Ecology of Ring-Tailed Lemurs (Lemur catta) at the Tsimanampetsotsa National Park, Madagascar: Implications for Female Dominance and the Evolution of Lemur Traits

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ECOLOGY OF RING-TAILED LEMURS (*Lemur catta*) AT THE TSIMANAMPETSOTSA NATIONAL PARK, MADAGASCAR: IMPLICATIONS FOR FEMALE DOMINANCE AND THE EVOLUTION OF LEMUR TRAITS

by

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B.Sc., University of Victoria, 2004
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A thesis submitted to the Faculty of the Graduate School of the University of Colorado Boulder in partial fulfillment of the requirements for the degree of Doctor of Philosophy

Department of Anthropology

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This thesis is entitled:
Ecology of ring-tailed lemurs (*Lemur catta*) at the Tsimanampetsotsa National Park, Madagascar: Implications for female dominance and the evolution of lemur traits
written by Marni LaFleur
has been approved for the Department of Anthropology

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ACU protocol # 1002.09
LaFleur, Marni (Ph.D., Anthropology)

Ecology of ring-tailed lemurs (*Lemur catta*) at the Tsimanampetsotsa National Park, Madagascar: Implications for female dominance and the evolution of lemur traits

Thesis directed by Associate Professor Michelle L. Sauther

Lemurs are an ancient, extant primate radiation and have a number of traits (e.g. female dominance, low basal metabolic rate, weaning synchrony, cathemerality) which are unusual when compared to other primates, or even other mammals. The Energy Conservation Hypothesis (ECH) posits that the lemur traits are part of an adaptive complex selected to enable lemurs to conserve and extract energy from their seasonally and stochastically resource-poor environments. Data were collected on two groups of ring-tailed lemurs in the dry spiny forests of the Tsimanampetsotsa National Park, Madagascar, and tested aspects of the ECH through the following hypotheses: 1) ring-tailed lemur foods are seasonally and stochastically limited, 2) ring-tailed lemur nutrients and/or calories are seasonally and stochastically limited, 3) ring-tailed lemurs use behavioral mechanisms to save energy, and 4) the dry season is differentially stressful for female ring-tailed lemurs. Results from these data suggest that ring-tailed lemur plant foods, nutrients, and calories are seasonally and stochastically limited. Males appear to use behavioral strategies to conserve energy and females appear differentially stressed by the harsh conditions of the dry season. This study also documented extensive cathemeral activity in the ring-tailed lemurs, which may function to increase food intake, and limit thermoregulatory stress during hot days and cool nights. The aforementioned results are consistent with ECH, indicating that the lemur traits are an adaptive response to the environmental pressures of Madagascar. Furthermore, since dominance facilitates a feeding advantage for female lemurs, this trait likely allows for costly mammalian reproduction during times of predictable resource scarcity.
For Sid, the lemur that never really had a chance, but slipped through my fingers anyhow. I am deeply sorry and will forever cherish your tooth comb garlic kisses.
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CHAPTER 1: Introduction to Lemur Traits and Primate Socioecology

Overview

This is the first study to document *Lemur catta* (ring-tailed lemurs) behavioral ecology in an intact spiny forest habitat. The vast majority of our knowledge on *L. catta* comes from gallery forest, where *Tamarindus indica* (tamarind) trees dominate the landscape. When they co-exist in this way, *T. indica* is a fallback and commonly used resource for *L. catta*, and we thus have very little information on ring-tailed lemurs in areas that are not dominated by tamarind trees. To date, only three studies have examined *L. catta* outside of gallery forests; two were in highly anthropogenically-degraded habitats, and the third was in the unusual high-altitude mountain range ring-tailed lemur population of Andringitra. This study provides new comparative data, and is of special interest in that it was collected on populations living within spiny forest habitat which may be the original habitat for this species. Thus, studying ring-tailed lemurs in an intact spiny forest offers the best possible opportunity to understand their adaptations, and subsequently understand the flexibility of the species.

Data were collected on two groups of *L. catta* over a consecutive nine month period at the Tsimanampetsotsa National Park (TNP), in southwestern Madagascar. This time period encompassed the latter portion and peak of the long annual dry season and the following short wet season. Additionally, during the study period Cyclone Bingiza occurred and resulted in heavy rains and a flash flood at TNP. Throughout the study, behavioral data were collected during the day and night. These data, along with camera trap photos, nutritional analyses of ring-tailed lemur plant foods, and assessments of stress, were used to test aspects of the Energy Conservation Hypothesis, including female dominance.
Background

The extant lemurs of Madagascar represent a primate radiation dating to at least the Eocene epoch (e.g. Yoder, 2004; Karanth et al., 2005). Within strepsirrhine primates (Lemuriformes and Lorisiformes), the lemurs (including the recently extinct "giant" forms), show the greatest variability in body size, activity patterns, feeding modes, locomotion styles, and social patterns (Scheumann et al., 2007). Several lemur features are puzzling as they demonstrate a very different adaptive pattern when compared to haplorrhine primates (van Schaik and Kappeler, 1996). For example, female dominance over males is extremely rare within mammalian social systems (Ralls, 1976; Kappeler, 1993), but is the norm within the lemurid primates (Kappeler, 1991, 1993). Factors favoring the evolution of female dominance have yet to be fully identified despite learned debate spanning more than two decades (see Pochron and Wright, 2005; Dunham, 2008). Understanding female dominance in lemurs is of particular interest because, unlike the few mammalian species showing female dominance, including hyenas (Crocuta crocuta [Kruuk, 1972]) and mole rats (Heterocephalus spp. [Sherman et al., 1991]), lemur females (with the exception of some mouse lemurs [e.g. Smith and Jungers, 1997]) do not have a size advantage over males and thus dominance is maintained socially rather than physically. In fact, uncovering the reasons for female dominance in lemurs has been deemed the “holy grail” of lemur research (Pochron and Wright, 2005). The predominant explanation in the current literature, the “Energy Conservation Hypothesis” (ECH), suggests that lemur female dominance results from an adaptation that allows females feeding priority, which counteracts high reproductive costs, along with seasonal and stochastic scarcity of food resources (Jolly, 1984; Young et al., 1990; Wright, 1999; Pochron et al., 2003). The ECH is a viable hypothesis, but has
yet to be fully tested and may contain incorrect information regarding some so-called “lemur traits.”

As described, the ECH for female dominance in lemurs has four key assumptions. Namely, it assumes that 1) lemur food resources are seasonally (and stochastically) limited, 2) a reduction in food availability results in a reduction in nutrient or caloric intake for lemurs, and that this reduction of nutrient or caloric intake is 3) stressful for all lemurs, but 4) particularly stressful for female lemurs who have the increased metabolic demands of gestation and lactation. This project examines the effects of season, sex and reproductive state on feeding behavior, nutrition, and stress on ring-tailed lemurs, in order test the aforementioned assumptions of ECH.

*Lemur catta* is an ideal species for testing the ECH as males and females are monomorphic in body size (Kappeler, 1991), females have strict dominance over males in all feeding and social situations (Jolly, 1966, 1984, 1998), and they have strict reproductive synchrony (Jolly, 1966). Additionally, *L. catta* is a monotypic species that up until only about 2000 years ago had been evolving for tens of millions of years within an environment free of humans and other major mammalian groups (Burney, 1987; Martin, 2000; Roos et al., 2004; Yoder and Yang, 2004). These traits render ring-tailed lemurs an ideal species for making direct comparisons between individuals, and understanding differences between sexes (see Gould, 2006). Moreover, TNP is an excellent site for testing the ECH because not only is it a good example of dry spiny habitat to which *L. catta* is proposed to be adapted (Goodman et al., 2006), it is also a large intact forest parcel, with few anthropogenic effects or invasive plant foods (Sussman et al., 2003). Gould (2006) noted that these conditions are optimal for understanding evolution and adaptation in *L. catta*.
Most of our knowledge of ring-tailed lemurs and how they differ in response to environmental variability, comes from the Beza Mahafaly Special Reserve or the Berenty Private Reserve, which are both highly fragmented and patchily degraded forest habitats, that are dominated by tamarind trees (See Gould et al., 1999; Sauther et al., 1999; Jolly et al., 2002; Cuozzo and Sauther, 2006; Koyama et al., 2006). As such, we know very little about ring-tailed lemur ecology outside gallery forest habitats (Gould, 2006). Though it is unclear when tamarind trees were introduced to Madagascar (Sauther and Cuozzo, 2009), when present, tamarind trees have a huge impact on ring-tailed lemur feeding ecology (Sauther, 1998; Yamashita, 2002; Simmen et al., 2006; Sauther and Cuozzo, 2009). In fact, L. catta in gallery forests spend 35-60% of their time feeding on tamarind fruits and leaves (Mertl-Milhollen et al., 2003), and Yamashita (2002, 2008) suggested that in gallery forests all other foods should be considered secondary to tamarind. Only two studies have observed L. catta in spiny environments, which are not dominated by tamarind trees, but in both cases the habitats were highly fragmented and affected by anthropogenic disturbance (Gould et al., 2011; Kelly, 2011). Additionally, although the ecology of L. catta has been briefly examined within the high-altitude populations of Andringitra (Goodman et al., 2006), the habitat of Andringitra is very different than what we believe ring-tailed lemurs are adapted to, and presents an entirely different suite of challenges to the ring-tailed lemurs residing there. Studying ring-tailed lemurs within a near pristine spiny forest habitat not dominated by tamarind trees provides insight into their ecology and behavior in their “natural” environment, meaning the habitat in which ring-tailed lemurs likely evolved and were living in up until human-induced alterations greatly changed much of Madagascar’s landscape (Goodman et al., 2006).
Rationale for Research

Unusual “lemur traits” include female dominance, targeted female-female aggression, lack of sexual dimorphism, sperm competition coupled with male-male aggression, high infant mortality, cathemerality, and strict seasonal breeding (Wright, 1999; Figure 1.0), and understanding the causal mechanisms of such traits has driven the research of many primatologists. Van Schaik and Kappeler (1996) noted distinct differences between gregarious lemurs and haplorrhine primates in several social, demographic, morphological and ecological features. Both ECH (Wright, 1999) and the evolutionary disequilibrium hypothesis (EDH) (van Schaik and Kappeler, 1996) have been presented to account for lemur traits. EDH argues that all extant lemur species were nocturnal and monogamous until the arrival of humans on Madagascar approximately 2000 years ago. Moreover, EDH states that the ensuing rapid ecological changes and extinctions of Madagascar's megafauna (both giant lemurs and large-bodied predatory raptors) reduced interspecific competition and predation pressure for surviving smaller-bodied lemurs, which opened up niches that modern diurnal lemurs are now exploiting. Characteristics such as monomorphism and female dominance are not seen as adaptations to current environments, but rather to ecological pressures present before the onset of the Holocene. For the purposes of this manuscript, all mention of the EDH will refer the hypothesis as specifically defined and proposed by van Schaik and Kappeler (1996) to account for the unusual traits found in lemurs.
There are several lines of evidence which suggest that lemurs are not in the type of evolutionary disequilibrium described by van Schaik and Kappeler (1996). The following three points outline the current evidence contrary to van Schaik and Kappeler's EDH.

First, EDH says that predator pressure is reduced for diurnal lemurs, because of the recent extinction of the large-bodied diurnal birds of prey (*Stephanoaetus maheryi*). However, extant endemic predators such as the harrier hawk (*Polyboroides radiatus*) are a real threat to diurnal lemurs, as they are subject to significant predation events that rival those of nocturnal lemurs (Wright et al., 1997; Karpanty, 2006; Brockman et al., 2008). Also, ring-tailed lemurs at the Beza Mahafaly Special Reserve are frequent prey victims of a number of species, including wild cats (e.g. Brockman et al., 2008; Sauther et al., 2011), and some evidence suggests that predation may be occurring both day and night, given the recovery of fresh lemur remains, and eye witness accounts, at various times during the day (Sauther et al., 2011). Furthermore, since there was also
a giant fossa (*Cryptoprocta spelea*) until about 2000 years ago, which was a large as 20kg (Goodman et al., 2004), by van Schaik and Kappeler's reasoning, we should expect that lemurs experience reduced predation pressure by modern fossa, which is simply not the case (Hawkins, 2003; Karpanty, 2003, 2006). It is more parsimonious to assume that the extinction of giant lemurs and their giant predators were coupled, and lemurs today are subject to predation by their extant predators, as we know they are.

Second, EDH predicts that cathemeral lemurs would have visual anatomy similar to that of nocturnal lemurs, given that they would have only recently diverged from their fully nocturnal lifestyle. Nocturnal species tend to have features that enhance visual sensitivity, such as increased size and curvature of cornea and lens, well-developed *tapetum lucidum* (a reflective layer which increases light available to receptors), and an increase in the proportion of rods to cones (Detwiler 1939, 1940, 1941; Walls, 1942; Prince, 1956; Duke-Elder, 1958; Tansley, 1965). By comparison, diurnal species typically have anatomical eye specializations that increase acuity, and may include *area centralis* (an area with a high density of receptors which increase acuity), reduction in the size and curvature of the cornea and lens, decreased retinal summation, and an increase in the proportion of cones to rods (Detwiler, 1939, 1940, 1941; Walls, 1942; Prince, 1956; Duke-Elder, 1958; Tansley, 1965). However, cathemeral lemurs have visual anatomy specializations, which differ from those of diurnal or nocturnal primates (Kirk, 2006). Moreover, eye morphology in cathemeral *Eulemur* are very similar to that found in other non-primate cathemeral mammals (Kirk, 2006). That is, cathemeral animals tend to have eye adaptations that are almost half-way between that of diurnal and nocturnal animals, such as poorly developed *tapetum lucidum* and *area centralis*, intermediate size and roundness of the cornea and lens, and intermediate proportion of rods compared to cones (Kirk, 2006). These
unique cathemeral lemur eye specializations along with the convergence of traits with other cathemeral animals suggest this visual anatomy is adaptive (Kirk, 2006). Kirk (2006) further suggests that the common ancestor of *Eulemur* was characterized by cathemerality, during the time period of 8-12MYA. Additionally, using phylogenetic analyses, Griffin et al. (2012) suggested that *Eulemur* share a cathemeral common ancestor 9MYA, and that the common ancestor of strepsirrhines was nocturnal. None of the aforementioned data is compatible with van Schaik and Kappeler's (1996) EDH.

Third, genetic analyses suggest a common ancestry of diurnal or cathemeral indriids and lemurids from between 32 and 32MYA, which implies that modern *cathemeral* and *diurnal* lemurs did not share a *nocturnal* common ancestor, and therefore ruling out the possibility of a recent (2000 years before present) nocturnal common ancestor (Roos et al., 2004). Though the culmination of these findings does not completely discount the possibility that some modern lemurs are in a state of evolutionary disequilibrium, the current evidence provides no support and indicates that this is not a promising direction for future research for understanding lemur traits.

Alternatively, ECH (Wright, 1999) does appear to be a promising direction in lemur research for understanding unusual lemur traits. In fact, this hypothesis has become normalized as the driving force in lemur adaptations though it has yet to be adequately scientifically tested (Dunham, 2008). ECH posits that the majority of lemur traits are either adaptations to conserve energy (e.g. low basal metabolic rate (BMR), torpor, sperm competition, small group size, seasonal breeding) or to maximize the use of scarce resources (e.g. female dominance, cathemerality, territoriality, fibrous diet, weaning synchrony) (Wright, 1999). Again, though prevalent throughout the literature, some of these suggested lemur traits or adaptations may not be truly representative of lemurs. For example, low basal metabolic rate is cited as an energy-
conserving trait of lemurs, and is prevalent throughout the literature (Richard and Nicol, 1987; Young et al., 1990; Wright, 1999; Tilden, 2008). Daniels (1984) demonstrated that some three individual Eulemur had BMRs just 28% of that predicted from the Kleiber relationship for same-sized mammals. However, Kappeler (1996) showed that reduced BMR is a characteristic of the strepsirrhine primates, rather than being uniquely lemur. In a recent review of BMR in primates, Harcourt (2008) also showed (using data from Genoud [2002] and White and Seymour [2003]) that strepsirrhines indeed have lower BMR when compared to haplorrhine primates, but that lemur BMRs are not significantly lower than that of other strepsirrhine primates. That being said, low BMR may very well be an important trait in lemurs, however, the extent to which this trait is a result of phylogenetic inertia is unknown. Though, from the current body of literature, you would presume that the this trait had been extensively tested and studied.

Costs of reproduction for female lemurs are also unclear, despite being mentioned frequently in the literature as though these costs are well understood. Some researchers argue that lemur females have unusually high costs of reproduction (Jolly, 1984; Richard and Nicol, 1987; Young et al., 1990), while others say that female lemurs invest less than expected into reproduction (Wright, 1995; Tilden and Oftedal, 1997; Wright, 1999; Tilden, 2008). Young et al. (1990) posits that female lemurs have a high rate of prenatal maternal investment (as measured by average neonate weight gain per day gestation) when compared to other strepsirrhine primates. However, Kappeler (1996) argued that postnatal growth rates, which represent the bulk of maternal investment, do not differ among lemurs and lorises, and concluded that lemur females do not invest significantly more energy in reproduction than other strepsirrhine primates. Wright (1995) stated that lemur females may invest less in reproduction when compared to other primates, as lemurs have low-quality milk and lower infant birth weights. However, subsequent research has
shown that milk quality is not universally low in lemurs, but rather, milk is more dilute in primate mothers whose infants “ride” rather than “park” (Tilden and Oftedal, 1997; Tilden, 2008). Furthermore, while lemur neonates weigh an average of 9% of maternal body mass, neonate weight in galagos is about 7% of maternal weight (Izard and Nash, 1988) and a mere 3% in lorises (Zimmermann, 1988). These data suggest that low milk quality and low neonate body weight are not idiosyncrasies of lemurs.

Wright (1995, 1999) also suggested that females invest little in their young because infant mortality is inordinately high and further maternal investment would not result in increased survivorship. As evidence, Wright (1999) cites infant mortality rates of 40-80% for *L. catta* and notes that these are twice the infant mortality rates of studied monkey populations. However, the *L. catta* mortality rates cited by Wright, which neared 80%, were in the reproductive season following a 2-year massive drought in southern Madagascar, and that during this time mortality rates were elevated throughout the entire population, not just within infants (Gould et al., 1999). As would be expected, primate populations experiencing natural disasters show increased mortality (Pavelka et al., 2007), so this is not a peculiarity of lemurs. What about the lower end (i.e. 40%) Wright (1999) cited for lemur infant mortality? Semi-free-ranging ring-tailed lemurs experience infant mortality rates of 28.6% (Parga and Lessnau, 2005), which is lower than their wild counterpart, but is likely due to food provisioning and protection from predators. Infant mortality rates for wild non-lemur strepsirrhine primates are largely lacking from the current literature, however wild haplorrhine primates show the following infant mortality rates: *Saimiri oerstedii* 50% (Boinski, 1987), *Semnopithecus entellus* 50% (Borries, 1997), *Callithrix* spp. > 50% (Ross et al., 2007), *Gorilla beringei beringei* 27% (Robbins et al., 2007). Given the data at hand, it does not seem that lemur infant mortality rates are elevated *per se*, and thus increased
infant mortality should not be interpreted as a trait unique to lemurs. However, it is important to consider the effects of frequent natural disasters on lemur evolution. In sum, no current evidence sufficiently demonstrates that lemur females have unusually high or low costs of reproduction, and thus low maternal investment, as currently measured, should not be interpreted as an energy-conserving strategy of lemurs.

If natural disasters are more prevalent in Madagascar and these disasters affect both infant and adult survivorship, selection is likely to shape traits that enable survival in unpredictable environments. The ECH has not been adequately been tested and remains promising in our understanding of lemur evolution. Understanding exactly how the environment shapes female dominance in lemurs will provide a powerful framework for understanding whether and how lemurs are adapted to conserve and extract energy.

**Review of pertinent literature**

The following review is primarily based on data and theories from the order Primates. The majority of information specific to lemurs and ring-tailed lemurs will be addressed in subsequent chapters.

*Social Groups*

Animal survival in a given habitat is dependent on their ability to find suitable and sufficient food resources. Acquiring and processing resources requires time and thus the number of animals in a group is limited by their ability to maintain nutritional requirement within a reasonable time frame (Dunbar et al., 2009). Increased group size leads to increased feeding competition between individuals (Wrangham, 1980; Terborgh and Janson, 1986), which at least
within primates, negatively affects fecundity (Dunbar, 1980, 1988; Hill et al., 2000). There is a trade off, however, between increased feeding competition and avoiding predation, since chances of any one animal being preyed upon decreases with larger group sizes (Hamilton, 1971). Hence, large group size is indirectly limited by fecundity, yet social groupings are maintained through the benefits of predator evasion (van Schaik, 1989; Hill and Lee, 1998).

The primate "ecological model" was proposed by Wrangham (1980), and later expanded upon by van Schaik (1989), Isbell (1991) and Sterck et al. (1997). This model posits that female gregariousness within primates creates feeding competition both within and between groups (Crook and Gartlan, 1966; Terborgh and Jansen, 1986; Isbell, 1991), but as we would predict, group living is beneficial to females through predation avoidance (van Schaik and van Hooff, 1983; Isbell, 1994; Boinski and Chapman, 1995) and possibly through infanticide prevention (Sommer, 2000; van Schaik and Janson, 2000; but also see Bartlett et al., 1993; Sussman et al., 1995). The types of feeding competition delineate the distribution of females, and in turn their social relationships (Wrangham, 1980). Males, on the other hand, are primarily affected by mating competition and the distribution of receptive females (Emlen and Oring, 1977; Vehrencamp and Bradbury, 1978; Stephens and Crebs, 1986).

Food resources, as described by Wrangham (1980) are either large and clumped, and therefore defendable, or small and dispersed, and thus not defendable. Primates with defendable food resources, such as fruits, likely have larger group sizes, are female bonded, and the social relationships are well defined (Wrangham, 1980). This is because females use cooperative defenses to protect food resources, and social ranking to distribute them. Conversely, primates with non-defendable foods, such as dispersed insects or certain leaves, likely have smaller group sizes, do not have female cooperative relationships, are not female bonded, and have very
loosely defined social relationships (Wrangham, 1980). This is because foods cannot be
defended against other groups or individuals. Relatedness within groups facilitates female
bonding, and dictates male philopatry (Wrangham, 1980). Groups with female, and/or male and
female philopatry have low relatedness, which does not generally lend to strong female bonds
(Wrangham, 1980).

Predation

Predation is likely a major factor shaping morphology and behavior in primates (see
Alexander, 1974; Clutton-Brock and Harvey, 1977; Cheney and Wrangham, 1987; Boinski et al.,
2000; Miller, 2000), and as mentioned, in the formation of social groups (see Jarman, 1974;
Busse, 1977; Anderson, 1986, but see Stanford, 1998, 2002). However, the effect of predation
on primates is notoriously difficult to understand given the elusiveness of predators, the rarity or
potential randomness of attacks, and lack of empirical evidence (Isbell, 1994; Boinski and
Chapman, 1995; Janson, 1998; Treves, 1999, Boinski et al., 2000; Treves, 2000). Furthermore,
although mounting anecdotal data exists, contextual information surrounding predation events
are often missing. Information such as predator attack strategy, prey age, sex, and status, along
with microhabitat type, and behavior of victims or survivors have been noted as crucial in
advancing our knowledge of the effects of predation on primate evolution (Miller and Treves,
2006). Also, existing anecdotal evidence has been criticized because it sheds little light on prey
vulnerability, and because even those predation events that are actually witnessed could be
random with regards to the prey genotype and/or phenotype (Miller and Treves, 2006).

The most direct method to explore the impact of predation on primates is to study the
predators themselves, which reveals prey profiles for each predator (Janson, 1998). Then by
combining prey profiles with demographic data of both predator and prey, we can assess predation rates (Karpanty, 2006). With predation rates, we can compare across individuals, populations and species of primate, with the intention of understanding the degree to which predation influences life history of the individual or shapes the phylogeny of a species (Hart, 2000). Though effective, it can be difficult to determine predation rates in primate populations, as predators are elusive by nature and may alter their behavior in the presence of researchers. A few studies have looked directly at primate predators, and have greatly improved our knowledge on the topic. The majority of this small body of work has come from the nest observations of predatory birds, radio tracking terrestrial predators, and collection and examination of bird regurgitory pellets or mammalian predator scat. Mitani et al. (2001) collected prey remains from under the nest of two pairs of crowned hawk-eagles (*Stephanoaetus coronatus*), along with census data on prey species at Kibale National Park. They found that monkeys were the primary prey of the eagle and that the eagles were preferentially selecting male redtail monkeys. Sanders et al. (2003) had similar findings at Ngogo, within Kibale National Park, and note that primates composed 81% of the crowned haw-eagles’ diet. In addition to collecting prey remains, Karpanty (2006) observed diurnal raptors (*Polyboroides radiatus* and *Accipiter hnestii*) at Ranomafana National Park in Madagascar. She found predation rates on lemurs to be significant, and suggested that raptor predation may depress the intrinsic growth rates and carrying capacity of some of the lemurs at the site. In their work, Zuberbuhler and Jenny (2002) radio tracked leopards in order to understand leopard predation on primates in the Tai Forest. They also examined leopard scat samples and found that monkeys constituted a large portion of the diet. Interestingly, Zuberbuhler and Jenny (2002) found that leopard predation was positively correlated to prey density, which suggests that leopards hunt according to abundance. Dollar
(2006) analyzed scat samples from fossa (*Cryptoprocta ferox*) and found that rather than being “lemur specialists” (Wright et al., 1997), fossa are flexible foragers that include a number of non-lemur prey in their diets. These few studies have vastly improved our knowledge on predation rates within primate communities, and similar studies have been deemed a priority in future.

It is important to realize, however, that the majority of research looking at primates and their predators has examined predation risk rather than rate. Predation risk aims to understand a primate’s perception of the chance of being taken by a predator (Hill and Dunbar, 1998; Janson, 1998; Miller, 2002). As Hill and Dunbar (1998) noted, predation risk could also be seen as a primate’s perception of the likelihood of encountering a predator. This perception is likely to affect a primate anti-predator behavior, namely vigilance, which has been extensively discussed elsewhere (see Hill and Dunbar, 1998). Additionally, perceptions of risk are likely to include memory of past predation attempts and present ecological variables (e.g. canopy cover, refuge availability, presence of neighboring primate groups, visibility, etc.), which can convolute our understanding of both the proximate and ultimate factors of the effects of predation on primate societies (Hill and Dunbar, 1998).

Recently, researchers examining primate anti-predator behavior have moved away from studies of vigilance and focused on how predation risk influences foraging behavior. Optimally finding food while avoiding becoming someone else’s food can be a difficult balance, as behaviors that increase foraging may also increase the risk of being preyed upon (Janson, 2000). For example, although increased inter-individual distance while foraging can increase food consumption, it also increases chances of predation (Cords, 2002). “Predator sensitive foraging” looks at the behaviors primates use when foraging, which minimize chances of predation.
Social and environmental factors are important influences in primate predator sensitive foraging (Lima and Dill, 1990; Miller, 2002). Other than group size, further social factors affecting predator sensitive foraging include group composition, cohesion, centrality, and rank. Adult or sub-adult males often play a protective role in their groups, and therefore having more or less males would likely increase or decrease group safety (Lima and Dill, 1990). Similarly, physical locations of group members affect individual safety. Individuals with close neighbors and whose physical location is near the center of the group are less likely to be targeted by predators; however, foraging efficiency is negatively correlated with increasing neighbors and centrality (Miller, 2002). Social rank influences on predator sensitive foraging are complicated (Miller, 2002; Sterck, 2002). For example, in sexually dimorphic species, higher-ranked individuals may be larger, and thus somewhat less vulnerable to predation, which allows them to engage in riskier foraging behaviors. However, lower-ranked individuals may also engage in risky foraging behaviors, which are motivated by restricted access to high-quality foods. Overall, higher-ranked individuals have greater freedom regarding their foraging strategy, as they can choose their location within the group (Miller, 2002).

The environment a primate lives in also influences predator sensitive foraging. Though habitat type is determined, primates can choose on which substrate and at what time they forage (Miller, 2002; Sauther, 2002). Predation risk is generally greater in open areas, since individuals are exposed to both aerial and terrestrial predators (Sauther, 2002; Sterck, 2002). However, with increased visibility, primates can also detect predators sooner, which may not be the case in dense forest cover, where range of sight and sound are restricted (Garber and Bicca-Marques, 2002; Miller, 2002). Though more data on predator-prey interactions are needed to fully understand the complex interactions, the type and hunting style of each predator likely influence
risk-factor in open versus closed habitats. Additionally, primates can alter the risk-factor associated with behaviors perceived as risky, such as foraging in an open environment. Larger group size or increased ability to detect predators may decrease predation risk. Or, increased risk may be ignored if the reward is high (as in crop raiding) and/or individuals are particularly nutrient depleted (Saj et al., 1999).

Given the necessary social and environmental factors, polyspecific associations may also be employed in primate predator sensitive foraging (Miller, 2002). Primate species may forage in groups with other primates, as in Saguinus (Garber and Bicca-Marques, 2002), or with ring-tailed lemurs and Verreaux’s sifaka (Sauther, 2002), or they may forage with non-primate animals, such as the coupling of baboons and gazelles (Devore and Hall, 1965) or langurs and deer (Newton, 1985). In cases where the species’ diets differ, costs of foraging in the larger group are greatly off-set. Moreover, given that species’ can interpret each others’ alarm systems, predator detection is likely significantly increased (Zuberbuhler, 2002).

The balance between finding food resources and avoiding predators is multifactorial and dependent upon social and environmental factors, but also individual choices. If predation accounts for a significant number of deaths in wild primates, we expect selection to favor traits which minimize predation events in an individual’s life. Future work examining the “synecological” relationships of primates and their predators that include predation rates, predation risk, and experimental manipulation are likely to yield valuable information on the proximate and ultimate affects of predation on primates (Colquhoun, 2006).
Feeding and Nutritional Ecology

Like activity pattern, adaptations to feeding may affect variables such as physiology, morphology, ontogeny, and ecology on individual, population and community levels (e.g. Oates et al., 1990; Fleagle et al., 1991; Ross, 1992; Leigh, 1994; Altmann, 1998; McGraw, 1998). In fact, diet has been called the single most important parameter underlying behavioral and ecological differences in primates (Oates, 1987; Fleagle, 1988).

Primates require the full suite of nutrients that are necessary for most mammals, which include both macronutrients (carbohydrates, proteins, fats, water) and micronutrients (minerals and vitamins) (Oftedal and Allen, 1996). With a few exceptions (Tarsius spp. [e.g. MacKinnon and MacKinnon, 1980] and Loris spp. [e.g. Nekaris and Rasmussen, 2003]), wild primates derive the majority of their nutritional and energetic requirements from plant parts including: fruits (ripe and unripe), seeds (immature and mature), leaves (all development phases), petioles, corms, rhizomes, bark, flowers, nectar, sap, and gum (Lambert, 2007). Plant foods contain both nutrients (feedants) and non-nutritive components (antifeedants). Feedants are desired nutrients such as protein and carbohydrates, while antifeedants are non-nutritious and may include components that reduce quality (fiber), and/or interfere with digestion (e.g. secondary compounds, toxins) (Wrangham et al., 1998). Primate food selection is thus influenced by both nutrients required for survival, but also chemicals and compounds that may interfere with nutrient absorption or even be poisonous (Wrangham et al., 1998).

Relative levels of feedants (e.g. protein) and antifeedants (e.g. fiber) are often used as a measure of dietary quality (Waterman and Kool, 1994), often by way of the protein to acid detergent fiber ratio (protein:ADF). Protein is an integral part of the primate diet because it provides the nitrogenous building blocks essential for DNA replication, body growth and
maintenance, and regulation of body functions (Ullrey et al., 2003). Protein is found in high concentrations in young leaves, flowers, some fruits and seeds (Waterman and Choo, 1981; Waterman et al., 1981). Non-structural carbohydrates are the primary source of energy for most primate species (Ullrey et al., 2003; Danish et al., 2006). Non-structural carbohydrates are a quick energy source, as they absorbed directly through the gut lining and into the bloodstream (Ullrey et al., 2003; Danish et al., 2006). Non-structural carbohydrates are found in high concentrations in fruits, nectars, flowers and some young leaves. Fats are also important in the primate diet, as they particularly rich energy source and because fats can be stored for later use (Ullrey et al., 2003; Danish et al., 2006). Fats can be found primarily in seeds, but also in non-plant primate foods such as insects and small vertebrate prey (Ullrey et al., 2003). Water is also an important macronutrient as it carries other nutrients throughout the body and is required for cell regulation (Bosco et al., 2001). Primates require water intake daily, which can be found directly in tree holes or streams, or indirectly in plant parts such as pulpy fruits and succulent leaves (Glander, 1978).

Micronutrients, such as some vitamins and minerals, are also essential for body development, growth, and maintenance and healing (National Research Council, 2003; Windmaier et al., 2004). For example, calcium and magnesium are required for bone growth and maintenance, and for function of muscles and nerves (National Research Council, 2003; Windmaier et al., 2004). Potassium is also necessary for nerve function and is important in maintaining normal body blood pressure (National Research Council, 2003; Windmaier et al., 2004). Similarly, sodium regulates body fluid volume and concentration (National Research Council, 2003; Windmaier et al., 2004). Vitamins, such as niacin, folic acid, and ascorbic acid are also important in body function and are integral to processes ranging from cell division to
building fat, muscle, and bone to oxygen transport and red blood cell generation (National Research Council, 2003; Windmaier et al., 2004). Micronutrients are found in plant foods, but can also be found in earthy deposits such as clay and soil (Mahaney et al., 1993).

Antifeedants are components of foods that do not contribute to body nourishment. Fiber, a structural carbohydrate, is the primary antifeedant consumed by most primates, as it is present in all plant foods (Van Soest, 1994; Conklin-Brittian et al., 1998). Fiber content is inversely related to digestibility (Van Soest, 1994), as high fiber levels can also interfere with fat and protein absorption (Ullrey et al., 2003). Mature leaves, unripe fruits, and plants such as bamboos are particularly fibrous, and should be avoided by primates who do not have specializations to ferment or otherwise deal with high fiber content (Yeager et al., 1990; Milton, 1993). In addition to fiber, secondary compounds can interfere with digestion and/or absorption on nutrients. Secondary compounds that primates commonly encounter include tannins and alkaloids. Tannins bind to proteins and thereby reduce the digestibility of the protein, while alkaloids act as toxins and disrupt metabolic processes (Lambert, 1998). Although some primates have evolved adaptations to deal with specific secondary compounds (e.g. Hapalemur spp., Tan, 1999; Glander et al., 1989), many largely circumvent ingesting significant quantities through diet diversification or avoiding foods high in secondary compounds (Fashing et al., 2007). Primates are highly selective feeders who discriminate finely between plant food species and parts (Milton, 1980; Glander, 1982); these foraging decisions can often be attributed to relative compositions of both feedants and antifeedants (Wrangham et al., 1998).

Sex based dietary differences are found throughout the primate order. Gautier-Hion et al. (1980) demonstrated that intraspecific sex differences in diet can be even greater than interspecific differences. To illustrate, while gestating or lactating, female cercopithecines
(Cercopithecus nictitans, C. pogonias, and C. cephus) chose protein-rich foods such as foliage and insects, while non-reproductive females and males chose foods lower in protein (Gautier-Hion et al., 1980). Increased protein intake has been observed in reproductive females in a variety of other primate species including: (e.g. Indi indri [Pollock, 1977], L. catta [Sauther, 1994], Varecia variegata rubra and Eulemur fulvus albifrons [Vasey, 2002]), (e.g. Cercocebus albigena [Waser, 1977], C. sabaeus [Harrison, 1983], Cebus olivacea [Fragaszy, 1986; Robinson, 1986], Saimiri oerstedii [Boinski, 1987], Cebus capucinus [Rose, 1994], and Pongo pygmaeus [Fox et al., 2004]). In addition to protein, reproductive females from a number of genera show dietary shift towards a higher quality diet that is low-fiber and rich in minerals (Waterman and Choo, 1981; Waterman et al., 1983; Sauther, 1994, 1998; Curtis, 2004). Since food is essential for reproduction and survival, natural selection is expected to exert a strong influence on foraging decisions (Pyke et al., 1977; Stephens and Krebs, 1986; Garber, 1987; ; Richard et al., 2000; Lewis and Kappeler, 2005). Females able to maximize energy intake or optimize the mix of nutrients consumed are likely to have higher reproductive output and success (van Noordwijk and van Schaik, 1987; Altmann, 1991; van Noordwijk and van Schaik, 1999; Dufour and Sauther, 2002). Strong selective pressure on adaptive traits, such as female food choice, can provide important insight into primate evolutionary ecology (Altmann, 1998; Milton, 1993).

The "Madagascar traits"

Madagascar's flora and fauna are unlike anywhere else on earth (Yoder and Nowak, 2006). It is characterized by high levels of endemicity and broad diversity from a select few orders, including lemurs, tenrecs, carnivores, and rodents (Goodman et al., 2003; Yoder et al., 2006).
2003). Within the diverse species of Madagascar, it is common to find unusual traits. For example the Madagascar giant jumping rat (*Hypogeomys antimena*) weighs in at over 1kg, and is a herbivore in which pair-bonded parents' cooperatively rear a single infant every two years (Eisenberg and Gould, 1970; Stephenson and Racey, 1997). Compare this with Madagascar's so-called "common" tenrec (*Tenrec ecaudatus*), which weighs up to 2kg and whose females are nearly semelparous yet have up to 32 infants at once (Sommer, 1997). And of course, the lemurs, are noted for their suite of unusual traits which are outlined throughout this manuscript.

Madagascar's unusual animals along with their unusual life history traits and adaptations have been largely attributed to its environmental properties. Long isolation, low colonization, chance dispersion, strong seasonality, poor soils, and frequent natural disasters have all been proposed to account for the peculiarities found on Madagascar. However, with nearly all of these traits we can find examples of similar situations outside of Madagascar which have not resulted in flora and fauna remotely similar to those in Madagascar as we know it.

In addition, as suggested by Richard and Dewar (2007), given current evidence no other land mass appears to have the same levels of hyper-variability in rainfall and frequent yet unpredictable natural disasters including cyclones and droughts. In its "Natural Disaster Hotspots" document, the World Bank (2005) states that Madagascar is at high risk of human mortality because it is prone to multiple hazards including overlapping regions with drought and cyclones. Severe droughts are common in the arid regions of the south and southwest, and may even be cyclical, but droughts also affect the eastern rainforests (Gould et al., 1999). Drought results in high canopy tree mortality, tree reproductive failure, fruit crop failure and a decrease in young leaf production. Storms and cyclones also frequent the island, with an average of seven major events per year (Donque, 1975; Ganzhorn, 1995). Cyclone activity can result in
defoliation, complete tree knockdowns, canopy destruction, landslides and flooding (Ganzhorn, 1995). Southern portions and highlands of Madagascar also experience cold temperatures and frost resulting from annual Antarctic storms in June through August (Terborgh, 1983). Moreover, destructive hailstorms in these regions are often lethal to vegetation, which have little frost tolerance. Dewar and Richard (2007) deemed the environment of Madagascar “hypervariable” and demonstrated that intra- and inter-annual rainfall patterns throughout Madagascar are unpredictable. Unpredictable rainfall along with frequent yet unpredictable natural disasters result in unpredictable phenological patterns, which Dewar and Richard (2007) argue has shaped the evolution of distinctive features of the lemurs and other mammalian fauna on Madagascar.

In vertebrates, exposure to a stressor (a noxious or unpredictable stimulus) elicits a stress response, which can be defined as the physiological, hormonal and/or behavioral changes that enable the animal to cope with a stressor (Romero, 2004). Physiological stress involves a cascade of neurological, hormonal and immunological responses that promote energy mobilization and behavioral responses to environmental changes and challenges (Sapolsky, 1992). One physiological stress response increases the release of catecholamine (the sympathetic “fight-or-flight” hormone), which is followed by an increase in secretion of glucocorticoid (GC) hormones into the bloodstream (Sapolsky, 1992). Many studies have used elevated GC, including cortisol levels, as a measure of stress in animals (Sapolsky, 1992; Wingfield and Romero, 2001). Cortisol functions to redirect energy from long-term storage to immediate use (Sapolsky et al., 1992), and thus has an associated metabolic cost. Chronic elevation of GC can suppress the immune system,
somatic cell growth, and/or sexual maturation, which can in turn alter life-history patterns and lower reproductive success (Sapolsky, 1992). Additionally, since chronic elevation in GC is a significant predictor of early adult mortality, relative GC levels can serve as a proxy for fitness (Romero and Wikelski, 2001; Pride, 2005).

GC levels are strongly influenced by ecological, social, and physiological variables (Cheney and Seyfarth, 2009). Many studies of mammals have shown that fGC (fecal glucocorticoid) levels are elevated during winter months, and during times of food or water scarcity (reviewed by Wingfield and Ramenofsky, 1999; Romero, 2002). Additionally, in species organized into dominance hierarchies, rank and aggressive interactions can elevate fGC (Creel, 2001; Abbott et al., 2003). Moreover, animals experiencing periods of elevated metabolic and energetic demands, such as costly reproductive periods in female mammals, also show increased fGC (Pepe and Albrecht, 1995; Wingfield and Ramenofsky, 1999; Romero, 2002).

While short-term (hourly) stressors are measured through fGC levels, longer-term stress or general health can be measured through an animals’ coat condition (Berg et al., 2009). Like fGC levels, coat condition can be affected by a plethora of factors, such as reproductive condition (Davis and Suomi, 2006), nutritional deficiencies (Isbell, 1995; Gerold et al., 1997), social stress (Isbell, 1995; Roloff et al., 1998; Steinmetz et al., 2006), parasites and skin diseases (Roloff et al., 1998; Steinmetz et al., 2006), and over-grooming (Reinhardt, 2005). However, hair loss related to nutritional deficiencies and/or general stressors tends to be bilaterally symmetrical, and results in an overall shaggy, dry, and dull appearance (Steinmetz et al., 2005). Isbell (1995) noted that wild vervet monkeys (Cercopithecus aethiops) exhibited significant hair loss on an annual basis and attributed this loss to both nutritional and social stressors. In these
cases, poor coat condition correlated with low food availability and low social rank (Isbell, 1995).

Hypotheses

This project compares adult male and female ring-tailed lemurs from two social groups in an endemic, non-disturbed xerophytic habitat during portions of southern Madagascar's distinct wet and dry seasons, to test some of the assumptions made by ECH with relation to the effect of fluctuations in resource availability on activity, behavior, nutrition, and stress in ring-tailed lemurs. Specific hypotheses include:

1. Lemur foods are seasonally and stochastically limited.
2. Lemur nutrients and/or calories are seasonally and stochastically limited.
3. Lemurs use behavioral mechanisms to save energy.
4. The dry season is differentially stressful for female lemurs.

Summary

Lemur traits are hypothesized to be part of an adaptive complex selected to help lemurs conserve energy in their seasonally and stochastically resource-poor environments. Female dominance and associated niche partitioning between the sexes may facilitate lemur energy conservation and frugality, which act to offset costs of reproduction in females. By integrating ecological, behavioral, nutritional, and biological data collected on wild ring-tailed lemurs in the spiny forest habitat at TNP, my aim is to understand the extent that male and female lemurs are constrained by seasonal fluctuations in resources availability. Data here is compared with data from localities where ring-tailed lemurs have been extensively studied, namely the Beza
Mahafaly and Berenty Reserves, as well as recent research from degraded spiny forest habitats, in order better understand how the environment has shaped adaptations in this species. This will be the first project to examine ring-tailed lemurs in a largely undisturbed spiny forest habitat, and provides the framework to better understand ring-tailed lemur ecology in all other habitat types.

**Outline of Dissertation**

To avoid unnecessary duplication of methodological and theoretical content, this dissertation is arranged as a monograph. The following briefly outlines the content of the subsequent chapters. In chapter two I describe the study site and methods used. Chapter three examines the nighttime behavior of ring-tailed lemurs. Nighttime activity was not expected to be part of the behavioral repertoire of these ring-tailed lemurs, however, since it was noticed early in the study period (through camera trap photos) and is likely to be of significant importance to this research and in understanding the adaptations of ring-tailed lemurs, it has been included in this manuscript. Chapter four encompasses the climate and weather conditions of southern Madagascar and TNP, along with plant phenology and plant food use by focal animals during the study period. Chapter five outlines ecology of ring-tailed lemurs at TNP including activity budgets, diet and nutrition, and stress. Finally, chapter six examines the implications of this research for understanding ECH, and its account of the unusual traits found in lemurs, including female dominance.
Chapter 2: Methods

Study Site

Data were collected at the Tsimanampetsotsa National Park (TNP), in southwestern Madagascar (24°03’-24°12’S, 43°46’-43°50’E), between September 2010 and April 2011. Figures 2.1-2.3. show the geographical locations Tsimanampetsotsa National Park, including base camp for this project, and locations of other ring-tailed lemur research locations discussed frequently throughout this manuscript. Tsimanampetsotsa represents the western most escarpment of the limestone Mahafaly Plateau. This area is highly seasonal, and is subject to high winds, frequent droughts and cyclones (Andriatsimietry et al., 2009). The majority of rainfall occurs between late December and February, with total rainfall rarely exceeding 400 ml per year (Donque, 1975). The dry season is long with average durations of nine to eleven months (Donque, 1975). Temperatures can be extreme, with daytime highs of well over 40°C, although mean daily temperatures range between 22.5°C and 35.8°C. Lake Tsimanampetsotsa occupies 45000 hectares of protected RAMSAR wetlands, and the park is another 43200 hectares of land protected by Madagascar National Parks.

Vegetation at Tsimanampetsotsa is characterized as dry, spiny, and xerophytic. It can be further divided into four zones (Figure 2.4.). The first zone consists of the land surrounding the lake, which is sparsely populated, but contains stands of invasive *Casuarina equisetifolia*, and patches of *Acrostichym aureum* and *Cyperus* sp. (Mamokatra, 1999). The second zone lies at the foot of the Mahafaly Plateau, where the forest ranges from partially canopied fruit trees (*Ficus megapoda, Tamarindus indica, Salvadoria angustifolia*, etc.) to degraded scrub and areas of induced desertification. In general, these fruit trees are found near ephemeral or permanent water sources, such as springs and seeps, along the border of the limestone plateau. The third zone is
the Mahafaly Plateau, and is populated by open-canopied dwarf flora, primarily from the families Euphorbiaceae, Didiereaceae, Bombaceae, and Fabaceae (Mamokatra, 1999). The fourth and eastern most zone emerges where the limestone gives way to red clays and flora and are composed of spiny bush formations with dominant plant families from Didiereaceae, Euphorbiaceae, and Burseraceae (Mamokatra, 1999). The plateau area is a relatively narrow formation, running north-south, and found between the lake margin and the vast "eastern zone." Numerous collapsed "sinks" which can contain some plants that rely on a minimum of ephemeral water sources mark the plateau.

**Figure 2.1.** Relative location of Tsimanampetsotsa National Park in Madagascar.
Figure 2.2. Location of Tsimanampetsotsa in relation to the Beza Mahafaly Special Reserve, Berenty Private Reserve, and Cap Sainte Marie, in southwestern Madagascar.

Figure 2.3. Map of Tsimanampetsotsa National Park with reference to the base living camp.
Figure 2.4. Examples of habitat zones at the Tsimanampetsotsa national park, including a) zone 1 (near) and zone 2 (distant), b) zone 2, c) zone 3, and d) zone 4. Photos a and b courtesy of Sauther, 2012.

Study animals and data collection

Ring-tailed lemurs are endemic to southwestern Madagascar and are currently listed as vulnerable to extinction, with declining population numbers (Mittermeir et al., 2006). Males and females have an average body weight of 2.2-2.7kg (Tattersall, 1982; Sauther et al., 2006), although the body weights of TNP animals may be lower than this range. Dutton et al. (2003) anesthetized 20 free ranging animals (10 females and 10 males) and note an average weight of 1.99 kg ± 0.342kg, and minima and maxima weights of 1.15kg and 2.45kg, respectively. Ring-tailed lemurs are the most terrestrial of the lemurs, spending up to one half of their foraging time on the ground (Sauther, 1994; Sauther et al., 1999). They live in multi-male multi-female social
groups ranging from approximately 9-22 individuals (Sussman, 1977). They are a remarkably plastic “edge” or “weed” species (Sussman, 1977; Gould et al., 1999; Sauther et al., 1999) and their diet is classified as opportunistic frugivore/folivore (Sauther et al., 1999). Their gut morphology includes a simple stomach, moderate length small intestine, a well-developed cecum and intermediately long colon (Campbell et al., 2000). These morphological adaptations allow for at least some microbially assisted fiber fermentation (Campbell et al., 2000).

*Lemur catta* are found in a variety of habitat types including: spiny and xerophytic forests, gallery and deciduous dry forests, anthropogenically induced savannah, scrub and brush land, and the mesic high altitude forests of the Andringitra mountain range (Sussman, 1977; Goodman and Langrand, 1996; Goodman and Rasolonandrasana, 2001; Sussman et al., 2003; Pride, 2005; Goodman et al., 2006). Ring-tailed lemurs are the only large-bodied lemurs present in the northern portion of TNP, where this study was conducted. However, there are unconfirmed reports of Verreaux’s sifaka (*Propithecus verreauxi*) being found 20km south of the study area, where the spiny forest canopy consists of larger and taller vegetation. The Vintany (n= 12-14 adults, 7 sub-adults and 4-7 infants) and ILove (n= 9-10 adults, 7 sub-adults, and 4-5 infants) groups were the focus of this research. Individual animals were identified by unique markings, scars, mask shapes, or in the case of the collared individuals (detailed below) by their collars. Animals, along with the names I used to identify them, age class, sex, and group are detailed in Table 2.1. These two groups inhabited similar, overlapping home ranges that included areas between the habitat zones 2-4. Both groups’ sleeping sites were on the Mahafaly Plateau (Zone 3). The Vintany group (VG) slept in a large *Ficus* tree (*Figure 2.5*), whereas the ILove group (IG) slept in small communal caves on the face of a 20 meter high limestone cliff (*Figure 2.6*). The Vintany group fissioned near the end of the dry season, after core females in Vintany
targeted aggression towards three specific adult females in the group. The three females left the Vintany group and were called the "Soccer Moms" once they began sleeping and spending days away from the main group. I was unable to reliably find and follow the Soccer Mom group, but did occasionally see them during the wet season when the two groups encountered one another. Additionally, Figures 2.7-2.8 shows two of the places where the animals drink water, which is available year-round.

<table>
<thead>
<tr>
<th>Rank</th>
<th>Name</th>
<th>Group</th>
<th>Sex</th>
<th>Infant noted (yes/no)</th>
<th>Infant survive (yes/no), death month</th>
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</tr>
<tr>
<td>5</td>
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<td>ILove</td>
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<tr>
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<td>5Head</td>
<td>ILove</td>
<td>F</td>
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<tr>
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<td>No, Nov</td>
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<td>M</td>
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<td>ILove</td>
<td>M</td>
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<td></td>
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<tr>
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<td>M</td>
<td></td>
<td></td>
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<td>ILove</td>
<td>M</td>
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<td>M</td>
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Figure 2.5. The cliff face where the ILove group sleeps (top left) and one of the ILove group females on a rocky outcrop of the cliff (bottom right).
Figure 2.6. The large *Ficus* tree where the Vintany group sleeps with (top left) western view of the tree, with the tree's aerial roots extending into the sink hole and (bottom right) the eastern view showing the tree's breadth (~22m).
Figure 2.7. Vintany group drinking sites, including male descending *Ficus megapoda* aerial roots (top left), and group members drinking (nervously) in the sink hole below their sleeping tree (bottom right).
Figure 2.8. I love group drinking sites, including the group drinking in the Mitoho cave (top left), and group members entering the Mitoho cave (bottom right).
With the assistance of a local Malagasy lemur darting team, six female animals from three distinct social groups were captured and fitted with radio tracking collars. Animals captured were fitted with VHS radio collars (MOD-080 transmitter configuration, Telonics Inc.) because during preliminary observations the animals were noted to be quiet and cryptic when moving, and thus difficult to continuously follow. We used the same veterinary protocols that were used during ring-tailed lemur captures at TNP in 2006 (see Sauther and Cuozzo, 2008) and at Beza Mahafaly since 2003 (e.g. Miller et al., 2007). Two of the groups (ILove and Vintany) were easily habituated to my presence within two weeks, while I was not able to habituate the third group (Akao). The Vintany and ILove groups had previous exposure to tourists, as some trails and the camping site are within their home ranges. Akao seemed differentially affected by the capture process and were extremely wary of human presence both before and after capture. Even with collared animals, I was unable to get within a reasonable viewing distance of the Akao group and chose to stop trying to following them after 5 months. During the study, one female's collar fell off and after the study 3 other females were recaptured to have their collars removed. The darting team was not able to find the Akao group in order to remove their collars.

Behavioral Sampling

I collected 526 hours of focal animal data in the daytime and 67 hours of scan data at night. Additionally, my assistants collected 275 hours of scan data in the daytime. Nocturnal observations were not part of the original data collection plan, but early on in the study I noted nocturnal lemur activity on camera trap photos, and decided to additionally observe the animals at night. These data were collected during weeks bracketing full moons, between 8pm and 1am, in October, November, and December 2010, and March 2011. Increased moon illumination aided
in my ability to observe animals in the dark. During the day, continuous, known-animal focal follows were conducted with the objective of sampling one animal daily. If the animal was lost for more than 30 minutes, however, I would switch to another animal. Scan data (Altmann, 1974), were collected at 5 minute intervals with the goal of including 10 adult animals in every scan. Dominance rank and changes in rank were noted for each focal animal, based on approach retreat repeated interactions (Hausfater, 1975). For a few animals, it was difficult to decipher their exact rank, and in these instances I used relative rank instead (e.g. low). Photographs and scores of coat and tail condition were taken at the beginning of every month (or when encountered, as in the case of the Soccer Moms) as per the methods outlined by Berg et al. (2009), where coat score of 0= good, 1= rough, 2= holes, 3= ragged, 4= sheared, and 5= bald; and tail score of 0= good, 1= pointy, 2= thin, 3= ragged or whorled, 4= sheared, and 5= bald. GPS position was recorded several times per day throughout the study period. Later, these data were entered into Google Earth © (2012) in order to generate home range maps, and then data were transferred to the online Earth Point © (2012) software (http://earthpoint.us/shapes.aspx), in order to calculate ranging areas.

During the day, animal locations were noted as being on or off the ground, and if off the ground, I recorded if they were in a shrub, tree, or other area. Animal location scores at night were categorized slightly differently, and included the following: tree/cave, ground/cliff, or other. Location data for "tree" and "cave", and "ground" and "cliff" were combined, because they served the same or comparable purposes to the animals. For example, the large Ficus tree and caves were sites for sleeping, while the ground and cliff were areas of travel between the sleeping spot and other destinations (primarily feeding trees).
Camera trap photos of lemurs at night serve as a proxy for nighttime activity levels (Griffiths and van Schaik, 1996). These both contribute to our knowledge of cathemeral lemurs, and provide valuable unbiased information on the nocturnal behavior of these L. catta groups (Griffiths and van Schaik, 1996). Cameras were stationed near the two lemur group’s sleeping sites (n=2-5), and along forest paths (n=1-3). The number and position of cameras in use varied from time to time, as lemurs would change ranging patterns, which required camera reposition trials, or because cameras required repairs. Resultant photos were reviewed for presence of one or more animal. Lemur nighttime photos were categorized by lemur group, and then a average nighttime photo rate was calculated as per the following formula (Griffiths and van Schaik 1996):

$$\text{Average nighttime photo rate per day} = \frac{\text{Number of nighttime photos in one day per lemur group}}{\text{Number of cameras per day}}$$

Similarly, the average lemur nighttime photo rate per month was calculated as per the following formula:

$$\text{Average nighttime photo rate per month} = \frac{\text{Number of nighttime photos in one month per lemur group}}{\text{Number of days per month}\times\text{number of cameras per day}}$$

Following the methods of van Schaik and Griffiths (1996), only the first of consecutive photos containing one (or more than one) of the same individual(s) was included in the data. A lapse of 5 minutes was used to delineate each photo event. Using only the first photo and delineating a time period between photos aids in achieving statistical independence (Griffiths and van Schaik, 1996). Colors of photographs varied according to light conditions. During the day, photos are in full color; during dawn and dusk, photos are in grey scale; and at night, photos are in black and white.
Activity patterns and feeding behavior

Focal animal data were used to calculate daytime activity budgets. These data were combined into the following categories: feed/forage, locomote, sit/stand/rest, and other (vigilance, groom, displace(d), scent mark, stink fight). These categories aid in not only understanding feeding activity, but also activities that vary according to their approximate energetic costs, such as moving or not moving. Average percentages of time spent in each behavioral category were obtained and summed according to animal sex and group, and season. Conversely, activity data from group scan sampling were used to calculate activity budgets and animal locations between the day and night. Similarly, average percentages of time spent in each behavioral category and location were summed according to day or night time, and group.

During focal follows, if an animal was feeding, the plant and plant part were noted. Usually, plant samples were collected at the same time and place where the animal was feeding, but this was not always possible. Given the variation that can occur between plant samples, I aimed to collect samples which best represented what an animal was eating and this was generally done within 24-hours of the feeding bout. A local Malagasy botanist later identified plants and samples were dried in the shade. Plants, such as Aloe divaricatha or Euphorbia stenoclada, that were succulent or particularly resistant to desiccation were sliced into thin strips that promoted drying. Exudate from E. stenoclada was collected by cutting small areas of the terminal tips of branches and catching the liquid in a glass jar. The jar was then kept in the shade until the liquid exudate had evaporated and a powder remained. Caterpillars used as lemur foods were also collected. These were cut in half and then left to dry in the shade. Once dry, all foods were weighed and an average weight was calculated. The number of plant samples weighed to produce an average weight depended on the type of sample, and on the amount of variation
between sample weights. Variation was largest in very small foods (those weighing <0.01 grams per unit), such as flowers from *Neobeguea mahafaliensis*, and so 100 individual flowers were weighed to produce an average weight per flower. With larger foods (those weighing >0.10 grams per unit) that had less variation between samples, such as young red leaf bundles leaves from *Neobeguea mahafaliensis*, 10 individual leaf bundles were weighed to produce and average weight per unit. Dry, weighed plant samples were stored in the shade, in zip lock bags with silica desiccant.

*Diet and Nutrition*

All nutritional analyses were conducted at the Department of Animal Ecology and Conservation of Hamburg University. A total of 80 food samples (79 plant, 1 insect) were analyzed. The food samples included: 28 fruits or parts of fruit, 24 types of leaves, 20 flowers or flower parts, 5 non-leaf non-reproductive plant parts, and two exudates. Samples were ground to pass through a 2mm sieve, and dried again (at 50-60°C) before laboratory analyses. Crude lipid (referred to hereafter as fat) content was determined by extraction using petroleum ether, followed by evaporation of the solvent. The amount of nitrogen was determined using the Kjeldahl method and 6.25 was used as the factor converting nitrogen to crude protein (referred to hereafter as protein). Soluble carbohydrates and procyanidin condensed tannins were extracted with 50% methanol. Concentrations of soluble sugars (referred to hereafter as sugar) were determined as the equivalent of galactose after acid hydrolization of the 50% methanol extract. Concentrations of procyanidin condensed tannin (referred to hereafter as tannin) were measured as equivalents of quebrancho tannin (Oates et al., 1977), and polyphenole following Folin-Ciocalteau (Bollen et al., 2004; Stolter et al., 2009). Neutral and acid detergent fibers (referred to
hereafter as NDF and ADF, respectively) (Goering and van Soest, 1970; van Soest, 1994; modified according to instructions for the use in "Ankom fiber analyzer") were analyzed.

In order to estimate the amount an animal consumed during a day, I multiplied the number of bites in each feeding bout by the average weight of the item eaten (Watts, 1984; Oftedal, 1992; Rode et al., 2006). I then summed the daily total of amount eaten by an animal for all foods and divided that total by the amount of time taken to consume the foods, to obtain a feeding rate per hour (Rothman et al., 2011). The feeding rate per hour was then multiplied by the average time spent feeding per day for the subgroup, such as females in the dry season (LaFleur and Gould, 2009; Gould et al., 2011). It was essential to calculate feeding rates in this way because the amount of focal data was not equally distributed between animals (Schulke et al., 2006).

Calories per macronutrient were calculated by multiplying the percentage of macronutrient in a food by the amount consumed and the following nutritional constants: protein, 4 kcal/gram; sugar 4 kcal/gram; and fat, 9 kcal/gram. Total calories per feeding bout were obtained by adding together the calories from each of the constituent macronutrients, as seen in the following formula:

\[
\text{Calories (kcal)} = \text{Amount consumed (grams)} \times \left( \frac{\% \text{ protein} \times 4 + \% \text{ fat} \times 9 + \% \text{ sugar} \times 4}{100} \right)
\]

Calories from each feeding bout per animal per day were added together in order to generate total calories. Total calories were divided by time taken to consume the foods and multiplied by the average time spent feeding per day, as outlined and explained above. For comparative purposes, nutrients, non-nutrients, dietary quality and calories consumed per day were averages for each subgroup of interest, such as males.
Environmental Abiotic data

Percentage of moon illuminated for the southern hemisphere was taken from the United States Naval Observatory Astronomical Applications Department website (NMOC, 2011). Temperature and humidity absolute and average minimums and maximums, along with millimeters of rainfall, were taken daily at base camp. These data, can be found in Appendix 1. During this study temperatures at base camp ranged from 10.4°C to 41.9°C, however temperatures can be significantly higher in certain areas of the forest. Much of the dwarf spiny forest is on the Mahafaly limestone plateau, and in addition to there being no protective tree canopy, solar radiation reflects intensely from the dark grey limestone formations. Though I was not able to constantly measure spiny forest temperatures, I did occasionally take readings, the highest of which was 53°C. For the purposes of this research, the dry season began at the onset of the study (Sept 1, 2011) and ended at the onset of the seasonal rains (December 22, 2010). The wet season began with the onset of seasonal rains (December 23, 2010), and ended when the study ended (April 7, 2011). The "wet" season was extended until the end of the study period, because at this time standing water was still abundant throughout the habitat and the vast majority of trees were foliated. It is also of note that on February 14 2011, Cyclone Bingiza collided with southwestern Madagascar and brought heavy rains (~125mm) and a flash flood to TNP.

Environmental biotic data

Phenological data were collected once per month. Nine line plots were established, by an expert Malagasy botanist, within each of the representative zones (2-4) of the animals' home ranges. To do this, a line of 25m was established and then any woody tree or shrub within 1
perpendicular meter of the line was marked with a numbered tree tag. Presence and abundance of mature leaves, young leaves, flowers, and fruits (along with ripeness) were record. Additionally, all *Tamarindus indica* and *Ficus megapoda* trees (which had a diameter at breast height of 10 cm or larger) within the lemurs' home ranges were monitored (for leaves, flowers, fruits, and fruit ripeness), as tamarind is an important food in other habitats of ring-tailed lemurs, and figs appeared to be an important lemur food source during this study.

Predator presence was measured through camera trap photos, nest monitoring, and opportunistically collected predator scats. One point was used to score a predator photo or scat on the day it was taken or collected. Points were tallied monthly to create an estimate of predator presence. Predator scores were categorized according to the activity pattern of the predator, where *P. radiatus* and *Canis familiaris* are diurnal, *Felis sylvestris* is nocturnal, and *C. ferox* is cathemeral.

**Data Analyses**

Chi-square was used to assess variation between and within groups’ day and nighttime activities, as the data are of nominal level. Sample sizes of these data were large (e.g. 4000), which can increase the power of chi-square (and thus artificially decreasing the p-value). As such, Cramer's V was used for determining strength of association within "significant" Chi-square data and the Contingency Coefficient C was also used in to compare "percent of max" between data. In these instances, findings were only considered significant when Chi-square p-values were equal to or less than 0.05, Cramer's V was greater than or equal to 0.15 (strong or very strong association), and the Contingency percent of max suggested a meaningful relationship.
Linear regression and Pearson's correlation were used to assess variation between the number of photos taken after dark in a time period (day or month) and the following independent variables: predator presence, day length, temperature maximum and minimum, humidity maximum and minimum, rainfall, phenology (including total phenological availability, plant part availability and fig fruiting patterns), and nightly moon illumination. Additionally, the relationships between nighttime activity and daytime activity budgets (feed/forage, locomote, sit/stand/rest, other), and relationships between the daytime activity independent variables were analyses using linear regression and Pearson's correlation. Data that may measure the same variables twice, such as rainfall and phenology, were examined separately.

The Student's T-Test was used to analyze differences in the mean between seasons, lemur sexes and groups for activity patterns and plant part eaten, daily intake of nutrients (protein, sugar, fat), non-nutrients (tannin, polyphenole, NDF, ADF), dietary quality (protein:ADF), and calories. For the dependant variables in this chapter and in Chapter 5, numerical codes were used in place of words when analyzing differences between sex (female=1, male=2), season (dry=1, wet=2), and group (ILove=1, Vintany=2). Therefore, the direction of $t$ reflected that of the coding. For example, a negative $t$ between sexes would imply that males had a higher value for a given variable, when compared to females.

Once again, the Student's T-test was used to assess variation in the means between coat and tail scores between sexes and seasons. Since results from the condition of coat and tail condition were not significantly different (i.e. a individual with a coat score of 3 also had a tail score of 3), only the data for coat condition are presented.

Values of $p$ that were less than or equal to 0.05 were considered significant and marked with an asterisk. SPSS 19.0 was used for all statistical analyses.
CHAPTER 3: Cathemeral activity in wild ring-tailed lemurs

Overview

Adaptations to diurnal or nocturnal living are vast, and may affect variables such as life history, diet, sociality, morphology, predator and prey dynamics, and sensory functioning (see Enright, 1970; Terborgh and Jackson, 1986; Jacobs, 1993; Rydell and Speakmen, 1995). It would thus seem unlikely that primates, or any mammal, would be active both during the day and night, given that day-active adaptations may hinder an animal during the night, and vice-versa (Charles-Dominique, 1975; Aschoff et al., 1982; Halle, 2006). Although it is rare for primates to exhibit cathemeral activity patterns, one haplorrhine genus, *Aotus* (Wright, 1989; Fernandez-Duque, 2003), and two strepsirrhine genera, *Eulemur* and *Hapalemur* (Curtis and Rasmussen, 2002, 2006) are currently regarded as cathemeral.

The Lemuriformes offer an excellent opportunity to understand factors that may drive cathemerality, given that lemurs are a monophyletic group exhibiting the three main activity patterns, namely they can be nocturnal, diurnal, or cathemeral (Tattersall, 1982; Donati and Borgognini-Tarli, 2006). Additionally, since cathemerality is, by comparison, found in many species of Malagasy primates, it seems likely that Madagascar has or had some environmental properties favoring flexible activity patterns (Tattersall, 1982). Dewar and Richard (2007) deemed the environment of Madagascar "hypervariable," due to its seasonality, unpredictability and frequent tropical cyclones. We thus know that the environment is unpredictable and that some lemurs use flexible activity patterns, however, teasing apart environmental factors promoting cathemeral activity patterns in lemurs have proved rather arduous (Curtis and Rasmussen, 2002). Some of the difficulties lie in the impracticality of monitoring animal's behavior over 24-hour periods, and our own shortcomings in the nocturnal environment (Curtis
and Rasmussen, 2002). Additionally, ever changing environmental factors can make understanding cause and effect factors complex (Curtis, 2006). Various models have even been proposed to account for cathemerality in different species and habitat types in Madagascar, yet what we are learning from these explanatory models is that there likely is no one-size-fits-all proximate or ultimate answer as to why cathemerality exists in lemurs (see Rasmussen, 1999; Curtis and Rasmussen, 2002; Curtis, 2006). Despite the difficulties associated with cathemeral research in lemurs, activity patterns are of basic importance in understanding adaptations behind primate radiations (Donati and Borgognini-Tarli, 2006), and should remain a priority in lemur evolutionary biology.

While adaptive reasons have been proposed to account for cathemerality in all primates (see Overdorff, 1988; Enqvist and Richard, 1991 Overdorff and Rasmussen, 1995; Curtis and Rasmussen, 2002), non-adaptive explanations have also been proposed to account for this in lemurs (van Schaik and Kappeler, 1996). Possible (non-mutually exclusive) ultimate environmental factors favoring flexible activity patterns include: thermoregulatory benefits (Curtis et al., 1999), predator avoidance (Overdorff, 1988; Curtis et al., 1999), competition minimization (Curtis, 1997; Rasmussen, 1999; but see Overdorff, 1993) and nutritional needs (Engqvist and Richard, 1991; Wright, 1999; Tarnaud, 2006). Alternatively, for lemurs, cathemerality has been suggested to be a non-adaptive transitional state or evolutionary disequilibrium, wherein nocturnal animals are in the process of becoming diurnal, resulting from relaxed selection pressure of diurnal living following the relatively recent mass extinctions of large diurnal raptors (van Schaik and Kappeler, 1996). The following will expand on aforementioned proposed adaptive and non-adaptive hypotheses accounting for cathemerality.
Background

Thermoregulation

Primates, as with other mammals, employ physiological means of thermoregulation (Heldmaier and Steinlechner, 1981; Ellison et al., 1992; Haim et al., 1995). For example, fur and fat act as insulators over long periods, and vasoconstriction and vasodilatation conserve or dissipate heat, respectively, during the short-term (e.g. Romanovsky, 2007). Physiologically, some nocturnal lemurs show torpor, seasonal fattening, and heterothermy (Petter-Rousseaux, 1980; Fietz and Ganzhorn, 1998; Giroud et al., 2010), yet limited shiver and sweat responses (Aujard et al., 1998). All lemur species that have been tested show lower than expected basal metabolic rates (BMR) as per the Kleiber equation (Jolly, 1984; Perret et al., 1998; Richard and Dewar, 1991; Wright, 1999; Richard et al., 2000; Genoud, 2002; Simmen et al., 2010). However, it has been debated as to whether reduced BMR is a phylogenetic trait shared with other strepsirrhine primates (e.g. Müller, 1985; Genoud, 2002), or if low BMR is an adaption to Madagascar's feast/famine environment (Richard and Dewar, 1991; Wright, 1999; Schmid and Stephenson, 2003). While more data are needed to understand if low BMR is a trait unique to lemurs, we do know that some lemurs have extremely low BMR. For instance, the BMR of *E. fulvus* is just 28-56% of the expected rate (Daniels, 1984). Low BMR, in this case, is coupled with a near constant and relatively high body temperature which ranges from 38.4-39.4°C (Daniels, 1984; Erkert and Cramer, 2006). Low BMR indicates a capacity for temperature regulation, while a high body temperature disallows a reduction in body temperatures during cool periods or times of inactivity (Daniels, 1984; Müller, 1985). For *E. fulvus* the resultant "thermoneutral zone," or temperature range wherein animals expend little or no energy to maintain their body temperature, lies between 22°C and 30°C (Daniels, 1984; Erkert and
Cramer, 2006). The thermoneutral zone of *L. catta* is unknown, however, BMR in *L. catta* is just 26-37% of that predicted (McNab in Simmen et al., 2010), and body temperature ranges from 36.9-38.9°C (Teare, 2002; Dutton et al., 2003). Given that ring-tailed lemurs are primarily adapted to the hot dry forests of southern Madagascar (although overnight temperatures can be low in the austral winter) (Goodman et al., 2006), while *Eulemur* are adapted to the cool eastern humid forests of northern Madagascar (see Tattersall and Sussman, 1998), we might expect the thermoneutral zone of ring-tailed lemurs to be slightly higher than that of *Eulemur spp.*, however this prediction does require testing to be confirmed.

Behavioral means of thermoregulation can both increase or decrease body temperature. Ring-tailed lemurs are well known for their sunning behavior, which acts to increase body temperature on cool days (Jolly, 1966). Other behavioral mechanisms used by lemurs that increase body temperature may include postures that decrease surface area (and reduce heat dissipation), and social thermoregulation, such as huddling (Jolly, 1966). For example, *Eulemur collaris* spends significantly more time in huddle or curled positions during the cold season of the tropical wet forests of Saint Luce (Donati et al., 2011). Conversely, behavioral mechanisms used to decrease body temperature (or prevent over-heating) include postures that increase surface area (and increase heat dissipation) (Donati et al., 2011). During the hottest periods of the day, *L. catta* rest in the shade in prone positions and hug onto the bases of cool trees or rocks. Animals also lick their hands and feet, and pant, all of which aid in heat reduction through dissipation (Jolly, 1966). Each of the aforementioned behaviors helps maintain optimal body temperatures, while minimizing use of comparatively energetically expensive physiological mechanisms.
Some lemurs also adjust activity patterns as a behavioral mechanism minimizing energy required for thermoregulation (see Curtis et al., 1999; Curtis, 2006). In the reed beds of lake Alaotra, *H. alaotrensis* avoids activity in particularly high daytime temperatures, and instead increases nighttime activity (Mutschler, 2002). Alternatively, in the deciduous forest of Anjamena and Kirindy, *E. mongoz* (Curtis et al., 1999) and *E. rufus* (Donati et al., 1999; Kappeler and Erkert, 2003) increase nighttime activity during low nighttime temperatures (e.g. 11°C [Kappeler and Erkert, 2003], 18°C [Curtis et al., 1999]). Limiting activity in high temperatures minimizes heat stress, while increasing activity during cool periods induces heat production generated through movement (Curtis et al., 1999). In these instances, cathemerality may be a behavioral mechanism that helps reduce thermoregulatory costs associated with heat or cold stress (Curtis et al., 1999). Though a contributing factor for some cathemeral lemurs, other cathemeral lemurs nocturnal activity levels are not related to thermoregulatory benefits (e.g. *E. macaco* [Andrews and Birkshaw, 1998], *E. fulvus* [Donati and Borgognini-Tarli, 2006], *E.f. collaris* [Tarnaud, 2006]). Thus, although thermoregulation may help explain some variation in lemur activity patterns, it cannot solely explain the variation.

**Anti-predator strategy**

Predation is a major force in shaping primate evolution (see van Schaik and van Hoof, 1983; Andewartha and Birch, 1984; Anderson, 1986; Cheney and Wrangham, 1987; Isbell, 1994; Stanford, 2002). Yet, there is a longstanding debate as to the extent to which lemurs experience predation, particularly predation from aerial predators (van Schaik and Kappeler, 1996; Kappeler, 1997; Wright, 1999). It has been suggested that extant lemurs are subject to relatively low levels of predation, especially aerial predation, due to the mass extinction of large-
bodied diurnal raptors that occurred about 2000 years ago (van Schaik and Kappeler, 1996). There is mounting evidence, however, which demonstrates that lemurs are subject to significant predation from diurnal raptors (Karpanty 1999, 2003, 2006). Additionally, lemurs are under threat of predation from their most formidable endemic predator, the fossa (*Cryptoprocta ferox*) (Hawkins, 2003; Colquhoun, 2006). Data on animal location (i.e. ground, low canopy, high canopy) in several *Eulemur* species may demonstrate a strategy for avoiding predation by diurnal raptors (Andrews and Birkinshaw, 1998; Overdorff, 1988; Curtis et al., 1999; Donati et al., 1999; Rasmussen, 2005; Gould and Sauther, 2006), and for avoiding predation by cathemeral fossa (Kohncke and Leonhardt, 1986; Dollar et al., 1997; Hawkins, 2003). These lemurs exploit the upper layer of the forest during the night, while using the middle to lower layers during the day (Overdorff, 1988; Curtis et al., 1999; Donati et al., 1999; Rasmussen, 2005). Feeding and traveling in the mid to low forest during the day may help evade detection from raptors (Curtis, 2007); while, feeding and traveling in the high canopy may help avoid detection from terrestrial predators, particularly the fossa (Hawkins, 2003), but also forest cats. The fossa is adept in the trees, but has difficulty in the highest canopy due to its body size (Hawkins, 2003). Though it may be the case that lemurs are less likely to attract fossa at night if they are in the high canopy, fossa are cathemeral (Colquhoun, 2006), which would put lemurs at greater risk of detection by fossa during the day. Aside from location, lemurs may use cathemerality as a mechanism of temporal crypsis, wherein predators are unable to focus efforts on a particular time for capturing prey (Colquhoun, 2006). Predation is an important factor in lemur ecology, however, it is once again central to note that although predation appears to play an key role in the cathemerality of some lemurs, other lemurs with known reduced predation threat also maintain cathemeral
activity patterns (Tarnaud, 2006). Thus, predation cannot solely account for variation in these activity patterns.

Avoidance of competition

Though interspecific competition is intrinsically linked to niche differentiation, the relationship between cathemerality and resource competition remains the most ambiguous to date (Curtis and Rasmussen, 2006). Rasmussen (1999) showed that *E. fulvus fulvus* and *E. mongoz* in a seasonal dry forest of northeastern Madagascar had overlapping core home ranges, along with preferred sleeping trees and diet. In this case, we would expect that species would favor the reduction of interspecific competition through temporal shifts (Rasmussen, 1999). However, these species groups actually displayed higher than expected encounter rates, many of which were neutral or positive, even in feeding contexts (Rasmussen, 1999). Additionally, the importance of competition in cathemeral activity patterns is less understood in communities that do not contain congeners (Curtis and Rasmussen, 2006). Given that *L. catta* is the sole species of the *Lemur* genus and that the present research took place in an area without intraspecific competitors, the avoidance of competition and its potential role in cathemeral activity will not be further addressed here.

Metabolic and dietary needs

Seasonal and stochastic fluctuations in food availability pose a significant problem to Malagasy primates (Richard and Dewar, 2007). Tattersall and Sussman (1975) linked the nocturnal feeding of *E. mongoz* to the temporally available nectar from *Ceiba pentaandra* flowers. Furthermore, Andrews and Birkshaw (1998) found that the presence of particular foods,
both during the day and night can help explain activity patterns. Yet, others have found few or no associations between temporal availability of food and diurnal or nocturnal behavior (Overdorff and Rasmussen, 1995; Colquhoun, 1998; Curtis et al., 1999; Rasmussen, 1999; Tarnaud, 2006). Rather than specific foods, Enqvist and Richards (1991) proposed that during times of fruit scarcity lemurs may include more fibrous leaves in their diets, thus requiring a 24-hr clock to maximize food spacing and digestive capacity. Results on this hypothesis are contradictory.

Tarnaud (2006) found that *E. f. mayottensis* females increased their leaf consumption during the daytime, when activity was extended through the night (Tarnaud, 2006). However, Curtis et al. (1999) found no relationship between fibrous diets and nighttime activity. As noted, some variation in cathemeral activity patterns may be explained by dietary needs, however diet cannot solely explain this variation.

**Transition between nocturnal and diurnal niche**

van Schaik and Kappeler's (1996) EDH argues that cathemeral lemurs are in a transitional state between nocturnal and diurnal lifestyles. However, since EDH was covered in Chapter 1 of this dissertation, and EDH does not appear to be a fruitful direction for elucidating causal mechanisms of lemur traits, it will not be further explored here.

**Cathemerality in *Lemur catta***

Although *L. catta* is considered "strictly diurnal" (Jolly, 1966; Sauther et al., 1999) there are anecdotal (Jolly, 1966; Sauther, 1989) and/or limited empirical (Traina, 2001; Parga, 2011) data suggesting a flexible activity pattern in this species. Jolly (1966) and Sauther (1989) have noted nocturnal yapping (a call in response to a potential predator) by *L. catta* at both Berenty
Private Reserve and Beza Mahafaly Special Reserve. Researchers at Beza Mahafaly Special Reserve have recently noted that when the moon was full (or near full) ring-tailed lemurs slept near heavily fruiting tamarind (*Tamarindus indica*) in camp and then fed on those fruits during the night (Sauthe, pers. obs.). Traina (2001) found that the nighttime activities of *L. catta* at Berenty included feeding, grooming, traveling, playing, mating, and fighting. Parga (2011) used GPS during a brief, one-week study of five, semi-captive, provisioned *L. catta* on St. Catherines Island, Georgia, USA, and found that animals did range between the hours of 1900 and 0530. Most recently, in July of 2011, ring-tailed lemurs at Beza Mahafaly Special Reserve were observed by local villagers engaging in crop raiding behaviors during the full moon (Enafa, pers. comm.). Albeit limited, these observations suggest that wild, free-ranging, and captive ring-tailed lemurs engage in some degree of cathemeral activity. Interestingly, *L. catta* may also have the patterns of eye morphology commonly found in cathemeral animals. In fact, they have both a well-developed *tapetum lucidum* and *area centralis*, which means that ring-tailed lemurs have both visual sensitivity for nighttime activity and visual acuity for daytime activity (Rohen and Castenholtz, 1967; Starck, 1995). *Lemur catta* is regarded as an extraordinarily flexible primate in many aspects (e.g. habitat type, feeding behavior, sleep sites) (Goodman et al., 2006; Gould, 2006; Jolly et al., 2006; Sussman et al., 2003) and cathemeral behavior may represent another way in which this species is adaptable. Cathemerality in *L. catta* may thus play a key role in our understanding of adaptations enabling flexibility in this species.

Accounting for cathemeral activity in lemur behavior and ecology is an extremely important aspect of future lemur studies, including that of *L. catta*. Nocturnal data are largely missing in all but a few studies in species of *Hapalemur* and *Eulemur*, which has likely created a bias towards daytime activities in many lemur study species (Curtis and Rasmussen, 2002).
Curtis and Rasmussen (2002) point out that many lemur research projects aimed at understanding "seasonal stress" likely provide inaccurate activity budgets and feeding data, given that nocturnal data are under-represented or absent. Nocturnal data of cathemeral lemurs could have a huge impact on our understanding lemur adaptations, including the 'holy grail' of lemur research, namely, understanding why female lemurs are dominant to males (Pochron & Wright, 2005).

Due to the nature of the study, data collection is biased towards daytime activities, and cannot account for all lunar phases or time periods. This schedule allowed for clearest observation of nighttime activities, and continuation of the larger research project. However, through animal observations, use of camera traps, and examination of prey remains, some insight into what animals were doing during nocturnal activities is provided. Results demonstrate that *L. catta* are in fact cathemeral, point to some of the proximate variables promoting cathemeral behavior, suggest ultimate benefits of cathemerality, and compares this research with the current literature on cathemerality in the Lemuridae.
Results

Animal data

Cathemeral activity occurred throughout the study period (Figure 3.1). Animal activity and location scores from scan samples are presented in Tables 3.1 and 3.2, respectively.

Figure 3.1. Nighttime activity levels in the ILove and Vintany groups from September to March.

Table 3.1. Day and Night animal activity scores from scan sampling with percentage of time spent engaging in each activity.

<table>
<thead>
<tr>
<th>Activity</th>
<th>Day</th>
<th>Night</th>
<th>Day: percentage of time in each activity</th>
<th>Night: percentage of time in each activity</th>
</tr>
</thead>
<tbody>
<tr>
<td>Locomotion</td>
<td>4709</td>
<td>602</td>
<td>44</td>
<td>26</td>
</tr>
<tr>
<td>Feed or Forage</td>
<td>4665</td>
<td>1256</td>
<td>43</td>
<td>53</td>
</tr>
<tr>
<td>Groom</td>
<td>756</td>
<td>196</td>
<td>8</td>
<td>8</td>
</tr>
<tr>
<td>Other</td>
<td>633</td>
<td>302</td>
<td>13</td>
<td>13</td>
</tr>
</tbody>
</table>

Table 3.2. Day and night animal location scores from scan sampling with percentage of time spent in each location.

<table>
<thead>
<tr>
<th>Location</th>
<th>Day</th>
<th>Night</th>
<th>Day: percentage of time at location</th>
<th>Night: percentage of time at location</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tree</td>
<td>7869</td>
<td>2528</td>
<td>72</td>
<td>96</td>
</tr>
<tr>
<td>Ground</td>
<td>2688</td>
<td>93</td>
<td>25</td>
<td>4</td>
</tr>
<tr>
<td>Cliff/Cave</td>
<td>75</td>
<td>3</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Other</td>
<td>228</td>
<td>4</td>
<td>2</td>
<td>0</td>
</tr>
</tbody>
</table>
All Chi-square values examining day and night animal activities, and animal day and night animal locations were significant (Table 3.3-3.4). Data with Cramer's V values that were strong or very strong are considered significant, while those with none or weak relationships were considered not significant. The Contingency Coefficient C (reported as percentage of max) reflect findings similar to those of Cramer's V, namely that there were much stronger relationships between day versus night activities or locations, when compared to within the day or night. There were significant differences in animal behavior and location between the day and the night, however, there were no significant differences found between animals groups.

**Table 3.3.** Chi-square, Cramer's V, and Contingency Coefficient C as percent of max ("C") values for between and within group variation in day and nighttime active lemur behaviors (locomote, feed/forage, groom, other).

<table>
<thead>
<tr>
<th>Activity</th>
<th>Chi-Square</th>
<th>df</th>
<th>p</th>
<th>Cramer's V</th>
<th>Relationship</th>
<th>C</th>
</tr>
</thead>
<tbody>
<tr>
<td>All animals day versus night</td>
<td>335.68</td>
<td>3</td>
<td>&lt;0.0001</td>
<td>0.16</td>
<td>Strong</td>
<td>19.35</td>
</tr>
<tr>
<td>VG day versus night</td>
<td>186.51</td>
<td>3</td>
<td>&lt;0.0001</td>
<td>0.1834</td>
<td>Strong</td>
<td>22.09</td>
</tr>
<tr>
<td>IG day versus night</td>
<td>175.46</td>
<td>3</td>
<td>&lt;0.0001</td>
<td>0.1522</td>
<td>Strong</td>
<td>18.43</td>
</tr>
<tr>
<td>VG day versus IG day</td>
<td>25.2</td>
<td>3</td>
<td>&lt;0.0001</td>
<td>0.0484</td>
<td>None</td>
<td>5.92</td>
</tr>
<tr>
<td>VG night versus IG night</td>
<td>10.17</td>
<td>3</td>
<td>0.0172</td>
<td>0.0657</td>
<td>None</td>
<td>8.03</td>
</tr>
</tbody>
</table>

**Table 3.4.** Chi-square, Cramer's V, and Contingency Coefficient C as percent of max ("C") values for between and within group variation in day and nighttime lemur locations.

<table>
<thead>
<tr>
<th>Location</th>
<th>Chi-Square</th>
<th>df</th>
<th>p</th>
<th>Cramer's V</th>
<th>Relationship</th>
<th>C</th>
</tr>
</thead>
<tbody>
<tr>
<td>All animals day versus night</td>
<td>1033.97</td>
<td>3</td>
<td>&lt;0.001</td>
<td>0.2566</td>
<td>Very Strong</td>
<td>32.68</td>
</tr>
<tr>
<td>VG day versus night</td>
<td>340.77</td>
<td>3</td>
<td>&lt;0.001</td>
<td>0.2467</td>
<td>Very Strong</td>
<td>29.34</td>
</tr>
<tr>
<td>IG day versus night</td>
<td>700.76</td>
<td>3</td>
<td>&lt;0.001</td>
<td>0.2639</td>
<td>Very Strong</td>
<td>34.98</td>
</tr>
<tr>
<td>VG day versus IG day</td>
<td>97.82</td>
<td>3</td>
<td>&lt;0.001</td>
<td>0.0951</td>
<td>Weak</td>
<td>11.57</td>
</tr>
<tr>
<td>VG night versus IG night</td>
<td>53.59</td>
<td>3</td>
<td>&lt;0.001</td>
<td>0.1051</td>
<td>Weak</td>
<td>17.31</td>
</tr>
</tbody>
</table>

Both groups of lemurs ranged extensively throughout the day (2018m on average, as presented in Chapter 5). Nighttime ranging, on the other hand, was restricted. Most animals stayed within a 100m circumference of their group's sleep site. That being said, on two occasions
I saw lone males leave their group at night, and have one camera trap photo (Figure 3.2) of a male in the "momma" baobab tree which is farther than 100m from either of the groups sleep sites.

**Figure 3.2.** Male ring-tailed lemur in the momma baobab tree at 12:09am on March 20, 2011.

*Camera trap data*

The camera traps stationed near animal sleeping sites resulted in 1314 unique lemur photographs from 422 camera trap days. Of these photos, 387 were at night (Figure 3.3).
Figure 3.3. Camera trap photos taken near animals sleep sites. Clockwise from top left: IG members during daylight at 6:02pm, IG mother and offspring during the night at 11:51pm, VG animal after dark at 8:50pm, and VG animals before daylight at 4:48am.

Nighttime Activity

Significant correlations were found between nighttime activity levels and daytime temperature maximum, nighttime temperature maximum, and to a lesser extent, amount of nighttime moon illumination (Table 3.5). Furthermore, linear regression showed significant relationships within the aforementioned variables (Table 3.6). In other words, the lemurs increased their nighttime activity levels when a) it had been hot during the day, or b) was warm during the night (Figure 3.4), and/or c) when there was greater moon illumination, although this
was marginal. High daily and nightly temperatures explained about 20% of the variation in nighttime activity levels, while increased moon illumination explained about 2%. No significant associations were found between nocturnal activity and day length, rainfall and/or phenology, or predator presence. However, the events surrounding the death of a predated ring-tailed lemur infant will be detailed below.

**Table 3.5.** Pearson's correlation between lemur nighttime activity levels and daytime high temperature, nighttime high temperature, and moon illumination.

<table>
<thead>
<tr>
<th></th>
<th>Pearson</th>
<th>N</th>
<th>p-value (1-tailed)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Daytime temperature</td>
<td>0.332</td>
<td>194</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Nighttime temperature</td>
<td>0.382</td>
<td>194</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Illumination</td>
<td>0.149</td>
<td>194</td>
<td>0.019</td>
</tr>
</tbody>
</table>

**Table 3.6.** Linear regression of lemur nighttime activity levels with daytime temperature maximum, nighttime temperature maximum, and moon illumination.

<table>
<thead>
<tr>
<th></th>
<th>R²</th>
<th>d.f.</th>
<th>p-value (1-tailed)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Daytime temperature, nighttime temperature, and illumination</td>
<td>0.216</td>
<td>193</td>
<td>&lt;0.000</td>
</tr>
</tbody>
</table>

**Figure 3.4.** Average nighttime activity levels with nighttime temperature
Pearson's correlation shows positive relationships between average monthly nighttime activity levels and daytime activities of feed/forage and sit/stand/rest, while negative correlations between average nighttime activity levels and daytime activities of locomotion and "other" (Figure 3.5, Table 3.7). Similarly, linear regression showed significant relationships between the amount of lemur nighttime activity and daytime activity budgets (Table 3.8). Additionally, there were significant correlations found within the daytime activity categories (independent variables) (Figure 3.6, Table 3.9).

**Figure 3.5.** Nighttime activity levels and regression lines with the following daytime activities: a) Feed/forage, b) Locomote, c) Other, d) Sit/stand/rest.
Table 3.7. Pearson's correlation between lemur nighttime activity levels and daytime activity budget categories (feed/forage, locomote, sit/stand/rest, other).

<table>
<thead>
<tr>
<th></th>
<th>Pearson</th>
<th>N</th>
<th>p-value (1-tailed)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Feed/forage</td>
<td>0.733</td>
<td>6</td>
<td>0.047</td>
</tr>
<tr>
<td>Locomote</td>
<td>-0.739</td>
<td>6</td>
<td>0.047</td>
</tr>
<tr>
<td>Sit/stand/rest</td>
<td>0.836</td>
<td>6</td>
<td>0.019</td>
</tr>
<tr>
<td>Other</td>
<td>-0.845</td>
<td>6</td>
<td>0.017</td>
</tr>
</tbody>
</table>

Table 3.8. Linear regression of lemur nighttime activity levels with daytime activity budgets (feed/forage, locomote, sit/stand/rest).

<table>
<thead>
<tr>
<th></th>
<th>R²</th>
<th>d.f.</th>
<th>p-value (1-tailed)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Feed/forage</td>
<td>0.538</td>
<td>5</td>
<td>0.049</td>
</tr>
<tr>
<td>Locomote</td>
<td>0.546</td>
<td>5</td>
<td>0.047</td>
</tr>
<tr>
<td>Sit/stand/rest</td>
<td>0.714</td>
<td>5</td>
<td>0.017</td>
</tr>
<tr>
<td>Other</td>
<td>0.699</td>
<td>5</td>
<td>0.019</td>
</tr>
</tbody>
</table>
Figure 3.6. Correlations and best fit lines within daytime activities, including: a) feed/forage and locomote, b) feed/forage and other, c) feed/forage and sit/stand/rest, d) locomote and other, e) locomote and sit/stand/rest, and f) other and sit/stand/rest.
Table 3.9. Pearson's correlation between lemur daytime activity budgets (feed/forage, locomote, sit/stand/rest).

<table>
<thead>
<tr>
<th></th>
<th>Pearson's</th>
<th>N</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Feed/forage, locomote</td>
<td>-0.927</td>
<td>7</td>
<td>0.001</td>
</tr>
<tr>
<td>Feed/forage, other</td>
<td>-0.784</td>
<td>7</td>
<td>0.018</td>
</tr>
<tr>
<td>Feed/forage, sit/stand/rest</td>
<td>0.772</td>
<td>7</td>
<td>0.021</td>
</tr>
<tr>
<td>Locomote, other</td>
<td>0.741</td>
<td>7</td>
<td>0.028</td>
</tr>
<tr>
<td>Locomote, sit/stand/rest</td>
<td>-0.935</td>
<td>7</td>
<td>0.001</td>
</tr>
<tr>
<td>Other, sit/stand/rest</td>
<td>-0.734</td>
<td>7</td>
<td>0.030</td>
</tr>
</tbody>
</table>

Daytime activities that were considered "other" are further detailed in Figure 3.7. Only males engaged in stink fighting, as we know, and scent marking was significantly correlated to males (Pearson's= 0.900, N=4, p=0.050), when compared to females. No other significant differences were found in these data.

Figure 3.7. Daytime "other" activities females and males in the dry and wet seasons.
Predation of an infant ring-tailed lemur

On October 26, 2010, a 3-4 week old dead infant *L. catta* was found under the Vintany sleep tree. Given the state of decay, the infant had likely died the previous day (Figure 3.8). The ventral surface of the infant's torso was absent and it was not possible to determine its sex. There were two puncture wounds on the infant's neck, with a distance of 16mm between them. This infant was probably killed (or at least bitten by) either an ampaha or a fossa, given that either of these animals can have an inter-canine distance of 16mm (Sauther, unpublished data).

**Figure 3.8.** Remains of *L. catta* infant a) as encountered with dorsal surface untouched, b) ventral surface after flipping carcass over, c) puncture wounds on side of torso.
During the entire study period, there were two instances, which I am aware of, when the Vintany group did not sleep at their usual tree. Those nights were October 25 and October 26, 2010. Instead of their usual sleeping site, the group slept north of camp at the base of the Mahafaly plateau. Using telemetry, I was able to locate their general location at about 10:00pm on Oct 25th, but could not pinpoint where exactly the animals were sleeping because of problems with nighttime visibility and there not being any paths in the vicinity.

There were camera trap images for the Vintany group after dark on October 20-23 and 25, and then not again until November 21, 2010 (27 days later). There were no camera trap images of predators surrounding the infant's death. Albeit circumstantial, it seems as though a predator had taken the infant ring-tailed lemur, probably at night, on the evening of October 25, 2010, and that after this event the Vintany group avoided their usual sleep tree for two nights, and avoided nighttime activities for nearly a month.
Discussion

This study of wild *L. catta* at Tsimanampetsotsa National Park, which is part of a long-term ecological assessment of this lemur population, documents for the first time in a wild ring-tailed lemur population that ring-tailed lemurs are frequently active during the night, and thus should be considered cathemeral. During nighttime activity, TNP lemurs engaged in more feeding behavior and less locomotion when compared to daytime activity. Furthermore, at night, most animals avoided being on the ground and spent the majority of their active time in trees within 100m of their usual sleeping spots. The amount of nighttime activity in these two lemur groups increased with high daily temperatures, nightly high temperatures, and greater moon illumination, although these three independent variables only explain 26% of the variation. Significant positive correlations were found between nighttime activity levels, daytime feeding and daytime resting, while significant negative correlations were found between nighttime activity levels and daytime locomotion and daytime "other" behaviors. While more data are needed to completely identify the underlying causes of cathemerality in *L. catta*, these results allow for some evaluation of the functional relevance of cathemeral activity in a comparative framework.

Increased moon illumination promotes nocturnal activity in many lemur species from various habitats (Colquhoun, 1998; Donati et al., 1999, 2001; Olivieri, 2002; Kappeler and Erkert, 2003; Donati and Borgognini-Tarli, 2006). Moreover, nocturnal activity is highest when the moon is above the horizon and at its brightest (Kappeler and Erkert, 2003; Donati and Borgognini-Tarli, 2006). Though moon rise and crest were not considered in this study, available moon light was significantly related to nocturnal activity, but only marginally. Given that moon illumination has been suggested to positively affect *L. catta* activity (Traina, 2001; Parga, 2011),

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it is likely that light availability is a factor in *L. catta* nocturnal activity, however it only accounts for a small amount of the variation in nighttime activity here.

Ambient temperature also affects nocturnal activity in some lemur species (Overdorff and Rasmussen, 1995; Colquhoun, 1998; Curtis et al., 1999; Donati et al., 1999; Rasmussen, 1999; Kappeler and Erkert, 2003; Donati and Borgognini-Tarli, 2006), which may be a means to minimize thermoregulatory energy requirements (Curtis et al., 1999; Curtis and Rasmussen, 2002). In fact, lemurs have a suite of physiological, behavioral, postural, and social activities, which appear to function as low-cost thermoregulatory mechanisms (Richard and Dewar, 1991; Morland, 1993; Ostner, 2002). These have been interpreted as adaptations to the distinct seasonality and unpredictability of resources in Madagascar (Jolly, 1984; Wright, 1999; Dewar and Richard, 2007). All lemurs that have been studied thus far appear to be hypometabolic (Daniels, 1984; Genoud, 2002; Simmen et al., 2010), and have limited capacity for sweat or shiver responses (Aujard et al., 1998). However, low BMR in *Eulemur* spp. seems to be coupled with high body temperature (Daniels, 1984; Müller, 1985), which may help explain high levels of activity in these animals (Donati et al., 2007). If these patterns are also present in other genera of lemur, such as *L. catta*, it is likely that lemurs have evolved physiological and behavioral traits that maintain high body temperatures even with their low metabolic rates (Donati et al., 2011). High activity levels resulting from a high resting body temperature may help lemurs exploit scarce and ephemeral resources when they are briefly available.

It has thus been proposed that lemurs should often use behavioral thermoregulation as an energy efficient way to maintain temperature homeostasis (Morland, 1993). Research here suggests that cathemerality could represent a behavioral mechanism for thermoregulation. I noted that during days with hot periods, particularly when temperatures were greater than 45°C,
lemurs spent long periods of time resting in the shade, while panting and licking their hands and feet, and were subsequently more likely to be active at night. Nighttime activity, in this case, may have allowed animals to make up for lost feeding or foraging time when conditions were much more favorable. Ellwanger and Gould (2011) note that activity rapidly declines in L. catta once ambient temperatures surpass 40°C and suggest that in order to compensate for the lost feeding time, animals use abbreviated but intense feeding periods in the late afternoon, wherein feeding rates increase. Data from this study suggests that L. catta increase nighttime activity during periods with particularly high daytime temperatures (i.e. >40°C). During nighttime active periods, animals spend the majority of their time feeding (53%), and as such, nighttime feeding may serve as an additional mechanism for making up for lost feeding time, when daytime conditions are not optimal. The avoidance of high daytime temperatures and increased nighttime foraging has also been found in H. alaotrensis (Mutschler, 1999, 2002).

These ring-tailed lemurs were more likely to be active at night when nighttime temperatures were warmer, and may have been limiting nighttime activity during particularly cold nights. Huddling and avoidance of activity during overnight cold temperatures have also been seen in H. g. alaotrensis (Mutschler, 1998) and Aotus aotus azarai (Fernandez-Duque, 2003). However, the opposite case where correlations between low nighttime temperatures and nighttime activity have been reported in several species of Eulemur (mongoz [Curtis et al., 1999], rufus [Donati et al., 1999], rubriventer [Overdorff and Rasmussen, 1995]). Donati and Borgognini-Tarli (2006) note that there seems to be a divide in the activity pattern and level of seasonality in the habitat. Correlations between increased nocturnal activity and low overnight temperatures tend to be seen in forests with reduced seasonality and smaller relative annual temperature fluctuations, whereas the avoidance of activity during cold nights occurs in highly
Nocturnal activity was not directly related to measures of predator presence in this study. However, measures may not have accurately reflected predator pressure, as other lines of evidence suggest predation may have played a role in nocturnal activity of *L. catta*. First, animals had a marked aversion to traveling on the ground and spend far less time in locomotion at night. While spending 25% of their travel time on the ground during the day, they spent only 2% of their time on the ground at night. Ground travel is likely associated with increased predation by nocturnal cats, and potentially by fossa, and may be why lemurs avoided the ground at night (Curtis, 2006). Additionally, nighttime activity was comparably low at the beginning of the study period, which corresponded to the lemur birth season, but increased every month after that, as the infants increased in size and improved their physical abilities (though nighttime temperatures were also low at the onset of the study). Infant *L. catta* are extremely precocial and actively move about their mother shortly after birth (Sauther, 1989). During the second week of life, infants engage in exploratory behavior through hopping off the mother and climbing around their environment (Gould, 1990). This can be a particularly dangerous time for infants, as their mothers may quickly flee if startled, leaving the exploring infants behind. During this study, a three week old infant was found dead on the ground at the Vintany group's sleep site. It had only been dead a few hours and had two puncture wounds on the side of its torso, which were consistent with the size and shape of either cat or fossa canine teeth (Figure 3.9). Camera trap photos revealed that animals were up the previous night, but this group was not seen after dark again until 27 days later. Furthermore, the group did not sleep in their regular sleep tree for two nights following my finding the dead infant. This was the only known occasion during the study...
when Vintany did not sleep in their normal tree. In addition to this infant, the remains of at least three adult ring-tailed lemur was found in predator scat from within the group’s overlapping home ranges. Of course, these remains could have been the result of scavenging rather than direct predation, but the lemurs behavior suggest animals are subject to predation, engaging in predator avoidance, and that anti-predator behaviors should be explored further in future research.

The diet hypothesis predicts that cathemerality is an adaptive response that enables animals to best utilize low-quality food resources during times of scarcity. For this hypothesis to be true, we would expect to see more cathemeral activity during periods when animals were eating markedly fibrous foods, or when food resources were most limited. Data presented in Chapter 5 of this manuscript demonstrates that fiber consumption was higher for both males and females during the dry season, which corresponds to periods of relatively low nocturnal activity by these lemurs. Additionally, the TNP ring-tailed lemurs were much more active during the wet season when foods are more abundant. This pattern of increased nocturnal activity with increased food abundance, was also found by Kappeler and Erkert (2003) in their work on *E. f. rufus* in the dry deciduous forests of Kirindy. Thus, it does not appear that *L. catta* at TNP increased nighttime activity in response to highly fibrous foods or scarcity of resources. All observed foods consumed during nighttime observations, were also consumed during the day, however, it was not possible to assess rates of feeding or amount consumed at night. Curtis (1999) suggested that feeding behaviors at night in *E. mongoz* were not significantly different from their daytime feeding habits. Since we do not know if feeding behaviors vary between night and day in ring-tailed lemurs, this should be explored further, as this data could impact the interpretation of fibrous food consumption. Proximity to food resource seemed to be the most important factor
determining what foods the animals would consume at night. Almost all nighttime observations of animals were within 100m of their sleep site. Males sometimes went off alone and ranged further at night (Figure 3.2), but in the vast majority of nighttime observations animals remained close to their sleeping site. This type of ranging was likely related to predator avoidance, since there is no continuous canopy and animals have to travel on the ground if they are to range further. The evidence from other lemur species is mixed on the relative importance of the diet hypothesis in relation to cathemeral activity. Donati et al. (2009) found that fiber was able to explain a significant portion of activity variation in *E. collaris* and *E. collaris X E.f. rufus* hybrids, while many other authors have found no such associations (Andrews and Birkinshaw, 1998; Colquhoun, 1998; Curtis et al., 1999; Rasmussen, 1999; Fernandez-Duque, 2003; Kappeler and Erkert, 2003). With reference to diet, cathemeral lemurs may simply increase their caloric intake in order to meet (or attempt to meet) their metabolic needs, and are achieving this through nighttime feeding. Nocturnal activity, however, by their thermoregulatory capacities, which may explain why animals were not more active at night during the times when foods were most scarce, and overnight temperatures were lowest. Nighttime feeding and foraging was positively correlated to daytime feeding and foraging and also resting, while negatively correlated with locomotion and "other" behavioral categories. These data follow the trends I have found for activity budgets of male and female ring-tailed lemurs, in that when food is more plentiful animals feed more and travel less. From an energetic point of view one might predict that nighttime feeding would be most beneficial to animals when foods were generally scarce and animals have to travel more and rest less, while feeding during the day. Once again however, the coincidence of low food availability and low overnight temperatures may impede these ring-tailed lemurs' ability to feed during the night, though this may also be related to the relative
vulnerability of infants to predation during this time period. Food is often limited for frugivorous/folivorous lemurs, and fruit abundance is cited as being the primary limiting factor in *L. catta* survival (Jolly et al., 2002). Ability to feed at night could be important for gaining fat during brief periods of food availability, and/or essential for survival during times of food shortages.

van Schaik and Kappeler's (1996) evolutionary disequilibrium hypothesis suggests that cathemerality is not an adaptive trait, but rather part of the transition from a nocturnal to diurnal lifestyle, resulting from relaxed selection pressure following the extinction of large-bodied diurnal raptors some 2000 years ago. Existing data on predation rates by diurnal raptors (Karpanty, 1999, 2003, 2006), eye morphology of cathemeral lemurs (Kirk, 2006), genetic analyses (Roos et al., 2004), and phylogenetic reconstructions (Griffin et al., 2012) have all indicated that cathemeral lemurs do not show evolutionary disequilibrium, nor do the data presented here. Also, pairs of *P. radiatus* were frequently seen within lemur territory, and two unsuccessful predation attempts on *L. catta* individuals were recorded. Lemurs sometimes reacted strongly (shrieks, alarm barks, moving into trees) to the presence of *P. radiatus*. When the groups were in areas of habitat that were dwarf forests or otherwise without canopy, they would illicit intense and long alarm responses. However, when lemur groups were in or under large trees, their reaction was very different in that they seldom alarm called, and continued to feed while frequently glancing at the hawk(s). Sauther (1989) suggested that Harrier hawks require open spaces in order to predate animals, because of their large wing span. From their behavioral response to Harrier hawks, it appears as if these lemurs a) recognize Harrier hawks as a potential predator, and b) assess the level of threat posed by hawks according to micro-habitat.

van Schaik and Kappeler (1996) suggested that lemurs' alarm responses to hawk were
inappropriate in modern times and a relic behavior left over from before the extinction of the giant crowned eagle, *S. mahery*. Given that Harrier hawks prey on other large-bodied lemurs (Karpanty 2002, 2006) and that *L. catta* appear to react to the level of threat posed by the hawks, I expect that the current behavioral reactions of lemurs are appropriate. Selection pressure in the diurnal niche is not likely relaxed, as proposed by van Schaik and Kappeler (1996), and cathemeral lemurs are not expected to be in a state of evolutionary disequilibrium.

Conditions of Madagascar's habitats are unusually harsh (Wright, 1997; Wright, 1999). Soils are of poorer quality than most in other primate habitats (Ganzhorn et al., 1999), and tree growth is slower and fruit production lower than in measured forests in South America and Africa (Terborgh, 1983; Sorg and Rohner, 1996; Terborgh et al., 1997; Struhsaker, 1997; Ganzhorn et al., 1999). Additionally, Madagascar is subject to frequent yet unpredictable cyclones, severe storms, and droughts, and all of Madagascar's forests are seasonal (Donque, 1975; Ganzhorn, 1995; Wright, 1997). For lemurs, the culmination of the aforementioned conditions result in frequent predictable and unpredictable shortages of foods (Jolly, 1984; Wright, 1999). Cathemerality could be one of the flexible responses employed by some lemurs, which enables them to secure resources, such that they meet caloric requirements. One thing is becoming increasingly clear in the study of cathemerality in lemurs; there is no one universal factor or mechanism determining cathemeral activity. Rather, cathemerality is an activity pattern employed by a variety of species, in various habitats, at different times, in response to a host of ever changing and non-mutually exclusive variables. The task at hand remains to examine more cathemeral lemur data, tease apart proximate mechanisms, and discover any patterns that may exist.
Conclusions

In summary, I argue that *L. catta* is in fact cathemeral. Proximate mechanisms promoting nighttime activity include daytime and overnight temperatures and moon illumination, although these variables can only explain 26% of the variation in nighttime activity levels. Ultimate factors of cathemerality likely include thermoregulation and predator avoidance. Food availability was not found to be an ultimate factor, *per se*, although I suggest that cathemeral feeding may allow animals to meet basic caloric needs. If this were true, diet would play an adaptive role in cathemerality. It remains unlikely that lemur cathemerality is a result of evolutionary disequilibrium, as proposed by van Schaik and Kappeler (1996). Since unaccounted nocturnal activities could greatly affect our interpretations of *L. catta* ecology, future work should at the very least monitor the amount of time animals are active at night, but we also need much more data on nighttime behavior, activity budgets, and nutritional profiles. Furthermore, given the potential importance of cathemerality on lemur ecology, cathemeral behavior should be investigated further in any species in which occasional flexible diel activity pattern has been reported. This information would be particularly pertinent for *Varecia variegata variegata*, which along with *L. catta*, has been regarded as diurnal, but has also been reported as nighttime active (Morland in Hoffmann et al., 1992; Balko in Wright, 1999; Britt in Donati and Borgognini, 2006). If *V. variegata* was cathemeral along with *Eulemur, Hapalemur* and now *Lemur*, parsimony would predict that the ancestral state of the Lemuridae clade is also cathemeral. This knowledge could advance our understanding on the evolution of flexible 24-hr activity patterns in lemurs, and therefore other mammals, given their shared physiology and phylogeny.
Chapter 4: Patterns of climate and weather in southern Madagascar, along with *Lemur catta* plant food use.

**Overview**

Strong seasonality, erratic rainfall, frequent cyclones, and cyclical droughts are characteristic of the climate and weather of Madagascar (Dewar and Richard, 2007). These climatic events have been suggested as primary proximate mechanisms shaping traits in the islands' flora and fauna (Dewar and Richard, 2007). For instance, lemur reproduction is timed such that females are pregnant, and at least begin lactating during the driest parts of the year, when food resources are reduced (Jolly, 1984; Wright, 1999). During these times, lemur females rely primarily on small burst of flowers and leaves, and in gallery forests, on tamarind fruits (Sauther, 1994, 1998). Through synchronous and seasonal reproduction, females begin weaning their infants at the time of year which coincides with the highest food availability and infants are thus given the best possible chances of survival during this critical life stage period (Jolly, 1984; Wright, 1999).

This chapter examines the climate in southern Madagascar and at Tsimanampetsotsa before and during the time of this research, which then sets the stage for understanding plant phenology, and whether or not plant foods are seasonally limited for ring-tailed lemurs.

**Background**

**Southern Madagascar climate and weather**

Madagascar's climatic features are often regarded as unusual, when compared to other landmasses, due in part to the island's large size, latitudinal expanse and topographic diversity (Jury, 2003). Southern Madagascar's climate alternates between a short, hot, wet austral summer and a long, cool and dry austral winter. Temperatures during austral summer days can be well
over 40°C, while austral winter night temperatures near 0°C. Cyclone season mirrors the austral summer wherein an average of seven significant storms hit Madagascar every year (based on data from 1920-1975 [Donque, 1975; Goodman 1995]). On average, 80% of these annual storms originate in the east and most affect the east coast, however, approximately 20% originate west of Africa and have the most impact on Madagascar's southwestern coast (Wright, 1999).

Additionally, storms originating in Madagascar's east often continue on a trajectory that includes the south, although the severity is generally reduced after initial touchdown.

Rainfall in southern Madagascar varies between approximately 300 and 900mm per year, although these tend to vary greatly. Richard and Dewar (2007) note that rainfall patterns, particularly those in western Madagascar are unpredictable both inter- and intra-annually. Severe droughts also occur in Madagascar and some suggest droughts are part of cyclical patterns (Sauther, 1991; Gould, 1992; Jolly, 1998; Sauther, 1998; Gould et al., 1999). Prior to 1999, drought years recorded in Betioky (25km southwest of BMSR), include: 1949, 1957, 1959, 1964, 1976, 1982, and 1991-1992 (Gould et al., 1999). Serious drought conditions in southern Madagascar and El Nino periods appear to occur simultaneously, and droughts also tend to linger in years after El Nino (Jury, 2003). Furthermore, the International Disaster Database (2012) suggests that between 1900 and 2012 there were an average of 0.16 droughts per year in Madagascar. In other words, on average, southern Madagascar can expect a significant drought once every 6.25 years.

Cyclones in southern Madagascar can result in massive destruction in Madagascar's forests. In January 2005, cyclone Ernest hit BMSR, and resulted in flooding, defoliation, tree knock-downs, soil erosion, and a fruiting failure within tamarind trees (LaFleur and Gould, 2009; Whitelaw, 2010). This storm, and associated reduction in forest foods, appeared to impede the
The ability of female ring-tailed lemurs to conceive, and impact the survivorship of infants that were born (Sauther, unpublished data).

Cyclones, but particularly drought, appear to negatively affect animal survivorship, through a reduction in water and food resources. Gould et al. (1999) describe the bottleneck effects of widespread drought on ring-tailed lemur populations, and note that in the second year of the 1991-1992 drought 80% of all infants and 20.8% of adult females died. Furthermore, in the following year, 57% of juveniles died and an additional 29.9% of adult females died. It wasn't until the 4th year following the drought that *L. catta* populations began to show signs of recovery (Gould et al., 1999). Southwestern Madagascar's habitat is harsh and difficult to begin with, but coupled with several annual cyclones and serious droughts which occur approximately every 6 years, results in an extremely challenging environment to survive in.

**Ring-tailed lemur feeding and important foods**

The availability of plant foods in southern Madagascar fluctuates dramatically according to season. Only a select few plant genera have the ability to maintain productivity during the long dry seasons, and thus there is a significant reduction in plant foods available during dry periods. However, once seasonal rains commence, many forest plant species are almost immediately productive and for a period of time there is an abundant and diverse array of plant foods available.

Ring-tailed lemurs are flexible foragers that consume ripe and unripe fruits, young and mature leaves, leaf stems, flowers, soil, dead wood, termite casts, insects, and in very rare occasions, vertebrate prey (Jolly, 1966; Sussman, 1972, 1974; Budnitz and Dainis, 1975; Sussman, 1976; Sauther, 1992; Rasamimanana and Rafidinarivo, 1993; Sauther, 1998;
The number of plants species fed on by ring-tailed lemurs at a given time can be diverse and varies according to time of year and location. For example, at BMSR, ring-tailed lemurs consume 40 different leaf species, 28 fruit species and 16 flower species, whereas at Berenty, they consume 82 different leaf species, 40 fruits and 38 flowers (Simmens et al., 2006). However, since ring-tailed lemurs use plant resources as they become available, the total number of species consumed during a given time period tends to be largely dominated by far fewer species (Sauther 1992, 1998; Simmen et al., 2006). When accounting for newly introduced species (such as those in the tourist areas of Berenty) and tamarind, ring-tailed lemur diet tends to focus on 15 or less plant species at a time (Sauther 1992, 1998; Simmen et al., 2006). However, if tamarind and introduced plant species are not present or not included in this tally, the diet tends to be dominated by three or less species at any one time (Sauther 1992, 1998; Simmen et al., 2006).

Though generally a trait reserved for species in temperate climates, the vast majority of lemur reproduction is strictly seasonal, and is induced by changes in photoperiod (van Horn and Resko, 1977; Petter-Rousseaux, 1980). In some genera, such as those within the Lemuridae, reproduction in groups is synchronized to within a week or two of surrounding groups (Richard, 1974; Pereira, 1991; Sauther, 1991; Wright, 1995; Pereira, 1998; Wright, 1999). Moreover, synchronous reproduction is deeply ingrained within lemur life history, and is maintained in lemurs even when they are in captivity and far from Madagascar, which is not the case for any other primate group (Rasmussen, 1985).

*Lemur catta* reproduction is highly tied to seasonal resources within gallery forest habitats such as BMSR or Berenty (Jolly, 1984; Sauther, 1992; Rasamimanana and Rafidinarivo, 1993; Sauther, 1993, 1998; Sauther et al., 1999; Yamashita, 2002), and females are in late...
gestation during the driest parts of the year (July-September), which has correspondingly low food availability (Sauther, 1994, 1998; Sauther et al., 1999). Furthermore, at Berenty and BMSR early lactation occurs at the onset of the wet season (October-November) and late lactation and early weaning occurs well into the wet season (January-April), which is normally associated with food abundance. At this time, all animals exploit increasing food resources (Sauther, 1994, 1998; Sauther et al., 1999). Furthermore, weanlings’ chances of autonomous survival are increased through “weaning synchrony” wherein weaning coincides during the time of year with the most predictably abundant food resources (Jolly, 1984; Sauther, 1994; Wright, 1999). Reproductive females in gallery forests rely heavily on a few key species (e.g. *Tamarindus indica*, *Maeurua filiformis*, and *Quivisianthe papinae*), which tend to be either consistently available or likely to produce short bursts of large quantities of foods during critical times (Sauther, 1994, 1998; Sauther et al., 1999).

In the few other habitats where ring-tailed lemurs have been studied, we see similar trends of reproduction and plant food use. For example, Kelly (2011) found that the diets of ring-tailed lemurs groups in Cap St. Marie, who's habitat is distinctly populated by stands of *Opuntia monacantha*, were similar to gallery forest ring-tailed lemurs' in species diversity, general food type and composition. Furthermore, these lemurs used the fruits of *O. monacantha* throughout the year and were able to sequester both nutrients and important water resources from the fruits. Gould (2011) noted that in fragmented gallery and spiny forest patches, ring-tailed lemur relied on a few key species of plants during lean times. Furthermore, many of the plant species used during the driest times of year are also those used by ring-tailed lemurs in the gallery forests of BMSR and Berenty including: *Gyrocarpus americanus* (flowers leaves, fruits), *Metaporana*
parvifolia (young leaves), *Tamarindus indica* (fruit, leaves), *Alluaudia procera* (flowers, leaves), mixed liana (young leaves), and *Salvadora angustifolia* (young leaves and flower bundles).

**Gallery forest ring-tailed lemurs and tamarind**

*Tamarindus indica* is of particular importance to gallery forest-residing *L. catta* as young leaves, flowers, and fruits are produced asynchronously throughout the year at riverine gallery forest habitats (Sauther, 1998), thus making them available year-round for consumption (Simmen et al., 2006; Irwin, 2008). As a member of the family Fabaceae, tamarind fruits are protein-dense and provide a rich source of energy (Morton, 1987). Young tamarind leaves and flowers are also important to *L. catta* diet as they too provide a readily digestible protein source (Sauther, 1993; Mertl-Milhollen et al., 2003). Furthermore, tamarind foods usually comprise upwards of 35-60% of gallery forest ring-tailed lemurs’ diet (Rasamimanana and Rafidinarivo, 1993; Mertl-Milhollen et al., 2003; Soma, 2004; Koyama et al., 2006). Fruits are ripe during the driest parts of the year and provide high-energy foods to females who are gestating or lactating, and infants as young as two months feed on and lick tamarind pods (Simmen et al., 2006). Because of the dietary importance of *T. indica* to *L. catta* at the BMSR as well as the large number of tamarind trees in this forest, Yamashita (2002) suggests that all other foods are secondary.

Several authors use the definition of a "fallback food" for any food for which there is a significant negative correlation between its use and the abundance of other foods (Marshall and Wrangham, 2007; Marshall et al., 2009; Sauther and Cuozzo, 2009). Fallback foods are often thought to be influential in primate morphology, and particularly dental morphology, since they influence adaptive shifts during critical periods (e.g. Lambert et al., 2004; Laden and Wrangham,
2005; Vogel et al., 2008; Strait et al., 2009). Du Puy et al. (2002) suggests that the importance of tamarind foods to gallery forest ring-tailed lemurs implies an adaptation to consuming a disproportionate amount of *T. indica*. However, Sauther and Cuozzo (2004, 2006, 2009) associate severe and premature dental wear and attrition with tamarind fruit use in ring-tailed lemurs at Beza Mahafaly. Similar wear and attrition has been found in Berenty ring-tailed lemurs, where tamarind is also the dominant gallery forest tree species and ring-tailed lemur fallback food (as noted by Crawford [Sauther and Cuozzo, 2006]). Yamashita's (2008) work showed that tamarind fruits are the hardest and toughest foods consumed by ring-tailed lemurs at BMSR, and since the lemurs use their teeth to crack and chew the hard casing of the tamarind fruits, these data lend further support to Sauther and Cuozzo's (Cuozzo and Sauther 2004, 2006, 2009) linkage of tamarind fruit consumption and the ring-tailed lemurs' dental pathology. Moreover, this work is further supported by the facts that dental pathologies are not found in the sifaka (*Propithecus verreauxi*) at Beza Mahafaly or in ring-tailed lemurs at Tsimanampetsotsa. The sifaka choose younger, softer fruits, and the Tsimanampetsotsa ring-tailed lemurs only occasionally consume tamarind fruits (Cuozzo and Sauther, 2004, 2006; Yamashita, 2008; Sauther and Cuozzo, 2009). Though very important to gallery forest residing ring-tailed lemurs, the current evidence suggests that the lemurs are not morphologically adapted to consume large quantities of tamarind, given the detrimental biological effects (but see DuPuy et al., 2002).

The goal of this chapter is to describe the climate and weather patterns bracketing the study period, and through measures of phenology, to determine if seasonality limits food resources for ring-tailed lemurs. Seasonal (or stochastic) restriction of resources is the first assumption of the Energy Conservation Hypothesis that is tested by this research, and
understanding if/how resources are limited to lemurs should provide insight into the unusual lemur traits, including female dominance.
Results

Climate and weather patterns

TNP generally receives less than 400mm of rain per year, with the majority of rainfall occurring between late December and February. During the study period, a total of 232.9mm of rain were measured (Table 4.1). The rain in February coincided with Cyclone Bingiza, which hit the northeast coast of Madagascar on Feb 14, 2011 and the southwest on Feb 17, 2011 (Figure 4.1). The intensity of the cyclone was dramatically reduced on the west coast, however within a 30 hour period between February 17 and 18, 2011, TNP received more than 125mm of rain. This rain caused a flash flood at the TNP camp, but did not cause significant tree damage or defoliation within the study area.

Figure 4.1. Amount of rainfall at TNP between September 2010 and March 2011.

<table>
<thead>
<tr>
<th>Month</th>
<th>Sept</th>
<th>Oct</th>
<th>Nov</th>
<th>Dec</th>
<th>Jan</th>
<th>Feb</th>
<th>March</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rain (mm)</td>
<td>0</td>
<td>6.3</td>
<td>0</td>
<td>16</td>
<td>76.5</td>
<td>134.1</td>
<td>0</td>
</tr>
</tbody>
</table>

Figure 4.1. Map of the trajectory of Cyclone Bingiza (UNCT Madagascar).
Phenology and food availability

Seasonal food availability changed dramatically over the study period (Figure 4.2-4.3; Table 4.2). At the onset of the study (August of 2010), mature leaf coverage was below 40%, but at the end of the study period (April 2011) coverage surpassed 80%. Young leaf availability peaked once (December 2010 through January 2011), while flower availability peaked twice (once in November 2010 and again in January 2011). Fruit availability also peaked twice, with some fruits available in November (2010) and others in January through March (2011).

Table 4.2. Average percentage of tree coverage on all phenological transect lines during the study period.

<table>
<thead>
<tr>
<th>Month</th>
<th>Mature leaves</th>
<th>Young leaves</th>
<th>Flowers</th>
<th>Fruits</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sept</td>
<td>39</td>
<td>4</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Oct</td>
<td>36</td>
<td>4</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Nov</td>
<td>34</td>
<td>13</td>
<td>4</td>
<td>3</td>
</tr>
<tr>
<td>Dec</td>
<td>31</td>
<td>25</td>
<td>3</td>
<td>1</td>
</tr>
<tr>
<td>Jan</td>
<td>62</td>
<td>21</td>
<td>3</td>
<td>1</td>
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<tr>
<td>Feb</td>
<td>84</td>
<td>14</td>
<td>0</td>
<td>4</td>
</tr>
<tr>
<td>Mar</td>
<td>86</td>
<td>10</td>
<td>1</td>
<td>6</td>
</tr>
<tr>
<td>Apr</td>
<td>83</td>
<td>11</td>
<td>2</td>
<td>3</td>
</tr>
</tbody>
</table>

Figure 4.2. Availability of fruits, flowers, young leaves, and leaves during the study period.
Figure 4.3. Photos taken of the same areas (angles vary somewhat) during the dry season (left) and wet season (right).

In addition to transects, I monitored all tamarind and fig trees (with a diameter at breast height over 10cm) within the two focal lemur group’s overlapping home ranges. In total, there were 59 T. indica and 96 Ficus megapoda trees within this area. With the exception of one
tamarind tree on the Mahafaly plateau (zone 3), tamarinds were only present at the base of the Mahafaly plateau or "zone two" as described in Chapter 2: Methods. Though *T. indica* trees in southwestern Madagascar are generally asynchronoust within gallery forests and noted for their ability to provide gallery forest ring-tailed lemurs with food year-round (Sauther 1992, 1994), the trees in this study appeared seasonal. During September and October tamarind trees had ripe fruit and mature leaves (see **Figure 4.4**). Shortly after there had been 6.3mm of rain in late October a few tamarind trees produced flowers, but these flowers did not seem to result in any fruits. By November there were little-to-no fruits remaining and trees rapidly lost all of their leaves and became completely defoliated. In late December, trees regained their leaves, and these leaves matured quickly. In late March, flowers began to appear. Trees were not monitored after the study period, though one would presume after flowering in March and April, fruits would mature and be again ripe in September. Local people confirmed that synchrony was the normal pattern for tamarind at TNP.

*Ficus megapoda* trees were distributed throughout zones 2 and 3 of the lemurs' home ranges. These trees did fruit asynchronously and provided bursts of ripe fruits throughout the study period (**Figure 4.5**). Most notably, the large fig tree that the Vintany group slept in produced great quantities of fruits during two separate periods, while another fig tree ("Fig 3") produced a large amount of fruits in late October and early November. These fruiting events attracted many frugivorous/herbivorous animals including lemur groups, a host of bird species, tortoises, and insects. When fig trees within the territory produced large quantities of fruits, the lemur groups would visit the trees several times daily to selectively feed on ripe fruits. Throughout the study period, there was continuous availability of figs (*F. megapoda* and *F. marmorata*), though the quantity and quality varied.
**Figure 4.4.** Availability of *T. indica* and *F. megapoda* foods

**Figure 4.5.** *Ficus megapoda* fruits.
Foods consumed by focal animals

During the study period, focal ring-tailed lemurs were observed consuming two types of unidentified insects (one species of large arthropod and one or possibly two species of caterpillar), along with 69 plant parts originating from 53 known and 7 unknown different plant species (See Appendix 2 for a complete list). As with previous studies (Sauther 1992, 1998), animals at TNP consumed foods as they became available, and the composition of the diet varied from month to month (Figure 4.6). During September to late December the average number of species consumed per month by focal animals was 6.7, while from January to April the average number of species consumed per month was 11.1. Plant species and part, and the relative amount that animals consumed per month are listed in Table 4.3. For each month, the highest percentage of feeding time was spent on the following: September, Neobeguea mahafaliensis, flowers, 94%; October, Gyrocarpus americanus, flowers, 57%; November, G. americanus, fruit aril, 43%; December, Alluaudia comosa, flowers, 44%; January, Pentarhopalopilia madagascariensis and other species of liana, young leaves, 21%; February, F. megapoda, fruit, 57%; and March, P. madagascariensis and other species of liana, young leaves, 35%. Of all of the focal feeding data collected, animals spent 10.9% of their feeding time consuming figs and less than 1% of their feeding time consuming tamarind foods. Neobeguea mahafaliensis flowers, G. americanus flowers and fruit arils, and A. cosmosa flowers fit the definition of fallback foods, as the consumption of these foods negatively correlated to availability of other same type foods. The use of F. megapoda fruits by ring-tailed lemurs in this study doesn't fit cleanly into any of the operationalized definitions of food resources, as specified by Marshall and Wrangham (2007). Figs are almost always available, though the quantity and quality vary. The lemurs over-exploited F. megapoda fruits when there was one particular tree within their range that had an
enormous amount of ripe fruits. This happened in October when the fruits of *Gyrocarpus* were plentiful (although the lemurs only ate the fruit aril of *Gyrocarpus* and not the entire fruit) but no other fruits available, in December when few other fruits were available, and in February, which was one of the months with highest food availability. Though figs tend to be a regular food source of relatively low nutritional content (see Chapter 5), in times of mast fruiting of one tree, figs appeared to be a preferred food (October and February), a fallback food (December), and a staple food in other months. Overall, female lemurs consumed significantly more leaves (t=6.353, df=2, p=0.0120), when compared to males, and both males and females fed on insects during the wet season but not the dry (t=-4.556, df=2, p=0.0220). There were no other significant differences found in the type of food eaten by lemur sexes or groups, or between seasons.
Figure 4.6. Percentage of plant food and part consumed each month (species contributing < 2% per month removed)
Table 4.3. Percentages of plant species and plant part that contributed 1% or more of the total amount consumed by ring-tailed lemurs during each complete month of the study period. The most consumed species per month are in bold.

<table>
<thead>
<tr>
<th>Plant*</th>
<th>Part</th>
<th>Sept</th>
<th>Oct</th>
<th>Nov</th>
<th>Dec</th>
<th>Jan</th>
<th>Feb</th>
<th>Mar</th>
</tr>
</thead>
<tbody>
<tr>
<td>Adansonia rubrostipa</td>
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<td></td>
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<tr>
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<td>44</td>
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<tr>
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<td>Pentarhopalopilia madagascariensis and other species of liana</td>
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<td>21</td>
<td>13</td>
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<td>Poupartia minor</td>
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<td>Rantsandaka</td>
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<td>Tallinella grevei</td>
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</tr>
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<td>Zygophyllum depauperatum</td>
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<td></td>
<td></td>
<td>7</td>
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</tr>
</tbody>
</table>

*Scientific name used unless unknown.
Discussion

There was a marked lack of both lemur plant foods and non-lemur plant foods during the dry portion of this study. It appears as though TNP has an even more restricted wet season and receives less annual precipitation, when compared to the well-studied ring-tailed lemur habitats in southern Madagascar. The following examines the effects of reduced rainfall on phenology, and in turn, the effects of low rainfall on ring-tailed lemurs.

During years without disrupting droughts or cyclones, the annual rainy season in southern Madagascar occurs between November and March (Sussman et al., 2012). At BSMR average rainfall measures 700mm (Sussman et al., 2012), while data for Berenty range is between 300-900mm (Jolly et al., 2012). Kelley (2011) notes 695mm of rainfall during a one-year period at Cap Sainte Marie, but interestingly, this area received rain every single month. Moreover, at all of these sites infant ring-tailed lemurs are born in late September and early October. At TNP, infants were also born in late September, but there is a marked decrease, at this site, in the amount and duration of rainfall. Annual rains begin in December (usually late December) and cease in February, with most of the year’s total rainfall measuring significantly less than 400mm (Donque, 1975). Though weather patterns are highly variable, what these sites do have in common is a generally predictable abundance of food at the onset of lemur infant weaning, which occurs in January. This pattern of infant weaning with most predictable food resources appears to be deeply engrained in the life histories of ring-tailed and many other lemur species.

The effects of cyclones and droughts on lemurs depend on the severity and duration of the storm or drought. During this study, cyclone Bingiza brought a large amount of rain (125mm) in a short period of time (30hrs), but it did not appear to be physically destructive to the habitat, or to adversely affect the lemurs. However, the full effects of natural disasters may
not be evident until the years following the event. For example, in 2005, following cyclone Ernest, massive defoliation and tree knock-downs occurred at BMSR, and for at least seven months after the cyclone, tamarind trees failed to produce fruits. This cyclone also may have impacted the ring-tailed lemurs, in that infant survivorship was reduced over the following two birth years (Sauther, unpublished data). Moreover, during the 1991-1992 severe droughts in southern Madagascar, Gould et al. (1999) detail significant mortality rates in ring-tailed lemur females and infants at BSMR. Pavelka et al. (2007) describe similar long-term effects of hurricanes on howler monkey populations. These authors point out that hurricanes affect the monkeys' food supply, diet, and activity (Pavelka et al., 2007). Given that these animals continue to have elevated rates of mortality long after normal patterns of rain ensue, it appears as though food supply, rather than water per se, most affects survival of these primates following natural disasters.

Both lemur plant foods and non-foods were extremely limited during the dry season at TNP. As we know, ring-tailed lemurs exploit foods as they become available (Sauther 1994, 1998). During the dry season the number of foods available at any one time was low. Neobeguea provided an incredible 97% (94% flowers, 3% young leaves) of all recorded food items in the month of September, and there were several days during this month where lemurs did not consume any other foods. The flowers and leaves from Neobeguea were important to focal animals for the following reasons: nutritional content, they became foliated and flowered en masse, and there were few other foods available. Other plant foods that were of particular importance to ring-tailed lemurs throughout this study included G. americanus, A. comosa, F. megapoda, and P. madagascariensis and other species of liana. Gyrocarpus was an important food during November and December and focal animals consumed flowers, fruit arils, and young
and mature leaves. Gould et al. (2011) also noted *G. americanus* young fruits as a ring-tailed lemur plant food, but I did not witness any consumption of the actual fruiting body. In fact, focal animals seemed to go out of their way to discard fruits, while feeding on fruit arils. In the analyses by Gould et al., (2009), concentrations of condensed tannins found in *G. americanus* fruits were more than seven times the concentration found in flowers, fruit arils, or leaves, which may explain why TNP animals avoided them, although it is unclear why the Berenty animals would consume the fruits. *Alluaudia* flowers were an important food source during November and December, and it is worth noting that the trees were also physically important to focal animals, in that their umbrella-like shape and thick canopy provided shady refuge for the lemurs during particularly hot periods when temperatures surpassed 45°C.

As per the definition of Sauther and Cuozzo (2009), *N. mahafaliensis*, *G. americanus*, and *A. comosa* were all fallback foods to the TNP lemurs, as there were negative correlations between the intensive use of these species and the abundance of other foods. *Ficus* sp. were also important foods during this study as they provided ripe fruits during every calendar month and were the only species to do so. The relationship of fig fruit use by ring-tailed lemurs at TNP is somewhat more complicated than that of other foods. The lemurs tend to over-exploit figs when there was a mast fruiting event of one fig tree within their home range, and their use of these fruits could be classified as fallback, preferred, or staple, depending on the time period and what other foods were available. It is also possible that these food classifications are not adequate or accurate in describing the patterns of use by ring-tailed lemurs. *Ficus megapoda* fruits are not a particularly high quality food and may be difficult for the lemurs to digest (see Chapter 5), however, the ease to which they can be obtained in a heavily fruiting tree appears to be an attractive quality to the lemurs, and many other species of animal at TNP (birds, tortoises,
insects), regardless of the availability of other fruits, which would not have been as spatially clumped as the fig fruits. Fig fruits are esteemed for their importance to frugivorous species world-wide (Terborgh, 1986), and their importance to animals in this research will be addressed further below. The last foods noted to be an important seasonal resource in this study includes the young leaves from *P. madagascariensis* and those from other lianas, which were ample during both January and March. Though high in fibrous matter, these leaves were an excellent protein source and contain little secondary compounds, which likely made them attractive, low-cost food sources. From the aforementioned species, both lianas and *G. americanus* have been noted to contribute to the diets of ring-tailed lemurs in other habitats. *Gyrocarpus* is an important seasonal food for ring-tailed lemurs at Beza (Sauther, 1998; Yamashita, 2002) and is also important for the ring-tailed lemurs in spiny forest fragments outside of Berenty (Gould et al., 2011). Figs are an important component of the Andringitra mountain range ring-tailed lemurs dry and wet season diets, and they spend 6.6% and 14.0% of their feeding time consuming fruits, respectively, over these seasons (Simmen et al., 2006). When comparing top quartile or seasonally important foods from the study period, *G. americanus*, liana leaves, and fig species appear to be the only overlapping food species between TNP and all other ring-tailed lemur study sites.

*Ficus* spp. have been noted as part of the ring-tailed lemur diet at Beza, Berenty, Cap. St. Marie, and in the Andringitra mountain range (Simmens et al., 2006). Most of the fruits consumed in these locations, such as those from *F. marmorata*, are from small shrub-like bushes, that don't tend to produce vast quantities of fruits at any one time. Koyoma et al. (2006) note that *F. megapoda* occur at Berenty (they include 6 individual trees within their habitat census), but there is little information on if and in what manner the ring-tailed lemurs use resources from
these trees at Berenty. In this research, lemurs used figs during every month of the study period and consumed large quantities from *F. megapoda*, when they were available. During February 2011, *F. megapoda* constituted 57% of the lemur’s diet. Figs are noted to be depauperate in Madagascar, which is thought to be one of the factors contributing to Madagascar's low frugivore diversity, particularly in birds (Langrand, 1990; Mittermeir et al., 1994; Goodman and Ganzhorn, 1997).

For the purposes of this research, it is important to know if these figs are endemic to Madagascar, and if not, the length of time that ring-tailed lemurs and figs have been co-existing. Machado et al. (2001) note that the separation of India and Madagascar, which occurred about 80 million years ago, coincided with the timing of the radiation of groups of wasps that pollinate flowers from the subgenera *Urostigma* (which includes *F. megapoda*), *Sycomorus*, *Ficus* and *Sycidium*. Machado et al. (2001) further state that *Ficus* and its pollinators could have dispersed by drifting with the fractured continents or by rafting, and that either scenario is consistent with the paleontological data (Sahni, 1984; Briggs, 1987). However, both Machado et al. (2001) and Goodman and Ganzhorn (1997) suggest that the lack of endemism of figs on Madagascar along with the high levels of endemism of other Malagasy species suggests a relatively recent introduction. We know that *F. megapoda* is not one of the historically introduced fig species, because there have been leaf imprints found in Benenitra, from alongside the Onilahy river which date to at least the early Quaternary (Perrier de la Bâthie, 1928). Lemurs’ historical use of figs and whether *F. megapoda* is endemic or an introduced species on Madagascar, would help in understanding to what degree lemurs have relied on these fruits in the past.

The findings that ring-tailed lemurs exploit available fig fruits is not surprising. What is surprising is that foods from tamarind trees were infrequently incorporated into the diets of these
animals. There are a few explanations for why the ring-tailed lemurs at TNP use tamarind foods infrequently. First, in gallery forests, the availability of foods from tamarind trees are asynchronous (Sauther, 1994). As such, throughout the year, there are almost always tamarind trees that have young leaves, flowers, and/or fruits available (Sauther, 1994). So, these trees are a reliable food source for lemurs, even in the dry season. This did not seem to be the case at TNP. The phenology of tamarind trees at TNP was highly synchronized (Figure 4.3), and although the lemurs did consume some tamarind foods when they were available, their total amount of feeding time dedicated to tamarind was < 1%. Second, at TNP figs appeared to be the only asynchronous food that was available during every month of the study (Figure 4.3). The lemurs did exploit ripe fig fruits frequently, and spent 16% of the total observed feeding time consuming figs. Third, fig fruits are substantially easier to process mechanically, compared to tamarind fruits. Pods of ripe tamarind fruits are very hard and inedible, and biting through this exocarp has been related to extreme tooth wear in the Beza Mahafaly ring-tailed lemurs (Sauther Cuozzo, 2004, 2006; Yamashita, 2008; Sauther and Cuozzo 2009). Figs, on the other hand, are soft and fleshy and do not require manipulation prior to being consumed. During the months of Sept-Nov 2010, both tamarind fruits and figs were available in the lemur’s home ranges. Animals spent 2%, 6%, and 19% of their feeding time consuming figs during these months, but less than 1% of their time consuming tamarind fruits, which suggests that the TNP lemurs prefer fig fruits to tamarind pods. Though the known dates of introduction of *F. megapoda* and *T. indica* are ultimately unknown, given the current evidence, it appears as though *F. megapoda* has a longer evolutionary history in Madagascar, when compared to that of *T. indica*. If TNP is the type of habitat that ring-tailed lemurs are primarily adapted to, it is possible that when ring-tailed lemurs dispersed throughout southern Madagascar via river ways (Goodman et al., 2006), they also
acted as seed dispersers for both *T. indica* and *F. megapoda*. Both fig and tamarind species need access to a certain amount of ground water to survive. However, given that *Ficus* species are less tolerant of certain soil types (Swagel et al., 1997), it would be much less likely that figs would be as readily distributed so widely, whereas tamarind is much more tolerant in reference to soil (Gillman and Watson, 1994). This would help explain the near lack of large fig trees in southern Madagascar's gallery forest, along with the dominance of tamarind trees. That being said, further data are needed before we can decide when and how these plant species dispersed in southern Madagascar. Use of different plant species than previously known for *L. catta*, exploitation of figs, and the unusual near exclusion of tamarind foods in the TNP ring-tailed lemurs further exemplifies the extreme flexibility of this species.

**Conclusions**

Southwestern Madagascar is highly seasonal, and although weather patterns are erratic and unpredictable, natural disasters such as cyclones and drought are frequent and common. Weather patterns directly impact primary productivity, even in dry adapted forests, and limited or unpredictable primary productivity is thought to be important in the unusual adaptations found in Madagascar's primates. This research was the first to document ecology of ring-tailed lemurs in an intact spiny forest. *Neobeguea, Alluaudia,* and *Gyrocarpus,* and figs all served as fallback foods. These ring-tailed lemurs, surprisingly, incorporate very little tamarind into their diets, which may be because the tamarind trees at TNP are seasonal in leaf coverage, flowering and fruiting, or because these lemurs have access to figs, which are comparably easier to consume.
Chapter 5: Feeding ecology and nutrition of *Lemur catta* at the Tsimanampetsotsa National Park

Overview

In Chapter 4 we saw that there are far less of plant foods present during southern Madagascar's long dry season. The question that still remains, however, is whether this reduction in overall plant food availability translates into a reduction of nutrients or calories consumed by lemurs (Yamashita, 2008). Previous research has noted differences between lemur female and male feeding behavior, such as plant part chosen and/or amount of time spent feeding, and these differences are thought to reflect the differential reproductive metabolic needs of female and male lemurs (Sauther 1994, 1998). However, nutritional data have been either lacking or provide no or weak support for the hypotheses (see Sauther 1994, 1998; Curtis, 2004; Yamashita 2008). Several authors have suggested that future research should examine gross amount consumed when comparing dietary components of lemur nutrition (Curtis, 2004; Yamashita, 2008). This chapter will explore the interspecific response of ring-tailed lemurs to variability in the availability of plant foods, along with caloric and nutritional profiles, activity budgets, and stress, in order to understand the degree to which ring-tailed lemurs may partition ecological niches between the sexes.

Background

Sex based feeding differences

In gallery forest ring-tailed lemurs, both seasonal and sex differences in feeding have been documented. At Beza, pregnant females consume more flowers and fruits, while males consume more leaves (Sauther, 1994, 1998). Once lactating, females focus on consuming young leaves which contain elements that are important for lactation, such as calories, protein, and
calcium, presumably, without large quantities of secondary compounds which can interfere with digestion (Sauther, 1994, 1998). At Berenty, pregnant females fed heavily on mature tamarind leaves and unripe tamarind fruit and then once lactating, these same females became increasingly frugivorous (Rasamimanana and Rafidinarivo, 1993). Unripe tamarind fruits and mature leaves contain considerable secondary compounds, which we would expect females to avoid, but Rasamimanana and Rafidinarivo (1993) suggest that in this case, females are exploiting the high protein content found in these foods.

These sex based differences in food selection and diet are hypothesized to aid females in securing sufficient resources to feed their rapidly growing young (Lee, 1996; Dufour and Sauther, 2002; Gould et al., 2003). Protein (or rather, the amino acids found in protein) and calcium have been noted as particularly important dietary components to reproductive mammals, as they are required in physiological processes ranging from DNA replication and cell division to bone deposition and hair growth (Ullrey et al., 2003; National Research Council, 2003). That being said, the current data on intraspecific lemur nutrition are all but lacking, and for those data on interseasonal differences in the diets of lemurs that have been explored, the data does not always support hypotheses proposed based on lemur feeding data. This topic will be further explored next.

**Diet and nutrition**

We know that Madagascar's forests are seasonal, particularly in the west and southwestern dry forests. However, an overall reduction in flora does not necessarily result in a proportional reduction in lemur plant foods or nutrients, since lemur plant foods are only a subset of the total plant biomass in the forest, and because lemurs exploit seasonal foods as they
become annually available (Sauther, 1994, 1998). In her analyses of gallery forest lemur (*L. catta* and *Propithecus verreauxi*) nutrition, Yamashita (2008) found that although there was a marked reduction in food availability in the dry season, nutrient intake (protein, sugars) was balanced between the wet and dry seasons. Furthermore, Yamashita (2008) notes that although the quantities of nutrients and contributing plant parts differ throughout the year, neither sifaka nor ring-tailed lemurs appear to be nutrient starved. Similarly, in her analyses of gallery forest *Eulemur mongoz* dietary nutrients (amino acids, lipids, carbohydrates) Curtis (2004) found vast differences in seasonal food availability, but little interseasonal difference in nutrient intake, and suggested that the lemurs' nutritional requirements were being met throughout the year. Although food resources are reduced, these lemurs appear to exploit resources such that their nutritional requirements are met during the wet and dry seasons (Curtis, 2004; Yamashita, 2008). Through these data both authors concluded that there was not a maximal exploitation of foods during periods of abundance, or that seasonality induces nutritional stress (Curtis, 2004; Yamashita, 2008).

Although nutrients were balanced between the seasons in the aforementioned studies, Curtis (2004) and Yamashita (2008) point out that calories are likely not balanced due to the reduction in overall food intake, along with the visible reduction in lemur body weight during the dry season. It is also possible that seasonal nutrient differences were not found in these studies because of the presence of tamarind trees (see Yamashita, 2008). At both of these study sites *T. indica* trees are the most common or at least a very common species throughout the habitats. As such, the aforementioned findings may be more reflective of *E. mongoz*, *L. catta*, and *P. verreauxi* when consuming a tamarind dense diet, which we know influences feeding patterns in lemurs.
Gould et al. (2011) examined nutrients and calories for reproductive female and male ring-tailed lemurs in the gallery and spiny forest fragments surrounding Berenty. This research spanned approximately two one-month periods during which the female lemurs were in early to mid lactation (2006) or early gestation (2007) (Gould et al., 2011). These authors found no sex differences in feeding behavior, nutrients, or calories consumed. In fact, the only significant difference found by Gould et al. (2011), was that spiny forest females tended to rest more than gallery forest females. The presence of tamarind fruits in the lemurs' diet may account for some of the findings, however, Gould et al. (2011) suggest that the lemurs' overall food availability may have played a role, given that the previous year had lower than average rainfall. LaFleur and Gould (2009) note an absence of feeding or nutritional differences in the diets of BMSR ring-tailed lemurs during a complete tamarind fruiting failure and suggest that sex based differences may cease when foods reach a critical low point. Gould et al. (2011) do not provide phenological data, and it is therefore difficult to decipher if the ring-tailed lemur plant foods were at critically low levels.

In the biomedical evaluations of ring-tailed lemurs at Cap Sainte Marie, Kelley (2011) found no evidence of dehydration or malnourishment in focal animals. These lemurs live in highly anthropogenically altered habitats, and depend on *O. monacantha* cactus hedges for both shelter, food, and water. Interestingly, Kelley (2011) notes that although the sleeping sites of focal animals were within agricultural fields or gardens, crop raiding was extremely rare. Furthermore, in contrast to ring-tailed lemurs at BSMR, Kelley (2011) did not witness any consumption of cooked human foods, cattle forage, or intraspecific coprophagy. We might expect that lemurs living in highly disturbed areas with would show signs of adverse health, poor diet, and/or behavioral adaptations to consuming crop or other non-typical foods, as has been
found elsewhere (MeNon and Poirier, 1996; Umapathy and Kumar, 2000; Irwin, 2006), and even within ring-tailed lemurs (Whitelaw, 2010). Furthermore, it is surprising that studies focused on nutrition in ring-tailed lemurs, a species for which we have well documented sex and seasonal dietary differences (Rasamimanana and Rafidinarivo, 1993; Sauther, 1994, 1998; Simmen et al., 2006; Soma, 2006), have failed to produce significant differences in the nutritional profiles. It is possible, of course, that feeding differences documented in these animals do not equate to nutritional differences, even though behavioral data would suggest so. Conversely, it is also possible that the presence and use of certain foods, such as potentially introduced species such as *T. indica* and invasive or sometimes cultivated species like *O. monacantha*, mask what would be the "normal" (i.e. what we would expect in the types of habitats that they are adapted to) dietary profile for ring-tailed lemurs.

**Activity patterns and ranging**

Seasonal patterns in activity budgets have been found throughout the Malagasy primates (Wright, 1999; Ganzhorn et al., 2000), including within ring-tailed lemurs (Jolly, 1966; Sussman, 1977; Sauther, 1992; Loudon, 2008; Whitelaw, 2010). These differences have been attributed to food availability, reproduction, temperature, and sex (Jolly, 1966; Sussman, 1977; Sauther, 1992; Gould, 2006; Rasamimanana et al., 2006). Gallery forest ring-tailed lemurs tend to rest more during the dry season, and ring-tailed lemurs in spiny forest fragments tend to rest more than those in gallery forests (Sauther, 1994; Loudon, 2008; Ellwanger and Gould, 2011). Furthermore, the amount of time spent resting seems to negatively correlate with the amount of time spent feeding (Gould, 2006). That being said, reported sex based differences in activity budget are inconsistent. For example, some authors report no sex differences in the amount of
time spent resting, feeding or locomoting (Simmen et al., 2010; Gould et al., 2011; Kelley, 2011) while others state that females move and travel significantly more than males (Rasamimanana et al., 2006). The trend of resting more during the dry season has been interpreted as an energy effective strategy by ring-railed lemurs, wherein periods of inactivity coincide with periods of high ambient temperature and low food availability (Sauther et al., 2006; Gould et al., 2011). Under this reasoning, it is unclear why female lemurs would engage in more active behaviors, when compared to males. Activity budgets will be examined here, in order to understand the relative amounts of energy expended by focal animals during different reproductive periods and seasons.

**Stress**

Studies of fecal glucocorticoid levels, a common measurement used to monitor stress in wild animals, have shown that lemur stress varies by species and can be triggered by a variety of stressors (Cavilgelli 1999; Pride, 2005; Fitchel et al., 2007; Ostner et al., 2008; Starling et al., 2010). For example *P. verreauxi* alpha males at Kirindy show significantly elevated fGC levels in the breeding season, when compared to subordinate males, but during the birthing season, no rank-related differences are found (Fitchel et al., 2007). Conversely, at the same site, no rank related differences were found in male *Eulemur fulvus rufus*, but there is an increase of fCG during the birthing season (Ostner et al., 2008). In the sifaka, alpha males likely experience significant stress guarding cycling females during the very short reproductive time period (Fitchel et al., 2007). In the red-fronted brown lemur, elevated stress during the birthing period may be in response to threat of infanticide (Ostner et al., 2008). In further comparison, female ring-tailed lemurs show an increase in fCG levels in response to low rainfall and low tamarind
fruit availability (Cavigelli, 1999), short term food scarcity and large group size (Pride, 2005), social rank, social instability and aggressive interactions (Starling et al., 2010), and with mating, pregnancy, and lactation (Cavigelli, 1999; Starling et al., 2010). Given that many of these factors co-occur (e.g. pregnancy and low food availability), it can be difficult to understand the causal mechanisms.

Coat condition can also be used as a long-term measure of stress, given that prolonged fGC correlates with poor coat condition (Pride, 2005; Steinmetz et al., 2005). A dull, shaggy, and dry looking coat in a free-ranging primate is likely an indicator of nutritional or social stress (Steinmetz et al., 2005). Long-term stress, such as that which is reflected in extended fGC level elevation or poor coat condition, can be indicators of early adult mortality and ultimately fitness (Pride, 2005; Romero and Wikelski, 2001). The ring-tailed lemur coat scoring system as outlined by Berg et al. (2009) was used to assess long-term stress in focal animals of this study, with the aim of better understanding which of the following stress factors most affected individuals: sex, reproductive state, dominance rank, and food availability.

Objectives

Research presented here includes the feeding behavior, nutritional and non-nutritional components of diet, activity patterns, and estimates of stress from two groups of ring-tailed lemurs residing at the Tsimanampetsotsa National Park. Data will be used to address the following questions:

1. Are ring-tailed lemur nutrients or calories seasonally constrained?
2. Do ring-tailed lemurs use behavioral mechanisms to save energy?
3. Is the dry season differentially stressful for female ring-tailed lemurs?
Results

Activity Patterns

The percentages of average daytime activities were calculated from focal animal data during the dry and wet seasons, and for animal groups and sexes (Table 5.1). Percentages for sex, season and group were calculated separately after removing any outliers, and thus the total percentages may differ slightly between categories. Outliers included data points which were unreasonable (such as daily caloric intake of 1.44Kcal or 4012Kcal) and likely resulting from measurement error. Significant differences were found for both seasons and sexes. However, when comparing the ILove and Vintany groups' activities, no significant differences were found (Table 5.2).

Table 5.1. Activity budgets (average percentage of daytime observation) for lemurs sexes, all animals across the dry and wet seasons, and lemur groups.

<table>
<thead>
<tr>
<th>Activity</th>
<th>Female</th>
<th>Male</th>
<th>Dry</th>
<th>Wet</th>
<th>ILove</th>
<th>Vintany</th>
</tr>
</thead>
<tbody>
<tr>
<td>Feed/Forage</td>
<td>32.3</td>
<td>20.8</td>
<td>22.2</td>
<td>30.9</td>
<td>30</td>
<td>28.9</td>
</tr>
<tr>
<td>Locomote</td>
<td>30.9</td>
<td>26.0</td>
<td>33.4</td>
<td>23.4</td>
<td>27.3</td>
<td>26.9</td>
</tr>
<tr>
<td>Sit/Stand/Rest</td>
<td>29.7</td>
<td>39.2</td>
<td>31.9</td>
<td>36.9</td>
<td>34.1</td>
<td>33.8</td>
</tr>
<tr>
<td>Vigilance</td>
<td>1</td>
<td>3.8</td>
<td>3.4</td>
<td>1.5</td>
<td>2.3</td>
<td>2.5</td>
</tr>
<tr>
<td>Scent</td>
<td>1.0</td>
<td>3.0</td>
<td>2.5</td>
<td>1.5</td>
<td>1.7</td>
<td>2.2</td>
</tr>
<tr>
<td>Stink Fight</td>
<td>N/A</td>
<td>3.2</td>
<td>0.5</td>
<td>3.5</td>
<td>3.0</td>
<td>3.3</td>
</tr>
<tr>
<td>Groom</td>
<td>1.6</td>
<td>2.5</td>
<td>4.1</td>
<td>0.7</td>
<td>2.3</td>
<td>2.5</td>
</tr>
<tr>
<td>Displace(d)</td>
<td>2.3</td>
<td>1.8</td>
<td>2.5</td>
<td>1.7</td>
<td>1.8</td>
<td>3</td>
</tr>
<tr>
<td>Misc. (Defecate, drink)</td>
<td>0.9</td>
<td>1.5</td>
<td>1.3</td>
<td>1.2</td>
<td>0.8</td>
<td>0.8</td>
</tr>
</tbody>
</table>
Table 5.2. Student's T-test for differences in the mean amount of time spent in each activity category by female and male lemurs, all lemurs between the dry and wet season, and the ILove and Vintany lemur groups.

<table>
<thead>
<tr>
<th>Sex</th>
<th>Feed/Forage</th>
<th>Locomote</th>
<th>Sit/Stand/Rest</th>
<th>Vigilance</th>
<th>Scent</th>
<th>Stink</th>
<th>Groom</th>
<th>Displace(d)</th>
<th>Misc. (defecate, drink)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>t</td>
<td>df</td>
<td>p</td>
<td>t</td>
<td>df</td>
<td>p</td>
<td>t</td>
<td>df</td>
<td>p</td>
</tr>
<tr>
<td></td>
<td>-2.11</td>
<td>87</td>
<td>0.0160*</td>
<td>-2.227</td>
<td>106</td>
<td>0.0140*</td>
<td>1.394</td>
<td>88</td>
<td>0.1670</td>
</tr>
<tr>
<td></td>
<td>2.232</td>
<td>62</td>
<td>0.0225*</td>
<td>3.544</td>
<td>62</td>
<td>0.0005*</td>
<td>1.082</td>
<td>61</td>
<td>0.2840</td>
</tr>
<tr>
<td></td>
<td>-2.058</td>
<td>76</td>
<td>0.0215*</td>
<td>-2.075</td>
<td>62</td>
<td>0.0385*</td>
<td>0.272</td>
<td>88</td>
<td>0.7860</td>
</tr>
<tr>
<td></td>
<td>-1.387</td>
<td>22</td>
<td>0.1790</td>
<td>2.054</td>
<td>22</td>
<td>0.0260*</td>
<td>-0.168</td>
<td>23</td>
<td>0.8680</td>
</tr>
<tr>
<td></td>
<td>-3.327</td>
<td>56</td>
<td>0.0001*</td>
<td>1.407</td>
<td>22</td>
<td>0.08250</td>
<td>-0.764</td>
<td>56</td>
<td>0.2240</td>
</tr>
<tr>
<td></td>
<td>N/A</td>
<td></td>
<td>N/A</td>
<td>-0.142</td>
<td>7</td>
<td>0.4455</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>-1.223</td>
<td>13</td>
<td>0.2430</td>
<td>2.610</td>
<td>21</td>
<td>0.0080*</td>
<td>-1.805</td>
<td>13</td>
<td>0.0940</td>
</tr>
<tr>
<td></td>
<td>0.301</td>
<td>12</td>
<td>0.7000</td>
<td>0.700</td>
<td>12</td>
<td>0.9950</td>
<td>-0.500</td>
<td>12</td>
<td>0.4540</td>
</tr>
<tr>
<td></td>
<td>-0.994</td>
<td>36</td>
<td>0.3270</td>
<td>-1.174</td>
<td>36</td>
<td>0.2480</td>
<td>-0.593</td>
<td>36</td>
<td>0.5570</td>
</tr>
</tbody>
</table>

N/A = females do not stink fight, only one occurrence of male stink fighting in the dry season.

Data were further categorized according to lemur sex and season, in order to understand where significant interactions were occurring, if any. Table 5.3 and Figure 5.1a-5.1b show the percentages of average daytime activities for female and male lemurs in the dry and wet seasons. Significant differences in these data can be found in Table 5.4-5.5. The percentages of time spent feeding by lemur sexes in each season, were multiplied the average day length (12hr) in order to determine differences in the number of hours spent feeding per day (Figure 5.2).
<table>
<thead>
<tr>
<th>Activity</th>
<th>Female Dry</th>
<th>Female Wet</th>
<th>Male Dry</th>
<th>Male Wet</th>
</tr>
</thead>
<tbody>
<tr>
<td>Feed/Forage</td>
<td>27.6</td>
<td>35</td>
<td>16</td>
<td>25.6</td>
</tr>
<tr>
<td>Locomote</td>
<td>37.5</td>
<td>23.2</td>
<td>27.6</td>
<td>23.6</td>
</tr>
<tr>
<td>Sit/Stand/Rest</td>
<td>26.6</td>
<td>35.8</td>
<td>38.2</td>
<td>38.4</td>
</tr>
<tr>
<td>Vigilance</td>
<td>1.4</td>
<td>0.6</td>
<td>5.3</td>
<td>2.3</td>
</tr>
<tr>
<td>Scent</td>
<td>1.3</td>
<td>0.6</td>
<td>3.3</td>
<td>2.3</td>
</tr>
<tr>
<td>Stink Fight</td>
<td></td>
<td>N/A</td>
<td>0.5</td>
<td>3.5</td>
</tr>
<tr>
<td>Groom</td>
<td>2.7</td>
<td>0.4</td>
<td>5.5</td>
<td>1.6</td>
</tr>
<tr>
<td>Displace(d)</td>
<td>1.9</td>
<td>2.7</td>
<td>3</td>
<td>0.6</td>
</tr>
<tr>
<td>Other (Defecate, drink)</td>
<td>0.3</td>
<td>1.5</td>
<td>2.2</td>
<td>0.8</td>
</tr>
</tbody>
</table>

NA= females do not stink fight
**Figure 5.1.a.** Activity budgets (average percentage of observed time) of female ring-tailed lemurs in the dry and wet seasons.

**Females Dry Season**

**Females Wet Season**
Figure 5.1.b. Activity budgets (average percentage of observed time) of male ring-tailed lemurs in the dry and wet seasons.

**Males Dry Season**

- Sit/Stand/Rest: 37.6%
- Locomote: 27.2%
- Feed/Forage: 15.7%
- Other: 19.5%
- Disp(d): 3.0%
- Misc: 2.2%
- Groom: 5.4%
- Scent: 3.2%
- Stink Fight: 0.5%
- Vigilance: 5.2%
- Other: 11.2%

**Males Wet Season**

- Sit/Stand/Rest: 38.9%
- Locomote: 23.9%
- Feed/Forage: 25.9%
- Other: 11.2%
- Disp(d): 0.6%
- Misc: 0.8%
- Scent: 2.3%
- Stink Fight: 3.5%
- Vigilance: 2.3%
- Groom: 1.6%
Table 5.4. Student's T-test for differences in the mean amount of time spent in each activity category by lemur females and males in the dry and wet seasons.

<table>
<thead>
<tr>
<th>Activity</th>
<th>Female Dry</th>
<th>t</th>
<th>df</th>
<th>p</th>
<th>Male Dry</th>
<th>t</th>
<th>df</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Feed/Forage</td>
<td>1.725</td>
<td>46</td>
<td>0.0450*</td>
<td>3.350</td>
<td>59</td>
<td>0.0001*</td>
<td>1.227</td>
<td>32</td>
</tr>
<tr>
<td>Locomote</td>
<td>-2.749</td>
<td>48</td>
<td>0.0040*</td>
<td>2.192</td>
<td>14</td>
<td>0.0230*</td>
<td>0.905</td>
<td>27</td>
</tr>
<tr>
<td>Sit/Stand/Rest</td>
<td>-3.350</td>
<td>59</td>
<td>0.0001*</td>
<td>-0.785</td>
<td>7</td>
<td>0.2260</td>
<td>n/a</td>
<td></td>
</tr>
<tr>
<td>Vigilance</td>
<td>2.192</td>
<td>14</td>
<td>0.0230*</td>
<td>-0.785</td>
<td>7</td>
<td>0.2260</td>
<td>n/a</td>
<td></td>
</tr>
<tr>
<td>Scent</td>
<td>0.905</td>
<td>27</td>
<td>0.3740</td>
<td>1.595</td>
<td>6</td>
<td>0.1620</td>
<td>1.422</td>
<td>34</td>
</tr>
<tr>
<td>Stink Fight</td>
<td></td>
<td></td>
<td>N/A</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Groom</td>
<td></td>
<td></td>
<td>n/a</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Displace(d)</td>
<td>-0.785</td>
<td>7</td>
<td>0.2260</td>
<td>n/a</td>
<td></td>
<td>n/a</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Misc. (Defecate, drink)</td>
<td>n/a</td>
<td></td>
<td>n/a</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

N/A= females do not stink fight, only one occurrence of male stink fighting in the dry season.
n/a = sample size too small

Table 5.5. Student's T-test for differences in the mean amount of time spent in each activity category during the dry and wet season by female and male lemurs.

<table>
<thead>
<tr>
<th>Activity</th>
<th>Female Dry</th>
<th>t</th>
<th>df</th>
<th>p</th>
<th>Female Wet</th>
<th>t</th>
<th>df</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Feed/Forage</td>
<td>3.084</td>
<td>23</td>
<td>0.0050*</td>
<td>1.754</td>
<td>54</td>
<td>0.0425*</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Locomote</td>
<td>2.611</td>
<td>22</td>
<td>0.0160*</td>
<td>-0.361</td>
<td>67</td>
<td>0.7190</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sit/Stand/Rest</td>
<td>-3.082</td>
<td>13</td>
<td>0.0090*</td>
<td>-1.388</td>
<td>7</td>
<td>0.1040</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Vigilance</td>
<td>-2.447</td>
<td>20</td>
<td>0.0120*</td>
<td>-3.934</td>
<td>41</td>
<td>0.0001*</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Scent</td>
<td>-2.447</td>
<td>20</td>
<td>0.0120*</td>
<td>-3.934</td>
<td>41</td>
<td>0.0001*</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Stink Fight</td>
<td></td>
<td></td>
<td>N/A</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Groom</td>
<td>-0.589</td>
<td>9</td>
<td>0.2850</td>
<td>n/a</td>
<td></td>
<td>n/a</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Displace(d)</td>
<td>-0.778</td>
<td>7</td>
<td>0.2285</td>
<td>n/a</td>
<td></td>
<td>n/a</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Misc. (Defecate, drink)</td>
<td>n/a</td>
<td></td>
<td>n/a</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

N/A= females do not stink fight
n/a= sample size too small
The average and maximum distances traveled per day, number of adults in group, and total home range sizes of both lemur groups can be found in Table 5.6. Additionally, a map of the two groups' semi-overlapping home ranges can be found in Figure 5.3.

**Table 5.6.** ILove and Vintany groups average distance traveled per day (meters) and number of adults in group during the dry and wet seasons, along with maximum day distance (meters) and home range size (km$^2$) throughout the study period.

<table>
<thead>
<tr>
<th></th>
<th>Dry Season</th>
<th>Wet Season</th>
<th>Study period</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Day distance</td>
<td>Adults in group</td>
<td>Day Distance</td>
</tr>
<tr>
<td>ILove</td>
<td>2081</td>
<td>10</td>
<td>1812</td>
</tr>
<tr>
<td>Vintany</td>
<td>2329</td>
<td>14</td>
<td>1848</td>
</tr>
</tbody>
</table>
Figure 5.3. Aerial satellite map displaying the Vintany and ILove groups semi-overlapping home ranges.

Nutritional Intake

From foods consumed by the lemurs, one insect sample and 79 plant samples were analyzed for their nutritional content. Complete nutrient composition along with specific details of plant part processing (i.e. seed removal, when appropriate) can be found in Appendix 3. Due to the abundance and diversity of lianas, which were often intertwined and difficult to distinguish, samples were combined into "mixed liana." The Pentarhopalopilia liana was analyzed solely because it was the most commonly consumed liana, and easy to identify given its five-lobed leaves and distinctive smell. Not all foods were analyzed due to factors such as rarity of consumption, insufficient sample availability, and sample spoilage. However, nutritional content of foods from varying phases and time periods were analyzed for 51 species of plant, which constituted 94.5% of the lemurs' diet.
Focal feeding data yielded feeding rates 76% of the time, as it was not always possible to count bites or see the focal animal's mouth, even when I knew they were eating. Of the data with feeding rates, I have nutritional information for 97.5% of the plant foods consumed. Therefore, the data presented here are likely approximately 27% lower than the average animal daily intakes. Additionally, these data do not include the amount of food focal animals consumed at night, which may have been significant. However, assuming that the excluded data are equally distributed between animals, and that the rates of feeding at night are comparable to those during the day, the data presented here represent an accurate fraction of the actual average animal daily intake.

The average daily intake and statistical analyses of macronutrients, non-nutrients, amount, protein to fiber ratio, and energy for each season, sex, and group can be found in Tables 5.7-5.8. In sum, there are significant differences within the following combinations: sexes and calories consumed; seasons and calories, tannin and the ratio of protein:ADF; and lemur groups and the amount of NDF and ADF (Figure 5.4). For comparative purposes, I divided the average number of calories consumed per day by all animals, by the average distance traveled per day in the dry and wet seasons. The value for the dry season is 0.0776 kcal/m (171.1 kcal/2205 m) and the value for the wet season is 0.129 kcal/m (235.8 kcal/1830 m).
### Table 5.7. Average daily intake by season, sex and group of macronutrient (g/day), non-nutrient (g/day), protein to fiber ratio, and energy (kcal/day).

<table>
<thead>
<tr>
<th>Sex</th>
<th>Protein</th>
<th>Fat</th>
<th>Sugar</th>
<th>Tannin</th>
<th>Polyphenole</th>
<th>NDF</th>
<th>ADF</th>
<th>Protein :ADF</th>
<th>Calories</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Female</td>
<td>Male</td>
<td>Dry</td>
<td>Wet</td>
<td>Ilove</td>
<td>Vintany</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dry</td>
<td>23.9</td>
<td>16.0</td>
<td>17.5</td>
<td>22.4</td>
<td>20.4</td>
<td>20.0</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Wet</td>
<td>19.1</td>
<td>16.0</td>
<td>16.4</td>
<td>18.7</td>
<td>18.0</td>
<td>17.0</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ilove</td>
<td>6.7</td>
<td>5.2</td>
<td>4.0</td>
<td>8.0</td>
<td>5.7</td>
<td>6.2</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Vintany</td>
<td>0.51</td>
<td>0.61</td>
<td>0.76</td>
<td>0.37</td>
<td>0.59</td>
<td>0.05</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

### Table 5.8. Statistical results from the Independent Student's T-test between sexes, seasons, and group for the consumption of macronutrients (g/day), non-nutrients (g/day), the protein to ADF ratio, and energy (kcal/day).

<table>
<thead>
<tr>
<th></th>
<th>Sex</th>
<th>Season</th>
<th>Group</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>t</td>
<td>df</td>
<td>p</td>
</tr>
<tr>
<td>Protein</td>
<td>0.154</td>
<td>93</td>
<td>0.878</td>
</tr>
<tr>
<td></td>
<td>-0.784</td>
<td>93</td>
<td>0.435</td>
</tr>
<tr>
<td></td>
<td>0.034</td>
<td>86</td>
<td>0.973</td>
</tr>
<tr>
<td>Fat</td>
<td>0.067</td>
<td>93</td>
<td>0.0947</td>
</tr>
<tr>
<td></td>
<td>-0.116</td>
<td>93</td>
<td>0.908</td>
</tr>
<tr>
<td></td>
<td>-1.442</td>
<td>86</td>
<td>0.153</td>
</tr>
<tr>
<td>Sugar</td>
<td>0.041</td>
<td>93</td>
<td>0.0968</td>
</tr>
<tr>
<td></td>
<td>-0.576</td>
<td>93</td>
<td>0.315</td>
</tr>
<tr>
<td></td>
<td>0.682</td>
<td>86</td>
<td>0.497</td>
</tr>
<tr>
<td>Tannin</td>
<td>1.374</td>
<td>34.132</td>
<td>0.178</td>
</tr>
<tr>
<td></td>
<td>1.171</td>
<td>77.883</td>
<td>0.0455*</td>
</tr>
<tr>
<td></td>
<td>-0.469</td>
<td>86</td>
<td>0.640</td>
</tr>
<tr>
<td>Polyphenol</td>
<td>0.165</td>
<td>87.213</td>
<td>0.840</td>
</tr>
<tr>
<td></td>
<td>-0.978</td>
<td>37.634</td>
<td>0.334</td>
</tr>
<tr>
<td></td>
<td>-0.620</td>
<td>86</td>
<td>0.537</td>
</tr>
<tr>
<td>NDF</td>
<td>-0.435</td>
<td>93</td>
<td>0.665</td>
</tr>
<tr>
<td></td>
<td>0.58</td>
<td>85</td>
<td>0.562</td>
</tr>
<tr>
<td></td>
<td>-1.758</td>
<td>86</td>
<td>0.0410*</td>
</tr>
<tr>
<td>ADF</td>
<td>-0.565</td>
<td>93</td>
<td>0.574</td>
</tr>
<tr>
<td></td>
<td>0.809</td>
<td>85</td>
<td>0.421</td>
</tr>
<tr>
<td></td>
<td>-1.678</td>
<td>86</td>
<td>0.0485*</td>
</tr>
<tr>
<td>Protein:ADF</td>
<td>0.141</td>
<td>93</td>
<td>0.888</td>
</tr>
<tr>
<td></td>
<td>-3.180</td>
<td>84.445</td>
<td>0.001*</td>
</tr>
<tr>
<td></td>
<td>1.525</td>
<td>86</td>
<td>0.131</td>
</tr>
<tr>
<td>Calories</td>
<td>2.064</td>
<td>66.902</td>
<td>0.0215*</td>
</tr>
<tr>
<td></td>
<td>-2.092</td>
<td>85</td>
<td>0.0209*</td>
</tr>
<tr>
<td></td>
<td>0.799</td>
<td>86</td>
<td>0.427</td>
</tr>
</tbody>
</table>
Average values and statistical results for data between and within sexes and seasons can be found in Table 5.9-5.10. Females consume more calories (Figure 5.5), protein, and have a higher protein:ADF (Figure 5.6) ratio both when compared to males, and when comparing female intake for the wet and dry seasons.

### Table 5.9. Average nutrients, non-nutrients, and calories consumed per day for female and male ring-tailed lemurs during the dry and wet seasons.

<table>
<thead>
<tr>
<th></th>
<th>Female Dry</th>
<th>Female Wet</th>
<th>Male Dry</th>
<th>Male Wet</th>
</tr>
</thead>
<tbody>
<tr>
<td>Protein</td>
<td>20.67</td>
<td>27.07</td>
<td>14.23</td>
<td>17.66</td>
</tr>
<tr>
<td>Sugar</td>
<td>18.93</td>
<td>19.30</td>
<td>13.93</td>
<td>18.06</td>
</tr>
<tr>
<td>Fat</td>
<td>4.82</td>
<td>8.63</td>
<td>3.09</td>
<td>7.29</td>
</tr>
<tr>
<td>Tannin</td>
<td>0.72</td>
<td>0.31</td>
<td>0.80</td>
<td>0.43</td>
</tr>
<tr>
<td>Polyphenole</td>
<td>3.20</td>
<td>3.37</td>
<td>3.40</td>
<td>3.52</td>
</tr>
<tr>
<td>NDF</td>
<td>52.28</td>
<td>55.48</td>
<td>44.85</td>
<td>39.87</td>
</tr>
<tr>
<td>ADF</td>
<td>34.76</td>
<td>34.16</td>
<td>40.98</td>
<td>22.98</td>
</tr>
<tr>
<td>Protein:ADF</td>
<td>0.59</td>
<td>0.89</td>
<td>0.47</td>
<td>0.77</td>
</tr>
<tr>
<td>Calories</td>
<td>201.8</td>
<td>263.1</td>
<td>142.5</td>
<td>208.5</td>
</tr>
</tbody>
</table>
Table 5.10. Statistical results from the Independent Student's T-test between seasons, and for female and male animals for the consumption of macronutrients (g/day), non-nutrients (g/day), the protein to ADF ratio, and energy (kcal/day).

<table>
<thead>
<tr>
<th></th>
<th>Female Dry Wet</th>
<th>Male Dry Wet</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>t</td>
<td>df</td>
</tr>
<tr>
<td>Protein</td>
<td>-2.147</td>
<td>50.221</td>
</tr>
<tr>
<td>Sugar</td>
<td>-0.01</td>
<td>58</td>
</tr>
<tr>
<td>Fat</td>
<td>-0.342</td>
<td>58</td>
</tr>
<tr>
<td>Tannin</td>
<td>0.688</td>
<td>58</td>
</tr>
<tr>
<td>Polyphenole</td>
<td>-0.099</td>
<td>58</td>
</tr>
<tr>
<td>NDF</td>
<td>-0.076</td>
<td>58</td>
</tr>
<tr>
<td>ADF</td>
<td>0.076</td>
<td>58</td>
</tr>
<tr>
<td>Protein:ADF</td>
<td>-1.9532</td>
<td>55.625</td>
</tr>
<tr>
<td>Calories</td>
<td>-2.074</td>
<td>46.933</td>
</tr>
</tbody>
</table>

Table 5.11. Statistical results from the Independent Student's T-test between sexes in the dry and wet seasons, for the consumption of macronutrients (g/day), non-nutrients (g/day), the protein to ADF ratio, and energy (kcal/day).

<table>
<thead>
<tr>
<th></th>
<th>Dry Female</th>
<th>Male</th>
<th>Wet Female</th>
<th>Male</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>t</td>
<td>df</td>
<td>p</td>
<td>t</td>
</tr>
<tr>
<td>Protein</td>
<td>2.203</td>
<td>19.78</td>
<td>0.0200*</td>
<td>0.282</td>
</tr>
<tr>
<td>Sugar</td>
<td>0.709</td>
<td>28</td>
<td>0.484</td>
<td>0.087</td>
</tr>
<tr>
<td>Fat</td>
<td>0.066</td>
<td>28</td>
<td>0.948</td>
<td>-0.089</td>
</tr>
<tr>
<td>Tannin</td>
<td>-1.108</td>
<td>28</td>
<td>0.277</td>
<td>0.0124</td>
</tr>
<tr>
<td>Polyphenole</td>
<td>-0.335</td>
<td>28</td>
<td>0.740</td>
<td>-0.151</td>
</tr>
<tr>
<td>NDF</td>
<td>0.417</td>
<td>28</td>
<td>0.680</td>
<td>1.218</td>
</tr>
<tr>
<td>ADF</td>
<td>-0.438</td>
<td>28</td>
<td>0.665</td>
<td>1.192</td>
</tr>
<tr>
<td>Protein:ADF</td>
<td>2.315</td>
<td>18.662</td>
<td>0.0320*</td>
<td>-0.502</td>
</tr>
<tr>
<td>Calories</td>
<td>-2.187</td>
<td>20.046</td>
<td>0.0200*</td>
<td>-0.320</td>
</tr>
</tbody>
</table>
Group membership and Dominance Rank

Group membership and dominance rank were monitored for all adult focal lemurs. During the study period, targeted female-female aggression was noted in the Vintany group, specifically during late October and November. At this time the group contained 20 animals of the following age/sex classes: 7 adult females, 6 adult males, 7 sub-adults, and 7 infants. Three
of the Vintany adult females ("Lucy," "Mutant Mom," "Mom2") exhibited targeted aggression towards three of the other females (the "soccer moms"), who eventually left the group to occupy semi-overlapping territory. The seventh female who neither directed nor received targeted aggression ("300"), was the lowest ranked female and spent more time with males than with other females. Additionally, one male ("Snooze") from the ILove group transferred to the Vintany group between December and January, and one of the males ("Scabbers") in the Vintany group was presumably in the process of transferring to another group because by the end of the study period he was not reliably present with the group.

Other than changes in dominance rank that related to group fission or transfer, the only dominance rank changes noted were fluctuations between the top two ILove females ("Pinky" and "Chubbers"). Neither female appeared to maintain dominance for more than a few weeks, after which the dominance would reverse.

**Coat and tail condition**

Average monthly coat conditions for females with and without infants and males can be found in Figure 5.7 (recall that coat condition score values represent the following: 0= "good", 1= "rough", 2= "holes", 3= "ragged", 4= "sheared", and 5= "bald" and that lower coat scores indicate a better coat condition). Tail scores reflected the same patterns as coat scores, and for simplicity are not presented here. No significant correlations were found between coat condition and season, group, or dominance rank. However, on average, females had significantly worse coat conditions than males (t=2.9593, df=12, p=0.0058). Female coats deteriorated faster during the dry season and took longer to improve after the onset of the wet season. Interestingly, one female's ("5Head") baby died in September within a few days of its birth. 5Head's coat condition
was significantly different than the average coat condition of all females with babies (t= 1.9659, df=12, p=0.038), but not different than the coat condition of the males (t=0.231, df=12, p=0.231) (Figure 5.8). Additionally, two other females' infants died (Dianne's infant in November and SLG's infant in December) later in the study period. There were no significant differences found between the coat condition of these females after they lost their babies, when compared to the coats of the females whose infants survived. Dianne and SLG, however, appeared to have additional stressors, which may have impacted their coat conditions including a large open wound that took weeks to close (SLG), and being aggressively kicked out her natal group (Dianne). The coat and overall body condition of all focal and sub-adult non-focal animals decreased throughout the dry season. The infants were the only sub-set of animals whose usual body condition did not decrease during the dry season.

Figure 5.7. Average coat condition for females with and without infants, and males

*Females with infants  ■ Females after loss of infant  ◇ Males

<table>
<thead>
<tr>
<th></th>
<th>Oct</th>
<th>Nov</th>
<th>Dec</th>
<th>Jan</th>
<th>Feb</th>
<th>Mar</th>
<th>Apr</th>
</tr>
</thead>
<tbody>
<tr>
<td>Females with infants</td>
<td>1</td>
<td>1.2</td>
<td>1.7</td>
<td>2.6</td>
<td>2</td>
<td>1.7</td>
<td>1.1</td>
</tr>
<tr>
<td>Females after loss of infant</td>
<td>0.5</td>
<td>0.7</td>
<td>0.7</td>
<td>0.4</td>
<td>0.1</td>
<td>0.7</td>
<td>0.1</td>
</tr>
<tr>
<td>Males</td>
<td>0.4</td>
<td>0.1</td>
<td>0.1</td>
<td>0.1</td>
<td>0.1</td>
<td>1</td>
<td>1</td>
</tr>
</tbody>
</table>
The following series of photographs (Figure 5.9-5.10) show the disparity between dry and wet season coat condition in one focal female and male. Additionally, changes in body weight are evident.
Figure 5.9. Female ring-tailed lemur ("The Patient") and her offspring from the ILove group on a) November 10, 2010, b) February 9, 2011, c) March 9, 2011, and d) April 2, 2011.
Figure 5.10. Male ring-tailed lemur ("Tumor") from the Vintany group on a/b) November 11, 2010, c) March 29, 2011, and d) April 6, 2011.
Qualitative results

Some observations from this research are important in interpreting lemur behavior, but were noted in an *ad libitum* fashion and/or not quantitatively measured. For instance, throughout this research focal lemurs drank from water sources from the subterranean system of caves beneath the Mahafaly plateau or from small watering holes throughout their territories. These lemurs have daily access to water. Additionally, short durations of geophagy were noted by at least some focal animals on a near daily basis.

A qualitative difference in feeding behavior occurred between male and female lemurs with regard to feeding on baobab (*Adansonia rubrostipa*) flowers (*Figure 5.11*), which were available in February and March. Flowers from this species were large (~15cm in length) and females were selective as to the flower parts eaten. Females fed on anther tubes, sepals, stigma and styles, but were once not seen ingesting petals, and were only occasionally seen consuming anther filaments. Males however, were not selective in their feeding on baobab flowers parts, and would often wait for females to discard petals and anther filaments, before them picking up and consuming the discarded parts. Nutritional analyses of *A. rubrostipa* are outlined in *Table 5.12*. We see from these nutritional data that baobab petals had similar nutrient contents of other flower parts in all areas except tannins, and that the tannin levels were more than twice as high as any other plant part. Moreover, the anther filaments and petals were the only portions of the flowers that qualitatively tested positive for alkaloids. However, the anther tubes had the highest polyphenole concentrations.
Figure 5.11. Baobab (*A. rubrostipa*) flower entire (above) and dissected (below) with flower parts labeled: a) sepals, b) petals, c) stigma and style, d) anther filaments, and e) anther tube.

Table 5.12. Percentages of nutrients and non-nutrients in parts from the flowers of *A. rubrostipa*.

<table>
<thead>
<tr>
<th>Plant Part</th>
<th>Protein</th>
<th>Fat</th>
<th>Sugar</th>
<th>Tannin</th>
<th>Polyphenole</th>
<th>NDF</th>
<th>ADF</th>
</tr>
</thead>
<tbody>
<tr>
<td>Anther filaments</td>
<td>1.3</td>
<td>27.2</td>
<td>14.5</td>
<td>8.9</td>
<td>29.9</td>
<td>2.4</td>
<td>3.6</td>
</tr>
<tr>
<td>Anther tubes</td>
<td>1.0</td>
<td>32.0</td>
<td>17.9</td>
<td>8.3</td>
<td>35.8</td>
<td>2.7</td>
<td>3.6</td>
</tr>
<tr>
<td>Petals</td>
<td>1.5</td>
<td>28.5</td>
<td>14.9</td>
<td>10.8</td>
<td>28.2</td>
<td>7.4</td>
<td>4.2</td>
</tr>
<tr>
<td>Sepals</td>
<td>1.2</td>
<td>32.2</td>
<td>15.6</td>
<td>7.8</td>
<td>28.5</td>
<td>3.6</td>
<td>2.6</td>
</tr>
<tr>
<td>Stigma &amp; style</td>
<td>1.5</td>
<td>42.0</td>
<td>25.7</td>
<td>8.7</td>
<td>17.4</td>
<td>2.6</td>
<td>2.2</td>
</tr>
</tbody>
</table>
Differences were also noted regarding dominance rank and feeding on *Ficus megapoda*. High ranking females would often exhibit targeted aggression, such as repeated displacement, chasing, cuffing, etc., towards low ranking females, and chase them out of feeding trees, regardless of the fact that the trees likely had thousands of ripe fruits available. This did not seem to impede feeding however, as low rank females and males would often sit below fig trees and forage from fruits that had fallen or been discarded. Fruits on the ground continued to ripen after they were off the tree, and no significant differences were found in nutritional content of ripe tree fruits and fruits from the ground.

The insect consumption was in response to a flush of caterpillars that were feeding on the leaves of the *Delonix floribunda* trees (Figure 5.12). Interestingly, when the caterpillars were present, the lemurs would run leaflettes from *D. floribunda* through their mouths while chewing, yet without consuming the leaves, in order to catch the caterpillars.

**Figure 5.12.** Caterpillars that were consumed by lemurs (left) and the *D. floribunda* trees, which the caterpillars fed on (right).
Discussion

The type and distribution of primary plant foods across the dry and wet seasons affected lemur behavior, including activity budget and ranging. Generally, during the wet season foods are much more abundant, closer to one another, and larger in size. Foods are much less abundant in the dry season, the most frequently consumed foods were small flowers, and required the lemurs to travel farther to garner appreciable quantities. These circumstances are further demonstrated through the average daily ratio of calories consumed per meter traveled, which is lower for the dry season (0.0776 kcal/m) and higher for the wet season (0.129 kcal/m), essentially indicating that in the dry season animals have to work harder for fewer calories.

When comparing the two seasons, locomotion, vigilance, and grooming are higher during the dry season, while feed/forage, sit/stand/rest, and scent marking increase in the wet season (Figure 4.1). During the dry season specifically, females spent more time feeding and locomoting, while males spent more time resting and scent marking. As mentioned, foods are much more limited during the dry season, and tend to be spread out over farther distances. For example, during three of the four months of the dry season studied here, the primary food source for these animals were small, widely distributed, synchronously blooming flowers (N. mahafaliensis, G. americana, and A. comosa) that each weighed <0.1g (Figure 5.13, below). Since ring-tailed lemur groups generally travel and feed as a unit, both females and males traveled long distances to these secure small spread out resources. The highest reported literature day range for ring-tailed lemurs is 1377m/day at Berenty (Jolly et al., 1993), while the average dry season day range at TNP was 2205m/day. Furthermore, while in a feeding patch, females spent more time feeding and continued to locomote between and around microhabitat, according to the distribution of flowers. Males would also feed while in patches, but dedicated more of their time within patches to
resting and engaging in scent marking. Isbell (1998) pointed out that foods that are widely dispersed have low densities and require animals to cover large distances to secure the sufficient quantities. Furthermore, Rasamimanana et al. (2006) also found the female ring-tailed lemurs moved and travelled more than males. Without more detailed data on energy expenditure, it is difficult to decipher the net cost/benefit of these behavioral strategies. However, these data likely reflect the priorities of female and male primates during this period, wherein females concentrate on resource acquisition, and males on future acquisition of females, which may be facilitated through maintaining territory boundaries and thereby securing food resources.

**Figure 5.13.** Flowers from *N. mahafaliensis* (left), and *A. comosa* (right) demonstrating the small size of the flowers.

Vigilance was much more frequent in the dry season for both sexes. During this time there is very little forest foliage, which can render animals easier visual targets for raptors (Eason 1989; Peetz et al., 1992; Isbell, 1994). Furthermore, infant ring-tailed lemurs are more vulnerable during early life, and may be particularly vulnerable to predation during about their second to
third week of life, when they begin exploring off their mothers, and during their 4th month of life, when they begin to feed/forage independent of their mothers (Sauther, 1989). Both lack of foliage and infant vulnerability likely contributed to the increased dry season vigilance. Males spend an incredible amount of time engaged in scent marking behaviors during both season, but in somewhat different ways. During the dry season, males mostly mark territories. As noted earlier, female primates are driven to secure resources, while males are driven to secure females (Emlen and Oring, 1977; Vehrencamp and Bradbury, 1978; Wrangham, 1980; Stephens and Crebs, 1986). Scent marking, in this case, could function to ward off other males, and/or secure foraging territory for females who may later favor them as potential mates. Energy requirements associated with stink fighting likely far surpass that of scent marking, given relative differences in the time and intensity of these two behaviors. Though scent marking could be over-represented in the wet season because of the nearing mating season, it is also possible that males opt to use scent marking more during the dry season, because of its relative decrease in energetic requirements, when compared to stink fighting. Females are more often expected to energy minimize, however, it appears as though male ring-tailed lemurs at TNP also engage in these behaviors, which will be addressed next.

Other authors have noted that gallery forest ring-tailed lemurs "energy minimize" during the dry season by increasing resting (Sauther, 1992; Loudon, 2008). Ellwanger and Gould (2011) note that ring-tailed lemurs in the dry season, in spiny forest fragments at Berenty rest ("rest" and "sit" as defined by the authors) an incredible 72.8% of the time and only feed/forage 14.9% of the time (see Table 5.14-5.15, below). However, increased dry season resting was not seen in the study by Kelley (2011), who notes that the Cap Sainte Marie ring-tailed lemurs rest about 30% of the time, and feed/forage between 9-13% of the time, year round. Increasing time spent resting
has been suggested to save energy during times of food scarcity (Sauther, 1992; Loudon, 2008; Whitelaw, 2010). Increased resting during the dry season was only observed within males of this study, which is counter to what we might expect, given that males have lower energetic requirements when compared to their reproductive female counterparts. Once again, females in this study appear to be more driven by the need to secure resources, while males forgo much of the time we might expect them to feed during the dry season. This results in females using what seems to be a more energy expensive means of acquiring more food resources, while males use little energy, yet secure few resources, comparatively. Male energy conservation may actually benefit females, in this case, since decrease in foraging on part of the males would act to decrease feeding competition and feeding patch depletion time for the group.

There are a few reasons why there are dramatic variations in activity budgets of ring-tailed lemurs may be occurring in different habitats. First, foods are distributed and used differently at these sites. For example, Gould (et al., 2011) notes the particular importance of *G. americanus* fruits to the ring-tailed lemurs in Berenty's spiny forest fragments. Remarkably, during the same time period, TNP ring-tailed lemurs actively avoid the actual fruiting portion of *G. americanus*, yet consume the fruit arils, flowers, and leaves from the species. *Gyrocarpus* is
not present at Cap Sainte Marie, but the feeding patterns in these lemur groups are affected by their use of the large *O. monacantha* fruits. Next, activity budgets could vary between sites if feeding rates vary between sites. Ellwanger and Gould (2011) suggest the Berenty ring-tailed lemurs feed rapidly during late afternoon bouts, although it is unknown if this is the case for the other populations. Third, temperatures can be extreme throughout southern Madagascar, but can be particularly problematic to animals in spiny forests where shade and water are limited (Ellwanger and Gould, 2011) and this could be contributing to differing activity budgets. Cold temperatures also limit ring-tailed lemur activities. During the dry season at BMSR sub-zero temperatures have been reported (see Gould et al., 1999; Sauther et al., 1999), during which time animals huddle and rest until late morning, when temperature increases. The lowest temperature recorded at TNP during this study was 10.4°C, and thus animals wouldn't be expected to huddle or rest through mid-morning because of low temperatures, in the same way that they do at BMSR. Last, as noted in Chapter 3, nighttime feeding activity is an important consideration for studies of ring-tailed lemurs and since those have not been accounted for here. Ambient temperature also affects nighttime activity in the TNP lemurs, and thus, non-mutually exclusive factors that appear to contribute to variation in activity budget in ring-tailed lemurs include distribution and use of food resources, feeding rates, high and low temperatures, and nighttime activity.

Nutritional profiles assembled here suggest that, when compared to the dry season, during the wet season when food availability is higher ring-tailed lemurs consume more calories and less tannin, and increase their dietary quality (as measured through protein:ADF). With the increase in available foods, animals have more choice in what they select and are simply able to consume more. *Cordia caffra* fruits, the young leaves from lianas (including *P.*
*madagascariensis*, and caterpillars were foods that were only available in the wet season, and these three foods had the highest protein:ADF ratios of any analyzed foods at 5.82, 5.55, and 5.32, respectively. The wet season also included the three most calorically dense foods, including *Ximenia perrieri* seeds (5.93 kcal/gram), caterpillars (3.82 kcal/gram), and *Ximenia perrieri* fruit flesh (2.08 kcal/gram). In addition, none of the aforementioned foods had any detectable levels of tannin.

Several authors (see Sauther 1994, 1998; Curtis 2004; Yamashita 2008) have suggested that food intake is likely reduced for lemurs in the dry season, because plant foods are scarce, and because both females and males lose dramatic amounts of weight. Furthermore, the protein:ADF ratio is known to be an important food selection criteria in primate diet and an indicator of the diet quality (Milton, 1979). Studies, including those in Madagascar (Ganzhorn, 1992), have demonstrated positive correlations between folivorous primate biomass and the ratio of protein:ADF in forests (Oates et al., 1990; Davis, 1994; Waterman and Kool, 1994; Chapman and Chapman, 2002). The effect of tannins in ring-tailed lemurs' diets are less clear, as Simmen et al. (2006) found a distinct seasonal difference in the concentrations of tannins found in gallery forest ring-tailed lemurs diet, while Yamashita (2008) did not. It is important to note there is currently controversy over the methods and interpretations of tannins and calories in primate diets. This will be further addressed later in this chapter.

When compared to males, females in this study consumed more calories and had a higher protein:ADF ratios. Moreover, when looking at just females, we see that their intake of calories, protein and their average protein:ADF ratio increases during the wet season. When looking at males, their calories consumed also increases, from the dry to wet season. Also, there are significant differences in the dry season intake of protein, the protein:ADF ratio, and the calories
consumed for females and males in the dry season, but no significant differences found between females and males in the wet season. In sum, female ring-tailed lemurs in this study consume more calories and have a better quality diet than males, and both females and males consume more calories in the wet season.

An increase in the amount eaten and protein intake have been documented in reproductive females, when compared to adult males, throughout the primate order (see Waser, 1977 [Cercocebus albigena]; Gautier-Hion 1980 [Cercopithecus spp.]; Fragaszy, 1986 [Cebus olivaceus]; Robinson, 1986 [Cebus olivaceus]; Rose 1994 [Papio anubis]; Remis, 1997 [Gorilla gorilla gorilla] ; McCabe and Fedigan, 2007 [Cebus capucinus]), including within lemurs (Meyers and Wright, 1993 [Propithecus tattersalli]; Overdorff, 1993 [Eulemur rubriventer and Eulemur fulvus rufus]; Vasey, 2002). Due to the costs associated with gestation and lactation, reproductive females require more energy than males (Lee, 1999; Dufour and Sauther, 2002). Protein, or the amino acids in protein, are necessary for growth and development, and thus, it is not surprising that females, when reproductive, consume significantly more of these building blocks (Lee, 1996; Jessop, 1997). Sauther (1994, 1998) predicted that the diets of female ring-tailed lemurs were high in protein, based on plant parts eaten by animals at BMSR, and those dietary predictions are reflected in these data. Gould et al. (2011) report no sex differences in the top five most consumed foods (including protein:ADF) between of ring-tailed lemurs in spiny forest fragments of Berenty. The work done by Gould et al. (2011) took place during two one-month periods of the dry season, and it is possible that the Berenty and TNP spiny forest ring-tailed lemurs employ different strategies in feeding behavior and nutrient consumption, or that the duration of data collection was not sufficient to detect significant differences. That being said, controversy also exists in methods and interpretations of protein in primate diet, and the
usefulness of protein:ADF as a measure of dietary quality. These issues will also be addressed later in this chapter.

The Vintany group consumed significantly more NDF and ADF when compared to the ILove group. This was likely due to the increased number of animals in the Vintany group. If we include sub-adults and infants the ILove group had a maximum of 21 members, while Vintany had 28. In primates and other animals, group size is limited by the ability to secure sufficient food resources (van Schaik, 1983; Terborgh and Janson, 1986; Wrangham et al., 1993; Janson and Goldsmith, 1995). When groups near upper limits for the number of members it can sustain, food patch deletion time increases, which may result in a decrease in the diet quality (Milton, 1984; Janson, 1988; Wrangham et al., 1993; Chapman et al., 1995; Chapman and Chapman, 2000). The Vintany group fissioned half way through this study, but even after the fission, more adult, sub-adult, and infants group members remained, when compared to the ILove group. Alternatively, it is also possible that variations in microhabitat lead to an increased consumption of fiber by the Vintany group, as their home range extended more into Alluaudia dominated forests. If this were the case, however, we might expect to find other dietary differences as well. Future work with these lemurs and analyses of plants by exact location would help elucidate differences in fiber intake between these two groups.

The data presented here suggest that there are differences in the consumption of nutrients and non-nutrients by TNP L. catta sexes, during dry and wet seasons, and between groups of animals. Females consumed significantly more calories, protein, and had a better quality diet (as measured through protein:ADF), when compared to males. Furthermore, all focal lemurs increased their caloric intake in the wet season, which implies that these lemurs were at least in some aspects "nutrient starved" during the dry season. This is in sharp contrast to Yamashita
(2008) and Curtis (2004), who found no significant differences in the interseasonal nutrition of *L. catta*, *P. verreauxi*, or *E. mongoz* and suggested that lemurs are not nutrient starved (see **Figure 5.16**, below). However, the data analyzed by these authors did not examine nutritional differences between sexes, the ratio of protein:ADF, or caloric intake. Also, the lemur populations studied by Yamashita (2008) and Curtis (2004) rely heavily on foods from tamarind trees, which may act to buffer nutritional stress. Tamarind trees were present at TNP, though their phenology was synchronous (which has not been documented elsewhere), and the lemurs spent less than 1% of their focal feeding time consuming tamarind foods. Kelley (2011) found that at Cap Sainte Marie, lemurs who rely on *O. monacantha* fruits, did not suffer from seasonal dehydration or malnutrition. Interestingly, *O. monacantha* and *T. indica* are both asynchronous species and not foods that *L. catta* have specific adaptations for eating. *Opuntia* is invasive or sometimes cultivated in Madagascar, and tamarind could be domesticated, but is at least a harvested and used as a human food in southern Madagascar. By their very nature, plants which are cultivated for human use are nutrient rich and can be valuable resources for wild primates (Forthman-Quick, 1986; Hill, 2005). The TNP lemurs had access to and regularly fed on fig fruits, which on first glance may seem to fill the role of tamarind or cactus fruits. However, *F. megapoda* is not a cultivated species and it is not particularly nutrient dense (exocarp, protein:ADF = 0.159, energy = 0.862 kcal/gram). Furthermore, though the figs are asynchronous and can be plentiful, the lemurs do not digest the seeds, and judging from the pieces of intact exocarp found in their feces, they also appear to have some difficulty digesting the fleshy exocarp (**Figure 5.17**, below). It is also possible that the high dietary fiber in *F. megapoda* (up to 60% NDF and 44% ADF) reduces gut retention time, and impedes these lemurs' ability to absorb nutrients, as is the case with other species of lemur (Campbell, 2002).
Figure 5.16. Results and conclusions of previous research examining nutrition in lemurs.

**Curtis (2004):**
No seasonal differences detected in diets of *E. mongoz*
↓
Concludes that:
Lemurs NOT nutritionally starved during the dry season
↓
However,
- Sex differences not examined
- Lemurs rely heavily of tamarind
- Calories not analyzed
- Protein:ADF not compared

**Yamashita (2008):**
No seasonal differences detected in the diets of *P. verreauxi* or *L. catta*
↓
Concludes that:
Lemurs NOT nutritionally starved during the dry season
↓
However,
- Sex differences not examined
- Lemurs rely heavily on tamarind
- Calories not analyzed
- Protein:ADF not compared

**Gould et al. (2011):**
No sex differences detected in the diets of *L. catta*
↓
Concluded that:
Animals use behavioral mechanisms to save energy rather than consuming increased nutrients
↓
However,
- Only two one-month periods compared
- Forest habitat highly degraded

Figure 5.17. *Ficus megapoda* fruits in a) a portion of a heavily fruiting tree, b) a cluster of unripe fruits from the tree and b) fruit and seed remains in feces of *L. catta.*

a) [Image]

b) [Image]

c) [Image]
In sum, in the dry season, both sexes of the TNP ring-tailed lemurs appear to be calorically starved, and females appear to be protein starved. Also, female lemurs who are reproductive consume more calories, protein, and have a higher quality diet than their male counterparts. These data are consistent with ECH and are important in our understanding of lemur reproductive timing and some of the unusual lemur traits. This topic will be explored further in Chapter 6.

Reproductive female lemurs in this research had poorer coat and tail conditions at the end of the long dry season, when compared to males, or females who's infants died. Additionally, it took longer for the coats and tails of reproductive females to improve following the onset of the wet season. Coat and tail condition are a good indicator of health and well being (Berg et al., 2009), and poor coat condition in ring-tailed lemurs correlates with high levels of fCG (Pride, 2003; Steinmetz et al., 2005), which is used to indicate stress levels in wild animals. Stressors found in ring-tailed lemurs which correlate with high fGC are numerous and including, but not limited to: reproduction, food shortages, dominance rank, aggressive encounters, and predator presence (Cavigelli, 1999; Pride, 2005; Fitchel et al., 2007; Ostner et al., 2008; Starling et al., 2010). The combination of gestating and lactating by female lemurs, during times of food scarcity, appeared to be the most stressful situation endured by these lemurs. Males, and sub-adult animals appeared to also suffer from stress related to scarcity of food resources, but their stress was not as severe as the females. Infants appear to be the only subclass of animals who are not affected by stress in this way.

Though widely used, some authors criticize using the measurements of nitrogen and a conversion factor of 6.25 to infer protein content, saying that it over estimates biologically available protein, given that nitrogen can be bound in fiber or part of non-protein molecules.
(Conklin-Brittain et al., 1999, Rothman et al., 2008, Rothman et al., 2011). Some authors have proposed a nitrogen to protein conversion ratio of 4.3 (Conklin-Brittain et al., 1999), but others suggest that this will underestimate available protein (Rothman et al., 2011). However, if present, any protein over-estimates are expected to be equally distributed across the data (Vogel et al., 2011), and these data can be more readily be compared to those from other species of primates within the literature. Perhaps more problematic, is the relationship between protein availability and tannin concentrations.

There are currently several major difficulties with interpreting significant differences in tannin intakes. First, the literature on ring-tailed lemur consumption of tannins is largely contradictory (Gould et al., 2009). Several authors note that *L. catta* do not discriminate between tannin rich foods (Yamashita, 2008), yet others have documented seasonal or annual differences in tannin intake are noted (Mowry et al., 1997; Simmen et al., 2006; Gould et al., 2009). Second, Yamashita (2008) only found negligible amounts of tannins in 135 tested ring-tailed lemur food samples at Beza where as other authors reported significant tannin contents of gallery forest ring-tailed lemur foods (Mowry et al., 1997; Simmen et al., 2006; Gould et al., 2009). Third, although we know that the interaction between protein and tannins are largely dependent on the types of protein and tannin, the mechanisms of these interactions are not completely understood (Rothman et al., 2011). For example, some tannin protein combination render the protein unusable (Waterman, 1984), yet others can actually enhance protein hydrolysis (Waterman and Kool, 1994). Fourth, many primates (including humans) have salivary proteins or gut bacteria which are able to neutralize tannins (Mould et al., 2005), and it is possible that ring-tailed lemurs possess mechanisms to degrade tannins, however, this is not known. And last, recently the very common, yet not always used, method of determining tannin content, "Quebracho" has been
called into question, and Rothman et al. (2011) suggest that tannin levels determined by this method are "erroneous" (Rothman et al., 2009). Generally we would expect animals to avoid the consumption of tannins, especially those animals with increased protein needs, and behaviorally, that appears to have been the case for the lemurs in this research. However, given the aforementioned problems with interpretation, the mixed and questioned literature data for tannins in primate diets, all inferences on tannin intake must currently remain tentative, pending a clearer understanding of the relationships between protein and tannins.

Yet another caution of the data analyses presented here is that of caloric content of lemur foods. Rothman et al. (2011) point out that gross energy of foods as released via combustion, is not the same as the energy that is available for digestion. They cite the example of wood having a higher energy content than sugar, yet being nearly indigestible (Rothman et al., 2011). A means to correct for this discrepancy is to account for the energy content in the animals' feces and subtract it from the energy of the foods (Rothman et al., 2011). This method will be used in the near future to better understand the data presented here.

Micronutrients of the diet were also not accounted for here, and could impact lemur dietary selection, and our understanding of their diet.

Conclusions

This chapter explored the interspecific response of ring-tailed lemurs to variability in the composition, abundance, and availability of plant foods, along with caloric and nutritional profiles, activity budgets, and stress, in order to understand the degree to which ring-tailed lemurs may partition ecological niches between the sexes. Calories and the diet quality of the TNP ring-tailed lemurs varied according to group, season and sex. The dry season constrains the
lemurs' ability to secure sufficient resources, and female ring-tailed lemurs in the spiny forests of TNP gain a nutritional advantage over males, which is likely critical in their ability to survive periods of food scarcity and reproduce. Previous research suggested that some lemurs are not nutritionally starved (see Curtis 2004, Yamashita 2008), but data presented here indicates that the ring-tailed lemurs at TNP are in fact lacking in some nutritional components. Nutritional differences in previous studies may not have been present due to the lemurs' in those studies being highly dependent on aseasonal foods, or because of differences in aspects of nutritional analyses. These data must remain preliminary given the current controversies within primate nutritional research. However, trends found here are expected to hold true. Nutrient excretion may alter some of the interpretations of this work, with reference to calories, and this will be addressed in the near future. At present, ECH is supported by this research. More data are needed to fully understand the ecological plasticity of ring-tailed lemurs throughout the highly variable habitats which they are found in. Future research should focus on innovative means of measuring metabolic processes, including work such as the protein recycling studies of Vogel at al., (2011).
Overview

Female dominance and the unusual traits found in lemurs are long debated. Some of this debate stems from uncertainty in whether or not the traits are adaptive and the relative costs of reproduction for female lemurs. Jolly (1984) suggested that female dominance was an adaptation to offset the unusually high costs of reproduction for female lemurs, when compared to other primates. This hypothesis was expanded to include "female need" wherein several authors proposed that female lemurs elevated their typically low basal metabolic rates during reproduction, and that this increased metabolism further exacerbated female lemurs' reproductive costs (Richard and Nicoll, 1987; Young et al., 1990; Ross, 1992). Young et al. (1990) suggested that female lemurs have unusually high prenatal investment, but Kappeler (1996) argued that there was no evidence for an increased metabolic rate in reproductive female lemurs, that postnatal growth is where the bulk of reproductive cost are concentrated, and that these costs are not significantly higher than in non-lemur strepsirrhines. Wright (1995) suggested that female lemurs invest less in their infants through low-quality milk and low infant birth weights, given that lemur infants have high mortality rates. However, Tilden and Oftedal (1997) and Tilden (2008) show that milk quality is not universally low in lemurs, but rather, of lower quality in species whose infants "ride" rather than "park," which suggests a strategy reflecting frequency of suckling rather than differential nutrient transfer. Also, Izard and Nash (1988) showed that lemur infants comprise a higher percentage of maternal weight at birth, when compared to other non-lemur strepsirrhines. Though data are somewhat limited for infant mortality rates within primates, it does not appear that lemur infants fare any better or worse in "normal" years (i.e.
those without natural disasters and mass fatalities) in Madagascar. As such, despite nearly thirty years of discussion, no evidence exists for abnormally high or low reproductive costs for female lemurs.

Wright (1999) proposed the Energy Conservation Hypothesis (ECH), which suggests that a number of the unusual traits found in lemurs, including female dominance, are the result of an adaptive complex whereby female lemurs conserve energy and maximally exploit scarce resources, because the environments in which they live are more difficult or "harsh," when compared to the habitats of other primates. ECH has been further broken down into the "energy conserving" traits (low BMR, small group size, torpor, sperm competition, and seasonal breeding), which aid in minimizing energy expenditure, and the "energy frugal" traits (female dominance, weaning synchrony, fibrous diets, territoriality, and cathemerality), which help animals extract the maximum amount of energy from their resources (Wright, 1999). In essence, ECH posits that female lemurs are dominant to males in order to gain an energy advantage, through food resources, and that if they did not have this advantage it is unlikely that female lemurs could successfully reproduce. When proposed in 1999, two critically important aspects of ECH remained unknown, including: a) whether the environment of Madagascar is more difficult for lemurs to live in when compared to other primates and their habitats, and b) if female lemurs gain a nutritional advantage through their dominance over males?

*Hypervariable Madagascar*

In 2007 Richard and Dewar demonstrated that intra- and inter-annual rainfall on Madagascar is less predictable that most other regions with similar precipitation, and deemed Madagascar's habitat as "hypervariable." Furthermore, Madagascar experiences an average of 7
cyclones per year and a major drought approximately once every 6 years. Rainfall, or lack thereof, and cyclones have major effects on plant food availability, which then affects lemur survivorship, and particularly that of infants and juveniles (Gould et al., 1999). Certainly, natural disasters such as this happen in other primate habitats, and we should not expect that high mortality rates during disasters to be a peculiarity of lemurs. However, intense seasonality, along with unpredictability and relatively high frequencies of natural disasters affecting Madagascar, appear sufficiently different from other primate habitats (Richard and Dewar, 2007), to warrant distinctive adaptations, such as those found in lemurs.

**Nutrition and Female Dominance**

The research presented in this dissertation suggests that female dominance in ring-tailed lemurs at TNP does facilitate a nutritional advantage for female lemurs, when compared to males, and that this advantage is of utmost importance during the most difficult time of year for reproductive females, namely the late dry season, when food resources are low, and females are simultaneously nursing and carrying their quickly developing offspring. While Wright (1999) has suggested that female lemurs invest little in their young, due to high infant mortality, my results do not support this. Gould et al. (1999) note that female ring-tailed lemurs will continue to lactate up until their own death by starvation, and as argued elsewhere, ring-tailed lemurs do not appear to have unusually high infant mortality in normal years. I argue that ring-tailed lemur females transfer the maximum amount of energy possible to their offspring, and that when they are in dry spiny forests, and are not depending on asynchronous and potentially introduced and domesticated plant resources, female dominance facilitates obtaining sufficient resources to sustain the lives of mother and infant. This is especially the case during the later portions of the
long dry season. Without this advantage it seems unlikely that mothers and their offspring could survive, and when combined with the "lost cohorts" resulting from natural disasters, it is further possible that without female feeding priority, survival at the species level may be jeopardized.

*Strategies of Lemur Females, Males, and Infants*

There are two further debates that are pertinent to this topic and understanding selection in ring-tailed lemurs. The first is male and female lemurs' ability to "prepare" for the long dry season, and the second is the timing of reproduction and weaning synchrony. Both large bodied male and female lemurs gain significant amounts of weight during the short wet season, when resources are plentiful. Simmen et al. (2010) note that ring-tailed lemurs at Berenty gain up to 26.5% of their body weight in subcutaneous fat during the wet season. At TNP there appears to be about a 3 month window in which resources are annually abundant. At Beza, Sauther (1989) found that males fatten and dramatically increase the size of their testes during this time in preparation for the short, intense mating season and the following long dry season, during which time they feed little. Additionally, females at Berenty and Beza also fatten during this time in preparation for reproduction during the long dry season (Sauther, 1989; Simmen et al., 2010). Similar trends of rapid fattening appear to occur at TNP, although the rate may be somewhat quicker, given that TNP has the shortest annual wet season.

By the end of the dry season both male and female ring-tailed lemurs are in poor body condition and appear extremely thin. It is during this period that we would expect selection to be the strongest, given that animals have very little fat reserves remaining and that there is little food available. It is thus surprising that Pereira et al. (1999) state the following: "confusion concerning female dominance in lemurs derives from failing to appreciate that adaptation should
have minimized prospects for seasonal stress and that success during months of food abundance, not months of food scarcity, is most likely the primary foraging factor influencing relative fitness among today's lemurs." I suspect that this conclusion stems from the authors' work with captive ring-tailed lemurs where nutritional stress is not seen, because upon viewing the body conditions of wild lemurs during the later portion of the dry season, it is visually obvious that these animals are stressed. The authors' own definition of nutritional stress, being that of nutrient demands exceeding rates of ingestion and extraction from storage, would qualify wild ring-tailed lemurs as nutritionally stressed. Pereira et al. (1999) further suggest that it is the wet season, and not the dry, which serves as a bottleneck in lemur populations. Though I agree with Pereira et al. (1999) in that the ability to maximally fatten during a short window of time when food is abundant may be an important factor in survival and fitness of these animals, I argue that the wet season could only act as a bottleneck if the fat reserves acquired during this time would carry animals through to the next wet season. Since lemurs deplete their fat stores during the dry season, well before the onset on the next wet season, my data indicate that the period in the late dry season wherein animals have little remaining fat and there is little food available, acts as the bottleneck for adult animals. Those able to make due during this difficult time are far more likely to be reproductively successful.

*Lemur catta* are by-and-large considered "income" breeders (see Gould et al., 2003; Brockman and van Schaik 2005; Lewis and Kappeler, 2005; Gould et al., 2011). There is some controversy here, but much of the disagreement is based on the terminology used and definition of "reproduction" (Lewis and Kappeler, 2005). Income breeders use food intake to support offspring, and the body mass of an income breeder varies little throughout the year, alternatively, capital breeders build and store resources (such as body fat), in order to support their young, and
are expected to have the highest body weights just before reproduction (Stearns, 1989, 1992; Jönsson, 1997). Reproduction itself can be broken into the categories of conception, gestation, birth, lactation and weaning. Gould et al. (2003, 2011) define reproduction by its costliest portion, being lactation and weaning, and suggest that ring-tailed lemurs are income breeders. Several researchers have noted rapid weight gain in ring-tailed lemurs, in which the body condition of both female and male animals dramatically improves near the end of the wet season or by the early dry season (Sauther, 1990; Jolly et al., 2002; Simmen et al., 2010). It is thus likely important for individuals of both sexes to be in peak condition around mating period. Males who are best able to rapidly fatten before mating may be able to outcompete other males for chances to mate, though this has yet to be documented. Also, since females can cycle up to three times in a breeding season (Evans and Goy, 1968), it is also possible that their fertility is dependent on a their ability to fatten, as has been suggested by Pereira et al. (1993, 1999). Infants born outside of peak birth cohorts, however, have dramatically reduced survivorship (Koyama et al., 2001), which may indicate that females who can fatten and conceive at the same time as other females, may gain a fitness advantage. Given that female ring-tailed lemurs have the most subcutaneous fat prior to conception (Sauther, 1990; Jolly et al., 2002; Simmen et al., 2010), I suggest that it is more appropriate to define conception as the start of reproduction in this species. I also argue that female ring-tailed lemurs are capital breeders until such time that they deplete their fat stores, and then become income breeders during the later portion of the dry season. It is possible that there is a discrepancy between the level of fattening in areas where lemurs routinely use asynchronous food resources, such as tamarind, when compared to areas such as TNP where they do not have year round access to such foods. It is also possible that this model of "income" and "capital" breeding, which was developed to explain reproductive strategies of birds (Drent and
Daan 1980), is simply not an appropriate measure for mammals, and particularly primates that tend to be relatively large-bodied and have long reproductive periods (Lewis and Kappeler, 2005). Further scholarly debate on the applicability of this model, and research comparing body fattening across habitats with and without introduced food resources would help elucidate the level of fattening and extent to which ring-tailed lemurs use fat stores during the dry season, and whether they are "capital" or "income" breeders.

The second area that is pertinent to this discussion of lemur traits and female dominance is that of reproductive timing. Reproduction in lemurs is timed such that infants are weaned during the annual time period that most predictably has abundant food resources (Jolly, 1984; Wright 1995, 1999). This ensures the best possible chances of autonomous survival in lemur infants/juveniles (Wright 1999). Yet as we know, this imposes great stress on reproductive females, who have the added costs of gestation and early lactation during the dry season when resources are scarce. Their strict reproductive synchrony also imposes stress on reproductive males, who experience intense competition during the short mating season. Timing such as this suggests that infant survivorship is ultimately the most critical and variable portion of lemur reproduction, and that weaning synchrony has been selected for despite there being considerable consequences for reproductive adults.

As noted earlier, mortality in infant ring-tailed lemurs at BMSR is not abnormally high during "normal" years in southern Madagascar. However, infant mortality is high during years with natural disasters such as cyclones and droughts that are frequent, although unpredictable. It appears that in response to both strong seasonality and frequent yet unpredictable natural disasters, selection has favored maximizing infant survivorship during normal years (Figure 6.1). Weaning synchrony, which increases infant survivorship, acts as a stressor for both adult
females and males. Although stress *still exists*, both sexes have adapted strategies to counter act some of this stress. Females, who have increased need for calories and nutrients are dominant to males, and thereby have priority of access to foods year-round. This is particularly important at the end of the dry season, when females are lactating, their stores of subcutaneous fat are low, and food resources are scarce. If females were unable to survive this annual time period, it is unlikely that infants would either, given that they will continue to nurse, albeit at decreasing rates, for approximately another three months. Males are in peak condition for the short mating season and then appear to consume little, thereby relying on fat stores and increasing periods of rest during the long dry season. As with females, the end of the dry season is a difficult period for males. They have little remaining subcutaneous fat, there is little food available, and unlike with females, males only have secondary access to the few resources that are available. However, males require far fewer calories when compared to females at this time, and seem to be able to make do on much less. Simmen et al. (2010) note that the high fat levels attained by males during the wet season suggests that their energy expenditure in the months following are comparable to those of reproductive females. At TNP, both females and males appear similarly fat at the end of the wet season and similarly thin at the end of the dry season, though males have longer relative time periods in which to gain fat, because females continue to lactate for about three months after the onset of late December rains, in this case. If this is true, I would agree that females and males use comparable amounts of stored resources during this time, although I would suggest a slight divergence in the mechanisms used between the sexes (*Table 6.1*), such that the net sum of energy intake and output were similar between females and males. Simmen et al. (2010) find no sex related differences in energy expenditure rates of ring-tailed lemurs activity patterns, and conclude that low BMR is the extent to which ring-tailed lemurs are
conserving energy. Though we might expect females to adopt low energy expenditure behaviors, the ring-tailed lemur males at TNP were the sex to do so. Through resting more, feeding less, and using scent marking as a low cost means of competing with other groups and other males, these males appear to be more energy frugal than females. This energy frugal strategy on behalf of male ring-tailed lemurs, may actually benefit females through a reduction in feeding competition and a decrease in feeding patch depletion time.

Figure 6.1. Weaning synchrony as a strategy of lemur infants, along with adaptive strategies of female and male ring-tailed lemurs.
Table 6.1. Usage of fat stores during the dry season by adult female and male ring-tailed lemurs.

<table>
<thead>
<tr>
<th>End of wet season</th>
<th>Mating season (approximately 2 weeks)</th>
<th>Gestation and Lactation (approximately 7 months)</th>
<th>End of dry season</th>
</tr>
</thead>
<tbody>
<tr>
<td>Females fat</td>
<td>Continue foraging, energy output not unusually high</td>
<td>Feed more than males, energy output increased due to gestation, lactation and foraging effort</td>
<td>Females thin</td>
</tr>
<tr>
<td>Males fat</td>
<td>Feed little-to-none, energy output extremely high</td>
<td>Feed little, reduce energy output by resting</td>
<td>Males thin</td>
</tr>
</tbody>
</table>

Conclusions

The research presented in this dissertation aimed to answer the following questions:

1. Are lemur foods seasonally/stochastically constrained?
2. Are lemur nutrients or calories seasonally constrained?
3. Do lemurs use behavioral mechanisms to save energy?
4. Is the dry season differentially stressful for female lemurs?

Results suggest that lemur foods are seasonally constrained, and that frequent but unpredictable natural disasters in southwestern Madagascar also constrain food resources stochastically. Furthermore, when food resources are low, female and male ring-tailed lemurs consume fewer calories and have a lower quality diet, although the diet of female ring-tailed lemurs across seasons appears to be higher in calories and quality when compared to that of males. Males, in this research seem to minimize energy use during the dry season, although females did not. This may be a reflection of the females' increased need for food, and that in order to secure more food, increased locomotion is necessary. Male behavior, which appears to be energy frugal, may aid in the females' being able to secure foods in that a reduction in male feeding decreases feeding competition and feeding patch depletion time. Females also appeared to be more stressed at the end of the dry season, and take longer to recover from this stress, as
measured through coat and tail condition, when compared to males. The metabolic requirements of lactation are likely why females are more stressed than males in the dry season and why females take longer to recover from stress after the onset of the wet season. During this time, males can increase feeding and immediately replenish their bodies' nutritional needs, and although females also increase feeding, they continue to lactate for about another three months. Cathemerality was also noted in this population of ring-tailed lemurs, and for these lemurs, nighttime activity likely eased thermoregulatory stressors and predator pressure, while also allowing animals to increase caloric consumption over the 24-hr period.

Results outlined here are consistent with the Energy Conservation Hypothesis and suggest that these lemurs use both energy efficient and energy frugal mechanisms to cope with resource scarcity. Since dominance facilitates a feeding advantage for female lemurs, dominance is likely an adaptive mechanism, which allows for costly mammalian reproduction during times of predictable resource scarcity. Reproductive timing favoring weaning synchrony suggests that infant survivorship is the most critical period in the life histories of lemurs, and that maximal survivorship during "normal" years is important, in part because of frequent yet unpredictable natural disasters, which result in high infant mortality, or lost cohorts. Weaning synchrony results in strong competition within male lemurs, for access to fertile females, and males prepare for this by quick annual fattening and increasing testes size. Male fitness is an important yet often overlooked aspect of lemur studies, and future work on tactics employed by males would likely aid in our understanding of the lemur traits. Fitness in females may also be linked to their ability to fatten quickly, although I argue that the "bottleneck" for both sexes is the period in the late in the dry season after they have used up all of their fat reserves and foods resources are scarce.
Future research detailing the amount of and patterns of fattening in wild female and male ring-tailed lemurs, along with the reproductive success according to ability to fatten would be useful in understanding how these animals exploit brief periods with abundant resources. Further data on cathemeral activity of ring-tailed lemurs along with detailed feeding data, and mechanisms of thermoregulation and relative energy expenditure according to ambient temperature also promise to be interesting directions for research, and pertinent to understanding adaptations of lemurs. And of course, data examining mechanisms of the Energy Conservation Hypothesis in other species of lemurs, including those where dominance is not strict as with ring-tailed lemurs, would likely elucidate proximate and ultimate mechanism underlying the unusual trait found in lemurs. Additionally, it is important to realize that many of the "so called" lemur traits were proposed as hypotheses, and that some of these hypotheses are based on very little data (e.g. high infant mortality, low BMR, etc.). Future research involving lemur traits, should take care to test both hypotheses of interest, and those underlying the traits themselves. Last, lemur research should move away from testing non-adaptive hypotheses, such as the Evolutionary Disequilibrium Hypothesis (Kappeler and van Schaik, 1996) which is not supported by current data, and concentrate on testing the more promising aspects of adaptation in the quest to understand evolution in lemurs.


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