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Date

Beyond Aggression and Dominance: The Effects of Social and Environmental Factors on  
Fecal Testosterone and Fecal Glucocorticoid Levels in Wild Female Verreaux's Sifaka  
(*Propithecus verreauxi*)

By

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Doctor of Philosophy

Anthropology

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B.S., Duke University, 1998

M.A., Emory University, 2007

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## Abstract

Beyond Aggression and Dominance: The Effects of Social and Environmental Factors on Fecal Testosterone and Fecal Glucocorticoid Levels in Wild Female Verreaux's Sifaka

(*Propithecus verreauxi*)

By Brandie L. Littlefield

The study of female competition in non-human primates has generated more attention over recent years and placed an increased focus on the proximate and ultimate causes of female competitive behavior. When contest competition for available resources is high, females form linear dominance hierarchies, which may result in rank-related differences in feeding efficiency, nutrient intake, and reproductive success. The field of socioendocrinology provides the opportunity to examine inter-individual differences in hormonal responses to social factors that may reflect the relative costs of social rank. Research across species of primates has investigated the extent to which dominance and competitive behavior are mediated by hormones associated with aggression (androgens) and stress (glucocorticoids). Despite these advances, relatively few of these studies have examined the relationships among dominance, aggression, and hormonal measures in wild female primates.

The goal of this study was to examine female competitive behavior within an endocrinological framework by assessing the extent to which dominance rank and aggression are mediated by androgens and glucocorticoids in wild female Verreaux's sifaka (*Propithecus verreauxi*), a lemuroid primate living in southwest Madagascar. Behavioral and hormonal data were collected on eight adult female sifaka with infants from July through December 2007 at Beza Mahafaly Special Reserve, Madagascar.

The results showed that neither dominance rank nor rates of aggression were significant predictors of fecal testosterone (fT) or fecal glucocorticoid (fGC) levels. However, male immigration and infanticide events had a profound effect on both hormonal measures. Females in groups that experienced male takeover events had significantly higher fT and fGC levels compared to females in stable groups. There was a strong seasonal effect on aggressive behavior, suggesting that contest competition increases during the period of resource abundance for female sifaka and that dominance relationships may be seasonally dependent. Fecal glucocorticoid levels dropped significantly after the first rainfall of the season, demonstrating that the endocrine response is particularly sensitive to exogenous cues for this species. These results highlight the need for longitudinal studies with repeated hormonal measures in order to assess the complex interactions of social and ecological factors on the endocrine response in female primates.

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## **Chapter I. Introduction: Female Competition in Non-human Primates and the Hormonal Correlates of Aggression and Dominance**

### **Introduction**

The combative and often despotic female of 21<sup>st</sup> century primatology is a much more complex and intriguing creature than the coy and choosy female Darwin struggled to defend in his 19<sup>th</sup> century model of sexual selection (Darwin, 1871). Over the past thirty years, field biologists, including primatologists, have increasingly focused on the evolution and impact of female competitive strategies, providing new insights into our understanding of sexual selection, parental investment, socioecology, and life history theories (Clutton-Brock, 2004; Hrdy, 1981; Smuts, 1987; Sterck et al., 1997; van Schaik, 1989; Wasser, 1983; Wrangham, 1980). Prior to this shift, the complexities of female competitive relationships were obscured by an emphasis on sexual selection theories highlighting male mating competition (Hrdy, 1981; Hrdy & Williams, 1983; Wasser, 1983). Proponents of these theories argued that a female's generally greater energetic investment in offspring (Trivers, 1972) constrains her reproductive rate and limits her availability relative to males (Clutton-Brock, 1991), minimizing the benefits of female mating competition (Bateman, 1948). However, long term research on non-human primates has demonstrated that females regularly engage in competitive interactions, although the selective pressures driving female competition are inherently different from those affecting males. Parental investment is prolonged for primates due to long lifespans, delayed reproduction, and extended juvenile periods compared to other mammals of similar body size (Chapais & Schulman, 1980). The duration of parental

care combined with the energetic burden of gestation and lactation suggest that reproductive variance in female primates is greater than originally thought (Drea, 2005; Hrdy & Williams, 1983), creating increased pressure for females to compete in any way that ensures offspring survival (Wasser, 1983). Female primates have a vested interest in improving reproductive success through the support and protection of offspring; therefore, as Hrdy (1981) states: “every female is essentially a competitive, strategizing creature” (pg. 97). The focus on female competition contributes to our understanding of sex differences in competitive behavior, providing insights into the effects of competition on several aspects of female reproduction (such as nutrition, maternal investment, and infant survival), as well as a greater understanding of sex-specific constraints that will determine the range of competitive tactics employed by each sex.

Recognition of the importance of female intrasexual competition in primate social evolution has generated debate about the meaning of “competition” as it relates to sex differences in behavior. In the broadest sense, competition can occur “whenever the use of a resource ... by one individual makes the resource harder to come by for others” (Andersson, 1994). In terms of reproductive competition, sexual selection focuses on access to mates as the prime determinant of male reproductive success. By contrast, the limiting resource for females is access to sufficient resources, which affects both survival and reproduction, presenting the challenge of how to conceptualize and categorize female competitive behavior. While male competition for access to mates generally functions to increase offspring quantity, female competition for resources that support reproduction (pregnancy and lactation) is generally thought to enhance offspring quality (Wasser, 1983). This has led some to suggest that sexual selection theory should be expanded to

include selection arising from competition over components of reproduction beyond mating competition (Clutton-Brock, 2004; Hrdy & Williams, 1983; Wasser, 1983), while others argue that competition related to aspects of reproduction such as parenting effort should be confined to the realm of natural selection (Hawkes, 2004). This distinction is worthy of further consideration and debate because there is a high degree of overlap between female competition for survival and female competition for reproductive success, obscuring the line between sexual and natural selection. For this reason, Clutton-Brock (2004) advocates refocusing attention on comparison of the differences in selection pressures operating on males and females. For example, if females are competing primarily to ensure offspring survival, reproductive competition among females should occur throughout the reproductive cycle, but intensify at times of increased energetic stress, such as during gestation and lactation (Wasser, 1983). In contrast, competition among males intensifies primarily during mating. Moreover, the relative costs and benefits of certain competitive strategies are inherently different for females and males. Since engaging in overt and aggressive forms of competition can be risky, females may engage in more opportunistic and subtle forms of competition in order to reduce these costs (Hrdy, 1981; Silk, 1993; Smuts, 1987). The shift in focus from overt agonistic displays to the outcome of competitive interactions, such as obtaining access to a limited resource, allows for the inclusion of more subtle forms of competition that may be particularly useful in assessing how females compete.

Female competition occurs under varying contexts in primates, including: access to resources to support the energetic requirements of reproduction (van Schaik, 1989; Wrangham, 1980), access to high-quality males (Berglund et al., 1993) or sperm (Zinner



et al., 1994), access to safe spatial positions (Ron et al., 1996), and access to male “friends” (Palombit et al., 2001). In addition, females may engage in reproductive competition such as copulatory harassment, reproductive suppression, and infanticide in order to eliminate potential competitors for their own offspring (Vervaecke et al., 2003; Wasser, 1983). Females may also compete for their own dominance status (Chapais & Schulman, 1983; Hrdy, 1981; Silk, 1987, 1993; Smuts, 1987), as well as the status of daughters (Chapais, 1992; Chapais & Schulman, 1980; Chapais & Schulman, 1983) and sons (de Waal, 2001). The degree and intensity of female intrasexual competition, as well as the specific tactics employed, are predicted to vary with ecological, demographic, and social factors. These factors include, but are not limited to, resource availability and distribution (Isbell, 1991; van Schaik, 1989; Wrangham, 1980), group size (Janson, 1988; Janson & Goldsmith, 1995), sex ratio (Berglund et al., 1993; Clutton-Brock & Vincent, 1991), reproductive state (Sauther, 1993; Wasser, 1983), degree of estrous synchrony (Berglund et al., 1993), breeding seasonality (Kappeler, 1997; Wright, 1993), male constraints on female competitive behavior (Kuester & Paul, 1996; Vervaecke et al., 2003), and the ability of females to form coalitions (Hrdy, 2000; Smuts, 1987, 1992, 1995). In addition, since engaging in overt and aggressive forms of competition can be risky, females may engage in more opportunistic and subtle forms of competition in order to reduce these costs (Hrdy, 1981; Silk, 1993; Smuts, 1987).

The extent to which aggressive and competitive behaviors are hormonally mediated provides an intriguing avenue through which to examine not only sex differences in aggressive behavior, but also the physiological costs associated with competition. Recent advances in the assessment of steroid hormones from fecal samples

have allowed researchers to non-invasively examine hormone-behavior interactions in wild populations (Whitten et al., 1998). This is especially important when assessing competitive and aggressive behavior, which can be altered in the artificial setting of captivity. Studies across species of non-human primates have examined aspects of competition and dominance by assessing levels of steroid hormones associated with aggression (androgens) and stress (glucocorticoids). Overwhelmingly, these studies have pointed to the complex interactions of social, demographic, and ecological factors that influence the endocrine response. For example, the extent to which aggression, dominance, and testosterone levels are associated depends entirely on the relative stability of the dominance hierarchy (Sapolsky, 1982), seasonal fluctuations in the intensity of inter-male conflict (Brockman et al., 2001; Lynch et al., 2002; Strier et al., 1999), and even individual personality styles (Sapolsky, 1991; Virgin & Sapolsky, 1997). It is therefore not always the case that the most dominant individual is the most aggressive, or shows the highest levels of testosterone. In a similar vein, there is growing evidence that subordinate status is not always associated with the highest levels of stress (Abbott et al., 2003; Goymann & Wingfield, 2004a). Rather, for social groups in which the acquisition and maintenance of dominance status is achieved via aggression, it is the dominant individuals that often display the highest glucocorticoid levels (Goymann & Wingfield, 2004a). These results point to the potential costs associated with dominance status, suggesting that even though dominant individuals may enjoy priority access to resources and reproductive opportunities, these benefits are balanced by the negative impacts on physiological systems resulting from increased endocrine output (Abbott et al., 2003). For example, increased testosterone levels have been associated with impaired

immune function and decreased parental care behavior (reviewed in Wingfield et al., 2001). The costs associated with chronic stress range from impaired digestive function and increased risk of cardiovascular disease to the suppression of reproduction and immune function (reviewed in Sapolsky, 2002). Most of the research examining hormone-behavior interactions in wild non-human primates has focused on males (reviewed in Cheney & Seyfarth, 2009), which is unfortunate given that the costs associated with aggression may be particularly salient for females, who must achieve a balance between being effective competitors and nurturing mothers (Sih et al., 2004).

#### *Research Goals and Organizing Questions*

The goals of this project were to examine aspects of female competitive behavior within an endocrinological framework to begin to elucidate the extent to which aggression and dominance are mediated by androgens and glucocorticoids. This study was conducted over a five month period (from July to December 2007) on lactating female Verreaux's sifaka (*Propithecus verreauxi*) at Beza Mahafaly Special Reserve, Madagascar. Verreaux's sifaka are particularly well-suited for this research for a number of reasons. (1) Verreaux's sifaka live in the highly unpredictable and seasonal environment of Madagascar (Wright, 1999), where access to resources during the dry season is limited and can have a profound effect on female fertility and reproductive success (Richard et al., 2000). (2) Female sifaka are highly seasonal breeders (Brockman, 1999), making it possible to control for reproductive state while assessing hormone levels. (3) Female sifaka often engage in intense intrasexual competition, such as harassment of immigrant females (Lewis, 2008) and copulatory harassment (Brockman,

1999). (4) Verreaux's sifaka, like most lemuroid primates, are female-dominant (Richard, 1978), which may provide the opportunity to examine female competitive relationships outside the context of male dominance and aggression (Kappeler, 1993b). Specifically, this study set out to answer the following questions:

- 1. Is female competition mediated by dominance status and aggression?** Are there costs associated with subordinate status (i.e., increased feeding competition)? Are dominant females more aggressive? How might female competitive relationships change throughout the transition from the lean season to the season of greater resource abundance?
- 2. What are the relationships among dominance, aggression, and testosterone levels?** Do dominant females have higher levels of testosterone and to what extent is aggression a significant predictor of testosterone levels? What other social factors, such as group stability, predict testosterone levels?
- 3. What are the social and environmental factors associated with stress?** Are rank and aggression significant predictors of glucocorticoid levels? Do glucocorticoid levels change during the transition from the dry season to the wet season?

In the sections that follow, I lay the background for addressing these questions by reviewing the existing literature on female competitive behavior and the associations among dominance, competition, and the hormonal mediators of aggression and stress. The first section examines the evidence across non-human primates for female competition, focusing primarily on resource competition. I then discuss evidence of competition among female lemurs, and place Verreaux's sifaka within the context of

socioecological models. The next two sections examine the extent to which aggression and dominance status are mediated by androgens and glucocorticoids, respectively, providing evidence from research with both male and female primates and then concluding with evidence from lemuroid primates. In the final section, I return to the questions posed above and provide a brief overview of the hypotheses tested in the subsequent chapters.

### **Overview of Female Resource Competition in Primates**

Resource competition within and between primate groups provides important evidence of female intrasexual competition. Most of these data have been collected by socioecologists concerned with explaining the evolution of sociality and optimal group size. Socioecological theories focus primarily on the effects of resource competition and predation pressure on group size and composition, particularly patterns of female gregariousness and the formation of formal dominance hierarchies (Isbell, 1991; Isbell & Young, 2002; Sterck et al., 1997; van Schaik, 1989; Wrangham, 1980). This research has shown that factors such as group size, resource availability, and predation threat affect individual competitive strategies to maximize foraging efficiency, survival, and reproductive success. Socioecological models posit that intragroup competition provides the upper limit to group size, but there is much disagreement regarding which factors (intergroup competition or predation pressure) set the lower limit, resulting in different categorizations of female affiliation and status differentiation that serve as adaptive responses to these pressures (Sterck et al., 1997; van Schaik, 1989; Wrangham, 1980).

### *Resource Distribution and Dominance Hierarchies*

The intensity and form of female feeding competition is influenced by numerous factors, including demography (group size and cohesion); ecology (resource distribution and availability); and physiology (nutrient requirements, activity budgets, and time constraints of digestion) (Janson, 1988). Of these, the interactions between group size and resource distribution have been most intensively studied, providing evidence that larger group size impairs individual feeding efficiency, and that resource distribution is strongly linked to the formation of dominance hierarchies (Table 1.1). Social ranking mitigates the risks associated with contest competition over resources and confers reproductive advantages for dominant females when social status is positively correlated with food intake and reproductive success (Sterck et al., 1997). In addition, results of numerous field studies (Table 1.1) yield unambiguous support for the proposition that clumped and monopolizable resources are associated with the formation of linear dominance hierarchies, resulting in rank-related differences in food intake and foraging efficiency. For example, among female Japanese macaques (*Macaca fuscata*) utilization of clumped resources is associated with linear dominance hierarchies and rank-related differences in feeding efficiency and energy intake, with subordinate females feeding on an alternative, lower-quality resource in order to alleviate the costs of feeding competition (Saito, 1996). Chimpanzees (*Pan troglodytes*) also form linear dominance hierarchies, with dominant females controlling priority access to monopolizable food items such as meat in 66% of agonistic interactions over food (Wittig & Boesch, 2003). In other studies, high ranking female sooty mangabeys (*Cercocebus torquatus atys*) exhibit better foraging efficiency ratios (time spent feeding/time spent searching) compared to lower-ranking females

(Range & Noe, 2002), and female vervet monkeys (*Chlorocebus aethiops*) show rank-related differences in food consumption when resources were clumped and easily defensible by dominant individuals (Whitten, 1983).

#### *Variation in Resource Availability and Quality*

While resource availability and distribution profoundly impact the degree of contest competition among females, it is becoming clear that other social and ecological factors also contribute to differences in female competitive relationships across primate groups. For example, seasonal changes in the availability and predictability of particular resources can influence the intensity of resource competition throughout the year (Barton et al., 1996; Overdorff, 1996). Variations in resource quality may also affect the degree of resource competition, as demonstrated by studies of folivorous primates. Because leaves are generally abundant, evenly distributed and low in nutrient quality, it has been assumed that feeding competition will be minimal in folivorous primates. However, recent studies contradict this assumption. For example, group size is known to effect travel time, day range, and home range in red colobus (*Procolobus badius*) populations at Kibale National Park, Uganda, suggesting that folivores in larger groups experience greater levels of feeding competition (Gillespie & Chapman, 2001). Gillespie & Chapman (2001) suggest that variation in nutrient quality and toxicity, as well as patch depletion rates, provides important new estimates of competition overlooked when examining resource distribution alone. Studies of Hanuman langurs (*Semnopithecus entellus*) confirm the importance food quality plays in rank effects on feeding competition (Borries, 1993; Koenig, 2000, 2002; Koenig et al., 1998). Hanuman langurs

were reported to feed primarily on three plant species that were clumped in distribution and low in abundance, two of which were found to be of superior nutritional quality compared to all other available plant species (Koenig et al., 1998). Under these circumstances, the monopolizability of high-quality resources resulted in the peripheralization of low-ranking females by high-ranking females (Koenig et al., 1998), rank-related differences in physical condition (Koenig, 2000), and better reproductive success among dominants (Borries, 1993). Seasonal distribution of resources, as well as variations in resource quality, may be particularly important for competition and the formation of dominance relationships among folivorous female lemurs.

### **Lemur Behavior, Ecology, and Social Structure: Implications for Socioecological Models**

Lemurs are strepsirrhine primates, which also include lorises and galagos, and mark the earliest evolutionary radiation of the primate order during the Eocene. They are found only on the island of Madagascar, and currently comprise 15 different genera, and close to 100 different species and subspecies (Mittermeier et al., 2008). With increased colonization by humans beginning 1600 years ago, rapid deforestation led to the mass extinction of several species of large bodied lemurs and raptors, opening up a diurnal niche for the smaller bodied, nocturnal lemurs (Martin, 1972; van Schaik & Kappeler, 1996; Wright, 1999). As a result of these particular circumstances, lemurs have been described as having a number of unique and “idiosyncratic” traits (Wright, 1999), including, but not limited to: female social dominance ((Jolly, 1984; Richard, 1987), although see (M. E. Pereira et al., 1990)), lack of sexual dimorphism (Kappeler, 1991),



targeted female intrasexual aggression (Vick & Pereira, 1989), balanced sex ratios (Kappeler, 1997; Richard et al., 1991), strict seasonal breeding (Brockman et al., 1995), the formation of monogamous pair-bonds in some species (Jolly, 1998; M. E. Pereira & McGlynn, 1998), and cathemerality (van Schaik & Kappeler, 1996). A number of hypotheses have been presented to account for these unique traits (Kappeler, 1996, 1997; van Schaik & Kappeler, 1996; Wright, 1999), but it is clear that lemurs have evolved specific adaptations to cope with living in the extreme island environment of Madagascar, which is characterized by seasonal fluctuations in resource availability, unpredictable climatic events such as cyclones and droughts, and increased human encroachment and habitat destruction (Wright, 1999). Despite these perplexing and divergent traits, lemurs also display a number of characteristics that are similar to anthropoids, such as variable mating systems ranging from monogamy to polyandry and polygyny (Pochron & Wright, 2003; Richard, 1992), situation-dependent copulations (Brockman, 1999), female mate choice and paternity confusion (Brockman, 1999; M. E. Pereira & Weiss, 1991), and infanticide (Erhart & Overdorff, 1998; Jolly et al., 2000; Lewis et al., 2003; Littlefield, 2010; Wright, 1995). As a result of these similarities and differences, strepsirrhines provide an evolutionary link between other mammals and anthropoid primates that can reveal important aspects of primate evolution in social structure, reproductive ecology, and life histories (Kappeler, 1996), as well as provide insight into adaptive responses to specific ecological pressures.

The unique aspects of lemur social organization and behavior have made it particularly challenging to categorize them using the socioecological models described above. Sterck et al. (1997) categorize lemurs as Dispersal-Egalitarian based on three main

criteria: (1) females emigrate from their natal groups, (2) female dominance hierarchies are either non-existent or unstable, and (3) female intrasexual competition is low.

However, these broad generalizations over-simplify the species-specific differences in social structure that exist within lemurs, particularly with respect to *Lemur catta* and species within the genus *Propithecus* (Erhart & Overdorff, 2008). Erhart and Overdorff (2008) conducted a meta-analysis on aspects of female dispersal, dominance patterns, and intrasexual competition across several species of *Lemur*, *Eulemur*, *Hapalemur*, *Varecia*, *Propithecus*, and *Indri*. Although most species are characterized by female dispersal, *Lemur catta* and some species of *Propithecus* demonstrate female philopatry. Even when females of these species remain in their natal group, they are sometimes evicted through targeted aggression by other females (Pochron et al., 2003; Vick & Pereira, 1989; Wright, 1995). Female dominance hierarchies across species of lemurs can be difficult to categorize, again with the notable exception of *Lemur catta* (Sauther, 1993). This may be attributable to the low levels of intrasexual aggression among female lemurs; compared to Old World monkeys, lemurs have significantly lower rates of aggression (although Erhart and Overdorff (2008) found no significant difference between lemurs and apes, or lemurs and New World monkeys). There is also a noticeable lack of female coalitional support and rank inheritance among lemur species that exhibit female philopatry (Erhart & Overdorff, 2008; M. E. Pereira & Kappeler, 1997). This has been attributed to both low social intelligence (Jolly, 1966) and the lack of formalized dominance signaling seen in other primates (M. E. Pereira & Kappeler, 1997). In addition, lemur groups are relatively small and may be comprised of closely related females. The close relatedness of females within the group may not necessitate the formation of formalized dominance

hierarchies and could explain why intragroup competition among females is relatively low. The lack of female coalitional support may also be explained to some degree by high infant and juvenile mortality rates. For example, an adult female Milne Edwards' sifaka (*Propithecus diadema edwardsi*) is only expected to have a single daughter that survives to reproductive age compared to 2.7 daughters in Old World monkeys and 3.4 in New World monkeys (Pochron et al., 2004). It may be that the low reproductive output of many lemur species precludes the formation of matrilineal networks as seen in anthropoid primates because adult females simply do not have an extended network of females and sisters (Pochron et al., 2004).

However, instead of focusing on the relatively low rates of aggression in lemurs, it may be more useful to examine the context and timing of female aggression, with their varied effects on dominance relationships. For example, dominance hierarchies of female *Propithecus verreauxi* may be easier to classify during particular seasons, such as the wet season when contest competition increases over access to higher quality resources (Richard, 1978). Rates of feeding agonism have also been observed to increase during the wet season among female ring-tailed lemurs (*Lemur catta*) (Sauther, 1993), with females showing higher rates of feeding aggression when resources were clumped and monopolizable (Gemmell & Gould, 2008). Given the extreme seasonal climate of Madagascar, it may be that many species of lemurs shift competitive tactics in response to variations in plant productivity. Scramble competition for mature leaves during the dry season may give way to contest competition over fruits, flowers, and young leaves during the season of resource abundance. If this is the case, the model of matrilineal dominance

hierarchies in Old World Monkeys may not be an appropriate comparison for species of lemurs, where dominance relationships may be seasonally dependent.

### **Behavioral Adaptation to an Ecological Niche: The Case of Verreaux's Sifaka**

Taken together, the unique traits described above make it exceedingly difficult to categorize lemurs within current socioecological models. Their adaptations to an extreme environment have led to social structures that deviate from the expected, which have in turn affected female relationships and competition. Though lemurs may appear “idiosyncratic” compared to the rest of the primate order, they provide an important evolutionary link between primates and other mammals. In order to fully understand the evolution of female competitive behavior within primates, it is necessary to examine the selective pressures that have shaped female reproductive strategies throughout primate evolution. Since lemurs are female dominant, they also provide the opportunity to examine female competition in a context where male constraints on female behavior tend to be more relaxed (Kappeler, 1993b). Finally, the geographical and climatic variation in Madagascar has led to a number of species and population level differences in adaptive responses, providing yet another opportunity to examine behavioral adaptations to particular ecological niches. These points will be examined further in the case of Verreaux's sifaka (*Propithecus verreauxi*).

Verreaux's sifaka are diurnal and arboreal lemurs that are found along the south and southwest region of Madagascar (Mittermeier et al., 2008). They live in groups of 2-13 individuals with approximately 1-3 females per group (Richard, 1992). Although female philopatry is the norm (Richard et al., 1991), there is evidence that females

emigrate when the number of females within a group exceeds three (Kubzdela, 1997). Like other lemur species living in the extreme environment of Madagascar, sifaka endure seasonal shifts in resource availability. In fact, the southwest region of Madagascar is characterized by a high degree of interannual variation in rainfall (Dewar & Richard, 2007; Lawler et al., 2009) that has a profound effect on the availability of fruits and flowers (Dewar & Richard, 2008). Sifaka are folivores, subsisting primarily on leaves during the dry season (April/May to October/November), with an increasing reliance on flowers and fruits with the onset of the rains (November to March) (Lewis & Kappeler, 2005; Yamashita, 2008). Seasonal fluctuations in resource availability have profound effects on the timing of reproduction for this species. Sifaka are highly seasonal breeders, with the mating season occurring between January and March, and females displaying estrus within the narrow window of 0.5 to 96 hours (Brockman, 1999). Births occur during mid-June to mid-August, and infants are weaned during the subsequent wet season (Brockman, 1994; Richard et al., 2002). Mating in this species is usually polygynous (Brockman, 1999; Brockman & Whitten, 1996), although monogamous and polyandrous mating have been observed (Kubzdela, 1997; Richard et al., 2002). The mating season is characterized by increased intramale aggression and competition for mates, as well as female competition for mates, particularly when females display estrous synchrony (Brockman, 1999). Females exercise a degree of mate choice, often preferring resident males, but also engage in mating opportunities with peripheral or extra-group males, displaying situation-dependent receptivity that may be a counter-strategy to infanticide (Brockman, 1999;

Brockman & Whitten, 1996). Males curtail female mate choice through mate-guarding and copulatory harassment (Brockman, 1999). Paternity data from Beza Mahafaly Special Reserve, Madagascar reveal that extra-group males do sire offspring, providing additional evidence for the influence of female mate choice on male reproductive success (Lawler, 2007; Lawler et al., 2003). However, paternity data from Kirindy shows high reproductive skew among males, with resident males siring 83% of the offspring (Kappeler & Schaffler, 2008). This points to important population differences within the species, suggesting slightly differing strategies across these habitats that may contribute to male and female reproductive success.

Female reproductive success is contingent upon a number of social and ecological factors that may have a profound impact on reproductive strategies, competition, and female dominance relationships. Female Verreaux's sifaka reach reproductive maturity around age five, with reproductive success increasing after age six and then dramatically decreasing after age 18 (Richard et al., 2002). Compared to haplorrhines, sifaka females display a "slower" life history continuum by delaying age of first reproduction and reproducing longer, suggesting a "bet hedging" reproductive strategy (Richard et al., 2002). This may be especially salient for species living in extreme environmental conditions with drastic fluctuations in resource availability, where it is beneficial to extend reproduction in order to increase the possibility of reproducing when conditions are optimal (Richard et al., 2002). In the Beza Mahafaly population, approximately 44% of females give birth during a given year, and only 52% of infants survive to one year, with peak deaths occurring immediately after birth and during the subsequent wet season when

infants are weaned (Richard et al., 2002; Richard et al., 1991). On average, females have an interbirth interval of one year and females with a surviving infant are more likely to have an infant the following year (Richard et al., 2000); however, this is not indicative of the genus *Propithecus*, and species and population differences exist (Erhart & Overdorff, 1998). Like many other lemur species, sifaka time the most energetically demanding reproductive stages (gestation and lactation) to the period of decreased resource availability, which is demonstrated by fluctuations in body mass throughout the year. Female body mass increases throughout the wet season and peaks just before the onset of the dry season (March – June), and then continues to decline throughout the dry season (Lewis & Kappeler, 2005; Richard et al., 2000). Body mass is linked to female reproductive success and heavier females are significantly more likely to give birth and successfully wean infants compared to lighter females (Lewis & Kappeler, 2005; Richard et al., 2000). These observations demonstrate that the timing of reproduction is crucial to infant survival and that individual reproductive success is contingent upon how well a female negotiates the period of decreased resource availability before the onset of the mating season (Lewis & Kappeler, 2005).

Given that access to resources appears to be paramount to individual female reproductive success, it follows that females should compete for access to high quality resources during periods of food abundance, and that dominance status and the number of females within a group may influence reproductive success. In fact, in large groups, resource competition may negatively impact subordinate females in this species through lower foraging efficiency and decreased reproductive success

(Kubzdela, 1997). Furthermore, there is evidence to suggest that resident females control female group size by harassing unrelated female immigrants (Lewis, 2008). Although females in this species do not display high rates of intrasexual aggression, competition among females will still occur when demographic and environmental conditions warrant. For example, intrasexual competition, especially in the form of intergroup encounters, may increase during the period of resource availability for access to high quality resources (Richard et al., 2000). Further exploration of this context-dependent competition may help to elucidate both population and species differences in the amount and degree of female competition in Verreaux's sifaka, and may contribute more to our understanding of both the similarities and differences in lemur female reproductive strategies compared to anthropoid primates.

### **The Endocrinology of Competition**

Understanding the evolution of female competition in primates requires a more comprehensive assessment of the costs and benefits of female social rank and aggression. The field of socioendocrinology investigates hormonal responses to the social environment, providing a physiological lens through which to examine the potential negative consequences of competition. For example, chronically elevated levels of hormones associated with stress (glucocorticoids) and aggression (androgens) can negatively impact health (Sapolsky, 2004), survival (Pride, 2005b), and parenting effort (Wingfield et al., 2001). Assessing the extent to which social rank and aggression are hormonally mediated may elucidate some of the constraints



placed on female competitive behavior. This section will provide an overview of the existing literature in this area, laying the groundwork for the current study.

### **Androgens, Aggression, and Dominance**

The physiological framework for the hormonal mediation of aggressive behavior begins with the sensory input of environmental (such as changes in photoperiod, temperature, rainfall) and social cues that stimulate the hypothalamic-pituitary-gonadal (HPG) axis, releasing steroid hormones into circulation that have affects both on peripheral tissues and the brain (Adkins-Regan, 2005). Androgens in circulation can bind to peripheral tissues or specific target areas of the brain (particularly the preoptic area, the hypothalamus, and the amygdala) via specific androgen receptors within the cell nucleus, which show a high affinity for both testosterone and dihydrotestosterone (Adkins-Regan, 2005). Once bound, these receptor-ligand complexes regulate gene transcription, resulting in the synthesis of enzymes and proteins responsible for the production of neurotransmitters, neuropeptides, and their associated receptors, which can have direct effects on the regulation of aggressive behavior (Adkins-Regan, 2005; Monaghan & Glickman, 2001). Genomic effects may take several hours, therefore they most likely prime neural systems associated with aggression for future behavioral reactions, possibly through varying target tissue sensitivity and/or affecting the threshold for maintaining and initiating a particular behavioral response (Adkins-Regan, 2005; Monaghan & Glickman, 2001; Whitten, 2000). Recent evidence suggests the potential for steroid hormones to have non-genomic effects (such as interactions with neurotransmitter receptors or effects on ion channels that regulate synaptic activity), which may have more

immediate results on behavior (Adkins-Regan, 2005; Whitten, 2000). Furthermore, interactions between hormones and behavior are bidirectional, so that changes in behavioral states may influence hormonal levels as well as vice versa (Adkins-Regan, 2005; Monaghan & Glickman, 2001; Sapolsky, 1997; Whitten, 2000). This may be especially true in the interaction between androgens and aggression, where more often than not, increases in aggressive behavior precipitate elevations in testosterone levels (Sapolsky, 1997). However, elevated testosterone levels can come with substantial costs and have been associated with impaired immune function and decreased parental care (reviewed in Wingfield et al., 2001).

Given these costs, it is particularly salient to investigate hormone-behavior interactions in female primates, who must constantly negotiate a fine balance between engaging in both maternal care and competition with other group members. However, much of the research on the associations among androgens, aggression, and dominance in non-human primates has focused on males, with relatively little study of these relationships in female primates. Therefore, I begin here with an overview of the existing knowledge of androgens and aggression in males, before moving on to examine the evidence in females, and in lemurs more specifically.

#### *Evidence for Male Non-human Primates*

Significant associations among testosterone, rank, and aggression in both captive and wild studies of male non-human primates have been found in: *Propithecus verreauxi* (Brockman et al., 2001; Brockman et al., 1998); *Lemur catta* (Cavigelli & Pereira, 2000); *Papio hamadryas anubis* (Sapolsky, 1991); *Papio hamadryas ursinus* (Beehner et al.,

2006); *Pan troglodytes* (Anestis, 2006; Muehlenbein et al., 2004; Muller & Wrangham, 2004a); and *Pan paniscus* (Marshall & Hohmann, 2005). No significant associations among these variables have been documented for: *Eulemur fulvus rufus* (Ostner et al., 2002); *Cebus apella nigrinus* (Lynch et al., 2002); *Macaca fuscata* (Barrett et al., 2002a); *Alouatta palliata* (Cristoal-Azkarate et al., 2006); and *Pan troglodytes* (Klinkova et al., 2004). These studies highlight the myriad of individual, social, and environmental factors that impact the degree to which testosterone is associated to dominance and aggression.

Social factors such as the relative stability of the dominance hierarchy (Sapolsky, 1991); the type of mating system (Whitten, 2000; Whitten & Turner, 2004); demographic changes, such as immigration events (Alberts et al., 1992; Brockman et al., 2001; Brockman et al., 1998); seasonal changes in inter-male aggression (Brockman et al., 2001; Lynch et al., 2002; Strier et al., 1999); and the presence of cycling females (Lynch et al., 2002; Muller & Wrangham, 2004a; Whitten, 2000) may all affect the degree to which testosterone is associated with rank in male non-human primates. For example, male rank is only positively associated with individual serum testosterone concentrations during periods of social instability in wild olive baboons (*Papio hamadryas anubis*) (Sapolsky, 1991, 1993a), when rank reversals are common and inter-male aggression is high. Similar results were found in chacma baboons (*Papio hamadryas ursinus*), where rates of aggression were significantly positively correlated to individual fecal testosterone levels only when the hierarchy was classified as unstable (Beehner et al., 2006).

The relationships among testosterone, aggression, and dominance are also expected to fluctuate based on mating system, particularly the degree to which dominant males maintain exclusive access to females, and the presence of cycling females

(Whitten, 2000; Whitten & Turner, 2004; Wingfield et al., 1990). This had led to the formation of the “challenge hypothesis,” which predicts that testosterone levels increase during periods characterized by intense inter-male competition and territory defense (such as the breeding season), and that this increase is especially pronounced for polygynous males (Wingfield et al., 1990). For example, in cercopithecoids, testosterone levels during the breeding season in males living in multi-male groups were higher compared to males residing in uni-male groups, reflecting differences in the duration and intensity of inter-male competition and aggression (Whitten, 2000). In wild male chimpanzees (*Pan troglodytes*), urinary testosterone concentrations paralleled increases in inter-male aggression associated with the presence of sexually receptive parous females (Muller & Wrangham, 2004a). However, for tufted capuchin monkeys (*Cebus apella nigritus*), a seasonally breeding primate living in multi-male/multi-female groups, fecal testosterone levels were significantly positively associated with sexual behavior, but not with rates of inter-male aggression (Lynch et al., 2002). The lack of association between testosterone and aggression in this species may be due to the fact that female choice, rather than inter-male aggression, appears to predict male reproductive success (Lynch et al., 2002).

The relative importance of using aggressive strategies in the acquisition of dominance will also affect species-level differences in the associations among testosterone, aggression, and status (Whitten, 2000). In particular, social primates exhibit a high degree of social tolerance that is not accounted for by predictions of the challenge hypothesis (Whitten & Turner, 2004), and often coalition and alliance formation can be equally or more important in maintaining dominance than overt aggression (de Waal,

1989). Studies of *Brachyteles arachnoids* (Strier et al., 1999), *Cebus apella nigrinus* (Lynch et al., 2002), *Alouatta palliata* (Cristoal-Azkarate et al., 2006), and *Pan paniscus* (Sannen et al., 2004) failed to find rank-related differences in testosterone, most likely attributable to the relatively low rates of overt inter-male aggression. For example, status for male bonobos (*P. paniscus*) is more contingent upon the rank of the mother than male-male competition (Sannen et al., 2004), and aggressive interactions among muriqui (*B. arachnoids*) are low due to the fact that the dominant male does not monopolize access to females (Strier et al., 1999). In determining the extent to which testosterone is associated with rank across primate species, it is necessary to consider the delicate balance between affiliative and aggressive behaviors that impact social cohesion and the relative extent to which aggression is necessary to maintain status (Whitten, 2000).

#### *Evidence for Female Non-human Primates*

The research on female aggression across taxa suggest that, similar to males, the extent to which female aggression is related to circulating levels of androgens may depend upon reproductive state (Beehner et al., 2005; Floody, 1983), season (Floody, 1983; Rubenstein & Wikelski, 2005; von Engelhardt et al., 2000), availability of resources (Beehner et al., 2005), social factors such as mating system (Langmore et al., 2002), interactions with conspecifics (Batty et al., 1986), and the ability to form coalitions (Goymann et al., 2001; Sannen et al., 2004), as well as individual factors, particularly the relative costs associated with increased androgen levels on female reproduction (Zysling et al., 2003). Unfortunately, there is very little data available examining the relationships among testosterone, dominance, and aggression in adult

female non-human primates, making it especially difficult to draw any strong conclusions about these associations. An early study of captive female talapoin monkeys (*Miopithecus talapoin*) determined rank-related differences in plasma testosterone and androstenedione, with subordinate females showing significantly lower concentrations of both androgens compared to intermediate- and high-ranking females (Batty et al., 1986). However, even though dominant females displayed the highest rates of aggression compared to intermediate-ranking and subordinate females, individual levels of testosterone were not correlated with individual rates of aggression (Batty et al., 1986). Wild hybrid baboon females (*Papio spp.*) demonstrated seasonal differences in fecal testosterone levels, displaying higher testosterone and aggression levels during the season when female resource competition was at its peak (Beehner et al., 2005). In addition, there were significant rank-related differences in testosterone levels, with high-ranking females showing higher testosterone levels compared to subordinates (Beehner et al., 2005). These rank-related differences occurred despite the fact that the female hierarchy remained stable throughout the study period. The authors suggest that this result reflects the linear nature of female dominance hierarchies in this species, where non-aggressive interactions reinforce the “losing” perception of subordinates and the “winning” perception of dominants, which in turn affect testosterone levels. After rank was controlled, there was no significant association between rates of aggression and testosterone level across individuals; however, there was a significant positive association between rates of aggression and testosterone levels within individuals (Beehner et al., 2005). Finally, a study of captive bonobos (*Pan paniscus*) revealed no rank-related differences in urinary metabolites of testosterone, and no rank-related differences in

aggression (Sannen et al., 2004). This may be due to the fact that aggression is relatively unimportant in the acquisition of rank in this species since females rely on coalitions with other females to maintain status (Sannen et al., 2004).

At this point, there is no available research on the possible negative impacts of increased androgen levels on female reproduction, survival, or immune function in non-human primates; although, androgens have been implicated in increased reproductive failures in a few cases (Brockman & Whitten, 1996; Packer et al., 1995; Pusey & Williams, 1997). An area of future research involves identifying the roles of weaker androgens, such as androstenedione and dihydroepiandrosterone (DHEA), or the aromatization of testosterone to estrogens as possible mechanisms for mediating female aggression, thereby avoiding the potential costs of maintaining elevated testosterone levels (Glickman et al., 1992; Rubenstein & Wikelski, 2005; van Jaarsveld & Skinner, 1991; Wingfield et al., 2001).

### *Evidence for Lemurs*

Research across species of lemuroid primates provides additional evidence for the complex relationship among testosterone, aggression, and dominance. A study of wild Verreaux's sifaka (*Propithecus verreauxi*) noted rank-related differences in testosterone levels, with dominant males showing fecal testosterone levels that were five times higher than subordinates; however, dominant males only had higher testosterone levels compared to subordinates in unstable social groups (Brockman et al., 2001). Furthermore, dominant males in unstable groups had testosterone concentrations that were three times higher than dominant males in stable groups, again suggesting that periods marked by

increased competition for rank strengthen associations between androgens and dominance status (Brockman et al., 2001). In studies of ring-tailed lemurs (*Lemur catta*), males showed higher levels of testosterone in the mating season during the peak of male-male competition, although individual rates of aggression were not significantly associated with testosterone levels and there were no rank-related differences in testosterone levels (Cavigelli & Pereira, 2000; Gould, 2005).

These studies demonstrate that social factors, particularly immigration events, may outweigh seasonal effects on testosterone and aggression for some lemur species (Brockman et al., 2001; Brockman et al., 1998; Ostner et al., 2002). For example, there was no significant difference in fecal testosterone levels between breeding and birth seasons in male Verreaux's sifaka (*Propithecus verreauxi*), most likely due to the influx of new males during the birth season (Brockman et al., 2001; Brockman et al., 1998). Contrary to expectations, alpha males appeared to sustain elevated testosterone levels after the breeding season, possibly to facilitate their ability to respond to challenges of group membership from immigrating males (Brockman et al., 2001). Since dominance confers reproductive advantages in terms of mating priority, Brockman et al. (2001) suggest that maintaining status throughout the non-breeding season may be particularly important for ensuring reproductive success in the next mating season. A study of wild red-fronted lemurs (*Eulemur fulvus rufus*) also demonstrated that fecal testosterone levels peaked in both the mating and birth seasons, but were actually higher in the birth season (Ostner et al., 2002). It is possible that, similar to sifaka, the increase in birth season testosterone levels is associated with male transfer events and the increased risk of infanticide, which requires males to remain aggressively vigilant. However, monthly



testosterone levels were not correlated to the frequency of inter-male agonistic encounters, and there was no significant relationship between individual aggression and testosterone levels, making it difficult to conclude that birth season testosterone levels are either responding to, or driving, inter-male conflict during this time (Ostner et al., 2002).

As in the broader primate literature, there is a paucity of available data on the relationships among testosterone, dominance, and aggression in female lemurs. The studies that do exist tend to focus on the mediating role of androgens in masculinized genitalia (Drea & Weil, 2008) and female social dominance (Drea, 2007; von Engelhardt et al., 2000) as a comparison to research conducted in female spotted hyenas (*Crocuta crocuta*). Two studies that focused on female androgen levels were conducted on captive ring-tailed lemurs (*Lemur catta*). The first study found no rank-related differences in fecal testosterone levels, and no association between testosterone and individual rates of aggression (von Engelhardt et al., 2000). However, both aggression and androgen levels increased during the mating season, a period that is marked by intense targeted female aggression and eviction (von Engelhardt et al., 2000). The second study examined both testosterone and androstenedione levels in females, and found similar results (Drea, 2007). Females showed a higher production of androstenedione than testosterone, and this difference was most pronounced during the breeding and birthing seasons. In the case of the breeding season, this peak in androgen activity corresponded to an increase in female intrasexual aggression. Drea (2007) suggests that androstenedione may be a strong candidate for mediating female aggression and dominance in this species as a way to mitigate the potential costs of elevated testosterone levels. Take together, these studies provide preliminary evidence that associations between androgens and aggression in

female lemurs may become more salient during the season when inter-female competition is highest. Despite this promising trend, it remains necessary to test these predictions in populations of wild lemurs, where competition is not constrained by aspects of captivity, in order to fully explore the relationships between androgens and competitive behavior in female lemurs.

### **Competition and the Stress Response**

Examining the endocrine response to stress is also an effective way of clarifying the potential costs associated with social rank and competition. The stress response begins with sensory input in the brain, alerting the body to a potential threat and resulting in a cascade of hormonal events that triggers the release of epinephrine from the adrenal medulla and glucocorticoids from the adrenal cortex (reviewed in Sapolsky, 2002). The release of glucocorticoids primes physiological systems for effectively responding to the immediate threat, while temporarily redirecting energy from non-essential activities. Glucocorticoids stimulate cardiac output and mobilize energy for the “fight or flight” response, but have suppressive effects on gonadal steroids and insulin secretion (Sapolsky, 2002). If the acute stressor continues for a prolonged period of time, this “emergency response” may temporarily halt life history stages, such as breeding, until conditions improve (Wingfield et al., 1998; Wingfield & Ramenofsky, 1999). Because of the suppressive effects of glucocorticoids, prolonged exposure to elevated levels can negatively impact other physiological systems (reviewed in Sapolsky, 2002). Chronic stress can result in an increased risk of cardiovascular disease and gastrointestinal

disorders, as well as suppression of immune and reproductive function (Sapolsky, 2002, 2005; Wingfield & Ramenofsky, 1999).

If competition results in increased risk of agonistic encounters among group members, then social status in and of itself may carry a certain degree of physical and psychosocial stress (Goymann & Wingfield, 2004a; Sapolsky, 1982). While there tends to be an assumption that subordinate status carries the majority of the burdens associated with competition, there is growing evidence to suggest that dominance may actually be associated with higher levels of glucocorticoids (Abbott et al., 2003; Creel, 2001, 2005; Goymann & Wingfield, 2004a). As the results from the previous section on androgens demonstrated, the extent to which stress hormones are related to social rank and rates of aggression remains complex and dependent on a number of demographic, social, and ecological factors.

#### *Evidence from Male Non-human Primates*

Some of the earliest research in primates examining the associations between social rank and glucocorticoid levels came from studies of wild male olive baboons (*Papio anubis*) (Sapolsky, 1982, 1991, 1992). Subordinate status appeared to be particularly stressful for male baboons because they are frequently on the receiving end of aggressive harassment from dominant males. This is reflected by the fact that subordinate males had higher serum cortisol levels compared to dominants (Sapolsky, 1982). However, this rank-related difference in cortisol only emerged when dominance hierarchies were stable (Sapolsky, 1992). When hierarchies were in flux and individuals were forced to actively defend their rank positions, dominant males showed the highest

cortisol levels (Sapolsky, 1992). Going one step further, this early work made it clear that there are significant differences in cortisol levels among individual males that appear to be influenced by particular “personality styles” (Ray & Sapolsky, 1992; Virgin & Sapolsky, 1997). For example, dominant males that associated more with females and had outlets for displacing aggression showed decreased cortisol levels compared to individuals that lacked these social buffers (Ray & Sapolsky, 1992). Other studies on male primates have demonstrated higher glucocorticoid levels in dominant individuals (Japanese macaques (*Macaca fuscata*) (Barrett et al., 2002a) and chimpanzees (*Pan troglodytes*) (Muller & Wrangham, 2004c)), while most have failed to detect rank-related differences in stress hormones (golden lion tamarins (*Leontopithecus rosalia*) (Bales et al., 2006), tufted capuchin monkeys (*Cebus apella*) (Lynch et al., 2002), rhesus macaques (*Macaca mulatta*) (Bercovitch & Clarke, 1995), and gorillas (*Gorilla gorilla beringei*) (Robbins & Czekala, 1997)).

The extent to which social status is associated with glucocorticoid levels is largely dependent upon how dominance is acquired and maintained across species (Goymann & Wingfield, 2004a). The term “allostatic load” refers to the energetic burden associated with maintaining homeostasis in the face of social and environmental perturbations (*sensu* Goymann & Wingfield, 2004a). Therefore, the energy required for maintaining balance during periods of acute stress is reflected in an increase in allostatic load, which is accompanied by a concomitant increase in glucocorticoid levels. Goymann & Wingfield (2004) argue that the concept of “allostatic load” represents a useful heuristic tool for determining the relative costs associated with dominance status. If dominance status is acquired through aggression and constant vigilance, dominant animals are

expected to have relatively higher energetic costs associated with maintaining status, and therefore, higher glucocorticoid levels. If, however, subordinates are consistently on the receiving end of aggression, they are predicted to have higher levels of stress. Finally, if social rank is not mediated via aggressive interactions, which is true for many primate species, then no rank-related differences in stress levels are expected to emerge (Bercovitch & Ziegler, 2002; Goymann & Wingfield, 2004a).

These predictions appear to be supported by the available evidence from male primates. For example, dominant male Japanese macaques (*Macaca fuscata*) had significantly higher cortisol levels compared to subordinates, which seems to be related to the increased energetic burdens associated with dominant male mate guarding (Barrett et al., 2002a). Male chimpanzees (*Pan troglodytes*) showed higher cortisol levels compared to subordinates, and rates of aggression were significantly correlated to cortisol levels during the season of increased food competition (Muller & Wrangham, 2004c). The authors suggest that for male chimpanzees, rank-related differences in cortisol levels are related to increased energy expenditure resulting from competition for high-quality resources. For male tufted capuchin monkeys (*Cebus apella*) (Lynch et al., 2002) and golden lion tamarins (*Leontopithecus rosalia*) (Bales et al., 2006), glucocorticoid levels were associated with the energetic requirements of reproduction and parental care rather than with rank or rates of aggression, which is not altogether surprising given that rates of inter-male aggression tend to be low for these species.

Of course, ecological perturbations such as severe droughts and storms (Wingfield et al., 1998), cold stress (Beehner & McCann, 2008), and seasonal fluctuations in resource availability (Muller & Wrangham, 2004c) can also elicit a

significant stress response. Male gelada baboons (*Theropithecus gelada*) had higher fecal glucocorticoid levels at high altitudes and low temperatures, providing physiological evidence for cold stress (Beehner & McCann, 2008). Glucocorticoid levels in male tufted capuchin monkeys (*Cebus apella*) were negatively correlated with rainfall and peaked during the dry season (Lynch et al., 2002). For male chimpanzees (*Pan troglodytes*), fecal glucocorticoid levels were negatively correlated with fruit abundance, suggesting energetic stress when high quality resources were less available (Muller & Wrangham, 2004c). It is possible that the energetic burdens associated with seasonal variations in resource availability and breeding effort may override any intrinsic differences in stress hormone levels related to social rank (Wingfield et al., 1998; Wingfield & Ramenofsky, 1999). These considerations may be particularly important when considering resource competition across seasons in female primates.

#### *Evidence from Female Non-human Primates*

Relatively fewer studies have focused on the stress response in female primates, but these studies have revealed that females may be particularly sensitive to social and ecological changes, such as male immigration events and seasonal fluctuations in resource availability (reviewed in Cheney & Seyfarth, 2009). The extent to which females demonstrate rank-related differences in glucocorticoid levels may be tied to the degree of reproductive skew (Cheney & Seyfarth, 2009). Research on cooperatively breeding mammals (dwarf mongoose (*Helogale parvula*), African wild dog (*Lycaon pictus*), and the gray wolf (*Canis lupus*)) has demonstrated that dominant females have higher glucocorticoid levels compared to subordinates (Creel, 2005), which is also true

for female primates with a high degree of reproductive skew (ring-tailed lemurs (*Lemur catta*): (Cavigelli, 1999; Cavigelli et al., 2003), although see (Pride, 2005a, 2005c); marmosets (*Callithrix jacchus*): (Saltzman et al., 1994), and cotton-top tamarins (*Saguinus oedipus*): (Ziegler et al., 1995)). There are no rank-related differences in glucocorticoid levels in female primates with a low degree of reproductive skew (mandrills (*Mandrillus sphinx*): (Setchell et al., 2008), cynomolgus monkeys (*Macaca fascicularis*): (Stavisky et al., 2001), and chacma baboons (*Papio hamadryas ursinus*): (Crockford et al., 2008; Engh et al., 2006; Weingrill et al., 2004). Most of these studies did not examine associations between aggression and stress hormones (although see Weingrill et al., 2004 and discussion of lemurs below), so the extent to which aggressive competition results in heightened stress for female primates remains unknown. However, as with male primates, we may expect that the degree to which aggression is associated with stress hormones is entirely dependent upon the extent to which social rank is mediated via overt agonistic encounters among females (Goymann & Wingfield, 2004a). For males, these associations may strengthen during the mating period, when rates of inter-male competition increase; whereas for females, these associations may emerge during seasons when contest competition for resources is high.

For example, female primates appear to be particularly sensitive to environmental changes, demonstrating marked endocrine responses to seasonal shifts in rainfall, temperature, and day length. Fecal glucocorticoid levels are associated with photoperiod and temperature for female chacma baboons (*Papio hamadryas ursinus*), suggesting that elevated levels during the winter months are a response to cold stress (Weingrill et al., 2004). However, for female yellow baboons (*Papio cynocephalus*), fecal glucocorticoid

levels were higher in the dry season compared to the wet season, especially during the hottest months (Gesquiere et al., 2008). The increased glucocorticoids during the dry season most likely reflect the seasonal shift to lower-quality foods as well as the reduced availability of drinking water (Gesquiere et al., 2008). These findings parallel results from other female mammals (African elephants (*Loxodonta africana*) (Foley et al., 2001), mule deer (*Odocoileus hemionus*) (Saltz & White, 1991), and Pampas deer (*Ozotoceros bezoarticus bezoarticus*) (R. J. G. Pereira et al., 2006)), which also showed elevated glucocorticoid responses during the season of decreased resource availability. However, these seasonal shifts in resources do not necessarily reflect acute stressors, especially since these changes are likely to be predictable events (Wingfield & Ramenofsky, 1999). Rather, the increased secretion of glucocorticoids triggers the mobilization of energy from fat storage, which serves as an adaptive physiological response to the energetic requirements during the lean season (Foley et al., 2001; Gesquiere et al., 2008; Romero, 2002). If rank-related differences in feeding competition emerge during seasons when resources are less readily available, then the relative costs associated with social rank may become particularly pronounced for females during this time. Examining the stress response across seasons in conjunction with feeding efficiency and nutrient intake may be a useful way of determining the extent to which resource competition is reflected in increased stress for females.

Although seasonal fluctuations may represent low-level chronic stress for female primates, male immigration events represent acute social stress. Female olive baboons (*Papio anubis*) and chacma baboons (*Papio hamadryas ursinus*) showed marked elevations in glucocorticoid levels after the immigration of a new male (Alberts et al.,



1992; Engh et al., 2006; Wittig et al., 2008), which appeared to be directly related to the threat of infanticide. Females with dependent offspring, who are at a high risk for infanticide, had the highest glucocorticoid levels (Engh et al., 2006; Wittig et al., 2008). Glucocorticoid levels were also higher in the months when infanticides occurred (Engh et al., 2006). For female mantled howler monkeys (*Alouatta palliate*), the mere presence of solitary males appeared to trigger a stress response, suggesting that females are sensitive to the perceived threat of infanticide even before males immigrate (Cristobal-Azkarate et al., 2007). These observations suggest that acute stress for females may be tied to events that directly impact infant survival.

#### *Evidence from Lemurs*

There are a limited number of studies examining the relationships among dominance, aggression, and stress hormones in lemuroid primates; those that have been conducted show disparate results. One study found that dominant male Verreaux's sifaka had higher fecal glucocorticoid levels compared to subordinate males during the mating season, but not the birth season (Fichtel et al., 2007). Since rates of aggression among males were not related to fecal glucocorticoid levels, the authors suggest that the rank-related differences were due to the increased energy required for dominant males to guard potential mates. By contrast, studies of male red-fronted lemurs (*Eulemur fulvus rufus*) (Ostner, Kappeler et al., 2008) and Verreaux's sifaka (Brockman et al., 2009) found that fecal glucocorticoids were elevated during the birth season, although neither rank nor aggression were related to hormone levels. It is possible that for these species, elevated

glucocorticoid levels are related to the threat of male immigration and infanticide during the birth season (Brockman et al., 2009; Ostner, Kappeler et al., 2008).

Studies of stress hormones in female lemurs have been restricted to *Lemur catta*, and also reveal some conflicting results. A study of female ring-tailed lemurs during the lactation period at Beza Mahafaly Special Reserve demonstrated that dominants had higher fecal glucocorticoid levels compared to subordinates (Cavigelli, 1999). These results were confirmed in a comparative study that included female ring-tailed lemurs from two separate field sites and the Duke University Primate Center (Cavigelli et al., 2003). However, another study of female ring-tailed lemurs at Beza Mahafaly failed to find rank-related differences in fecal glucocorticoid levels (Pride, 2005c). The reason for this apparent discrepancy may be related to the time frame of the two studies. While Cavigelli et al. (2003) collected data only during the lactation period, Pride (2005a,c) collected data year round. Because the lactation period coincides with the end of the dry season, it is possible that the rank-related differences emerged during this time due to increased contest competition for resources (Cavigelli et al., 2003). In fact, groups that showed higher rates of aggression also showed the highest fecal glucocorticoid levels, leading the authors to conclude that feeding competition is particularly stressful during this time (Cavigelli et al., 2003). Rates of within-group competition did not predict fecal glucocorticoid levels in the Pride (2005a,c) study, although rates of aggressive participation in intergroup encounters were a strong predictor of stress hormones. This suggests that the form of competition, as well as its relative predictability, may influence the extent to which a competitive encounter is deemed stressful (Pride, 2005a). Low food intake was also associated with elevated fecal glucocorticoid levels (Pride, 2005a), and

these levels were higher during the period of decreased rainfall and reduced fruit availability (Pride, 2005c). Females may show elevated glucocorticoid levels during the lean season in order to mobilize energy from fat stores when resources are not readily available (Pride, 2005c). Taken together, these results suggest that the energetic stress associated with feeding competition is reflected in elevated glucocorticoid levels for female lemurs. However, these hormone-behavior interactions may be seasonally dependent, becoming more pronounced during periods of increased contest competition and decreased food availability. Examining these interactions across seasons may have profound implications for the relative costs associated with competition and social rank in female lemurs.

### **General Research Aims**

This study focused on examining aspects of competition, dominance, and aggression within an endocrinological context in wild female Verreaux's sifaka (*Propithecus verreauxi*) at Beza Mahafaly Special Reserve, Madagascar. I chose to limit this study to adult females with infants in order to control for reproductive state when assessing hormonal levels, as well as to examine female competitive behavior during this energetically expensive stage of reproduction. Since lactation is timed to the lean, dry season (Brockman, 1999; Richard et al., 2000), this also provided the opportunity to examine competitive behavior during a time when females may be energetically stressed (Richard et al., 2000). This study also encompassed the transition from the dry to the wet season, which allowed me to track changes in behavior and endocrine measures across this transitional period. As stated above, seasonal shifts in resource availability may be

particularly salient for dominance relationships, aggression, and hormone-behavior interactions in female lemuroid primates. Despite the fact that lemurs are generally categorized as egalitarian, it is likely that dominance relationships are seasonally dependent, emerging when contest competition for resources increases (Erhart & Overdorff, 2008; Richard, 1978). Referring back to the questions posed at the beginning of the chapter, I set out to test the following predictions:

**1. Is female competition mediated by dominance status and aggression?**

*Hypothesis 1A:* Dominant females are expected to show higher rates of aggression compared to subordinate females. In addition, rates of aggression are expected to increase with increased competition for high-quality resources; therefore, rates of aggression are expected to be higher in the period after the onset of rains compared to the dry season. Previous research on Verreaux's sifaka suggested that contest competition increases during the wet season (Richard, 1978), but there is no available data on rates of female aggression across seasons.

*Hypothesis 1B:* Subordinate females are expected to show decreased feeding efficiency (measured by decreased feeding time and increased travel time) relative to dominant females. This prediction is supported by evidence from a previous study on this population where subordinate females showed decreased feeding efficiency and decreased reproductive success compared to dominants (Kubzdela, 1997). In addition, subordinate females are expected to spend more time in close proximity to group members while feeding compared with dominant females.

**2. What are the relationships among dominance, aggression, and testosterone levels?**

***Hypothesis 2A:*** Aggression is positively associated with fecal testosterone levels.

However, the association between aggression and fecal testosterone levels may strengthen after the onset of rains, when contest competition for resources increases. This prediction is supported by previous research on ring-tailed lemurs (*Lemur catta*) demonstrating that testosterone levels increase during periods of heightened aggression among females (Drea, 2007; von Engelhardt et al., 2000).

***Hypothesis 2B:*** Since dominant females are expected to show higher rates of aggression, they are also expected to show higher fecal testosterone levels compared to subordinate females.

**3. What are the social and environmental factors associated with stress?**

***Hypothesis 3A:*** Since sifaka live in the highly seasonal environment of Madagascar, fecal glucocorticoid levels are expected to be higher in the dry season compared to the period after the onset of rain. This elevation in glucocorticoid levels reflects the increased energetic demands for lactating females during the lean season.

***Hypothesis 3B:*** Since contest competition is expected to be low during the dry season, then fecal glucocorticoid levels are not expected to vary by rank during this time. This prediction is supported by prior research on male sifaka from the Beza Mahafaly population demonstrating that glucocorticoid levels are not related to social rank during the birth season (Brockman et al., 2009).

## Conclusions

Research over the past three decades has shifted focus towards understanding the complexities of female intrasexual competition and its impact on female relationships, behavior, and reproductive strategies. The emphasis on female competition continues to highlight the ways in which females are responding to sex-specific selective pressures, particularly infant survival, with a myriad of behavioral tactics that vary across species, social groups, and individuals. Females compete over access to resources that enhance reproduction throughout the year, and the intensity of competition is expected to vary depending on the availability of specific resources, energetic burden, and the degree of reproductive variance associated with a particular social group. This means that female intrasexual competition is influenced by environmental, social, and life history parameters.

It is important to note that while research on this topic has increased substantially over the past thirty years, there remain significant gaps in our understanding of female competitive behavior. A closer look at Table 1.1 reveals that most research on female intrasexual competition has focused on Old World monkeys, particularly species of baboons and macaques. This phylogenetic bias makes it difficult to draw broad conclusions about the evolution of female competition within the primate order.

In addition, there is still relatively little known about hormone-behavior interactions in female primates. Understanding the endocrinology of competition can elucidate the potential physiological costs associated with female competitive behavior. While research across the animal kingdom has demonstrated considerable intrasexual variation in reproductive behavior that can be attributed to subtle differences in neural

and endocrine activity, most of this research has focused on males, leaving the area of female intrasexual variation open for future research (Rhen & Crews, 2002). So far research on this topic has demonstrated that the hormonal correlates of stress and aggression are affected by a myriad of complex interactions among social and ecological factors. Assessing hormonal levels in relation to competitive behaviors will expand our understanding of the proximate mechanisms influencing aggression, dominance, and reproductive variance across individuals, as well as determine the potential costs associated with certain competitive strategies, and the extent to which aggression and stress may affect reproductive success.

The goal of the present study was to investigate hormone-behavior interactions in a strepsirrhine primate in order to offer preliminary evidence on the social and ecological factors that affect endocrine measures of aggression and stress. The results presented in the following chapters examine the extent to which social rank and aggression are mediated by androgen and glucocorticoid levels. In addition, these results provide evidence for seasonal changes in competitive behavior and hormone levels that may underlie potential shifts in female dominance relationships across seasons. This study adds to the growing body of research on hormone-behavior interactions in wild female primates by offering new insight into the complexities of female competitive behavior in one of the earliest branches of the primate order.

TABLE 1.1. RESOURCE COMPETITION IN NONHUMAN PRIMATES

Species	Resource Distribution	Female Hierarchy	Group size effect	Rank Related Differences in Feeding	Reference(s)
<i>Cercopithecus mitis erythrarchus</i>	?	formal	N/A	no significant rank related variations in diet or time spent feeding	(Payne et al., 2003); (Cords, 2002)
<i>Cercocebus torquatus atys</i>	N/A	linear	N/A	better foraging efficiency for dominants	(Range & Noe, 2002)
<i>Chlorocebus aethiops</i>	N/A	N/A	yes	no rank related differences in measures of reproductive success	(Cheney & Seyfarth, 1987)
<i>Chlorocebus aethiops</i>	clumped or distributed based on population	linear, stable	N/A	rank related differences in birth rate and timing when resources clumped	(Whitten, 1983)
<i>Chlorocebus aethiops and Erythrocebus patas</i>	clumped evenly distributed based on population	formal non-linear	N/A	N/A	(Pruetz & Isbell, 2000)
<i>Eulemur fulvus rufus and Eulemur rubriventer</i>	<i>E. f. rufus</i> utilized larger patches	N/A	yes	N/A	(Overdorff, 1996)
<i>Gorilla gorilla beringei</i>	N/A	N/A	yes	dominants displaced other females from feeding sites at higher rate	(David P. Watts, 1985);(D.P. Watts, 1990); (D. P. Watts, 1991);(D. P. Watts, 1994)
<i>Lemur catta</i>	N/A	N/A	N/A	priority access to food for dominants	(Hood & Jolly, 1995)
<i>Lemur catta</i>	?	?	?	dominants have fewer close neighbors while feeding	(Sauter, 1993)
<i>Macaca fascicularis and Presbytis thomasi</i>	clumped larger patch size	linear, stable non-linear	?	N/A	(Sterck & Steenbeek, 1997)
<i>Macaca fuscata</i>	varies by population	varies by population	yes?	N/A	(Nakagawa, 1998)
<i>Macaca fuscata</i>	clumped	?	?	priority access to high quality foods for dominants	(Saito, 1996)



TABLE 1.1. RESOURCE COMPETITION IN NONHUMAN PRIMATES

Species	Resource Distribution	Female Hierarchy	Group size effect	Rank Related Differences in Feeding	Reference(s)
<i>Macaca sinica</i>	?	?	yes	priority access to greater proportion of high-quality foods for dominants	(Dittus, 1977); (Dittus, 1979); (Dittus, 1988)
<i>Pan troglodytes</i>	N/A	linear	N/A	priority access to high quality foods that are monopolizable for dominants	(Wittig & Boesch, 2003)
<i>Papio anubis and Papio ursinus</i>	clumped evenly distributed	linear	N/A	higher feeding rate ( <i>Papio anubis</i> only) for dominants	(Barton & Whiten, 1993); (Barton et al., 1996)
<i>Papio ursinus</i>	?	?	N/A	no rank related differences in feeding time	(Ron et al., 1996)
<i>Semnopithecus entellus</i>	? *provisioning occurs	linear	N/A	greater feeding time for dominants	(Borries, 1993)
<i>Semnopithecus entellus</i>	clumped	linear	yes	priority access to high quality foods; overall better physical condition for dominants	(Koenig et al., 1998); (Koenig, 2000)
<i>Presbytis thomasi</i>	evenly distributed	relaxed	no effect on diet	N/A	(Sterck & Steenbeek, 1997); (Sterck, 1999); (Steenbeek & van Schaik, 2001)
<i>Procolobus pennantii and Cercopithecus ascanius</i>	N/A	N/A	yes	N/A	(Chapman & Chapman, 2000); (Gillespie & Chapman, 2001)
<i>Propithecus v. verreauxi</i>	N/A	relaxed	yes	better feeding efficiency for dominants	(Kubzdela, 1997)
<i>Propithecus v. verreauxi</i>	seasonal	relaxed	N/A	greater reproductive advantage due to increased body mass for dominants	(Richard et al., 2000)
<i>Saimiri sciureus, S. oerstedii, and S. boliviensis</i>	clumped moderate distribution large distribution	linear, stable not evident linear, stable	N/A	N/A	(Mitchell et al., 1991); (Boinski et al., 2002)

## References

- Abbott, D. H., Keverne, E. B., Bercovitch, F. B., Shively, C. A., Mendoza, S. P., Saltzman, W., et al. (2003). Are subordinates always stressed? A comparative analysis of rank differences in cortisol levels among primates. *Hormones and Behavior*, *43*, 67-82.
- Adkins-Regan, E. (2005). *Hormones and Animal Social Behavior*. Princeton: Princeton University Press.
- Alberts, S. C., Sapolsky, R. M., & Altmann, J. (1992). Behavioral, endocrine, and immunological correlates of immigration by an aggressive male into a natural primate group. *Hormones and Behavior*, *26*(2), 167-178.
- Andersson, M. (1994). *Sexual Selection*. Princeton: Princeton University Press.
- Anestis, S. F. (2006). Testosterone in juvenile and adolescent male chimpanzees (*Pan troglodytes*): effects of dominance rank, aggression, and behavioral style. *American Journal of Physical Anthropology*, *130*(4), 536-545.
- Bales, K. L., French, J. A., McWilliams, J., Lake, R. A., & Dietz, J. M. (2006). Effects of social status, age, and season on androgen and cortisol levels in wild male golden lion tamarins (*Leontopithecus rosalia*). *Hormones and Behavior*, *49*(1), 88-95.
- Barrett, G. M., Shimizu, K., Bardi, M., Asaba, S., & Mori, A. (2002). Endocrine correlates of rank, reproduction, and female-directed aggression in male Japanese Macaques (*Macaca fuscata*). *Hormones and Behavior*, *42*(1), 85-96.
- Barton, R. A., Byrne, R. W., & Whiten, A. (1996). Ecology, feeding competition and social structure in baboons. *Behavioral Ecology and Sociobiology*, *38*, 321-329.
- Barton, R. A., & Whiten, A. (1993). Feeding competition among female olive baboons *Papio anubis*. *Animal Behaviour*, *46*, 777-789.
- Bateman, A. J. (1948). Intra-sexual selection in *Drosophila*. *Heredity*, *2*, 349-368.
- Batty, K. A., Herbert, J., Keverne, E. B., & Vellucci, S. V. (1986). Differences in blood levels of androgens in female talapoin monkeys related to their social status. *Neuroendocrinology*, *44*, 347-354.
- Beehner, J. C., Bergman, T. J., Cheney, D. L., Seyfarth, R. M., & Whitten, P. L. (2006). Testosterone predicts future dominance rank and mating activity among male chacma baboons. *Behavioral Ecology and Sociobiology*, *59*(4), 469-479.

- Beehner, J. C., & McCann, C. (2008). Seasonal and altitudinal effects on glucocorticoid metabolites in a wild primate (*Theropithecus gelada*). *Physiology and Behavior*, *95*, 508-514.
- Beehner, J. C., Phillips-Conroy, J. E., & Whitten, P. L. (2005). Female testosterone, dominance rank, and aggression in an Ethiopian population of hybrid baboons. *American Journal of Primatology*, *67*, 101-119.
- Bercovitch, F. B., & Clarke, A. S. (1995). Dominance rank, cortisol concentrations, and reproductive maturation in male rhesus macaques. *Physiology and Behavior*, *58*, 215-221.
- Bercovitch, F. B., & Ziegler, T. E. (2002). Current topics in primate socioendocrinology. *Annual Review of Anthropology*, *31*, 45-67.
- Berglund, A., Magnhagen, C., Bisazza, A., König, B., & Huntingford, F. (1993). Female-female competition over reproduction. *Behavioral Ecology*, *4*(2), 184-187.
- Boinski, S., Sughrue, K., Selvaggi, L., Quatrone, R., Henry, M., & Cropp, S. (2002). An expanded test of the ecological model of primate social evolution: competitive regimes and female bonding in three species of squirrel monkeys (*Saimiri oerstedii*, *S. boliviensis*, and *S. sciureus*). *Behaviour*, *139*, 227-261.
- Borries, C. (1993). Ecology of female social relationships: Hanuman langurs (*Presbytis entellus*) and the van Schaik model. *Folia Primatologica*, *61*(1), 21-30.
- Brockman, D. K. (1994). *Reproduction and Mating System of Verreaux's Sifaka (Propithecus verreauxi) at Beza Mahafaly, Madagascar*. Yale University, New Haven.
- Brockman, D. K. (1999). Reproductive behavior of female *Propithecus verreauxi* at Beza Mahafaly, Madagascar. *International Journal of Primatology*, *20*(3), 375-398.
- Brockman, D. K., Cobden, A. K., & Whitten, P. L. (2009). Birth season glucocorticoids are related to the presence of infants in sifaka (*Propithecus verreauxi*). *Proceedings of the Royal Society B-Biological Sciences*, *276*, 1855-1863.
- Brockman, D. K., & Whitten, P. L. (1996). Reproduction in free-ranging *Propithecus verreauxi*: estrus and the relationship between multiple partner matings and fertilization. *American Journal of Physical Anthropology*, *100*, 57-69.
- Brockman, D. K., Whitten, P. L., Richard, A. F., & Benander, B. (2001). Birth season testosterone levels in male Verreaux's sifaka, *Propithecus verreauxi*: insights into socio-demographic factors mediating seasonal testicular function. *Behavioral Ecology and Sociobiology*, *49*(2-3), 117-127.

- Brockman, D. K., Whitten, P. L., Richard, A. F., & Schneider, A. (1998). Reproduction in free-ranging male *Propithecus verreauxi*: the hormonal correlates of mating and aggression. *American Journal of Physical Anthropology*, *105*(2), 137-151.
- Brockman, D. K., Whitten, P. L., Russell, E., Richard, A. F., & Izard, M. K. (1995). Application of fecal steroid techniques to the reproductive endocrinology of female Verreaux's sifaka (*Propithecus verreauxi*). *American Journal of Primatology*, *36*, 313-325.
- Cavigelli, S. A. (1999). Behavioural patterns associated with faecal cortisol levels in free-ranging female ring-tailed lemurs, *Lemur catta*. *Animal Behaviour*, *57*, 935-944.
- Cavigelli, S. A., Dubovick, T., Levash, W., Jolly, A., & Pitts, A. (2003). Female dominance status and fecal corticoids in a cooperative breeder with low reproductive skew: ringtailed lemurs (*Lemur catta*). *Hormones and Behavior*, *43*, 166-179.
- Cavigelli, S. A., & Pereira, M. E. (2000). Mating season aggression and fecal testosterone levels in male ring-tailed lemurs (*Lemur catta*). *Hormones and Behavior*, *37*(3), 246-255.
- Chapais, B. (1992). The role of alliances in social inheritance of rank among female primates. In A. Harcourt & F. B. M. de Waal (Eds.), *Coalitions and alliances in humans and other animals*: Oxford University Press.
- Chapais, B., & Schulman, S. R. (1980). Evolutionary model of female dominance relations in primates. *Journal of Theoretical Biology*, *82*(1), 47-89.
- Chapais, B., & Schulman, S. R. (1983). Fitness and female dominance relationships. In R. A. Hinde (Ed.), *Primate social relationships* (pp. 271-278). Oxford: Blackwell Scientific Publications.
- Chapman, C. A., & Chapman, L. J. (2000). Constraints on group size in red colobus and red-tailed guenons: examining the generality of the ecological constraints model. *International Journal of Primatology*, *21*(4), 565-585.
- Cheney, D. L., & Seyfarth, R. M. (1987). The influence of intergroup competition on the survival and reproduction of female vervet monkeys. *Behavioral Ecology and Sociobiology*, *21*, 375-386.
- Cheney, D. L., & Seyfarth, R. M. (2009). Stress and coping mechanisms in female primates. *Advances in the Study of Behavior*, *39*, 1-44.
- Clutton-Brock, T. H. (1991). *The evolution of parental care*. Princeton: Princeton University Press.

- Clutton-Brock, T. H. (2004). What is sexual selection? In P. M. Kappeler & C. P. van Schaik (Eds.), *Sexual selection in primates: new and comparative perspectives* (pp. 24-36). New York: Cambridge University Press.
- Clutton-Brock, T. H., & Vincent, A. C. J. (1991). Sexual selection and the potential reproductive rates of males and females. *Nature*, *351*, 58-60.
- Cords, M. (2002). Friendship among adult female blue monkeys (*Cercopithecus mitis*). *Behaviour*, *139*, 291-314.
- Creel, S. (2001). Social dominance and stress hormones. *Trends in Ecology & Evolution*, *16*(9), 491-497.
- Creel, S. (2005). Dominance, aggression, and glucocorticoid levels in social carnivores. *Journal of Mammalogy*, *86*, 255-264.
- Cristoal-Azkarate, J., Chavira, R., Boeck, L., Rodriguez-Luna, E., & Veal, J. J. (2006). Testosterone levels of free-ranging resident mantled howler monkey males in relation to the number and density of solitary males: a test of the challenge hypothesis. *Hormones and Behavior*, *49*(2), 261-267.
- Cristobal-Azkarate, J., Chavira, R., Boeck, L., Rodriguez-Luna, E., & Veal, J. J. (2007). Glucocorticoid levels in free ranging resident mantled howlers: a study of coping strategies. *American Journal of Primatology*, *69*, 866-876.
- Crockford, C., Wittig, R. M., Whitten, P. L., Seyfarth, R. M., & Cheney, D. L. (2008). Social stressors and coping mechanisms in wild female baboons (*Papio hamadryas ursinus*). *Hormones and Behavior*, *53*, 254-265.
- Darwin, C. (1871). *The descent of man, and selection in relation to sex*: J. Murray.
- de Waal, F. B. M. (1989). Dominance 'style' and primate social organization. In V. Standen & R. A. Foley (Eds.), *Comparative socioecology: the behavioral ecology of humans and other mammals* (pp. 243-263). Boston: Blackwell Scientific Publications.
- de Waal, F. B. M. (2001). Apes from Venus: bonobos and human social evolution. In F. B. M. de Waal (Ed.), *Tree of origin* (pp. 39-68). Cambridge: Harvard University Press.
- Dewar, R. E., & Richard, A. F. (2007). Evolution in the hypervariable environment of Madagascar. *Proceedings of the National Academy of Sciences of the United States of America*, *104*, 13723-13727.
- Dittus, W. P. J. (1977). The social regulation of population density and age-sex distributions in the toque monkey. *Behaviour*, *63*, 281-322.

- Dittus, W. P. J. (1979). The evolution of behaviors regulating density and age-specific sex ratios in a primate population. *Behaviour*, 69, 265-302.
- Dittus, W. P. J. (1988). Group fission among wild toque macaques as a consequence of female resource competition and environmental stress. *Animal Behaviour*, 36, 1626-1645.
- Drea, C. M. (2005). Bateman revisited: the reproductive tactics of female primates. *Integrative and Comparative Biology*, 45(5), 915-923.
- Drea, C. M. (2007). Sex and seasonal differences in aggression and steroid secretion in *Lemur catta*: are socially dominant females hormonally 'masculinized'? *Hormones and Behavior*, 51, 555-567.
- Drea, C. M., & Weil, A. (2008). External genital morphology of the ring-tailed lemur (*Lemur catta*): females are naturally "masculinized". *Journal of Morphology*, 269, 451-463.
- Engh, A. L., Beehner, J. C., Bergman, T. J., Whitten, P. L., Hoffmeier, R. R., Seyfarth, R. M., et al. (2006). Female hierarchy instability, male immigration and infanticide increase glucocorticoid levels in female chacma baboons. *Animal Behaviour*, 71, 1227-1237.
- Erhart, E. M., & Overdorff, D. J. (1998). Infanticide in *Propithecus diadema edwardsi*: an evaluation of the sexual selection hypothesis. *International Journal of Primatology*, 19(1), 73-81.
- Erhart, E. M., & Overdorff, D. J. (2008). Rates of agonism by diurnal lemuroids: implications for female social relationships. *International Journal of Primatology*, 29, 1227-1247.
- Fichtel, C., Kraus, C., Ganswindt, A., & Heistermann, M. (2007). Influence of reproductive season and rank on fecal glucocorticoid levels in free-ranging male Verreaux's sifakas (*Propithecus verreauxi*). *Hormones and Behavior*, 51, 640-648.
- Floody, O. R. (1983). Hormones and aggression in female mammals. In B. B. Svare (Ed.), *Hormones and Aggressive Behavior* (pp. 39-89). New York: Plenum Press.
- Foley, C. A. H., Papageorge, S., & Wasser, S. K. (2001). Noninvasive stress and reproductive measures of social and ecological pressures in free-ranging African elephants. *Conservation Biology*, 15, 1134-1142.
- Gemmill, A., & Gould, L. (2008). Microhabitat variation and its effects on dietary composition and intragroup feeding interactions between adult female *Lemur*

*catta* during the dry season at Beza Mahafaly Special Reserve, Madagascar. *International Journal of Primatology*, 29, 1511-1533.

- Gesquiere, L. R., Khan, M., Shek, L., Wango, T. L., Wango, E. O., Alberts, S. C., et al. (2008). Coping with a challenging environment: effects of seasonal variability and reproductive status on glucocorticoid concentrations of female baboons (*Papio cynocephalus*). *Hormones and Behavior*, 54, 410-416.
- Gillespie, T. R., & Chapman, C. A. (2001). Determinants of group size in the red colobus monkey (*Procolobus badius*): an evaluation of the generality of the ecological-constraints model. *Behavioral Ecology and Sociobiology*, 50, 329-338.
- Glickman, S. E., Frank, L. G., Pavgi, S., & Licht, P. (1992). Hormonal correlates of masculinization in female spotted hyaenas (*Crocuta crocuta*). 1. Infancy to Sexual Maturity. *Journal of Reproduction and Fertility*, 95(2), 451-462.
- Gould, L. (2005). Variation in fecal testosterone levels, intermale aggression, dominance rank and age during mating and post-mating periods in wild adult male ring-tailed lemurs (*Lemur catta*). *American Journal of Primatology*, 69, 1325-1339.
- Goymann, W., East, M. L., & Hofer, H. (2001). Androgens and the role of female "hyperaggressiveness" in spotted hyenas (*Crocuta crocuta*). *Hormones and Behavior*, 39(1), 83-92.
- Goymann, W., & Wingfield, J. C. (2004). Allostatic load, social status and stress hormones: the costs of social status matter. *Animal Behaviour*, 67, 591-602.
- Hawkes, K. (2004). Mating, parenting, and the evolution of human pair bonds. In B. Chapais & C. Berman (Eds.), *Kinship and behavior in primates* (pp. 443-473). Oxford: Oxford University Press.
- Hood, L. C., & Jolly, A. (1995). Troop fission in female *Lemur catta* at Berenty Reserve, Madagascar. *International Journal of Primatology*, 16(6), 997-1015.
- Hrdy, S. B. (1981). *The woman that never evolved*. Cambridge: Harvard University Press.
- Hrdy, S. B. (2000). The optimal number of fathers: evolution, demography, and history in the shaping of female mate preferences. *Annals of the New York Academy of Sciences*, 907, 75-96.
- Hrdy, S. B., & Williams, G. C. (1983). Behavioral biology and the double standard. In S. K. Wasser (Ed.), *Social behavior of female vertebrates* (pp. 3-17). New York: Academic Press.
- Isbell, L. A. (1991). Contest and scramble competition: patterns of female aggression and ranging behavior among primates. *Behavioral Ecology*, 2(2), 143-155.

- Isbell, L. A., & Young, T. P. (2002). Ecological models of female social relationships in primates: Similarities, disparities, and some directions for future clarity. *Behaviour*, *139*, 177-202.
- Janson, C. H. (1988). Intra-specific food competition and primate social structure: a synthesis. *Behaviour*, *105*, 1-17.
- Janson, C. H., & Goldsmith, M. L. (1995). Predicting group size in primates: foraging costs and predation risk. *Behavioral Ecology*, *6*(3), 326-336.
- Jolly, A. (1966). Lemur social behaviour and primate intelligence. *Science*, *153*, 501-506.
- Jolly, A. (1984). The puzzle of female feeding priority. In M. F. Small (Ed.), *Female Primates: Studies by Women Primatologists*. New York: A.R. Liss, Inc.
- Jolly, A. (1998). Pair bonding, female aggression and the evolution of Lemur societies. *Folia Primatologica*, *69*(suppl 1), 1-13.
- Jolly, A., Caless, S., Cavigelli, S. A., Gould, L., Pereira, M. E., Pitts, A., et al. (2000). Infant killing, wounding and predation in *Eulemur* and *Lemur*. *International Journal of Primatology*, *21*(1), 21-40.
- Kappeler, P. M. (1991). Patterns of sexual dimorphism in body weight among prosimian primates. *Folia Primatologica*, *57*(3), 132-146.
- Kappeler, P. M. (1993). Variation in social structure: the effects of sex and kinship on social interactions in 3 lemur species. *Ethology*, *93*(2), 125-145.
- Kappeler, P. M. (1996). Causes and consequences of life-history variation among strepsirrhine primates. *American Naturalist*, *148*(5), 868-891.
- Kappeler, P. M. (1997). Determinants of primate social organization: comparative evidence and new insights from Malagasy lemurs. *Biological Reviews of the Cambridge Philosophical Society*, *72*(1), 111-151.
- Kappeler, P. M., & Schaffler, L. (2008). The lemur syndrome unresolved: extreme male reproductive skew in sifakas (*Propithecus verreauxi*), a sexually monomorphic primate with female dominance. *Behavioral Ecology and Sociobiology*, *62*, 1007-1015.
- Klinkova, E., Heistermann, M., & Hodges, J. K. (2004). Social parameters and urinary testosterone level in male chimpanzees (*Pan troglodytes*). *Hormones and Behavior*, *46*(4), 474-481.
- Koenig, A. (2000). Competitive regimes in forest-dwelling Hanuman langur females (*Semnopithecus entellus*). *Behavioral Ecology and Sociobiology*, *48*, 93-109.



- Koenig, A. (2002). Competition for resources and its behavioral consequences among female primates. *International Journal of Primatology*, 23(4), 759-783.
- Koenig, A., Beise, J., Chalise, M. K., & Ganzhorn, J. U. (1998). When females should contest for food - testing hypotheses about resource density, distribution, size, and quality with Hanuman langurs (*Presbytis entellus*). *Behavioral Ecology and Sociobiology*, 42, 225-237.
- Kubzdela, K. S. (1997). *Sociodemography in diurnal primates: The effects of group size and female dominance rank on intra-group spatial distribution, feeding competition, female reproductive success, and female dispersal patterns in white sifaka, Propithecus verreauxi verreauxi*. University of Chicago, Chicago.
- Kuester, J., & Paul, A. (1996). Female-female competition and male mate choice in barbary macaques (*Macaca sylvanus*). *Behaviour*, 133, 763-790.
- Langmore, N. E., Cockrem, J. F., & Candy, E. J. (2002). Competition for male reproductive investment elevates testosterone levels in female dunnocks, *Prunella modularis*. *Proceedings of the Royal Society of London Series B-Biological Sciences*, 269(1508), 2473-2478.
- Lawler, R. R. (2007). Fitness and extra-group reproduction in male Verreaux's sifaka: an analysis of reproductive success from 1989-1999. *American Journal of Physical Anthropology*, 132, 267-277.
- Lawler, R. R., Caswell, H., Richard, A. F., Ratsirarson, J., Dewar, R. E., & Schwartz, M. (2009). Demography of Verreaux's sifaka in a stochastic rainfall environment. *Oecologia*, 161, 491-504.
- Lawler, R. R., Richard, A. F., & Riley, M. A. (2003). Genetic population structure of the white sifaka (*Propithecus verreauxi verreauxi*) at Beza Mahafaly Special Reserve, southwest Madagascar (1992-2001). *Molecular Ecology*, 12(9), 2307-2317.
- Lewis, R. J. (2008). Social influences on group membership in *Propithecus verreauxi verreauxi*. *International Journal of Primatology*, 29, 1249-1270.
- Lewis, R. J., & Kappeler, P. M. (2005). Seasonality, body condition, and timing of reproduction in *Propithecus verreauxi verreauxi* in the Kirindy forest. *American Journal of Primatology*, 67, 347-364.
- Lewis, R. J., Razafindrasamba, S. M., & Tolojanahary, J. P. (2003). Observed infanticide in a seasonal breeding prosimian (*Propithecus verreauxi verreauxi*) in Kirindy Forest, Madagascar. *Folia Primatologica*, 74, 101-103.
- Littlefield, B. L. (2010). Infanticide following male takeover event in Verreaux's sifaka (*Propithecus verreauxi verreauxi*). *Primates*, 51, 83-86.

- Lynch, J. W., Ziegler, T. E., & Strier, K. B. (2002). Individual and seasonal variation in fecal testosterone and cortisol levels of wild male tufted capuchin monkeys, *Cebus apella nigritus*. *Hormones and Behavior*, 41(3), 275-287.
- Marshall, A. J., & Hohmann, G. (2005). Urinary testosterone levels of wild male bonobos (*Pan paniscus*) in the Lomako Forest, Democratic Republic of Congo. *American Journal of Primatology*, 65(1), 87-92.
- Martin, R. (1972). Adaptive radiation and behavior of the Malagasy lemurs. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, 264, 295-353.
- Mitchell, C. L., Boinski, S., & van Schaik, C. P. (1991). Competitive regimes and female bonding in two species of squirrel monkeys (*Saimiri oerstedii* and *S. sciureus*). *Behavioral Ecology and Sociobiology*, 28(1), 55-60.
- Mittermeier, R. A., Ganzhorn, J. U., Konstant, W. R., Glander, K., Tattersall, I., Groves, C. P., et al. (2008). Lemur diversity in Madagascar. *International Journal of Primatology*, 29, 1607-1656.
- Monaghan, E. P., & Glickman, S. E. (2001). Hormones and aggressive behavior. In J. B. Becker, S. M. Breedlove & D. Crews (Eds.), *Behavioral Endocrinology*. Cambridge, Massachusetts: The MIT Press.
- Muehlenbein, M. P., Watts, D. P., & Whitten, P. L. (2004). Dominance rank and fecal testosterone levels in adult male chimpanzees (*Pan troglodytes schweinfurthii*) at Ngogo, Kibale National Park, Uganda. *American Journal of Primatology*, 64(1), 71-82.
- Muller, M. N., & Wrangham, R. W. (2004a). Dominance, aggression and testosterone in wild chimpanzees: a test of the 'challenge hypothesis'. *Animal Behaviour*, 67, 113-123.
- Muller, M. N., & Wrangham, R. W. (2004b). Dominance, cortisol and stress in wild chimpanzees (*Pan troglodytes schweinfurthii*). *Behavioral Ecology and Sociobiology*, 55, 332-340.
- Nakagawa, N. (1998). Ecological determinants of the behavior and social structure of Japanese monkeys: a synthesis. *Primates*, 39(3), 375-383.
- Ostner, J., Kappeler, P. M., & Heistermann, M. (2002). Seasonal variation and social correlates of androgen excretion in male redfronted lemurs (*Eulemur fulvus rufus*). *Behavioral Ecology and Sociobiology*, 52(6), 485-495.

- Ostner, J., Kappeler, P. M., & Heistermann, M. (2008). Androgen and glucocorticoid levels reflect seasonally occurring social challenges in male redfronted lemurs (*Eulemur fulvus rufus*). *Behavioral Ecology and Sociobiology*, *62*, 627-638.
- Overdorff, D. J. (1996). Ecological correlates to social structure in two lemur species in Madagascar. *American Journal of Physical Anthropology*, *100*(4), 487-506.
- Packer, C., Collins, D. A., Sindimwo, A., & Goodall, J. (1995). Reproductive constraints on aggressive competition in female baboons. *Nature*, *373*(6509), 60-63.
- Palombit, R. A., Cheney, D. L., & Seyfarth, R. M. (2001). Female-female competition for male 'friends' in wild chacma baboons, *Papio cynocephalus ursinus*. *Animal Behaviour*, *61*, 1159-1171.
- Payne, H. F. P., Lawes, M. J., & Henzi, S. P. (2003). Competition and the exchange of grooming among female samango monkeys (*Cercopithecus mitis erythrarchus*). *Behaviour*, *140*, 453-471.
- Pereira, M. E., & Kappeler, P. M. (1997). Divergent systems of agonistic behaviour in lemurid primates. *Behaviour*, *134*, 225-274.
- Pereira, M. E., Kaufman, R., Kappeler, P. M., & Overdorff, D. J. (1990). Female dominance does not characterize all of the Lemuridae. *Folia Primatologica*, *55*, 96-103.
- Pereira, M. E., & McGlynn, C. A. (1998). Special relationships instead of female dominance for red fronted lemurs, *Eulemur fulvus rufus*. *American Journal of Primatology*, *44*(1), 85-85.
- Pereira, M. E., & Weiss, M. L. (1991). Female mate choice, male migration, and the threat of infanticide in ringtailed lemurs. *Behavioral Ecology and Sociobiology*, *28*(2), 141-152.
- Pereira, R. J. G., Duarte, J. M. B., & Negrao, J. A. (2006). Effects of environmental conditions, human activity, reproduction, antler cycle and grouping on fecal glucocorticoids of free-ranging Pampas deer stags (*Ozotoceros bezoarticus bezoarticus*). *Hormones and Behavior*, *49*, 114-122.
- Pochron, S.T., Fitzgerald, J., Gilbert, C.C., Lawrence, D., Grgas, M., Rakotonirina, G., Ratsimbazafy, R., Rakotosoa, R., Wright, P.C. (2003). Patterns of female dominance in *Propithecus diadema edwardsi* of Ranomafana National Park, Madagascar. *American Journal of Primatology*, *61*, 173-185.
- Pochron, S. T., Tucker, W. T., & Wright, P. C. (2004). Demography, life history, and social structure in *Propithecus diadema edwardsi* from 1986-2000 in Ranomafana

- National Park, Madagascar. *American Journal of Physical Anthropology*, 125(1), 61-72.
- Pochron, S. T., & Wright, P. C. (2003). Variability in adult group compositions of a prosimian primate. *Behavioral Ecology and Sociobiology*, 54(3), 285-293.
- Pride, R. E. (2005a). Foraging success, agonism, and predator alarms: behavioral predictors of cortisol in *Lemur catta*. *International Journal of Primatology*, 26(2), 295-319.
- Pride, R. E. (2005b). High faecal glucocorticoid levels predict mortality in ring-tailed lemurs (*Lemur catta*). *Biology Letters*, 1(1), 60-63.
- Pride, R. E. (2005c). Optimal group size and seasonal stress in ring-tailed lemurs (*Lemur catta*). *Behavioral Ecology*, 16(3), 550-560.
- Pruetz, J. D., & Isbell, L. A. (2000). Correlations of food distribution and patch size with agonistic interactions in female vervets (*Chlorocebus aethiops*) and patas monkeys (*Erythrocebus patas*) living in simple habitats. *Behavioral Ecology and Sociobiology*, 49, 38-47.
- Pusey, A., & Williams, J. (1997). The influence of dominance rank on the reproductive success of female chimpanzees. *Science*, 277(5327), 828-831.
- Range, F., & Noe, R. (2002). Familiarity and dominance relations among female sooty mangabeys in the Tai National Park. *American Journal of Primatology*, 56(3), 137-153.
- Ray, J. C., & Sapolsky, R. M. (1992). Styles of male social behavior and their endocrine correlates among high-ranking wild baboons. *American Journal of Primatology*, 28, 231-250.
- Rhen, T., & Crews, D. (2002). Variation in reproductive behavior within a sex: neural systems and endocrine activation. *Journal of Neuroendocrinology*, 14, 517-531.
- Richard, A. F. (1978). *Behavioral Variation: Case study of a Malagasy Lemur*. Lewisburg: Bucknell University Press.
- Richard, A. F. (1987). Malagasy prosimians: female dominance. In B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham & T. T. Struhsaker (Eds.), *Primate Societies* (pp. 25-33). Chicago: University of Chicago Press.
- Richard, A. F. (1992). Aggressive competition between males, female-controlled polygyny and sexual monomorphism in a Malagasy primate, *Propithecus verreauxi*. *Journal of Human Evolution*, 22, 395-406.

- Richard, A. F., Dewar, R. E., Schwartz, M., & Ratsirarson, J. (2000). Mass change, environmental variability and female fertility in wild *Propithecus verreauxi*. *Journal of Human Evolution*, 39, 381-391.
- Richard, A. F., Dewar, R. E., Schwartz, M., & Ratsirarson, J. (2002). Life in the slow lane? Demography and life histories of male and female sifaka (*Propithecus verreauxi verreauxi*). *Journal of Zoology*, 256, 421-436.
- Richard, A. F., Rakotomanga, P., & Schwartz, M. (1991). Demography of *Propithecus verreauxi* at Beza Mahafaly, Madagascar: sex ratio, survival, and fertility, 1984-1988. *American Journal of Physical Anthropology*, 84, 307-322.
- Robbins, M. M., & Czekala, N. M. (1997). A preliminary investigation of urinary testosterone and cortisol levels in wild male mountain gorillas. *American Journal of Primatology*, 43, 51-64.
- Romero, L. M. (2002). Seasonal changes in plasma glucocorticoid concentrations in free-living vertebrates. *General and Comparative Endocrinology*, 128, 1-24.
- Ron, T., Henzi, S. P., & Motro, U. (1996). Do female chacma baboons compete for a safe spatial position in a southern woodland habitat? *Behaviour*, 133, 475-490.
- Rubenstein, D. R., & Wikelski, M. (2005). Steroid hormones and aggression in female Galapagos marine iguanas. *Hormones and Behavior*, 48(3), 329-341.
- Saito, C. (1996). Dominance and feeding success in female Japanese macaques, *Macaca fuscata*: effects of food patch size and inter-patch distance. *Animal Behaviour*, 51, 967-980.
- Saltz, D., & White, G. C. (1991). Urinary cortisol and urea nitrogen responses to winter stress in mule deer. *The Journal of Wildlife Management*, 55, 1-16.
- Saltzman, W., Schultz-Darken, N. J., Scheffler, G., Wegner, F. H., & Abbott, D. H. (1994). Social and reproductive influences on plasma cortisol in female marmoset monkeys. *Physiology and Behavior*, 56, 801-810.
- Sannen, A., van Elsacker, L., Heistermann, M., & Eens, M. (2004). Urinary testosterone-metabolite levels and dominance rank in male and female bonobos (*Pan paniscus*). *Primates*, 45, 89-96.
- Sapolsky, R. M. (1982). The endocrine stress-response and social status in the wild baboon. *Hormones and Behavior*, 16, 279-292.
- Sapolsky, R. M. (1991). Testicular function, social rank and personality among wild baboons. *Psychoneuroendocrinology*, 16(4), 281-293.

- Sapolsky, R. M. (1992). Cortisol concentrations and the social significance of rank instability among wild baboons. *Psychoneuroendocrinology*, *17*, 701-709.
- Sapolsky, R. M. (1993). Endocrinology alfresco: psychoendocrine studies of wild baboons. In *Recent Progress in Hormone Research, Vol 48* (Vol. 48, pp. 437-468).
- Sapolsky, R. M. (1997). *The Trouble with Testosterone and Other Essays on the Biology of the Human Predicament*. New York: Simon & Schuster.
- Sapolsky, R. M. (2002). Endocrinology of the stress response. In J. B. Becker, S. M. Breedlove, D. Crews & M. M. McCarthy (Eds.), *Behavioral Endocrinology* (pp. 409-450). Cambridge: The MIT Press.
- Sapolsky, R. M. (2004). Social status and health in humans and other animals. *Annual Review of Anthropology*, *33*, 393-418.
- Sapolsky, R. M. (2005). The influence of social hierarchy on primate health. *Science*, *308*, 648-652.
- Sauther, M. L. (1993). Resource competition in wild populations of ringtailed lemurs (*Lemur catta*): implications for female dominance. In P. M. Kappeler & J. U. Ganzhorn (Eds.), *Lemur social systems and their ecological basis* (pp. 135-152). New York: Plenum Press.
- Setchell, J. M., Smith, T., Wickings, E. J., & Knapp, L. A. (2008). Factors affecting fecal glucocorticoid levels in semi-free-ranging female mandrills (*Mandrillus sphinx*). *American Journal of Primatology*, *70*, 1023-1032.
- Sih, A., Bell, A. M., Johnson, J. C., & Ziemba, R. E. (2004). Behavioral syndromes: an integrative overview. *Quarterly Review of Biology*, *79*(3), 241-277.
- Silk, J. B. (1987). Social behavior in evolutionary perspective. In B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham & T. T. Struhsaker (Eds.), *Primate societies* (pp. 318-329). Chicago: The University of Chicago Press.
- Silk, J. B. (1993). The evolution of social conflict among female primates. In W. A. Mason & S. P. Mendoza (Eds.), *Primate social conflict* (pp. 49-83). Albany: State University of New York Press.
- Smuts, B. B. (1987). Gender, aggression, and influence. In B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham & T. T. Struhsaker (Eds.), *Primate societies* (pp. 400-412). Chicago: The University of Chicago Press.
- Smuts, B. B. (1992). Male aggression against women: an evolutionary perspective. *Human Nature*, *3*(1), 1-44.

- Smuts, B. B. (1995). The evolutionary origins of patriarchy. *Human Nature*, 6(1), 1-32.
- Stavisky, R. C., Adams, M. R., & Watson, S. L. (2001). Dominance, cortisol, and behavior in small groups of female cynomolgus monkeys (*Macaca fascicularis*). *Hormones and Behavior*, 39, 232-238.
- Steenbeek, R., & van Schaik, C. P. (2001). Competition and group size in Thomas's langurs (*Presbytis thomasi*): the folivore paradox revisited. *Behavioral Ecology and Sociobiology*, 49, 100-110.
- Sterck, E. H. M. (1999). Variation in langur social organization in relation to the socioecological model, human habitat alteration, and phylogenetic constraints. *Primates*, 40(1), 199-213.
- Sterck, E. H. M., & Steenbeek, R. (1997). Female dominance relationships and food competition in the sympatric Thomas langur and long-tailed macaque. *Behaviour*, 134, 749-774.
- Sterck, E. H. M., Watts, D. P., & van Schaik, C. P. (1997). The evolution of female social relationships in nonhuman primates. *Behavioral Ecology and Sociobiology*, 41, 291-309.
- Strier, K. B., Ziegler, T. E., & Wittwer, D. J. (1999). Seasonal and social correlates of fecal testosterone and cortisol levels in wild male muriquis (*Brachyteles arachnoides*). *Hormones and Behavior*, 35(2), 125-134.
- Trivers, R. (1972). Parental investment and sexual selection. In B. Campbell (Ed.), *Sexual selection and the descent of man: 1871-1971* (pp. 136-179). Chicago: Aldine Publishing Company.
- van Jaarsveld, A. S., & Skinner, J. D. (1991). Plasma androgens in spotted hyaenas (*Crocuta crocuta*): influence of social and reproductive development. *Journal of Reproduction and Fertility*, 93(1), 195-201.
- van Schaik, C. P. (1989). The ecology of social relationships amongst female primates. In V. Standen & R. A. Foley (Eds.), *Comparative socioecology: the behavioral ecology of humans and other mammals* (pp. 195-218). Oxford: Blackwell Scientific Publications.
- van Schaik, C. P., & Kappeler, P. M. (1996). The social systems of gregarious lemurs: lack of convergence with anthropoids due to evolutionary disequilibrium? *Ethology*, 102(11), 915-941.
- Vervaecke, H., Stevens, J., & Van Elsacker, L. (2003). Interfering with others: female-female reproductive competition in *Pan paniscus*. In C. B. Jones (Ed.), *Sexual*

*selection and reproductive competition in primates: new perspectives and directions* (pp. 231-253). Norman, OK: The American Society of Primatologists.

- Vick, L. G., & Pereira, M. E. (1989). Episodic targeting aggression and the histories of *Lemur* social groups. *Behavioral Ecology and Sociobiology*, *25*, 3-12.
- Virgin, C. E., & Sapolsky, R. M. (1997). Styles of male social behavior and their endocrine correlates among low-ranking baboons. *American Journal of Primatology*, *42*, 25-39.
- von Engelhardt, N., Kappeler, P. M., & Heistermann, M. (2000). Androgen levels and female social dominance in *Lemur catta*. *Proceedings of the Royal Society of London Series B-Biological Sciences*, *267*(1452), 1533-1539.
- Wasser, S. K. (1983). Reproductive competition and cooperation among female yellow baboons. In S. K. Wasser (Ed.), *Social behavior of female vertebrates* (pp. 349-390). New York: Academic Press.
- Watts, D. P. (1985). Relations between group size and composition and feeding competition in mountain gorilla groups. *Animal Behaviour*, *33*, 72-85.
- Watts, D. P. (1990). Ecology of gorillas and its relation to female transfer in mountain gorillas. *International Journal of Primatology*, *11*(1), 21-45.
- Watts, D. P. (1991). Harassment of immigrant female mountain gorillas by resident females. *Ethology*, *89*, 135-153.
- Watts, D. P. (1994). Agonistic relationships between female mountain gorillas (*Gorilla gorilla beringei*). *Behavioral Ecology and Sociobiology*, *34*(5), 347-358.
- Weingrill, T., Gray, D. A., Barrett, L., & Henzi, S. P. (2004). Fecal cortisol levels in free-ranging female chacma baboons: relationship to dominance, reproductive state and environmental factors. *Hormones and Behavior*, *45*, 259-269.
- Whitten, P. L. (1983). Diet and dominance among female vervet monkeys (*Cercopithecus aethiops*). *American Journal of Primatology*, *5*, 139-159.
- Whitten, P. L. (2000). Evolutionary endocrinology of the cercopithecoids. In P. F. Whitehead & C. J. Jolly (Eds.), *Old World Monkeys* (pp. 269-297). New York: Cambridge University Press.
- Whitten, P. L., Brockman, D. K., & Stavisky, R. C. (1998). Recent advances in noninvasive techniques to monitor hormone-behavior interactions. *Yearbook of Physical Anthropology*, *41*, 1-23.



- Whitten, P. L., & Turner, T. R. (2004). Male residence and the patterning of serum testosterone in vervet monkeys (*Cercopithecus aethiops*). *Behavioral Ecology and Sociobiology*, 56(6), 565-578.
- Wingfield, J. C., Hegner, R. E., Dufty, A. M., & Ball, G. F. (1990). The "challenge hypothesis": theoretical implications for patterns of testosterone secretion, mating systems, and breeding strategies. *The American Naturalist*, 136(6), 829-846.
- Wingfield, J. C., Lynn, S. E., & Soma, K. K. (2001). Avoiding the 'costs' of testosterone: ecological bases of hormone-behavior interactions. *Brain Behavior and Evolution*, 57(5), 239-251.
- Wingfield, J. C., Maney, D. L., Breuner, C. W., Jacobs, J. D., Lynn, S., Ramenofsky, M., et al. (1998). Ecological bases of hormone-behavior interactions: the 'emergency life history stage'. *American Zoologist*, 38, 191-206.
- Wingfield, J. C., & Ramenofsky, M. (1999). Hormones and the behavioral ecology of stress. In P. H. M. Balm (Ed.), *Stress Physiology in Animals* (pp. 1-51). Boca Raton, FL: CRC Press.
- Wittig, R. M., & Boesch, C. (2003). Food competition and linear dominance hierarchy among female chimpanzees of the Tai National Park. *International Journal of Primatology*, 24(4), 847-867.
- Wittig, R. M., Crockford, C., Lehmann, J., Whitten, P. L., Seyfarth, R. M., & Cheney, D. L. (2008). Focused grooming networks and stress alleviation in wild female baboons. *Hormones and Behavior*, 54, 170-177.
- Wrangham, R. W. (1980). An ecological model of female-bonded primate groups. *Behaviour*, 75, 262-300.
- Wright, P. C. (1993). Variations in male-female dominance and offspring care in non-human primates. In B. Miller (Ed.), *Sex and gender hierarchies* (pp. 127-145). Cambridge: Cambridge University Press.
- Wright, P. C. (1995). Demography and life history of free-ranging *Propithecus diadema edwardsi* in Ranomafana National Park, Madagascar. *International Journal of Primatology*, 16(5), 835-851.
- Wright, P. C. (1999). Lemur traits and Madagascar ecology: coping with an island environment. *Yearbook of Physical Anthropology*, 42, 31-72.
- Yamashita, N. (2008). Chemical properties of the diets of two lemur species in southwestern Madagascar. *International Journal of Primatology*, 29, 339-364.

- Ziegler, T. E., Scheffler, G., & Snowdon, C. T. (1995). The relationship of cortisol levels to social environment and reproductive functioning in female cotton-top tamarins, *Saguinus oedipus*. *Hormones and Behavior*, 29, 407-424.
- Zinner, D., Schwibbe, M. H., & Kaumanns, W. (1994). Cycle synchrony and probability of conception in female hamadryas baboons (*Papio hamadryas*). *Behavioral Ecology and Sociobiology*, 35, 175-183.
- Zysling, D. A., Greives, T. J., Demas, G. E., & Ketterson, E. D. (2003). Effects of testosterone on female aggression and immune function: possible evidence of intersexual conflict in dark-eyed juncos (*Junco hyemalis*). *Integrative and Comparative Biology*, 43(6), 927-927.

## Chapter II. Seasonal Changes in Behavior and Competition: Implications for Female Dominance Relationships in Verreaux's Sifaka (*Propithecus verreauxi*)

### Introduction

The unique aspects of lemur social organization and behavior have made it particularly challenging to categorize them within socioecological models (Erhart & Overdorff, 2008). Lemurs have been classified as Dispersal-Egalitarian due to the fact that dominance hierarchies are often either non-existent or unstable and female intrasexual competition is low (Sterck et al., 1997). However, researchers have suggested that this may be an oversimplification of species-specific differences in lemur social structure, particularly with respect to *Lemur catta* and species within the genus *Propithecus* (Erhart & Overdorff, 2008). Although *Lemur catta* and *Propithecus* cannot be considered female-bonded (e.g. Wrangham, 1980) because they do not show strong female bonds along matriline or coalition formation (Kappeler, 1997), they do engage in targeted female aggression and are best characterized by female philopatry, which makes their classification as Dispersal-Egalitarian problematic (Erhart & Overdorff, 2008). In fact, lemurs display several “idiosyncratic” traits that most likely serve as adaptations to the highly seasonal and unpredictable island environment of Madagascar (Wright, 1999). These unique characteristics, coupled with demographic constraints and life history traits, separate lemurs from other anthropoid primates in noticeable ways such that attempting to fit lemurs into models that emerged from observations of Old World monkeys and apes may be problematic from the start. For example, a study of *Propithecus diadema edwardsi* demonstrated that an adult female had only one daughter that survived to

reproduce compared with 2.7 daughters for Old World monkeys, suggesting that small group size and a slow life history trajectory make it impossible for sifaka to form the types of large kin matriline seen in many anthropoid primates (Pochron et al., 2004). Furthermore, dominance relationships among female lemurs can be difficult to quantify and may be seasonally dependent, with stronger dominance relationships emerging during periods when resource competition is high (Erhart & Overdorff, 2008; Kubzdela, 1997; Richard, 1978).

Lemurs, particularly Verreaux's sifaka (*Propithecus verreauxi*), provide a unique context within which to examine aspects of female competition and dominance relationships. First, Verreaux's sifaka live in the extremely seasonal environment of the spiny desert forest in southwest Madagascar, marked by a wet season from October through March followed by a prolonged dry season (April-September) when resources become scarce (Richard et al., 1991). Verreaux's sifaka also time lactation, the most energetically expensive stage of reproductive, to the period of decreased resource availability so that infants are then weaned in the subsequent wet season (Lewis & Kappeler, 2005; Richard et al., 2000). Furthermore, Verreaux's sifaka, like many lemur species, are female-dominant, providing an opportunity to examine aspects of female aggression and competition in the absence of male constraints (Kappeler, 1993a). Finally, female Verreaux's sifaka are known to compete in a variety of contexts: harassment of immigrant females (Lewis, 2008), copulatory harassment (Brockman, 1999), and intergroup encounters (Richard, 1978). However, the context of female aggression and competition is concentrated over access to contestable resources (both high quality food

items and mates) and may increase as these resources become available during the wet season (Richard, 1978).

Although Verreux's sifaka are primarily folivorous, previous research has documented dietary shifts that occur with the onset of rains (Lewis & Kappeler, 2005; Norscia et al., 2006; Yamashita, 2008). Flowers and young leaves begin to make up more of the sifaka diet from October through December, while fruits become a larger portion of the diet from January through April (Lewis & Kappeler, 2005; Yamashita, 2002; 2008). These dietary shifts occur simultaneously with seasonal fluctuations in home range use, such that daily path length and core area use is significantly increased in the wet season (Norscia et al., 2006). As high quality, patchy resources such as flowers and fruits become more available in the wet season; it is likely that intra-individual feeding competition increases such that subordinate females are at a disadvantage. In fact, a study of Verreux's sifaka showed that subordinate females traveled more, displayed decreased feeding efficiency, and had fewer offspring compared to dominant females (Kubzdela, 1997). The seasonal distribution of resources is also linked to female fertility and reproductive success. Females with a higher body mass in the mating season are more likely to give birth in the subsequent birth season (Richard et al., 2000) and successfully wean infants (Lewis & Kappeler, 2005). These results suggest that acquiring and maintaining access to high-quality resources is of paramount importance for female sifaka, providing the incentive to engage in competition when the benefits outweigh the costs.

The goal of the current study was to examine aspects of female competition and dominance relationships in a wild population of Verreaux's sifaka. The specific objectives were as follows:

- 1) To examine seasonal shifts in competition during the transitional period from the dry to wet season, measured by changes in feeding and traveling behavior as well as close proximity to group members.
- 2) To examine possible rank-related differences in feeding, traveling, and presence of nearest neighbors to determine if there are competitive costs to subordinate females.
- 3) To examine the factors that contribute to infant death in this population as well as possible rank-related differences in infant survival.

## **Methods**

### *Study site and population*

This study was conducted on a population of wild sifaka (*Propithecus verreauxi*) at Beza Mahafaly Special Reserve, an area of protected spiny desert forest in southwest Madagascar, just south of the Tropic of Capricorn (Fig. 2.1 from Brockman et al., 2008). The southwest is characterized by a high degree of variation in interannual rainfall (Dewar & Richard, 2007; Lawler et al., 2009). Fifty years of annual rainfall data from Beza Mahafaly demonstrated periods of drought as well as periods characterized by high rainfall due to cyclones (Lawler et al., 2009). The unpredictable rainfall in southwest Madagascar may have profound effects on the availability of resources (Dewar & Richard, 2007), which in turn affects sifaka survival and fertility (Lawler et al., 2009; Richard et al., 2002). For the population

of Verreaux's sifaka at Beza Mahafaly, demographic factors such as adult survival and population growth rate seem to be particularly sensitive to low rainfall (below 300 mm) (Lawler et al., 2009). Recent evidence suggests this population may be declining as much as 2% every year (Lawler et al., 2009).

In addition to unpredictable annual rainfall, this region is also highly seasonal and semi-arid, with an average of 720 mm annual rainfall (Richard et al., 1991). There is a cooler, dry period from April through September (3°C to 36°C) and a hot, rainy season from October through March (21°C to 42°C) (Richard et al., 1991).

Beza Mahafaly Special Reserve consists of two parcels of protected forest (Fig. 2.1). The research from this study was conducted in Parcel 1, which is approximately 80 hectares and is bordered by the Sakamenga River on the eastern side. Vegetation in the reserve ranges from a high-canopy gallery forest in the east to a more semi-arid and thorny forest in the west, with sifaka groups occupying both ranges of habitats. *Tamarindus indica* is largely found in the eastern section of the reserve, with *Euphorbia* sp. and *Acacia bellula* becoming more pronounced in the west (Yamashita, 2002). Flowers and fruits are found in greater abundance in the reserve after the onset of rains in October/November (Yamashita, 2002).

The reserve itself is gridded with north to south and east to west trails, allowing greater accessibility for following groups (Fig. 2.1). There are about 50 separate sifaka groups, ranging in size from 2-13 individuals with 1-3 females per group (Richard, 1992). Although female philopatry is the norm, there is evidence that females emigrate when the number of females within a group exceeds three

(Kubzdela, 1997). The animals within the reserve are habituated, and individuals have unique color collar and tag combinations with numbers for identification purposes. Demographic data have been collected on this population since 1984 (Richard et al., 1991). Although the reserve is enclosed by a barbed wire fence to prevent trespassing by herds of goats and zebu, there has been an influx of invasive wildcats (*Felis silvestris*) and domestic dogs (*Canis lupus familiaris*) that, along with harrier hawks (*Polyboroides radiatus*), predate on this population of sifaka (Brockman, 2003; Brockman et al., 2008).

Verreaux's sifaka are diurnal and primarily arboreal, although sifaka in this population are frequently observed traveling and feeding on the ground (Brockman et al., 2008). Sifaka are folivores, subsisting primarily on mature leaves of *Tamarindus indica*, *Euphorbia* sp., and *Acacia* sp. during the dry season, with an increasing reliance on flowers and fruits with the onset of the rains (Yamashita, 2002; 2008). Sifaka tend to lose body mass during the lean season, and body mass predicts female fertility in this population (Richard et al., 2000). The mating season occurs from January to March, with females displaying estrus within a narrow window of time (0.5 to 96 hours) (Brockman, 1999). Births occur from June to August, and infants are weaned in January to March during the subsequent wet season (Richard et al., 2000). There is a high infant mortality rate in this population (only 52% of infants survive the first year), with infant deaths peaking after birth and weaning (Richard et al., 2002; Richard et al., 1991).



### *Sample Individuals and Behavioral Observations*

Behavioral observations were conducted on adult female sifaka with infants (N=8), two from each of four groups (Table 2.1) from July through December of 2007. The author collected data on two of the groups, while the remaining two groups were followed by a field research assistant. Four consecutive days of behavioral data were collected from both females within a group before switching to the second group, and this procedure was duplicated each month so that data were collected on all females at comparable stages of lactation. Each observer completed four 30 minute focal animal samples (Altmann, 1974) of each female in the group every day, alternating females and with 10-15 minute breaks of *ad libitum* sampling in between each focal block. Focal observations were conducted from approximately 0700 to 1700 hr, with an hour mid-day break. However, as temperatures began to rise in October, the sifaka often rested during the mid-day for 3 hours or more, but were active earlier in the morning and later in the evening. At this point, the schedule shifted from approximately 0600 to 1800 hr with an extended mid-day break as temperatures reached their daily peak. This resulted in a total of 606.5 hours of observation ( $M = 75.81$ ,  $SD = 4.78$ ). Instantaneous scan samples were recorded at five minute intervals throughout the focal. The observer noted the behavior of the focal female, the number of nearest neighbors within 2 meters and their identities, and the number of nearest neighbors between 2-5 meters and their identities. Instantaneous scan samples were used to assess activity budgets, whereas the focal samples were used primarily to record social interactions and mother-infant interactions. Behaviors were recorded during focal and scan samples using a 63 word ethogram previously established for this species (Brockman, 1994) and included feeding, resting, traveling, social

interactions (including approaches, retreats, supplants, other agonistic and submissive behaviors, grooming), vocalizations, and anogenital marking. Since rates of social behaviors are low among sifaka, *ad libitum* sampling was used to record any additional social behaviors and intergroup encounters. In all of the focal groups, the two females were mother-daughter pairs. The mother of each pair was determined to be the dominant female in the dyad based on direction of submissive behaviors (Brockman, 1994; Lewis & van Schaik, 2007).

In addition to in-depth focal sampling, census data were collected on 19 groups comprised of at least one adult female with an infant. Data were collected on all adult females within the group for a total of 37 females (23 mothers and 14 non-mothers) (Table 2.2). F290 and F86 both lost their infants early in the season, so they were subsequently considered non-mothers in the analyses and only those scans after the death of infants were used. Census scans were conducted on two days every week, although there were some weeks when groups could not be located, resulting in a range of 5-20 scans for each female ( $M = 14.41$ ,  $SE = 3.16$ ). Using scan sampling techniques, the observers scanned each female in the group in turn, recording current behavior (i.e., feeding, resting, traveling, social interactions), mother-infant proximity (where applicable), and number of nearest neighbors within 2 meters and between 2 and 5 meters. Since aggressive interactions are unlikely to be captured by scan samples, female age served as an indirect measure of female dominance status since the dominant female is older in 90% of the groups previously studied (Kubzdela, 1997). This observation was confirmed in the present study, where in each of the four focal groups, the dominant female was also the oldest female.

*Variable Definitions*

Weekly rates of grooming given, grooming received, and genital marking were calculated as bouts per hour from the focal data for each female. Proportions of time spent feeding and traveling were calculated from the instantaneous scan data for each female as the number of scans spent feeding/traveling over the total number of scans each week. Nearest neighbor variables were also calculated from the instantaneous scan sample. Proportions of time spent in the presence of nearest neighbors within 2 m for each female were calculated by dividing the number of scans in which a neighbor was present by the total number of scans for that week. This was repeated for the number of nearest neighbors between 2 to 5 m. The proportion of nearest neighbors present during feeding for each female was calculated by dividing the number of scans in which a neighbor was present during feeding divided by the total number of scans in which a female was feeding. This was repeated for the presence of nearest neighbors while resting.

For the scan sample females, the proportion of time spent feeding or traveling was calculated by dividing the number of scans in which a female was observed feeding/traveling by the total number of scans for that female. The proportion of nearest neighbors within 2 m (and between 2 to 5 m) was calculated as the number of instances in which a female had a nearest neighbor divided by the total number of scans for each female. There was insufficient data to break this up by feeding and resting.

### *Statistical Analyses*

MANOVAs for repeated measures were used to assess the effects of season and rank on behavioral variables for the focal and scan data. Proportion of scans spent feeding (Kolmogorov-Smirnov test:  $Z = 0.740$ ,  $p = 0.643$ ), traveling (Kolmogorov-Smirnov test:  $Z = 0.812$ ,  $p = 0.525$ ), in the presence of neighbors within 2 meters (Kolmogorov-Smirnov test:  $Z = 0.516$ ,  $p = 0.953$ ), in the presences of neighbors between 2 and 5 meters (Kolmogorov-Smirnov test:  $Z = 0.689$ ,  $p = 0.729$ ), as well as rates of genital marking (bouts/hr) (Kolmogorov-Smirnov test:  $Z = 1.150$ ,  $p = 0.142$ ) all satisfied assumptions of normality. Rates of grooming received (bouts/hr) were log-transformed to satisfy assumptions of normality. All analyses were run using SPSS v. 16.0.

## **Results**

### *Season and Rainfall*

October 15, 2007 marked the first rainfall of the season, occurring just after observation week 6 for focal females. October and November marked a transitional period between the dry and wet seasons, with less than 10 mm of rainfall for each of those months (Fig. 2.2). Heavier rains began in December, with a total of 54.6 mm of rain accumulating before the end of the study period (December 15). For the purpose of analyses, the term “season” is used for simplicity, but the term refers to the periods before and after the onset of rain.

*Effects of Rank and Season on Feeding, Traveling, Genital Marking, and Grooming Received Behavior for Focal Females*

A  $2 \times (2)$  MANOVA was used to assess the effects of rank and season on four behaviors: feeding, traveling, genital marking, and grooming received. Multivariate test results showed a significant main effect for season ( $F(4, 69) = 11.69, p = 0.00, \eta^2 = 0.40$ ) and rank ( $F(4, 69) = 4.83, p = 0.00, \eta^2 = 0.22$ ), but not for the interaction of season  $\times$  rank ( $F(4, 69) = 1.05, p = 0.39, \eta^2 = 0.06$ ). Univariate test results showed significant effects of season on traveling, genital marking, and grooming received, but no significant effect on feeding (Table 2.3; Fig. 2.3a-d). Both traveling (proportion of scans pre-rain:  $M = 0.09, SE = 0.01$ ; post-rain:  $M = 0.12, SE = 0.01$ ) and rates of genital marking (bouts per hour pre-rain:  $M = 0.52, SE = 0.09$ ; post-rain:  $M = 1.42, SE = 0.12$ ) increased significantly from the pre-rain to the post-rain season, while rates of grooming received significantly decreased (bouts per hour pre-rain:  $M = 0.64, SE = 0.06$ ; post-rain:  $M = 0.37, SE = 0.08$ ). There was also a significant effect of rank on traveling (Fig. 2.3b), but no significant effect of rank on feeding, genital marking, or grooming received. Subordinate females traveled significantly more compared to dominant females (proportion of scans spent traveling for subordinates:  $M = 0.13, SE = 0.01$ ; dominants:  $M = 0.09, SE = 0.01$ ).

*Effects of Relative Age and Having an Infant on Feeding and Traveling Behavior for Scan Sample Females*

A  $2 \times (2)$  MANOVA was used to assess the effects of relative age (as a proxy for rank) and having an infant on feeding and traveling behaviors for the scan sample females. There was insufficient data to examine seasonal differences in feeding and

traveling behavior for scan sample females. Multivariate test results revealed no significant main effect for relative age ( $F(2, 32) = 0.03, p = 0.97, \eta^2 = 0.00$ ) or for having an infant ( $F(2, 32) = 2.06, p = 0.14, \eta^2 = 0.11$ ). The interaction of relative age  $\times$  having an infant was also not significant ( $F(2, 32) = 1.57, p = 0.22, \eta^2 = 0.09$ ).

*Effects of Season and Rank on the Presence of Nearest Neighbors while Feeding and Resting for Focal Females*

A  $2 \times (2 \times 2)$  MANCOVA was used to assess the effects of season, rank, and behavior on the presence of nearest neighbors within 2 m and the presence of nearest neighbors between 2 to 5 m while feeding and resting. Group size was used as a covariate. Multivariate test results revealed a significant main effect for season ( $F(2, 64) = 5.71, p = 0.01, \eta^2 = 0.15$ ), a trend for the main effect of rank ( $F(2, 64) = 2.87, p = 0.06, \eta^2 = 0.08$ ), and no significant interaction of season  $\times$  rank ( $F(2, 64) = 0.79, p = 0.46, \eta^2 = 0.02$ ). There was also no significant main effect for behavior (i.e., feeding or resting) ( $F(2, 64) = 0.05, p = 0.96, \eta^2 = 0.00$ ) or for any of its interaction terms: behavior  $\times$  season ( $F(2, 64) = 1.14, p = 0.33, \eta^2 = 0.04$ ), behavior  $\times$  rank ( $F(2, 64) = 0.11, p = 0.90, \eta^2 = 0.00$ ), or behavior  $\times$  season  $\times$  rank ( $F(2, 64) = 0.54, p = 0.59, \eta^2 = 0.02$ ). Univariate tests showed a significant effect of season on the presence of nearest neighbors within 2 m ( $F(1, 65) = 11.52, p = 0.00, \eta^2 = 0.15$ ) and a trend for the effect of season on the presence of nearest neighbors between 2 to 5 m ( $F(1, 65) = 2.91, p = 0.09, \eta^2 = 0.04$ ). The presence of nearest neighbors within 2 m decreased significantly from pre-rain to post-rain (proportion of scans pre-rain:  $M = 0.36, SE = 0.02$ ; post-rain:  $M = 0.27, SE = 0.02$ ), while the presence of nearest neighbors between 2 to 5 m showed a trend towards

decreasing from pre-rain to post-rain (proportion of scans pre-rain:  $M = 0.27$ ,  $SE = 0.02$ ; post-rain:  $M = 0.22$ ,  $SE = 0.02$ ). Univariate test results revealed a significant effect of rank on the presence of nearest neighbors within 2 m ( $F(1, 65) = 5.55$ ,  $p = 0.02$ ,  $\eta^2 = 0.08$ ), but no significant effect of rank on the presence of nearest neighbors between 2 to 5 m ( $F(1, 65) = 2.19$ ,  $p = 0.14$ ,  $\eta^2 = 0.03$ ). Subordinate females spent significantly more time in the presence of nearest neighbors within 2 m compared to dominant females (proportions of scans for subordinates:  $M = 0.35$ ,  $SE = 0.02$ ; dominants:  $M = 0.29$ ,  $SE = 0.02$ ). The estimated marginal means for the presence of nearest neighbors within 2 m and between 2 to 5 m for feeding and resting are shown in Figures 2.4 and 2.5.

*Effects of Relative Age and Having an Infant on the Presence of Nearest Neighbors for Scan Sample Females*

A  $2 \times (2)$  MANCOVA was used to assess the effects of relative age (as a proxy for rank) and having an infant on the presence of nearest neighbors (within 2m and between 2 to 5 m). Group size was used as a covariate. Multivariate test results showed no significant main effect of relative age ( $F(2, 31) = 0.20$ ,  $p = 0.82$ ,  $\eta^2 = 0.01$ ) or having an infant ( $F(2, 31) = 0.67$ ,  $p = 0.52$ ,  $\eta^2 = 0.04$ ). The interaction of relative age  $\times$  having an infant was also not significant ( $F(2, 31) = 0.14$ ,  $p = 0.87$ ,  $\eta^2 = 0.01$ ).

*Case Study: Targeted Aggression and Eviction in Vavy Goa*

At the time of the study, the scan group Vavy Goa consisted of 10 individuals: two adult females with infants, three subadult females, two adult males, and three subadult males (Table 2.4). F367 and F438 were unrelated, and F367 was the mother of

both F518 and M634. Prior to the beginning of scan samples, adult F506 was not found with the group. She was subsequently spotted by another researcher near the village of Efitranga, approximately 3.5 km away from the reserve (A. Axel, personal communication). On September 11, 2007 at 1556 hrs, Vavy Goa was located for the weekly scan. F438 was observed chasing and attacking subadult F518, lunging, biting, and cuffing the subadult female. F518 would chatter at and retreat from F438, but F438 continued to display aggressive behavior towards F518. This attack continued for a total of five minutes, until F518 withdrew approximately 20 m away from the core group, where she remained resting and panting in a nearby tree until the scan was complete. The following week, on September 19, we were only able to locate F438 and F367 from Vavy Goa, traveling with M451 and M664. The other three subadult females could not be located. On September 25, F510 and F518 were seen traveling with M483 and an unmarked individual in the northernmost part of Vavy Goa's range. F504 was finally located on October 26, traveling south of Vavy Goa's range with two unmarked individuals. By October 31, it was clear that Vavy Goa had fissioned into two groups: one consisting of the adult females with infants, and the other consisting of the two subadult females F510 and F518 (Fig. 2.6). It became more difficult to locate these groups as their ranges began to shift, with the splinter group moving to the northeast border of the reserve and the core group utilizing the southern part of the Vavy Goa range. We were unable to locate the core Vavy Goa group again until November 11, where F438 was not seen. By December 6, we were still unable to locate F438 and she had not been seen by the census team.



*Male Takeover Events and Infanticides*

Beginning in mid-October, two of the focal groups (NB and MB) were subject to male takeover events that resulted in the observed or inferred infanticides of all infants (Table 2.1). In the case of NB, three new males (M331, M599, and M9051) immigrated into the group sometime just prior to October 12. The resident alpha male, M661, was seen on the periphery of the group panting heavily and missing large tufts of hair, suggesting the takeover event had occurred either earlier that morning or the previous day. Another resident adult male, M448, had left the group. F463's infant was badly injured, with a bleeding puncture wound in the chest and another long gash across the right upper thigh near the groin. The infant was confirmed dead at 1039hr. Ten days later, on October 26, one of the new immigrant males, M331, was seen attacking F315's infant. At 0741hr, F315 lunged at M331, cuffing and biting at him. I-315 was dislodged from F315's back and was left out of arm's reach behind her on the tree branch. M331 did not display aggression towards F315. Instead, he circumvented F315, grabbed I-315 with both hands, bit the infant in the neck and then dropped her onto the tree branch. In addition to a puncture wound to the neck, there was an additional small wound on the back. The three new males remained with the group and the resident alpha male remained peripheralized until the end of the study period. M448 was seen in November traveling with another neighboring group. Although the study ended before the onset of the next mating season, monthly census data up to September 2008 revealed that M331 remained with the group. M599 and M9051 were not seen with NB during the February 2008 census, but returned to the group in March and remained there until at least September. The resident male, M661, finally left the group in February and was later seen with group

LL2. F463 was seen with a new infant in August, 2008, while F315 did not have another infant. At this time, the paternity of F463's new infant is unknown.

In the case of MB, several unmarked males were seen with the group beginning in mid-October, which resulted in increased aggression towards new males by both resident males and females. In addition to the two focal females, F422 and F449, another adult female F346 also had an infant. On October 12, F346's infant was missing and presumed dead. On Oct 29, F422's infant was seen with a puncture wound to the upper back. The infant was still moving normally by the end of the observation day. The next day marked the switch to another focal group, so MB was not seen for another 10 days. On November 9, F422's infant was missing and the body was later recovered within MB's home range. The cadaver was too decomposed to determine if there were any additional wounds. Later that week, on November 13, F449's infant was also missing and presumed dead. The unmarked males were still present throughout this time period, resulting in increased instability within the group. Towards the end of the study period, MB appeared to be fissioning around the two adult females F422 and F449. While these two females still occupied MB's range, they were often not seen with each other. The resident males, along with several unmarked males, appeared to be floating between these two females. By December, it was difficult to define group composition for MB.

A full discussion of infanticidal events can be found at [http://www.springerlink.com/openurl.asp?genre=article&id=doi:10.1007/s10329-009-0162-1&sa\\_campaign=Email/ACE/OF](http://www.springerlink.com/openurl.asp?genre=article&id=doi:10.1007/s10329-009-0162-1&sa_campaign=Email/ACE/OF). This publication is available at [www.springerlink.com](http://www.springerlink.com).

### *Infant Survival in Focal and Scan Groups*

Combining all focal and scan females that had an infant at some point during the study (N=34) (Tables I & II), there was a 29.4% infant survival rate to one year, which is much lower than the 52% infant survival rate reported for the reserve (Richard et al., 2002). Subordinate females (N=15) had 46.7% infant survival compared to 15.8% in dominant females (N=19), which is a difference that approaches significance (Fisher's exact test,  $p=0.057$ ). Since age was used as a proxy for female dominance status, infant survival rates were compared between age classes. Previous research on this population suggests that infant survival remains fairly constant from age 6 to 17, but then begins to decline for females 18 years of age and older (Richard et al., 2002). Infant survival for females less than 18 years of age (N=26, 34.6%) was not significantly greater compared to infant survival for females 18 years of age and older (N=8, 12.5%) (Fisher's exact test,  $p=0.231$ ). Eleven groups from the focal and scan groups had two or more females with infants. Of these, only one group (RG) had both infants survive to one year. Five groups had at least one infant survive to one year, while in the remaining five groups, both infants died before one year.

## **Discussion**

### *Seasonality of Competition*

After the onset of the rains in October, there was a significant shift in several behaviors such that females traveled more, genital marked more, and received grooming less often compared to the period of time before the rains. The proportion of scans spent feeding was not significantly different pre- and post-rain, which is not entirely surprising

given the constraints on increasing foraging effort placed on folivores due to digestion time (Janson, 1988). The post-rain increase in travel observed in the present study supports predictions derived from socioecological models that individuals will increase day travel length when resources become clumped and easily depleted (Isbell, 1991). During the transitional months between the dry and wet season, sifaka in this population shift to a greater reliance on patchy food items such as flowers and young leaves (Yamashita, 2008), resulting in the need to increase travel to locate these higher-quality resources. The subsequent decrease in grooming received by females after the onset of rains may also indicate a shift in activity budgets as more time is allotted to traveling and foraging, leaving less time for social interactions.

Scent marking in female lemurs has been associated with both intra-female competition (Kappeler, 1998; Pochron et al., 2005) and inter-group defense (Mertl-Millhollen, 2006). Previous studies of *Propithecus* have shown seasonal effects on rates of scent-marking in females, with the highest rates occurring just before the mating season (Brockman, 1999; Pochron et al., 2005). Brockman (1999) found that Verreaux's sifaka at Beza Mahafaly showed increased rates of genital marking in December, just prior to the onset of mating. The results of the current study demonstrate that females increase rates of genital marking well in advance of mating activity, suggesting a possible role of olfactory communication in female territory defense. A study of scent marking in *Lemur catta* showed that females mark significantly more in boundary zones that overlapped with neighboring troops, and that these zones contained 67% of frequented feeding patches (Mertl-Millhollen, 2006). This, coupled with the observation that females increased marking rates during intergroup encounters, led the author to conclude that

scent-marking functioned as a form of territory defense in these contested areas (Mertl-Millhollen, 2006). Territory defense may become even more important for females as higher quality, patchy resources become more available. More research is needed to specifically determine the extent to which genital marking is used by females for territory defense in this population, as well as to parse out the degree to which the early seasonal rise in scent marking behavior is a precursor to the mating period.

Females also showed a decrease in the presence of nearest neighbors after the onset of the rains, suggesting that as females shift their dietary focus to more monopolizable items, they increase their distance to other group members and possible competitors. These results support previous findings that females will increase inter-individual distances when food items are patchily distributed (Barton & Whiten, 1993; Janson, 1988; Saito, 1996). The increase in female aggression after the onset of rains provides additional evidence that females are competing more actively for these clumped resources (Chapter III). Taken together, these results suggest seasonal changes in female resource competition. When sifaka feed primarily on lower-quality, evenly dispersed leaves during the dry season, competition may be primarily of the scramble type. However, as their diet shifts to patchy, higher-quality flowers and fruits, contest competition increases as females aggressively exclude other group members from feeding in the same area.

#### *Costs of Subordinance*

Subordinate females in this study traveled more and spent more time in close proximity to group members compared to dominant females. These results support

previous research conducted on this population which demonstrated that subordinate females had decreased foraging efficiency and traveled more compared to dominants (Kubzdela, 1997). Although the present study did not find a rank difference in the proportion of time spent feeding, data were not collected on inter-individual differences in food consumption, which is a necessary step in determining the extent to which there may be nutritional costs to subordinates. For example, studies of Hanuman langurs (*Semnopithecus entellus*) revealed variation in nutritional quality among preferred plant resources which appeared to translate into rank-related differences in overall body condition (Koenig, 2000; Koenig et al., 1998). Although competition among folivores is expected to be low, many have argued the importance of considering not only seasonal fluctuations in plant availability, but also variations in nutrient quality that may have significant consequences for female survival and reproductive success (Gillespie & Chapman, 2001; Koenig et al., 1998; Overdorff, 1996). Although a phenological study of the diet of Verreaux's sifaka at Beza Mahafaly failed to demonstrate seasonal differences in nutrient quality, that study did not examine overall caloric intake across seasons or rank-related differences in resource consumption (Yamashita, 2008). Since body mass predicts a degree of reproductive success in this species (Lewis & Kappeler, 2005; Richard et al., 2000), it is likely that there are variations in nutrient intake that may negatively impact subordinate female reproduction.

Subordinate females may suffer the additional cost of having more competitors for resources, reflected by the fact that they spend more time in the presence of nearest neighbors in close proximity (within 2 m) compared to dominants. A study of ringtailed lemurs (*Lemur catta*) showed that subordinate females tended to have more males

feeding in close proximity (Sauther, 1993). As a result, subordinate females displayed more aggression towards males, suggesting an energetic cost of competition for these lower-ranking females (Sauther, 1993). Since the focal groups in the present study were comprised of only two or three adult females, this did not afford the opportunity to examine significant sex-differences in nearest neighbors, although it is an intriguing avenue for further research with a larger sample of females. However, it is possible that the potential feeding costs associated with close proximity of group members may be balanced by the benefits of added predator detection. Predation on sifaka by harrier hawkes (*Polyboroides radiatus*) (Brockman, 2003) and invasive wildcats (*Felis silvestris*) (Brockman et al., 2008) has been documented at Beza Mahafaly. Sifaka in this population also demonstrate anti-predator vocalizations, such as growls and roars, suggesting that these predators are a measurable threat (Brockman, 2003; Brockman et al., 2008). No predation attempts were observed during this study; although examining the fitness benefit of having close neighbors for predator detection deserves consideration in future research.

Another form of female competition that may have consequences for subordinate females comes in the form of targeted aggression and eviction, which has been documented in *Lemur catta* (Hood & Jolly, 1995; Vick & Pereira, 1989) and *Propithecus diadema edwardsi* (Pochron et al., 2003; Wright, 1995). The group fission that occurred in Vavy Goa provides further evidence for this behavior in Verreaux's sifaka. F438 was seen attacking subadult female F518 and over the course of several weeks the younger, subordinate females of Vavy Goa emigrated to form new groups of their own. The costs of fission on subordinate females can be high and is only expected to occur when the

benefits of starting a new group outweigh the potential reproductive costs associated with remaining in the current group (Dittus, 1988). In the case of troop fission in *Lemur catta*, subordinate females suffered from increased resource competition, intergroup harassment, and even separation from infants (Hood & Jolly, 1995). Previous research on Verreaux's sifaka at Beza Mahafaly demonstrated that subordinate females often emigrate when the number of females in the group exceeds three, presumably to avoid the added costs of resource and reproductive competition in larger groups (Kubzdela, 1997). It appears that, at least in some cases, these emigrations may be forced. The forced eviction of subordinate females in some lemur species is perplexing since increased group size may aid with predator detection and intergroup territory defense; however, many folivorous primates form smaller groups than would be expected based on feeding competition alone (Janson & Goldsmith, 1995). This has led several researchers to suggest that small group size in folivorous primates may serve as infanticide avoidance (Crockett & Janson, 2000; Janson & Goldsmith, 1995; Steenbeek & van Schaik, 2001). In the case of lemurs, dominant females may limit group size by evicting females to not only eliminate competitors (Kappeler, 1997), but also to protect against male takeover events and infanticides (Kappeler, 1997; Lewis, 2008). Further research is needed to determine how often targeted eviction occurs in Verreaux's sifaka in the wild, as well as to assess the costs and benefits of this strategy for dominant and subordinate females in order to fully understand how this behavior functions as female competition for this species.

It is important to note that analyses of the scan sample data failed to replicate the findings of the focal data in that there were no significant effects of age (as a proxy for



rank) on the proportion of scans spent feeding or traveling, or on the presence of nearest neighbors. There also appeared to be no effect of the presence of an infant on these variables. It is likely that there were too few scan data points to determine significant differences, especially since it was difficult to locate several of the scan groups on a weekly basis. The longitudinal data from the focal sample provided a better opportunity to examine shifts in behavior over time, but the sample size was necessarily small. Therefore, these findings serve as a starting point for continued research on seasonal shifts in competition in female sifaka.

#### *Factors Affecting Infant Survival*

Perhaps the most surprising observation from the study period was the loss of half of the focal infants to male takeover events and infanticides. Although infanticide has been documented across species of lemurs (*Lemur catta* (Hood, 1994; Jolly et al., 2000), *Eulemur fulvus rufus* (Jolly et al., 2000), *Propithecus diadema edwardsi* (Erhart & Overdorff, 1998; Wright, 1995), *Propithecus verreauxi* (Lewis et al., 2003; Littlefield, 2010), and *Lepilemur edwardsi* (Rasoloharijaona et al., 2000)), its occurrence in these highly-seasonal breeders has been difficult to explain within the existing theoretical framework of infanticide as a sexually selected trait (Hausfater & Hrdy, 1984; Hrdy, 1979; van Schaik & Janson, 2000).

Researchers have proposed several hypotheses to explain infanticidal behavior in strepsirrhines. Infanticide may provide a reproductive advantage to immigrant males by enhancing breeding opportunities for the next season, especially in species such as *Propithecus diadema edwardsi* where males and females often exhibit stable breeding

relationships for several years (Wright, 1995), or in *Lemur catta* where females often display priority mating with resident males (M. E. Pereira & Weiss, 1991). While females in this population of *Propithecus verreauxi* also display priority mating with resident males, they occasionally mate with peripheral males (Brockman & Whitten, 1996), and males sire infants outside of their resident groups (Lawler, 2007). Infanticide also may decrease the interbirth interval, as in *Propithecus diadema edwardsi* (Erhart & Overdorff, 1998). However, in this population, females with a surviving infant are more likely to have an infant the following year compared to females without an infant (Richard et al., 2002). For some primate species, the loss of an infant may increase the survival of a subsequent infant born the following year (Hausfater & Hrdy, 1984; Hood, 1994; Jolly et al., 2000; M. E. Pereira & Weiss, 1991). Given that lactation is energetically expensive, and that body mass is predictive of the ability to conceive in this species (Richard et al., 2000), it is possible that curtailing reproductive effort in one year may improve a female's condition, enhancing the survival of a subsequent infant. However, the presence of a sibling from the previous birth cohort does not appear to affect an infant's chance of survival to one year (Richard et al., 2002). Finally, infanticide may be a form of intrasexual competition, where the killing of male infants functions to eliminate future rivals (van Schaik and Janson 2000). The victims of infanticide reported here include both sexes and a larger sample size of infanticidal victims is required to adequately test this hypothesis.

Regardless of whether infanticide serves as a reproductive strategy for males in this species, it is certainly a behavior that occurs with more frequency in this population than expected. The observations from the present study suggest that transferring males

provide a measurable threat to infants (e.g. Brockman and Whitten 1999), which has a profound impact on female reproductive strategies and success in this species. This provides some supporting evidence to the hypothesis that females limit group size as a strategy for infanticide avoidance in this species (e.g. Lewis, 2008). More research is needed in this population to determine the possible advantages of infanticide to males, the extent to which infanticidal males are the sires of subsequent surviving offspring, and the extent to which group size is related to infanticidal events

It is difficult to tease out from the present study the degree to which there are rank-related differences in infant survival. Previous research in this population showed that subordinate females had fewer offspring compared to dominants; however, it was impossible to make any definitive conclusions about these rank-related differences given that rank and age were so tightly correlated (Kubzdela, 1997). The present sample of focal and scan females included both subordinate and dominant females in the 7-18 age class, but only one subordinate female in the 18 years or older age class (Table 2.2). Subordinate females appeared to have a greater proportion of infants surviving to one year compared to dominants, but given that infant survival for females 18 years and older tends to decline (Richard et al., 2002), this result is most likely a function of female age rather than rank. Even though females 18 years and older seemed to have lower infant survival (only 12.5%), this result was not significant, most likely due to the small sample size. It appears as though age may be a better predictor of female fertility and infant survival, but whether there are rank-related differences in lifetime reproductive success across females remains to be seen.

It is interesting to note that of the 11 groups with two or more infants, there was only one group where both infants survived to one year. Of the remaining groups, half had one infant survive while the other half had no infants survive. Verreaux's sifaka in this population tend to only have one infant per group, with no more than three infants in a group (Kubzdela, 1997; Richard et al., 1991). Given that body mass is predictive of female fertility in this population (Richard et al., 2000), it is likely that only one female in a group achieves the necessary body mass to support reproduction in a given year. However, there may be years marked by milder dry seasons when resources are more plentiful, providing the opportunity for two or more females in a group to reproduce at the same time. Yet the results from this study suggest that having more than one infant in a group at a time negatively impacts the chances of survival for one or both infants. It is possible that competition for resources remains too pronounced to support the energetic costs of lactation, or that the presence of another infant translates into additional feeding competition after weaning. It is also possible that these groups are particularly attractive to new males and thereby suffer an increased probability of infanticide as seen in the groups NB and MB. An area for future research is to examine if there is a relationship between annual rainfall and the presence of groups with multiple infants, and the extent to which having more than one infant in a group results in decreased infant survival.

## **Conclusions**

The small sample size of the current study necessitates the use of caution when generalizing these results to the population of Verreaux's sifaka as a whole. Regardless of this caveat, the extensive behavioral data collected on these focal females provided the

opportunity to note behavioral changes over the transitional period from the dry to the wet season, as well as the opportunity to witness the effects of male takeover events.

These results demonstrate that female sifaka experience behavioral shifts as early as mid-October, coinciding with the onset of the first rains of the season and the dietary shift to monopolizable resources. As this dietary shift occurs, females travel more in search of these patchy food items and decrease the number of nearest neighbors while feeding. These observations, coupled with the fact that females also show a marked increase in aggression during this time period (Chapter III), suggest that contest competition among females begins to increase as the seasons change. This may have profound effects on subordinate females, who travel more and spend more time in the presence of nearest neighbors compared to dominant females, and are sometimes targeted for aggression and evicted from their natal group.

The seasonal change in contest competition may provide support for the hypothesis that dominance relationships among female Verreaux's sifaka are seasonally dependent, becoming more pronounced during the period of increased resource abundance (Richard, 1978). However, the present study did not extend throughout the wet season and therefore only offers preliminary evidence for increased competition during the transition period. Further research is needed on competition and dominance relations among females throughout the wet season. In addition, nutritional analyses of dietary shifts across seasons are needed to provide a complete picture of female competition. In particular, it is necessary to examine whether the consumption of different plant items by females results in rank-related nutritional differences and the extent to which this affects fertility and reproductive success.

Due to the small sample size, it was difficult to assess rank-related differences in infant survival, although previous research seems to suggest that age, rather than rank, may be a more important factor (Kubzdela, 1997; Richard et al., 1991). This study did point to the profound impact that immigrating males have on infant survival in this population, and raises several questions as to why male lemurs commit infanticide and how they target specific groups. If males target groups with more females (Crockett & Janson, 2000), then linking the occurrence of infanticide to group sex ratios in this population would provide further support to the hypothesis that females limit group size as a method of avoiding male takeover events (Lewis, 2008).

The fact that groups with more than one infant had such low infant survival seems to suggest that the presence of multiple infants in a group negatively impacts infant survival. Whether this increased infant mortality occurs via increased competition among lactating females, increased competition among infants for weaning foods, or some combination of both remains to be seen. Favorable ecological conditions may create a situation in which multiple females within a group are able to reproduce, but these positive effects on fertility may be outweighed by decreased infant survival. Further research in this area could impact conservation management practices by providing evidence for increasing protected areas in order to support population growth.

This study points to the complex nature of female relationships among female Verreaux's sifaka, demonstrating that the classification of lemurs as Dispersal-Egalitarian may obscure some important species-level differences (Erhart & Overdorff, 2008). Competition and dominance relationships among female Verreaux's sifaka are most likely seasonally dependent, with rank-related disparities becoming more pronounced in

the season of increased competition. These disparities can affect female fertility (Lewis, 2008; Richard et al., 2000), weaning success (Lewis & Kappeler, 2005), and possibly lifetime reproductive success. While lemurs do not form the extended matrilineal alliances and hierarchies seen in Old World monkeys, females do exert some degree of control over group membership through targeted aggression and eviction of subordinates (Pochron et al., 2003; Vick & Pereira, 1989; Wright, 1995), as well as harassment of immigrant females (Lewis, 2008). Female aggression in lemurs can be intense, but may occur less frequently compared to Old World monkeys (Erhart & Overdorff, 2008), and only occurs in the context of increased competition for quality resources or mates. For these reasons, as Erhart & Overdorff (2008) argue, it may be beneficial to move away from attempting to classify lemuroids within these broader models given their divergence from other anthropoid primates (Kappeler & Heymann, 1996), as well as their specific social and behavioral adaptations to the harsh environment of Madagascar (Wright, 1999).

Table 2.1. Demographic descriptions and data totals for focal females.

Lemur ID	Group	Group Size	Age	Rank	Occurrence of Infanticide	Observation Weeks	Focal Hours	Fecal Samples	Infant Survival 1 yr	Infant Last Seen	Infant Sex	Infant Born 2008
268	RG	8	14	Dom	No	10	80.5	39	Yes		M	
379	RG	8	8	Sub	No	10	80	40	Yes		M	Yes
9016	KK	5	20	Dom	No	10	80	41	No	01/21/08	UK	
429	KK	5	11	Sub	No	10	80.5	40	Yes		M	Yes
315	NB	7	13	Dom	Yes	9	70.5	36	No	10/26/07	F	
463	NB	7	7	Sub	Yes	9	71	35	No	10/12/07	M	
422	MB	8	17	Dom	Yes	9	71.5	34	No	11/09/07	UK	Yes
449	MB	8	11	Sub	Yes	9	72.5	36	No	11/13/07	UK	



Table 2.2. Demographic descriptions and data totals for scan females.

Lemur ID	Group	Group Size	Age	Rank	Total No. Scans	Has Infant	Infant Survival 1 yr	Infant Last Seen	Infant Sex
318	AF2	10	13	Sub	16	Yes	No	03/27/08	UK
260	CH	9	11	Sub	16	Yes	Yes		M
9049	EM	4	13	Dom	18	Yes	No	03/31/08	UK
108	EN	6	14	Sub	13	Yes	UK	06/19/08	UK
9160	EN	6	22	Dom	13	Yes	Yes		F
389	EN3	3	7	Dom	18	Yes	No	11/21/07	UK
559	FE	10	7	Sub	13	Yes	Yes		F
553	FN	4	8	Dom	17	Yes	Yes		F
153	FX	9	18	Dom	15	Yes	No	02/05/08	UK
287	FX2	5	11	Dom	17	Yes	No	02/26/08	UK
220	HN	3	20	Dom	16	Yes	No	01/21/08	UK
360	KT	4	10	Sub	11	Yes	No	03/29/08	UK
376	KT	4	20	Dom	6	Yes	No	10/16/07	UK
9102	MK	4	14	Dom	15	Yes	UK	05/07/08	M
255	NI	8	11	Sub	15	Yes	Yes		M
399	PL	7	8	Sub	15	Yes	Yes		F
403	PP	7	7	Sub	16	Yes	No	01/22/08	UK
432	SV	4	7	Sub	15	Yes	No	03/08/08	UK
103	TE	5	13	Dom	20	Yes	UK	06/19/07	F
176	TE	5	12	Sub	20	Yes	Yes		M
367	VG	10	9	Dom	10	Yes	No	03/29/08	UK
438	VG	10	7	Sub	9	Yes	No	10/31/07	UK
107	ZM2	2	14	Dom	16	Yes	UK	06/30/08	UK
266	AF2	10	14	Dom	16	No			
190	CH	9	18	Dom	16	No	No	08/01/07	UK
409	CH	9	8	Sub	16	No			
402	EN	6	21	Sub	13	No			
9043	FE	10	13	Dom	13	No			
529	FX	9	5	Sub	14	No			
9077	FX	9	12	Sub	14	No			
249	NI	8	25	Dom	13	No			
306	NI	8	13	Sub	14	No			
434	NI	8	6	Sub	5	No			
498	NI	8	5	Sub	14	No			
290	PL	7	21	Dom	15	No	No	08/13/07	UK
86	PP	7	22	Dom	14	No	No	07/17/07	UK
497	PP	7	5	Sub	16	No			

Table 2.3. MANOVA results for season and rank effects on feeding (proportion of scans), traveling (proportion of scans), genital marking (bouts/hr), and grooming received (bouts/hr) for focal females.

Effect	Dependent Variable	F	Hypothesis df	Error df	<i>p</i> -value	Partial $\eta^2$
Season	Feeding	2.17	1	72	0.15	0.03
	Traveling*	5.29	1	72	0.02	0.07
	Genital Marking*	37.84	1	72	0.00	0.35
	Grooming Received*	7.47	1	72	0.01	0.09
Rank	Feeding	0.16	1	72	0.69	0.00
	Traveling*	18.1	1	72	0.00	0.20
	Genital Marking	0.68	1	72	0.41	0.01
	Grooming Received	0.05	1	72	0.82	0.00
Season $\times$ Rank	Feeding	0.01	1	72	0.91	0.00
	Traveling	1.53	1	72	0.22	0.02
	Genital Marking	0.44	1	72	0.51	0.01
	Grooming Received	1.13	1	72	0.29	0.02

Table 2.4. Group Composition of Vavy Goa.

Lemur ID	Sex	Age	Last seen with Group
367	F	9	
438	F	7	
506	F	5	Jun-07
504	F	4	09/11/07
510	F	4	09/11/07
518	F	3	09/11/07
451	M	14	
278	M	11	09/11/07
483	M	3	09/11/07
664	M	2	
634	M	2	09/11/07

Figure 2.1. Location and map of Beza Mahafaly Special Reserve, including map of Parcel 1 showing gridded trails. This map is used by permission from D.K. Brockman from Brockman et al., 2008. Maps were drawn by D.K. Brockman, D. Godfrey, and R. Dewar.

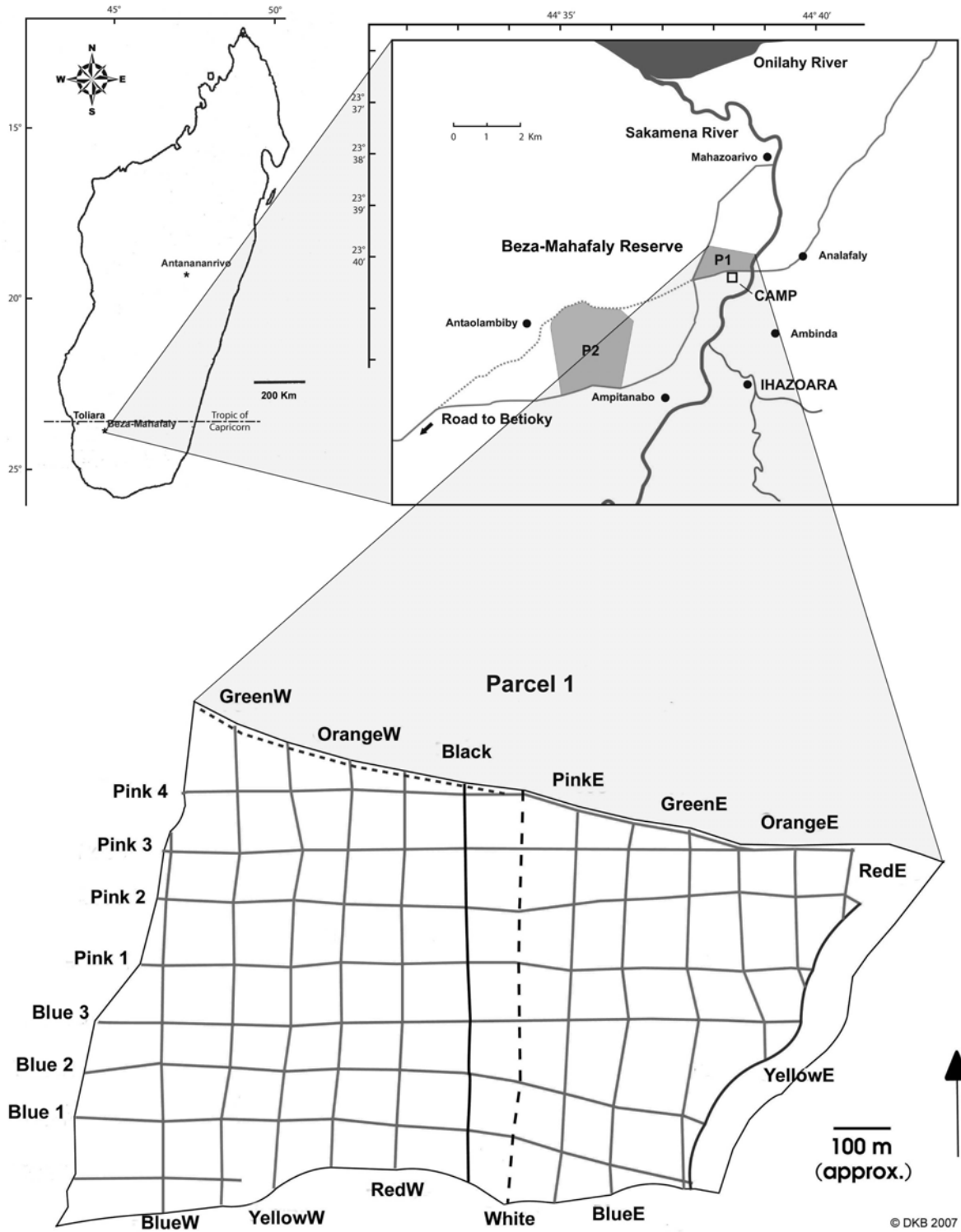


Figure 2.2. Total rainfall (mm) per month at Beza Mahafaly across study months in 2007.

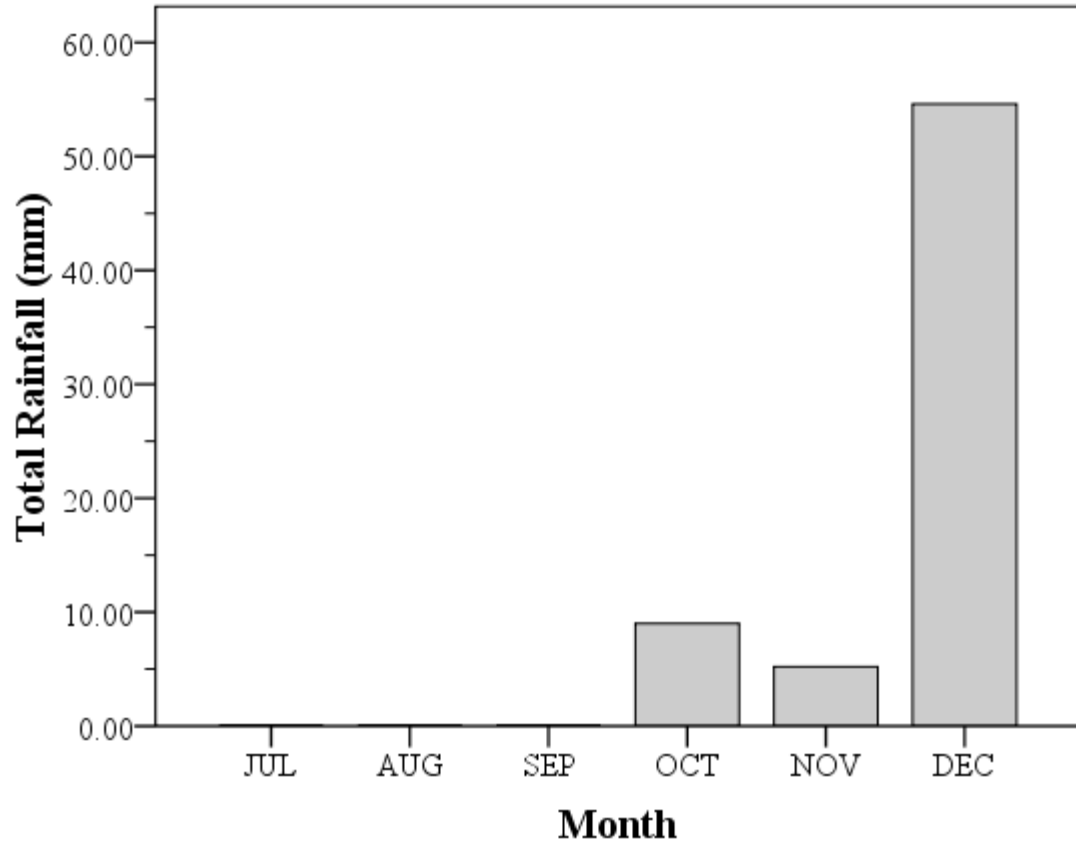
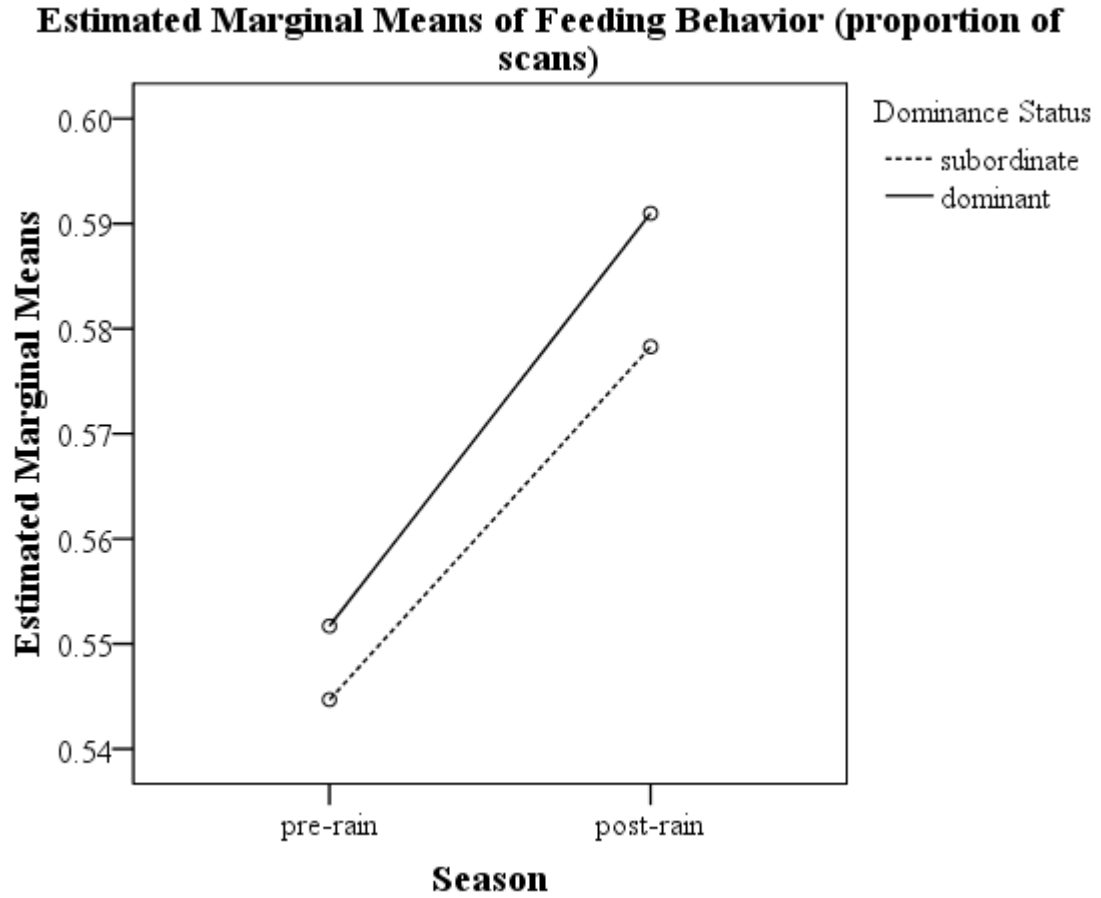
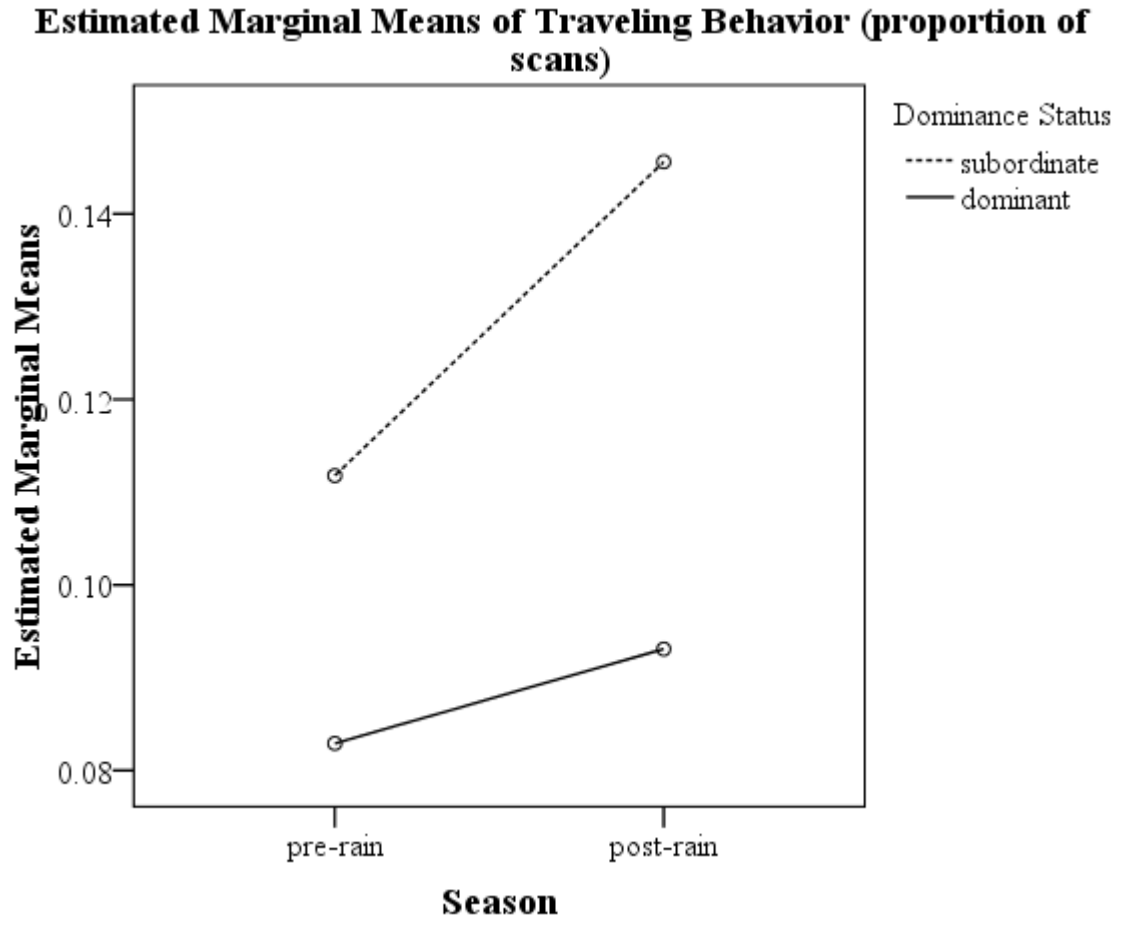


Figure 2.3. Estimated marginal means of the proportion of scans spent a) feeding and b) traveling, and rates of c) genital marking, and d) grooming received across seasons by dominance rank.

2.3a)

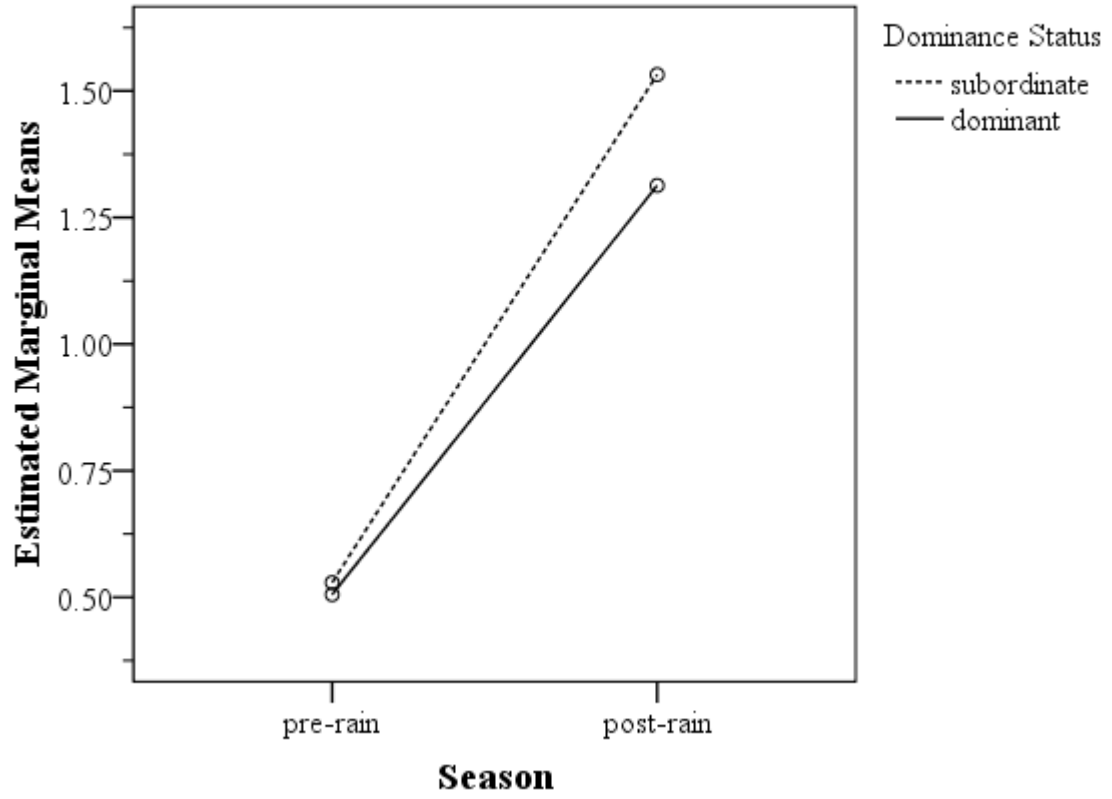


2.3b)



2.3c)

**Estimated Marginal Means of Rates of Genital Marking Behavior  
(bouts/hr)**





2.3d)

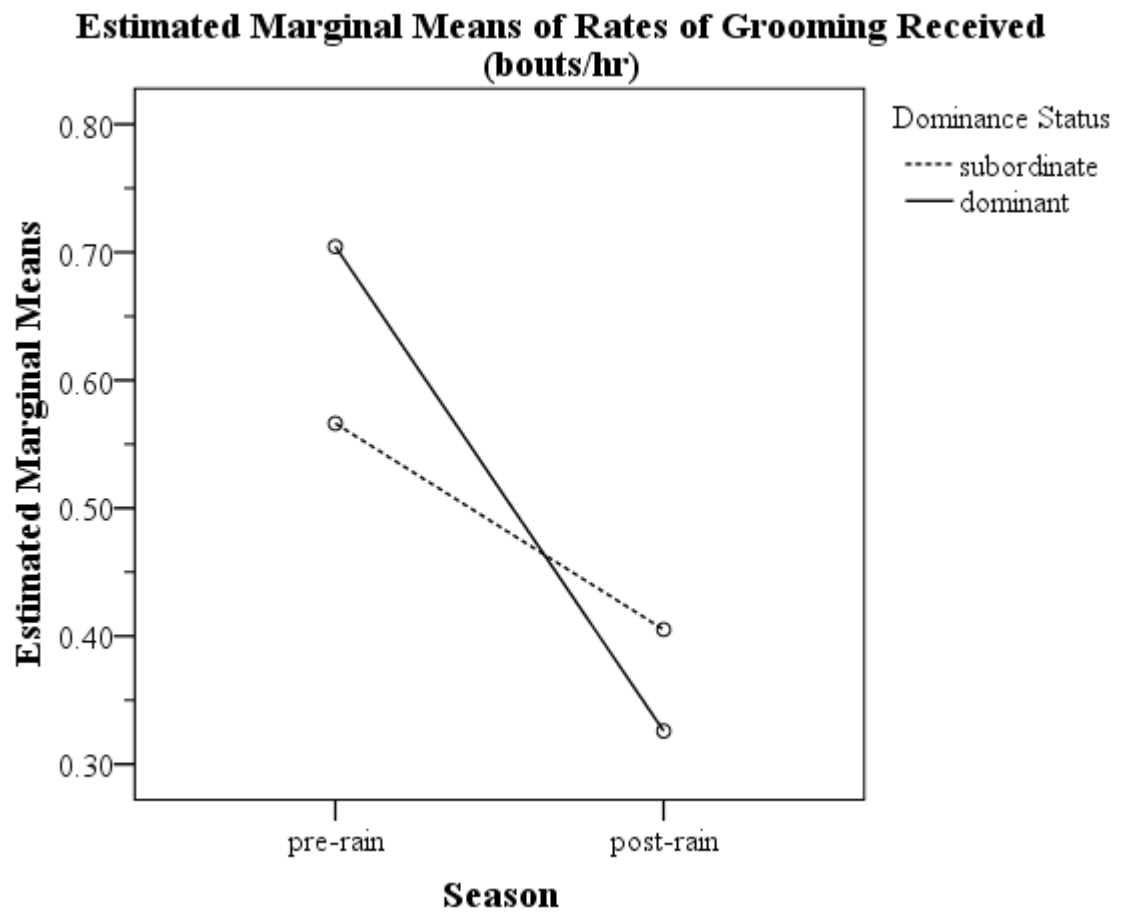
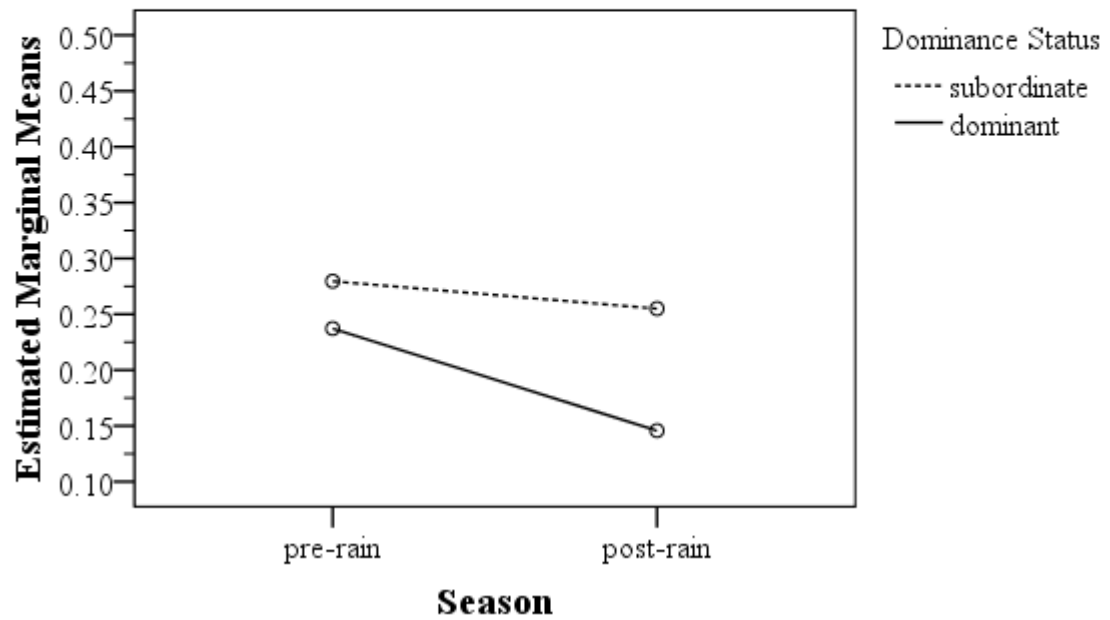


Figure 2.4. Estimated marginal means of the proportion of scans in the presence of nearest neighbors within 2m while a) feeding and b) resting across seasons by dominance rank.

2.4a)

**Estimated Marginal Means of Presence of Nearest Neighbors 0-2m  
(proportion of scans)**

at behavior = feeding



2.4b)

**Estimated Marginal Means of Presence of Nearest Neighbors 0-2m  
(proportion of scans)**

at behavior = resting

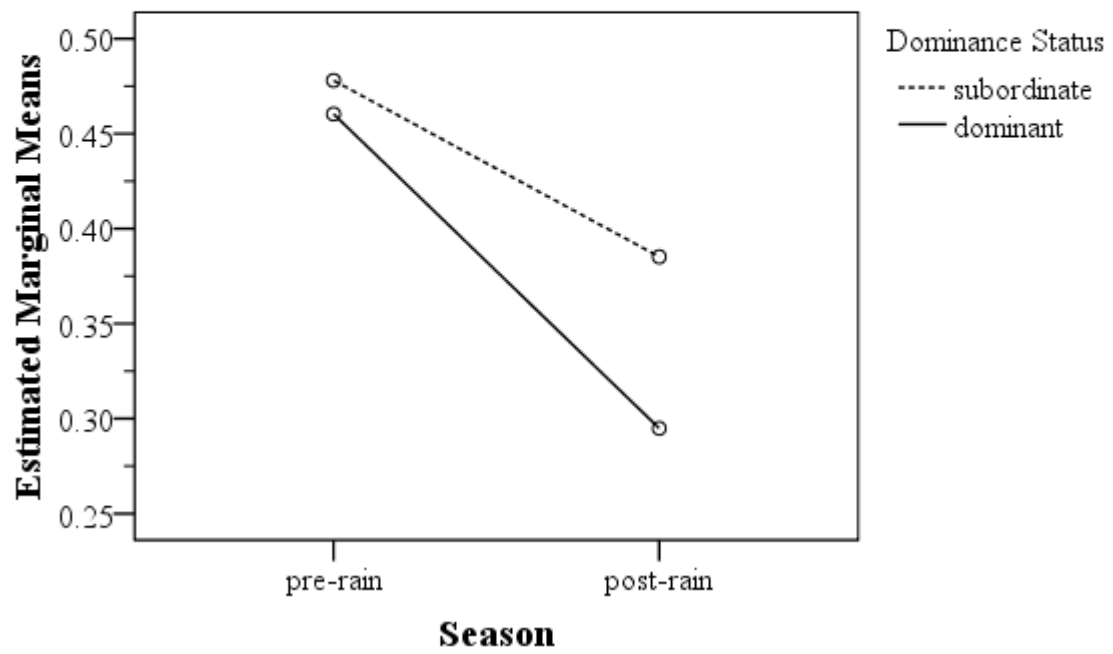
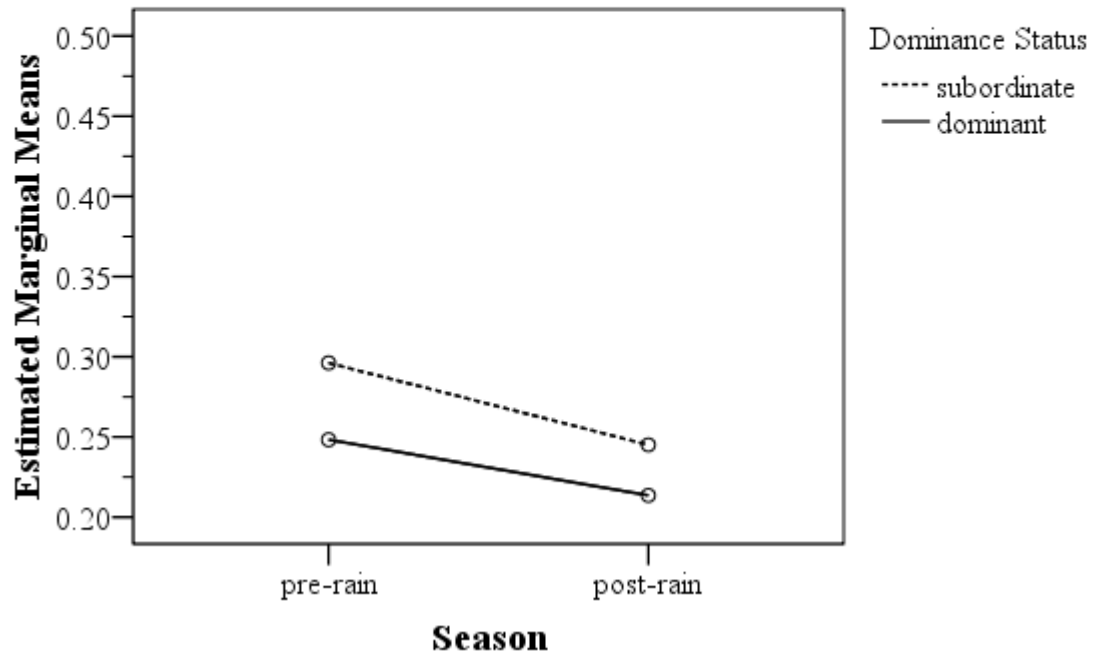


Figure 2.5. Estimated marginal means of presence of nearest neighbors between 2 to 5m while a) feeding and b) resting across seasons by dominance rank.

2.5a)

**Estimated Marginal Means of Presence of Nearest Neighbors 2-5m  
(proportion of scans)**

at behavior = feeding



2.5b)

**Estimated Marginal Means of Presence of Nearest Neighbors 2-5m  
(proportion of scans)**

at behavior = resting

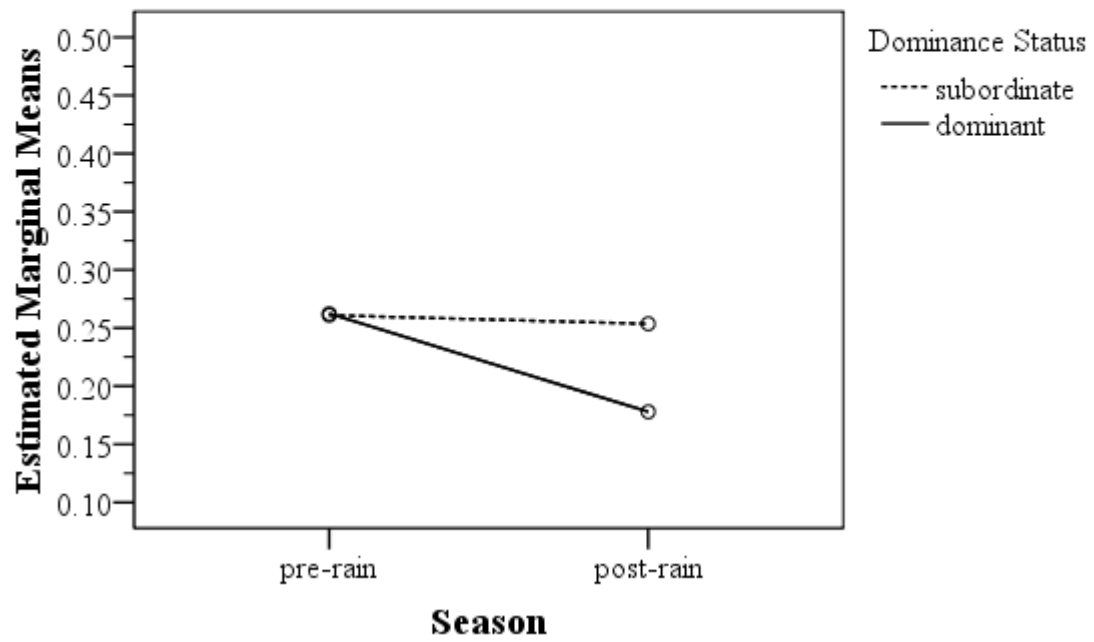
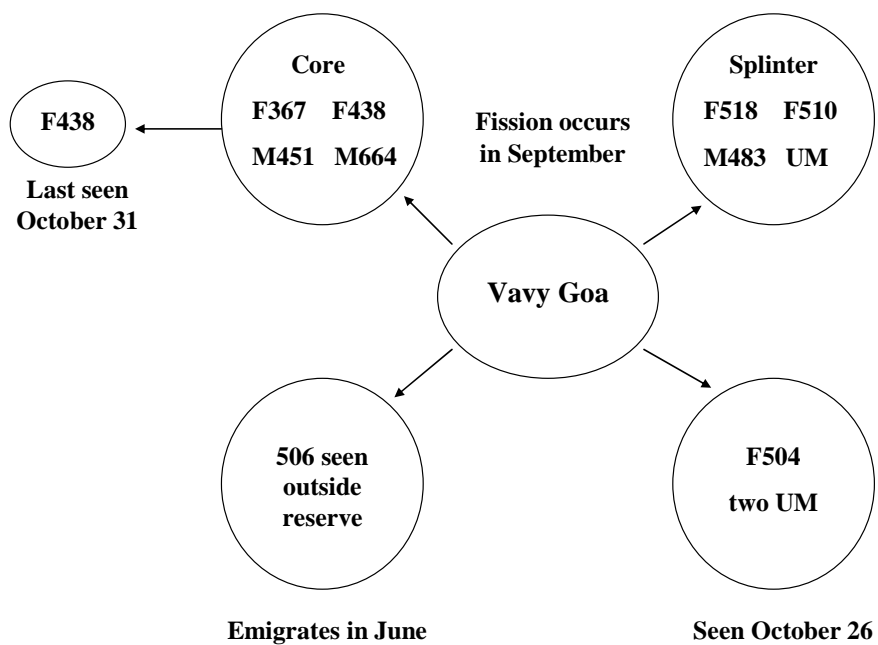


Figure 2.6. Diagram of group composition changes in Vavy Goa during period of targeted female aggression and eviction.



## References

- Altmann, J. (1974). Observational study of behavior: sampling methods. *Behaviour*, *49*, 229-267.
- Barton, R. A., & Whiten, A. (1993). Feeding competition among female olive baboons *Papio anubis*. *Animal Behaviour*, *46*, 777-789.
- Brockman, D. K. (1994). *Reproduction and Mating System of Verreaux's Sifaka (Propithecus verreauxi) at Beza Mahafaly, Madagascar*. Yale University, New Haven.
- Brockman, D. K. (1999). Reproductive behavior of female *Propithecus verreauxi* at Beza Mahafaly, Madagascar. *International Journal of Primatology*, *20*(3), 375-398.
- Brockman, D.K. (2003). *Polyboroides radiatus* predation attempts on *Propithecus verreauxi*. *Folia Primatologica*, *74*, 71-74.
- Brockman, D. K., Godfrey, L. R., Dollar, L. J., & Ratsirarson, J. (2008). Evidence of invasive *Felis silvestris* predation on *Propithecus verreauxi* at Beza Mahafaly Special Reserve, Madagascar. *International Journal of Primatology*, *29*, 135-152.
- Brockman, D. K., & Whitten, P. L. (1996). Reproduction in free-ranging *Propithecus verreauxi*: estrus and the relationship between multiple partner matings and fertilization. *American Journal of Physical Anthropology*, *100*, 57-69.
- Crockett, C. M., & Janson, C. H. (2000). Infanticide in red howlers: female group size, male membership, and a possible link to folivory. In C. P. van Schaik & C. H. Janson (Eds.), *Infanticide by Males* (pp. 75-98). New York: Cambridge University Press.
- Dewar, R. E., & Richard, A. F. (2007). Evolution in the hypervariable environment of Madagascar. *Proceedings of the National Academy of Sciences of the United States of America*, *104*, 13723-13727.
- Dittus, W. P. J. (1988). Group fission among wild toque macaques as a consequence of female resource competition and environmental stress. *Animal Behaviour*, *36*, 1626-1645.
- Erhart, E. M., & Overdorff, D. J. (1998). Infanticide in *Propithecus diadema edwardsi*: an evaluation of the sexual selection hypothesis. *International Journal of Primatology*, *19*(1), 73-81.
- Erhart, E. M., & Overdorff, D. J. (2008). Rates of agonism by diurnal lemuroids: implications for female social relationships. *International Journal of Primatology*, *29*, 1227-1247.

- Gillespie, T. R., & Chapman, C. A. (2001). Determinants of group size in the red colobus monkey (*Procolobus badius*): an evaluation of the generality of the ecological-constraints model. *Behavioral Ecology and Sociobiology*, *50*, 329-338.
- Hausfater, G., & Hrdy, S. B. (Eds.). (1984). *Infanticide: Comparative and Evolutionary Perspectives*. New York: Aldine Publishing Co.
- Hood, L. C. (1994). Infanticide among ringtailed lemurs (*Lemur catta*) at Berenty Reserve, Madagascar. *American Journal of Primatology*, *33*, 65-69.
- Hood, L. C., & Jolly, A. (1995). Troop fission in female *Lemur catta* at Berenty Reserve, Madagascar. *International Journal of Primatology*, *16*(6), 997-1015.
- Hrdy, S. B. (1979). Infanticide among animals: a review, classification, and examination of the implications for the reproductive strategies of females. *Ethology and Sociobiology*, *1*, 13-40.
- Isbell, L. A. (1991). Contest and scramble competition: patterns of female aggression and ranging behavior among primates. *Behavioral Ecology*, *2*(2), 143-155.
- Janson, C. H. (1988). Intra-specific food competition and primate social structure: a synthesis. *Behaviour*, *105*, 1-17.
- Janson, C. H., & Goldsmith, M. L. (1995). Predicting group size in primates: foraging costs and predation risk. *Behavioral Ecology*, *6*(3), 326-336.
- Jolly, A., Caless, S., Cavigelli, S. A., Gould, L., Pereira, M. E., Pitts, A., et al. (2000). Infant killing, wounding and predation in *Eulemur* and *Lemur*. *International Journal of Primatology*, *21*(1), 21-40.
- Kappeler, P. M. (1993). Sexual selection and lemur social systems. In P. M. Kappeler & J. U. Ganzhorn (Eds.), *Lemur Social Systems and Their Ecological Basis* (pp. 223-240). New York: Plenum Press.
- Kappeler, P. M. (1997). Determinants of primate social organization: comparative evidence and new insights from Malagasy lemurs. *Biological Reviews of the Cambridge Philosophical Society*, *72*(1), 111-151.
- Kappeler, P. M. (1998). To whom it may concern: the transmission and function of chemical signals in *Lemur catta*. *Behavioral Ecology and Sociobiology*, *42*, 411-421.
- Kappeler, P. M., & Heymann, E. W. (1996). Nonconvergence in the evolution of primate life history and socioecology. *Biological Journal of the Linnean Society of London*, *59*, 297-326.



- Koenig, A. (2000). Competitive regimes in forest-dwelling Hanuman langur females (*Semnopithecus entellus*). *Behavioral Ecology and Sociobiology*, 48, 93-109.
- Koenig, A., Beise, J., Chalise, M. K., & Ganzhorn, J. U. (1998). When females should contest for food - testing hypotheses about resource density, distribution, size, and quality with Hanuman langurs (*Presbytis entellus*). *Behavioral Ecology and Sociobiology*, 42, 225-237.
- Kubzdela, K. S. (1997). *Sociodemography in diurnal primates: The effects of group size and female dominance rank on intra-group spatial distribution, feeding competition, female reproductive success, and female dispersal patterns in white sifaka, Propithecus verreauxi verreauxi*. University of Chicago, Chicago.
- Lawler, R. R. (2007). Fitness and extra-group reproduction in male Verreaux's sifaka: an analysis of reproductive success from 1989-1999. *American Journal of Physical Anthropology*, 132, 267-277.
- Lawler, R. R., Caswell, H., Richard, A. F., Ratsirarson, J., Dewar, R. E., & Schwartz, M. (2009). Demography of Verreaux's sifaka in a stochastic rainfall environment. *Oecologia*, 161, 491-504.
- Lewis, R. J. (2008). Social influences on group membership in *Propithecus verreauxi verreauxi*. *International Journal of Primatology*, 29, 1249-1270.
- Lewis, R. J., & Kappeler, P. M. (2005). Seasonality, body condition, and timing of reproduction in *Propithecus verreauxi verreauxi* in the Kirindy forest. *American Journal of Primatology*, 67, 347-364.
- Lewis, R. J., Razafindrasamba, S. M., & Tolojanahary, J. P. (2003). Observed infanticide in a seasonal breeding prosimian (*Propithecus verreauxi verreauxi*) in Kirindy Forest, Madagascar. *Folia Primatologica*, 74, 101-103.
- Lewis, R. J., & van Schaik, C. P. (2007). Bimorphism in male Verreaux's sifaka in the Kirindy Forest of Madagascar. *International Journal of Primatology*, 28, 159-182.
- Littlefield, B. L. (2010). Infanticide following male takeover event in Verreaux's sifaka (*Propithecus verreauxi verreauxi*). *Primates*, 51, 83-86.
- Mertl-Millhollen, A. S. (2006). Scent marking as resource defense by female *Lemur catta*. *American Journal of Primatology*, 68, 605-621.
- Norscia, I., Carrai, V., & Borgognini-Tarli, S. M. (2006). Influence of dry season and food quality and quantity on behavior and feeding strategy of *Propithecus verreauxi* in Kirindy, Madagascar. *International Journal of Primatology*, 27(4), 1001-1022.

- Overdorff, D. J. (1996). Ecological correlates to social structure in two lemur species in Madagascar. *American Journal of Physical Anthropology*, 100(4), 487-506.
- Pereira, M. E., & Weiss, M. L. (1991). Female mate choice, male migration, and the threat of infanticide in ringtailed lemurs. *Behavioral Ecology and Sociobiology*, 28(2), 141-152.
- Pochron, S.T., Fitzgerald, J., Gilbert, C.C., Lawrence, D., Grgas, M., Rakotonirina, G., Ratsimbazafy, R., Rakotosoa, R., Wright, P.C. (2003). Patterns of female dominance in *Propithecus diadema edwardsi* of Ranomafana National Park, Madagascar. *American Journal of Primatology*, 61, 173-185.
- Pochron, S. T., Morelli, T. L., Scirbona, J., & Wright, P. C. (2005). Sex differences in scent marking in *Propithecus edwardsi* of Ranomafana National Park, Madagascar. *American Journal of Primatology*, 66, 97-110.
- Pochron, S. T., Tucker, W. T., & Wright, P. C. (2004). Demography, life history, and social structure in *Propithecus diadema edwardsi* from 1986-2000 in Ranomafana National Park, Madagascar. *American Journal of Physical Anthropology*, 125(1), 61-72.
- Rasoloharijaona, S., Rakotosamimanana, B., & Zimmermann, E. (2000). Infanticide by a male Milne-Edwards' sportive lemur (*Lepilemur edwardsi*) in Ampijoroa, NW-Madagascar. *International Journal of Primatology*, 21(1), 41-45.
- Richard, A. F. (1978). *Behavioral Variation: Case study of a Malagasy Lemur*. Lewisburg: Bucknell University Press.
- Richard, A. F. (1992). Aggressive competition between males, female-controlled polygyny and sexual monomorphism in a Malagasy primate, *Propithecus verreauxi*. *Journal of Human Evolution*, 22, 395-406.
- Richard, A. F., Dewar, R. E., Schwartz, M., & Ratsirarson, J. (2000). Mass change, environmental variability and female fertility in wild *Propithecus verreauxi*. *Journal of Human Evolution*, 39, 381-391.
- Richard, A. F., Dewar, R. E., Schwartz, M., & Ratsirarson, J. (2002). Life in the slow lane? Demography and life histories of male and female sifaka (*Propithecus verreauxi verreauxi*). *Journal of Zoology*, 256, 421-436.
- Richard, A. F., Rakotomanga, P., & Schwartz, M. (1991). Demography of *Propithecus verreauxi* at Beza Mahafaly, Madagascar: sex ratio, survival, and fertility, 1984-1988. *American Journal of Physical Anthropology*, 84, 307-322.

- Saito, C. (1996). Dominance and feeding success in female Japanese macaques, *Macaca fuscata*: effects of food patch size and inter-patch distance. *Animal Behaviour*, *51*, 967-980.
- Sauther, M. L. (1993). Resource competition in wild populations of ringtailed lemurs (*Lemur catta*): implications for female dominance. In P. M. Kappeler & J. U. Ganzhorn (Eds.), *Lemur social systems and their ecological basis* (pp. 135-152). New York: Plenum Press.
- Steenbeek, R., & van Schaik, C. P. (2001). Competition and group size in Thomas's langurs (*Presbytis thomasi*): the folivore paradox revisited. *Behavioral Ecology and Sociobiology*, *49*, 100-110.
- Sterck, E. H. M., Watts, D. P., & van Schaik, C. P. (1997). The evolution of female social relationships in nonhuman primates. *Behavioral Ecology and Sociobiology*, *41*, 291-309.
- van Schaik, C. P., & Janson, C. H. (Eds.). (2000). *Infanticide by Males and its Implications*. New York: Cambridge University Press.
- Vick, L. G., & Pereira, M. E. (1989). Episodic targeting aggression and the histories of *Lemur* social groups. *Behavioral Ecology and Sociobiology*, *25*, 3-12.
- Wrangham, R. W. (1980). An ecological model of female-bonded primate groups. *Behaviour*, *75*, 262-300.
- Wright, P. C. (1995). Demography and life history of free-ranging *Propithecus diadema edwardsi* in Ranomafana National Park, Madagascar. *International Journal of Primatology*, *16*(5), 835-851.
- Wright, P. C. (1999). Lemur traits and Madagascar ecology: coping with an island environment. *Yearbook of Physical Anthropology*, *42*, 31-72.
- Yamashita, N. (2002). Diets of two lemur species in different microhabitats in Beza Mahafaly Special Reserve, Madagascar. *International Journal of Primatology*, *23*, 1025-1051.
- Yamashita, N. (2008). Chemical properties of the diets of two lemur species in southwestern Madagascar. *International Journal of Primatology*, *29*, 339-364.

### **Chapter III. The Effects of Dominance, Aggression, and Male Immigration Events on Fecal Testosterone Levels in Female Verreaux's Sifaka (*Propithecus verreauxi*)**

#### **Introduction**

Androgens are associated with sexual differentiation, gonadal development, the expression of secondary sexual characteristics, spermatogenesis, the regulation of sexual behavior and motivation, and the expression of aggression (Adkins-Regan, 2005; Monaghan & Glickman, 2001). Extensive research across a variety of taxa has examined the mediating effects of circulating androgen levels on male aggressive behavior (Adkins-Regan, 2005; Dixson, 1980; Soma, 2006; Wingfield et al., 1990). The complex relationship between testosterone and aggression is influenced by a myriad of social and ecological variables, including variations in resource availability affecting the timing and duration of reproduction (Adkins-Regan, 2005), differences in mating systems and the degree of paternal care (Wingfield et al., 1990), and the relative costs associated with increased testosterone (Wingfield et al., 2001). Each of these factors will impact the strength of the association between testosterone and aggression, particularly as the intensity of inter-individual aggression and competition fluctuates across breeding seasons and social contexts. Furthermore, as individuals enter into different life history stages, there is a trade-off between mating and parental effort that is reflected in the costs of maintaining elevated testosterone levels, particularly in inappropriate contexts (Wingfield et al., 2001). While endocrine systems are responding to ecological cues that regulate reproductive behavior, they must also be sensitive to external social stimuli, thereby influencing the expression of aggression in a context-dependent and appropriate

manner (Wingfield et al., 2001). This is particularly important given that elevated testosterone levels may come with substantial costs, particularly decreased paternal care behaviors (Ketterson et al., 1992; Soma, 2006; Wingfield et al., 1990; Wingfield et al., 2001; Ziegler, 2000), as well as increased metabolic rate, decreased body mass, and impaired immune function (Mougeot et al., 2005; Soma, 2006; Wingfield et al., 2001; Zysling et al., 2003).

Less is known about the role of androgens in female behavior, although studies in birds (Gill et al., 2007; Goymann & Wingfield, 2004b; Jawor et al., 2006; Langmore et al., 2002; Sandell, 2007; Veiga et al., 2004; Zysling et al., 2003), fish (Desjardins et al., 2008; Taves et al., 2009), the marine iguana (Rubenstein & Wikelski, 2005), the rock hyrax (Koren & Geffen, 2009), the ibex (Shargal et al., 2008), and the spotted hyaena (Dloniak et al., 2006; Drea et al., 1998; Licht et al., 1998; van Jaarsveld & Skinner, 1991) have examined the role of androgens in female aggressive behavior, territory defense, and dominance status. The costs of aggression and elevated testosterone may be particularly salient for females, who are required to intermittently switch between competitive contexts and offspring care (Sih et al., 2004). Research has focused on the possible mediating roles of weaker androgens such as androstenedione (Drea, 2007) and dihydroepiandrosterone (DHEA) (Soma & Wingfield, 2001), and the aromatization of testosterone to estrogens (Rubenstein & Wikelski, 2005) in female aggression as possible mechanisms for mediating the costs associated with increased testosterone levels (Goymann & Wingfield, 2004b; Wingfield et al., 2001; Zysling et al., 2003).

In primates, the relationships among testosterone, aggression, and dominance in males have been well documented (*Propithecus verreauxi* (Brockman et al., 2001;

Brockman et al., 1998); *Lemur catta* (Cavigelli & Pereira, 2000); *Colobus vellerosus* (Teichroeb & Sicotte, 2008); *Papio hamadryas anubis* (Sapolsky, 1991, 1993b); *Papio hamadryas ursinus* (Beehner et al., 2006); *Pan troglodytes* (Anestis, 2006; Muehlenbein et al., 2004; Muller & Wrangham, 2004a); and *Pan paniscus* (Marshall & Hohmann, 2005; Sannen et al., 2004). Factors such as the relative stability of the dominance hierarchy (Sapolsky, 1991), the type of mating system (Whitten, 2000; Whitten & Turner, 2004), demographic changes, such as immigration events (Alberts et al., 1992; Brockman et al., 2001; Brockman et al., 1998), seasonal changes in inter-male aggression (Brockman et al., 2001; Lynch et al., 2002; Strier et al., 1999), and the presence of cycling females (Lynch et al., 2002; Muller & Wrangham, 2004a; Whitten, 2000) may all affect the degree to which testosterone is associated with rank in male non-human primates. However, there is still a paucity of data available on androgens in female primates (Barrett et al., 2002a; Batty et al., 1986; Beehner et al., 2005; Sannen et al., 2004). The only field study assessed fecal testosterone levels in female hybrid baboons (*Papio* spp.) and demonstrated that higher-ranking females had higher levels of testosterone compared to subordinates, as well as a positive association between testosterone levels and rates of aggression within individuals (Beehner et al., 2005).

There is even less known about the relationships among testosterone, aggression, and dominance rank in lemurs. Again, most of these studies have focused on males with conflicting results. Dominant males were reported to have higher testosterone levels compared to subordinates in Verreaux's sifaka (*Propithecus verreauxi*) (Brockman et al., 2001; Brockman et al., 1998; Kraus et al., 1999) and ring-tailed lemurs (*Lemur catta*) (Gould, 2005), although no rank-related differences in testosterone were found in red-

fronted lemurs (*Eulemur fulvus rufus*) (Ostner et al., 2002). A relationship between aggression and testosterone has been reported for Verreaux's sifaka (Brockman et al., 2001) and ring-tailed lemurs (Cavigelli & Pereira, 2000), while another study of ring-tailed lemurs (Gould, 2005) and a study of red-fronted lemurs (Ostner et al., 2002) found no association between individual levels of testosterone and rates of aggression. Studies examining testosterone levels in female lemurs have tended to expand upon research on female spotted hyenas (*Crocuta crocuta*) on the role of androgens in masculinized genitalia (Drea & Weil, 2008; Ostner et al., 2003) and female social dominance (Drea, 2007; von Engelhardt et al., 2000). Two separate studies on captive female ring-tailed lemurs found increased androgen levels during the breeding season, which is characterized by increased female aggression (Drea, 2007; von Engelhardt et al., 2000). However, von Engelhardt et al. (2000) reported that neither individual rates of aggression nor rank were significantly associated with testosterone levels. Currently, there are no available data on factors that predict female testosterone levels in a wild lemur population.

The goal of the present study was to examine the factors that predict testosterone levels in wild female Verreaux's sifaka (*Propithecus verreauxi*), a highly seasonally breeding lemur characterized by female dominance (Richard, 1978). Although previous research has examined the endocrinology of female reproduction (Brockman & Whitten, 1996; Brockman et al., 1995), as well as female competition and aggression (Kubzdela, 1997; Richard et al., 2000), there are no available data on the relationships among female aggression, dominance, and testosterone in this species. Behavioral data were collected and fecal testosterone (fT) levels were assessed for females during lactation, which

coincides with the dry season and is a period that is marked by lower resource availability (Kubzdela, 1997). Competition may be crucial for females at this stage to ensure adequate resource acquisition to support the energetics of lactation, but this may be balanced by the costs associated with increased aggression during this period of pronounced maternal care. Specifically, this study examined the extent to which 1) aggression rates (both within- and between-group), 2) dominance rank, 3) group instability (marked by male takeover events and infanticides), and 4) season predict fT levels in females. It was predicted that higher rates of within- and between-group aggression would be associated with higher fT levels, and that dominant females would show higher fT levels and higher rates of aggression compared to subordinates. Females in groups that experienced male takeover events and infanticides were expected to have higher fT levels and rates of aggression due to increased group instability. Finally, as the onset of rains marked the beginning of the season of increased resource availability, this was expected to result in higher rates of aggression and higher fT levels as competition for higher quality resources increased.

## **Methods**

### *Study site and population*

This study was conducted on a population of wild sifaka (*Propithecus verreauxi*) at Beza Mahafaly Special Reserve, an area of protected spiny desert forest in southwest Madagascar, just south of the Tropic of Capricorn. The southwest is characterized by a high degree of variation in interannual rainfall (Dewar & Richard, 2007; Lawler et al., 2009). Fifty years of annual rainfall data



from Beza Mahafaly demonstrated periods of drought as well as periods characterized by high rainfall due to cyclones (Lawler et al., 2009). The unpredictable rainfall in southwest Madagascar may have profound effects on the availability of resources (Dewar & Richard, 2007), which in turn affects sifaka survival and fertility (Lawler et al., 2009; Richard et al., 2002). For the population of Verreaux's sifaka at Beza Mahafaly, demographic factors such as adult survival and population growth rate seem to be particularly sensitive to low rainfall (below 300 mm) (Lawler et al., 2009). Recent evidence suggests this population may be declining as much as 2% every year (Lawler et al., 2009).

In addition to unpredictable annual rainfall, this region is also highly seasonal and semi-arid, with an average of 720 mm annual rainfall (Richard et al., 1991). There is a cooler, dry period from April through September (3°C to 36°C) and a hot, rainy season from October through March (21°C to 42°C) (Richard et al., 1991).

Beza Mahafaly Special Reserve consists of two parcels of protected forest. The research from this study was conducted in Parcel 1, which is approximately 80 hectares and is bordered by the Sakamenga River on the eastern side. Vegetation in the reserve ranges from a high-canopy gallery forest in the east to a more semi-arid and thorny forest in the west, with sifaka groups occupying both ranges of habitats. *Tamarindus indica* is largely found in the eastern section of the reserve, with *Euphorbia* sp. and *Acacia bellula* becoming more pronounced in the west (Yamashita, 2002). Flowers and fruits are found in greater abundance in the reserve after the onset of rains in October/November (Yamashita, 2002).

The reserve itself is gridded with north to south and east to west trails, allowing greater accessibility for following groups. There are about 50 separate sifaka groups, ranging in size from 2-13 individuals with 1-3 females per group (Richard, 1992). Although female philopatry is the norm, there is evidence that females emigrate when the number of females within a group exceeds three (Kubzdela, 1997). The animals within the reserve are habituated, and individuals have unique color collar and tag combinations with numbers for identification purposes. Demographic data have been collected on this population since 1984 (Richard et al., 1991). Although the reserve is enclosed by a barbed wire fence to prevent trespassing by herds of goats and zebu, there has been an influx of invasive wildcats (*Felis silvestris*) and domestic dogs (*Canis lupus familiaris*) that, along with harrier hawks (*Polyboroides radiatus*), predate on this population of sifaka (Brockman, 2003; Brockman et al., 2008).

Verreaux's sifaka are diurnal and primarily arboreal, although sifaka in this population are frequently observed traveling and feeding on the ground (Brockman et al., 2008). Sifaka are folivores, subsisting primarily on mature leaves of *Tamarindus indica*, *Euphorbia* sp., and *Acacia* sp. during the dry season, with an increasing reliance on flowers and fruits with the onset of the rains (Yamashita, 2002; 2008). Sifaka tend to lose body mass during the lean season, and body mass predicts female fertility in this population (Richard et al., 2000). The mating season occurs from January to March, with females displaying estrus within a narrow window of time (0.5 to 96 hours) (Brockman, 1999). Births occur from June to August, and infants are weaned in January to March during the subsequent wet season (Richard et al., 2000). There is a high

infant mortality rate in this population (only 52% of infants survive the first year), with infant deaths peaking after birth and weaning (Richard et al., 2002; Richard et al., 1991).

### *Sample Individuals and Behavioral Observations*

Behavioral observations were conducted on adult female sifaka with infants (N=8), two from each of four groups (Table 3.1) from July through December of 2007. The author collected data on two of the groups, while the remaining two groups were followed by a field research assistant. Four consecutive days of behavioral data and fecal samples were collected from both females within a group before switching to the second group, and this procedure was duplicated each month so that data were collected on all females at comparable stages of lactation. Each observer completed four 30 minute focal animal samples (Altmann, 1974) of each female in the group every day, alternating females and with 10-15 minute breaks of *ad libitum* sampling in between each focal block. Focal observations were conducted from approximately 0700 to 1700 hr, with an hour mid-day break. However, as temperatures began to rise in October, the sifaka often rested during the mid-day for 3 hours or more, but were active earlier in the morning and later in the evening. At this point, the schedule shifted from approximately 0600 to 1800 hr with an extended mid-day break as temperatures reached their daily peak. This resulted in a total of 606.5 hours of observation ( $M = 75.81$ ,  $SD = 4.78$ ). Behaviors were recorded during focal follows using a 63 word ethogram previously established for this species (Brockman, 1994) and included feeding, resting, traveling, social interactions (including approaches, retreats, supplants, other agonistic and submissive behaviors, grooming),

vocalizations, and anogenital marking. Since rates of social behaviors are low among sifaka, *ad libitum* sampling was used to record any additional social behaviors and intergroup encounters. In all of the focal groups, the two females were mother-daughter pairs. The mother of each pair was determined to be the dominant female in the dyad based on direction of submissive behaviors (Brockman, 1994; Lewis & van Schaik, 2007).

#### *Fecal Sample Collection and Extraction*

During the focal week, daily fecal samples were collected from each female immediately after voiding, and preferably in the morning. A total of 301 fecal samples (34-41 samples per female) were obtained, with an average of  $37.63 \pm 2.67$  samples per female (Table 3.1). The samples were dried in a Coleman camping oven within four hours of collection, wrapped tightly in plastic wrap, and then packaged and preserved in small plastic whirlpaks with silica gel inserts as previously described (Brockman & Whitten, 1996; Brockman et al., 1998). Samples were transported back to the Laboratory of Reproductive Ecology at Emory University for analysis. Steroid extraction was performed by homogenizing a 0.1 gm sample of feces in 2 ml methanol:acetone (8:2, v/v) and filtered with a 0.2  $\mu\text{m}$  nylon centrifuge filter (Centrex MF; Scheicher & Schuell, Keene, NH). The filtrate was extracted on Sep-Pak VAC C18 columns (500 mg) (Water Corp. Milford, MA). The sample was diluted with 2 ml distilled water and layered onto a Sep-Pak column primed according to manufacturer's instructions. The column was washed with 5 ml distilled water, and the steroid fraction was eluted with 3 ml methanol.

### *Testosterone Assay*

The fecal testosterone assay was a modification of immunoassay procedures developed by Worthman & Stallings, 1997 and Shirtcliff et al., 2001, and used reagents from the Diagnostic Systems Laboratories (Webster, TX) double antibody radioimmunoassay  $^{125}\text{I}$ -Testosterone kit.

A serial dilution of fecal sample extracts pooled from several different females confirmed that a dilution of 1:50, previously reported for sifaka males (Brockman et al., 1998), was appropriate for sifaka females. Working buffer was 0.1% gelatin phosphate buffered saline (pH 7.4). Diluted antiserum (20  $\mu\text{l}$ , diluted with working buffer 1:4) was added to 400  $\mu\text{l}$  aliquots of standards (diluted 1:6 to give concentrations of 1.0-250 pg/ml), controls (diluted 1:6), and samples (diluted 1:50). After 30 min incubation at 37 C,  $^{125}\text{I}$ -Testosterone tracer (50  $\mu\text{l}$ ) was added and all tubes except total count tubes were incubated at 37 C for 3 hr. After incubation, precipitating reagent (500  $\mu\text{l}$ ) was added and the tubes were vortexed, incubated for 20 min at room temperature, and then centrifuged at room temperature for 20 min at 1500 x g. Following decanting of the supernatants, the radioactivity of the precipitate was determined by 5 minute counts in the gamma counter. Intra- and interassay coefficients of variation were 5.5% (N=10) and 11.9% (N=11), respectively.

### *Season and Infanticide Events*

October 15, 2007 marked the first rain of the season, occurring just after observational week 6 for all females. Mid-October through November marked a transitional period between the dry season and the wet season, characterized by periodic

and light rainfall. The term “season” is used in the analyses for simplicity, but the term refers to the periods before and after the onset of rain. Around this same time period beginning in mid-October (week 6), two of the groups were involved in male takeover events that resulted in the observed or inferred infanticides of all the infants of focal females (Littlefield, 2010).

### *Variable Definitions*

For the focal females, weekly means were calculated for all hormone and behavior variables, resulting in 76 data points (four of the females had ten weeks of observation, while the other four had nine weeks of observation, Table 3.1). Weekly means of fT levels (ng/g) were calculated for each female. There were several daily fT values across females that were extreme outliers. Daily values that were greater than two standard deviations above the mean for each female were removed, and an adjusted fT weekly mean was used for all statistical analyses. Weekly rates of aggression given and anogenital marking were calculated as bouts per hour for each female. Aggressive participation in intergroup encounters was also recorded. An encounter was defined as any time two groups came in contact with each other such that at least one member from each group displayed aggressive behavior towards the other. This was to distinguish actual intergroup encounters from intergroup acknowledgements, where neighboring groups traveled past each other, resulting in monitoring and vocalizing, but no members of the groups interacted with each other. Encounters with roving males were not considered as intergroup encounters. A female was determined to have aggressively participated in an intergroup encounter if she displayed any of the behaviors categorized

as aggressive in the ethogram against at least one member from the other group. Weekly values for the variable for between-group aggression were categorized as “0” if the female did not aggressively participate in an intergroup encounter, and “1” if she did aggressively participate in an intergroup encounter. A dichotomous variable was used instead of a weekly rate (e.g. Pride, 2005a), because the calculated rates of aggressive participation in intergroup encounters were too low. For the purposes of analyses, females were coded as “yes” or “no” on the occurrence of infanticide. Females were categorized in this way to examine whether there were intrinsic differences in behavior and hormone levels in females in unstable groups compared to stable groups even before the actual male takeover events occurred. The interaction of season  $\times$  infanticide accounts for the time period after week 6 when the takeover events occurred.

### *Statistical Analyses*

A general linear mixed model (GLMM) using first-order autoregressive covariance structure with subject included as a random factor was used to model the association between various predictors and the outcomes fT level (ng/g) and rates of aggression given (bouts/hr). This model accounts for correlated errors due to the repeated measures within each subject. Observations between subjects are considered independent, but observations within subject are assumed to be correlated. The covariance structure of the model also takes into account that adjacent observations (e.g. week 1-2 or week 2-3) may be more highly correlated than observations further apart in time. Model selection was completed by considering the association between each predictor and outcome separately. Predictors found to be significantly associated with the outcome variable

(using  $\alpha=0.05$ ) were included in the final model for each outcome. Although this is not ideal, it was necessary to test variables individually rather than all together to avoid over-saturating the model.

The adjusted fT level variable satisfied assumptions of normality (Kolmogorov-Smirnov test:  $Z = 0.802, p = 0.541$ ) and was within acceptable ranges for skewness and kurtosis. The variable for rates of aggression given was log-transformed to satisfy assumptions of normality. GLMMs were run using SAS v. 9.1.3. A MANOVA was used to assess the effects of season and rank on rates of aggression given. The MANOVA was run using SPSS 16.0.

## **Results**

### *Age and Dominance Rank*

The age of focal females ranged from 7 to 20 years ( $M = 12.66, SD = 4.13$ ). There was a trend towards a significant association between age and dominance rank (Wilcoxon signed ranks test:  $Z = -1.89, p = 0.06$ ).

### *Testosterone Levels*

Weekly fT levels (ng/g) were predicted using the following set of 7 independent variables (3 continuous and 4 dichotomous): season (pre-rain = 0, post-rain = 1); weekly rates of within-group aggression given (bouts/hr); between-group aggression (female did not aggressively participate=0, female aggressively participated=1); occurrence of infanticide (no = 0, yes = 1); rank (subordinate = 0, dominant = 1); age (years); and weekly rates of genital marking (bouts/hr). Since infanticides occurred simultaneously



with the transition to rains, the interaction term  $\text{season} \times \text{infanticide}$  was also tested, along with the interaction terms  $\text{season} \times \text{rank}$ ,  $\text{season} \times \text{within-group aggression given}$ , and  $\text{season} \times \text{between-group aggression}$ . Season, occurrence of infanticide, and between-group aggression were all individually significant predictors of fT level, and were included in the final model (Table 3.2). In the final model, season is no longer significant. Occurrence of infanticide is significant such that females that experienced male takeover events and infanticides had higher fT levels than females in stable groups (Fig. 3.1). Females that aggressively participated in intergroup encounters tended to have higher fT levels compared to females that did not aggressively participate in encounters, but this difference only approached significance.

#### *Rates of Aggression Given*

Weekly rates of aggression given (ng/g) were predicted by the following set of 5 independent variables (2 continuous and 3 dichotomous): weekly fT levels (ng/g); season (pre-rain = 0, post-rain = 1); occurrence of infanticide (no = 0, yes = 1); rank (subordinate = 0, dominant = 1); age (years); and the interaction terms of  $\text{season} \times \text{rank}$  and  $\text{season} \times \text{infanticide}$ . Season, occurrence of infanticide, and the interaction of  $\text{season} \times \text{infanticide}$  were all individually significant predictors of rates of aggression given and were included in the final model (Table 3.3). In the final model, season was significant such that females displayed higher rates of aggression after the rains compared to before the rains. The interaction of  $\text{season} \times \text{infanticide}$  was also significant such that females that experienced male takeover events showed higher rates of aggression after the rains compared to females in stable groups (Fig. 3.2).

### *Effects of Season and Rank on Aggression Given to Males and Females*

A  $2 \times (2)$  MANOVA was used to assess the effects of season and rank on rates of aggression given (bouts/hr) to males and females. Multivariate test results revealed a significant main effect for season ( $F(1, 6) = 12.95, p = 0.01, \eta^2 = 0.68$ ) and for sex ( $F(1, 6) = 9.52, p = 0.02, \eta^2 = 0.61$ ). The interaction of season  $\times$  sex was also significant ( $F(1, 6) = 20.14, p = 0.00, \eta^2 = 0.77$ ). Multivariate test results showed no significant main effect for rank ( $F(1, 6) = 0.02, p = 0.90, \eta^2 = 0.00$ ). The interactions of season  $\times$  rank ( $F(1, 6) = 0.19, p = 0.68, \eta^2 = 0.03$ ), sex  $\times$  rank ( $F(1, 6) = 0.03, p = 0.87, \eta^2 = 0.00$ ), and season  $\times$  sex  $\times$  rank ( $F(1, 6) = 0.03, p = 0.87, \eta^2 = 0.00$ ) were also not significant. Rates of aggression (bouts/hr) given by females were significantly higher post-rain compared to pre-rain (pre-rain:  $M = 0.20, SE = 0.04$ ; post-rain:  $M = 0.49, SE = 0.11$ ). Aggression was directed towards males at significantly higher rates compared to females (males:  $M = 0.56, SE = 0.14$ ; females:  $M = 0.13, SE = 0.04$ ). These sex differences were even more pronounced in the post-rain season compared to pre-rain (pre-rain males:  $M = 0.30, SE = 0.09$ ; post-rain males:  $M = 0.83, SE = 0.20$ ; pre-rain females:  $M = 0.11, SE = 0.05$ ; post-rain females:  $M = 0.15, SE = 0.05$ ). Estimated marginal means of rates of aggression given to females and males across seasons is shown in Fig. 3.3.

## **Discussion**

### *Rates of Aggression and Testosterone*

Contrary to expectations, weekly rates of within-group aggression given by females were not a significant predictor of fT levels. Previous studies on ring-tailed lemurs (*Lemur catta*) have demonstrated increased androgen levels corresponding to

periods of increased aggression among females, particularly during the mating season (Drea, 2007; von Engelhardt et al., 2000), although von Engelhardt et al. (2000) did not find a significant association between individual rates of aggression and testosterone levels. The disassociation of aggression and fT levels may reflect the behavioral styles of a species characterized as egalitarian (Sterck et al., 1997), where overt displays of aggression may not necessarily be important for the acquisition and maintenance of dominance status (e.g. Whitten, 2000). For example, testosterone levels in both male muriquis (*Brachyteles arachnoides*) (Strier et al., 1999) and tufted capuchin monkeys (*Cebus apella nigritus*) (Lynch et al., 2002) were not associated with aggression, most likely due to the lack of overt mating aggression seen in these species. Rates of intra-group aggression tend to also be low across lemur species (Erhart & Overdorff, 2008), with the notable exception of periods of intense female-female competition, marked by targeted aggression and eviction that occur in both *Lemur catta* (Vick & Pereira, 1989) and *Propithecus diadema edwardsi* (Pochron et al., 2003; Wright, 1995). Targeted aggression and eviction of females has been observed in the Beza Mahafaly population (Chapter II). The event occurred in a relatively large group (10 individuals; 2 adult females and 3 subadult females) and the behavior was initiated by an adult female towards an unrelated subadult female. All of the focal females in the present study were in groups containing only two or three adult females, and were mother-daughter pairs. Dominance relationships were stable across dyads, and most aggression was directed towards male group members (see below). It is possible that intra-group aggression is relatively low-stakes, and therefore does not elicit a marked endocrine response. Furthermore, the energetic demands of lactation may place a restriction on engaging in

costly aggressive behaviors, especially during the time of decreased resource availability. At the same time, a stronger relationship between testosterone and aggression may emerge when the stakes of intra-group aggression for females are raised due to increased competition over resources or mating opportunities. Since this study did not examine these relationships during the mating season, this presents an avenue for further research (see below).

On the other hand, aggressive participation in between-group encounters may be a stronger predictor of fT levels, suggesting that intra-female competition and aggression may be more important in the context of territory defense. In general, the form of female aggression is expected to be context-dependent, with females showing marked aggression in defense of offspring and territory (Floody, 1983). Several researchers have noted the crucial role that intergroup encounters may have on resource defense for female lemurs (Erhart & Overdorff, 2008; Pride, 2005c; Richard et al., 2000). These encounters often escalate quickly, and can involve prolonged chases and risky aggressive interactions. It is interesting to note that these results parallel those found in male sifaka at the same site, where mean fT levels were significantly associated with frequency of intergroup encounters, but not rates of within-group aggression (Brockman et al., 1998). It must be stressed that in the present model this relationship only approached statistical significance, but it provides an avenue for future research. It may be that the relative intensity of agonistic encounters is a better predictor of testosterone levels (e.g. Ross et al., 2004) and that intergroup encounters, while infrequent, are marked by the potential for heightened aggression in female sifaka.

*Dominance Rank, Testosterone, and Aggression*

Rank was not a significant predictor of either fT levels or rates of within-group competition. Dominant females were found to have higher fT levels in hybrid baboons (*Papio* spp.) (Beehner et al., 2005), but no rank-related differences in testosterone levels were found in a study of captive ring-tailed lemurs (*Lemur catta*) (von Engelhardt et al., 2000) or captive bonobos (*Pan paniscus*) (Sannen et al., 2004). These results suggest that rank-related differences in testosterone levels do not emerge when aggression is relatively unimportant for the maintenance of dominance status. Whereas female baboons, like many Old World monkeys, often rely on aggression to maintain dominance hierarchies (Beehner et al., 2005; Sterck et al., 1997), lemurs show less aggression compared to Old World monkeys (Erhart & Overdorff, 2008) and bonobos use socio-sexual behaviors to mediate competition (Parish & de Waal, 2000). These results support the hypothesis that dominance relationships in Verreaux's sifaka, particularly between related females, are not dependent upon overt aggressive displays. However, it is likely that dominance relationships among female sifaka are seasonally dependent, becoming more pronounced during the season of resource abundance when food items are highly contestable (Richard, 1978). An area of future research is to examine these relationships throughout the wet season to determine whether rank-related differences in aggression and testosterone levels emerge during the time of increased female competition. In addition, rank-related differences in testosterone may be relatively unpronounced in related individuals (Bales et al., 2006). Another necessary step is to examine these relationships in sifaka groups where females are unrelated to explore whether aggression plays a more mediating role in dominance relationships among unrelated females.

### *Male Takeover Events and Testosterone*

The data support the prediction that females who experienced male takeover events and infanticides had higher fT levels compared to females in stable groups, even prior to the actual immigration of males. There is evidence from the focal data that both MB and NB were visited by roving males as early as mid-August (week 2). In the case of NB, one of the males involved in the subsequent takeover of the group was involved in an encounter with resident males in late August (week 3). It is possible that these groups were being targeted by males. It has been suggested that infanticide risk increases with the number of adult females in a group (Crockett & Janson, 2000). Although there are too few confirmed infanticides in this sifaka population to test this hypothesis, it is possible that the two groups in the present study were attractive to immigrant males due to the presence of several reproductively viable females. The weeks leading up to the takeover events may have marked a period of increased instability for these two groups as they encountered new males. Previous research from male primates suggests that testosterone levels increase during periods of group instability, often related to immigration events (Alberts et al., 1992; Brockman et al., 2001; Brockman et al., 1998; Cristoal-Azkarate et al., 2006; Sapolsky, 1991). In resident male mantled howler monkeys (*Alouatta palliata*), testosterone levels were positively associated with the number of solitary males in the area, suggesting that hormonal levels may be responding to the potential threat of male immigration. Similar results were found in male Verreaux's sifaka, where males showed elevated testosterone levels during the birth season, a period marked by immigration events (Brockman et al., 2001; Brockman et al., 1998). It is possible that the females in

these two vulnerable groups had elevated fT levels in response to the perceived threat of new males.

### *Seasonal Differences in Rates of Aggression*

Season was not a predictor of fT levels, but it was a strong predictor for rates of within-group aggression. Aggression increased after the onset of the rains, and much of this aggression was targeted towards males. This increase in aggression is partly due to directed aggression towards new immigrant males by females in groups that experienced male takeover events; however, both stable and unstable groups showed increased female aggression after the onset of rains (Fig. 3.2). During the rainy season, sifaka include more contestable resources such as fruits and flowers in their diet (Yamashita, 2008), which may lead to more competition and aggression over resources (Richard, 1978). Although the present study stops short of the wet season, it captures the transitional period at the onset of the rains and reveals a significant shift in aggressive behavior that accompanies the beginning of dietary shifts. Behavioral data also show that females travel more and spend less time in the presence of nearest neighbors within 2m while feeding after the onset of the rains (Chapter II). This suggests that females are increasing travel to search for higher quality food items, and increasing the distance to other group members as they feed on contestable resources. Taken together with the increase in aggression, these data offer further confirmation that female competition and aggression may be seasonally dependent for lemurs (Erhart & Overdorff, 2008).

## Conclusions

Due to the small sample size and time schedule of this study, these results must be interpreted with caution and are not meant to provide generalized conclusions about testosterone-behavior relationships across female sifaka. These limitations notwithstanding, the strength of this study lies in the collection of in-depth repeated measures over time that captured hormonal fluctuations throughout changing social conditions and during a seasonal transition period. The male takeover events in two of the four focal groups provided an opportunity to examine the hormonal responses of females to male immigration. Females in groups that experienced male takeover events and infanticides had higher fT levels compared to females in stable groups, providing preliminary evidence that group stability is a strong predictor of testosterone levels for female sifaka. Although females are dominant and displayed increased aggression towards these new males, they were unable to prevent new males from establishing residence. Males appear to be a viable threat to female reproductive success in this species (Littlefield, 2010), and more research is needed on female behavioral and hormonal responses to male immigration events, particularly when these events are overtly aggressive and hostile.

This preliminary evidence also suggests that intergroup aggression is more predictive of fT levels than intra-group aggression, a finding that is not altogether unexpected given that levels of aggression among female sifaka are generally low. In addition, between-group aggression appears to take on a different form, characterized primarily by chases and an increased potential for injury. It may be that territory defense against neighboring groups is “high stakes,” eliciting more of a hormonal response than



most aggressive interactions with other group members. This is not to say that aggression between female group members lacks intensity. Female sifaka display targeted aggression towards subordinates (Chapter II), harass immigrant females (Lewis, 2008), and engage in copulatory harassment (Brockman, 1999). Yet these interactions are still context-dependent and occur when the stakes of competition are raised (i.e. eliminating competitors for resources or mates). Dominance relationships among female sifaka may also be context-dependent, with stronger relationships emerging during times when resources are contestable (Erhart & Overdorff, 2008; Richard, 1978). During the transition from the dry to the wet season (October to December), sifaka begin shifting their diet to include more flowers and eventually fruit (Norscia et al., 2006; Yamashita, 2008). As competition for these higher-quality items increases, females may be more likely to use aggression to exert dominance and maintain priority access to resources. The fact that rates of aggression increased with the onset of rains in the present study suggests that females are actively competing with other group members for resources. This competition is expected to increase throughout the wet season, providing another context within which to examine the relationships among testosterone, aggression, and dominance. Although dominance was not a significant predictor of fT levels or rates of aggression, it is possible that rank-related differences in aggression become more pronounced as the wet season progresses. If competition results in aggressive displays between females, such as targeted aggression and eviction, a relationship between testosterone levels and intra-group aggression may also emerge during this season.

Finally, this study points again to the overwhelming complexity in assessing hormone-behavior interactions. There is a great deal of variance unaccounted for by the

present model, such as inter-individual differences in steroid metabolism (Rubinow & Schmidt, 1996) and behavioral style (Sapolsky, 1991). Furthermore, prolonged elevations in testosterone levels come with significant costs (Wingfield et al., 2001), which may be particularly salient for females as they negotiate the balance between competition and parental care (Sih et al., 2004). This has led many researchers to explore weaker androgens such as DHEA and androstenedione, or the aromatization to estrogens, in the expression of aggression in females (Drea, 2007; Rubenstein & Wikelski, 2005; Soma & Wingfield, 2001). Androstenedione levels are higher than testosterone levels in female ring-tailed lemurs, suggesting a possible mediating role for this hormone in female aggression and dominance in this species (Drea, 2007), although no studies have examined androstenedione levels in female sifaka. This study offers a first step in disentangling the social and ecological factors that influence testosterone levels in female sifaka, but more research is needed to contribute to our understanding of the role of testosterone in female primate behavior, as well as other proximate mechanisms that influence female aggression and competition.

Table 3.1. Demographic descriptions and data totals for focal females.

<b>Lemur ID</b>	<b>Group</b>	<b>Group Size</b>	<b>Age</b>	<b>Rank</b>	<b>Occurrence of Infanticide</b>	<b>Observation Weeks</b>	<b>Focal Hours</b>	<b>Fecal Samples</b>
268	RG	8	14	Dom	No	10	80.5	39
379	RG	8	8	Sub	No	10	80	40
9016	KK	5	20	Dom	No	10	80	41
429	KK	5	11	Sub	No	10	80.5	40
315	NB	7	13	Dom	Yes	9	70.5	36
463	NB	7	7	Sub	Yes	9	71	35
422	MB	8	17	Dom	Yes	9	71.5	34
449	MB	8	11	Sub	Yes	9	72.5	36

Table 3.2. Variables included in final general linear mixed model for fecal testosterone levels (ng/g).

<b>Predictor</b>	<b>Estimate</b>	<b>SE</b>	<b>DF</b>	<b><i>F</i> value</b>	<b><i>t</i> value</b>	<b><i>p</i> value</b>
Intercept	28.964	2.602	6		11.13	0.000
Season	-2.016	2.608	66	0.60	-0.77	0.442
Between group aggression	3.939	2.236	66	3.10	1.76	0.083
Occurrence of infanticide	11.479	3.503	6	10.74	3.28	0.017

Table 3.3. Variables included in final general linear mixed model for log-transformed rates of aggression given (bouts/hr).

<b>Predictor</b>	<b>Estimate</b>	<b>SE</b>	<b>DF</b>	<b><i>F</i> value</b>	<b><i>t</i> value</b>	<b><i>p</i> value</b>
Intercept	0.231	0.030	6		7.74	0.000
Season	0.286	0.079	66	13.07	3.61	0.000
Occurrence of infanticide	-0.076	0.042	6	3.28	-1.81	0.120
Season × infanticide	0.374	0.125	66	8.91	2.99	0.004

Figure 3.1. Predicted fT values from final linear mixed model separated by females that experienced male takeover events and infanticides (N=4) and females in stable groups (N=4).

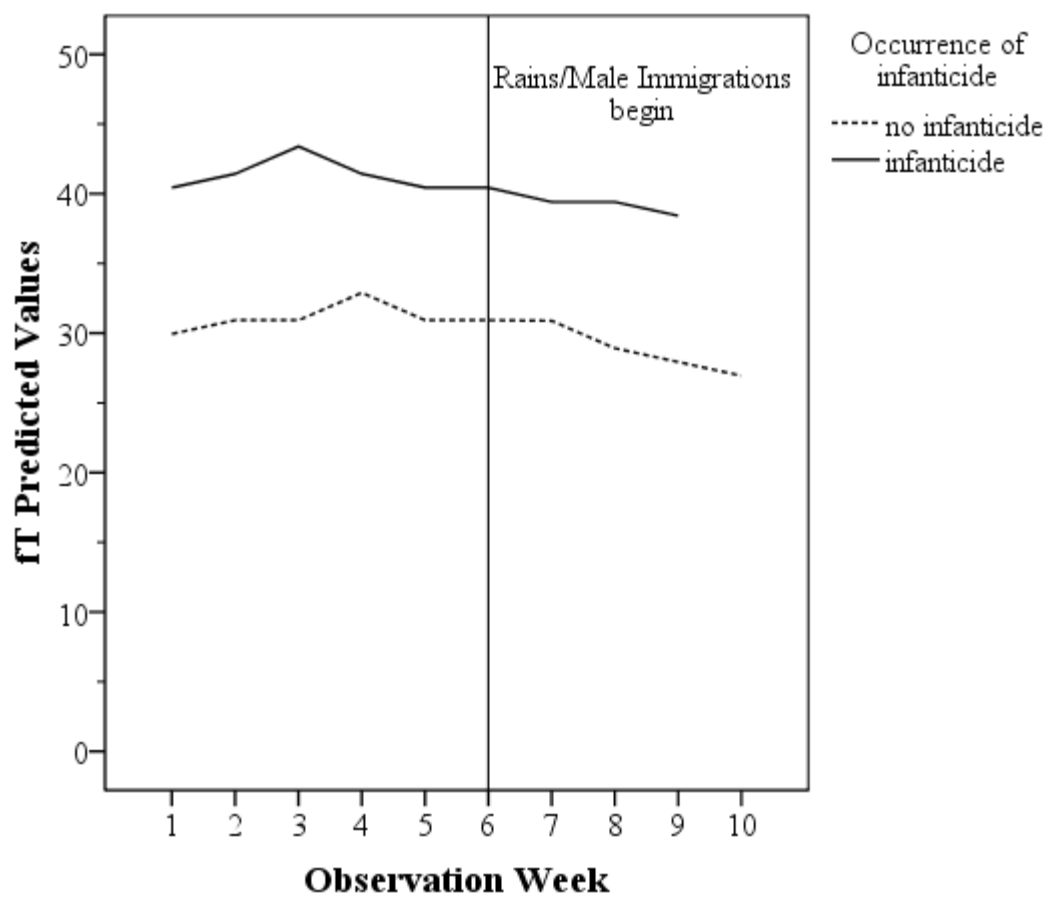


Figure 3.2. Predicted values of rates of within-group aggression (bouts/hr) from final linear mixed model separated by females that experienced male takeover events and infanticides (N=4) and females in stable groups (N=4) across seasons.

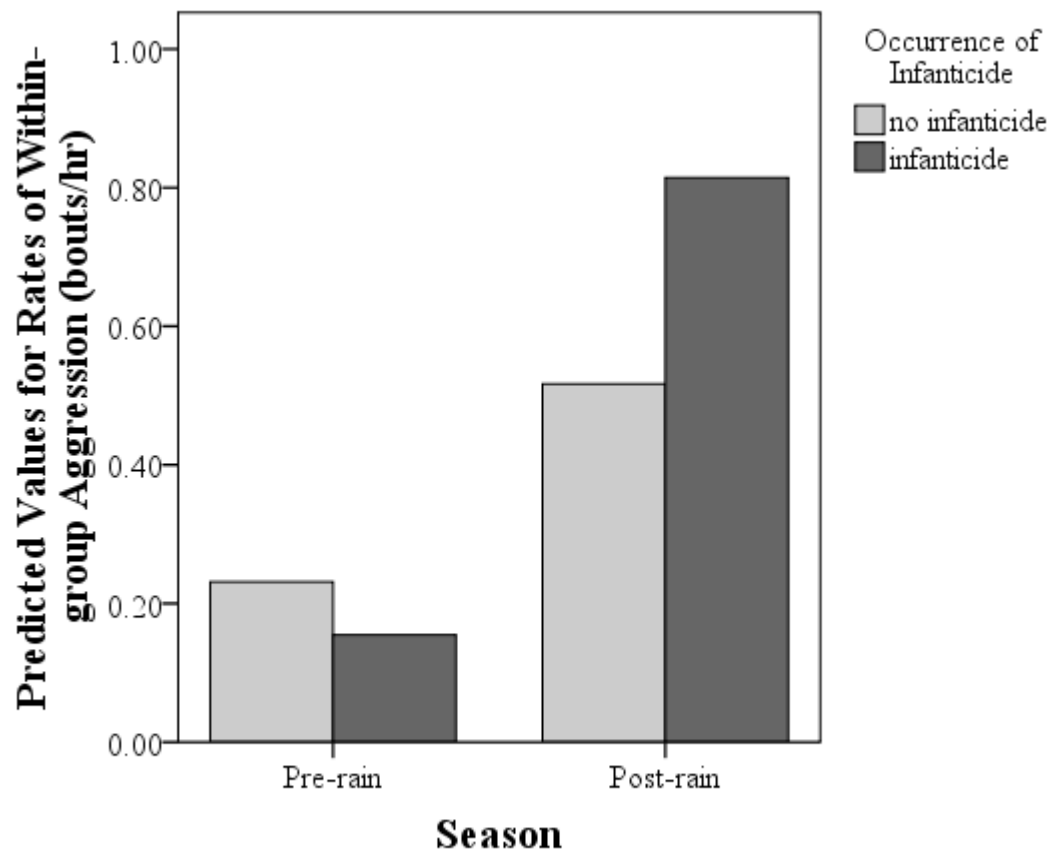
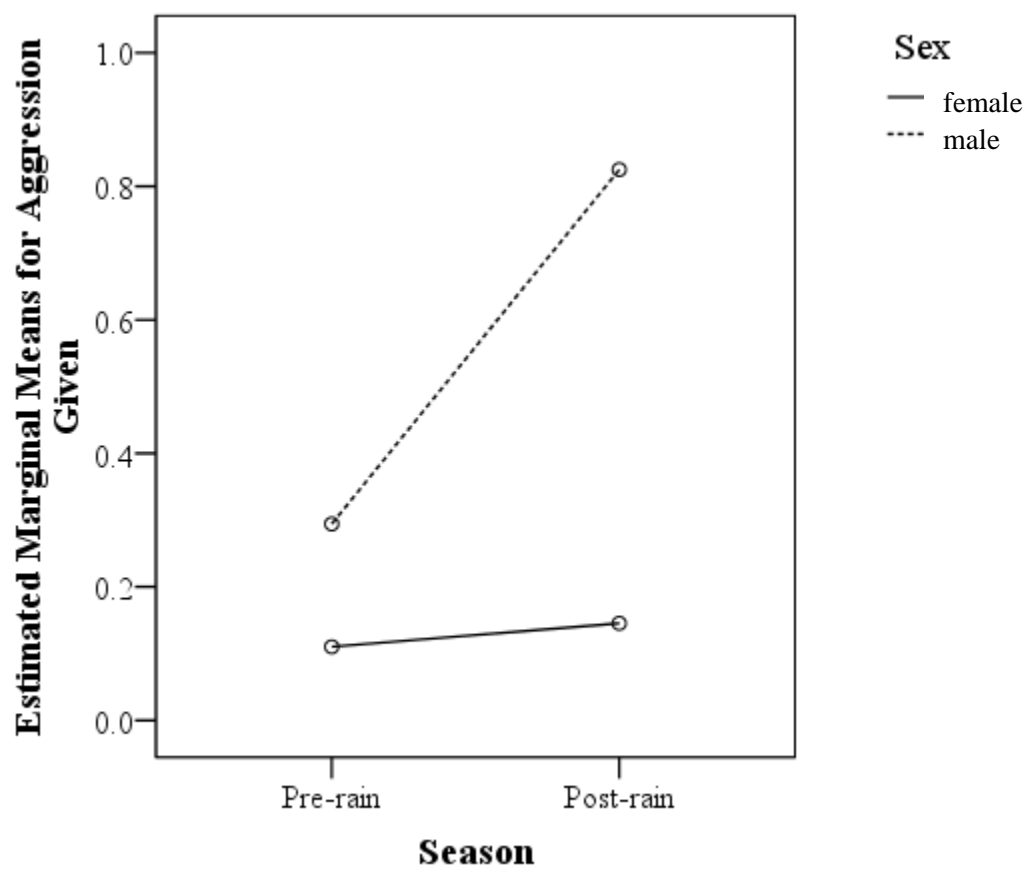


Figure 3.3. Estimated marginal means of rates of aggression given (bouts/hr) to females and males across seasons.





## References

- Adkins-Regan, E. (2005). *Hormones and Animal Social Behavior*. Princeton: Princeton University Press.
- Alberts, S. C., Sapolsky, R. M., & Altmann, J. (1992). Behavioral, endocrine, and immunological correlates of immigration by an aggressive male into a natural primate group. *Hormones and Behavior*, 26(2), 167-178.
- Altmann, J. (1974). Observational study of behavior: sampling methods. *Behaviour*, 49, 229-267.
- Anestis, S. F. (2006). Testosterone in juvenile and adolescent male chimpanzees (*Pan troglodytes*): effects of dominance rank, aggression, and behavioral style. *American Journal of Physical Anthropology*, 130(4), 536-545.
- Bales, K. L., French, J. A., McWilliams, J., Lake, R. A., & Dietz, J. M. (2006). Effects of social status, age, and season on androgen and cortisol levels in wild male golden lion tamarins (*Leontopithecus rosalia*). *Hormones and Behavior*, 49(1), 88-95.
- Barrett, G. M., Shimizu, K., Bardi, M., Asaba, S., & Mori, A. (2002). Endocrine correlates of rank, reproduction, and female-directed aggression in male Japanese Macaques (*Macaca fuscata*). *Hormones and Behavior*, 42(1), 85-96.
- Batty, K. A., Herbert, J., Keverne, E. B., & Vellucci, S. V. (1986). Differences in blood levels of androgens in female talapoin monkeys related to their social status. *Neuroendocrinology*, 44, 347-354.
- Beehner, J. C., Bergman, T. J., Cheney, D. L., Seyfarth, R. M., & Whitten, P. L. (2006). Testosterone predicts future dominance rank and mating activity among male chacma baboons. *Behavioral Ecology and Sociobiology*, 59(4), 469-479.
- Beehner, J. C., Phillips-Conroy, J. E., & Whitten, P. L. (2005). Female testosterone, dominance rank, and aggression in an Ethiopian population of hybrid baboons. *American Journal of Primatology*, 67, 101-119.
- Brockman, D. K. (1994). *Reproduction and Mating System of Verreaux's Sifaka (Propithecus verreauxi) at Beza Mahafaly, Madagascar*. Yale University, New Haven.
- Brockman, D. K. (1999). Reproductive behavior of female *Propithecus verreauxi* at Beza Mahafaly, Madagascar. *International Journal of Primatology*, 20(3), 375-398.
- Brockman, D.K. (2003). *Polyboroides radiatus* predation attempts on *Propithecus verreauxi*. *Folia Primatologica*, 74, 71-74.

- Brockman, D. K., Godfrey, L. R., Dollar, L. J., & Ratsirarson, J. (2008). Evidence of invasive *Felis silvestris* predation on *Propithecus verreauxi* at Beza Mahafaly Special Reserve, Madagascar. *International Journal of Primatology*, *29*, 135-152.
- Brockman, D. K., & Whitten, P. L. (1996). Reproduction in free-ranging *Propithecus verreauxi*: estrus and the relationship between multiple partner matings and fertilization. *American Journal of Physical Anthropology*, *100*, 57-69.
- Brockman, D. K., Whitten, P. L., Richard, A. F., & Benander, B. (2001). Birth season testosterone levels in male Verreaux's sifaka, *Propithecus verreauxi*: insights into socio-demographic factors mediating seasonal testicular function. *Behavioral Ecology and Sociobiology*, *49*(2-3), 117-127.
- Brockman, D. K., Whitten, P. L., Richard, A. F., & Schneider, A. (1998). Reproduction in free-ranging male *Propithecus verreauxi*: the hormonal correlates of mating and aggression. *American Journal of Physical Anthropology*, *105*(2), 137-151.
- Brockman, D. K., Whitten, P. L., Russell, E., Richard, A. F., & Izard, M. K. (1995). Application of fecal steroid techniques to the reproductive endocrinology of female Verreaux's sifaka (*Propithecus verreauxi*). *American Journal of Primatology*, *36*, 313-325.
- Cavigelli, S. A., & Pereira, M. E. (2000). Mating season aggression and fecal testosterone levels in male ring-tailed lemurs (*Lemur catta*). *Hormones and Behavior*, *37*(3), 246-255.
- Cristoal-Azkarate, J., Chavira, R., Boeck, L., Rodriguez-Luna, E., & Veal, J. J. (2006). Testosterone levels of free-ranging resident mantled howler monkey males in relation to the number and density of solitary males: a test of the challenge hypothesis. *Hormones and Behavior*, *49*(2), 261-267.
- Crockett, C. M., & Janson, C. H. (2000). Infanticide in red howlers: female group size, male membership, and a possible link to folivory. In C. P. van Schaik & C. H. Janson (Eds.), *Infanticide by Males* (pp. 75-98). New York: Cambridge University Press.
- Desjardins, J. K., Stiver, K. A., Fitzpatrick, J. L., Milligan, N., Van der Kraak, G. J., & Balshine, S. (2008). Sex and status in a cooperative breeding fish: behavior and androgens. *Behavioral Ecology and Sociobiology*, *62*, 785-794.
- Dewar, R. E., & Richard, A. F. (2007). Evolution in the hypervariable environment of Madagascar. *Proceedings of the National Academy of Sciences of the United States of America*, *104*, 13723-13727.
- Dixon, A. F. (1980). Androgens and aggressive behavior in primates: a review. *Aggressive Behavior*, *6*, 37-67.

- Dloniak, S. M., French, J. A., & Holekamp, K. E. (2006). Rank-related maternal effects of androgens on behaviour in wild spotted hyaenas. *Nature*, 440(7088), 1190-1193.
- Drea, C. M. (2007). Sex and seasonal differences in aggression and steroid secretion in *Lemur catta*: are socially dominant females hormonally 'masculinized'? *Hormones and Behavior*, 51, 555-567.
- Drea, C. M., & Weil, A. (2008). External genital morphology of the ring-tailed lemur (*Lemur catta*): females are naturally "masculinized". *Journal of Morphology*, 269, 451-463.
- Drea, C. M., Weldele, M. L., Forger, N. G., Coscia, E. M., Frank, L. G., Licht, P., et al. (1998). Androgens and masculinization of genitalia in the spotted hyaena (*Crocuta crocuta*). 2. Effects of prenatal anti-androgens. *Journal of Reproduction and Fertility*, 113(1), 117-127.
- Erhart, E. M., & Overdorff, D. J. (2008). Rates of agonism by diurnal lemuroids: implications for female social relationships. *International Journal of Primatology*, 29, 1227-1247.
- Floody, O. R. (1983). Hormones and aggression in female mammals. In B. B. Svare (Ed.), *Hormones and Aggressive Behavior* (pp. 39-89). New York: Plenum Press.
- Gill, S. A., Alfson, E. D., & Hau, M. (2007). Context matters: female aggression and testosterone in a year-round territorial neotropical songbird (*Thryothorus leucotis*). *Proceedings of the Royal Society of London Series B-Biological Sciences*, 274, 2187-2194.
- Gould, L. (2005). Variation in fecal testosterone levels, intermale aggression, dominance rank and age during mating and post-mating periods in wild adult male ring-tailed lemurs (*Lemur catta*). *American Journal of Primatology*, 69, 1325-1339.
- Goymann, W., & Wingfield, J. C. (2004). Competing females and caring males. Sex steroids in African black coucals, *Centropus grillii*. *Animal Behaviour*, 68, 733-740.
- Jawor, J. M., Young, R., & Ketterson, E. D. (2006). Females competing to reproduce: dominance matters but testosterone may not. *Hormones and Behavior*, 49, 362-368.
- Ketterson, E. D., Nolan, V., Wolf, L., & Ziegenfus, C. (1992). Testosterone and avian life histories: effects of experimentally elevated testosterone on behavior and correlates of fitness in the dark-eyed junco (*Junco hyemalis*). *The American Naturalist*, 140(6), 980-999.

- Koren, L., & Geffen, E. (2009). Androgens and social status in female rock hyraxes. *Animal Behaviour*, 77, 233-238.
- Kraus, C., Heistermann, M., & Kappeler, P. M. (1999). Physiological suppression of sexual function of subordinate males: a subtle form of intrasexual competition among male sifakas (*Propithecus verreauxi*)? *Physiology and Behavior*, 66, 855-861.
- Kubzdela, K. S. (1997). *Sociodemography in diurnal primates: The effects of group size and female dominance rank on intra-group spatial distribution, feeding competition, female reproductive success, and female dispersal patterns in white sifaka, Propithecus verreauxi verreauxi*. University of Chicago, Chicago.
- Langmore, N. E., Cockrem, J. F., & Candy, E. J. (2002). Competition for male reproductive investment elevates testosterone levels in female dunnocks, *Prunella modularis*. *Proceedings of the Royal Society of London Series B-Biological Sciences*, 269(1508), 2473-2478.
- Lawler, R. R., Caswell, H., Richard, A. F., Ratsirarson, J., Dewar, R. E., & Schwartz, M. (2009). Demography of Verreaux's sifaka in a stochastic rainfall environment. *Oecologia*, 161, 491-504.
- Lewis, R. J. (2008). Social influences on group membership in *Propithecus verreauxi verreauxi*. *International Journal of Primatology*, 29, 1249-1270.
- Lewis, R. J., & van Schaik, C. P. (2007). Bimorphism in male Verreaux's sifaka in the Kirindy Forest of Madagascar. *International Journal of Primatology*, 28, 159-182.
- Licht, P., Hayes, T., Tsai, P., Cunha, G., Kim, H., Golbus, M., et al. (1998). Androgens and masculinization of genitalia in the spotted hyaena (*Crocuta crocuta*). 1. Urogenital morphology and placental androgen production during fetal life. *Journal of Reproduction and Fertility*, 113(1), 105-116.
- Littlefield, B. L. (2010). Infanticide following male takeover event in Verreaux's sifaka (*Propithecus verreauxi verreauxi*). *Primates*, 51, 83-86.
- Lynch, J. W., Ziegler, T. E., & Strier, K. B. (2002). Individual and seasonal variation in fecal testosterone and cortisol levels of wild male tufted capuchin monkeys, *Cebus apella nigrinus*. *Hormones and Behavior*, 41(3), 275-287.
- Marshall, A. J., & Hohmann, G. (2005). Urinary testosterone levels of wild male bonobos (*Pan paniscus*) in the Lomako Forest, Democratic Republic of Congo. *American Journal of Primatology*, 65(1), 87-92.

- Monaghan, E. P., & Glickman, S. E. (2001). Hormones and aggressive behavior. In J. B. Becker, S. M. Breedlove & D. Crews (Eds.), *Behavioral Endocrinology*. Cambridge, Massachusetts: The MIT Press.
- Mougeot, F., Redpath, S. M., Piertney, S. B., & Hudson, P. J. (2005). Separating behavioral and physiological mechanisms in testosterone-mediated trade-offs. *American Naturalist*, *166*(2), 158-168.
- Muehlenbein, M. P., Watts, D. P., & Whitten, P. L. (2004). Dominance rank and fecal testosterone levels in adult male chimpanzees (*Pan troglodytes schweinfurthii*) at Ngogo, Kibale National Park, Uganda. *American Journal of Primatology*, *64*(1), 71-82.
- Muller, M. N., & Wrangham, R. W. (2004). Dominance, aggression and testosterone in wild chimpanzees: a test of the 'challenge hypothesis'. *Animal Behaviour*, *67*, 113-123.
- Norscia, I., Carrai, V., & Borgognini-Tarli, S. M. (2006). Influence of dry season and food quality and quantity on behavior and feeding strategy of *Propithecus verreauxi* in Kirindy, Madagascar. *International Journal of Primatology*, *27*(4), 1001-1022.
- Ostner, J., Heistermann, M., & Kappeler, P. M. (2003). Intersexual dominance, masculinized genitals and prenatal steroids: comparative data from lemurid primates. *Naturwissenschaften*, *90*(3), 141-144.
- Ostner, J., Kappeler, P. M., & Heistermann, M. (2002). Seasonal variation and social correlates of androgen excretion in male redfronted lemurs (*Eulemur fulvus rufus*). *Behavioral Ecology and Sociobiology*, *52*(6), 485-495.
- Parish, A. R., & de Waal, F. B. M. (2000). The other 'closest living relative': how bonobos (*Pan paniscus*) challenge traditional assumptions about females, dominance, intra- and intersexual interactions, and hominid evolution. *Annals of the New York Academy of Sciences*, *907*, 97-113.
- Pochron, S.T., Fitzgerald, J., Gilbert, C.C., Lawrence, D., Grgas, M., Rakotonirina, G., Ratsimbazafy, R., Rakotosoa, R., Wright, P.C. (2003). Patterns of female dominance in *Propithecus diadema edwardsi* of Ranomafana National Park, Madagascar. *American Journal of Primatology*, *61*, 173-185.
- Pride, R. E. (2005a). Foraging success, agonism, and predator alarms: behavioral predictors of cortisol in *Lemur catta*. *International Journal of Primatology*, *26*(2), 295-319.
- Pride, R. E. (2005b). Optimal group size and seasonal stress in ring-tailed lemurs (*Lemur catta*). *Behavioral Ecology*, *16*(3), 550-560.

- Richard, A. F. (1978). *Behavioral Variation: Case study of a Malagasy Lemur*. Lewisburg: Bucknell University Press.
- Richard, A. F. (1992). Aggressive competition between males, female-controlled polygyny and sexual monomorphism in a Malagasy primate, *Propithecus verreauxi*. *Journal of Human Evolution*, 22, 395-406.
- Richard, A. F., Dewar, R. E., Schwartz, M., & Ratsirarson, J. (2000). Mass change, environmental variability and female fertility in wild *Propithecus verreauxi*. *Journal of Human Evolution*, 39, 381-391.
- Richard, A. F., Dewar, R. E., Schwartz, M., & Ratsirarson, J. (2002). Life in the slow lane? Demography and life histories of male and female sifaka (*Propithecus verreauxi verreauxi*). *Journal of Zoology*, 256, 421-436.
- Richard, A. F., Rakotomanga, P., & Schwartz, M. (1991). Demography of *Propithecus verreauxi* at Beza Mahafaly, Madagascar: sex ratio, survival, and fertility, 1984-1988. *American Journal of Physical Anthropology*, 84, 307-322.
- Ross, C. N., French, J. A., & Patera, K. J. (2004). Intensity of aggressive interactions modulates testosterone in male marmosets. *Physiology & Behavior*, 83(3), 437-445.
- Rubenstein, D. R., & Wikelski, M. (2005). Steroid hormones and aggression in female Galapagos marine iguanas. *Hormones and Behavior*, 48(3), 329-341.
- Rubinow, D. R., & Schmidt, P. J. (1996). Androgens, brain, and behavior. *American Journal of Psychiatry*, 153(8), 974-984.
- Sandell, M. I. (2007). Exogenous testosterone increases female aggression in the European starling (*Sturnus vulgaris*). *Behavioral Ecology and Sociobiology*, 62, 255-262.
- Sannen, A., van Elsacker, L., Heistermann, M., & Eens, M. (2004). Urinary testosterone-metabolite levels and dominance rank in male and female bonobos (*Pan paniscus*). *Primates*, 45, 89-96.
- Sapolsky, R. M. (1991). Testicular function, social rank and personality among wild baboons. *Psychoneuroendocrinology*, 16(4), 281-293.
- Sapolsky, R. M. (1993). Endocrinology alfresco: psychoendocrine studies of wild baboons. *Recent Progress in Hormone Research*, 48, 437-465.
- Shargal, D., Shore, L., Roteri, N., Terkel, A., Zorovsky, Y., Shemesh, M., et al. (2008). Fecal testosterone is elevated in high ranking female ibexes (*Capra nubiana*) and

associated with increased aggression and a preponderance of male offspring. *Theriogenology*, 69, 673-680.

- Shirtcliff, E. A., Reavis, R., Overman, W. H., & Granger, D. A. (2001). Measurement of gonadal hormones in dried blood spots versus serum: verification of menstrual cycle phase. *Hormones and Behavior*, 39, 258-266.
- Sih, A., Bell, A. M., Johnson, J. C., & Ziemba, R. E. (2004). Behavioral syndromes: an integrative overview. *Quarterly Review of Biology*, 79(3), 241-277.
- Soma, K. K. (2006). Testosterone and aggression: Berthold, birds and beyond. *Journal of Neuroendocrinology*, 18(7), 543-551.
- Soma, K. K., & Wingfield, J. C. (2001). Dehydroepiandrosterone in songbird plasma: seasonal regulation and relationship to territorial aggression. *General and Comparative Endocrinology*, 123, 144-155.
- Sterck, E. H. M., Watts, D. P., & van Schaik, C. P. (1997). The evolution of female social relationships in nonhuman primates. *Behavioral Ecology and Sociobiology*, 41, 291-309.
- Strier, K. B., Ziegler, T. E., & Wittwer, D. J. (1999). Seasonal and social correlates of fecal testosterone and cortisol levels in wild male muriquis (*Brachyteles arachnoides*). *Hormones and Behavior*, 35(2), 125-134.
- Taves, M. D., Desjardins, J. K., Mishra, S., & Balshine, S. (2009). Androgens and dominance: sex-specific patterns in a highly social fish (*Neolamprologus pulcher*). *General and Comparative Endocrinology*, 161, 202-207.
- Teichroeb, J. A., & Sicotte, P. (2008). Social correlates of fecal testosterone in male ursine colobus monkeys (*Colobus vellerosus*): the effect of male reproductive competition in aseasonal breeders. *Hormones and Behavior*, 54, 417-423.
- van Jaarsveld, A. S., & Skinner, J. D. (1991). Plasma androgens in spotted hyaenas (*Crocuta crocuta*): influence of social and reproductive development. *Journal of Reproduction and Fertility*, 93(1), 195-201.
- Veiga, J. P., Vinuela, J., Cordero, P. J., Aparicio, J. M., & Polo, V. (2004). Experimentally increased testosterone affects social rank and primary sex ratio in the spotless starling. *Hormones and Behavior*, 46, 47-53.
- Vick, L. G., & Pereira, M. E. (1989). Episodic targeting aggression and the histories of *Lemur* social groups. *Behavioral Ecology and Sociobiology*, 25, 3-12.

- von Engelhardt, N., Kappeler, P. M., & Heistermann, M. (2000). Androgen levels and female social dominance in *Lemur catta*. *Proceedings of the Royal Society of London Series B-Biological Sciences*, 267(1452), 1533-1539.
- Whitten, P. L. (2000). Evolutionary endocrinology of the cercopithecoids. In P. F. Whitehead & C. J. Jolly (Eds.), *Old World Monkeys* (pp. 269-297). New York: Cambridge University Press.
- Whitten, P. L., & Turner, T. R. (2004). Male residence and the patterning of serum testosterone in vervet monkeys (*Cercopithecus aethiops*). *Behavioral Ecology and Sociobiology*, 56(6), 565-578.
- Wingfield, J. C., Hegner, R. E., Dufty, A. M., & Ball, G. F. (1990). The "challenge hypothesis": theoretical implications for patterns of testosterone secretion, mating systems, and breeding strategies. *The American Naturalist*, 136(6), 829-846.
- Wingfield, J. C., Lynn, S. E., & Soma, K. K. (2001). Avoiding the 'costs' of testosterone: ecological bases of hormone-behavior interactions. *Brain Behavior and Evolution*, 57(5), 239-251.
- Worthman, C. M., & Stallings, J. F. (1997). Hormone measures in finger-prick blood samples: new field methods for reproductive endocrinology. *American Journal of Physical Anthropology*, 104, 1-21.
- Wright, P. C. (1995). Demography and life history of free-ranging *Propithecus diadema edwardsi* in Ranomafana National Park, Madagascar. *International Journal of Primatology*, 16(5), 835-851.
- Yamashita, N. (2002). Diets of two lemur species in different microhabitats in Beza Mahafaly Special Reserve, Madagascar. *International Journal of Primatology*, 23, 1025-1051.
- Yamashita, N. (2008). Chemical properties of the diets of two lemur species in southwestern Madagascar. *International Journal of Primatology*, 29, 339-364.
- Ziegler, T. E. (2000). Hormones associated with non-maternal infant care: A review of mammalian and avian studies. *Folia Primatologica*, 71(1-2), 6-21.
- Zysling, D. A., Greives, T. J., Demas, G. E., & Ketterson, E. D. (2003). Effects of testosterone on female aggression and immune function: possible evidence of intersexual conflict in dark-eyed juncos (*Junco hyemalis*). *Integrative and Comparative Biology*, 43(6), 927-927.



**Chapter IV. The Interaction of Ecological and Social Factors on the Stress Response: The Effects of Rainfall and Male Immigration Events on Fecal Glucocorticoid Levels in Female Verreaux's Sifaka (*Propithecus verreauxi*)**

**Introduction**

The adrenocortical response prepares the body to effectively deal with the physiological demands of physical stressors. The release of glucocorticoids mobilizes energy stores and increases cardiac output in the face of potential threats, while diverting energy from nonessential tasks (reviewed in Sapolsky, 2002). In some cases, the acute stressor may activate an “emergency response” that temporarily interrupts a life history stage, such as reproduction, in favor of behaviors essential to survival until conditions improve (Wingfield et al., 1998; Wingfield & Ramenofsky, 1999). Stressors that activate this response can be environmental, social, or even psychological (Sapolsky, 2002). Glucocorticoids rise in response to serious environmental perturbations, such as prolonged drought or severe storms (Wingfield & Ramenofsky, 1999), and have been shown to vary across seasons in response to changes in food availability and behavior (such as mating and migration) (reviewed in Romero, 2002). For non-human primates, a number of demographic and social factors are related to glucocorticoid levels, such as group size (Pride, 2005c), male immigration events (Alberts et al., 1992; Engh et al., 2006; Wittig et al., 2008), social status (reviewed in Abbott et al., 2003; Sapolsky, 1982), and the stability of the hierarchy (Sapolsky, 1982), as well as individual factors such as personality style (Ray & Sapolsky, 1992; Virgin & Sapolsky, 1997) and access to social support (Abbott et al., 2003; Crockford et al., 2008). While the stress response is adaptive

in the short-run, prolonged elevation of glucocorticoids can have a negative impact on several physiological systems, resulting in impaired digestion, suppression of the immune system, increased cardiovascular disease, reproductive suppression, and neuron death (reviewed in Sapolsky, 1994, 2002).

Studies across species of non-human primates, especially male primates, have tended to focus on rank-related differences in glucocorticoid levels, with disparate results. While some studies demonstrated higher levels in subordinate males (Assamese macaques (*Macaca assamensis*) (Ostner, Heistermann et al., 2008) and olive baboons (*Papio anubis*) (Sapolsky, 1982, 1992, 1993b)), others have shown elevated glucocorticoid levels in dominant males (Verreaux's sifaka (*Propithecus verreauxi*) (Fichtel et al., 2007), Japanese macaques (*Macaca fuscata*) (Barrett et al., 2002b), and chimpanzees (*Pan troglodytes*) (Muller & Wrangham, 2004c)). For male chimpanzees, elevated glucocorticoid levels in dominant males appeared to be associated with higher rates of aggression, particularly during the period of decreased resource abundance (Muller & Wrangham, 2004c). However, most studies of male primates have found no rank-related differences in glucocorticoid levels (ring-tailed lemurs (*Lemur catta*) (Gould et al., 2005), red-fronted lemurs (*Eulemur fulvus rufus*) (Ostner, Kappeler et al., 2008), Verreaux's sifaka (*Propithecus verreauxi*) (Brockman et al., 2009), golden lion tamarins (*Leontopithecus rosalia*) (Bales et al., 2006), tufted capuchin monkeys (*Cebus apella*) (Lynch et al., 2002), rhesus macaques (*Macaca mulatta*) (Bercovitch & Clarke, 1995), and gorillas (*Gorilla gorilla beringei*) (Robbins & Czekala, 1997)), as well as no association between rates of aggression and glucocorticoid levels (ring-tailed lemurs (Gould et al., 2005), red-fronted lemurs (Ostner, Kappeler et al., 2008), tufted capuchin

monkeys (Lynch et al., 2002)). It is now well established that the degree to which rank is associated with glucocorticoid levels is dependent upon a number of social and individual factors. For example, subordinate baboons show higher serum cortisol levels when the dominance hierarchy is stable; however, when ranks are threatened, dominant individuals show the highest levels (Sapolsky, 1992, 2005). In addition, the relative costs associated with acquiring and maintaining dominance status will determine the extent to which dominants are more “stressed” than subordinates (Goymann & Wingfield, 2004a). Similarly, the degree to which subordinate status is associated with higher stress levels depends upon the availability of social support (Abbott et al., 2003). Furthermore, stress levels also may correspond to certain “personality styles,” such as the ability to respond effectively to threats and displace aggression (Ray & Sapolsky, 1992; Virgin & Sapolsky, 1997). Taken together, these results reaffirm that the relationship between stress and social rank is mediated by the complex nuances of primate social life.

Relatively less is known about stress hormones in female primates, and very few of these studies have been conducted on wild populations (reviewed in Cheney & Seyfarth, 2009). It is expected that the relationship between rank and glucocorticoids may differ between the sexes (Goymann & Wingfield, 2004a). For female primates, the extent to which rank is associated with glucocorticoids may be dependent upon the degree of reproductive skew (Cheney & Seyfarth, 2009; Creel, 2001). In cooperative breeders, elevated glucocorticoid levels are associated with dominance status (Creel, 2001, 2005), and this appears to be the case for female primates in groups with high reproductive skew (ring-tailed lemurs (*Lemur catta*) (Cavigelli, 1999; Cavigelli et al., 2003, although see Pride, 2005a, 2005c), marmosets (*Callithrix jacchus*) (Saltzman et al., 1994), and cotton-

top tamarins (*Saguinus oedipus*) (Ziegler et al., 1995)). When reproductive skew is low, there are no rank-related differences in female glucocorticoid levels (mandrills (*Mandrillus sphinx*) (Setchell et al., 2008), cynomolgus monkeys (*Macaca fascicularis*) (Stavisky et al., 2001), and chacma baboons (*Papio hamadryas ursinus*) (Crockford et al., 2008; Engh et al., 2006; Weingrill et al., 2004)). Although the relationship between aggression and glucocorticoid levels has not been well examined in female primates, there appears to be no relationship between intragroup aggression and glucocorticoid levels for either chacma baboons (Weingrill et al., 2004) or ring-tailed lemurs (Pride, 2005a, although see discussion of lemurs below). It may be for female primates that factors other than rank and aggression are more salient, including seasonal fluctuations in food availability and male immigration events.

Several studies have found elevated glucocorticoid levels in females during the dry season, when high-quality resources are less readily available (Cavigelli, 1999; Gesquiere et al., 2008; Lynch et al., 2002; Pride, 2005a, 2005c). One hypothesis for these seasonal fluctuations, termed the “energy mobilization hypothesis,” suggests that seasonally elevated glucocorticoid levels correspond to increased energetic demands, such as the energy required for breeding or for sustaining an individual through the lean season (reviewed in Romero, 2002). These elevations in glucocorticoids may not reflect an acute stressor, particularly when seasonal fluctuations in food availability are predictable (Wingfield et al., 1998; Wingfield & Ramenofsky, 1999). Rather the increase in glucocorticoid secretion may aid an individual in mobilizing energy from fat stores until ecological conditions are more favorable (Romero, 2002).

There is also growing evidence to suggest that male immigration events and the threat of infanticide are particularly stressful events for many female primates (Alberts et al., 1992; Cristobal-Azkarate et al., 2007; Engh et al., 2006; Wittig et al., 2008). In baboons (*Papio spp.*), females show a marked increase in glucocorticoid levels immediately following the immigration of a new male, when the threat of infanticide is greatest (Alberts et al., 1992; Engh et al., 2006; Wittig et al., 2008). Fecal glucocorticoid levels were elevated higher and longer for females with dependent offspring, and females sustained elevated levels for as long as 15 weeks (Wittig et al., 2008).

Relatively less is known about the factors that are associated with stress levels in lemuroid primates compared to Old World monkeys, although several studies have examined the effects of rank and aggression on both male and female lemurs. Although dominant male Verreaux's sifaka (*Propithecus verreauxi*) were found to have higher fecal glucocorticoid levels compared to subordinates in one study (Fichtel et al., 2007), most studies have found no rank-related differences among males (ring-tailed lemurs (*Lemur catta*) (Gould et al., 2005), red-fronted lemurs (*Eulemur fulvus rufus*) (Ostner, Kappeler et al., 2008), and Verreaux's sifaka (Brockman et al., 2009)). There also appears to be no association between rates of aggression and fecal glucocorticoid levels in male ring-tailed lemurs (Gould et al., 2005), red-fronted lemurs (Ostner, Kappeler et al., 2008), or Verreaux's sifaka (Fichtel et al., 2007). For males, elevated glucocorticoid levels during the mating season may be related to the energetics of mate guarding (Fichtel et al., 2007), while elevated levels in the birth season may be associated with the potential for male immigrations and the threat of infanticide (Brockman et al., 2009; Ostner, Heistermann et al., 2008). Research on wild female lemurs has been restricted to

populations of ring-tailed lemurs, with some conflicting results. Dominant female lemurs had higher fecal glucocorticoid levels compared to subordinates in two studies (Cavigelli, 1999; Cavigelli et al., 2003), while no rank-related differences were detected in another study (Pride, 2005c). Cavigelli et al. (2003) found that rates of aggression were correlated with glucocorticoid levels, particularly for high-ranking females. However, Pride (2005b) found that intergroup aggression, but not intragroup aggression, was predictive of female glucocorticoid levels. It appears that for female ring-tailed lemurs, elevated glucocorticoid levels correspond with the dry season (Cavigelli, 1999) and are associated with decreased daily food intake (Pride, 2005a), which is not surprising given the highly seasonal and unpredictable environment of Madagascar (Wright, 1999). These studies demonstrate the need to examine the association between glucocorticoid levels and different types of aggressive encounters (both intra- and intergroup) in female lemurs. In addition, it is necessary to investigate seasonal variations in female glucocorticoid levels in response to climatic variables such as rainfall and temperature.

The objective of the present study was to examine the ecological and social factors that predict fecal glucocorticoid levels in wild female Verreaux's sifaka (*Propithecus verreauxi*). Verreaux's sifaka are highly seasonally breeding primates that time lactation to the dry season, a period marked by lower resource availability (Whitten & Brockman, 2001). The birth season is also associated with male immigration events (Brockman et al., 2009), which sometimes result in infanticide (Lewis et al., 2003; Littlefield, 2010). This study focused on lactating females during a five month study period encompassing the transition from the dry to the wet season. Specifically, this study examined the extent to which the following factors predict female glucocorticoid levels:

1) season, 2) rank, 3) aggression (both intra- and intergroup), 4) male takeover events and infanticide, 5) grooming, and 6) proximity of conspecifics. Given that female ring-tailed lemurs showed elevated glucocorticoid levels in the dry season (Cavigelli, 1999), it was expected that females would show higher fecal glucocorticoid levels before the onset of rain than after the first rain. Since most of the previous studies on lemurs have failed to show a strong rank effect on glucocorticoid levels, rank-related differences in glucocorticoid levels were not predicted for female Verreaux's sifaka. Rates of aggression are low among female sifaka, especially during the dry season (Chapter III), so intragroup aggression rates were not expected to predict glucocorticoid levels. However, it was expected that between-group aggression would predict glucocorticoid levels. Male immigrations and infanticides are stressful events for females (Engh et al., 2006; Wittig et al., 2008); therefore, it was expected that glucocorticoid levels would be higher in females that experienced these events compared to females in stable groups. Because grooming has been shown to have a mitigating effect on stress levels in female baboons (Crockford et al., 2008), it was expected that glucocorticoid levels would be lower in females that received more grooming. Finally, glucocorticoid levels were related to group size in female ring-tailed lemurs (Pride, 2005c). If increased proximity to other group members is a mark of increased feeding competition during the dry season, and therefore considered stressful, then glucocorticoid levels should be higher in females that spend more time in close proximity to group members.

## Methods

### *Study site and population*

This study was conducted on a population of wild sifaka (*Propithecus verreauxi*) at Beza Mahafaly Special Reserve, an area of protected spiny desert forest in southwest Madagascar, just south of the Tropic of Capricorn. The southwest is characterized by a high degree of variation in interannual rainfall (Dewar & Richard, 2007; Lawler et al., 2009). Fifty years of annual rainfall data from Beza Mahafaly demonstrated periods of drought as well as periods characterized by high rainfall due to cyclones (Lawler et al., 2009). The unpredictable rainfall in southwest Madagascar may have profound effects on the availability of resources (Dewar & Richard, 2007), which in turn affects sifaka survival and fertility (Lawler et al., 2009; Richard et al., 2002). For the population of Verreaux's sifaka at Beza Mahafaly, demographic factors such as adult survival and population growth rate seem to be particularly sensitive to low rainfall (below 300 mm) (Lawler et al., 2009). Recent evidence suggests this population may be declining as much as 2% every year (Lawler et al., 2009).

In addition to unpredictable annual rainfall, this region is also highly seasonal and semi-arid, with an average of 720 mm annual rainfall (Richard et al., 1991). There is a cooler, dry period from April through September (3°C to 36°C) and a hot, rainy season from October through March (21°C to 42°C) (Richard et al., 1991).

Beza Mahafaly Special Reserve consists of two parcels of protected forest. The research from this study was conducted in Parcel 1, which is approximately 80



hectares and is bordered by the Sakamenga River on the eastern side. Vegetation in the reserve ranges from a high-canopy gallery forest in the east to a more semi-arid and thorny forest in the west, with sifaka groups occupying both ranges of habitats. *Tamarindus indica* is largely found in the eastern section of the reserve, with *Euphorbia* sp. and *Acacia bellula* becoming more pronounced in the west (Yamashita, 2002). Flowers and fruits are found in greater abundance in the reserve after the onset of rains in October/November (Yamashita, 2002).

The reserve itself is gridded with north to south and east to west trails, allowing greater accessibility for following groups. There are about 50 separate sifaka groups, ranging in size from 2-13 individuals with 1-3 females per group (Richard, 1992). Although female philopatry is the norm, there is evidence that females emigrate when the number of females within a group exceeds three (Kubzdela, 1997). The animals within the reserve are habituated, and individuals have unique color collar and tag combinations with numbers for identification purposes. Demographic data have been collected on this population since 1984 (Richard et al., 1991). Although the reserve is enclosed by a barbed wire fence to prevent trespassing by herds of goats and zebu, there has been an influx of invasive wildcats (*Felis silvestris*) and domestic dogs (*Canis lupus familiaris*) that, along with harrier hawks (*Polyboroides radiatus*), predate on this population of sifaka (Brockman, 2003; Brockman et al., 2008).

Verreaux's sifaka are diurnal and primarily arboreal, although sifaka in this population are frequently observed traveling and feeding on the ground (Brockman et al., 2008). Sifaka are folivores, subsisting primarily on mature leaves of *Tamarindus*

*indica*, *Euphorbia* sp., and *Acacia* sp. during the dry season, with an increasing reliance on flowers and fruits with the onset of the rains (Yamashita, 2002; 2008). Sifaka tend to lose body mass during the lean season, and body mass predicts female fertility in this population (Richard et al., 2000). The mating season occurs from January to March, with females displaying estrus within a narrow window of time (0.5 to 96 hours) (Brockman, 1999). Births occur from June to August, and infants are weaned in January to March during the subsequent wet season (Richard et al., 2000). There is a high infant mortality rate in this population (only 52% of infants survive the first year), with infant deaths peaking after birth and weaning (Richard et al., 2002; Richard et al., 1991).

#### *Sample Individuals and Behavioral Observations*

Behavioral observations were conducted on adult female sifaka with infants (N=8), two from each of four groups (Table 4.1) from July through December of 2007. The author collected data on two of the groups, while the remaining two groups were followed by a field research assistant. Four consecutive days of behavioral data and fecal samples were collected from both females within a group before switching to the second group, and this procedure was duplicated each month so that data were collected on all females at comparable stages of lactation. Each observer completed four 30 minute focal animal samples (Altmann, 1974) of each female in the group every day, alternating females and with 10-15 minute breaks of *ad libitum* sampling in between each focal block. Instantaneous scan samples were recorded at five minute intervals throughout the focal block, where the observer noted the number of nearest neighbors within 2 m and the

number of nearest neighbors between 2 and 5 meters. Focal observations were conducted from approximately 0700 to 1700 hr, with an hour mid-day break. However, as temperatures began to rise in October, the sifaka often rested during the mid-day for 3 hours or more, but were active earlier in the morning and later in the evening. At this point, the schedule shifted from approximately 0600 to 1800 hr with an extended mid-day break as temperatures reached their daily peak. This resulted in a total of 606.5 hours of observation ( $M = 75.81$ ,  $SD = 4.78$ ). Behaviors were recorded during focal follows using a 63 word ethogram previously established for this species (Brockman, 1994) and included feeding, resting, traveling, social interactions (including approaches, retreats, supplants, other agonistic and submissive behaviors, grooming), vocalizations, and anogenital marking. Since rates of social behaviors are low among sifaka, *ad libitum* sampling was used to record any additional social behaviors and intergroup encounters. In all of the focal groups, the two females were mother-daughter pairs. The mother of each pair was determined to be the dominant female in the dyad based on direction of submissive behaviors (Brockman, 1994; Lewis & van Schaik, 2007).

#### *Fecal Sample Collection and Extraction*

During the focal week, daily fecal samples were collected from each female immediately after voiding, and preferably in the morning. A total of 301 fecal samples (34-41 samples per female) were obtained, with an average of  $37.63 \pm 2.67$  samples per female (Table 4.1). The samples were dried in a Coleman camping oven within four hours of collection, wrapped tightly in plastic wrap, and then packaged and preserved in small plastic whirlpaks with silica gel inserts as previously described (Brockman &

Whitten, 1996; Brockman et al., 1998). Samples were transported back to the Laboratory of Reproductive Ecology at Emory University for analysis. Steroid extraction was performed by homogenizing a 0.1 gm sample of feces in 2 ml methanol:acetone (8:2, v/v) and filtered with a 0.2  $\mu$ m nylon centrifuge filter (Centrex MF; Scheicher & Schuell, Keene, NH). The filtrate was extracted on Sep-Pak VAC C18 columns (500 mg) (Water Corp. Milford, MA). The sample was diluted with 2 ml distilled water and layered onto a Sep-Pak column primed according to manufacturer's instructions. The column was washed with 5 ml distilled water, and the steroid fraction was eluted with 3 ml methanol.

#### *Corticosterone Radioimmunoassay*

Fecal glucocorticoids were assessed using a corticosterone radioimmunoassay. The corticosterone assay is a modification of the ImmuChem Double Antibody Corticosterone  $^{125}$ I RIA kit (MP Biomedicals (Orangeview, NY). The primary antibody in this kit has been shown to have high cross-reactivity with the major fecal metabolites of cortisol and was found to be superior to other antibodies in a number of mammalian species (Wasser et al., 2000) and has been previously validated for this species (Brockman et al., 2003).

Working buffer was 0.1% gelatin phosphate buffered saline (pH 7.4).  $^{125}$ I tracer (50  $\mu$ l) and antiserum (200  $\mu$ l), diluted 1:3 in working buffer, were added to 100  $\mu$ l aliquots of the standards (diluted 1:3 to give concentrations of 40-1670 pg/ml), samples (diluted 1:4), and controls (diluted 1:3). Samples, standards, and controls were vortexed and incubated 2 hours at room temperature. After incubation, 500  $\mu$ l of second antibody (diluted 1:3) was added, and the incubates were vortexed, incubated an additional 15 min

at room temperature, and centrifuged at 1500 x g for 30 min at room temperature. Following decanting of the supernatant, the radioactivity of the precipitate was determined by 5 min counts in a gamma counter. Intra- and interassay coefficients of variation were 7.2% (N=10) and 15.8% (N=9), respectively.

#### *General Linear Mixed Model (GLMM)*

A general linear mixed model (GLMM) using first-order autoregressive covariance structure with subject included as a random factor was used to assess the association between various predictors and the outcome variable, fecal glucocorticoid (fGC) level. This model accounts for correlated errors due to the repeated measures within each subject. Observations between subjects are considered independent, but observations within subject are assumed to be correlated. The covariance structure of the model also takes into account that adjacent observations (e.g. week 1-2 or week 2-3) may be more highly correlated than observations further apart in time. Model selection was completed by considering the association between each predictor and outcome separately. Predictors found to be significantly associated with the outcome variable (using  $\alpha=0.05$ ) were included in the final model for each outcome. Although this is not ideal, it was necessary to test variables individually rather than all together to avoid over-saturating the model. Analysis was run using SAS v. 9.1.3.

#### *Variable Definitions*

For the focal females, weekly means were calculated for all hormone and behavior variables, resulting in 76 data points (four of the females had ten weeks of

observation, while the other four had nine weeks of observation, Table 4.1). Weekly means of fGC levels (ng/g) were calculated for each female. The outcome variable, fGC level, satisfied assumptions of normality (Kolmogorov-Smirnov test:  $Z = 0.663$ ,  $p = 0.771$ ) as was within acceptable ranges for skewness and kurtosis. The 11 predictors (4 dichotomous and 7 continuous) and interaction terms were as follows:

1. *Season*. The term season is used in the following analyses for simplicity, but refers to observation weeks before first rains (pre-rain=0) and observation weeks after the first rain (post-rain=1).
2. *Occurrence of Infanticide*. Females were classified into two groups: those that did not experience male takeover events or observed/suspected infanticides (=0) and those that did (=1) regardless of what week the takeover events and infanticides occurred. This allowed the opportunity to test if there were intrinsic differences in fGC levels in these two groups.
3. *Rank*. Females were classified as subordinate (=0) or dominant (=1).
4. *Age*. Age was determined in years from the demographic data on this population (Richard et al., 1991).
5. *Aggression*. Both intragroup *aggression given* and *aggression received* were calculated as rates per hour of observation time.
6. *Between-group aggression*. Female sifaka often engage in intergroup encounters. An encounter was defined as any time two groups came in contact with each other such that at least one member from each group displayed aggressive behavior towards the other. This was to distinguish actual intergroup encounters from intergroup acknowledgements, where neighboring groups traveled past each other, resulting in monitoring and

vocalizing, but no members of the groups interacted with each other. Encounters with roving males were not considered as intergroup encounters. A female was determined to have aggressively participated in an intergroup encounter if she displayed any of the behaviors categorized as aggressive in the ethogram against at least one member from the other group. Weekly values for the variable for between-group aggression were categorized as “0” if the female did not aggressively participate in an intergroup encounter, and “1” if she did aggressively participate in an intergroup encounter. A dichotomous variable was used instead of a weekly rate (e.g. Pride, 2005a), because the calculated rates of aggressive participation in intergroup encounters were too low for the purposes of statistical analyses.

7. *Grooming*. Both *grooming given* and *grooming received* were calculated as rates per hour of observation time.

8. *Presence of nearest neighbors*. Nearest neighbor variables were calculated from the instantaneous scan sample. Weekly proportions of time spent in proximity to group members for each female were calculated by dividing the number of scans in which a neighbor was present within 2m by the total number of scans for that week. This was repeated for distances between 2 to 5 m.

9. *Interaction terms*. Since the onset of male takeover events coincided with the first rains (see Results), the interaction of *season*  $\times$  *rank* was used to denote the time period after male takeover and infanticides occurred. Evidence suggests that aggression increases after the onset of rains (Chapter III), so the interaction terms *season*  $\times$  *aggression given* and *season*  $\times$  *between-group aggression* were also tested.

## Results

### *Season and Fecal Glucocorticoid Levels*

October 15, 2007 marked the first rainfall of the season, occurring just after observation week 6 for focal females. October and November marked a transitional period between the dry and wet seasons, with less than 10 mm of rainfall for each of those months (Fig. 4.1). Heavier rains began in December, with a total of 54.6 mm of rain before the end of the study period (December 15). Temperature also began to steadily increase with the transition from the dry to the wet season (Fig. 4.2). Fecal glucocorticoid levels (ng/g) across all focal females dropped precipitously just after observation week 6, coinciding with the first rain of the season (Fig. 4.3) (pre-rain:  $M=97.92$ ,  $SE=5.85$ , post-rain:  $M=62.13$ ,  $SE=2.71$ ).

### *Male Takeover and Infanticide Events*

Beginning in mid-October (observation week 6), both NB and MB were involved in male immigration and takeover events that resulted in the observed and inferred infanticides of all the focal infants over the next couple of weeks (Littlefield, 2010). Figure 4.4 shows mean fGC levels (ng/g) for females that experienced male takeover events and infanticides and females that remained in stable groups.

### *Final GLMM Model*

Of the 11 predictors tested, only season, occurrence of infanticide, and the interaction of season and infanticide were included in the final model (Table 4.2). Fecal glucocorticoid levels decreased after the onset of the rains; however, the interaction term



of season and infanticide was also significant. Females that lost infants due to male immigration events had higher fGC levels after the rains (which coincided with male takeover events) compared to females that remained in stable groups (Figure 4.5).

Dominance rank, along with behavioral measures of aggression and grooming, were not included in the model, suggesting that fGC levels were unaffected by these social variables during this time.

## **Discussion**

### *Seasonal Effects on Glucocorticoid Levels*

There is a strong environmental effect on fGC levels in female Verreaux's sifaka, with females showing higher fGC levels in the dry season compared to the onset of rains (Figs. 3 & 5). Several studies have demonstrated similar results, with individuals showing higher glucocorticoid levels during periods of reduced food availability. Glucocorticoids were elevated in the dry season and negatively correlated with rainfall in male tufted capuchin monkeys (*Cebus apella nigrinus*) (Lynch et al., 2002). Female baboons (*Papio cynocephalus*) also showed higher fGC levels during the dry months (Gesquiere et al., 2008), and fGC levels in male chimpanzees (*Pan troglodytes*) were negatively correlated with the abundance of fruit (Muller & Wrangham, 2004c). In female ring-tailed lemurs (*Lemur catta*), fGC levels were higher during the months of lowest rainfall and fruit availability (Pride, 2005c) and were associated with low food intake (Pride, 2005a). Verreaux's sifaka at Beza Mahafaly Special Reserve subsist primarily on mature leaves during the dry months, adding higher quality items such as young leaves, flowers, and fruits into their diet as they move into the wet season (Yamashita, 2008). Both sexes

show loss in body mass as the dry season progresses, but this loss is especially pronounced in female sifaka and can have a profound effect on female fertility (Richard et al., 2000). Elevated glucocorticoids have been associated with decreased body weight during the lean season in African elephants (*Loxodonta africana*) (Foley et al., 2001), mule deer (*Odocoileus hemionus*) (Saltz & White, 1991), and Pampas deer (*Ozotoceros bezoarticus bezoarticus*) (R. J. G. Pereira et al., 2006). It is therefore not surprising that females show elevated fGC levels during this time period, especially given the added energetic burden associated with lactation. However, these elevated levels are not necessarily tantamount to acute stress for these females. Although Madagascar is a highly unpredictable environment (Wright, 1999), seasonal fluctuations in resource availability are most likely predictable events and are not expected to cause acute stress responses (Wingfield et al., 1998; Wingfield & Ramenofsky, 1999). Rather, elevated glucocorticoid levels in lemurs during the dry season most likely function to mobilize energy from fat stores until higher quality food items become more available (Pride, 2005a).

These results also suggest that the glucocorticoid response in female sifaka is extremely sensitive to exogenous cues. Fecal glucocorticoid levels dropped precipitously from observation week 6 to week 7 (Fig. 4.3), just after the first rainfall of the season, despite the fact that the rain was light (only 2mm). Verreaux's sifaka have been classified as relaxed income breeders ((Brockman & van Schaik, 2005), although see (Richard et al., 2000)) due, in part, to the fact that gonadal steroids are extremely sensitive to photoperiod (Brockman & Whitten, 1996; Whitten & Brockman, 2001). Data on day length were not collected during this study, so it is not possible to rule out the possibility that fGC levels are responding to changes in photoperiod. In addition, previous research

at Beza Mahafaly demonstrated that the abundance of young leaves and flowers peaked in November with the onset of rains (Yamashita, 2002) and that sifaka increased the percent of time spent feeding on these items in November (Yamashita, 2008). The focal females in this study began to feed on more flowers after the onset of rains in late October (personal observation), so it is possible the dietary shift from mature leaves to young leaves and flowers is primarily responsible for the decrease in glucocorticoid levels during this time. However, the possibility that environmental variables such as rainfall, temperature, and day length may regulate glucocorticoid secretion in lemuroid primates provides an intriguing avenue for further research.

#### *Male Immigration and Infanticide*

The results also show that the effect of rainfall on fGC levels is attenuated in females that experienced male takeover events and infanticide (Figure 4.5). Male immigration events and the threat of infanticide have been shown to have profound effects on the stress response for both male and female primates. The immigration of a particularly aggressive male into a group of savannah baboons (*Papio cynocephalus*) resulted in a significant increase in cortisol levels for all group members, especially females, who were most often on the receiving end of the immigrant male's aggressive attacks (Alberts et al., 1992). Female chacma baboons (*Papio hamadryas ursinus*) showed elevated fGC levels after the immigration of a new male (Engh et al., 2006; Wittig et al., 2008). This response was especially pronounced in lactating females at a greater risk of infanticide, such that females with dependent infants maintained elevated fGC levels for a longer period of time compared to females with a lower risk of

infanticide (Wittig et al., 2008). Females also displayed higher fGC levels during the months when infanticide occurred (Engh et al., 2006). For female mantled howler monkeys (*Alouatta palliata*), the strongest predictor of fGC levels was the density of solitary males, suggesting that females are responding to the potential threat of infanticide (Cristobal-Azkarate et al., 2007). Although there are no studies that have examined the relationship between glucocorticoid levels and male immigration events in female lemurs, a study of male Verreaux's sifaka found that elevated glucocorticoid levels during the birth season were related to the presence of infants, which may reflect the stress associated with male immigration and the threat of infanticide (Brockman et al., 2009). This study offers the first evidence that female sifaka also demonstrate a marked endocrine response to male immigration and infanticide events, although it is important to note that fGC levels were not higher after the infanticides occurred compared to the period of time prior to male immigration. Rather, these females showed less of a decrease in fGC levels after the rains. It appears as though the transition to the rainy season has the most pronounced effect on fGC levels, but this effect is mitigated by the social stress associated with male immigration and infanticide.

#### *Dominance Rank, Aggression, and Glucocorticoid Levels*

Fecal glucocorticoid levels were not predicted by either dominance rank or rates of aggression. Previous research on female ring-tailed lemurs has produced equivocal results as to whether there are rank-related differences in glucocorticoid levels. Dominant females were found to have higher fGC levels across two field sites in Madagascar (Cavigelli, 1999; Cavigelli et al., 2003), while another study did not find rank-related

differences in fGC levels (Pride, 2005a, 2005c). In the case of the former, fGC levels were also related to rates of aggression such that groups with the highest rates of aggression also displayed the highest fGC levels (Cavigelli et al., 2003). In addition, rates of initiated aggression were the best predictor of fGC levels in dominant females, while rates of aggression received were the best predictor of fGC levels for subordinate females (Cavigelli et al., 2003). This study took place during the lactation phase coinciding with the end of the dry season, leading the authors to conclude that feeding competition among female ring-tailed lemurs during the period of decreased resource availability may be particularly stressful. Pride (2005), on the other hand, examined associations among rank, aggression, and fGC levels across seasons and found no association between rates of intragroup aggression and fGC levels. The discrepancy between these studies might be explained by the fact that associations among rank, aggression, and glucocorticoid levels may only occur during time periods when there is increased contest competition for available resources (Cavigelli et al., 2003). Although the current study also examined fGC levels during the lean season, evidence from this population suggests that contest competition for resources actually emerges when more high-quality and monopolizable resources become available during the wet season (Richard, 1978). Female rates of aggression were relatively low during the dry season (only about 0.2 bouts/hour), but significantly increased after the onset of rains (Chapter III). It is possible that rank-related differences in fGC levels may emerge for female sifaka during the wet season, especially if contest competition for resources results in differences in food acquisition and nutrient intake for dominant and subordinate females. The extent to which this results in higher stress levels for dominant females, who must maintain preferential access to resources

through increased aggression, or for subordinate females, who are on the receiving end of this aggression and may suffer from decreased access to high-quality food items, remains to be seen. Overall, the lack of rank-related differences in fGC levels in the current study support similar findings for male sifaka during the birth season (Brockman et al., 2009; Fichtel et al., 2007), suggesting that the potential costs associated with social rank for sifaka are not reflected in elevated glucocorticoid levels during the dry season.

The fact that aggressive participation in intergroup encounters did not predict fGC levels for female sifaka was surprising. Previous research in ring-tailed lemurs demonstrated that between-group aggression was a better predictor of fGC levels than within-group aggression (Pride, 2005a). Since intergroup encounters among sifaka can often result in prolonged chases, or even escalate to contact aggression, it seemed probable that these encounters would trigger the release of glucocorticoids for the mobilization of energy. It is possible that the strong seasonal effects on fGC levels for these females, coupled with the male immigration events, may have masked any possible effects of intergroup encounters, especially given that these encounters are rare. At this stage, it is premature to conclude that intergroup encounters do not elicit a stress response from female sifaka. More data are needed on intergroup encounters over the course of the year in order to thoroughly examine the possible activation of the stress response during territory defense.

Finally, neither grooming rates nor close proximity to group members were significant predictors of fGC levels. In many species of primates, access to kin networks and social support may mitigate the costs associated with social status (Abbott et al., 2003). For example, fGC levels were lower in female chacma baboons (*Papio hamadryas*

*ursinus*) that focused their grooming on a small, selective group of partners (Crockford et al., 2008; Wittig et al., 2008). Lemurs lack the extensive kin networks and strong female bonds seen in Old World monkeys (Kappeler, 1997), which may explain why grooming is not a strong predictor of fGC levels in Verreaux's sifaka. Furthermore, the presence of nearest neighbors does not appear to affect female fGC levels, either by decreasing stress levels via affiliation or increasing stress levels due to feeding competition. While evidence from ring-tailed lemurs demonstrated that fGC levels are associated with group size (Pride, 2005c), there was little variation in group size in the present study (Table 4.1). Comparable data from females residing in groups of various sizes are needed to determine the extent to which group size and composition may affect stress levels in Verreaux's sifaka.

## **Conclusions**

The results from the current study provide a unique opportunity to examine the interaction of environmental and social factors on the stress response. Female sifaka showed a pronounced decrease in fGC levels following the first initial rainfall of the season, but this effect was attenuated in females that experienced male immigration events and infanticides. The decrease in fGC levels after the onset of rain suggests that the stress response in female sifaka may be particularly sensitive to exogenous cues. An avenue for future research is to examine the extent to which the stress response is modulated by climatic factors such as temperature and photoperiod for both male and female sifaka. The elevated fGC levels during the dry season most likely reflect the need to mobilize energy from fat stores during a period of increased energetic burden

(lactation) that coincides with the season of decreased resource abundance. Comparable data from males and non-lactating females during this period would elucidate the extent to which the dry season represents a stressful period for sifaka.

This is also the first study to examine hormonal responses to infanticide in a female lemuroid primate. Similar to research on baboons (Engh et al., 2006; Wittig et al., 2008), this study shows that male immigration events, particularly those that result in infanticide, are stressful for female sifaka. However, it is interesting to note that the social stress of these events appears to be secondary to the fGC response to the seasonal shift. These results point to the importance of considering the many social, ecological, and individual factors that interact in complimentary and opposing ways to influence the stress response.

Other social factors, such as dominance rank and aggression, did not predict female fGC levels during this time. Dominance relations among female lemuroid primates are generally considered to be more relaxed compared to other anthropoid primates (Kappeler, 1997), and the acquisition and maintenance of dominance for females may not depend upon aggressive interactions (Erhart & Overdorff, 2008). Therefore, based upon the definition of “allostatic load” (Goymann & Wingfield, 2004a), rank-related differences are not expected to emerge for female sifaka. However, dominance relationships among female sifaka may be seasonally dependent, with stronger relationships emerging during the season of increased contest competition for resources (Chapters II & III). When assessing the associations among rank, aggression, and glucocorticoid levels in lemuroid primates, it is necessary to compare these relationships across seasons.



Due to the small sample size of this study, these results offer only preliminary evidence of the factors that influence fGC levels in female sifaka and cannot be generalized to the population as a whole. In addition, this study lacks comparable data from the wet season. It is entirely probable that fGC levels increase during the wet season in response to both mating and feeding competition such that there are no discernible differences in fGC levels across seasons. However, the strength of this study lies in the repeated measures collected from the females throughout the transition from the dry to the wet season, which revealed a marked endocrine response to an environmental cue. This response would not have been detected if samples were only collected on a monthly basis. Although this sampling schedule necessitated a smaller number of focal individuals in the study, the weekly data provided an opportunity to examine immediate endocrine responses to environmental and social changes. There is always a trade-off between collection schedule and sample size in primate studies, but there is much to be gained from increasing the number of repeated measures, especially when examining the interaction of complex social and ecological factors affecting the endocrine response.

Table 4.1. Demographic descriptions and data totals for focal females.

Lemur ID	Group	Group Size	Age	Rank	Occurrence of Infanticide	Observation Weeks	Focal Hours	Fecal Samples
268	RG	8	14	Dom	No	10	80.5	39
379	RG	8	8	Sub	No	10	80	40
9016	KK	5	20	Dom	No	10	80	41
429	KK	5	11	Sub	No	10	80.5	40
315	NB	7	13	Dom	Yes	9	70.5	36
463	NB	7	7	Sub	Yes	9	71	35
422	MB	8	17	Dom	Yes	9	71.5	34
449	MB	8	11	Sub	Yes	9	72.5	36

Table 4.2. Variables included in final general linear mixed model for fecal glucocorticoid levels (ng/g).

<b>Predictor</b>	<b>Estimate</b>	<b>SE</b>	<b>DF</b>	<b>F value</b>	<b>t value</b>	<b>p value</b>
Intercept	106.140	4.573	6		23.21	<0.0001
Season	-41.782	5.816	66	51.61	-7.18	< 0.0001
Occurrence of infanticide	-12.317	6.468	6	3.63	-1.90	0.1055
Season × infanticide	32.700	8.288	66	15.57	3.95	0.0002

Figure 4.1. Total rainfall (mm) per month at Beza Mahafaly Special Reserve during study months.

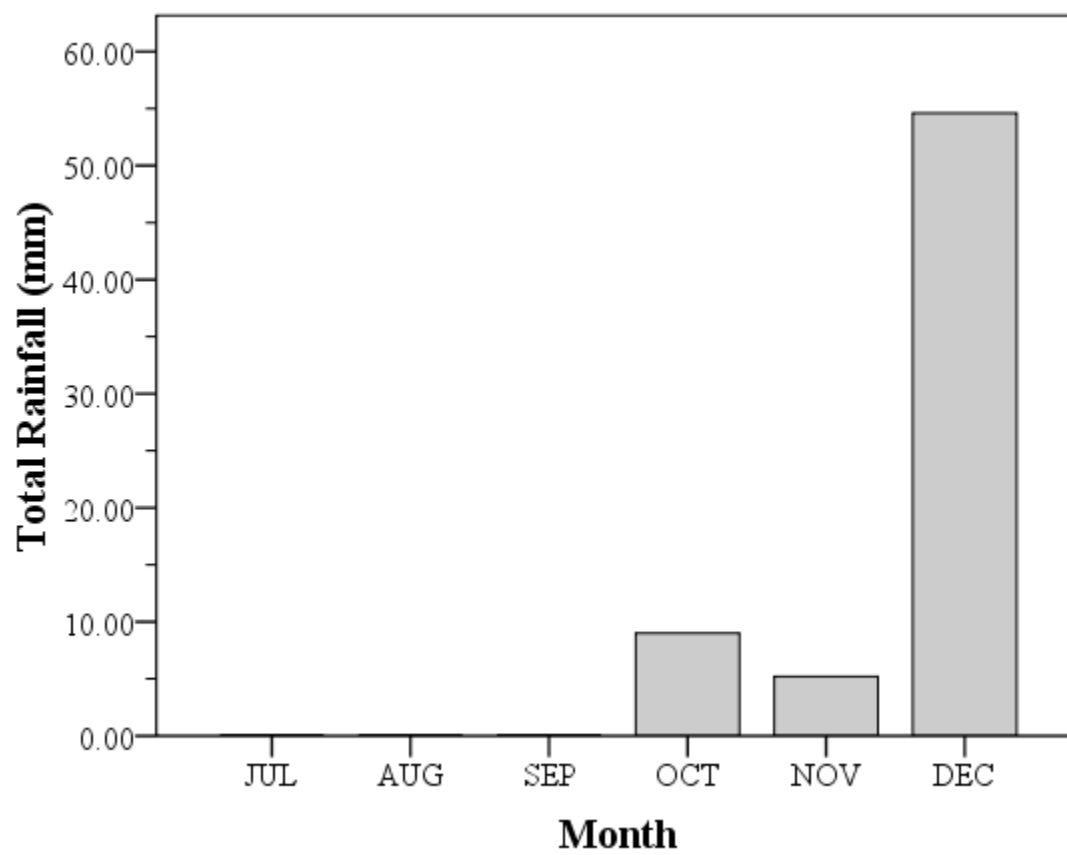


Figure 4.2. Mean ( $\pm$  SE) minimum and maximum temperatures ( $^{\circ}$ C) at Beza Mahafaly Special Reserve across study months.

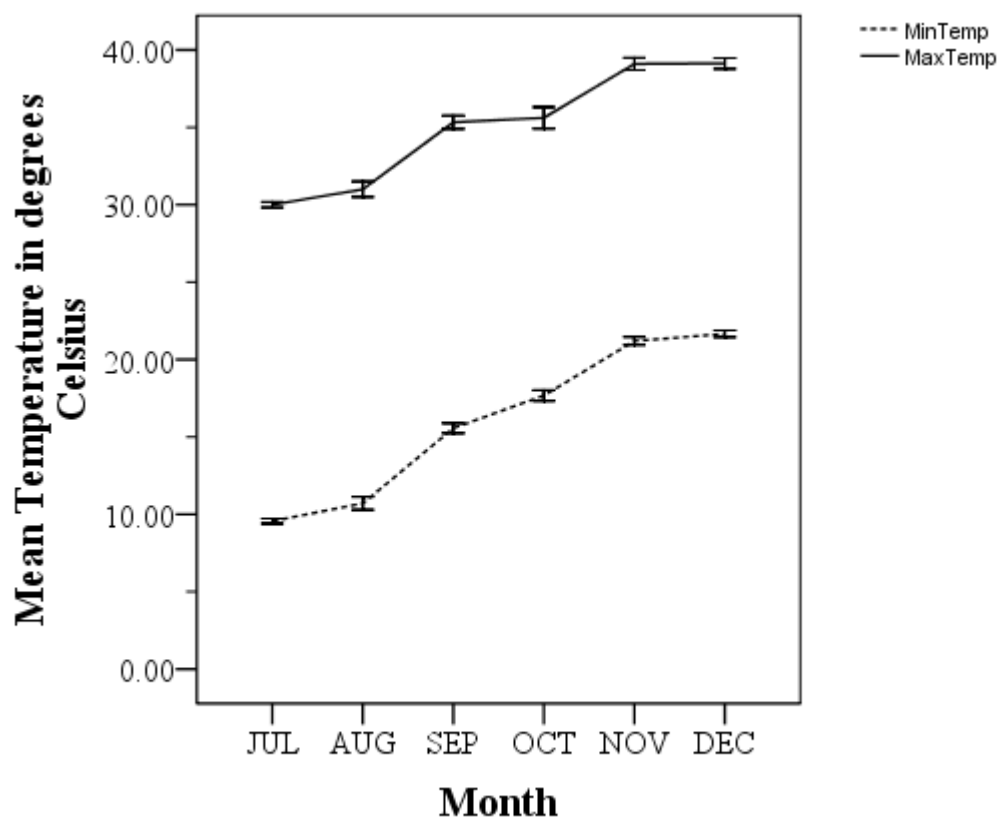


Figure 4.3. Mean ( $\pm$  SE) fecal glucocorticoid levels for all females (N=8) by observation week.

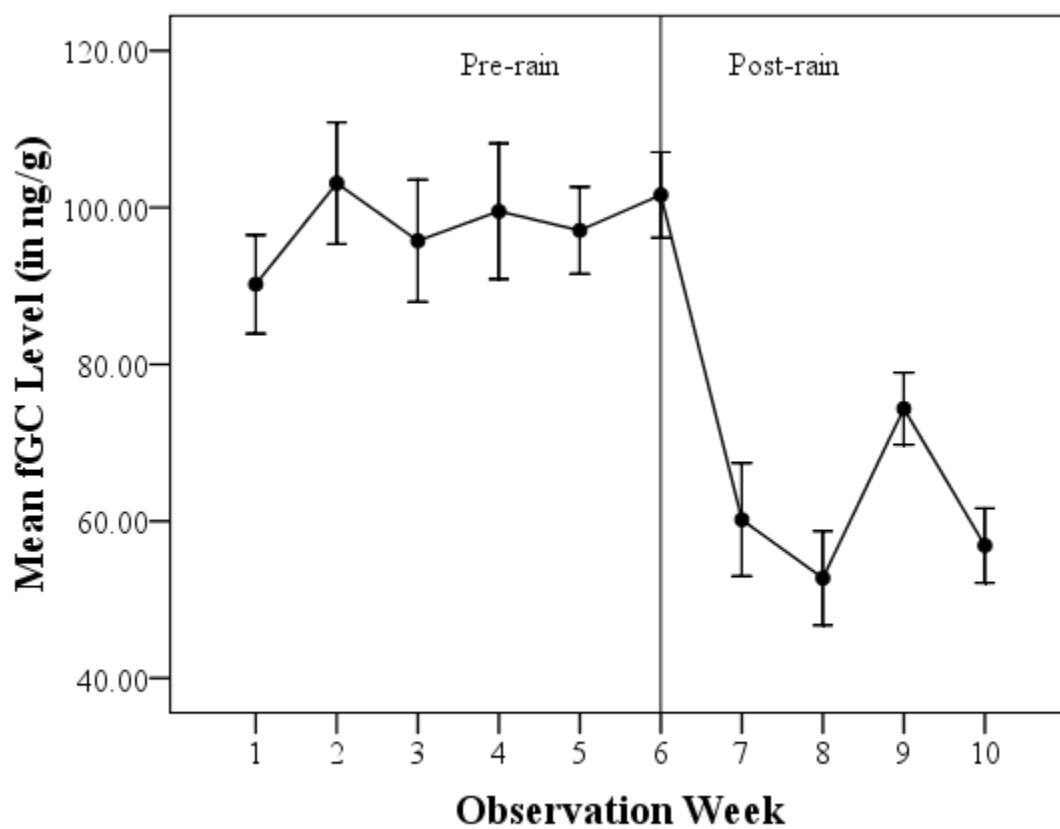


Figure 4.4. Mean ( $\pm$  SE) fecal glucocorticoid levels for females that experienced male takeover events and infanticides (N=4) and females that remained in stable groups (N=4) across observation weeks.

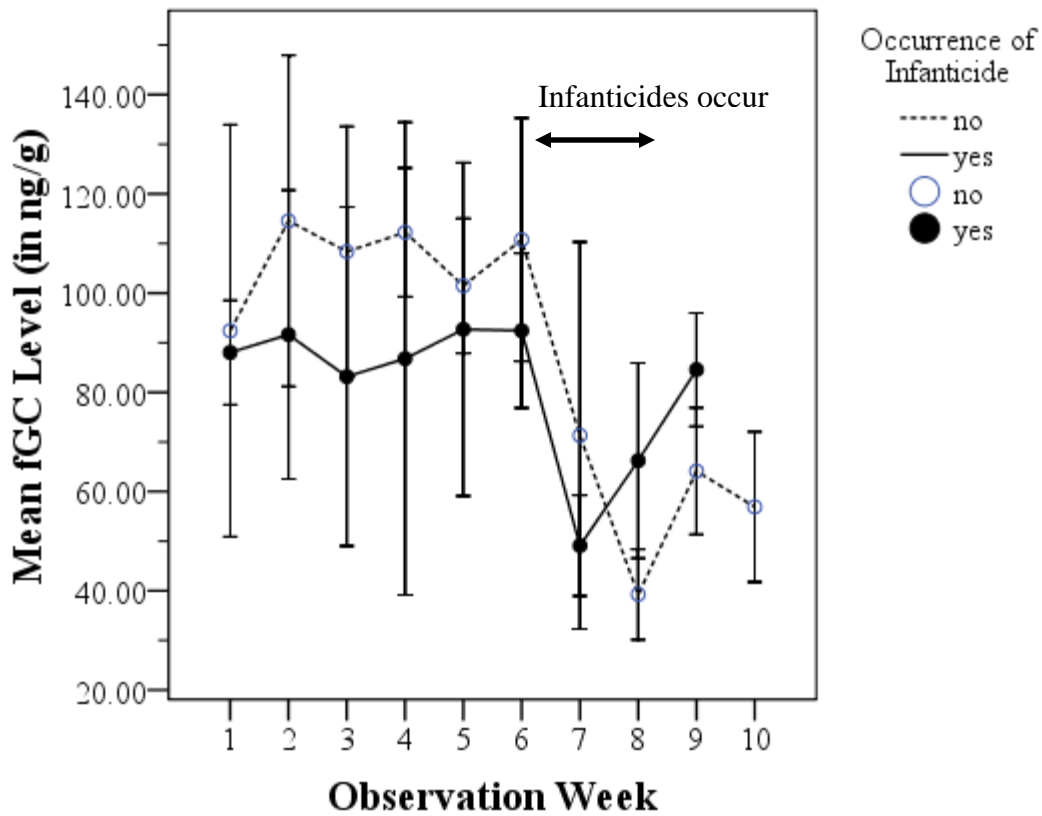
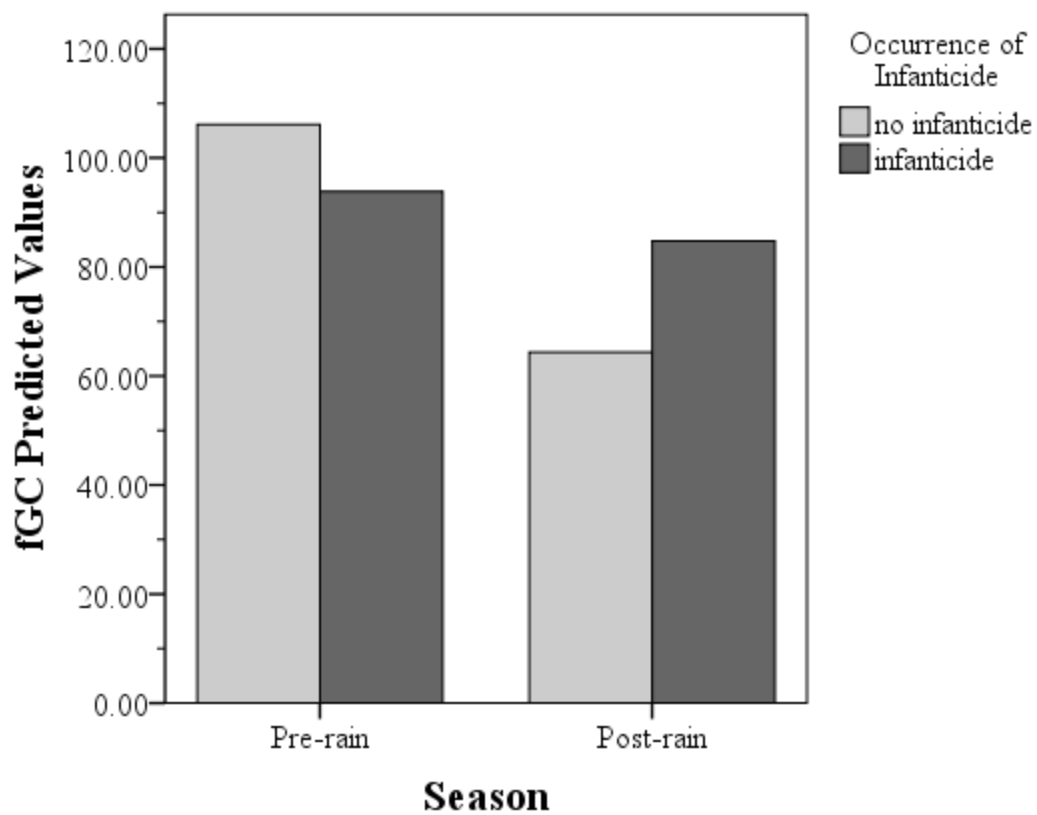


Figure 4.5. Predicted fecal glucocorticoid values from final general linear mixed model separated by females that experienced male takeover events and infanticides (N=4) and females in stable groups (N=4) across seasons.





## References

- Abbott, D. H., Keverne, E. B., Bercovitch, F. B., Shively, C. A., Mendoza, S. P., Saltzman, W., et al. (2003). Are subordinates always stressed? A comparative analysis of rank differences in cortisol levels among primates. *Hormones and Behavior*, *43*, 67-82.
- Alberts, S. C., Sapolsky, R. M., & Altmann, J. (1992). Behavioral, endocrine, and immunological correlates of immigration by an aggressive male into a natural primate group. *Hormones and Behavior*, *26*(2), 167-178.
- Altmann, J. (1974). Observational study of behavior: sampling methods. *Behaviour*, *49*, 229-267.
- Bales, K. L., French, J. A., McWilliams, J., Lake, R. A., & Dietz, J. M. (2006). Effects of social status, age, and season on androgen and cortisol levels in wild male golden lion tamarins (*Leontopithecus rosalia*). *Hormones and Behavior*, *49*(1), 88-95.
- Barrett, G. M., Shimizu, K., Bardi, M., Asaba, S., & Mori, A. (2002). Endocrine correlates of rank, reproduction, and female-directed aggression in male Japanese macaques (*Macaca fuscata*). *Hormones and Behavior*, *42*, 85-96.
- Bercovitch, F. B., & Clarke, A. S. (1995). Dominance rank, cortisol concentrations, and reproductive maturation in male rhesus macaques. *Physiology and Behavior*, *58*, 215-221.
- Brockman, D. K. (1994). *Reproduction and Mating System of Verreaux's Sifaka (Propithecus verreauxi) at Beza Mahafaly, Madagascar*. Yale University, New Haven.
- Brockman, D.K. (2003). *Polyboroides radiatus* predation attempts on *Propithecus verreauxi*. *Folia Primatologica*, *74*, 71-74.
- Brockman, D. K. (1999). Reproductive behavior of female *Propithecus verreauxi* at Beza Mahafaly, Madagascar. *International Journal of Primatology*, *20*(3), 375-398.
- Brockman, D. K., Cobden, A. K., & Whitten, P. L. (2009). Birth season glucocorticoids are related to the presence of infants in sifaka (*Propithecus verreauxi*). *Proceedings of the Royal Society B-Biological Sciences*, *276*, 1855-1863.
- Brockman, D. K., Godfrey, L. R., Dollar, L. J., & Ratsirarson, J. (2008). Evidence of invasive *Felis silvestris* predation on *Propithecus verreauxi* at Beza Mahafaly Special Reserve, Madagascar. *International Journal of Primatology*, *29*, 135-152.

- Brockman, D. K., Meltz, K., & Whitten, P. L. (2003). Noninvasive assessments of stress in male sifaka (*Propithecus verreauxi*). *American Journal of Physical Anthropology, (Suppl)* 35, 72.
- Brockman, D. K., & van Schaik, C. P. (2005). Seasonality and reproductive function. In D. K. Brockman & C. P. van Schaik (Eds.), *Seasonality in Primates* (pp. 269-305). Cambridge: Cambridge University Press.
- Brockman, D. K., & Whitten, P. L. (1996). Reproduction in free-ranging *Propithecus verreauxi*: estrus and the relationship between multiple partner matings and fertilization. *American Journal of Physical Anthropology, 100*, 57-69.
- Brockman, D. K., Whitten, P. L., Richard, A. F., & Schneider, A. (1998). Reproduction in free-ranging male *Propithecus verreauxi*: the hormonal correlates of mating and aggression. *American Journal of Physical Anthropology, 105*(2), 137-151.
- Cavigelli, S. A. (1999). Behavioural patterns associated with faecal cortisol levels in free-ranging female ring-tailed lemurs, *Lemur catta*. *Animal Behaviour, 57*, 935-944.
- Cavigelli, S. A., Dubovick, T., Levash, W., Jolly, A., & Pitts, A. (2003). Female dominance status and fecal corticoids in a cooperative breeder with low reproductive skew: ringtailed lemurs (*Lemur catta*). *Hormones and Behavior, 43*, 166-179.
- Cheney, D. L., & Seyfarth, R. M. (2009). Stress and coping mechanisms in female primates. *Advances in the Study of Behavior, 39*, 1-44.
- Creel, S. (2001). Social dominance and stress hormones. *Trends in Ecology & Evolution, 16*(9), 491-497.
- Creel, S. (2005). Dominance, aggression, and glucocorticoid levels in social carnivores. *Journal of Mammalogy, 86*, 255-264.
- Cristobal-Azkarate, J., Chavira, R., Boeck, L., Rodriguez-Luna, E., & Veà, J. J. (2007). Glucocorticoid levels in free ranging resident mantled howlers: a study of coping strategies. *American Journal of Primatology, 69*, 866-876.
- Crockford, C., Wittig, R. M., Whitten, P. L., Seyfarth, R. M., & Cheney, D. L. (2008). Social stressors and coping mechanisms in wild female baboons (*Papio hamadryas ursinus*). *Hormones and Behavior, 53*, 254-265.
- Dewar, R. E., & Richard, A. F. (2007). Evolution in the hypervariable environment of Madagascar. *Proceedings of the National Academy of Sciences of the United States of America, 104*, 13723-13727.

- Engh, A. L., Beehner, J. C., Bergman, T. J., Whitten, P. L., Hoffmeier, R. R., Seyfarth, R. M., et al. (2006). Female hierarchy instability, male immigration and infanticide increase glucocorticoid levels in female chacma baboons. *Animal Behaviour*, *71*, 1227-1237.
- Erhart, E. M., & Overdorff, D. J. (2008). Rates of agonism by diurnal lemuroids: implications for female social relationships. *International Journal of Primatology*, *29*, 1227-1247.
- Fichtel, C., Kraus, C., Ganswindt, A., & Heistermann, M. (2007). Influence of reproductive season and rank on fecal glucocorticoid levels in free-ranging male Verreaux's sifakas (*Propithecus verreauxi*). *Hormones and Behavior*, *51*, 640-648.
- Foley, C. A. H., Papageorge, S., & Wasser, S. K. (2001). Noninvasive stress and reproductive measures of social and ecological pressures in free-ranging African elephants. *Conservation Biology*, *15*, 1134-1142.
- Gesquiere, L. R., Khan, M., Shek, L., Wango, T. L., Wango, E. O., Alberts, S. C., et al. (2008). Coping with a challenging environment: effects of seasonal variability and reproductive status on glucocorticoid concentrations of female baboons (*Papio cynocephalus*). *Hormones and Behavior*, *54*, 410-416.
- Gould, L., Ziegler, T. E., & Wittwer, D. J. (2005). Effects of reproductive and social variables on fecal glucocorticoid levels in a sample of adult male ring-tailed lemurs (*Lemur catta*) at the Beza Mahafaly Reserve, Madagascar. *American Journal of Primatology*, *67*, 5-23.
- Goymann, W., & Wingfield, J. C. (2004). Allostatic load, social status and stress hormones: the costs of social status matter. *Animal Behaviour*, *67*, 591-602.
- Kappeler, P. M. (1997). Determinants of primate social organization: comparative evidence and new insights from Malagasy lemurs. *Biological Reviews of the Cambridge Philosophical Society*, *72*(1), 111-151.
- Kubzdela, K. S. (1997). *Sociodemography in diurnal primates: The effects of group size and female dominance rank on intra-group spatial distribution, feeding competition, female reproductive success, and female dispersal patterns in white sifaka, Propithecus verreauxi verreauxi*. University of Chicago, Chicago.
- Lawler, R. R., Caswell, H., Richard, A. F., Ratsirarson, J., Dewar, R. E., & Schwartz, M. (2009). Demography of Verreaux's sifaka in a stochastic rainfall environment. *Oecologia*, *161*, 491-504.

- Lewis, R. J., Razafindrasamba, S. M., & Tolojanahary, J. P. (2003). Observed infanticide in a seasonal breeding prosimian (*Propithecus verreauxi verreauxi*) in Kirindy Forest, Madagascar. *Folia Primatologica*, *74*, 101-103.
- Lewis, R. J., & van Schaik, C. P. (2007). Bimorphism in male Verreaux's sifaka in the Kirindy Forest of Madagascar. *International Journal of Primatology*, *28*, 159-182.
- Littlefield, B. L. (2010). Infanticide following male takeover event in Verreaux's sifaka (*Propithecus verreauxi verreauxi*). *Primates*, *51*, 83-86.
- Lynch, J. W., Ziegler, T. E., & Strier, K. B. (2002). Individual and seasonal variation in fecal testosterone and cortisol levels of wild male tufted capuchin monkeys, *Cebus apella nigrinus*. *Hormones and Behavior*, *41*(3), 275-287.
- Muller, M. N., & Wrangham, R. W. (2004). Dominance, cortisol and stress in wild chimpanzees (*Pan troglodytes schweinfurthii*). *Behavioral Ecology and Sociobiology*, *55*, 332-340.
- Ostner, J., Heistermann, M., & Schulke, O. (2008). Dominance, aggression and physiological stress in wild male Assamese macaques (*Macaca assamensis*). *Hormones and Behavior*, *54*, 613-619.
- Ostner, J., Kappeler, P. M., & Heistermann, M. (2008). Androgen and glucocorticoid levels reflect seasonally occurring social challenges in male redfronted lemurs (*Eulemur fulvus rufus*). *Behavioral Ecology and Sociobiology*, *62*, 627-638.
- Pereira, R. J. G., Duarte, J. M. B., & Negrao, J. A. (2006). Effects of environmental conditions, human activity, reproduction, antler cycle and grouping on fecal glucocorticoids of free-ranging Pampas deer stags (*Ozotoceros bezoarticus bezoarticus*). *Hormones and Behavior*, *49*, 114-122.
- Pride, R. E. (2005a). Foraging success, agonism, and predator alarms: behavioral predictors of cortisol in *Lemur catta*. *International Journal of Primatology*, *26*(2), 295-319.
- Pride, R. E. (2005b). Optimal group size and seasonal stress in ring-tailed lemurs (*Lemur catta*). *Behavioral Ecology*, *16*(3), 550-560.
- Ray, J. C., & Sapolsky, R. M. (1992). Styles of male social behavior and their endocrine correlates among high-ranking wild baboons. *American Journal of Primatology*, *28*, 231-250.
- Richard, A. F. (1978). *Behavioral Variation: Case study of a Malagasy Lemur*. Lewisburg: Bucknell University Press.

- Richard, A. F. (1992). Aggressive competition between males, female-controlled polygyny and sexual monomorphism in a Malagasy primate, *Propithecus verreauxi*. *Journal of Human Evolution*, 22, 395-406.
- Richard, A. F., Dewar, R. E., Schwartz, M., & Ratsirarson, J. (2000). Mass change, environmental variability and female fertility in wild *Propithecus verreauxi*. *Journal of Human Evolution*, 39, 381-391.
- Richard, A. F., Dewar, R. E., Schwartz, M., & Ratsirarson, J. (2002). Life in the slow lane? Demography and life histories of male and female sifaka (*Propithecus verreauxi verreauxi*). *Journal of Zoology*, 256, 421-436.
- Richard, A. F., Rakotomanga, P., & Schwartz, M. (1991). Demography of *Propithecus verreauxi* at Beza Mahafaly, Madagascar: sex ratio, survival, and fertility, 1984-1988. *American Journal of Physical Anthropology*, 84, 307-322.
- Robbins, M. M., & Czekala, N. M. (1997). A preliminary investigation of urinary testosterone and cortisol levels in wild male mountain gorillas. *American Journal of Primatology*, 43, 51-64.
- Romero, L. M. (2002). Seasonal changes in plasma glucocorticoid concentrations in free-living vertebrates. *General and Comparative Endocrinology*, 128, 1-24.
- Saltz, D., & White, G. C. (1991). Urinary cortisol and urea nitrogen responses to winter stress in mule deer. *The Journal of Wildlife Management*, 55, 1-16.
- Saltzman, W., Schultz-Darken, N. J., Scheffler, G., Wegner, F. H., & Abbott, D. H. (1994). Social and reproductive influences on plasma cortisol in female marmoset monkeys. *Physiology and Behavior*, 56, 801-810.
- Sapolsky, R. M. (1982). The endocrine stress-response and social status in the wild baboon. *Hormones and Behavior*, 16, 279-292.
- Sapolsky, R. M. (1992). Cortisol concentrations and the social significance of rank instability among wild baboons. *Psychoneuroendocrinology*, 17, 701-709.
- Sapolsky, R. M. (1993). Endocrinology alfresco: psychoendocrine studies of wild baboons. *Recent Progress in Hormone Research*, 48, 437-465.
- Sapolsky, R. M. (1994). *Why Zebras Don't Get Ulcers*. New York: W.H. Freeman and Company.
- Sapolsky, R. M. (2002). Endocrinology of the stress response. In J. B. Becker, S. M. Breedlove, D. Crews & M. M. McCarthy (Eds.), *Behavioral Endocrinology* (pp. 409-450). Cambridge: The MIT Press.

- Sapolsky, R. M. (2005). The influence of social hierarchy on primate health. *Science*, 308, 648-652.
- Setchell, J. M., Smith, T., Wickings, E. J., & Knapp, L. A. (2008). Factors affecting fecal glucocorticoid levels in semi-free-ranging female mandrills (*Mandrillus sphinx*). *American Journal of Primatology*, 70, 1023-1032.
- Stavisky, R. C., Adams, M. R., & Watson, S. L. (2001). Dominance, cortisol, and behavior in small groups of female cynomolgus monkeys (*Macaca fascicularis*). *Hormones and Behavior*, 39, 232-238.
- Virgin, C. E., & Sapolsky, R. M. (1997). Styles of male social behavior and their endocrine correlates among low-ranking baboons. *American Journal of Primatology*, 42, 25-39.
- Wasser, S. K., Hunt, K. E., Brown, J. L., Cooper, K., Crockett, C. M., Bechert, U., et al. (2000). A generalized fecal glucocorticoid assay for use in a diverse array of nondomestic mammalian and avian species. *General and Comparative Endocrinology*, 120, 260-275.
- Weingrill, T., Gray, D. A., Barrett, L., & Henzi, S. P. (2004). Fecal cortisol levels in free-ranging female chacma baboons: relationship to dominance, reproductive state and environmental factors. *Hormones and Behavior*, 45, 259-269.
- Whitten, P. L., & Brockman, D. K. (2001). Strepsirrhine reproductive ecology. In P. T. Ellison (Ed.), *Reproductive Ecology and Human Evolution* (pp. 321-350). New York: Aldine de Gruyter.
- Wingfield, J. C., Maney, D. L., Breuner, C. W., Jacobs, J. D., Lynn, S., Ramenofsky, M., et al. (1998). Ecological bases of hormone-behavior interactions: the 'emergency life history stage'. *American Zoologist*, 38, 191-206.
- Wingfield, J. C., & Ramenofsky, M. (1999). Hormones and the behavioral ecology of stress. In P. H. M. Balm (Ed.), *Stress Physiology in Animals* (pp. 1-51). Boca Raton, FL: CRC Press.
- Wittig, R. M., Crockford, C., Lehmann, J., Whitten, P. L., Seyfarth, R. M., & Cheney, D. L. (2008). Focused grooming networks and stress alleviation in wild female baboons. *Hormones and Behavior*, 54, 170-177.
- Wright, P. C. (1999). Lemur traits and Madagascar ecology: coping with an island environment. *Yearbook of Physical Anthropology*, 42, 31-72.
- Yamashita, N. (2002). Diets of two lemur species in different microhabitats in Beza Mahafaly Special Reserve, Madagascar. *International Journal of Primatology*, 23, 1025-1051.

- Yamashita, N. (2008). Chemical properties of the diets of two lemur species in southwestern Madagascar. *International Journal of Primatology*, 29, 339-364.
- Ziegler, T. E., Scheffler, G., & Snowdon, C. T. (1995). The relationship of cortisol levels to social environment and reproductive functioning in female cotton-top tamarins, *Saguinus oedipus*. *Hormones and Behavior*, 29, 407-424.

## Chapter V. Summary and Conclusions

The study of female competition in non-human primates has generated more attention over recent years and placed an increased focus on the proximate and ultimate causes of female competitive behavior. It is clear that female primates compete in a variety of contexts, and that the form of female competition is often functionally different from that seen in males. While males often compete for access to mates, females may primarily compete in ways that promote reproductive effort and ensure infant survival (Hrdy & Williams, 1983; Wasser, 1983). Since access to resources is tantamount to reproductive success for female primates, much of the research on female competitive behavior has emphasized the role of resource competition. The formation of socioecological models provided a heuristic tool by which to classify female dominance hierarchies based upon the relative degree of within- and between-group aggression (Sterck et al., 1997; van Schaik, 1989; Wrangham, 1980). Based upon these models, females are predicted to form formalized, linear dominance hierarchies when there is a high degree of contest competition for available resources. The extent to which food items are contestable will depend in large part upon whether these items are monopolizable and easily depleted (Isbell, 1991), and the degree to which they vary in nutrient quality (Koenig et al., 1998). This last point is especially crucial for folivorous primates, who are thought to exhibit low rates of intra-group aggression because leaves are generally abundant and evenly distributed. However, differences in resource nutrient quality can have a profound impact on female body condition and reproductive success in folivorous primates (Koenig, 2000). Therefore, the distribution of high-quality resources



may impact the intensity of female competition across seasons, which may in turn influence the relative importance of female dominance hierarchies throughout the year.

Although the formation of dominance hierarchies mitigates the risks associated with aggressive interactions, social rank may come with substantial costs for subordinate females, who often display decreased foraging efficiency and reproductive success compared to dominants (reviewed in Bercovitch, 1991). Therefore, most of the research on the costs of competition for female primates has tended to focus on the potential consequences associated with low rank. However, there is much to be learned about the costs of competition from examining the hormonal mediators of aggression and stress. Both androgens and glucocorticoids are associated with considerable physiological costs to health and survival (Sapolsky, 2002; Wingfield et al., 2001). Chronically elevated levels of these hormones can have deleterious effects on reproduction and immune function, and may even inhibit the expression of parental care behaviors (Wingfield et al., 2001). Yet these costs are not always associated with low rank; in fact, it is often the most dominant individuals who show the highest levels of stress hormones, providing evidence for the possible consequences associated with acquiring and maintaining dominance status (Abbott et al., 2003; Goymann & Wingfield, 2004a). While most of the research conducted on hormone-behavior interactions has tended to focus on males, these physiological costs may be particularly salient for female primates, who are constantly negotiating the delicate balance between competing for resources and caring for offspring.

The purpose of this study was to examine female competitive behavior within an endocrinological framework by assessing the extent to which dominance rank and

aggression are mediated by androgens and glucocorticoids in wild female Verreaux's sifaka (*Propithecus verreauxi*) at Beza Mahafaly Special Reserve, Madagascar.

Behavioral and hormonal data were collected on eight females with infants from July through December 2007. Since lactation is timed to the period of decreased resource abundance, this afforded the opportunity to investigate these relationships when females may be energetically stressed. In addition, the study period encompassed the transition from the dry season to the wet season, providing the opportunity to examine how female competition and endocrine responses are influenced by climatic changes and the seasonal distribution of resources.

#### *Seasonality of Competition*

The results from this study provide evidence for a seasonal shift in behavior brought about by the onset of the rains in mid-October. Females showed a significant increase in traveling and genital marking behaviors and a decrease in grooming received after the rains. Previous research on this population has demonstrated a dietary shift during this seasonal transition period from mature leaves to an increased reliance on flowers and fruits (Yamashita, 2008). The fact that females increased travel during this time is consistent with predictions that individuals increase foraging effort when resources are clumped and easily depleted (Isbell, 1991). The increase in genital marking behavior also suggests heightened territory defense as females use these olfactory cues to mark their home ranges (Mertl-Millhollen, 2006). The concurrent decrease in grooming behavior may demonstrate a shift away from social behaviors as more time is spent on locating high-quality food items. Females also showed a decrease in the presence of

nearest neighbors after the rains, which, coupled with the significant increase in aggression, signifies an increase in contest competition. These results suggest that as females shift their diet to include more monopolizable resources, they increase their distance to nearest neighbors, often relying on aggressive displacements in order to maintain control of food patches.

The hypothesis that subordinate females have decreased foraging efficiency was somewhat supported by the data. Subordinate females traveled more across seasons compared to dominants and also spent more time in the presence of nearest neighbors while feeding, suggesting increased resource competition. Furthermore, the observed group fission in Vavy Goa is the first recorded instance of female targeted aggression in the Beza Mahafaly population and supports previous observations of female targeted aggression and eviction in *Propithecus diadema edwardsi* (Pochron et al., 2003; Wright, 1995). Previous research on this population demonstrated that when group size increases beyond an optimal number of females, subordinate females often leave their natal group and either immigrate into an existing group or form a new group (Kubzdela, 1997), both of which are associated with substantial risks (Dittus, 1988; Hood & Jolly, 1995). The observations from this study suggest that these emigration events may result from increased harassment from dominant females. Whether these observations translate into decreased reproductive success for subordinate females still remains to be seen. Previous research on this population provided some evidence that subordinate females show decreased fertility and infant survival rates compared to dominants, but this result was complicated by the tight correlation between female dominance rank and age (Kubzdela, 1997). The fact that female fertility is dependent upon body mass in this species (Richard

et al., 2000) suggests that subordinate females may be at a disadvantage for attaining optimal reproductive weight, especially if they have restricted access to high-quality food items. However, due to the small sample size in this study, it was not possible to examine rank-related differences in reproductive success.

The shifts in behavior after the onset of rain may provide intriguing insight into dominance relationships among female sifaka. Lemuroid primates are classified as Dispersal-Egalitarian in socioecological models because they display low rates of within-group aggression and relaxed dominance hierarchies among females (Erhart & Overdorff, 2008). However, female competition in Verreaux's sifaka may emerge during the season of resource abundance when high-quality food items become more available, providing a context for increased aggression. If access to these resources ensures optimal body weight for reproduction, then enforcing dominance relationships during this time may guarantee priority access for dominant females. In addition, the season of resource abundance also coincides with the mating period, which is marked by increased aggression in the form of copulatory harassment among females (Brockman, 1999). Competition for mates may provide additional incentive for females to exert dominance status. By contrast, the low rates of aggression displayed during the dry season may signify that competition for evenly distributed leaves is simply not worth the energy expenditure required for females to enforce dominance relationships. If dominance relationships are seasonally-dependent, then the classification of lemurs within the existing socioecological models may be inappropriate (Erhart & Overdorff, 2008). In fact, Erhart & Overdorff (2008) argue that it may be more useful to devise a separate model that describes female dominance relationships in lemuroid primates, especially

considering that they display nonconvergence in many traits compared with haplorrhines (Kappeler & Heymann, 1996).

*Dominance Rank, Aggression, and Endocrine Response*

Contrary to expectations, neither dominance rank nor rates of within-group aggression were significant predictors of fecal testosterone (fT) levels in females. In addition, the hypothesis that dominant females display the most aggression was not supported by the data. The lack of association among dominance, aggression, and fT levels may be explained by the following: (1) aggression is relatively unimportant in the acquisition and maintenance of dominance for female Verreaux's sifaka, (2) within-group aggression is low-stakes and does not elicit an endocrine response, and (3) competition is relaxed among related females due to kin selection.

In general, lemuroid primates display low rates of aggression (Erhart & Overdorff, 2008), which seems to suggest that dominance relationships are not mediated via agonistic interactions. This is somewhat supported by the current study, which demonstrated that during the dry season, female rates of aggression were very low (about 0.2 bouts per hour). However, as stated above, the increase in aggression after the rains may be related to the relative costs and benefits of intra-group competition across seasons. The energetic requirements of lactation during the lean season may place constraints on female aggressive behavior during this time. This may be especially true for female strepsirrhines, who have relatively low basal metabolic rates compared with haplorrhines and must expend extra energy to raise metabolic rates during reproduction (Young et al., 1990). Therefore, contest competition for low-quality resources may be too

costly for females during this time. Instead, females may display scramble competition throughout the dry season, which is not dependent upon overtly aggressive interactions. This “low stakes” form of intragroup competition may not elicit a strong endocrine response. The lack of association between intragroup aggression and androgen levels during this period also may aid in avoiding the physiological costs of competition when females are energetically stressed and resources are scarce. By contrast, the intensity of between-group aggressive encounters may be relatively “high stakes” and elicit a marked endocrine response from females. Although rates of within-group aggression did not predict fT levels, aggressive participation in inter-group encounters was marginally related to fT levels (although this predictor only approached significance in the final model). Since intergroup encounters are potentially risky and are often marked by high speed chases, this result supports previous research that the association between aggression and testosterone is entirely dependent on the relative intensity of the aggressive encounter (Ross et al., 2004). If the intensity of competition for resources and mates increases during the wet season, then we might predict a stronger association between within-group aggression and testosterone levels for female sifaka. In addition, if dominance relationships are exerted through contest competition during this time, it is possible that rank-related differences in both aggression and testosterone may emerge.

Finally, the fact that the females in this study were mother-daughter pairs also may explain the lack of association among dominance, aggression, and fT levels. Most of the aggression observed in this study was directed at males, demonstrating that there were very few agonistic encounters among related females in stable dyads. In primate social groups, aggressive interactions are expected to be relatively low among closely related

individuals due to kin selection (Clutton-Brock & Harvey, 1976). Furthermore, there is evidence to suggest that the degree of relatedness among individuals affects the extent to which there are rank-related differences in androgen levels. For example, in wild golden lion tamarins (*Leontopithecus rosalia*), related male duos showed no rank differences in fecal androgen levels, while dominant males in unrelated duos had significantly higher levels compared to subordinates. It is entirely possible that rank-related differences in aggression and FT levels may emerge among unrelated female sifaka, providing an intriguing avenue for further research.

The results also show disassociations among dominance rank, aggression, and fecal glucocorticoid (fGC) for females. Neither dominance rank nor rates of within-group aggression were significant predictors of fGC levels. Again, these results were not entirely unexpected given the low rates of aggression during the dry season. Previous research on ring-tailed lemurs (*Lemur catta*) suggests that associations between aggression and fGC levels emerge when contest competition is high (Cavigelli et al., 2003); therefore, rates of aggression may only be associated with fGC levels for female sifaka during the wet season. In this study, fGC levels declined during the period after the rains when rates of aggression began to increase. However, the study period stopped short of the wet season and there were only 3-4 observational weeks of data for each female after the onset of rains. It is entirely possible that fGC levels begin to increase throughout the wet season as contest competition becomes more intense. Given the strong seasonal effect on fGC levels (see below), the rapid decline in fGC levels after the rains may have overridden any behavioral effects on the stress response. There is also the possibility that the switch to higher-quality resources may offset any additional social

stress that emerges due to increased contest competition. Comparative data from the wet season are needed in order to fully investigate the relationship between aggression and fGC levels for female sifaka.

Since dominance status does not appear to be mediated through aggressive interactions during the dry season, rank-related differences in glucocorticoid levels were not expected to emerge. The concept of “allostatic load” suggests that intrinsic differences in physiological stress associated with rank will result in rank-related differences in glucocorticoid levels (Goymann & Wingfield, 2004a). For dominant individuals, the stress associated with rank acquisition and maintenance may cause elevated glucocorticoid levels, while for subordinate individuals, the threat of dominants may result in chronic stress. If dominance relationships are relatively relaxed, as in the case of female sifaka during the lean season, then there should be no rank-related differences in stress hormone levels. However, if during the wet season dominance relationships become more pronounced, we might expect rank-related differences to emerge as a measure of the relative costs of social rank. At least during the dry season, the results of the present study suggest that there are no significant costs in terms of increased stress levels that are associated with rank for female sifaka.

#### *Effects of Environmental and Social Factors on Endocrine Response*

There was a strong seasonal effect on fGC levels, such that fGC levels were significantly lower after the first rains. Elevated glucocorticoid levels during the dry season have been documented across several mammalian species (Foley et al., 2001; Muller & Wrangham, 2004b; R. J. G. Pereira et al., 2006; Pride, 2005a), and may reflect



the seasonal stress associated with decreased food availability. However, these seasonal shifts in resources are expected and predictable events, and therefore may not characterize an acute stressor (Wingfield & Ramenofsky, 1999). Rather, elevated glucocorticoids during the dry season may serve to mobilize energy from fat stores while resources are scarce (Pride, 2005a; Romero, 2002). This may be especially true for the females in this study, who had to sustain the energetic burden of lactation throughout the latter half of the lean season. What is interesting to note is that fGC levels dropped immediately after the first light rain, suggesting that stress hormones are particularly sensitive to exogenous cues for female sifaka. These results demonstrate the importance of considering environmental factors such as rainfall, temperature, and photoperiod when assessing hormonal levels in primates.

Perhaps the most unanticipated events to occur during the study period were the aggressive male immigration events that resulted in the observed and inferred infanticides of half of the infants from the focal groups. This provided the opportunity to examine female endocrine responses to these male takeover events. Females that experienced male takeover events had significantly higher fT and fGC levels compared to females in stable groups. Fecal testosterone levels were higher in females that experienced male takeover events across the study period, suggesting that females mounted a testosterone response in anticipation of the potential threat of male immigration. Fecal glucocorticoid levels were only significantly higher for these females after the actual immigration events occurred, which coincided with the first rains of the season. For females in groups that experienced male takeover events, the seasonal decrease in fGC levels was attenuated by the social stress of infanticides. These results support findings in chacma baboons (*Papio*

*hamadryas ursinus*) that infanticide is an acute stressor for females (Crockford et al., 2008; Engh et al., 2006), but also provide some intriguing evidence for the interaction of social and environmental factors on the stress response. The empirical data from this study reveal that these factors can often have opposing effects on the stress response, demonstrating the need to control for these interactions when assessing hormonal levels.

### *Future Directions*

The small sample size of this study precludes generalizing these results to female sifaka as a whole, but the preliminary finding that dominance relationships may be seasonally dependent provides an intriguing avenue for future research. First and foremost, the hypothesis that female sifaka increase contest competition during the wet season rests entirely upon the assumption that resources during this time are unevenly distributed and are of a higher quality compared to food items during the dry season. This is a reasonable assumption given that previous research showed that, after October, sifaka include more flowers and fruits in their diet (Yamashita, 2008), items that are generally considered to be clumped and high-quality resources that incite contest competition (Isbell, 1991). However, there is scant data on resource distribution for this population. One study examined the chemical properties of food items across seasons and found no differences in overall nutrient quality between the dry and wet season (Yamashita, 2008). However, this study did not examine overall caloric intake or inter-individual differences in nutrient intake, both of which may have profound effects on female body condition. Examining patch size distribution and depletion rates, as well as rank-related differences in food intake, would provide much needed information about the potential costs of

resource competition for female sifaka. Combining these observations with behavioral data during the wet season would allow for a more thorough testing of the hypothesis that dominance relationships among females emerge during the season of resource abundance.

Examining shifts in nutrient intake across seasons may provide further support that female sifaka are energetically stressed during the dry season, which is reflected in elevated glucocorticoid levels. Nutritional analysis combined with behavioral and hormonal data during the wet season would aid in determining whether the switch to higher-quality resources offsets the stress associated with competition. In addition, placing these results in a cross-species comparative context may reveal some intriguing differences in hormone-behavior interactions for primates with low metabolic rates. The energetic costs associated with elevating metabolic rates during reproduction for female strepsirrhines (Richard & Nicoll, 1987; Young et al., 1990) may be magnified by the physiological costs associated with elevated glucocorticoid levels during this time. If nutritional stress triggers glucocorticoid secretion as a way of mobilizing energy during the lean season, this may place severe constraints on female aggression and competition. Examining the relative costs of nutritional and psychosocial stress across seasons in lemuroid primates provides an exciting opportunity to continue to disentangle the myriad of ecological and social factors that influence hormone-behavior interactions throughout the primate order.

It is also necessary to collect hormonal data throughout the year in order to examine whether associations among dominance, aggression, and endocrine measures strengthen during the wet season. If aggression among female sifaka increases during this

time, rank-related differences in both testosterone and glucocorticoids may emerge, providing the opportunity to assess the relative physiological costs associated with rank. In addition, the females of this study were all mother-daughter pairs and lived in groups of comparable size. The degree of relatedness may affect competitive interactions as well as the extent to which there are rank-related differences in hormonal measures (Goymann & Wingfield, 2004a); therefore, assessing these relationships in pairs of unrelated females could provide an interesting contrast to the results presented here. It has also been well established that group size has an effect on within-group contest competition (Isbell, 1991), foraging effort (Chapman & Chapman, 2000), and hormonal measures of stress (Pride, 2005c). Previous research on this sifaka population demonstrated that feeding competition increased with group size, which had the greatest negative impact on subordinate females in large groups (Kubzdela, 1997). Extending these observations by examining the effects of group size on glucocorticoid levels may provide additional insights into the costs associated with resource competition and social rank for this species.

Finally, the lack of association among dominance, aggression, and fecal testosterone levels for female sifaka in this study might implicate the role of weaker androgens, such as androstenedione or dihydroepiandrosterone (DHEA), in the regulation of aggressive behavior. There is growing evidence in research across species of birds that elevated DHEA levels during the non-breeding season may modulate aggression as a way of decreasing the costs associated with elevated levels of circulating testosterone (Soma & Wingfield, 2001; Wingfield et al., 2001). DHEA is secreted from the adrenals and other peripheral tissues, and has a low affinity for testosterone and estrogen receptors.

Wingfield et al. (2001) argue that DHEA is converted to testosterone or estradiol in the brain, thereby having a direct effect on aggressive behavior and avoiding the need to elevate circulating testosterone levels (Soma & Wingfield, 2001). Androstenedione also does not bind to androgen receptors and can be converted to testosterone or estrogens, and may play a prominent role in female aggressive behavior and dominance in the spotted hyena (*Crocuta crocuta*) (van Jaarsveld & Skinner, 1991). Preliminary evidence from captive ring-tailed lemurs (*Lemur catta*) showed that females had higher levels of androstenedione than testosterone and that this difference was most pronounced during the breeding season when female aggression was at its height (Drea, 2007). These results suggest the intriguing possibility that female aggression is mediated via weaker androgens in lemuroid primates, but currently there is no available data on the associations between aggression and androstenedione or DHEA levels in wild female lemurs.

In summary, the results from this study demonstrated a strong seasonal effect on female sifaka behavior and endocrine responses, but failed to support hypotheses regarding the associations among dominance, aggression, and hormonal measures. Although this study set out to examine the endocrinology of female competitive behavior, the unexpected infanticide events provided the unique opportunity to assess hormonal responses to extreme social events. As previous research with male primates has demonstrated, factors that impact group stability seem to have a more pronounced effect on endocrine markers than dominance status alone. There is a continuing shift away from focusing solely on the effects of dominance and aggression on hormonal levels towards examining the myriad of social, ecological, and individual factors that influence the

endocrine response. Yet there are still relatively few studies that examine these factors in female primates in the wild, demonstrating the need for longitudinal research on hormone-behavior interactions across species of primates. This study also illustrates the importance of collecting repeated hormone measures over time. While repeated sampling may necessitate a trade-off in sample size, it provides the opportunity to assess the complex interactions of social and ecological factors on hormonal measures. The results presented here only begin to address the gaps in our understanding of hormone-behavior interactions in wild female primates. The focus on socioendocrinology will continue to reveal the potential physiological costs of female aggression, providing valuable information on the evolution of female competition within the primate order.

## References

- Abbott, D. H., Keverne, E. B., Bercovitch, F. B., Shively, C. A., Mendoza, S. P., Saltzman, W., et al. (2003). Are subordinates always stressed? A comparative analysis of rank differences in cortisol levels among primates. *Hormones and Behavior*, *43*, 67-82.
- Bercovitch, F. B. (1991). Social stratification, social strategies, and reproductive success in primates. *Ethology and Sociobiology*, *12*(4), 315-333.
- Brockman, D. K. (1999). Reproductive behavior of female *Propithecus verreauxi* at Beza Mahafaly, Madagascar. *International Journal of Primatology*, *20*(3), 375-398.
- Cavigelli, S. A., Dubovick, T., Levash, W., Jolly, A., & Pitts, A. (2003). Female dominance status and fecal corticoids in a cooperative breeder with low reproductive skew: ringtailed lemurs (*Lemur catta*). *Hormones and Behavior*, *43*, 166-179.
- Chapman, C. A., & Chapman, L. J. (2000). Constraints on group size in red colobus and red-tailed guenons: examining the generality of the ecological constraints model. *International Journal of Primatology*, *21*(4), 565-585.
- Clutton-Brock, T. H., & Harvey, P. H. (1976). Evolutionary rules and primate societies. In P. P. G. Bateson & R. A. Hinde (Eds.), *Growing points in ethology* (pp. 195-237). Cambridge: Cambridge University Press.
- Crockford, C., Wittig, R. M., Whitten, P. L., Seyfarth, R. M., & Cheney, D. L. (2008). Social stressors and coping mechanisms in wild female baboons (*Papio hamadryas ursinus*). *Hormones and Behavior*, *53*, 254-265.
- Dittus, W. P. J. (1988). Group fission among wild toque macaques as a consequence of female resource competition and environmental stress. *Animal Behaviour*, *36*, 1626-1645.
- Drea, C. M. (2007). Sex and seasonal differences in aggression and steroid secretion in *Lemur catta*: are socially dominant females hormonally 'masculinized'? *Hormones and Behavior*, *51*, 555-567.
- Engh, A. L., Beehner, J. C., Bergman, T. J., Whitten, P. L., Hoffmeier, R. R., Seyfarth, R. M., et al. (2006). Female hierarchy instability, male immigration and infanticide increase glucocorticoid levels in female chacma baboons. *Animal Behaviour*, *71*, 1227-1237.
- Erhart, E. M., & Overdorff, D. J. (2008). Rates of agonism by diurnal lemuroids: implications for female social relationships. *International Journal of Primatology*, *29*, 1227-1247.

- Foley, C. A. H., Papageorge, S., & Wasser, S. K. (2001). Noninvasive stress and reproductive measures of social and ecological pressures in free-ranging African elephants. *Conservation Biology*, *15*, 1134-1142.
- Goymann, W., & Wingfield, J. C. (2004). Allostatic load, social status and stress hormones: the costs of social status matter. *Animal Behaviour*, *67*, 591-602.
- Hood, L. C., & Jolly, A. (1995). Troop fission in female *Lemur catta* at Berenty Reserve, Madagascar. *International Journal of Primatology*, *16*(6), 997-1015.
- Hrdy, S. B., & Williams, G. C. (1983). Behavioral biology and the double standard. In S. K. Wasser (Ed.), *Social behavior of female vertebrates* (pp. 3-17). New York: Academic Press.
- Isbell, L. A. (1991). Contest and scramble competition: patterns of female aggression and ranging behavior among primates. *Behavioral Ecology*, *2*(2), 143-155.
- Kappeler, P. M., & Heymann, E. W. (1996). Nonconvergence in the evolution of primate life history and socioecology. *Biological Journal of the Linnean Society of London*, *59*, 297-326.
- Koenig, A. (2000). Competitive regimes in forest-dwelling Hanuman langur females (*Semnopithecus entellus*). *Behavioral Ecology and Sociobiology*, *48*, 93-109.
- Koenig, A., Beise, J., Chalise, M. K., & Ganzhorn, J. U. (1998). When females should contest for food - testing hypotheses about resource density, distribution, size, and quality with Hanuman langurs (*Presbytis entellus*). *Behavioral Ecology and Sociobiology*, *42*, 225-237.
- Kubzdela, K. S. (1997). *Sociodemography in diurnal primates: The effects of group size and female dominance rank on intra-group spatial distribution, feeding competition, female reproductive success, and female dispersal patterns in white sifaka, Propithecus verreauxi verreauxi*. University of Chicago, Chicago.
- Mertl-Millhollen, A. S. (2006). Scent marking as resource defense by female *Lemur catta*. *American Journal of Primatology*, *68*, 605-621.
- Muller, M. N., & Wrangham, R. W. (2004). Dominance, cortisol and stress in wild chimpanzees (*Pan troglodytes schweinfurthii*). *Behavioral Ecology and Sociobiology*, *55*(4), 332-340.
- Pereira, R. J. G., Duarte, J. M. B., & Negrao, J. A. (2006). Effects of environmental conditions, human activity, reproduction, antler cycle and grouping on fecal glucocorticoids of free-ranging Pampa deer stags (*Ozotoceros bezoarticus bezoarticus*). *Hormones and Behavior*, *49*, 114-122.



- Pochron, S.T., Fitzgerald, J., Gilbert, C.C., Lawrence, D., Grgas, M., Rakotonirina, G., Ratsimbazafy, R., Rakotoaso, R., Wright, P.C. (2003). Patterns of female dominance in *Propithecus diadema edwardsi* of Ranomafana National Park, Madagascar. *American Journal of Primatology*, 61, 173-185.
- Pride, R. E. (2005a). Foraging success, agonism, and predator alarms: behavioral predictors of cortisol in *Lemur catta*. *International Journal of Primatology*, 26(2), 295-319.
- Pride, R. E. (2005b). Optimal group size and seasonal stress in ring-tailed lemurs (*Lemur catta*). *Behavioral Ecology*, 16(3), 550-560.
- Richard, A. F., Dewar, R. E., Schwartz, M., & Ratsirarson, J. (2000). Mass change, environmental variability and female fertility in wild *Propithecus verreauxi*. *Journal of Human Evolution*, 39, 381-391.
- Richard, A. F., & Nicoll, M. E. (1987). Female social dominance and basal metabolism in a Malagasy primate, *Propithecus verreauxi*. *American Journal of Primatology*, 12, 309-314.
- Romero, L. M. (2002). Seasonal changes in plasma glucocorticoid concentrations in free-living vertebrates. *General and Comparative Endocrinology*, 128, 1-24.
- Ross, C. N., French, J. A., & Patera, K. J. (2004). Intensity of aggressive interactions modulates testosterone in male marmosets. *Physiology & Behavior*, 83(3), 437-445.
- Sapolsky, R. M. (2002). Endocrinology of the stress response. In J. B. Becker, S. M. Breedlove, D. Crews & M. M. McCarthy (Eds.), *Behavioral Endocrinology* (pp. 409-450). Cambridge: The MIT Press.
- Soma, K. K., & Wingfield, J. C. (2001). Dehydroepiandrosterone in songbird plasma: seasonal regulation and relationship to territorial aggression. *General and Comparative Endocrinology*, 123, 144-155.
- Sterck, E. H. M., Watts, D. P., & van Schaik, C. P. (1997). The evolution of female social relationships in nonhuman primates. *Behavioral Ecology and Sociobiology*, 41, 291-309.
- van Jaarsveld, A. S., & Skinner, J. D. (1991). Plasma androgens in spotted hyaenas (*Crocuta crocuta*): influence of social and reproductive development. *Journal of Reproduction and Fertility*, 93(1), 195-201.
- van Schaik, C. P. (1989). The ecology of social relationships amongst female primates. In V. Standen & R. A. Foley (Eds.), *Comparative socioecology: the behavioral*

*ecology of humans and other mammals* (pp. 195-218). Oxford: Blackwell Scientific Publications.

Wasser, S. K. (1983). Reproductive competition and cooperation among female yellow baboons. In S. K. Wasser (Ed.), *Social behavior of female vertebrates* (pp. 349-390). New York: Academic Press.

Wingfield, J. C., Lynn, S. E., & Soma, K. K. (2001). Avoiding the 'costs' of testosterone: ecological bases of hormone-behavior interactions. *Brain Behavior and Evolution*, 57(5), 239-251.

Wingfield, J. C., & Ramenofsky, M. (1999). Hormones and the behavioral ecology of stress. In P. H. M. Balm (Ed.), *Stress Physiology in Animals* (pp. 1-51). Boca Raton, FL: CRC Press.

Wrangham, R. W. (1980). An ecological model of female-bonded primate groups. *Behaviour*, 75, 262-300.

Wright, P. C. (1995). Demography and life history of free-ranging *Propithecus diadema edwardsi* in Ranomafana National Park, Madagascar. *International Journal of Primatology*, 16(5), 835-851.

Yamashita, N. (2008). Chemical properties of the diets of two lemur species in southwestern Madagascar. *International Journal of Primatology*, 29, 339-364.

Young, A. L., Richard, A. F., & Aiello, L. C. (1990). Female dominance and maternal investment in strepsirhine primates. *American Naturalist*, 135(4), 473-488.