition of study animals. A1=Ankoba 1, A2=Ankoba 2, M=Malaza. Lactating females: n=5. Males: n=5.

Individual	**Group**	**Sex**	**Number of Focal Sessions**	**Total Time Observed (hh:mm:ss)**
Blackspot	A1	F	72	21:38:18
Blondie	A2	F	72	16:29:47
Bob	A1	M	72	18:55:43
Dido	M	M	72	18:26:55
Fred	A1	M	72	19:17:12
Jenny	A2	F	72	16:10:48
Katrina	A1	F	72	19:20:31
Sarah Louise	M	F	72	16:59:21
Sofina	A2	M	72	17:25:30
Ted	A2	M	72	17:38:20

3.2 DATA COLLECTION

I collected data over six weeks at Berenty Reserve in southern Madagascar. Data were collected with the aid of a Malagasy master's degree student, Saotra Rakotonomenjanahary, from the Ecole Normale Supérieure department at the Université d'Antananarivo.

Continuous focal animal data (Altman, 1974) were collected for fifteen-minute increments to record activity: rest, self-groom, groom, feed, locomote, vigilance, and aggression. An ethogram that was previously used to conduct behavioral observations of P. verreauxi at Berenty (Richard, 1978) was adapted to suit the needs of my study (see Appendix I). At the start of each session, the date, time, and individual identification were recorded. The focal animal was then observed for fifteen minutes. The activity of the focal animal was recorded as per the ethogram (Appendix I) to the second. In instances when the focal animal moved out of view, the time was noted and the activity was recorded as "out of sight" until the focal animal was visible again.

I collected data six days per week for approximately seven hours per full day rotating through each troop to ensure all focal animals were represented as equally as possible. Because data were collected on only two individuals in Malaza troop, this troop was observed for a half day as opposed to a full day. Collection for Malaza troop alternated equally between morning sessions and afternoon sessions so that a realistic representation of their behavior was obtained. A focal session was disregarded if the total time the focal animal was in view was less than ten minutes. Seventy-two focal sessions (≥10min) were collected on each individual (Table 3.1).

Calculation of activity budget data

In order to obtain the percentage of time a focal devoted to a specific behavior, the summed time in said behavior (in seconds) per focal was divided by the total time the focal animal was observed. Results were then transformed into a percentage. This calculation was performed for each behavior and focal animal.

GPS data collection and home range calculations

Home range is the area the animal uses in normal activities such as foraging, mating, and caring for young (Burt, 1943). There are many ways to measure home range and some are only crude outlines of an animal's travels, which may be satisfactory if the researcher does not seek to understand why an animal has chosen that range (Powell, 2013). The bivariate normal, which uses a 2D ellipse (Jennrich and Turner, 1969), the harmonic mean, which calculates harmonic mean values at grid points (Dixon and Chapman, 1980), and the adaptive kernel estimation, which also uses a grid structure but is non-parametric (Worton, 1989) are all examples of methods used to estimate home range. I used the minimum convex polygon (MCP) method of estimating home range. The MCP encloses all data points, connecting outer points so that a convex polygon is created (Mohr, 1947). This method is advantageous because it is simple to do, but areas of high usage and areas of low usage are given the same value (White and Garrott, 1990). The MCP is also sensitive to outliers (White and Garrott, 1990).

The home range for each troop was determined with the aid of the DeLorme Earthmate PN-60 handheld GPS instrument. GPS points were collected along the furthest points each troop was observed ranging. Coordinates were recorded in degree: minute format and entered into Google Earth software. Area calculations were computed using the Earth Point Shapes tool (http://www.earthpoint.us/Shapes.aspx).

3.3 DATA COLLECTION-FEEDING SPECIFIC

The activity “feeding” occurred when an individual was observed continually chewing and swallowing a food item. As reported by Richard (1977) *P. verreauxi* almost always detached food parts with their teeth and food was consumed where it was found. Thus, foraging or handling time was nonexistent for the food items the animals consumed during my study. A feeding bout is defined as the amount of time a focal animal was observed continuously feeding. A feeding bout ended when the focal animal resumed a behavior other than feeding as was noted to the nearest second. The food item consumed (young leaf, mature leaf, flower bud, flower, ripe fruit, and unripe fruit) and the species of plant were recorded. The number of bites each individual consumed of a food item was counted and then recorded. A pitch counter allowed observers to simply press a button each time an individual took a bite and the count was summed and displayed. At times, the focal animal consumed two or more plant parts from the same feeding tree. Given the fast rate at which the focal animals often fed, it was not typically possible to separate the count of one food item from another. For example, individuals would often ingest the occasional young leaf in addition to the flowers the individual was primarily consuming. These instances were recorded as 121 bites of “young leaves and flowers” for example and were analyzed as a specific food type separate from “young leaves” and “flowers.”

This distinction is important as feeding rate may differ significantly among food items (Hladik, 1977).

Because this project required counting the precise number of mouthfuls an individual consumed of a food item, data collection began later and ended earlier than typical for primate field studies (7:30-16:00), as it was difficult to observe individuals in low light. Collecting accurate data on intake rates of wild primates is challenging due to arboreal feeding, dense vegetation, and other factors (Nakagawa, 2009). To obtain precise counts of food items consumed, adequate sunlight was needed and the focal animal needed to be placed in foliage so that the observer could see the mouth of the individual.

Calculation of feeding ingestion rates

Ingestion rate is an important component when determining primate energy intake and should be calculated when possible (Schülke et al., 2006), as feeding time may differ from intake rate. Hladik (1977) was the first to report that intake rate varied depending on the food item consumed. Calculating food ingestion by multiplying average ingestion rates of food items by feeding time was found to deviate from true ingestion amounts by 8-50% (Zinner, 1999). Rate of ingestion was calculated for every feeding bout recorded by dividing the total number of bites consumed per bout by the feeding bout length and then transforming intake rate to represent hourly rates (Equation 3.0). There is no unified definition of intake rate (Nakagawa, 2009) and multiple methods have been used to determine this variable (cf. Hladik, 1977; Stacey, 1986; Shopland, 1987; Janson, 1988; Schulke et al., 2006;

Gould et al., 2011). Average intake rates of all feeding bouts and average intake rates for specific food types (flowers, leaves, etc.) were then computed for each focal animal. As noted in Gould et al., 2011, this methodology is important because the amount of data collected per individual varied (some individuals were observed for approximately 16 hours whereas one individual was observed for 21 hours). All feeding intake rate data represent bite rate per hour, as number of bites was the measurement recorded.

$$\frac{\#\,\text{bites consumed}}{\text{length(sec) feeding bout}} = \text{intake rate} \rightarrow \text{intake rate*3600=(hourly) intake rate}$$

Equation 3.0 Calculation of intake rate per individual feeding bout

Calculation of water content for plant species and food type

Plant samples consumed by *P. verreauxi* were collected from the same plants used by the focal animals on the same day the sample was consumed to ensure proper identification and accurate description of diet. Samples were also collected to determine water content of the food items consumed. When possible, twenty representative amounts of plant sample ingested (flowers, leaves, etc.) were collected. The sample was then weighed using a portable scale (My Weigh DuraScale D2 300), which was accurate to 0.01g, and the wet weight was recorded. Samples were then hung or placed to dry indoors for a minimum of three days and then weighed and recorded again for dry weight. Average weight for each food item consumed was calculated. If ten full size leaves were collected of a species but a typical bite for an individual would only have been half of a leaf, calculations were adjusted to report average water content for one bite's worth of the sample (see Equation 3.1). Samples were not hung outside due to the concern the abundance of habituated lemurs around the reserve would consume the samples. As data collection occurred during the dry season, humidity was low throughout the study period. No biological samples were exported from Madagascar.

$$\frac{\text{avg water content (g) of one sample}}{\text{approx. \# of bites required to ingest one sample}} = \text{avg water content per bite of food item}$$

Equation 3.1. Calculation of water content when item was not wholly ingested in one bite. Example of "one sample" includes large, mature leaf ingested in multiple bites.

Mean total water intake (grams) for each sex was calculated by computing the total water intake of each individual (multiplying the number of bites by the water content per bite for each plant species and part). Once total water intake was calculated for each individual, averages were computed for each sex by summing total water intake rate per individual and then dividing this sum by the number of individuals for each sex.

3.4 PHENOLOGY

Phenological transects are used to describe leaf, flower, and fruit availability of the forest based on random samples and are an appropriate choice of measurement in heterogeneous habitats because they sample increased variety of microhabitats (Ganzhorn, 2003). Measurements allow for an understanding of seasonal changes in habitat types and food abundance for primates (Ganzhorn, 2003). Understanding seasonal changes in food availability is difficult because detailed data of the species' diet are needed prior to phenological measurement (Ganzhorn, 2003). Two phenological transects (One in Ankoba forest and one in Malaza forest) were constructed approximately one and a half weeks into the research project, after study troops were selected, and an idea of the types of foods the animals consumed was obtained. Vegetation was tagged with flagging tape and assigned a number for identification if it met the following conditions: 1) it was roughly three meters from the transect line, 2) it had a DBH greater than 10cm, and 3) if the sifakas had been observed feeding on the species. Measuring vegetation with a DBH greater than 10cm is standard (Chapman et al., 1990; Ganzhorn, 2003) in order to exclude immature vegetation. Any vegetation meeting the first two requirements that the sifakas may have fed on, based on the knowledge of my Malagasy assistant, was also included. The Ankoba forest transect was approximately fifty meters long. The Malaza forest transect was approximately 75 meters long in order to include all species the sifakas had been observed consuming. In total, phenological data were collected on sixteen trees.

Phenological data were recorded every two weeks (Ganzhorn, 2003). Abundance of plant parts was rated on a relative scale from 0 to 4 (Ganzhorn, 2003), with the following plant parts recorded: young leaves, mature leaves, flowers, ripe fruit, and unripe fruit. A rating of 0 indicates not present, 1 indicates item is present in less than 25% of the tree or shrub's foliage, 2 25% or greater but less than 50%, 3 50% or greater but less than 75%, and 4 75% or greater but less than 100%. Both my Malagasy assistant and myself were present for phenological data collection to agree upon ratings.

3.5 DATA ANALYSIS

Data from field notebooks were entered into Microsoft Excel 2011, version 13. Data were then exported into the statistical software RStudio, versions 97.332 and 98.501. Sample size (n=5 for both sexes) was not large enough to reach normal distribution in my study, thus nonparametric tests, in which normal distribution is not assumed, were appropriate. Graphs were made using the package "ggplot2" (Wickman, 2009).

The package "sm" (Bowman and Azzalini, 2014) was used to obtain a kernel density plot of intake rates for males and females of all food types consumed. A popular alternative to the histogram, kernel density estimation places a kernel on each value (Parzen, 1962). It is preferred to histograms because, as n converges to infinity, the kernel density estimate converges in mean square and in probability to the true probability density function (Parzen, 1962; Duda et al., 2001). Also, histograms are sensitive to the number of bins used and thus using different bins can result in different histogram shapes (Levy, in progress).

Chi square goodness of fit test was used to determine differences of observed and expected values in activity budget of both sexes and of each sex separately. The Chi square test measures the association of two variables by two-way tables of observed values and theoretical values (Daniel, 2009).

A linear model was used to determine if water content of plant species and plant parts differed significantly. Because the water content of a single young leaf could not be measured given the scale used (accurate to 0.01g) and water content of young leaves represented the summed wet weight of multiple young leaves minus the summed dry weight of multiple leaves, this plant part was not factored into the linear model.

The Mann-Whitney *U*-test was used to examine if sex-based differences in feeding intake rate, activity budget, most frequently consumed plant species, plant species comprising the highest proportion of total feeding time, and differences in water content existed. The Mann-Whitney *U*-test determines if two samples are from the same population (Daniel, 2009). It is the nonparametric equivalent of the Student's *t*-test and does not assume normal distribution. Because multiple Mann-Whitney *U*-tests were run on the same data set, p-values were Bonferroni corrected and significance level set to 0.002. The Bonferroni correction controls for the likelihood of making type I errors when performing multiple comparisons (Dunnett, 1955).

CHAPTER FOUR: RESULTS

4.0 HOME RANGE

Home range at the time of study was measured to be 0.74, 0.66, and 0.48 ha for A1, A2 and Malaza respectively. Home range of A2 overlapped with that of A1 (Figure 4.0). A1, A2, and M troops were observed for approximately a total of 43:44, 46:07, and 21:43 hours and minutes each respectively.

Figure 4.0 Home ranges of troops studied. Polygons from left to right are the home ranges for A2, A1, and M. Google Earth 7.1 Accessed on July 31, 2014.

4.1 FOREST TREE PHENOLOGY

Figures 4.1, 4.2, and 4.3 display the phenological data for the duration of the study period for flowers, young leaves, and mature leaves respectively. Of the sixteen trees samples, *P. verreauxi* was observed feeding on all but *Bauhirria sp. Morua alba,* and *Albizia polyphylla*. Mature leaves were widely available during the study and young leaves were observed on five and six trees at the start and the end of sampling period, respectively. Two species were observed flowering during my study: *Pithecellobium dulce* and *Rinorea greveana*. *P. verreauxi* was observed consuming flowers from both of these species. The only fruit available during the study period was ripe fruit from the *Tamarindus indica* trees and *P. verreauxi* was observed consuming this food item.

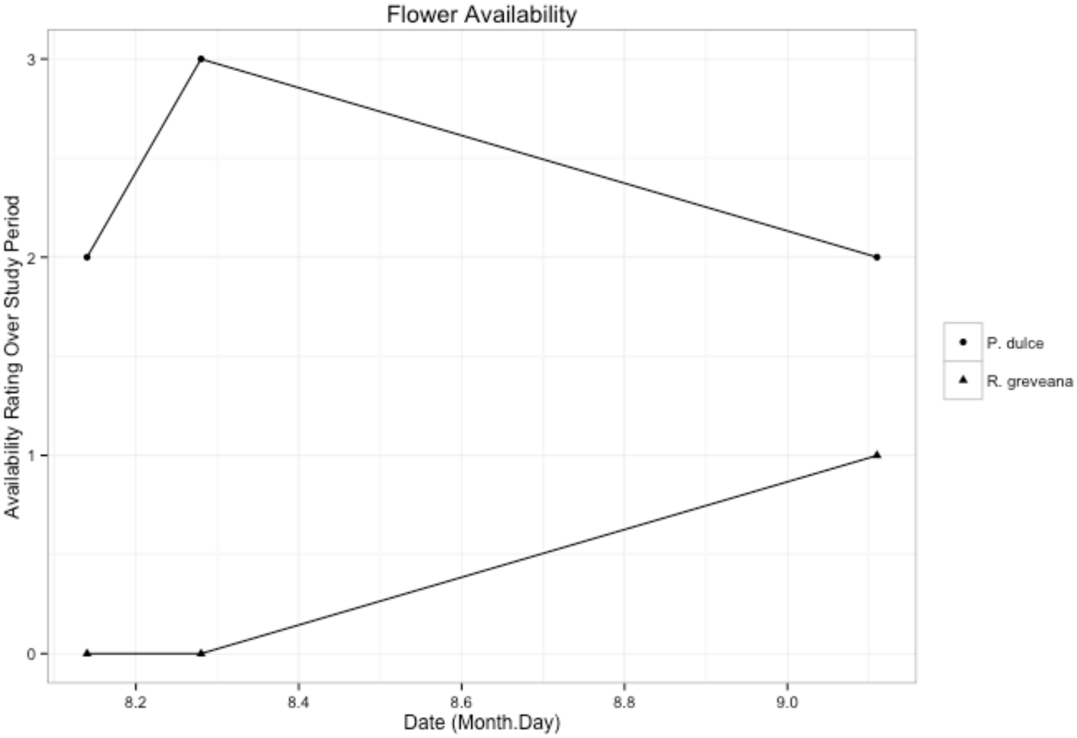


Figure 4.1 Flower availability over course of study. A rating of 0 indicates not present, 1 indicates item is present in less than 25% of the tree or shrub's foliage, 2 25% or greater but less than 50%, 3 50% or greater but less than 75%, and 4 75% or greater.

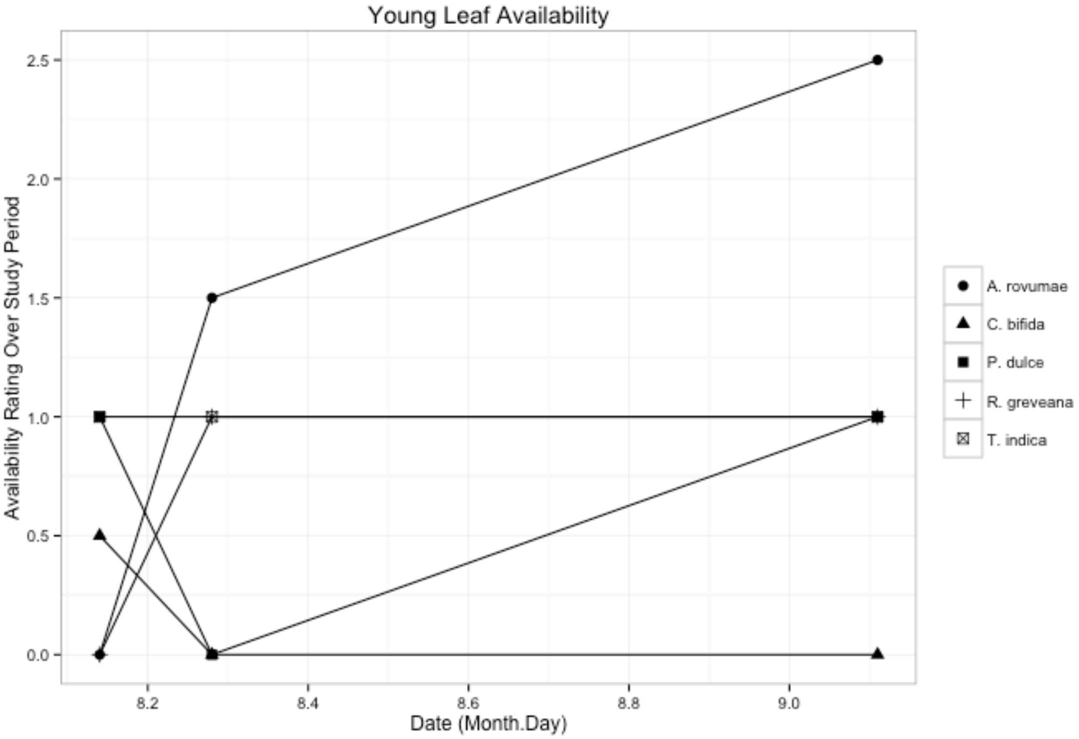


Figure 4.2 Young leaf availability over course of study. A rating of 0 indicates not present, 1 indicates item is present in less than 25% of the tree or shrub's foliage, 2 25% or greater but less than 50%, 3 50% or greater but less than 75%, and 4 75% or greater.

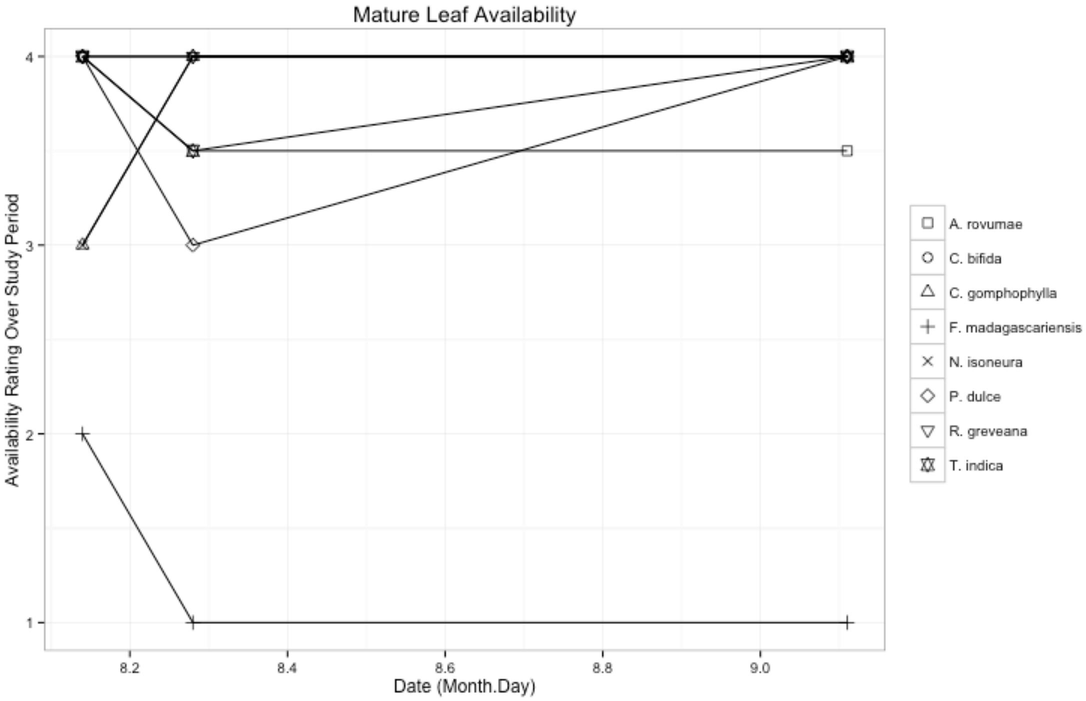


Figure 4.3 Mature leaf availability over course of study. A rating of 0 indicates not present, 1 indicates item is present in less than 25% of the tree or shrub's foliage, 2 25% or greater but less than 50%, 3 50% or greater but less than 75%, and 4 75% or greater.

4.2 INTAKE RATES OF MALES AND FEMALES: ALL FOOD TYPES

The difference in average intake rates (measured in bites per hour) of males and females, regardless of food type or plant species, did not reach significance (U_{10}=3 [subscript denotes sample size for test is 10], P=0.06; male intake rate = 1130.15 bites/hour, SD=145.74; female intake rate = 935.07 bites/hour, SD=139.51). Figure 4.4 shows the distribution of average intake rate values of both males and females.

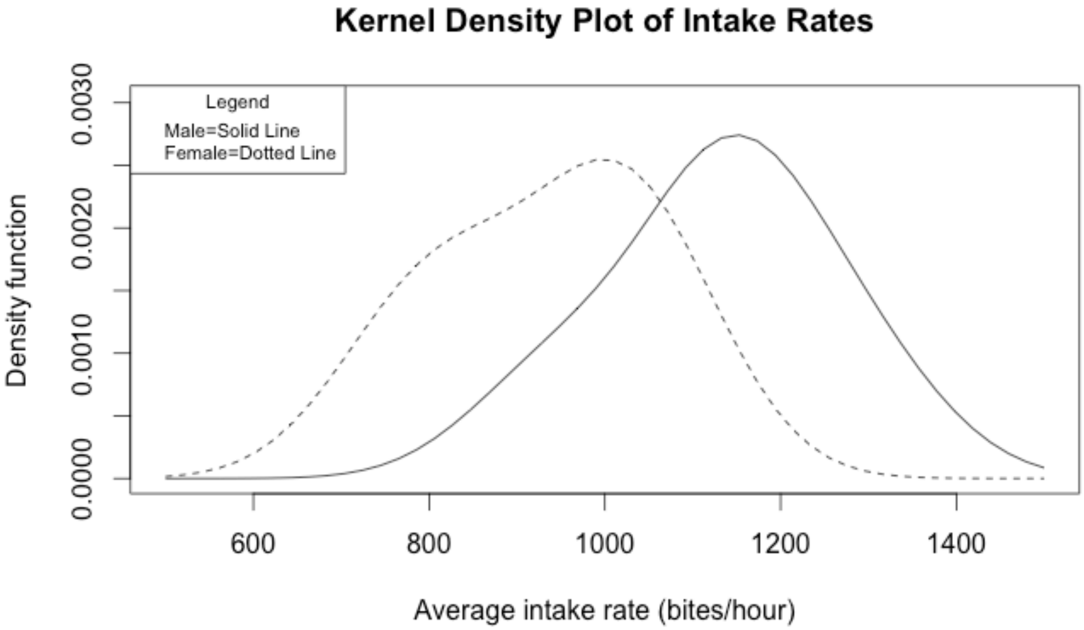


Figure 4.4 Kernel density plot showing the distribution of average intake rate values of both sexes (females N=5, males N=5) of all food types consumed over six weeks. Refer to table 3.2 for exact lengths of time individuals were observed.

4.3 INTAKE RATES OF MALES AND FEMALES: BY FOOD TYPE

Flowers

Males and females did not differ in the average intake rate of flowers (U_{10}=3, P=0.06), mature leaves (U_{10}=3, P=0.6), or young leaves (U_{10}=3, P=0.06).

Figures 4.5 and 4.6 illustrate intake rates of the sexes regardless of food type consumed and by food type.

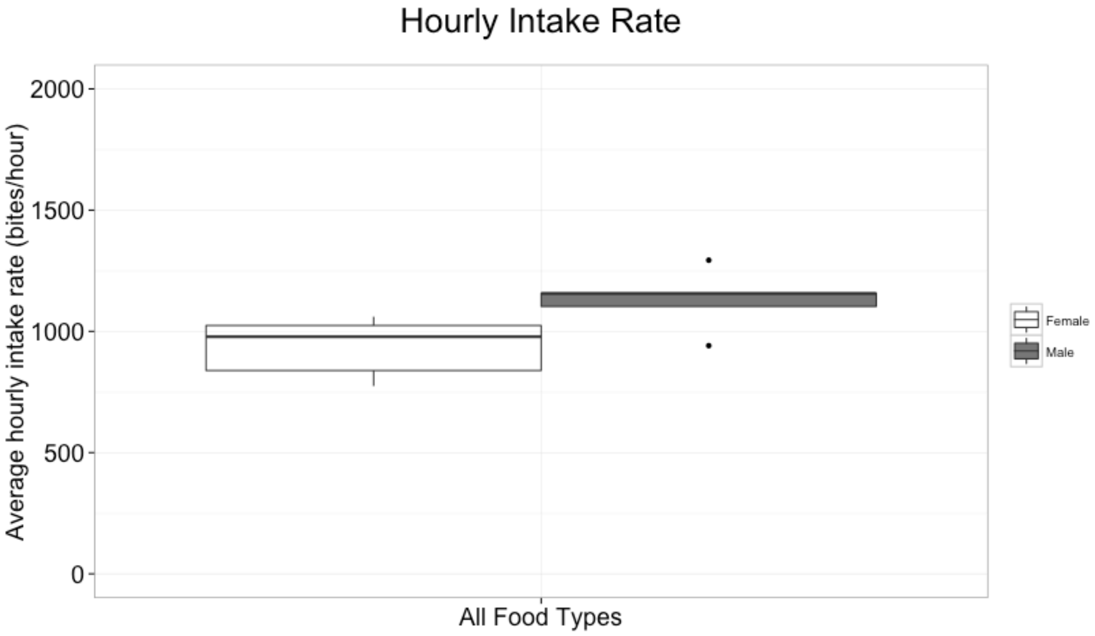


Figure 4.5 Average hourly intake rates regardless of food type consumed. Whiskers are the first and third quartiles. Bars indicate median values and diamonds mean values. Outliers plotted as individual points.

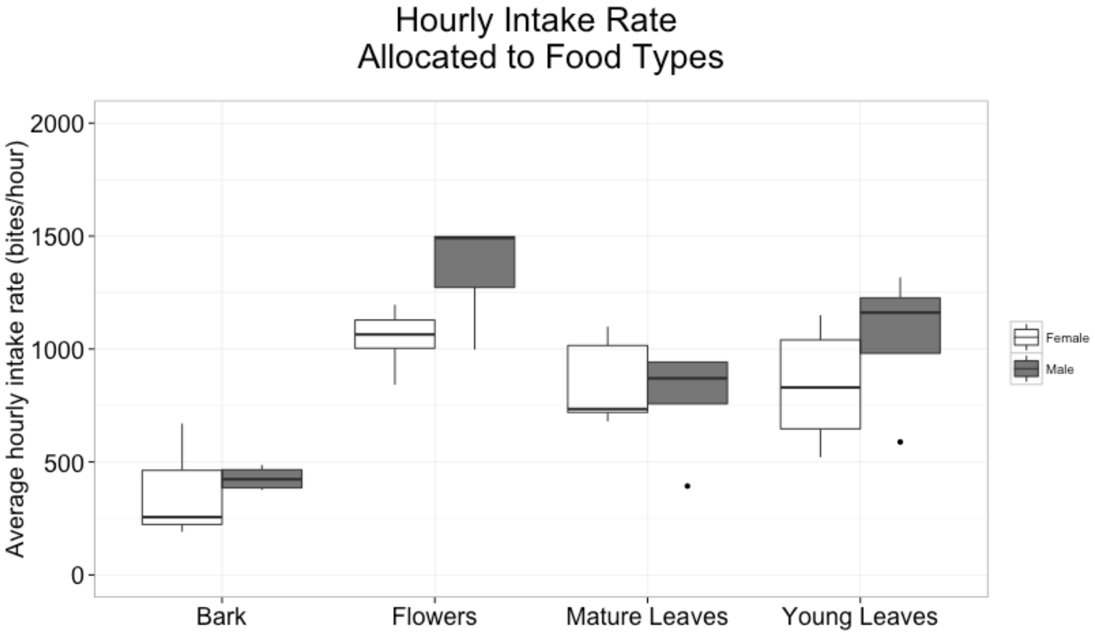


Figure 4.6 Average hourly intake rates by food type consumed. Whiskers are the first and third quartiles. Bars indicate median values and diamonds mean values. Outliers plotted as individual points. Note: sample size for bark was too small to test for significant differences (n=4 for both males and females).

4.4 PROPORTION OF TIME DEVOTED TO FEEDING ON SPECIFIC FOOD TYPES

Males and females did not differ in the average percentage of feeding time devoted to any of the three food types (flowers: U_{10}=13, P=1.0, mature leaves: U_{10}=17, P=0.42, young leaves: U_{10}=8, P=0.42). Figure 4.7 illustrates average proportion of time allocated to each food type.

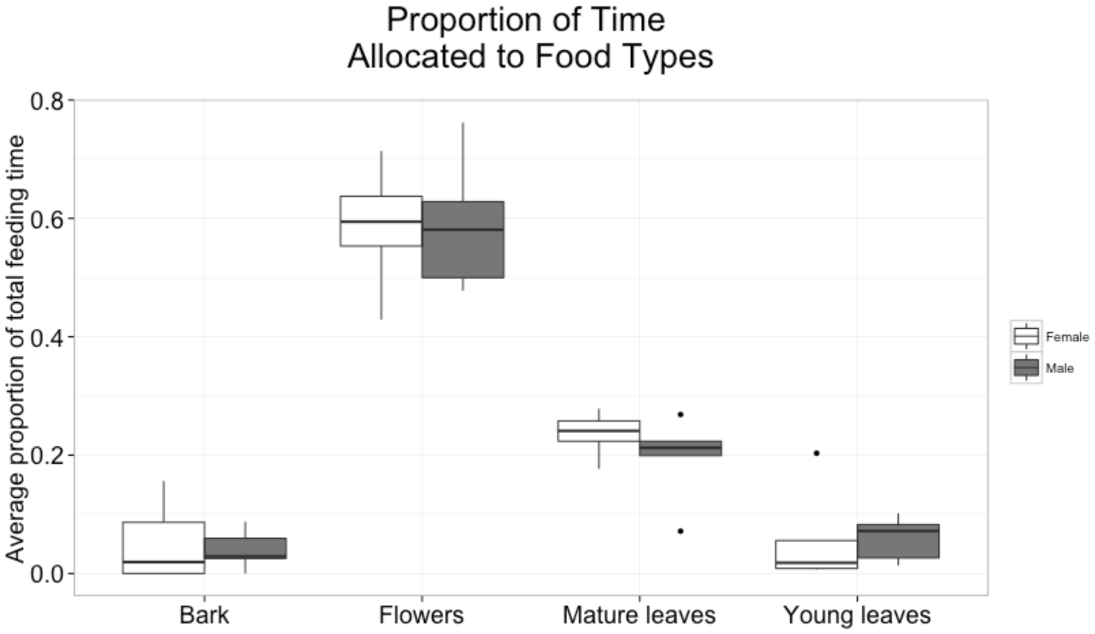


Figure 4.7 Average proportion of total feeding time devoted to specific food type. Whiskers are the first and third quartiles. Bars indicate median values and diamonds mean values. Outliers plotted as individual points. Note: sample size for bark was too small to test for significant differences.

4.5 PROPORTION OF TIME DEVOTED TO SPECIFIC BEHAVIORS

Activity budgets for males and females were analyzed using the chi square goodness of fit test and comparisons between males and females examined through the Mann-Whitney *U*-test. Chi square analysis showed substantial deviation in the proportion of time devoted to each behavior from expected values in which time was equally distributed amongst all behaviors (χ^2=234.97, P=<0.0001, n=10). When each sex was analyzed separately, males and females both differed significantly from expected values (χ^2=223.36, two-tailed P =<0.0001, n=10 and χ^2=252.91, two-tailed P =<0.0001, n=10 for males and females respectively). Major contributors to the significant χ^2 value found for female behaviors, as determined by standardized residuals greater than 2.0, which indicate that there is a significant difference between observed and expected frequencies (Tabachnick and Fidell, 2001), include other (-3.3), feed (10.2), allo-groom (-2.8), play (-3.3), rest (10.6), scent-mark (-3.3), vigilance (-3.1), vocalization (-3.3) (negative values indicate the behavior occurred less than expected). Major contributors to the significant χ^2 value found for male behaviors, as determined by standardized residuals greater than 2.0, include other (-3.3), feed (8.3), allo-groom (-2.9), play (-2.2), rest (10.8), scent-mark (-3.2), vigilance (-3.1), vocalization (-3.3).

Females allocated more time to feeding than did males (U_{10}=25, P=0.01). Males spent a significantly greater proportion of time devoted to scent-marking than did females (U_{10}=1.5, P=0.02). Males also allocated a greater proportion of time to playing than did females (U_{10}=2.5, P=0.03). However, given that multiple tests were conducted on the same data set, the significance of these results should be interpreted carefully. The aforementioned p-values are higher than the Bonferroni calculated p-value (P=0.002).

Males and females did not differ in the proportion of time devoted to any behavior: allo-grooming (U_{10}=10, P=0.68), resting (U_{10}=10, P=0.68), locomoting (U_{10}=9, P=0.53), self-grooming (U_{10}=8, P=0.42), vigilance (U_{10}=13, P=1.0), or vocalizing (U_{10}=9, P=0.49).

Figures 4.8 illustrate the average percentage of time spent in each behavior for males and females.

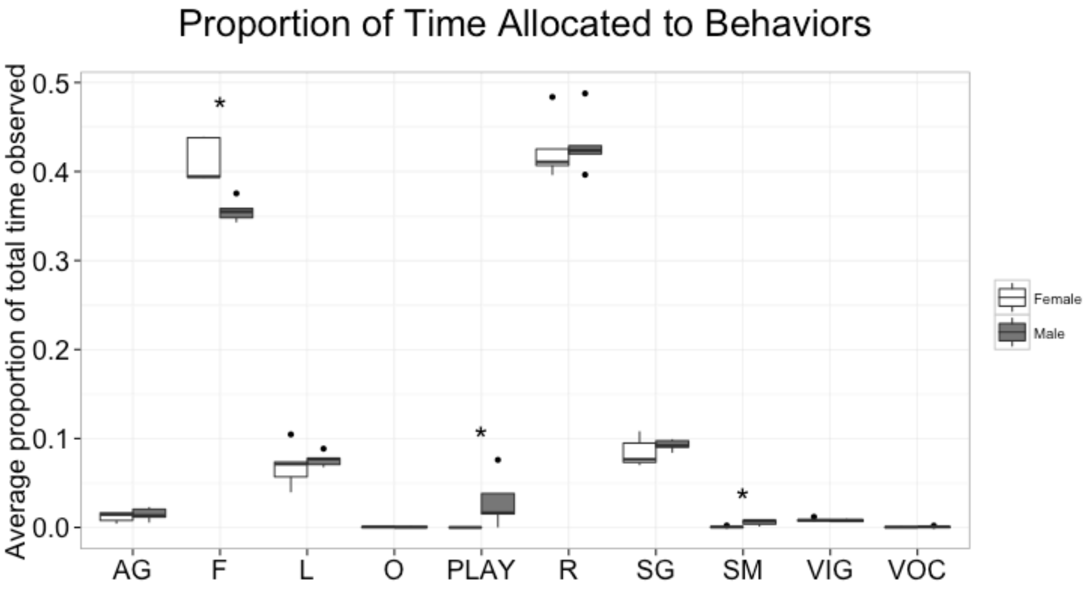


Figure 4.8 Average proportion of total time observed allocated to behaviors. Whiskers are the first and third quartiles. Bars indicate median values and diamonds mean values. Outliers plotted as individual points. (AG=Allo-groom, F=Feed, L=Locomote, O=Other, R=Rest, SG=Self-groom, SM=Scent-mark, VIG=Vigilance, VOC=Vocalize.) Asterisks indicate significant differences between males and females.

4.6 AMOUNT OF FOOD CONSUMED

Accounting for time observed feeding (by taking total food consumed divided by the amount of observation time the focal was observed over the study), males and females did not differ in the total amount of food consumed (U_{10}=22, P=0.55). On average, males consumed 1197.28 (SD=117.41) and females 1009.63 (SD=112.17) total bites of food over the duration of my study (Figure 4.9).

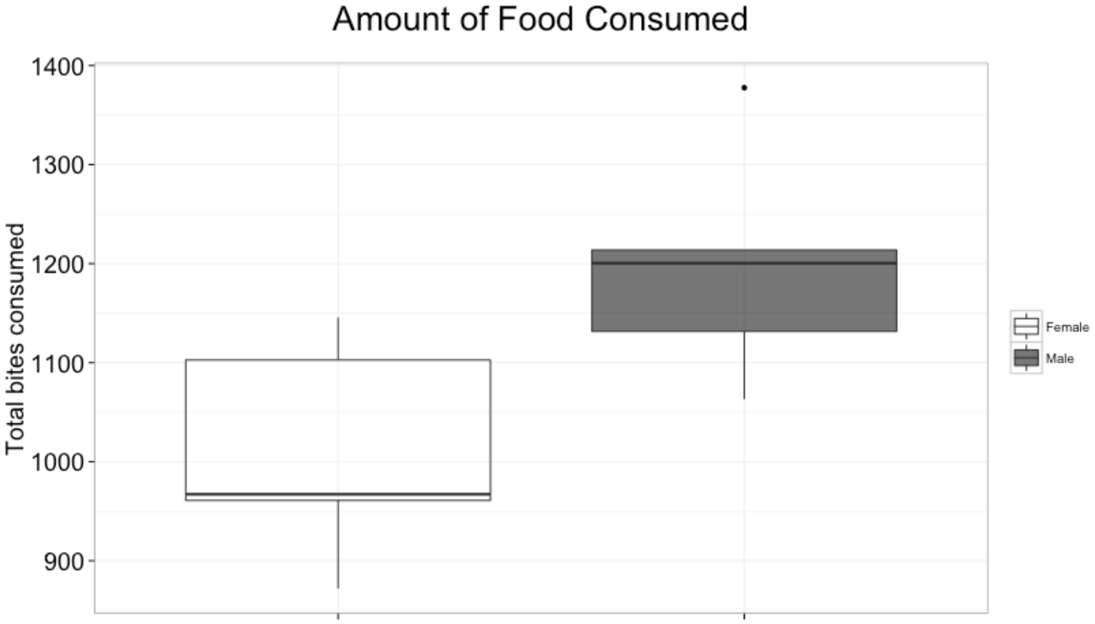


Figure 4.9 Total amount of food each individual consumed over course of study. Whiskers are the first and third quartiles. Bars indicate median values and diamonds mean values. Outliers plotted as individual points.

4.7 ANALYSIS OF PLANT SPECIES CONSUMED

Table 4.0 details the food items consumed and the percentage of feeding time all focal animals allocated to those items. *P. verreauxi* consumed thirteen plant species over the course of the study, four of which are not endemic to the area. Refer to Figure 4.7 for the percent of total feeding time devoted to each plant part regardless of species.

Table 4.0 Species consumed along with plant parts consumed, percentage of total feeding time allocated to species, and number of feeding bouts allocated to species.

Species	Percent of total feeding time for females	Percent of total feeding for males	Plant parts consumed	Recorded instances of females feeding on this species	Recorded instances of males feeding on this species
Acacia rovumae	17.00	12	FL, ML, YL	103	68
Azadirachta indica†	6.00	5	Bark, YL	34	32
Celtis gomphophylla	<1.00	<1.00	ML	3	1
Cordia sinensis†	0.00	<1.00	ML, YL	0	6
Crateva excelsa	1.00	1	ML	4	10
Ficus madagascarensis	1.00	2	FL, ML, YL	11	19
Grewia saligna	0.00	<1.00	ML	0	1
Neotina isoneura	<1.00	<1.00	ML	4	5
Pithecellobium dulce†	66.00	76	FL, ML, YL	490	498
Quisivanthe papinae	0.00	<1.00	ML	0	4
Rinorea greveana	3.00	1	FL, ML	41	20
Strychnos madagascariensis	1.00	0	ML	2	0
Tamarindus indica†	3.00	<1.00	ML, YL, Fruit	29	4

†= Species not native to Madagascar.

Most frequently consumed plant species as determined by number of feeding bouts

Table 4.0 details the number of feeding bouts allocated to the thirteen species *P. verreauxi* consumed during my study. The species *P. verreauxi* devoted the greatest number of feeding bouts to, *P. dulce*, was consumed five times more frequently than the second most frequently consumed species, *A. rovumae*.

The top five plant species consumed, as determined by the number of feeding bouts, was calculated for each sex separately. In comparing these rankings for males and females, the top four most frequently consumed plant species were identical for both sexes. Females and males differed only in the fifth ranking, with *T. indica* and *F. madagascariensis* ranking fifth for female and males respectively (Table 4.0).

The top five most frequently consumed species regardless of sex were determined and analyzed in a Mann Whitney *U*-test. No significant sex-based differences were found in the number of feeding bouts of *P. dulce* (U_{10}=12, P=1.0), *A. rovumae* (U_{10}=19, P=0.21), or *A. indica* (U_{10}=12.5, P=1.0) or *T. indica* (U_{10}=21, P=0.08) (Figure 4.10). However, there were significant differences in the frequency of feeding bouts for *R. greveana* (U_{10}=24, P=0.02) with females consuming this species more frequently than males (Figure 4.10). Because multiple tests were conducted on the same data set, the significance of this reported difference between the sexes in *R. greveana* should be interpreted carefully. The aforementioned p-value is higher than the Bonferroni calculated p-value (P=0.002).

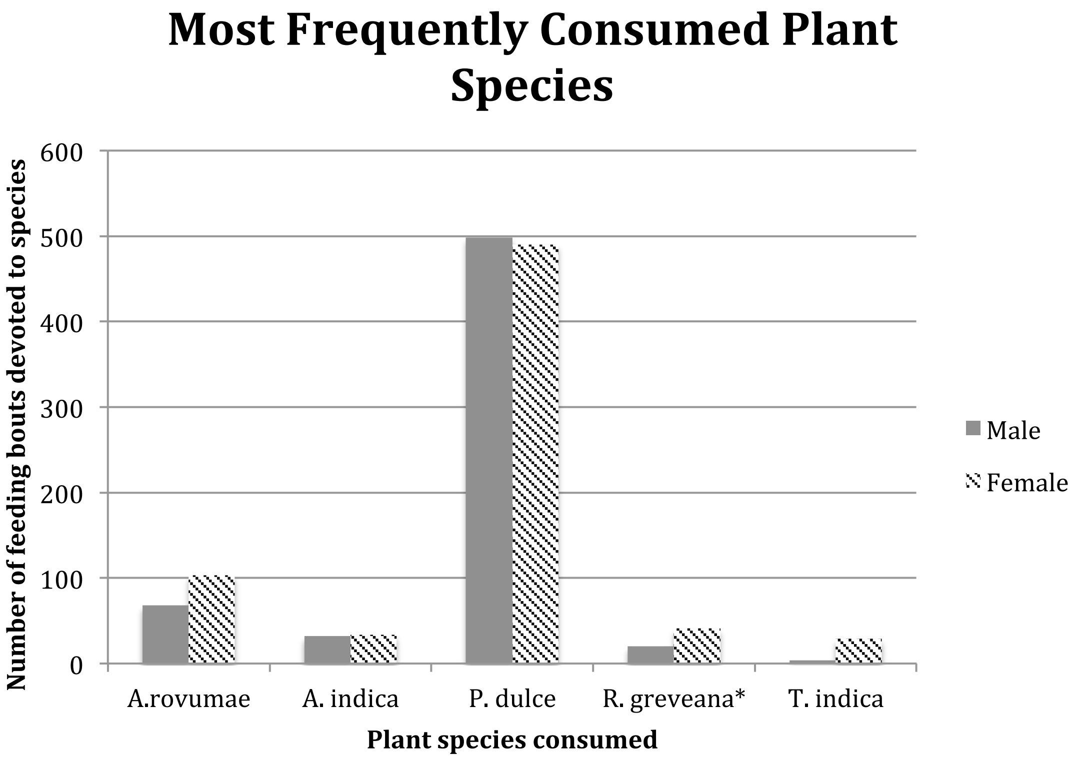


Figure 4.10 Most frequently consumed plant species determined by number of feeding bouts. Asterisks indicate significant differences between the sexes.

Amount of time devoted to specific plant species as a percentage of total feeding time

Table 4.0 details the percentage of total feeding time allocated to each species. Of all species on which *P. verreauxi* was observed feeding, over 78% of feeding time was allocated to non-native plant species.

To test for sex-based differences in the plant species comprising the greatest proportion of *P. verreauxi* feeding time as listed in Table 4.0, the Mann-Whitney *U*-test was used. Proportion of total feeding time for males and females for the top five species (regardless of sex) were analyzed. There were no significant differences between the sexes when comparing *P. dulce* (U_{10}=5, P=0.15), *A. rovumae* (U_{10}=21, P=0.10), *A. indica* (U_{10}=12.5, P=1.0), and *T. indica* (U_{10}=19.5, P=0.16). There was a significant difference between the sexes in time devoted to *R. greveana* (U_{10}=25, P=0.01) with females allocating more time to this species. Figures 4.11 displays the proportion of feeding time devoted to the top plant species.

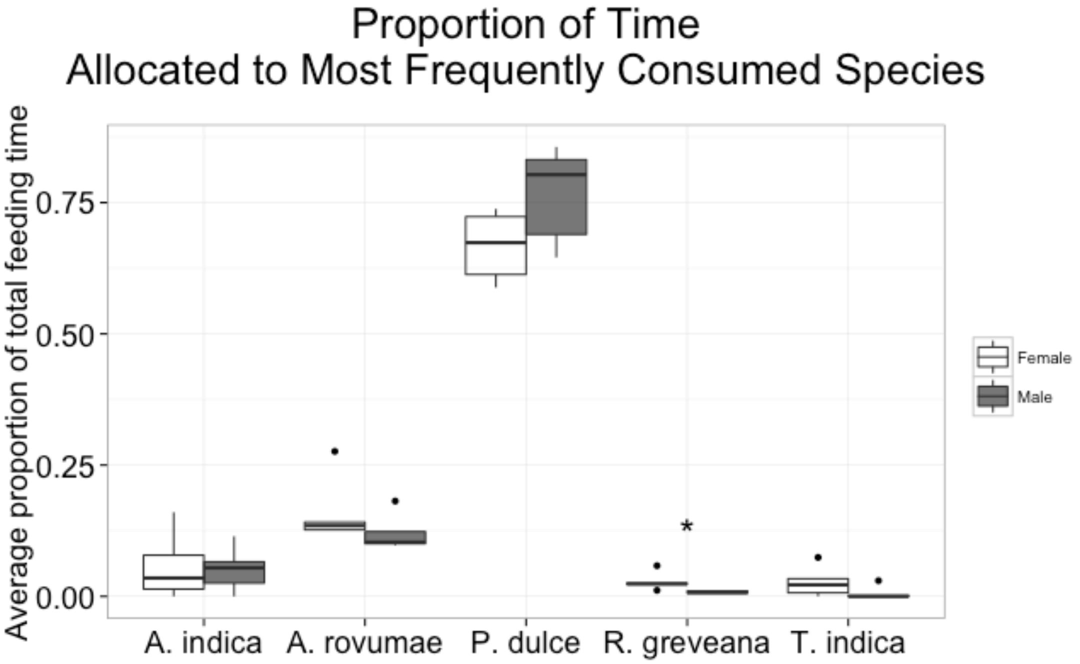


Figure 4.11 Average proportion of total feeding time allocated to species. Whiskers are the first and third quartiles. Bars indicate median values. Outliers plotted as individual points. Asterisk indicates significant differences between males and females.

Mann-Whitney *U*-tests for sex-based differences in the percentage of total feeding time devoted to each species/food type showed no significant difference of *A. rovumae* mature leaves (U_{10}=18, P=0.31), *A. rovumae* young leaves (U_{10}=13, P=1.0), *C. gomphophylla* mature leaves (U_{10}=13, P=1.0), *F. madagascariensis* mature leaves (U_{10}=10.5, P=0.75, *N. isoneura* mature leaves (U_{10}=10, P=0.61), *P. dulce* flowers (U_{10}=12, P=1.0), *P. dulce* mature leaves (U_{10}=9, P=0.55), *R. greveana* flowers (U_{10}=17, P=0.42), or of *T. indica* mature leaves (U_{10}=18.5, P=0.24). A significant difference was found in the proportion of feeding time devoted to *R. greveana* mature leaves between males and females (U_{10}=21, P=0.01). As before, this result should be interpreted with caution, because the aforementioned p-value is higher than the Bonferroni calculated p-value (P=0.002).

4.8 WATER CONTENT ANALYSIS

Water content was measured and calculated for ten combinations of plant species and food type. The average water content of one bite's worth of each food item is shown in Table 4.1.

Table 4.1 Percentage of feeding time and average water content of each plant species and part.

Species	Plant part	% of total feeding time devoted to food item	Average water content of one mouthful of food item (grams)	Average water content of one leaf/flower (%)
A. rovumae	ML	11.42	0.00	
A. rovumae	YL	2.89	0.00	26.47
C. gomphophylla	ML	0.06	0.14	51.90
F. madagascariensis	ML	1.44	0.25	86.10
N. isoneura	ML	0.25	0.15	55.70
P.dulce†	FL	57.07	0.10	71.82
P.dulce†	ML	3.82	0.05	40.38
R. grevenea	FL	0.76	0.11	65.68
R. grevenea	ML	1.06	0.06	60.16
T. indica†	ML	1.08	0.01	43.31

(FL=flowers, ML=mature leaves, YL=young leaves). †= Species not native to Madagascar.

A linear model was used to determine the relationship between water content and plant species and food type (flowers or mature leaves) consumed (Table 4.2).

	Estimate	Std. error	t-value	p-value
Intercept	0.60	0.05	12.24	<0.001
F. madagascariensis	0.35	0.05	7.70	<0.001
N. isoneura	0.03	0.05	0.58	0.56
P. dulce	-0.11	0.04	-2.58	0.01
R. greveana	0.08	0.04	1.92	0.06
T. indica	-0.09	0.06	-1.58	0.12
Mature Leaves	-0.08	0.04	-2.17	0.03

Table 4.2 Linear model used to determine relationship between water content and plant species and food type.

Of the species measured, *F. madagascariensis* and *C. gomphophylla* had the highest water content on average (Table 4.2). Water content for *N. isoneura* was also high but the p-value for this species was not significant (Table 4.2). None of these three species made up a particularly large quantity of *P. verreauxi* feeding time (Table 4.1). Indeed, the species that composed a high amount of feeding time, *P. dulce*, had significantly lower water content. Mature leaves had lower water content when compared to flowers.

Average observed water intake of males and females

Average observed water intake (measured in grams) did not differ between males and females (U_{10}=13, P=1.0). Total observed water intake was 526 (SD=138.80) grams and 500.47 (SD=109.69) grams on average for males and females respectively.

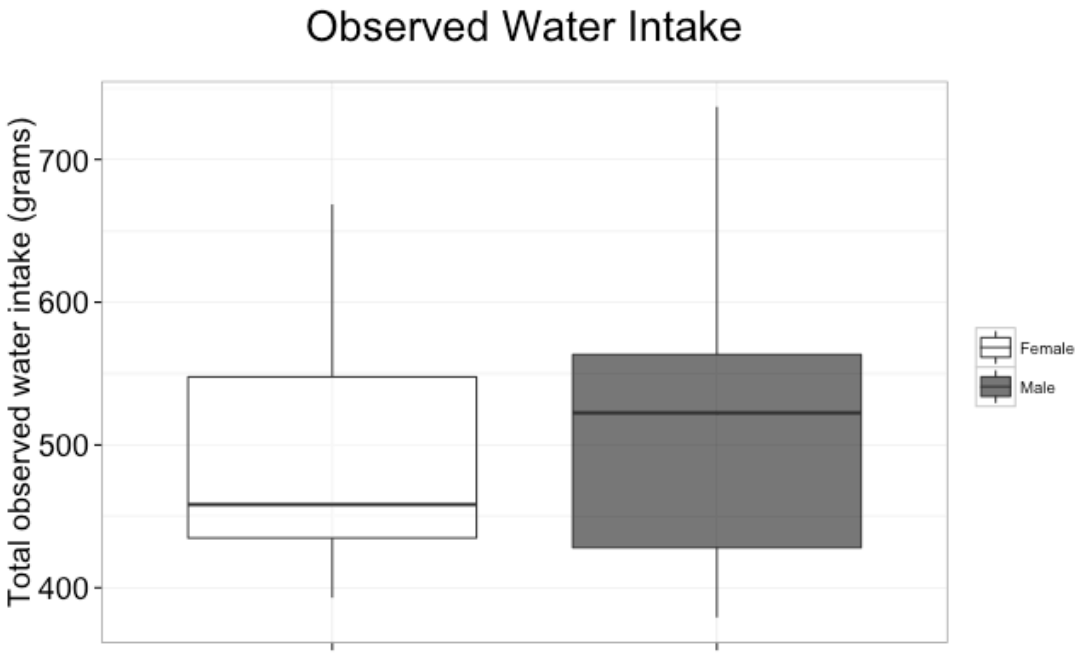


Figure 4.12 Total observed water intake of males and females. Whiskers are the first and third quartiles. Bars indicate median values. Outliers plotted as individual points.

4.9 POST-HOC POWER ANALYSIS

Because sample sizes were so small for this research (n=5 for females and for males), a post-hoc power analysis was completed. Post-hoc power analyses inform the researcher if he/she had adequate sample sizes to determine with statistics the effect found. Effect sizes ranged from 0.02 to 3.32 for the Mann Whitney *U*-tests completed. With a significance level of p=0.05, an effect size of roughly three gives a significant power of 0.8. However, with the Bonferroni corrected significance level of p=0.002, an effect size slightly over four is needed to achieve the same power of significance, an effect size which was not reached for any of the tests performed.

CHAPTER FIVE: DISCUSSION

5.0 KEY FINDINGS

The purpose of my study was to determine if lactating female *Propithecus verreauxi* exhibit any differences in diet or behavior compared to males. My results do not overwhelmingly suggest females employ behavioral and dietary changes in comparison to males during the early stage of lactation. Males had a slightly higher intake rate in total, although this difference approached but did not reach significance, when compared to females. Females devoted a greater portion of time to feeding than did males but both sexes allocated similar amounts of time to resting (Figure 4.8). Females and males did not differ significantly in the amount of total food consumed (Figure 4.9) or total water intake on average (Figure 4.12).

5.1 FEEDING DIFFERENCES

Intake Rate

Considering the costs of lactation, one method females might use to counter this stress is to increase the amount of total food consumed by feeding at a greater rate in comparison to males. Alternative hypothesis 1 states that there is a difference in intake rate between the sexes, and I predicted females would feed at a higher intake rate (bites per hour) than males during the period of the study.

When examining intake rates for all food types and plant species, males fed at a somewhat higher intake rate (bites per hour) than did females on average, but this was not significant. Thus I failed to reject null hypothesis one. Four of the five focal males fed at rates of higher than 1100 bites per hour on average, whereas only two of the five females fed at rates greater than 1000 bites per hour on average over the course of my study. These results concur with earlier research that found lactating *Propithecus edwardsi* females did not differ from males in intake rate (Hemingway, 1999). Data are limited on other members of the genus *Propithecus* as studies on sex-based differences in diet have yet to be conducted.

However, findings on sex-based differences in intake rate are available from studies on other Strepsirhine species. My results are consistent with the majority of findings published on *L. catta,* which have not found sex-based differences in intake rate (Sauther, 1992; LaFleur, 2012; Gould et al., 2011). Although, Rasamimanana (1999) found that *L. catta* males in gallery forest in Berenty were more efficient at feeding than females in all seasons, possibly because females were more selective in foods consumed. It is possible a more selective feeding criterion could be the reason why female intake rate was slightly low in comparison to males for *P. verreauxi* during my study. Overdorff and colleagues (2005), studying sex-based differences in intake rates of male and female black-and-white ruffed lemurs (*Varecia variegata*), report one female fed at a higher intake rate and one at a lower intake rate when compared to males. Thus, results from my study are inconsistent with Overdorff and colleagues ’ findings (2005).

Varying habitat, social systems, physiology and/or other interspecies differences may cause my results to conflict with those reported for other species. (Limitations such as sample size, temporal constraints, and others are discussed in Section 5.7 titled, “Limitations of Study.”) Lemuriformes, including *P. verreauxi,* are found in differing forest types (spiny, gallery, deciduous dry), which will obviously affect the types of foods that may be consumed. Species also have specific adaptations that influence nutrient absorption (Chapman et al., 2012), such as the sacculated stomach found in colobine monkeys that allows them to break down cellulose and hemicellulose in plant walls (Milton, 1996). Socioecological differences, such as lower food intake values due to feeding competition in large groups, differing social statuses, or varying female social relationships (Janson, 1988; van Schaik, 1989; Janson and Goldsmith, 1995), will also cause interspecies differences in dietary behavior.

Food Type Consumed

Examining potential differences in food types consumed is one method of studying primate diet. Generally speaking, flowers have high to moderate levels of protein, low to moderate levels of fiber, and moderately accessible calories overall

(Milton, 1996). Although variable across species, fruits are a source of readily accessible calories, high in nonstructural carbohydrates, low in protein, and contain moderate levels of fiber (Milton, 1987; Milton, 1996; Simmen et al., 1999; Ortmann et al., 2006). Mature leaves are generally low in terms of readily accessible calories, and contain moderate levels of protein, and high levels of fiber (Milton, 1996; Lambert, 2011). Again, although variable across species, immature leaves are characteristically low in terms of readily accessible calories, high in protein and contain moderate levels of fiber (Milton, 1996; Ortmann et al., 2006; Lambert, 2011). Protein: fiber ratios of leaves are positively correlated with folivorous primate biomass (Waterman et al, 1984; Oates et al., 1990; Ganzhorn, 1992; Davies 1994; Chapman et al., 2002). Shoots, flowers, and fruit are more commonly consumed than mature leaves because of higher protein levels and lower levels of fiber found in these items (Clutton-Brock, 1977; Milton, 1987; Hamilton and Galdikas, 1994; Conklin-Brittan et al., 1998; McConkey et al., 2003). Protein intake levels are highest when *P. verreauxi* in Kirindy consume flowers and fruits (Norscia et al., 2006).

Assumed differences in energy and nutritional content dependent on food type may result in females consuming specific food types at a different rate than males. Alternatively, females may devote a larger proportion of their total feeding time to specific food types in comparison to males. Two reproductive strategies, income and capital breeding, are relevant to this discussion (examined in detail in Section 5.6). Capital breeders accumulate and store energy needed for reproduction, whereas income breeders increase food intake simultaneously with gestation and lactation (Thomas, 1988; Stearns, 1992). Female *P. verreauxi* are dominant over males in feeding situations, thus they can make behavioral changes to cope with the increased costs of lactation and acquire preferred food items at a greater frequency than males. There were no differences between the sexes in the amount of feeding time or in average intake rate of any food type consumed, therefore I failed to reject null hypothesis one in regards to any food type.

Because data were collected only during the early lactation period, it is not possible to determine if *P. verreauxi* consume young leaves at a higher intake rate during gestation and lactation, as do *P. tattersalli* and *P. edwardsi* (Meyers and Wright, 1993). Results compare with the lack of sex-based differences in percent of feeding time allocated to specific items found in *P. edwardsi* (Hemingway, 1999). My results are in part consistent with that of Pollock (1977), who reports mixed findings as to whether or not female *Indri indri* allocate a greater percentage of feeding time to leaves than males. Female *L. catta* have been found to consume a greater amount of leaves in comparison to males (in gallery forest: Sauther, 1992, 1993), but a lack of sex-based differences in food types have also been reported for this species (in spiny forest: LaFleur, 2012; Gould et al., 2011).

While it is often assumed that nutrition gained from a food item is the same across species, species-specific adaptations need to be considered (Chapman et al., 2012). The effectiveness at which members of a species gain nutrients is linked with species-specific metabolism and digestion (Robbins, 1977). One shortcoming of my study is the lack of nutritional data. Nutrient and chemical composition of plants was not measured or calculated for my study. Thus, it is impossible to make any definitive statements about differences or lack thereof in nutrient intake of males and females (although an absence of intersex differences in food type consumption would suggest nutrient intake was analogous). It is also not prudent to compare my results with other published findings of sex-based nutritional differences in primates due to aforementioned species-specific adaptations. My results are also specific to the early lactation period in Berenty only, and changes in plant parts consumed may occur during the later stages.

Plant Species Consumed

Sex differences in feeding time devoted to specific plant species may exist due to differences in body size, strength, or nutritional requirements (Clutton-Brock, 1977). Of the top plant species *P. verreauxi* consumed, females devoted significantly more time to *Rinorea greveana* than did males, but this species was not fed upon frequently (see Table 4.0). *R. greveana* composed the fourth greatest percentage of feeding time for females in comparison to males for which it ranked fifth. Thus, sex-based differences in plant species consumed for *P. verreauxi* at Berenty do not appear to be common during the period of my study.

5.2 DIFFERENCES IN TOTAL FOOD CONSUMED

Males and females did not differ in the total amount of food they were observed to have consumed over the duration of my study. Although females consumed significantly fewer bites of food per hour than did males, it appears they compensated for this lower rate by increasing feeding time, obtaining similar food intake totals in comparison to males.

5.3 BEHAVIORAL DIFFERENCES

Females may also respond to the costs of lactation by using available stored energy or reducing time devoted to certain activities (Lappan, 2009). In many primate species, adult males spend proportionally less time feeding and more time resting or in inactive behaviors than do females or juveniles (Chivers, 1974; 1977: Symphalangus syndactylus; Dunbar, 1977: Theropithecus gelada; Pollock, 1977: Indri indri; Smith, 1977: Alouatta palliata; Waser, 1977: Cercocebus albigena). Females may increase the proportion of time spent feeding or reduce activity levels while feeding at a steady rate in order to consume greater amounts of energy and protein (Silk, 1987; Altmann, 1980; Hytten, 1980). If following an income breeding strategy, dominant P. verreauxi females have feeding priority and can exclude males from foraging if needed, consequently affecting the time budget of males and females. Thus, I predicted females would allocate more time to feeding and resting in comparison to males due to the increased costs of lactation.

Females did allocate a greater proportion of their observed time feeding than did males, thus I rejected null hypothesis 2 (no difference in feeding time). Richard (1978), studying *P. verreauxi* both in northern deciduous and mixed evergreen forest and in southern didierea forest, found no sex-based differences in amount of time devoted to feeding. Richard (1978) reports *P. verreauxi* males and females spend 24% of time observed feeding during the dry season in the south in comparison to 35 and 41% for males and females respectively found during my study. It is possible *P. verreauxi* at Berenty have a lower intake rate and thus respond by feeding for a greater portion of time and allocating less time to other behaviors (play, groom, and others). Differences in forest composition between Berenty and Richard's southern site, Hazafotsy, may also be responsible for the varying results, as it is possible foods at Hazafotsy were easier to access and/or of higher nutritional quality, thus allowing individuals to feed for less time to meet energy needs. Charrier and colleagues (2007) studying *P. verreauxi* at Berenty in March and April (when females are gestating) found no difference in amount of time spent feeding. My results are inconsistent with the lack of sex-based differences *P. edwardsi* exhibits in the amount of time spent feeding during lactation (Hemingway, 1999).

While it was predicted that *P. verreauxi* females at Berenty would rest more than males to minimize energy expenditure, there was no such difference between the sexes and null hypothesis four was rejected. My results are consistent with the lack of sex-based differences in time allocated to resting found for *P. edwardsi* (Hemingway, 1999) and for *P. verreauxi* during gestation (Charrier et al., 2007). It is possible that both sexes rested more during the dry season in comparison to the wet season as part of a strategy to decrease energy expenditure during a time of limited resource availability, as was found to be the case for *P. verreauxi* at Kirindry (Norscia et al., 2006). Given that data for my study were only collected during part of the dry season, whether or not both sexes rest more in comparison to other times is uncertain.

Males allocated significantly more time than females to the behaviors play and scent-marking. Females were never observed engaging in play over the course of my study, possibly because the rough and tumble play observed would not be feasible/wise for a female with an infant and in order to reduce energy expenditure. My findings are consistent with the reduction of social behaviors seen in lactating female baboons (*Papio hamadryas ursinus*) when infant feeding demand is high (Barrett et al., 2006). However, *P. verreauxi* females did not significantly differ from males in the social behavior allo-grooming. Charrier and colleagues (2007) studying *P. verreauxi* at Berenty during the gestation period found no considerable difference between the sexes in time allocated to social interactions or miscellaneous activities. A lack of sex-based differences in time allocated to social behaviors has also been reported for *P. edwardsi* (Hemingway, 1999).

5.4 WATER INTAKE DIFFERENCES

Lactating females lose water through milk production and thus have increased water requirements (see Hulbert and Gordon, 1972 for brown bandicoots [*Isoodon macrourus]*; Kurta et al., 1990 for big brown bats [*Eptesicus fuscus]*; Krockenberger, 2003 for koalas [*Phascolarctos cinereus]*; Degen et al., 2004 for Cario spiny mice [*Acomys cahirinus]*). *P. verreauxi* exhibit seasonal reproduction (Richard et al., 2000), giving birth typically in July and August during the dry season (Richard et al., 2002; Erkert and Kappeler, 2004; Lewis and Kappeler, 2005). Average yearly rainfall in Berenty is 500mm (Koyama et al., 2002) with 70% occurring between November and February (Jolly et al., 2002). Climatic conditions such as rainfall may significantly affect a species' reproduction. For example, populations of the grey mouse lemur, *Microcebus murinus*, living in rainforest give birth at least twice a year (Lahann et al., 2006) in comparison to those in dry forests that produce one litter (Fietz, 1999; Eberle and Kappeler, 2004). The infants born to *P. edwardsi* mothers older than 18 years require elevated rainfall if they are to survive the lactation period (King et al., 2005). Considering *P. verreauxi* females may lose water through lactation, I predicted females would differ from males in measurements of mean water intake.

Throughout my study, male and female *P. verreauxi* did not differ in total water intake, hence I failed to reject null hypothesis three. However, there was substantial variation within the sexes (see Figure 4.13). Lactating females did not exhibit any behavioral indications of water deprivation and *P. verreauxi* have never been observed drinking water (Jolly, 1966; Simmen et al., 2003; Loudon and Sauther, 2013). Although lemurs commonly drink freestanding water and from wells in Berenty, I observed one *P. verreauxi* troop drinking water from a well during my study, and none of my focal troops were witnessed drinking. This lack of behavioral signs indicating water deprivation suggests that *P. verreauxi* lactating females acquire the necessary water through food sources. However, given that individuals were not observed continuously, it is possible lactating females employed feeding behaviors not directly observed during which they obtained sufficient water. Lactating female *P. verreauxi* may have increased water intake in relation to other stages of reproduction. However, without water intake data from other seasons, it is impossible to determine whether lactating females consume more/less water in their diet during the early dry season.

5.5 HOME RANGE

Home range at the time of my study was measured to be 0.74, 0.66, and 0.48 ha for A1, A2 and Malaza troops respectively. While *P. verreauxi* at Kirindy forest reduce home range during the dry season, measurements from my study are particularly low (Table 5.0). The smaller home ranges reported in my study may be due in part to the high density of *P. verreauxi* at Berenty, especially in Ankoba forest (Jolly et al., 2006). Counting 206 individuals in total, Norscia and Palagi (2008) found densities of 2.75 and 0.41 individuals/ha in Ankoba and Malaza forests respectively.

Table 5.0 Home ranges reported for *P. verreauxi* across forest types and research sites.

Home range size (ha)	Site	Forest type	Study
2.5-8.5	Berenty	Gallery	Richard, 1977
0.93 and 1.62; 2.08	Berenty	Gallery; Spiny	Prew, 2005
4.0-6.0	Beza Mahafaly	Gallery	Richard et al., 1991
1.5-4.5	Kirindy	Dry deciduous	Norscia et al., 2006
0.48-0.74	Berenty	Gallery	This study

Because *P. verreauxi* is a folivore and leaves are a widely available resource, home range size is predicted to be small in comparison to more frugivorous primates (Isbell, 1991). However, home range measurements for troops observed during this research appear much smaller than previously reported sizes (see Table

5.0). Smaller home ranges may indicate that troops at Berenty are able to obtain adequate energy in a limited amount of space. This is unexpected due to the challenges associated with the dry season. Introduced tree species, such as *P. dulce* and *A. rovumae*, may be a contributing factor to the small home ranges, as *P. verreauxi* in Ankoba forest are known to prefer introduced tree species and troops in Malaza rely on them as well (Simmen et al., 2003). Results from my study show that *P. verreauxi* allocated a large proportion (~70%) of feeding time to *P. dulce*, an introduced tree species rich in protein (Jolly et al., 2006). Malaza troop's especially small home range is likely a result of their daily feeding pattern; this troop would often spend the first few hours of the morning (~7:00-10:00) feeding on one large *P. dulce* tree, return to this same tree mid-afternoon (~14:00), and were still feeding on it when data collection ended for the day (~16:00). Given that population density is lower in Malaza than in Ankoba forest (Jolly et al., 2006; Norscia and Palagi, 2008), it is unlikely Malaza troop's small home range was a function population size.

A1 and A2 overlapped spatially in their home ranges but they were never observed in these shared areas at the same time nor were they ever observed in conflict over common areas. Previous results from Kirindy show *P. verreauxi* do not differ behaviorally or in their use of resources when in areas of their home range that are shared with other troops compared to unshared areas of their home range (Benadi et al., 2008). Benadi and colleagues conclude that potential of meeting neighboring troops does not have a strong effect behaviorally or in terms of resource use for *P. verreauxi*.

5.6 THE ENERGY CONSERVATION HYPOTHESIS AND REPRODUCTIVE STRATEGIES

Primatologists have long thought increased reproductive stress due to Madagascar's extreme seasonality may have resulted in female lemurs adopting feeding priority and dominance (Jolly, 1984; Wright, 1999). Wright (1999) suggests Malagasy primates must cope with a multitude of challenges, such as droughts and extreme variation in rainfall. Wright (1999) also states that El Niño events and cyclones contribute to the country's extreme seasonality and unpredictable environment (Wright, 1999). Female dominance has been argued as a response to the ecology of Madagascar: feeding priority allows females greater access to food needed to sustain offspring in a particularly challenging environment (Jolly, 1984).

A common adaptation of mammals living in seasonal environments is seasonal reproduction, in which the animal maps reproductive stages to fluctuating food resources (see for review Baker, 1938; Bronson, 1985; Bronson, 1989). Compared with primates of a similar diet, body mass, and latitude, Malagasy primates appear to react to seasonality with a significantly more narrow birth peak than primates in Africa, Asia, and the Americas (Janson and Verdolin, 2005). Within the genus *Propithecus,* the birth season lasts approximately a month: *P. verreauxi* at Berenty give birth between mid-June and mid-July (Richard et al., 1991), 75% of *P. verreauxi* births occur in the month of July at Kirindy (Lewis and Kappeler, 2005), and 73% of *P. edwardsi* births occur in June (Pochron et al., 2004). Interspecies birth asynchrony of lemur species in Madagascar is suggested to occur so that infants are weaned during periods of high fruit, young leaf, and insect abundance (Jolly, 1984;

Wright, 1999). *P. diadema* and *P. tattersalli* wean infants when young leaves are highly abundant (Myers and Wright, 1993). Consequently, *P. verreauxi* birth and lactation occur during the dry season (Richard et al., 2002; Erkert and Kappeler, 2004; Lewis and Kappeler, 2005) when leaves, fruit, and flowers are produced sporadically in southern Madagascar (Richard, 1978; Sauther, 1998).

It has been suggested that, like other members of the genus Propithecus, *P. verreauxi* is a “capital breeder” (Richard et al., 2000; Janson and Verdolin, 2005). Whereas income breeding is beneficial when resources are neither limited nor unpredictable in their availability, as storing resources is costly, capital breeding is beneficial when resources are limited and varied in occurrence and abundance (Jonsson, 1997). The use of energy stores means a capital breeder is less reliant on foraging during reproduction than an income breeder (Jonsson, 1997).

Loss of body mass is part of the capital breeding tactic, as stores are used for successful reproduction (Jonsson, 1997). Reproductive female *P. verreauxi* lose more body mass than males and non-reproductive females during the dry season (Richard et al., 2000). *P. diadema* females in Ranomafana National Park lose 12% of their body mass over the course of a year (Glander et al., 1992). *P. verreauxi* females that weigh more during the mating season are also more likely to give birth (Richard et al., 2000), and their offspring are more likely to survive past weaning (Lewis and Kappeler, 2005), suggesting fertility and individual fitness follows a capital breeding trajectory, in which the condition of the breeding female is important year-round.

Capital breeders may compete over food at any time regardless of season (Richard et al., 2000). Further evidence that *P. verreauxi* is a capital breeder is provided by the finding that resource-linked aggression is highest in *P. verreauxi* during the wet season, as opposed to in the dry season when females need to ingest enough energy for the immediate costs of reproduction (Richard, 1978; Richard et al., 2000). Aggression is most likely to occur when food resources are the most abundant and will thus yield high returns (Richard et al., 2000).

The designations income breeder and capital breeder are subjective and not always interpreted consistently (Stephens et al., 2009). As opposed to considering capital and income breeders as two distinctly disparate terms, it has been suggested that an income-capital continuum model be used instead (Brockman and van Schaik, 2005). When using a continuum, *P. verreauxi* is classified as a "relaxed income breeder" rather than a strict capital breeder due to the fact that individuals become less seasonally reproductive in captivity when food is plentiful (Brockman and van Schaik, 2005). It has also been suggested that *P. verreauxi* follows a "classic" breeding strategy (Lewis and Kappeler, 2005), in which conception occurs during high but declining resource availability so that the most energetically costly phase of reproduction, mid/late lactation (Moen, 1973), falls during a period of high resource availability. When considering that a high enough body mass is required to resume cycling after lactation (Bercovitch, 1987), mass potentially lost while lactating may be regained as infants are weaned and food availability increases. Females rely on stores during reproduction rather than on increased feeding rates, thus body mass loss is coupled with reproduction in capital breeding (Jonsson, 1997). As food availability is unpredictable, females take advantage of periods of high availability and store energy rather than follow a strategy in which they must increase intake rate during reproduction, which may or may not be possible (Jonsson, 1997).

Given that, in my study, 1) females and males spent an equal amount of total time observed resting and; 2) there were no sex-based, significant differences in total food intake or average intake rate, it may be that *P. verreauxi* is a "capital breeder," or a species that stores resources needed for reproduction (Richard et al., 2000). In contrast, if *P. verreauxi* is more of an "income breeder," an increase in food intake during gestation and lactation would be expected (Richard et al., 2000). As a capital breeder, *P. verreauxi* may compete over resources at any time during the year (Richard et al., 2000). My findings may indicate that it is more important for *P. verreauxi* females to maintain a healthy state year-round as opposed to consuming substantially more food during lactation because females do not consume more food than males during lactation. My results tentatively support that *P. verreauxi* follows a capital breeding strategy, as I did not compare lactating with non-lactating females. This important limitation, discussed further (along with others) in the next section, results in uncertainty as to the extent to which lactating female *P. verreauxi* do or do not modify their behavior during the birth season and should be kept in mind.

If female dominance is an evolutionary response to increased energetic stress females experience during reproduction (Wright, 1999), the lack of significant difference in total food consumed between the sexes is surprising. Females did not consume particular food types at a greater rate or at a greater proportion when compared to males. Despite taking place during the dry season, when resource availability was low, males fed at a comparable rate to females and rates of agonism were low (< 0.07% of observation time), suggesting there is little competition over food between the sexes during the early period of lactation.

Thus, it is possible lactating females at Berenty, through a combination of physiological traits and a modified environment with introduced plant species, may not be particularly stressed even in the early dry season. Hemingway (1999) complied available data on Lemuridae and Indriidae species across multiple sites and concluded that female dominance and sex-based differences in foraging are not strongly associated, supporting the idea that female *P. verreauxi* may be a "capital breeder," as suggested by Richard and colleagues (2000), and do not increase feeding during gestation or lactation but feed and store energy needed year-round. That *P. verreauxi* is a capital breeder is further supported by the fact that this species, like many lemurs, times the period of the greatest food availability with weaning (Wright, 1999) as opposed to gestation or lactation. My findings support Pereira and colleagues' (1999) suggestion that female dominance does not relieve the abnormal amount of reproductive energetic stress, but that it allows females to avoid normal (when compared to other mammals) levels of reproductive stress by dominating males in feeding contexts.

Female dominance may be one of many adaptations helping lemurs avoid reproductive stress but it may not have evolved in response to peculiar levels of reproductive stress, as suggested by Jolly (1984) and Wright (1999) (Pereira et al., 1999). Because capital breeders compete over resources throughout the year, this may be one reason females are dominant year-round (Richard et al., 2000). As a capital breeder, the rewards of female dominance may be most greatly felt during the dry season, if females are able to adequately build up fat stores during the rest of the year.

Alternatively, the lack of sex-based differences in feeding behaviors across Strepsirhines (see Table 5.1) may indicate reproductive females are not especially energetically stressed. Acute cycles of resource availability do not necessarily mean a species will experience periods of nutritional stress (Pereira et al., 1999) and nutritional quality of habitat does not necessarily indicate the quality of a primate's diet (Hohmann et al., 2010). King and Murphy (1985: 955) wisely said, "…it is unjustified to assume, and even more so to conclude, that there is 'not enough' when 'enough' has not been defined."

P. verreauxi in Kirindy significantly alter time spent foraging on different food types dependent on season and feed at a higher rate on mature leaves with a lower condensed tannin content (Norscia et al., 2006). In southeastern rainforest *P. verreauxi* consume different food types dependent on the season but the average macronutrient and energy content of the most consumed foods in each season was comparable (Irwin et al., 2013).

Table 5.1 Sex-based differences in feeding behavior. *Species does not exhibit complete female dominance (Harrington, 1975; Pereira et al., 1990; Pereira and McGlynn, 1997; Ostner and Kappeler, 1999)

Species	Variable	Result	Forest type	Reference
L. catta	% feed and fruit time	Female=male	Tropical dry forest	Sauther, 1992, 1993
	Plant parts eaten	Female>male leaf		
	Intake food items	Female=male; male>female		
	Feeding efficiency	Female<male (*Tamarindus* fruit)		
L. catta	% feed time	Female=male	Southern gallery forest	LaFleur, 2008
	Amount food consumed	Female=male		
	Intake rate	Female=male		
	Nurtient intake	Female=male (Ca, Mg Protein, ADF, NDF); Female>male (P and K)		
L. catta	% feed time	Female=male	Spiny forest	Gould et al., 2011
	% feed time food items	Female=male		
	Intake rate	Female=male		
	Nutrient intake (top five species)	Female=male		
	Water intake	Female=male		
*E. rufus**	Feeding bout duration	Female>male (3/13 mos)	Southeastern rainforest	Overdorff, 1991
	Number of feeding bouts	Female=male		
E. rubriventer	Feeding bout duration	Female=male (12/13 mos)	Southeastern rainforest	Overdorff, 1991
	Number of feeding bouts	Female=male		
V. variegata	% feed time	Female=male	Lowland rainforest	Morland, 1991
	Plant parts eaten	Female<male fruit; female>male nectar		
V. variegata	Intake rate	Female<male (Group 1); Female>male (Group 2)	Southeastern rainforest	Overdorff et al., 2005
I. indri	% feed time	Female>male	Upland rainforest and cloud forest	Pollock, 1977
	% feed time food items	Female=male (group V); female>male (group P)		
	Plant parts eaten	Female=male (group P); female<male fruit (group V)		
P. verreauxi	% feed time	Female=male	Southern gallery forest	Richard, 1978
P. verreauxi	% feed time	Female=male	Southern gallery forest	Charrier et al., 2007
	Amount food consumed	Female>male		
P. verreauxi	Intake rate	Female=male	Southern gallery forest	This study
	% feed time	Female>male		
	Water intake	Female=male		
P. coquereli	% feed time	Female=male		Richard, 1978
P. edwardsi	% feed time	Female=male	Southeastern rainforest	Hemingway, 1999
	% feed time food items	Female=male (most months)		
	Feed duration	Female=male (most months)		
	Feed rate	Female=male (most months)		
	Plant parts eaten	Varied across groups and months		
H. griseus	Dietary diversity	Female>male	Southeastern rainforest	Grassi, 2002

While it is often assumed Madagascar's ecology is particularly challenging, further studies need to be done to better quantify this assumption. Inter-annual variability in rainfall is not unusually high and cannot be considered a general characteristic of the island (Dewar and Richard, 2007). In contrast, the consistency and the amount of rainfall from month to month across Madagascar is significantly less predictable when compared to continental Africa (Dewar and Richard, 2007).

In regards to primary production, while the timing and quantity of fruit availability in in eastern Madagascar is variable (Meyers and Wright, 1993; Hemingway, 1996), studies in other parts of the island and on other food items have yet to be undertaken. Leaf production (the main food type *P. verreauxi* consumes) in Madagascar is similar to production found in other seasonal forests (Hladik, 1980; Ranaivoson et al., in press). Average protein and acid detergent fiber do not differ between folivorous Malagasy primates and folivorous colobine monkeys found in *analogous* habitats (i. e. riverine forests) (Powzyk and Mowry, 2003; Simmen et al., 2012). Average leaf chemistry (total protein, extractable protein, acid detergent fiber, condensed tannin) does not differ significantly between sites across Madagascar, and averages recorded at colobine sites across continental Africa and Asia (Ganzhorn, 1992). The dry forest found at Beza Mahafaly in southern Madagascar does not differ in regards to plant density, diversity, and the size classes of individual fauna when compared to dry forests found in continental Africa and in the Neotropics (Sussman and Rakotozafy, 1994). Thus, supposed uniqueness of Madagascar's environment and its seasonality needs to be further investigated.

The lack of a significant difference between males and lactating females for intake rate and total food consumption may support the idea that female strepsirhines are *not* under abnormal energetic stress during reproduction (Kappeler, 1996). Kappeler (1996) reports that postnatal offspring growth rates, which are a good reflection of maternal energetic investment, do not differ between lemurs, which display female dominance, and lorises, which do not (although see Hager and Welker, 2001). These results imply that female lemurs do not invest more energy in reproduction during lactation than other primates (Kappeler, 1996). Analysis of milk composition and offspring care found that most Lemuridae produce milk that is similarly diluted compared to anthropoids (Tilden and Oftedal, 1997), suggesting that Lemuridae are not unique in reproductive costs. While *P. verreauxi* is a member of the family Indriidae and not Lemuridae, the two families are closely related, and recent research has shown *P. coquereli* milk is low in oligosaccharide content (1.0%) and diversity (Taufik et al., 2012). Given that synthesis of oligosaccharides is metabolically costly (Taufik et al., 2012), it is logical to assume *P. verreauxi* milk is comparably dilute.

To conclude, while energy intake and hormonal data are not available, the lack of feeding differences between lactating females and males may hint lactating females do not experience extreme energetic stress during this time. The lack of intersex differences may be due to use of a capital breeding strategy, requiring females to maintain a sufficiently healthy body condition year-round to reproduce successfully. Without data from non-lactating females however, it is impossible to determine for certain if females change their behavior and diet to accommodate the energetic costs of supporting an infant in the early stage of lactation.

5.7 LIMITATIONS OF STUDY

My results generally agree with previous research suggesting that *P. verreauxi* is a capital breeder. The lack of significant differences between males and females in intake indicates that females do not compensate for the costs of early lactation through consuming more bites of food per unit of time. Nor do females conserve energy through increasing time spent resting when compared to males. There is evidence that females spend a greater proportion of time observed engaged in feeding than males, but this increase in proportion of observation time allocated to feeding does not result in significantly greater total food intake than males. In addition to the obvious limitation of the short time period of my study, which was limited to six weeks of observations when lactation lasts between six to nine months (Richard, 2003), there are other factors that may lessen the impact of my research.

One potential issue affecting the robustness of my results is that nutritional analysis of food items consumed is unavailable. Given that males and females did not differ in the proportion of time devoted to most plant species except for *R. greveana* (which accounted for less than three percent of female feeding time), this shortcoming may not present a great impact.

Information on intake rates and food types/species consumed across multiple stages of reproduction would strengthen my study. It is impossible to determine whether females adjusted their intake rate while lactating when data are not available from non-lactation periods. The same can be said for the composition of female diet: knowledge of the amount of plant parts consumed during other periods could show females do consume certain food types more/less when lactating. Because information is not available on behaviors and diet during maintenance periods, results presented here are limited.

Another interfering factor may be the timing in which observational data were recorded. Because it was necessary to count the number of bites the focal animal consumed, observations were only possible during times of sufficient light. Thus, early morning and late afternoon were excluded because it was impossible to accurately count the number and type of food an individual consumed. Observations were often terminated while animals were still feeding because light conditions were poor. Consequently, it is possible that intake rate, food type consumed, and activity budget of males and females differed during the late afternoon, as activity budget has been shown to be affected by time of day in other primate species such as *Macaca sylvanus* (Majolo et al., 2013), *Cercopithecus aethiops* (Baldellou and Adan, 1997), *Callithrix geoffroyi* (Passamani, 1998), and *Procolobus rufomitratus* (Marsh, 1981).

Also, it is worth noting that *P. verreauxi* devoted the majority of feeding time to a plant species, *P. dulce,* which is not native to the area. The number of introduced plant species at Berenty Reserve may affect the diet composition of many animals, such as *L. catta, M. murinus,* and fruit bats (*Pteropus rufus*). Plant species and plant parts that would not naturally be available to *P. verreauxi* in unaltered forest at Berenty are present. Analysis of *P. verreauxi* diet at Kirindy found that leaves composed at least 79% of diet from April-November, with the exception of September (Lewis and Kappeler, 2005). Results from my study spanning from August to early September show almost 60% of feeding time was devoted to flowers.

P. verreauxi at Kirindy lose body mass around the same time their diet composition shifts to primarily mature leaves (Lewis and Kappeler, 2005). Females in Berenty consumed primarily flowers during my study, thus perhaps this difference in diet composition lessens the energetic costs of lactation for females at Berenty. Generally, flowers have high to moderate levels of protein, low to moderate levels of fiber, and moderately accessible calories overall and are typically more desirable than leaves (Milton, 1987; Milton, 1996), the greatest contributor to *P. verreauxi*'s diet at Kirindy (Lewis and Kappeler, 2005). Leaves are available almost year-round but flowering is much less common and are usually available for less than three months (Milton, 1996; Zjhra, 2006; Zhjra, 2008). Some flowering Malagasy species are available only for days (Spaulding and Kociolek, 2003), although no species was observed during this study flowering for this short a time in gallery forest. Given that flowers generally contain more easily accessible calories than both immature and mature leaves (Hamilton and Galdikas, 1994; Milton, 1996; Conklin-Brittan et al., 1998; McConkey et al., 2003), the greater availability of this resource is an advantage for *P. verreauxi* females.

5.8 CONSERVATION IMPLICATIONS

At the most recent meeting of the International Union for Conservation of Nature Specialist Meeting, Schwitzer and colleagues (2013) report that *P. verreauxi* is now classified as "endangered" and is threatened by habitat loss, forest degradation, and hunting for consumption. Habitat loss across Madagascar is thought to be the largest contributor to the loss of species diversity and numbers of lemurs (Schwitzer et al., 2013). The most recent estimates show between 16.9% and 29.5% of the island is covered by forest (Dufils, 2008; Harper et al., 2007). Lemurs are also threatened across Madagascar due to hunting (Golden, 2009; Golden et al., 2011; Jenkins et al., 2011). A recent survey of wildlife consumption reports that 12-29% of the 1,851 people surveyed across Madagascar consumes *Propithecus* species (Razafimanahaka et al., 2012). A lack of livelihood strategies and the need to provide food for families create an incentive for wildlife hunting (Schwitzer et al., 2013). Declines in social values and political support for conservation may contribute to increased hunting (Jenkins et al., 2011).

Schwitzer and colleagues (2013) state that *P. verreauxi* is currently found in the spiny and gallery forests of the Mandrare Valley, Amboasary, Ifotaka, Angavo, Ankodida, and Andabolava as well as the Mahafaly Plateau, where future conservation objectives include increasing participation of local communities in monitoring lemurs, patrolling forests, standardizing monitoring methods, and developing associated conservation and development activities. *P. verreauxi* is also found in the Makay region where reforestation, research, ecotourism and an attempt to obtain protected status are all in progress in an effort to conserve this area (Schwitzer et al., 2013; Makay Nature Project, 2014). The dry deciduous Kirindy and Ambadira forests are home to *P. verreauxi* as well, and efforts are underway to formally protect this area (Gray and Jongepier, 2008; Schwitzer et al., 2013; Schaffler and Kappeler, 2014). Schwitzer and colleagues (2013) report that the conservation objectives for this are: 1) improved understanding of the distribution, ecology and threats to endangered lemurs and 2) better environmental education and threat mitigation.

That *P. verreauxi* females in Berenty displayed no overt behavioral or dietary differences compared to males during the early lactation period is unexpected. It is possible the number of introduced plant species play a key role in females' success by providing foods of higher energy/nutrient content in comparison to species naturally occurring at Berenty. Particularly, the availability of *P. dulce* flowers, which troops fed on frequently, may have been instrumental in alleviating the effects of the dry season if calories were easily obtained from this flower. Over 71% of this flower on average was composed of water, thus this food item may also have acted as an important source of water for *P. verreauxi* females over the duration of my study.

Results from my study represent only a snapshot of *P. verreauxi* reproduction, and it is difficult to make any solid conclusions about the welfare of Berenty population. The sex ratio of *P. verreauxi* populations at Berenty was skewed in favor of males in 2006, suggesting population stress (Norscia and Palagi, 2008). However, Norscia and Palagi (2008) state that no significant difference between the number of males and females was found across a greater period of time (1963-2006), potentially indicating that populations at Berenty are generally doing well.

5.9 CONCLUSIONS

The objectives of my study were to determine how lactating females compare to males 1) in food intake rate; 2) in the amount of time spent feeding and resting 3) and in diet composition and; 4) water intake. Results show that lactating females do not consume more or different foods than males during the dry season. Males had slightly higher intake rates overall in comparison to females, although results did not reach significance. Females and males also did not differ in mean water intake during my study. While females were found to spend a greater proportion of time devoted to feeding, there was no difference between males and females in the proportion of time spent resting. There was also no significant difference between males and females in the total amount of food consumed.

A lack of results consistent with the idea that lactating females must cope with increased energetic costs than males through behavioral and/or dietary changes may be due to the following: 1) *P. verreauxi* is a capital breeder and does not increase intake rate during lactation but feeds and stores energy at all times, 2) the cost of reproduction for *P. verreauxi* is not great enough to warrant significant changes in female behavior/diet (Kappeler, 1996; Hemingway, 1999), 3) species inhabiting an unpredictable environment may display flexible reproductive physiology that evolved in response to these fluxes and protect against their effects (Canale et al., 2012). A combination of these factors may also be in effect.

Future research should examine *P. verreauxi* during lactation and non-lactation periods in order to compare behaviors and diet and water intake during multiple stages of *P. verreauxi* reproduction. Nutritional analysis of food items eaten while females are lactating and during other periods would provide a more complete understanding of the stresses *P. verreauxi* encounters while lactating.

LITERATURE CITED

Madagascar. 2012. https://www.cia.gov/library/publications/the-world-factbook/geos/ma.html ed. Washington, DC: Central Intelligence Agency.

Makay Nature Project. 2014. http://www.outdoorconservation.eu/project-detail.cfm?projectid=21 ed. Kanton Zug, Switzerland: European Outdoor Conservation Association.

Ali J, Krause D. 2011. Late cretaceous bioconnections between Indo-Madagascar and Antarctica: Refutation of the Gunnerus Ridge Causeway Hypothesis. J Biogeogr 38(10):1855-1872.

Altmann J. 1974. Observational study of behavior: Sampling methods. Behaviour 49(3/4):227-267.

Axel AC, Maurer BA. 2011. Lemurs in a complex landscape: Mapping species density in subtropical dry forests of southwestern Madagascar using data at multiple levels. Am. J. Primatol., 73: 38-52.

Baker J. 1938. The evolution of breeding seasons. In: De Beer G, editor. Evolution; essays on aspects of evolutionary biology. Oxford: Clarendon Press. p 161-179.

Baldellou M, Adan A. 1997. Time, gender, and seasonality in vervet activity: A chronobiological approach. Primates 38(1):31-43.

Bercovitch FB. (1987), Female weight and reproductive condition in a population of olive baboons (*Papio anubis*). Am. J. Primatol., 12: 189–195.
doi: 10.1002/ajp.1350120206

Bell R. 1971. A grazing ecosystem in the Serengeti. Sci Am 225:86-93.

Benadi G, Fichtel C, Kappeler P. 2008. Intergroup relations and home range use in Verreaux's sifaka (*Propithecus verreauxi*). Am J Primatol 70(10):956-965.

Beehner J, Onderdonk J, Alberts S, Altmann J. 2006. The ecology of conception and pregnancy failure in wild baboons. Behav Ecol 17(5):741-750.

Bodin O, Tengö M, Norman A, Lundberg J, Elmqvist T. 2006. The value of small size: Loss of forest patches and ecological thresholds in southern Madagascar. Ecological Applications : A Publication of the Ecological Society of America 16(2):440-451.

Bowman AW, Azzalini A. 2014. sm: Smoothing Methods for Nonparametric Regression and Density Estimation. University of Glasgow, UK and Universita di

Padova, Italia. R package version 2.2-5.4. http://www.stats.gla.ac.uk/~adrian/sm, http://azzalini.stat.unipd.it/Book_sm

Brockman D, van Schaik C. 2005. Seasonality and reproductive function. In: Brockman D, van Schaik C, editors. Seasonality in primates: studies of living and extinct human and non-human primates. Cambridge: Cambridge University Press. p 269-305.

Brockman D, Whitten P. 2003. Hormonal basis of reproductive competition in female *Propithecus v. coquereli*: Mothers and daughters in conflict. 8th ed. Lemur News.

Brockman D, Whitten P. 1996. Reproduction in free-ranging *Propithecus verreauxi*: Estrus and the relationship between multiple partner matings and fertilization. Am J Phys Anthropol 100(1):57-69.

Brockman D, Whitten P, Richard A, Schneider A. 1998. Reproduction in free-ranging male *Propithecus verreauxi*: The hormonal correlates of mating and aggression. Am J Phys Anthropol 105(2):137-151.

Brockman D. 1999. Reproductive behavior of female *Propithecus verreauxi* at Beza Mahafaly, Madagascar. Int J Primatol 20(3):375-398.

Bronson FH. 1985. Mammalian reproduction: An ecological perspective. Biol Reprod 32(1):1-26.

Bronson FH. 1989. Seasonal strategies: Ultimate factors. In: Bronson FH, editor. Mammalian Reproductive Biology. University of Chicago Press. p 28-60.

Burney L, Burney D, Godfrey L, Jungers W, Goodman S, Wright H, Jull A. 2004. A chronology for late prehistoric Madagascar. J Hum Evol 47(1):25-63.

Canale CI, Huchard E, Perret M, Henry P. 2012. Reproductive resilience to food shortage in a small heterothermic primate. PloS One 7(7):e41477.

Chalk J, Vogel ER. 2012. Insights into primate dietary ecology: Methods and theory. Int J Primatol 33(3):515-519.

Chapman CA, Chapman LJ, Gillespie TR. 2002. Scale issues in the study of primate foraging: Red colobus of kibale national park. Am J Phys Anthropol 117(4):349-363.

Chapman CA, Chapman LJ, Wrangham R, Hunt K, Gebo D, Gardner L. 1992. Estimators of fruit abundance of tropical trees. Biotropica 24(4):527-531.

Chapman CA, Rothman JM, Lambert JE. 2012. Food as a selective force in primates. In: Mitani J, Call J, Kappeler P, Palombit R, Silk J, The Evolution of Primate Societies. Chicago University Press, pp. 149-168.

Charrier A., Hladik A., Simmen B. 2007. Stratégie alimentaire et dominance des femelles propithèque de verreaux (*Propithecus v. verreauxi*) dans la forêt à Didiereaceae du sud de Madagascar. *Revue d'Ecologie, Terre et Vie*, 62:257-263.

Chivers D. 1974. The siamang in Malaya: a field study of a primate in tropical rain forest. Contrib. primt. 4: 1-335. Karger, Basel.

Chivers D. 1977. The feeding behaviour of siamang (*Symphalangus syndactylus*). In: Clutton-Brock TH, editor. Primate Ecology: Studies of Feeding and Ranging Behavior in Lemurs, Monkeys, and Apes. London: Academic Press. p 355-382.

Clutton-Brock TH. 1977. Some aspects of intraspecific variation of feeding and ranging behaviour in primates. In: Clutton-Brock TH, editor. Primate Ecology: Studies of Feeding and Ranging Behavior in Lemurs, Monkeys, and Apes. London: Academic Press. p 539-576.

Clutton-Brock T, Albon S, Guinness F. 1989. Fitness costs of gestation and lactation in wild mammals. Nature 337(6204):260-262.

Dammhahn M, Kappeler PM. 2014. Stable isotope analyses reveal dense trophic species packing and clear niche differentiation in a Malagasy primate community. Am J Phys Anthropol 153(2):249-259.

Cowlishaw G. 1999. Predicting the pattern of decline of African primate diversity: An extinction debt from historical deforestation. Conserv Biol 13(5):1183-1193.

Conklin-Brittain NL, Wrangham RW, Hunt KD. 1998. Dietary response of chimpanzees and cercopithecines to seasonal variation in fruit abundance. II. macronutrients. Int J Primatol 19(6):971-998.

Cyr NE, Michael Romero L. 2007. Chronic stress in free-living European starlings reduces corticosterone concentrations and reproductive success. Gen Comp Endocrinol 151(1):82-89.

Daniel WW. 2009. Biostatistics: A foundation for analysis in the health sciences. 9th ed. Hoboken, NJ: John Wiley & Sons.

Davies AG. 1994. Colobine populations. In: Davies AG, Oates JF, editors. Colobine Monkeys: Their Ecology, Behaviour, and Evolution. Cambridge: Cambridge University Press. p 285-310.

Degen AA, Khokhlova IS, Kam M, Snider I. 2004. Water budget during reproduction in female common spiny mice (*Acomys cahirinus*). J Mammal 85(6):1106-1110.

Dene H, Goodman M, Prychodko W, Moore GW. 1976. Immunodiffusion systematics of the primates. III. the strepsirhini. Folia Primatol 25(1):35-61.

de Wit M. 2003. Madagascar: Heads it's a continent, tails it's an island. Annu Rev Earth Planet Sci 31(1):213-248.

Dewar R, Richard A. 2012. Madagascar: A history of arrivals, what happened, and will happen next. Annu Rev Anthropol 41:495-517.

Dewar RE, Richard AF. 2007. Evolution in the hypervariable environment of Madagascar. Proc Natl Acad Sci USA 104(34):13723-13727.

Dewar R, Wallis J. 1999. Geographical patterning of interannual rainfall variability in the tropics and near tropics: An L-moments approach. J Clim 12(12):3457-3466.

Dixon KR, Chapman JA. 1980. Harmonic mean measure of animal activity areas. Ecology 61:1040-1044.

Duda RO, Hart PE, Stork DG. 2001. Pattern classification. New York: Wiley.

Dufils JM. 2008. Couvert forestier restant. In: Goodman, SM, editor. Paysages Naturels et Biodiversite de Madagascar. Paris, France: Museum Naturelle d'Histoire Naturelle. P. 67-79.

Du Puy D, Moat J. 2003. Using geological substrate to identify and map primary vegetation types in Madagascar and the implications for planning biodiversity conservation. In: Goodman S, Benstead J, editors. The Natural History of Madagascar. Chicago: University of Chicago Press.

Dunbar R. 1977. Feeding ecology of gelada baboons: A preliminary report. In: Clutton-Brock TH, editor. Primate Ecology: Studies of Feeding and Ranging Behavior in Lemurs, Monkeys, and Apes. London: Academic Press. p 251-273.

Dunnett CW. 1955. A multiple comparisons procedure for comparing several treatments with a control. J. Am. Statist. Assoc. 50 (272): 1096–1121.

Eaglen R, Boskoff K. 1978. The birth and early development of a captive sifaka, *Propithecus verreauxi coquereli*. Folia Primatol 30(3):206-219.

Eberle M, Kappeler PM. 2004. Sex in the dark: determinants and consequences of mixed male mating tactics in *Microcebus murinus*, a small solitary nocturnal primate. Behav Ecol Sociobiol 57:77–90

Emery Thompson M, Muller M, Wrangham R. 2012. The energetics of lactation and the return to fecundity in wild chimpanzees. Behav Ecol 23(6):1234-1241.

Erkert H, Kappeler P. 2004. Arrived in the light: Diel and seasonal activity patterns in wild Verreaux's sifakas (*Propithecus v. verreauxi* ; primates: Indriidae). Behav Ecol Sociobiol 57(2):174-186.

Fietz J. 1999. Mating system of *Microcebus murinus*. Am J Primatol 48:127-133.

Fichtel C, Kappeler PM. 2012. A 15-year perspective on the social organization and life history of sifaka in Kirindy forest. In: Kappeler PM, Watts D, editors. Long-Term Field Studies of Primates Berlin, Heidelberg: Springer Berlin Heidelberg. p 101-121.

Fenn MD. 2003. The spiny forest ecoregion. In: Goodman S, Benstead J, editors. The Natural History of Madagascar. Chicago: University of Chicago Press.

Foerster S, Cords M, Monfort SL. 2012. Seasonal energetic stress in a tropical forest primate: Proximate causes and evolutionary implications. PloS One 7(11):e50108.

Foley CAH, Papageorge S, Wasser SK. 2001. Noninvasive stress and reproductive measures of social and ecological pressures in free-ranging African elephants. Conserv Biol 15(4):1134-1142.

Ganzhorn JU. 1992. Leaf chemistry and the biomass of folivorous primates in tropical forests. Test of a hypothesis. Oecologia 91(4):540-547.

Ganzhorn J, Goodman S, Dehgan A. 2003. Effects of forest fragmentation on small mammals and lemurs. In: Goodman S, Benstead J, editors. The Natural History of Madagascar. Chicago: University of Chicago Press. p 1228-1234.

Ganzhorn J. 2003. Habitat description and phenology. In: Setchell J, Curtis D, editors. Field and laboratory methods in primatology: a practical guide. Cambridge: Cambridge University Press. p 40-56.

Gautier L, Goodman S. 2003. Introduction to the flora of Madagascar. In: Goodman S, Benstead J, editors. The Natural History of Madagascar. Chicago: University of Chicago Press. p 229-250.

Gittleman J, Thompson S. 1988. Energy allocation in mammalian reproduction. Integrative and Comparative Biology 28(3):863-875.

Global Facility for Disaster Reduction and Recovery. 2011. Climate risk and adaptation country profile for Madagascar. The World Bank Group.

Godfrey LR, Samonds KE, Jungers WL, Sutherland MR, Irwin MT. 2004. Ontogenetic correlates of diet in Malagasy lemurs. Am J Phys Anthropol 123(3):250-276.

Golden CD, Lia F, C.H., Brashares J, Rasolofoniaina BJR, Kremen C. 2011. Benefits of wildlife consumption to child nutrition in a biodiversity hotspot. Proceedings of the National Academy of Sciences 108(49):19653-19656.

Golden CD. 2009. Bushmeat hunting and use in the Makira forest, north-eastern Madagascar: A conservation and livelihoods issue. Oryx 43(3):386-392.

Goodman M, Porter CA, Czelusniak J, Page SL, Schneider H, Shoshani J, Gunnell G, Groves CP. 1998. Toward a phylogenetic classification of primates based on DNA evidence complemented by fossil evidence. Mol Phylogenet Evol 9(3):585-598.

Gould L, Power M, Ellwanger N, Rambeloarivony H. 2011. Feeding behavior and nutrient intake in spiny forest-dwelling ring-tailed lemurs (*Lemur catta*) during early gestation and early to mid-lactation periods: Compensating in a harsh environment. Am J Phys Anthropol 145(3):469-479.

Grassi C. 2002. Sex differences in feeding, height, and space use in *Hapalemur griseus.* Int J Primatol 23(3):677-693.

Gray C, Jongepier E. 2008. Effect of human disturbance on arthropod diversity at Kirindy Forest, western Madagascar. Tropical Biology Association.

Hager R, Welker C. 2001. Female dominance in African lorises (*Otolemur garnettii*). Folia Primatol (Basel) 72(1):48-50.

Hamilton RA, Galdikas BMF. 1994. A preliminary study of food selection by the orangutan in relation to plant quality. Primates 35(3):255-263.

Hammond K, Diamond J. 1992. An experimental test for a ceiling on sustained metabolic rate in lactating mice. Physiol Zool 65(5):952-977.

Hanwell A, Peaker M. 1977. Physiological effects of lactation on the mother. UK, Zoological Society of London: Comparative Aspects of Lactation.:297-312.

Harper G, Steininger M, Tucker C, Juhn D, Hawkins F. 2007. Fifty years of deforestation and forest fragmentation in Madagascar. Environ Conserv 34(4):325-333.

Harrington J. 1975. Field observations of social behavior of *Lemur fulvus fulvus* E. Geoffroy 1812. In: Tattersall I, Sussman R, editors. Lemur biology. New York: Plenum Press. p 259-279.

Harrison MJS. 1983. Age and sex differences in the diet and feeding strategies of the green monkey, *Cercopithecus sabaeus*. Anim Behav 31(4):969-977.

Hemingway, CA. 1995. Feeding and reproductive strategies of the Milne-Edwards' sifaka, *Propithecus diadema edwardsi*. Ph.D. thesis, Duke University, Durham, North Carolina.

Hemingway, CA. 1996. Morphology and phenology of seeds and whole fruit eaten by Milne-Edwards' sifaka, *Propithecus diadema edwardsi*): implications for folivory and seed eating. Int J Primatol 17(5); 637-59.

Hill WCO. 1953. Primates: Comparative anatomy and taxonomy. I. Strepsirhini. New York: Interscience Publishers.

Hladik C. 1977. A comparative study of the feeding strategies of two sympatric species of leaf monkeys: *Presbytis senex* and *Presbytis entellus*. In: Clutton-Brock TH (ed) Primate ecology. Academic Press, London. p. 324–353

Hladik A. 1980. The dry forest of the west coast of Madagascar: climate, phenology, and food available for Prosimians. In Charles-Dominique, P., Cooper, H. M., Hladik, A., Hladik, C. M., Pagès, E., Pariente, G. F., Petter-Rousseaux, A., Petter, J.-J. & Schilling, A. (eds.). Nocturnal Malagasy primates. Ecology, physiology, and behavior. Academic Press, New York. p. 3–40

Hohmann G, Potts K, N'Guessan A, Fowler A, Mundry R, Ganzhorn JU, Ortmann S. 2010. Plant foods consumed by pan: Exploring the variation of nutritional ecology across Africa. Am J Phys Anthropol 141(3):476.

Houghton, RA. 2005. Tropical deforestation as a source of greenhouse gas emissions. *Tropical deforestation and climate change.* 13.

Hulbert AJ, Gordon G. 1972. Water metabolism of the bandicoot *Isoodon macrourus* gould in the wild. Comparative Biochemistry and Physiology.A, Comparative Physiology 41(1):27-34.

Hytten, FE. 1980. Nutrition. Weight gain in pregnancy. In: Hytten, FE and Chamberlain, G, editors. Clinical Psychology in Obstetrics, Blackwell Scientific Publishers, Oxford. p. 163-223.

Irwin MT, Raharison J, Raubenheimer D, Chapman CA, Rothman JM. 2014. Nutritional correlates of the "lean season": Effects of seasonality and frugivory on the nutritional ecology of diademed sifakas. Am J Phys Anthropol 153(1):78.

Irwin M. 2007. Ecologically enigmatic lemurs: The sifakas of the eastern forests (*Propithecus candidus, P. diadema, P. edwardsi, P. perrieri,* and *P. tattersalli*). In: Gould L, Sauther M, editors. Lemurs: Ecology and Adaptation. Boston, MA: Springer US. p 305-326.

Isbell LA. 1991. Contest and scramble competition: Patterns of female aggression and ranging behavior among primates. Behav Ecol 2(2):143-155.

Janson CH. 1988. Intra-specific food competition and primate social structure: A synthesis. Behaviour 105(1/2):1-17.

Janson CH, Goldsmith ML. 1995. Predicting group size in primates: Foraging costs and predation risks. Behav Ecol 6(3):326-336.

Janson C, Verdolin J. 2005. Seasonality of primate births in relation to climate. In: Brockman DK, van Schaik C, editors. Seasonality in primates: studies of living and extinct human and non-human primates. Cambridge: Cambridge University Press. p 307-350.

Jennrich RI, Turner FB. 1969. Measurement of non-circular home range. J. Theoretical Biol. 22:227-237.

Jenkins RKB, Keane A, Rakotoarivelo AR, Rakotomboavonjy V, Randrianandrianina FH, Razafimanahaka HJ, Ralaiarimalala SR, Jones JPG. 2011. Analysis of patterns of bushmeat consumption reveals extensive exploitation of protected species in eastern Madagascar. PloS One 6(12):e27570.

Jolly A. 1972. Troop continuity and troop spacing in *Propithecus verreauxi* and *Lemur catta* at Berenty (Madagascar). Folia Primatol 17(5-6):335-362.

Jolly A. 1984. The puzzle of female feeding priority. In: Small M, editor. Female Primates: Studies by Women Primatologists. New York: Liss. p 197-215.

Jolly A, Gustafson H, Oliver WL, O'Connor SM. 1982. *Propithecus verreauxi* population and ranging at Berenty, Madagascar, 1975 and 1980. Folia Primatologica; Folia Primatologica.

Jolly A. 1966. Lemur behavior: A Madagascar field study. Chicago: University of Chicago Press.

Jolly A. 2004. Lords and Lemurs: Mad scientists, kings with spears, and the survival of diversity in Madagascar. New York: Houghton Mifflin Co.

Jolly A, Dobson A, Rasamimanana H, Walker J, O'Connor S, Solberg M, Perel V. 2002. Demography of *Lemur catta* at Berenty Reserve, Madagascar: Effects of troop size, habitat and rainfall. Int J Primatol 23(2):327-353.

Jolly A, Koyama N, Rasamimanana H, Crowley H. 2006. Berenty Reserve: A research site in southern Madagascar. In: Lords and Lemurs. Boston, MA: Springer US. p 32-42.

Jönsson KI. 1997. Capital and income breeding as alternative tactics of resource use in reproduction. Oikos 78(1):57-66.

Jury M. 2003. The climate of Madagascar. In: Goodman S, Benstead J, editors. The Natural History of Madagascar. Chicago: University of Chicago Press.

Kappeler PM. 1991. Patterns of sexual dimorphism in body-weight among prosimian primates. Folia Primatol 57(3):132-146.

Kappeler PM. 1993. Sexual selection and lemur social systems. In: Kappeler PM, Ganzhorn JU, editors. Lemur social systems and their ecological basis. New York: Plenum Press. p 223-240.

Kappeler PM. 1996. Causes and consequences of life-history variation among strepsirhine primates. Am Nat 148(5):868-891.

Kappeler PM, Schäffler L. 2008. The lemur syndrome unresolved: Extreme male reproductive skew in sifakas (*Propithecus verreauxi*), a sexually monomorphic primate with female dominance. Behav Ecol Sociobiol 62(6):1007-1015.

Key C, Ross C. 1999. Sex differences in energy expenditure in non-human primates. Proceedings.Biological Sciences / the Royal Society 266(1437):2479-2485.

King SJ, Arrigo-Nelson SJ, Pochron ST, Semprebon GM, Godfrey LR, Wright PC, Jernvall J. 2005. Dental senescence in a long-lived primate links infant survival to rainfall. Proc Natl Acad Sci U S A 102(46):16579-16583.

King J., Murphy M. 1985. Periods of nutritional stress in the annual cycles of endotherms: Fact or fiction? Am Zool 25(4):955-964.

Kounig B, Riester J, Markly H. 1988. Maternal care in house mice (*Mus musculus*): II. The energy cost of lactation as a function of litter size. J Zool 216(2):195-210.

Koyama N, Nakamichi M, Ichino S, Takahata Y. 2002. Population and social dynamics changes in ring-tailed lemur troops at Berenty, Madagascar between 1989 - 1999. Primates; Journal of Primatology 43(4):291-314.

Krockenberger A. 2003. Meeting the energy demands of reproduction in female koalas, *Phascolarctos cinereus*: Evidence for energetic compensation. Journal of Comparative Physiology.B, Biochemical, Systemic, and Environmental Physiology 173(6):531-540.

Kurta A, Kunz TH, Nagy KA. 1990. Energetics and water flux of free-ranging big brown bats (*Eptesicus fuscus*) during pregnancy and lactation. J Mammal 71(1):59-65.

LaFleur MM, University of Victoria (B.C.). Dept. of Anthropology, University of Victoria (B.C.). 2008. Feeding behavior and nutrition of male and late-gestation female gallery forest *Lemur catta* at the Beza Mahafaly Special Reserve, Madagascar.

LaFleur MM, University of Colorado Boulder. Dept. of Anthropology, University of Colorado Boulder (C.O.). 2012. Ecology of Ring-Tailed Lemurs (*Lemur catta*) at the Tsimanampetsotsa National Park, Madagascar: Implications for Female Dominance and the Evolution of Lemur Traits.

Lahann P, Schmid J, Ganzhorn JU. 2006. Geographic variation in life history traits of *Microcebus murinus* in Madagascar. Int J Primatol 27:983–99

Lambert J. 2011. Primate nutritional ecology. In: Campbell CJ, editor. Primates in Perspective. New York: Oxford University Press. p 512-522.

Lee PC. 1987. Nutrition, fertility and maternal investment in primates. J Zool 213(3):409-422.

Lee PC, Bowman, JE. 1995. Influence of ecology and energetics on primate mothers and infants. In: Pryce CR, Martin RD, Skuse, D, editors. Motherhood in human and nonhuman primates. Basel: Karger. p 47-58.

Lewis R. 2005. Sex differences in scent-marking in sifaka: Mating conflict or male services? Am J Phys Anthropol 128(2):389-398.

Lewis R. 2006. Scent marking in sifaka: No one function explains it all. Am J Primatol 68(6):622-636.

Lewis RJ. 2008. Social influences on group membership in *Propithecus verreauxi verreauxi*. Int J Primatol 29(5):1249-1270.

Lewis R, Kappeler P. 2005. Seasonality, body condition, and timing of reproduction in *Propithecus verreauxi verreauxi* in the Kirindy Forest. Am J Primatol 67(3):347-364.

Levy, R. In progress. Probabilistic Models in the Study of Language.

Lewis RJ, van Schaik CP. 2007. Bimorphism in male Verreaux's sifaka in the Kirindy forest of Madagascar. Int J Primatol 28(1):159-182.

Loudon J, Sauther M. 2013. Verreaux's sifaka (*Propithecus verreauxi*) and ring-tailed lemur (*Lemur catta*) endoparasitism at the Bezà Mahafaly special reserve. Madagascar Conservation & Development 8(1):21-28.

Majolo B, McFarland R, Young C, Qarro M. 2013. The effect of climatic factors on the activity budgets of Barbary macaques (*Macaca sylvanus*). Int J Primatol 34(3):500-514.

Marsh CW. 1981. Time budget of Tana River Colobus. Folia Primatol 35:30-50.

McCabe GM, Fedigan LM. 2007. Effects of reproductive status on energy intake, ingestion rates, and dietary composition of female *Cebus capucinus* at Santa Rosa, Costa Rica. Int J Primatol 28(4):837-851.

McConkey KR, Ario A, Aldy F, Chivers DJ. 2003. Influence of forest seasonality on gibbon food choice in the rain forests of Barito Ulu, central Kalimantan. Int J Primatol 24(1):19-32.

Mclean JA, Speakman JR. 1999. Energy budgets of lactating and non-reproductive brown long-eared bats (*Plecotus auritus*) suggest females use compensation in lactation. Funct Ecol 13(3):360-372.

McNab BK. 2002. The physiological ecology of vertebrates: a view from energetics. Cornell University Press.

Meyers D, Wright P. 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.

Milton K. 1987. Primate diet and gut morphology: Implications for hominid evolution. In: Harris M, Ross EB, editors. Food and evolution: toward a theory of human food habits. Philadelphia: Temple University Press. p 93-115.

Milton K. 1996. Diet and Primate Evolution. *Scientific American*.269:86-93.

Mittermeier R. 1994. Lemurs of Madagascar. Conservation International.

Mittermeier RA, Cemex SAdCV, Agrupacio´n Sierra Madre, Conservation International. 2004. Hotspots revisited. Mexico City: CEMEX.

Mittermeier RA, Konstant WR, Hawkins F, Louis EE, Langrand O, Ratsimbazafy J, Rasoloarison R, Ganzhorn JU, Rajaobelina S, Tattersall I, Meyers DM. 2006. Lemurs of Madagascar, 2nd ed. Washington DC: Conservation International.

Moat J, Smith P. 2007. Atlas of the vegetation of Madagascar Vegetation.

Moberg GP. 2000. Biological Response to Stress: Implications for Animal Welfare. In: Moeberg GP, Mench JA, editors. The Biology of Animal Stress: Basic Principles and Implications for Animal Welfare. Oxon: CABI. p 1-22.

Moen AN. 1973. Wildlife ecology. An analytical approach. San Francisco: W.H. Freeman and Co.

Mohr CO. 1947. Table of equivalent populations of North American mammals. Am. Midland Nat. 37:223-249.

Morland HS. 1991. Yale University. Social organization and ecology of black and white ruffed lemurs (*Varecia variegata variegata)* in lowland rain forest, Nosy Mangabe, Madagascar.

Myers N, Mittermeier RA, Mittermeier CG, da Fonseca GA, Kent J. 2000. Biodiversity hotspots for conservation priorities. Nature 403(6772):853-858.

Negus N, Berger P. 1972. Environmental Factors and Reproductive Processes in Mammalian Populations.

Norscia I, Carrai V, Borgognini-Tarli S. 2006. Influence of dry season and food quality and quantity on behavior and feeding strategy of *Propithecus verreauxi* in Kirindy, Madagascar. Int J Primatol 27(4):1001-1022.

Norscia I, Palagi E. 2008. Berenty 2006: Census of *Propithecus verreauxi* and possible evidence of population stress. Int J Primatol 29(4):1099-1115.

Norscia I, Antonacci D, Palagi E. 2009. Mating first, mating more: Biological market fluctuation in a wild prosimian. PloS One 4(3):e4679.

Oda R. 1998. The responses of Verreaux's sifakas to anti-predator alarm calls given by sympatric Ring-tailed lemurs. Folia Primatol 69(6):357-360.

Ostner J, Kappeler P.M. 1999. Central males instead of multiple pairs in redfronted lemurs, *Eulemur fulvus rufus* (primates, lemuridae)? Anim Behav 58(5):1069-1069.

Overdorff DJ. 1991. Duke University. Ecological and reproductive correlates to social structure in two prosimians primates: (*Eulemur rubriventer* and *Eulemur fulvus rufus*).

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. New York: Plenum. p 61-74.

Overdorff DJ, Erhart EM, Mutschler T. 2005. Does female dominance facilitate feeding priority in black-and-white ruffed lemurs (*Varecia variegata*) in southeastern Madagascar? Am J Primatol 66(1):7-22.

Parra R. 1978. Comparison of foregut and hindgut fermentation in herbivores. The Ecology of Arboreal Folivores:205-229.

Parzen E. 1962. On estimation of a probability density function and mode. The Annals of Mathematical Statistics 33(3):1065-1076.

Passamani M. 1998. Activity budget of Geoffrey's marmoset (*Callithrix geoffroyi*) in an Atlantic forest in southeastern Brazil. Am J Primatol 46(4):333-340.

Pastorini J, Martin RD, Ehresmann P, Zimmermann E, Forstner MR. 2001. Molecular phylogeny of the lemur family cheirogaleidae (primates) based on mitochondrial DNA sequences. Mol Phylogenet Evol 19(1):45-56.

Pereira ME, Kaufman R, Kappeler PM, Overdorff DJ. 1990. Female dominance does not characterize all of the Lemuridae. Folia Primatol 2:96-103.

Pereira ME, McGlynn CA. 1997. Special relationships instead of female dominance for Redfronted Lemurs, *Eulemur fulvus rufus*. Am J Primatol 43(3):239-258.

Pereira M, Strohecker R, Cavigelli S, Hughes C, Pearson D. 1999. Metabolic Strategy and Social Behavior in Lemuridae. In: Rakotosamimanana B, Rasamimanana H, Ganzhorn J, Goodman S, editors. New Directions in Lemur Studies. New York: Kluwer Academic/Plenum Publishers. p 93-118.

Perrigo G. 1987. Breeding and feeding strategies in deer mice and house mice when females are challenged to work for their food. Anim Behav 35(5):1298-1316.

Petter J. 1972. Order of primates: sub-order of lemurs. In Battistini R.,Richard-Vindard G., editors. Biogeography and Ecology in Madagascar. The Hague: Junk.

Petter-Rousseaux J. 1962. Recherches sur l'écologie et l'éthologie des lémuriens Malgaches. Editions du Muséum.

Pinkus SE. 2004. Impact of an Introduced Population of *Eulemur fulvus* on a Native Population of *Lemur catta* at Berenty Reserve, Madagascar. MSc thesis, Department of Zoology, University of British Columbia, Vancouver.

Pollock J. 1977. The ecology and sociology of feeding in *Indri indri* . In: Clutton-Brock TH, editor. Primate Ecology: Studies of Feeding and Ranging Behavior in Lemurs, Monkeys, and Apes. London: Academic Press. p 38-68.

Pond, C.M. 1977. The significance of lactation in the evolution of mammals. *Evolution*. 31, 177-199.

Porter CA, Page SL, Czelusniak J, Schneider H, Schneider MPC, Sampaio I, Goodman M. 1997. Phylogeny and evolution of selected primates as determined by sequences of the e-globin locus and 5' flanking regions. Int J Primatol 18(2):261-295.

Powell RA. 2013. Animal home ranges and territories and home range estimators. In: Boitani L, Fuller TK, editors. Research Techniques in Animal Ecology: Controversies and Consequences. Columbia University Press. P 65-110.

Powzyk JA, Mowry CB. 2003. Dietary and feeding differences between sympatric *Propithecus diadema diadema* and *Indri indri*. Int J Primatol 24(6):1143-1162.

Ralls K. 1976. Mammals in which females are larger than males. Q Rev Biol 51(2):245-276.

Ranaivoson, TN, Razakanirina, H, Rajeriarison, C, Hladik, A. Roger, E. In press. Structure de l'habitat et disponibilites alimentaires de *Propithecus coronatus* dans la foret seche de Badrala (Station Forestiere a Usages Multiples d'Antrema, Madagascar): application de la methode des tris de litiere et interpretations des adaptations des especes arborescentes et lianescentes. Proceedings of the 19th congress of the AETFAT. April, 25-30. Antananarivo, Madagascar.

Randolph JC, Randolph PA, Mattingly K, Foster MM. 1977. Energy costs of reproduction in the cotton rat, *Sigmodon hispidus*. Ecology 58(1):31-45.

Rasamimanana H. 1999. Influence of social organization patterns on food intake of *Lemur catta* in the Berenty Reserve. In: Rakotosamimanana B, Rasamimanana H, Ganzhorn J, Goodman S, editors. New Directions in Lemur Studies. New York: Kluwer Academic/Plenum Publishers. p 173-188.

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. ed. Durham, North Carolina.: Duke University.

Ratsirarson J. 2003. Reserve Speciale de Beza Mahafaly. In: Goodman S, Benstead J, editors. The Natural History of Madagascar. Chicago: University of Chicago Press. p 1520-1525.

Razafimanahaka JH, Jenkins R, Andriafidison D, Randrianandrianina F, Rakotomboavonjy V, Keane A, Jones J. 2012. Novel approach for quantifying illegal bushmeat consumption reveals high consumption of protected species in Madagascar. Oryx 46(4):584.

Richard A. 1977. The feeding behaviour of *Propithecus verreauxi*. Primate Ecology: Studies of Feeding Behavior in Lemurs, Monkeys and Apes, Academic Press, London:71-96.

Richard A. 1978. Bucknell University. Behavioral variation: Case study of a Malagasy lemur. Associated University Press.

Richard A. 1985. Social boundaries in a Malagasy prosimian, the sifaka (*Propithecus verreauxi*). Int J Primatol 6(6):553-568.

Richard A, Rakotomanga P, Schwartz M. 1991. Demography of *Propithecus verreauxi* at Beza Mahafaly, Madagascar: Sex ratio, survival, and fertility, 1984-1988. Am J Phys Anthropol 84(3):307.

Richard A. 2003. *Propithecus*, sifaka. In: Goodman S, Benstead J, editors. The natural history of Madagascar. Chicago: University of Chicago Press. p 1345-1348.

Richard A, Dewar R, Schwartz M, Ratsirarson J. 2000. Mass change, environmental variability and female fertility in wild *Propithecus verreauxi*. J Hum Evol 39(4):381-391.

Richard A, Dewar R, Schwartz M, Ratsirarson J. 2002. Life in the slow lane? Demography and life histories of male and female sifaka (*Propithecus verreauxi verreauxi*). J Zool 256(4):421-436.

Robbins C. 1983. Wildlife feeding and nutrition. New York: Academic Press.

Robbins M, Hohmann G. 2006. Primate feeding ecology: an integrative approach. In: Hohmann G, Robbins MM, Boesch C , editors. Feeding ecology in apes and other primates: ecological, physiological and behavioral aspects. Cambridge University Press, New York, p 1–13.

Saito C. 1998. Cost of lactation in the Malagasy primate *Propithecus verreauxi:* estimates of energy intake in the wild. Folia Primtol 69 (suppl 1):414.

Sauther M., Nash L. 1987. Effect of reproductive state and body size on food consumption in captive *Galago senegalensis braccatus*. Am J Phys Anthropol 73: 81–88.

Sauther ML. 1992. Washington University in St. Louis. The effect of reproductive state, social rank and group size on resource use among free-ranging ringtailed lemurs (*Lemur catta*) of Madagascar.

Sauther ML. 1993. Resource competition in wild populations of ringtailed lemurs (*Lemur catta*): implications for female dominance. In: Kappeler PM, Ganzhorn JU, editors. Lemur social systems and their ecological basis. New York: Plenum Press. p 135-152.

Sauther ML. 1994. Wild plant use by pregnant and lactating ringtailed lemurs with implications for early hominid foraging. In: Etkin NL, editor. Eating on the wild side. Tuscon, AZ: University of Arizona Press. p 240–256.

Schäffler L, Kappeler PM. 2014. Distribution and abundance of the world's smallest primate, *Microcebus berthae,* in central western Madagascar. Int J Primatol 35(2):557-572.

Schwitzer C, Mittermeier RA, Davies N, Johnson S, Ratsimbazafy J, Razafindramanana J, Louis Jr. EE, Rajaobelina S (eds). 2013. Lemurs of Madagascar: A Strategy for Their Conservation 2013–2016. Bristol, UK: IUCN SSC Primate Specialist Group, Bristol Conservation and Science Foundation, and Conservation International.

Serio-Silva JC, Hernández-Salazar LT, Rico-Gray V. 1999. Nutritional composition of the diet of *Alouatta palliata mexicana* females in different reproductive states. Zoo Biol 18(6):507-513.

Selye H. 1950. The Physiology and Pathology of Exposures to Stress. Montreal: Acta Medica Publ.

Silk JB. 1987. Activities and feeding behavior of free-ranging pregnant baboons. Int J Primatol 8(6):593-613.

Simmen B, Hladik A, Ramasiarisoa P, Laconelli S, Hladik CM. 1999. Taste discrimination in lemurs and other primates, and the relationship to distribution of plant allelochemicals in different habitats in Madagascar. In: Rakotosamimanana H, Rasamimanana H, Ganzhorn J, Goodman S, editors. New directions in Lemur studies. New York: Kluwer Academic/Plenum Press. p 201-219

Simmen B, Hladik A, Ramasiarisoa P. 2003. Food intake and dietary overlap in native *Lemur catta* and *Propithecus verreauxi* and introduced *Eulemur fulvus* at Berenty, southern Madagascar. Int J Primatol 24(5):948-967.

Simmen B, Tarnaud L, Hladik A. 2012. Leaf nutritional quality as a predictor of primate biomass: Further evidence of an ecological anomaly within prosimian communities in Madagascar. J Trop Ecol 28(2):141-151.

Smith C. 1977. Feeding behaviour and social organization in howling monkeys. In: Clutton-Brock TH, editor. Primate Ecology: Studies of Feeding and Ranging Behavior in Lemurs, Monkeys, and Apes. London: Academic Press. p 97-126.

Sorg JP, Ganzhorn JU, Kappeler PM. 2003. Forestry and research in the Kirindy Forest/Centre de Formation Professionnelle Forestiere. In: Goodman S, Benstead J, editors. The Natural History of Madagascar. Chicago: University of Chicago Press. p 1512-1519.

Speakman JR, McQueenie J. 1996. Limits to sustained metabolic rate: The link between food intake, basal metabolic rate, and morphology in reproducing mice, *Mus musculus*. Physiol Zool 69(4):746-769.

Stearns S. 1992. The evolution of life histories. Oxford: Oxford University Press.

Stearns S. 1976. Life-history tactics: A review of the ideas. Q Rev Biol 51(1):3-47.

Stephens PA, Boyd IL, McNamara JM, Houston AI. 2009. Capital breeding and income breeding: Their meaning, measurement, and worth. Ecology 90(8):2057-2067.

Sussman R. 1972. An ecological study of two Madagascar Primates: *Lemur fulvus rufus* (Audebert) and *Lemur catta* (Linnaeus). PhD thesis, Department of Anthropology, Duke University, Durham.

Sussman R. 1999. Primate ecology and social structure volume 1: Lorises, lemurs and tarsiers. Needham Heights, MA: Pearson Custom Publishing.

Sussman, R, Rakotozafy, A. 1994. Plant diversity and structural analysis of a tropical dry forest in southwestern Madagascar. Biotropica 26(3): 241-254

Sussman R, Sweeney S, Green G, Porton I. 2006. A preliminary estimate of *Lemur catta* population density using satellite imagery. In: Jolly A, editor. Ringtailed Lemur Biology: *Lemur catta* in Madagascar. Boston, MA: Springer US. p 16-31.

Sussman RW, Richard AF, Ratsirarson J, Sauther ML, Brockman DK, Gould L, Lawler R, Cuozzo FP. 2012. Beza Mahafaly Special Reserve: Long-term research on lemurs in southwestern Madagascar. In: Anonymous Berlin, Heidelberg: Springer Berlin Heidelberg. p 45-66.

Tabachnick BG, Fidell LS. 2001. Using multivariate statistics. Boston, MA: Allyn and Bacon.

Tattersall I. 1987. Cathemeral activity in primates: A definition. Folia Primatol 49:200-202.

Taufik E, Fukuda K, Senda A, Saito T, Williams C, Tilden C, Eisert R, Oftedal O, Urashima T. 2012. Structural characterization of neutral and acidic oligosaccharides in the milks of strepsirrhine primates: Greater galago, aye-aye, coquerel's sifaka and mongoose lemur. Glycoconj J 29(2-3):119-134.

Terborgh J, van Schaik C. 1987. Convergence vs. nonconvergence in primate communities. In: Gee J, Giller P, editors. Organization of communities, past and present. Oxford: Blackwell Scientific. p 205-226.

Thomas VG. 1988. Body condition, ovarian hierarchies, and their relation to egg formation in anseriform and galliform species. In: Ouellet H, editor. Acta XIX Congressus Internationalis Ornithologici. Ottawa: University of Ottawa Press. p 353-363.

Tilman D, May RM, Nowak MA, Lehman CL. 1994. Habitat destruction and the extinction debt. Nature 371(6492):65-66.

Tilden CD, Oftedal OT. 1997. Milk composition reflects pattern of maternal care in prosimian primates. Am J Primatol 41(3):195.

Tirado Herrera ER, Heymann EW. 2004. Does mom need more protein? preliminary observations on differences in diet composition in a pair of red titi monkeys (*Callicebus cupreus*). Folia Primatol (Basel) 75(3):150-153.

van Schaik CP, Kappeler PM. 1996. The social systems of gregarious lemurs: Lack of convergence with anthropoids due to evolutionary disequilibrium? Ethology 102(7):915-941.

van Schaik CP, Noordwijk MA. 1985. Interannual variability in fruit abundance and the reproductive seasonality in Sumatran Long-tailed macaques (*Macaca fascicularis*). J Zool 206(4):533-549.

van Schaik, CP. 1989. The ecology of social relationships amongst female primates. *Comparative socioecology: The behavioural ecology of humans and other mammals*, 195-218.

van Schaik C, Brockman DK. 2005. Seasonality in primate ecology, reproduction, and life history: An overview. In: Brockman DK, van Schaik C, editors. Seasonality in primates: studies of living and extinct human and non-human primates. Cambridge: Cambridge University Press. p 3-20.

Virah-Sawmy M, Willis K, Gillson L, Williams J. 2010. Evidence for drought and forest declines during the recent megafaunal extinctions in Madagascar. J Biogeogr 37(3):506-519.

Waser P. 1977. Feeding, ranging and group size in the managabey *Cercocebus albigena*. In: Clutton-Brock TH, editor. Primate Ecology: Studies of Feeding and Ranging Behavior in Lemurs, Monkeys, and Apes. London: Academic Press. p 183-222.

Waterman PG. 1984. Food acquisition and processing as a function of plant chemistry. In: Chivers DJ, Wood BA, Bilsborough A, editors. Food Acquisition and Processing in Primates. New York: Plenum Press. p 177-211.

Wells N. 2003. Geology and soils. In: Goodman S, Benstead J, editors. The Natural History of Madagascar. Chicago: University of Chicago Press.

White GC. Garrott RA. 1990. Analysis of wildlife radio-tracking data. San Diego: Academic Press.

Wickham H. 2009. ggplot2: elegant graphics for data analysis. Springer New York. http://had.co.nz/ggplot2/book

Wingfield JC, Sapolsky RM. 2003. Reproduction and resistance to stress: When and how. J Neuroendocrinol 15(8):711-724.

Worton BJ. 1989. Kernel methods for estimating the utilization distribution in home-range studies. Ecology 70:164-168.

Wrangham R. 1980. An ecological model of female-bonded primate groups. Behaviour 75:262–300

Wright PC. 1993. The evolution of female dominance and biparental care among non-human primates. In: Miller B, editor. Sex and gender hierarchies. Cambridge: Cambridge University Press. p 127-147.

Wright P. 1984. Biparental care in *Aotus trivirgatus* and *Callicebus moloch.* In: Small MF, editor. *Female primates: Studies by women primatologists.* New York: Alan R. Liss. p 59-75.

Wright P. 1995. Demography and life history of free-*ranging Propithecus diadema edwardsi* in Ranomafana National Park, Madagascar. Int J Primatol 16(5):835-854.

Wright P. 1999. Lemur traits and Madagascar ecology: Coping with an island environment. Yearbook of Physical Anthropology 42:31-72.

Yamashita N. 2008. Chemical properties of the diets of two lemur species in southwestern Madagascar. Int J Primatol 29(2):339-364.

Yoder AD, Cartmill M, Ruvolo M, Smith K, Vilgalys R. 1996a. Ancient single origin for Malagasy primates. Proc Natl Acad Sci U S A 93(10):5122-5126.

Yoder AD, Vilgalys R, Ruvolo M. 1996b. Molecular evolutionary dynamics of cytochrome b in strepsirrhine primates: The phylogenetic significance of third-position transversions. Mol Biol Evol 13(10):1339.

Yoder A, Yang Z. 2004. Divergence dates for Malagasy lemurs estimated from multiple gene loci: Geological and evolutionary context. Mol Ecol 13(4):757-773.

Young A, Richard A, Aiello L. 1990. Female dominance and maternal investment in strepsirhine primates. Am Nat 135(4):473-488.

Zinner D. 1999. Relationship between feeding time and food intake in Hamadryas baboons (*Papio hamadryas*) and the value of feeding time as predictor of food intake. Zoo Biol 18(6):495-505.

Zjhra ML. 2006. New taxa of coleeae (*bignoniaceae*) from Madagascar. I. A collection from Masoala Peninsula. Annn Bot Fennici 43:225-239.

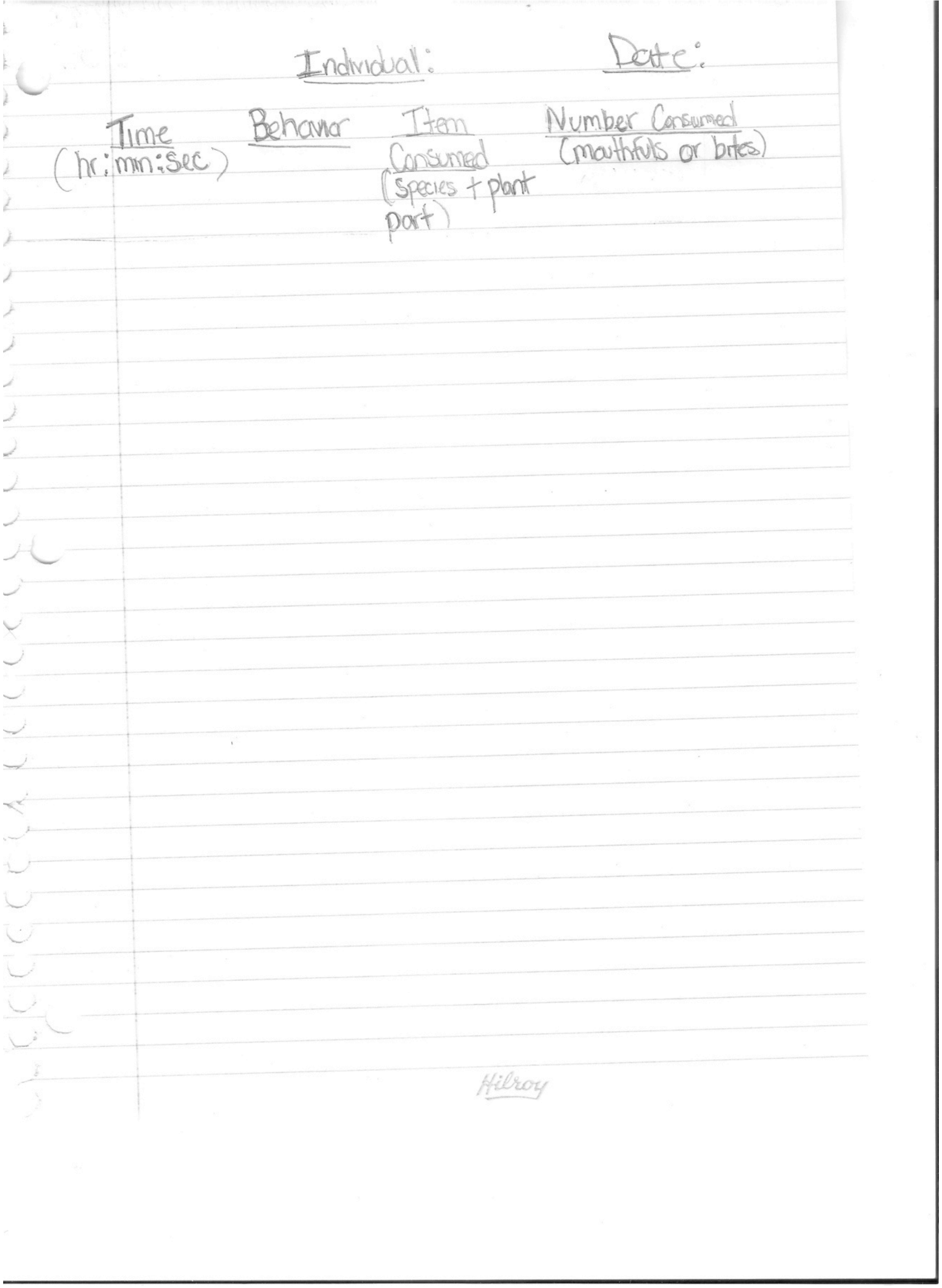
Zjhra ML. 2008. Facilitating sympatric species coexistence via pollinator partitioning in endemic tropical trees of Madagascar. Plant Syst Evol 271(3):157-176.

APPENDIX I-ETHOGRAM

Activity:	Definition:
Rest(R)	Any period focal animal is inactive, including sleep.
Feed(F)	Any period focal animal is ingesting, masticating, or swallowing food.
Locomote(L)	Any period focal animal is moving, including but not limited to jumping on ground, climbing quadrupedally in trees, and leaping in vertical, upright position from tree to tree.
Self-groom(SG)	Focal animal is inspecting or combing its own coat via tooth-comb, hands, or feet.
Allo-groom(AG)	Focal animal is inspecting or combing the coat of another individual via tooth-comb, hands, or feet or focal is receiving such inspection/combing.
Scent-mark(SM)	Focal animal is rubbing areas known to have scent-glands on a branch or object.
Vocalize(VOC)	Focal animal is making repeated noises using its vocal folds such as “tchi-fak” or a roaring bark. (Note: Intermittent vocalizations such as a quick grunt were not recorded.)
Vigilance(VIG)	Focal animal raises head and is alertly scanning the area for perceived threats.
Play(PLAY)	Focal animal is physically interacting with one or more individuals in a non-agonistic manner, such as wrestling, jumping on another individual, etc.
Other(O)	Any behavior the focal animal engages in that cannot not accurately be described by the above activities.

APPENDIX II-DATA COLLECTION SHEETS

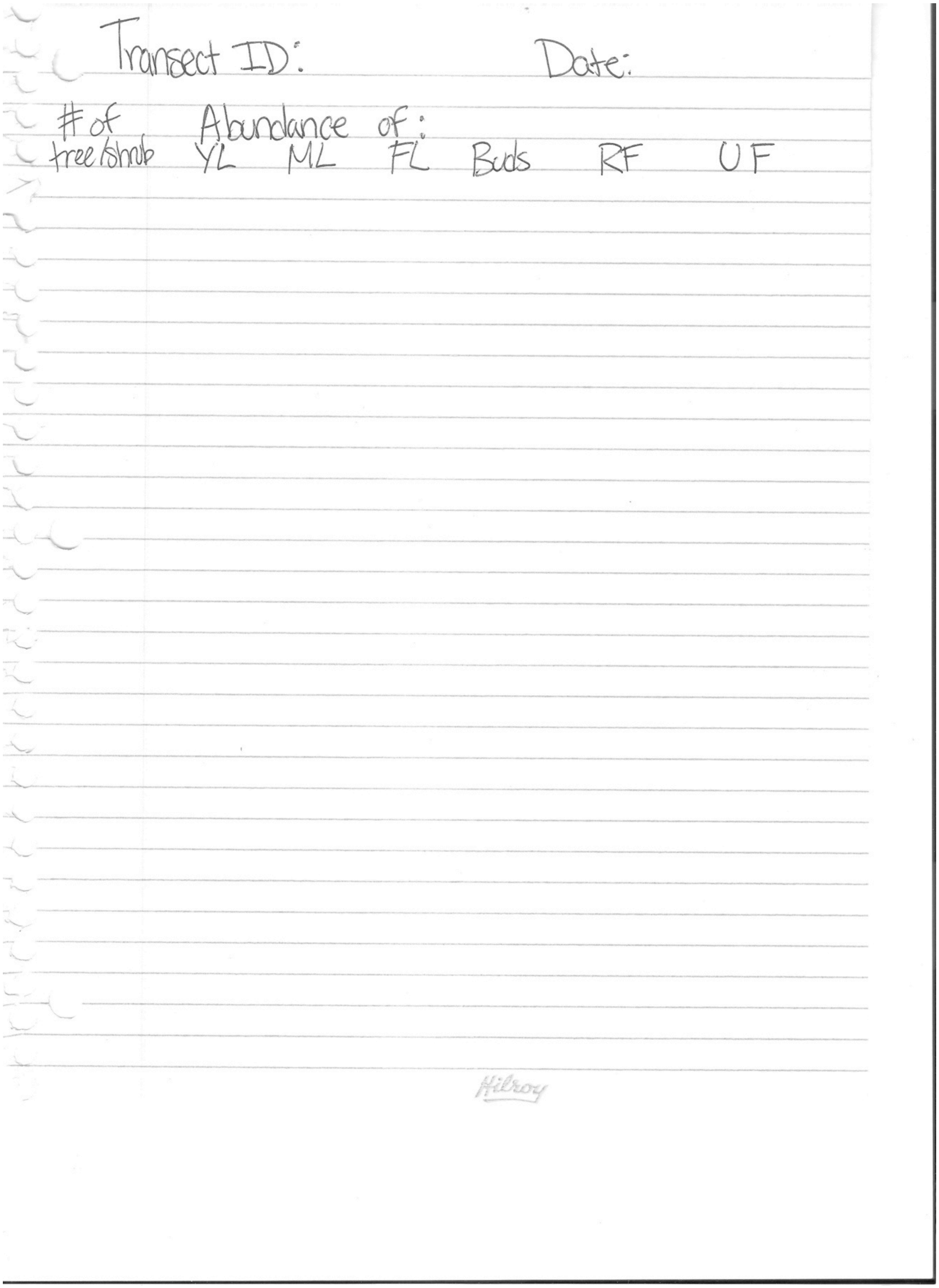
Behavioral Data Sampling



Individual: Date:

Time (hr:min:sec)	Behavior	Item Consumed (species + plant part)	Number Consumed (mouthfuls or bites)

Phenological Data Sampling



Transect ID: Date:

# of tree/shrub	Abundance of:					
	YL	ML	FL	Buds	RF	UF

APPENDIX III-INDEX OF KNOWN PLANTS CONSUMED AT BERENTY

Plant family	**Species**	**Plant part consumed**
Anacardiaceae	*Operculicarya* cf. *decaryi*	Mature leaves
Anacardiaceae	*Poupartia minor*	Young leaves, mature leaves
Anacardiaceae	*Sclerocarya birrea*	Flowers, young leaves, mature leaves
Apocynaceae	*Hazunta modesta*	Ripe fruit pulp and seed, unripe fruit, mature leaves
Asclepdiadaceae	*Pentopetia androsaemifolia*	Stem, petiole, mature leaves
Asclepdiadaceae	*Secamone uncinata*	Young leaves, mature leaves, unripe fruit
Asteraceae	*Vernonia pectoralis*	Mature leaves
Boraginaceae	*Cordia caffra*	Mature leaves
Caesalpiniaceae	*Caesalpinia bonduc*	Stem, young leaves
Caesalpiniaceae	*Tamarindus indica*	Young leaves, mature leaves, flowers
Capparidaceae	*Crataeva* sp.	Mature leaves
Combretaceae	*Combretum albiflorum*	Stem, young leaves, mature leaves, unripe fruit
Combretaceae	*Combretum* sp.	Young leaves, mature leaves
Combretaceae	*Terminalia mantaly*	Flowers, unripe fruit
Convolvulaceae	*Ipomoea cairica*	Stem, young leaves, mature leaves
Convolvulaceae	*Metaporana parvifolia*	Mature leaves
Cucurbitaceae	*Xerosicyos perrieri*	Mature leaves
Euphorbiaceae	*Antidesma madagascariense*	Unripe fruit, young leaves
Euphorbiaceae	*Euphorbia famatamboay*	Young leaves, stem
Euphorbiaceae	*Euphorbia laro*	Stem, young leaves
Euphorbiaceae	*Euphorbia plagiantha*	Ripe fruit
Euphorbiaceae	*Phyllanthus casticum*	Young leaves, flowers
Flacourtiaceae	*Physena sessiliflora*	Mature leaves
Icacinaceae	*Apodytes dimidiate*	Young leaves, mature leaves
Loganiaceae	*Strychonos madagascariensis*	Mature leaves
Lythraceae	*Lawsonia* sp.	Leaves (unknown maturity)

Malvaceae	*Hibiscus* sp.	Mature leaves
Meliaceae	*Azadirachta indica Jussieu*	Young leaves, mature leaves, floral bud, ripe fruit
Meliaceae	*Quivisianthe papinae Baill.*	Young leaves
Mimosaceae	*Acacia rovumae Oliv.*	Young leaves, unripe fruit, flowers
Mimosaceae	*Acacia* sp.	Young leaves
Mimosaceae	*Albizia polyphylla*	Petiole
Mimosaceae	*Calliandra surinamensis*	Young leaves, ripe fruit seed and pulp, flowers
Mimosaceae	*Leucaena leucocephala*	Mature leaves, unripe fruit
Mimosaceae	*Pithecellobium dulce*	Young leaves, mature leaves, ripe fruit seed and pulp, flowers, unripe fruit
Moraceae	*Ficus cf. polita*	Mature leaves
Moraceae	*Ficus cf. sycomorus*	Ripe fruit, young leaves, mature leaves
Moraceae	*Ficus sp.*	Young leaves, mature leaves, unripe fruit
Myrtaceae	*Eucalyptus sp. ****	Young leaves
Nyctaginaceae	*Bougainvillaea spectabilis*	Young leaves, stem
Rhamnaceae	*Zizyphus cf. spina-cristi*	Leaves (unknown maturity)
Rubiaceae	*Enterospermum sp.****	Mature leaves
Salvadoraceae	*Azima tetracantha*	Ripe fruit, mature leaves
Sapindaceae	*Allophyllus decaryi*	Mature leaves
Sapindaceae	*Neotina isoneura*	Ripe seed, ripe fruit, young leaves, mature leaves, wood
Solanaceae	*Solanum croatii*	Young leaves, floral bud, unripe fruit
Sterculiaceae	*Byttneria voulily*	Mature leaves
Tiliaceae	*Grewia grandidieri*	Young leaves, mature leaves
Tiliaceae	*Grewia saligna*	Young leaves, mature leaves
Ulmaceae	*Celtis bifida*	Young leaves, ripe fruit
Ulmaceae	*Celtis gomphophylla*	Ripe fruit
Ulmaceae	*Celtis philippensis*	Young leaves, mature leaves
Violaceae	*Rinorea greveana*	Young leaves, mature leaves, unripe fruit
Vitaceae	*Cissus quadrangularis*	Mature leaves

APPENDIX IV-FOOD AVAILABILITY RATINGS FOR DURATION OF STUDY

		14-Aug			28-Aug			11-Sep		
Forest	**Species**	**ML**	**YL**	**FL**	**ML**	**YL**	**FL**	**ML**	**YL**	**FL**
Ankoba	*Rinorea greveana*	4	0	0	4	1	0	4	1	1
Ankoba	*Morua alba*	4	1	0	3	0	0	4	0	0
Ankoba	*Celtis gomphophylla*	3	0	0	4	0	0	4	0	0
Ankoba	*Bauhirria sp.*	4	0	0	2	0	0	2	0	0
Ankoba	*Pithecellobium dulce*	4	1	2	3	0	3	4	1	2
Ankoba	*Tamarindus indica*	4	1	0	3	1	0	4	1	0
Ankoba	*Celtis bifida*	4	1	0	4	0	0	4	0	0
Ankoba	*Acacia rovumae*	4	0	0	3	2	0	3	3	0
Malaza	*Celtis bifida*	4	0	0	4	0	0	4	0	0
Malaza	*Rinorea greveana*	4	0	0	3	0	0	4	1	1
Malaza	*Celtis gomphophylla*	4	0	0	3	0	0	3	0	0
Malaza	*Neotina isoneura*	3	0	0	4	0	0	4	0	0
Malaza	*Tamarindus indica*	4	1	0	4	1	0	4	1	0
Malaza	*Ficus madagascariensis*	2	0	0	1	0	0	1	0	0
Malaza	*Acacia rovumae*	4	0	0	4	1	0	4	2	0
Malaza	*Albizia polyphylla*	4	0	0	4	0	0	4	0	0

Note: ML=mature leaves, YL=young leaves, FL=flowers. A rating of 0 indicates not present, 1 indicates item is present in less than 25% of the tree or shrub's foliage, 2 25% or greater but less than 50%, 3 50% or greater but less than 75%, and 4 75% or greater.