Correlates of Dominance Rank in Female Ring-tailed Lemurs (*Lemur catta*) During Birth and Lactation at the Beza Mahafaly Special Reserve, Madagascar.

by

Renee N. Bauer
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ABSTRACT

Dominance status in female ring-tailed lemurs (*Lemur catta*) has a pervasive effect upon social organization, however the proximate mechanisms underlying female rank-relations remain poorly understood. I investigated how four such attributes – weight, age, agonistic frequency, and fecal testosterone levels – relate to female rank-order wild ring-tailed lemurs at the Beza Mahafaly Special Reserve, Madagascar. My results indicated that: (1) The mean weight of high-ranking females is significantly greater than in lower-ranking females; (2) The relationship of age in relation to rank follows an inverted J-shaped pattern, with old adults attaining the highest average rank, followed by prime adults, young adults, and very old adults; (3) Significant, positive correlations between rank and rates of agonism exist in four of the six study groups; and (4) The effect of rank on mean testosterone concentration was significant in one social troop, in which the two highest ranking females exhibited significantly lower mean testosterone levels.

Examiners:

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CHAPTER ONE

INTRODUCTION

Reviewing the changes and developments of researchers' views of the social dominance concept can provide important insights into our understanding of social structure in animals. This history begins with the classic work of Norwegian naturalist Schjelderup-Ebbe (1922, 1935) who was the first to describe the existence of a hierarchical system in vertebrates which he termed the "peck order." Through a number of experiments involving domestic chickens, he discovered that hens - who were initially strangers to each other - fought in a manner such that aggression directed towards flock members was highly consistent and unidirectional. Once a hierarchical system was established, Schjelderup-Ebbe found that rank-order was highly influential in determining who had access to food, water, and preferred roosting sites. The concept of social dominance quickly grew in momentum and decades later dominance hierarchies had been studied in almost all vertebrate taxa (reviewed in Wilson, 1975). As research initiatives broadened to include the complex social lives of nonhuman primates, adult males were the primary focus of attention (Blaffer Hrdy, 1984) in part because it was widely assumed that males were the focal point in structuring social organization (Zuckerman, 1932, Maslow 1936; 1940, reviewed in Wilson, 1975). However, several important studies began to uncover that females also competed with each other for access to key resources, and that the dominance concept was equally applicable to females (Hrdy, 1981). From the mid-1970s to mid-1980s, the role that female rank-relations played in determining group dynamics, social structure, and ultimate reproductive success took the center stage (i.e. Drickamer, 1974; Dunbar, 1980; Cheney et al., 1981; Gouzoules et al., 1982).

For as long as the dominance concept has been deliberated, researchers have sought to uncover the proximate mechanisms underlying an individual's social position, as well as the benefits accrued to higher-ranking individuals. In several non-human primates, including vervet monkeys, several species of baboons, and some macaques, a female's rank is essentially determined by the matriline into which she is born (Seyfarth, 1976; Chapais and Schulman, 1980; Dunbar, 1980; Hausfater et al., 1982; Horrocks and Hunte, 1983; Prud'Homme and Chapais, 1993). This system, termed matrilineal rank inheritance, is in part ensured by the high degree of female third party alliances[1] that occur often on behalf of kin (Wrangham, 1980; Datta, 1983; Chapais, 1983; Bernstein and Ehardt, 1985; van Schaik, 1989; van Hoof and van Schaik, 1992). Female ring-tailed lemurs (*Lemur catta*) provide a unique opportunity to examine individual attributes which may confer higher-rank, as matrilineal rank inheritance is absent in this species, and third-party alliances are extremely rare (Sauther, 1992; Kappeler, 1993b; Nakamichi and Koyama, 1997; Pereira and Kappeler, 1997). The goal of the current research is to examine how four such factors - age, weight, frequency of aggression, and testosterone levels - may influence a female's social position within the well-structured dominance hierarchy.

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[1] Alliances occur whenever a third individual intervenes in an aggressive interaction between two others, to aid one of the antagonists in either attack or defence (Walters and Seyfarth, 1987: 309).

CHAPTER TWO
Correlates of dominance rank in female ring-tailed lemurs in relation to age, weight and frequency of aggression

ABSTRACT

Although dominance status in female ring-tailed lemurs (*Lemur catta*) has a pervasive effect upon social organization, the proximate mechanisms underlying dominance rank in females of this species remain poorly understood. With the rarity of alliances and lack of maternal rank inheritance in this species, it appears that adult females are reliant upon individual attributes and aggressive abilities to earn their respective rank positions. I investigated how three such attributes – weight, age, and agonistic frequency – relate to female rank-order in six wild troops of ring-tailed lemurs during the birth and lactation season at the Beza Mahafaly Special Reserve in southwestern Madagascar. I used continuous-time focal animal sampling methods to calculate rates of agonism and delineate female rank-order in six social groups. My results indicated that: (1) the mean weight of high-ranking females (i.e. those occupying the alpha, beta, and gamma positions in the dominance hierarchy) are significantly higher than that of lower-ranking females; (2) the relationship of age in relation to rank follows an inverted J-shaped pattern, with old adults attaining the highest average rank, followed by prime adults, young adults, and very old adults; (3) significant, positive correlations between rank and rates of agonism exist in four of the six study groups. Results of this research will contribute to our understanding of the intricacies of female social interactions, while providing key insights into how female rank-relations govern several important aspects of social organization in this species, including feeding ecology and possibly infant survivorship.

INTRODUCTION:

Since the original description of the "peck-order" concept of dominance relations in domestic fowl by the Norwegian biologist, Schjeldrup-Ebbe (1922; 1935), dominance orders have been described in a host of group-living vertebrates, including fish, amphibians, birds and mammals (reviewed in Wilson, 1975). Topics pertaining to dominance relationships in the highly complex social life of nonhuman primates have garnered much attention, and have extended to examine both the proximate causes and ultimate evolutionary significance of dominance rank (e.g. Maslow, 1940; Carpenter, 1954; Kawai, 1958; Maroney et al., 1959; Rowell, 1966, 1974; Sade, 1967; Gartlan, 1968; Bernstein, 1970, 1981; Richards, 1974; Hinde, 1978; Noë et al., 1980; Chapais and Schulman, 1980; Dunbar, 1980, 1988; Small, 1981; Dewsbury, 1982; Whitten, 1983; Zumpe and Michael, 1986; de Waal, 1986, 1989; Hausfater et al., 1987; Giacoma and Messeri, 1992; Gust, 1995; Furuichi, 1997; Sprague, 1998; Kubzdela, 1998; Koenig, 2000; Setchell and Dixson, 2002; Gerald, 2002; Takahashi, 2002; Wittig and Boesch, 2003; Bergman et al., 2003). However, to date the majority of research investigating the determinants of adult social status within the primate order has focused on anthropoids – cercopithecines in particular. Surprisingly few studies have addressed this important question in prosimians (but see Taylor, 1986; Digby and Kahlenberg, 2002; Pochron and Wright, 2003), thus highlighting the need for future research in order to elucidate the correlates of rank in females of this sub-order.

For a number of reasons, female ring-tailed lemurs (*Lemur catta*) are excellent subjects in which to explore the determinants of dominance rank. First, in contrast to males whose dominance hierarchies are unstable over time due to male migration and extreme male-male competition during the brief mating season (Budnitz and Dainis, 1975; Taylor, 1986; Sauther, 1992; Sauther and Sussman, 1993; Pereira, 1993; Gould, 1994; 1997), the rank-order of females remains relatively stable (Budnitz and Dainis, 1975; Sauther, 1992). In addition, adult females are often described as the focal point of group activity (Jolly, 1966; Budnitz and Dainis, 1975; Sauther and Sussman, 1993; Sauther et al., 1999) and hence play an important role in structuring group organization. Finally, as ring-tailed lemurs are sexually monomorphic (Kappeler, 1990a, 1991; Sauther et al., 2001) and female dominant (Jolly, 1966, 1984; Budnitz and Dainis, 1975; Taylor, 1986; Pereira et al., 1990; Kappeler, 1990b, 1993a; Sauther, 1992), the behavior of females is not constrained by the actions of larger, dominant males as seen in many sexually dimorphic anthropoids (Kappeler, 1993b).

One way to gain insight into the mode of rank acquisition in female ring-tailed lemurs is to compare them with other primate taxa that share similar social organization and key life-history attributes. Cercopithecines, including some species of baboons, macaques, and vervet monkeys (Seyfarth, 1976; Cheney, 1977; Chapais and Schulman, 1980; Dunbar, 1980; Hausfater et al., 1982; Horrocks and Hunte, 1983; Chapais, 1988; Prud'Homme and Chapais, 1993) are an excellent group to compare with *L. catta* as both reside in multi-male, multi-female social groups (Jolly, 1966; Budnitz and Dainis, 1975; Sussman, 1991), and both exhibit female philopatry which accounts for the high degree of intra-troop relatedness of females (Sussman, 1974, 1992; Budnitz and Dainis, 1975; Jones, 1983). However in contrast to cercopithecines, in which third-party alliances - often on behalf of kin (Massey, 1977; Watanabe, 1979; Wrangham, 1980; Datta, 1983; Chapais, 1983; Bernstein and Ehardt, 1985; van Schaik, 1989; van Hoof and van Schaik, 1992), and maternal rank inheritance play crucial roles in determining female rank (reviewed in Chapais, 1992), agonistic aiding occurs very rarely among ring-tailed lemurs (Sauther, 1992; Kappeler, 1993b; Nakamichi and Koyama, 1997; Pereira and Kappeler, 1997) and does “not ensure matrilineal inheritance of dominance status” (Pereira, 1995: 143). Thus, while inheritance of maternal rank and agonistic aiding contribute substantially to socially inherited or ‘dependent rank’ (Kawai, 1958) of many cercopithecines, status relationships in female ring-tailed lemurs are likely influenced by individual attributes, such as “age, size, fighting ability” (Nakamichi et al., 1997: 332), which is reflective of their ‘basic rank’ (Kawai, 1958) and independent of social coalitions.

Previous research into the biological correlates of dominance rank in female nonhuman primates has yielded interesting results. For example, several species have positive associations between weight, body fat, and body condition to status in females, while other species yield no such correlation (Table 1). Such equivocal results have also been reported in those studies relating a female’s social position to her age (Table 1).

In addition to physical traits, behavioral correlates of female social rank can provide important insights into why particular females are dominant. Agonism is one group of behaviors which are argued to have pervasive influences on group dynamics and social order in nonhuman primate groups (Mason and Mendoza, 1993), and is reflected by the plethora of studies that have found positive associations between patterns of aggression and rank (Table 1).

Although high-ranking individuals are often perceived as the most aggressive members of the group, this is not invariably the case (Table 1). This variation highlights the fact that aggression is not simply a synonym for dominance (Bernstein, 1981). Dominance refers to the direction and outcome of interactions between two individuals and not necessarily to the absolute amount of aggressive behavior displayed (Hinde,

Table 1. A review of the variable relationships between physical and behavioural parameters and female dominance rank in several species of non-human primates.

WEIGHT, BODY FAT, OR CONDITION IN RELATION TO FEMALE RANK:		
positive relationship		**no relationship**
pigtailed mcaques (Tokuda and Jensen, 1969)		Hanuman langurs (Hrdy and Hrdy, 1976)
rhesus macaques (Small, 1981)		bonnet macaques (Cooper et al., 2004)
vervet monkeys (Whitten, 1983)		
toque macaques (Dittus, 1998)		
Hanuman langurs (Koenig, 2000)		
AGE IN RELATION TO FEMALE RANK:		
positive relationship	**negative relationship**	**no relationship**
bonobos (Furuichi, 1989, 1997)	Hanuman langurs (Hrdy and Hrdy, 1976)	Hanuman langurs (Dolhinow et al., 1979)
blue-eyed black lemurs (Digby and Kahlenberg, 2002)	mantles howling monkeys (Jones, 1980, Clarke and Glander, 1984; Zucker et al., 1998, 2001a, 2001b)	Japanese macaques (McDonald Pavelka et al., 1991)
Milne-Edwards' sifaka (Pochron and Wright, 2003)		sooty mangabeys (Gust, 1995)
		red-fronted lemurs (Overdorff et al., 1999)
		chimpanzees (Wittig and Boesch, 2003)
AGGRESSION IN RELATION TO FEMALE RANK:		
positive relationship		**no relationship**
gelada baboons (Dunbar, 1984)		Japanese macaques (Yamada, 1963)
talapoin monkeys (Batty et al., 1986)		chacma baboons (Seyfarth, 1976)
white-fronted capuchins (Robinson and Janson, 1987)		bonobos (Sannen et al., 2004)
stumptail monkeys (Nieuwenhuijsen et al., 1988)		
ring-tailed lemurs (Sauther, 1992)		
proboscis monkeys (Suryana, 1992)		

1983, Walters and Seyfarth, 1987). Furthermore, as Rowell (1966) points out, the avoidance behavior of subordinates can be as influential in maintaining dominance relationships as the overt aggression of dominants.

Despite decades of research into the biology and behavioral ecology of female *L. catta* - including several studies of rank relations in particular (e.g. Taylor, 1986; Nakamichi and Koyama, 1997) - the question still remains: how do female ring-tailed lemurs achieve and maintain their position in the dominance hierarchy? With the relative lack of alliances and maternal rank inheritance in this species, I hypothesized that adult females are reliant upon individual attributes and aggressive abilities to earn their respective rank positions. The goal of the current study is to investigate how three such attributes – age, weight, and agonistic frequency – relate to female rank-order in six troops of wild ring-tailed lemurs in southwestern Madagascar.

This research represents the first of its kind to attempt to validate the concept of dominance in a wild, female *L. catta*, which will serve to refute a number of doubts regarding the validity of the dominance concept in this species. Moreover, by providing key insights into the attributes of social dominance rank, this research will strengthen our understanding of how female rank influences group composition, competitive interactions, and possibly reproductive success of female *L. catta*.

METHODS:

Research site

The Beza Mahafaly Special Reserve (Fig. 1), located in southwestern Madagascar (23°30'S lat., 44°40'E long; Sussman, 1991), was established in 1978 and declared a Special Government Reserve in 1986 (Richard *et al.*, 1987). The climate at Beza Mahafaly is highly seasonal and is characterized by a hot/wet season from November to

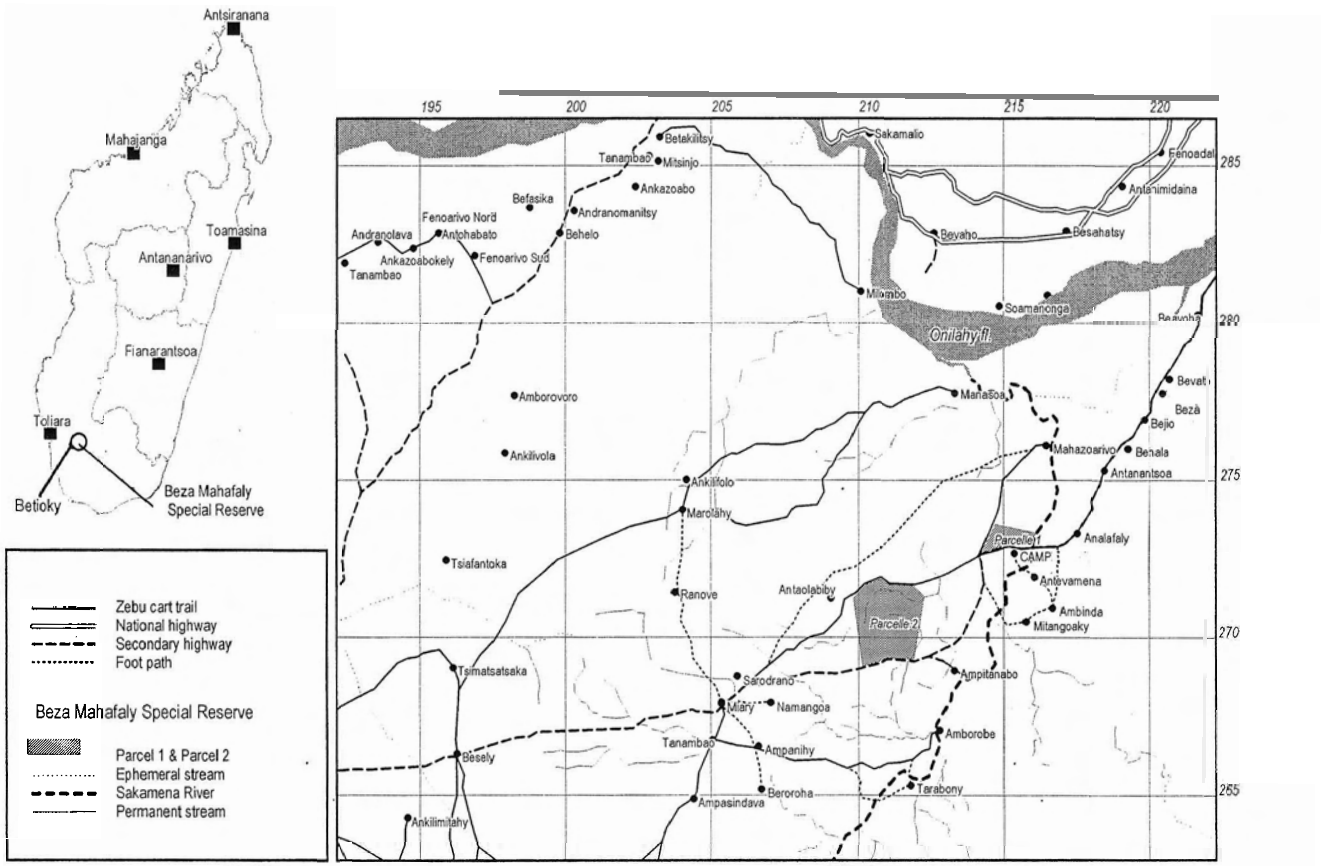


Figure 1. Location of the Beza Mahafaly Special Reserve in southwestern Madagascar produced by the ESSA/FORETS lab. The map on the right shows an enlargement of the reserve and surrounding area.

March, and a cool/dry season from June to August, with transitional seasons in between (Sussman, 1991; Sauther, 1992). A more detailed description of the habitat and vegetation at this site can be found elsewhere (Sussman, 1991; Sauther, 1991, 1992, 1993). My study population included six ring-tailed lemur troops residing in and around a section of the reserve termed 'parcel one' which contains two distinct habitat types: gallery forest bordering the Sakamena River, and xerophytic forest in the western portion of the reserve. The home ranges of the three 'gallery' groups (fitted with red, green, and lavender collars) included a composite of vegetation dominated by *Tamarindus indica* (Sauther, 1992, 1998). The diet of these groups was supplemented by frequent visits (mean = 0.60 ± .08 S.E. visits/day) to adjacent fields to raid human food crops (*pers. obs.).* The remaining troops (fitted with teal, yellow, and black collars) have home ranges which encompassed xerophytic forest in which *Salvadora augustifolia* is co-dominant with *Tamarindus indica* (Sauther, 1992, 1998). In addition, the diets of yellow and black troops are supplemented though access to human food and water from the nearby village and research station (Sauther et al., 2004; *pers. obs.*; Table 2).

Focal animals and observation methods

Ring-tailed lemurs (*Lemur catta*) are diurnal prosimian primates that live in social groups which range from 8-15 adults (mean 8.2; Gould et al., 2003), and typically consist of multiple matrilines (Taylor and Sussman, 1985; Taylor, 1986; Sauther, 1992). Females usually remain in their natal troops (Budnitz and Dainis, 1975; Jones, 1983; Sussman, 1992; Gould et al., 1999) and they undergo a strict estrous synchrony which results in a well-defined and brief reproductive period (Jolly, 1966; van Horn and Resko, 1977; Sauther, 1991; Pereira, 1991).

Table 2. Group size, age-sex distribution, patterns of habitat utilization, and level of provisioning of the six *L. catta* study troops at the Beza Mahafaly Special Reserve.

				group composition					
group	**habitat use**[1]	**food/water provisioning**[2]	**group size**[3]	**AM**	**SM**	**AF**	**SF**	**Juv**	**Inf**[4]
red	gallery forest & crops	no	9	4	0	4	1	2	5
green	gallery forest & crops	no	13	6	1	6	0	1	5
lavender	gallery forest & crops	no	8	3	0	4	1	1	4
teal	xerophytic forest	no	15	6	2	6	1	4	6
yellow	xerophytic forest	yes	11	5	0	5	1	2	4
black	xerophytic forest	yes	9	4	0	4	1	1	4

Note: AM = adult male, SM = sub-adult male, AF = adult female, SF = sub-adult female, Juv = juvenile, Inf = infant

1,2 - for a description of habitat use and provisioning, see methods.

3 - the values for group size and composition represent data collected at the onset of the study in August, 2003. Infants and juveniles were not included in the calculation of group size or other statistical analyses.

4 - the number of infants represents those born during the four month study period.

From August - November, 2003 I observed all adult and sub-adult *L. catta* females (n = 34) residing in six social groups during the well-defined birth and lactation season. The highly terrestrial nature of ring-tailed lemurs (Jolly, 1966; Sussman, 1974, 1977) combined with the fact that these particular study troops were well-habituated to human observers, allowed for behavioral observations at close range (2 - 3m) and precise sampling of subtle and rapid behaviors. Prior to data collection, two field assistants and I engaged in a training period until an inter-observer reliability test was passed ($R > 0.95$). Each study group was followed for five to six consecutive days and observations commenced in the early morning (0600-0730 hours) and continued until dusk (16:30-18:00 hours) with a 2-3 hour break in the afternoon which coincided with the lemurs' extended siesta.

I collected focal animal samples of 12-minutes in duration using continuous time focal animal sampling (Altmann, 1974). The order of focal animal observation was determined randomly at the onset of each observation day, and the number of focal animal samples for each individual was distributed approximately evenly between the morning and afternoon sessions.

Determining age and weight

As a part of a long-term, ongoing study of the effects of habitat differences and endocrine profiles on the health and behavior of ring-tailed lemurs at Beza Mahafaly, M. Sauther, L. Gould and I captured all females (≥ 2 years) from six study troops (with the exception of four females in lavender and red groups whose exact ages were known from previous capture from 1987-1990 and 1995 and subsequent demographic study; Sussman, 1991; Gould et al., 2003). The animals were darted using a Telinject blowpipe and tranquilized with 0.25 – 0.30cc of Tiletamine (Telazol). While the animals were immobilized, I fit all animals with colored, nylon collars (denoting group) and numbered tags for individual identification. I also obtained weight measurements for all individuals in teal, black, and yellow groups using a standard digital scale accurate to 0.01 kg. Finally, I assigned all females (n = 34) to one of five age-classes: very old (≥ 18 years), old (9 ≤ x < 18 years), prime (5 ≤ x < 9), young (3 ≤ x < 5 years), or sub-adult (2 ≤ x < 3 years) on the basis of dental attrition and nipple length (see Sauther *et al.*, 2002 for a more detailed description of age assignments). All methods were approved by the Animal Care Committee at the University of Victoria.

Previous studies examining age-rank effects in nonhuman primates are inconsistent in terms of the inclusion or exclusion of maturing individuals; while some authors include sub-adults/adolescents in their analysis (i.e. Noë et al., 1980; Setchell and Dixson, 2002), others exclude them (i.e. Furuichi, 1997; Koenig, 2000; Takahishi, 2002). I justify their inclusion in the current analysis, as all sub-adults (n = 5) were already unambiguously dominant to males - a landmark which has previously been described to occur in females only after their first mating season (Sauther, 1993; but see Pereira, 1993). In addition, they were consistently challenging higher-ranking females, and as a result were not invariably the lowest-ranking group members (see also Nakamichi and Koyama, 1997; Kappeler, 1993b for similar finding across different *L. catta* study sites). However, due to the lack of consensus as to whether or not to include maturing individuals in such analyses, I also present the statistical tests of age in relation to rank excluding the sub-adults.

Definitions and determination of female aggressiveness

I collected data on conflicts and competitive interactions via using terms previously described by Jolly (1966), Gould (1994), and Pereira and Kappeler (1997). Agonistic behaviors included 'chase', 'lunge', 'bite', 'grab', 'cuff' and 'attack'; and submissive signals included 'flee', 'cower', 'jump away' and 'spat call' or 'submissive chatter'. Approach - retreat interactions were scored when the actor approached the recipient to a distance of ≤ 2m and the recipient subsequently emitted an unambiguous submissive signal in response. I define a "bout" of agonism as conflict between two individuals that lasted ≤ 10 seconds. I used this definition to compute the rate of agonism per hour of focal animal observation (i.e. the number of bouts of agonism per hour initiated by females towards other group members, excluding infants and juveniles). Agonistic rates were further divided to examine such rates initiated by females towards group members of differing sex (male vs. female) and in differing contexts (contact vs. non-contact aggression).

Dominance relationships and alliances

Agonistic interactions were considered 'decided' (Bernstein, 1981) when one animal exhibited only submissive signals in response to a clear approach or other agonistic behavior by its opponent. Following Rowell (1966), Seyfarth (1976), and Dolhinow et al. (1979), female rank-order was determined by the direction of approach-retreat interactions among females with decided outcomes. I chose to assess female rank-order in terms of the directionality of approach - retreat interactions (herein termed the 'supplant hierarchy') as it is unrelated to the criterion used to assess the relative aggressiveness of females. Female rank-order was determined by ordering the females in the matrices which allowed for the minimum number of reversals while maintaining the maximum degree of linearity (Martin and Bateson, 1993). As changes in female rank were not detected across reproductive seasons (i.e. late gestation, early lactation, and mid-lactation), dominance relationships and frequencies of aggressive interactions were calculated using the data from the entire study period.

I recorded the occurrence of alliances that took place during focal animal sampling according to Walters and Seyfarth (1987: 309) in which "alliances occur whenever a third individual intervenes in an aggressive interaction between two others, to aid one of the antagonists in either attack or defense." I calculated the percentage of total approach-retreat and agonistic interactions involving alliances, and noted the percentage of both approach-retreat and agonistic interactions involving rank reversals.

Finally, to determine if the female rank-order remained consistent independent of the measure used to define it - termed "external validity" (Syme, 1974: 933) - I re-constructed dominance hierarchies for all six groups according to the direction and outcome of agonistic interactions in both feeding and non-feeding contexts, and compared these results to the supplant hierarchy.

Statistical analysis

As subtle differences in habitat (Singh, 1966; Isbell et al., 1999) and demographic parameters (Dunbar, 1984; Itoigawa, 1993; Silk, 1993) between groups have been demonstrated to influence the effects of weight and aggressive patterns on rank, I examined these variables in my analysis. The data revealed no statistically significant effects of either group size (one-way ANOVA: $F_{2,17} = 0.612$; $P = 0.555$) nor the presence or absence of provisioning (one-way ANOVA: $F_{1,17} = 1.040$; $P = 0.323$) on the variation in weight of focal females residing in teal, yellow or black troops. Similarly, there were no significant effects of either group size (one-way ANOVA: $F_{4,31} = 0.524$; $P = 0.719$), the presence or absence of provisioning (one-way ANOVA: $F_{1,31} = 1.616$; $P = 0.213$), nor habitat type (one-way ANOVA: $F_{1,31} = 2.162$; $P = 0.152$) on the mean rate of aggression initiated by females of all troops. Based on these results, I pooled the data for all individuals of the six study groups in the subsequent analysis.

Due to the relatively small sample size for female weight (n = 18 females), I categorized ranks into 'high-rank' (i.e. those individuals occupying the alpha, beta and gamma positions in the dominance hierarchy; n = 9) and 'low-rank' (i.e. all remaining individuals; n = 9) for the analysis of weight in relation to rank. In addition, a visual inspection of the dataset for weight in relation to female rank revealed an outlier in which the top-ranking female of teal group (F187) was also the lightest individual in her group (1.89 kg), I therefore presented the results of weight-rank relationships with the inclusion and exclusion of this individual, herein termed the 'lightweight' female.

Statistical tests I performed included both parametric (one-way ANOVA, independent samples t-test) and non-parametric (Kendall's correlation, Kruskal-Wallis test) using the SPSS (version 11.5) statistical software package. The significance level was set at $\alpha = 0.05$ for all analyses and all data are presented as means ± 2 SE unless otherwise noted.

RESULTS:

Female dominance hierarchies, rank reversals, and alliances

A summary of the age-sex distribution, patterns of habitat utilization, and level of provisioning of the six study troops is presented in Table 2. The mean group size was 10.5 ± 0.99 SE (range 8 to 15 adult and sub-adult individuals).

I collected 2715 focal animal sessions of 12-minutes in duration. I observed the six troops for a total of 1743 hr, which included 543 hr of focal-animal sampling and 1200 hr of *ad libitum* notes. The proportion of unknown female-female dyadic relationships was low, as I was able to clearly identify dominance relationships in 72 of 73 (98.6%) of possible female dyads on the basis of supplant interactions (Fig. 2). All focal females in the six groups could be arranged in a linear rank-order, with the exception of green group in which a non-transitive relationship existed between F459 and F34 (Fig. 2). In addition, the female rank-orders constructed on the basis of the direction and outcome of female dyadic agonistic interactions in the context of feeding (Fig. 3) and non-feeding (Fig. 4) were identical to the female hierarchical order obtained on the basis of supplants (Fig 2).

The dominance hierarchies were relatively stable, as indicated by the low percentage of interactions involving rank reversals between F-F dyads (Table 3 and Table 4). In addition, the majority of rank reversals in the context of supplant and agonistic interactions were initiated by sub-adults in comparison to all other age-classes: yellow group 85.7% (n = 6); black group 75.0% (n = 6); teal group 50.0% (n = 5). I was unable to calculate the absolute percentages of rank-reversals involving the two sub-adults in red and green groups due to the fact that data on these individuals were collected on an *ad lib* basis only. The percentage of approach-retreat (Table 3) and agonistic interactions (Table 4) involving alliances by focal females were low (range 0% to 2.5%), and all observed recipients of aid were females only.

Figure 2. Supplant dominance matrices for focal females of the six study troops. Female rank-order was determined by the direction and outcome of decided female-female interactions. Numbers in the matrices represent instances of approach-retreat interactions recorded during focal animal sessions.

yellow group

dominant → **subordinate**

recipient actor	**F489**	**F172**	**F155**	**F159**	**F157**	**F187**
F489	▨	2	8	8	6	2
F172	0	▨	19	8	24	7
F155	0	0	▨	4	6	2
F159	0	0	0	▨	4	1
F157	0	0	0	0	▨	6
F187	2	0	1	0	2	▨

green group

dominant → **subordinate**

recipient actor	**F9**	**F34**	**F23**	**F459**	**F24**	**F46**
F9	▨	15	28	9	24	14
F34	0	▨	26	0	7	14
F23	0	1	▨	14	24	19
F459	0	4	0	▨	5	6
F24	0	0	1	0	▨	12
F46	0	0	0	0	0	▨

teal group

dominant → **subordinate**

recipient actor	**F158**	**F144**	**F147**	**F162**	**F150**	**F142**	**F148**
F158	▨	13	5	20	20	8	4
F144	0	▨	10	4	16	10	4
F147	0	0	▨	1	10	7	2
F162	0	0	0	▨	11	6	8
F150	1	1	0	0	▨	5	0
F142	0	0	0	0	2	▨	2
F148	0	1	0	0	0	1	▨

black group

dominant → **subordinate**

recipient actor	**F112**	**F432**	**F111**	**F110**	**F116**
F112	▨	17	12	28	11
F432	1	▨	6	15	10
F111	0	0	▨	5	5
F110	1	0	0	▨	7
F116	1	0	1	3	▨

lavender group

dominant → **subordinate**

recipient actor	**F33**	**F428**	**F38**	**F139**
F33	▨	11	8	4
F428	0	▨	6	8
F38	0	0	▨	14
F139	0	0	0	▨

red group

dominant → **subordinate**

recipient actor	**F114**	**F55**	**F44**	**F59**
F114	▨	7	8	9
F55	0	▨	21	32
F44	1	1	▨	39
F59	0	0	0	▨

Figure 3. Agonistic dominance matrices during feeding contexts. Female rank-order was determined by the direction and outcome of decided agonistic interactions (i.e. chase, lunge, bite, grab, cuff, and attack). Numbers in the matrices represent instances of agonistic interactions recorded during focal animal sessions.

yellow group

dominant → **subordinate**

recipient actor	**F489**	**F172**	**F155**	**F159**	**F157**	**F187**
F489	▨	3	5	6	8	8
F172	0	▨	4	1	9	3
F155	0	0	▨	2	1	1
F159	0	0	0	▨	1	1
F157	0	0	0	1	▨	2
F187	0	0	0	0	0	▨

black group

dominant → **subordinate**

recipient actor	**F112**	**F432**	**F111**	**F110**	**F116**
F112	▨	4	4	6	4
F432	0	▨	1	1	4
F111	0	0	▨	2	2
F110	0	0	0	▨	1
F116	0	0	1	0	▨

green group

dominant → **subordinate**

recipient actor	**F9**	**F34**	**F23**	**F459**	**F24**	**F46**
F9	▨	2	1	2	1	1
F34	0	▨	7	0	2	1
F23	0	0	▨	7	6	6
F459	0	1	0	▨	2	2
F24	0	0	0	0	▨	1
F46	0	0	1	0	0	▨

lavender group

dominant → **subordinate**

recipient actor	**F33**	**F428**	**F38**	**F139**
F33	▨	9	2	4
F428	0	▨	1	6
F38	0	0	▨	6
F139	0	0	0	▨

teal group

dominant → **subordinate**

recipient actor	**F158**	**F144**	**F147**	**F162**	**F150**	**F142**	**F148**
F158	▨	2	3	3	16	6	1
F144	0	▨	1	1	3	6	2
F147	0	0	▨	1	2	3	1
F162	0	0	1	▨	4	2	2
F150	0	0	0	0	▨	1	1
F142	1	0	0	0	2	▨	2
F148	0	0	0	0	0	1	▨

red group

dominant → **subordinate**

recipient actor	**F114**	**F55**	**F44**	**F59**
F114	▨	1	10	1
F55	0	▨	5	2
F44	0	0	▨	5
F59	0	0	0	▨

Figure 4. Agonistic dominance matrices during non-feeding contexts. Female rank-order was determined by the direction and outcome of decided agonistic interactions (i.e. chase, lunge, bite, grab, cuff, and attack). Numbers in the matrices represent instances of agonistic interactions recorded during focal animal sessions.

yellow group

dominant → **subordinate**

recipient actor	F489	F172	F155	F159	F157	F187
F489		3	4	2	5	13
F172	0		7	2	4	13
F155	0	0		1	1	3
F159	0	0	0		2	3
F157	0	0	0	0		1
F187	0	0	0	0	1	

black group

dominant → **subordinate**

recipient actor	F112	F432	F111	F110	F116
F112		2	1	6	13
F432	0		5	7	7
F111	0	0		2	5
F110	0	0	0		2
F116	0	0	0	0	

green group

dominant → **subordinate**

recipient actor	F9	F34	F23	F459	F24	F46
F9		11	3	1	3	1
F34	0		7	0	1	1
F23	0	0		3	8	8
F459	0	2	0		1	1
F24	0	0	0	0		3
F46	0	0	0	0	0	

lavender group

dominant → **subordinate**

recipient actor	F33	F428	F38	F139
F33		4	11	3
F428	0		2	8
F38	0	0		9
F139	0	0	0	

teal group

dominant → **subordinate**

recipient actor	F158	F144	F147	F162	F150	F142	F148
F158		10	4	17	11	10	2
F144	0		3	2	7	8	3
F147	1	0		2	1	1	1
F162	0	0	1		7	1	6
F150	0	0	0	0		1	2
F142	0	2	0	0	0		3
F148	0	0	0	0	0	0	

red group

dominant → **subordinate**

recipient actor	F114	F55	F44	F59
F114		1	3	1
F55	0		1	9
F44	0	0		8
F59	0	0	0	

Table 3. Percentages of rank reversals and alliances involving focal females and group members (excluding juveniles and infants) that occurred in the context of approach-retreat interactions.

group	number of focal females	total number of supplants	F-F rank reversals	M-F rank reversals	alliances
teal	7	252	6 (2.4%)	3 (1.2%)	0
yellow	6	140	5 (3.6%)	1 (0.7%)	0
green	6	256	6 (2.3%)	2 (0.8%)	0
black	5	169	7 (4.1%)	1 (0.6%)	0
lavender	5	58	0	0	0
red	5	155	2 (1.3%)	1 (0.6%)	0

note: Rank reversals and alliances were calculated as a percentage of the total number of approach-retreat interactions recorded during focal animal sampling

Table 4. Percentages of rank reversals and alliances involving focal females and group members (excluding juveniles and infants) that occurred in the context of agonistic interactions.

group	number of focal females	total number of agonistic interactions	F-F rank reversals	M-F rank reversals	alliances
teal	7	175	6 (3.4%)	0	3 (1.7%)
yellow	6	134	2 (1.5%)	1 (0.7%)	1 (0.7%)
green	6	81	4 (4.9%)	0	2 (2.5%)
black	5	127	1 (0.8%)	0	0
lavender	5	81	0	0	0
red	5	75	0	1 (1.3%)	1 (1.3%)

note: Rank reversals and alliances were calculated as a percentage of the total number of agonistic interactions recorded during focal animal sampling

Weight in relation to female rank

The mean weight of females (n = 18) in black, yellow and teal groups was 2.23 ± .20 kg (range 1.88 – 2.58 kg). The mean weight of females did not differ significantly across the four age-classes (one-way ANOVA: $F_{3,17} = 2.898$; P = 0.072). Females holding high-ranking positions (i.e. alpha, beta, and gamma positions in the dominance hierarchy) had a mean weight which was significantly greater than the mean weight of those females occupying lower positions (mean weight high-ranking = 2.34 ± 0.06 kg; n = 9 and mean weight low-ranking = 2.12 ± 0.06 kg; n = 9 respectively; Fig. 5). These statistically significant differences became even more pronounced by excluding the 'lightweight' female from teal group (Fig. 5).

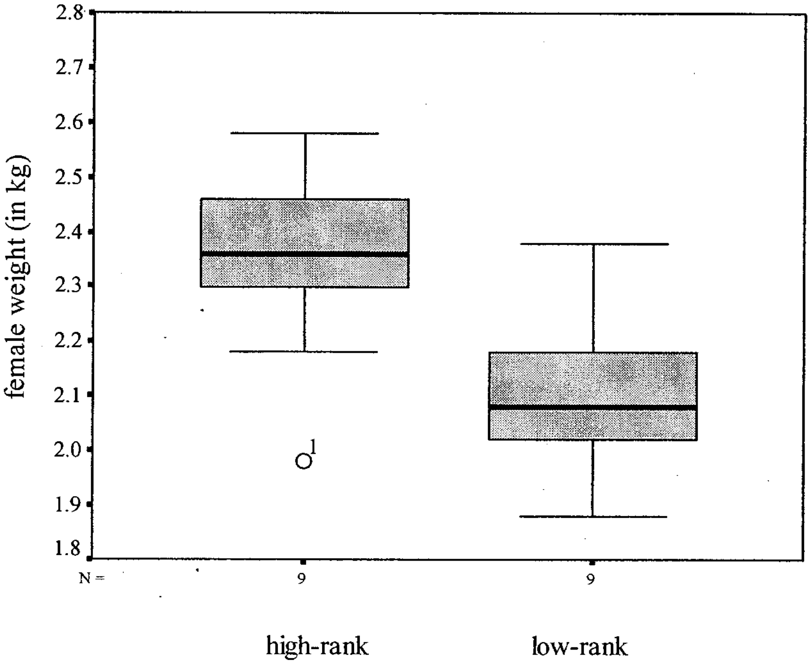
Age in relation to female rank

The age of focal females had a significant effect upon mean rank-position Kruskal-Wallis Test N = 34; H = 9.81; P = .044; Table 5) and this trend followed an inverted J-shaped pattern with old adults attaining the highest average rank, followed by prime adults, young adults, very old adults, and finally sub-adults. Such statistically significant differences were affected by the inclusion of sub-adults in the analysis, as the exclusion of this age-class resulted in non-significance (Kruskal-Wallis Test N = 29; H = 1.68; P = 0.643; Table 5). While there was a trend for older individuals to be heavier, the relationship between weight and age was not statistically significant (Fig. 6).

Rates of agonism in relation to female rank

Significant, positive correlations were found between rank and rates of agonism initiated by focal females in four of the six study groups (Fig. 7), and it was the top-

Figure 5. Differences in mean weight (± 2 S.E.) of high-ranking vs. low-ranking females in three study groups (teal, yellow, and lavender). Independent samples t-test: including extreme value $t_{16(2).05} = 2.627$; $P = .018$; excluding extreme value $t_{15(2).05} = 3.568$; $P = .003$.

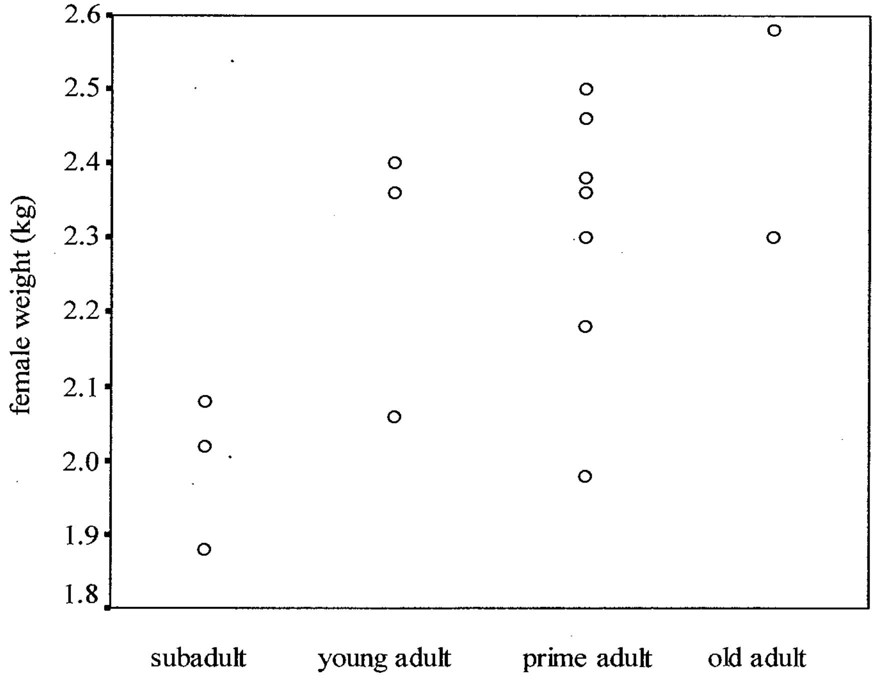


[1] represents an outlier value in which the highest-ranking female from teal group is the lightest individual in the group (1.98 kg).

Table 5. Average female rank in relation to age of focal females in six ring-tailed lemur social troops at the Beza Mahafaly Special Reserve. Kruskall-Wallis Test: sub-adults included: N = 34; H = 9.81; P = .044; sub-adults excluded: N = 29; H = 1.68; P = .643

	AGE CLASS				
rank	**sub-adult**	**young adult**	**prime adult**	**old adult**	**very old**
1		1	3	2	
2		1	4	1	
3			6		
4		1	2	2	1
5	3	2	1		
6	2		1		
7			1		
Total	5	5	18	5	1
Average rank	5.40	3.40	3.06	2.40	4.00
Std. error	± 0.70	± 0.70	± 0.37	± 0.68	n/a

Figure 6. Correlation between age and weight of focal females (n = 18) in teal, yellow and black groups. Kendall's correlation coefficient $K_{dw} = 0.369$; P = .057



ranking female in five of the six study groups that initiated the highest rate of agonistic interactions towards group members (Table 6). Although age did not have a significant effect upon the mean rates of agonism, (one-way ANOVA: $F_{4,31} = 2.005$; $P = 0.122$), an interesting trend emerged in which females of prime-adult age were 1.3 to 2.5 times more aggressive than younger individuals.

By pooling the data for all groups, and dividing the recipients of the aggression into categories by sex, the data revealed that the correlations between rank and rates of agonism were significant for both male recipients (i.e. F-M dyads), and female recipients (i.e. F-F dyads - Figure 8). Similarly, both rates of contact-aggression and non-contact aggression initiated by focal females were positively and significantly correlated to rank (Figure 9).

A closer look at the mean rates of agonism revealed that 'lightweight' female (F158) in teal group was not only the most aggressive member of her group, but also the most aggressive individual in the entire study population, as the mean rate of agonism she initiated (4.32 ± .21 bouts/hour) was significantly higher than the mean group rate (1.29 ± bouts/hour; one sample t-test: $t = -18.18$; $P = 0.000$).

Figure 7. Correlations between female social rank and mean rates of agonism initiated by females (n = 32) of six study troops at the Beza Mahafaly Special Reserve. (* represents statistically significant differences at $\alpha = .05$ level).

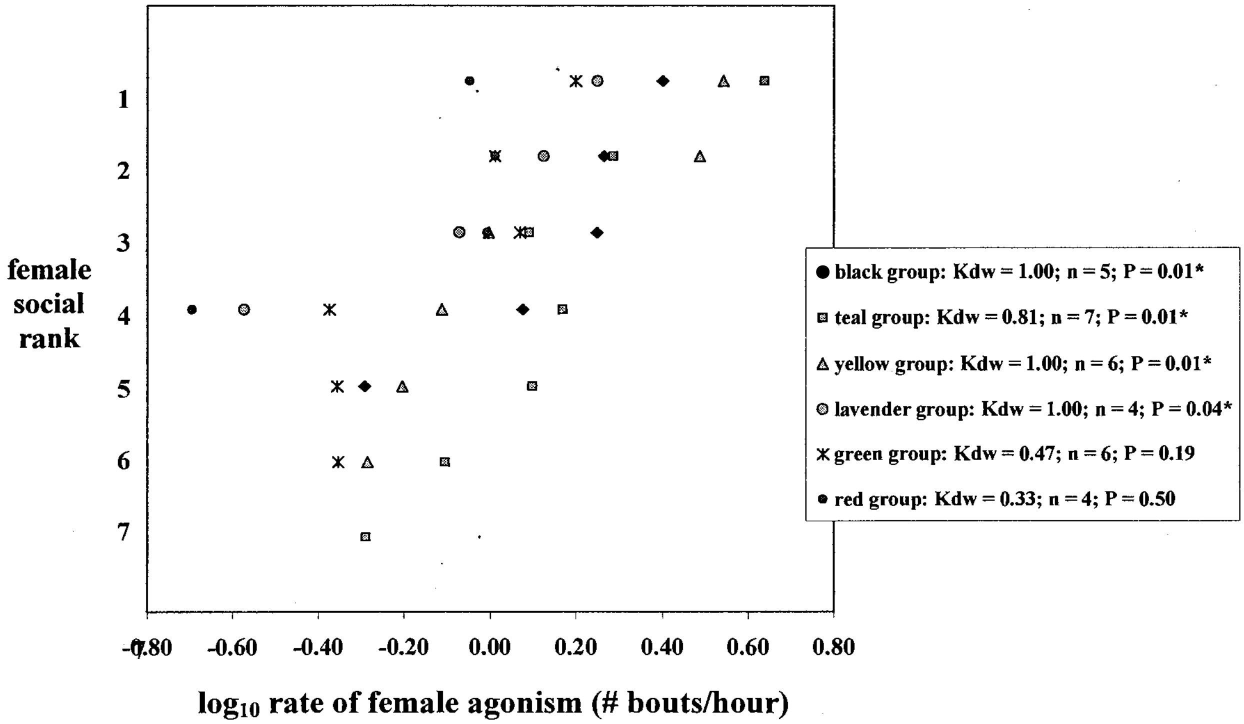


Table 6. Mean rate of agonism initiated by females of differing social ranks at the Beza Mahafaly Special Reserve. Mean rates refer to the mean hourly rate of aggression females initiated towards group members (excluding juveniles and infants).

	rank position		
group	**alpha**	**beta**	**gamma**
teal	4.34	1.93	1.23
yellow	3.48	3.06	0.99
black	2.51	1.84	1.77
lavender	1.33	0.85	0.27
green	1.58	1.03	1.17
red	0.89	1.02	0.98
mean rate (±SE)	2.36 ● 0.55	1.62 ± 0.34	1.07 ± 0.20

Note: rate of agonism is defined as the number of bouts of aggressive interactions per hour of focal animal sampling (see methods).

Figure 8. The relationship between mean rate of female initiated agonism and social rank of all females (n = 32) residing in six social troops at the Beza Mahafaly Special Reserve. Kendall's correlation efficient for F-F dyads: $T_{dw} = 0.662$, $P = .000$; F-M dyads: $T_{dw} = 0.274$, $P = .039$

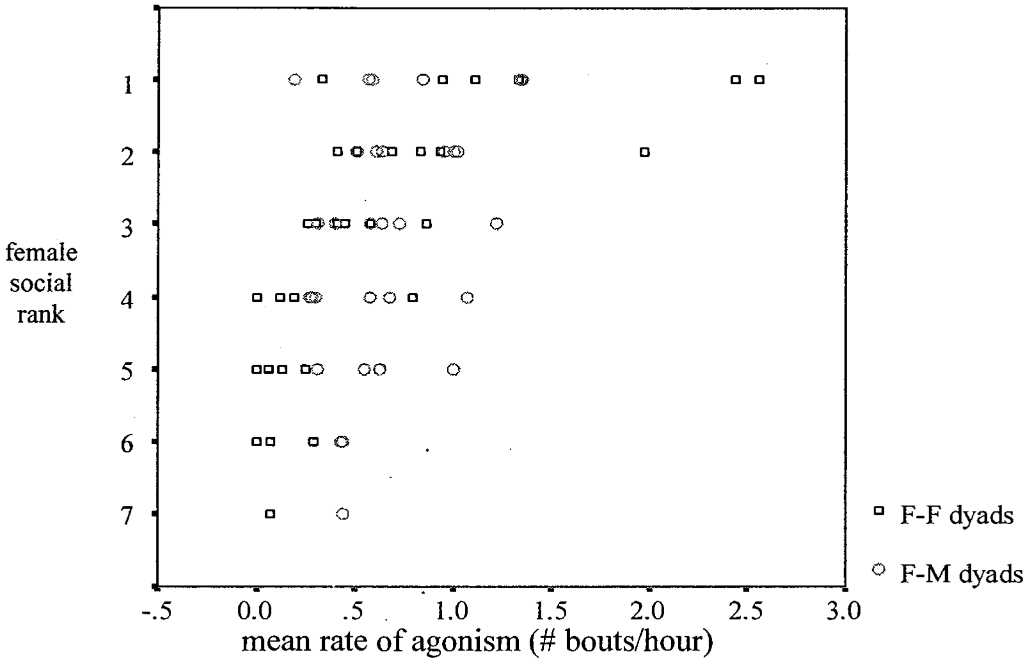
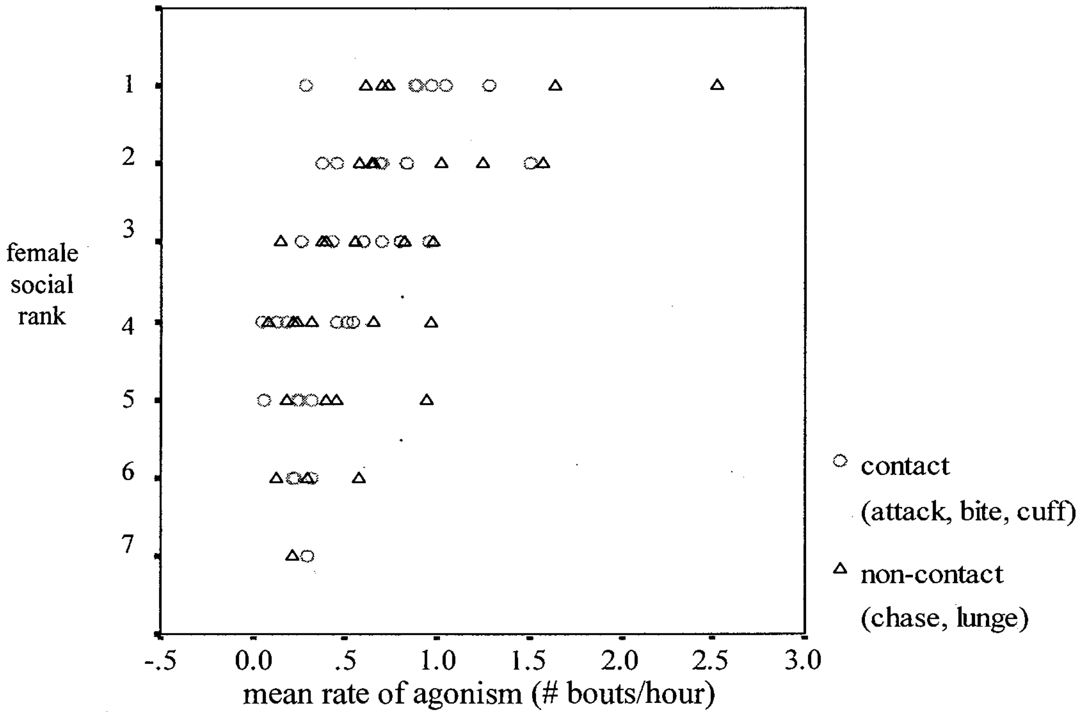


Figure 9. The relationship between mean rates of contact and non-contact aggression initiated by females and social rank of all females (n = 32) residing at the Beza Mahafaly Special Reserve. Kendall's correlation efficient for contact aggression: $T_{dw} = 0.545$, $P = .000$; non-contact aggression: $T_{dw} = 0.502$, $P = .000$



DISCUSSION

Third-party alliances and the stability and validity of dominance hierarchies

While the manner in which female nonhuman primates acquire and maintain their respective rank positions is an important topic in primatology (Hausfater et al., 1987), the validity of the social dominance paradigm in nonhuman primates has been questioned on several accounts. Some researchers suggest that rank-order in nonhuman primates represents an invention of the observer in response to an "unconscious anthropomorphism" (Rowell: 1974: 132) rather than a legitimate construction recognized by the primates themselves (Altmann, cited in Bernstein, 1981). Others attribute the formation of dominance hierarchies to pathological, behavioral responses to stressful conditions in captivity (Gartlan, 1968; Rowell, 1974). Moreover, critics have questioned the use of a single measure to assess social status (Wade, 1977; Altmann, 1980; Bernstein, 1981) as it undermines the ability to use dominance rank as a unifying property in which to predict a variety of behaviors (Rowell, 1974; Bernstein, 1976, Deag, 1977).

In reconciling such arguments, it is essential to assess the degree to which the dominance hierarchy maintains "external validity" (Syme, 1974). In other words, if rank-orders based on one parameter (such as supplants) coincides to one or more alternative measures, (i.e. aggressive interactions, feeding priority, grooming, or mating) under a variety of incentives (i.e. food, water, space), the dominance hierarchy is said to have external validity (Syme, 1974, Dunbar, 1988), and thus rank can be used to predict many behaviors (Bernstein, 1981).

While a number of authors have reported the existence of discernable dominance hierarchies in wild, female *L. catta* (i.e. Jolly, 1966; Sauther, 1992; Nakamichi and

Koyama, 1997), the results of the current study take these findings one step further in validating the dominance concept in wild troops of this species. Evidence for the validity of the dominance hierarchy is derived from my findings that female rank-order was predicted – to varying degrees – by both biological parameters, such as age and weight, and behavioral correlates, under a variety of contexts. The rate of female-initiated agonism tightly corresponded to the supplant dominance hierarchy in four of the six groups studied. In addition, the data revealed that rank-orders produced from approach-retreat interactions were identical to those constructed using the agonistic data, in both feeding and non-feeding contexts. This result deviates slightly from Taylor (1986), who studied a free-ranging troop of ring-tailed lemurs at the Duke University Primate Center. She found that female ranks derived from approach-withdrawal interactions, were consistent with the agonistic dominance hierarchy only for the alpha and omega female.

While these findings are of crucial importance to enhance our understanding of the complementary influences of biology and behavior in relation to female rank in *L. catta*, more research is required to elucidate the extent to which alternative measures of social status (i.e. affiliative patterns, grooming, feeding priority, and access to mates; Taylor, 1986) produce female rank-orders similar to the ones based on supplants and aggression. If all variables are indeed tightly correlated, this would allow the dominance concept to be used as a unifying mechanism (Syme, 1974) which would increase the utility and predictive power of female dominance rank in this species.

The percentages of agonistic and approach-retreat interactions involving third party intervention (herein termed "alliances," Walters and Seyfarth, 1987) were extremely rare (Table 3 & Table 4) and were consistent with values reported for females in two wild ring-tailed lemur social groups at the Berenty Reserve in Madagascar (2.6%

and 1.4%; Nakamichi and Koyama, 1997) and a semifree-ranging troop at the Duke University Primate Center (<0.7%; Pereira and Kappeler, 1997). Moreover, this study confirms Nakamichi and Koyama's (1997) assertion that stereotypical solicitation behaviors used for alliance recruitment – as seen in many anthropoid species (Cheney, 1977; de Waal, 1977; Gouzoules et al., 1984; Gouzoules and Gouzoules, 1989; Schaffner and French, 1997) are lacking in ring-tailed lemurs. In this study, which included over 500 hours of focal animal sampling and 1200 hours of *ad lib* data, no such behaviors were witnessed. Researchers have speculated that characteristic patterns of agonistic intervention and recruitment are absent in *L. catta* due to a relatively low visual acuity, which is approximately one-fifth of that of anthropoids and humans (Pereira, 1995), or to a lack of stereotyped solicitation behaviors in which to recruit support from allies (Nakamichi and Koyama, 1997).

Given that female rank is independent of maternal rank in this species, and that adult females in the six troops I observed did not demonstrate a high degree of social support from others in the form of alliances, I postulated that rank would likely reflect individual attributes, such as age, size, and/or aggressiveness of females. The relationship between rank and these three aforementioned variables will be addressed in turn.

Age in relation to social rank of females:

An extensive review of the literature revealed that the significant relationships between age and social rank in non-human primates fall into one of two categories: age-graded systems (Eisenberg et al., 1972) or "inverted J-shaped" systems (Sprague, 1992), which have also been described as "humped curves" (Takahashi, 2002). In age-graded systems, status follows a linear pattern in which rank increases with age (positively age-graded) or decreases with age (negatively age-graded). While positively age-graded systems are common to number of nonhuman primates including male mandrills (Setchell and Dixson, 2002), female bonobos (Furuichi, 1989, 1997), female blue-eyed black lemurs (Digby and Kahlenberg, 2002), and female Milne-Edwards' sifaka (Pochron and Wright, 2003), negatively age-graded systems occur less frequently, and to date have only been described in mantled howler monkeys (Jones, 1980; Clarke and Glander, 1984, Zucker et al., 1998, 2001a, 2001b) and female common langurs (Hrdy and Hrdy, 1976). Inverted J-shaped age-rank relations show positive correlations between age and rank until the latter life-history stages when rank declines with increasing age. Most known examples of this pattern occur in female hamadryas baboons (Meishveli, 2001) and male Japanese macaques (Sprague, 1992, 1998; Takahashi 2002; but see Norikoshi and Koyama, 1975).

My data indicate that age is an important factor in determining female rank-order in *L. catta* (Table 5): female rank-relations followed an inverted J-shaped pattern. Upon removing sub-adults from the analysis, however, the results lost statistical significance which indicates that the real age differences in relation to rank occur between sub-adult and older age-classes. I argue that rank acquisition in females appears to follow a step-wise process that begins as sub-adult females initiate challenges toward higher-ranking females. Sub-adults were the age-class responsible for the majority of rank reversals overall, and although they held the lowest mean rank (Table 5), they were not invariably the lowest-ranking members of the group (i.e. sub-adult F142 was second-ranking female in teal group). Similar results have been reported at the Duke University Primate Center (Kappeler, 1993a) and at Berenty Reserve in Madagascar (Nakamichi and Koyama, 1997). By the time the females' reached the young adult stage, their mean rank was notably higher. This trend could be explained by their propensity to demonstrate their "increasing agonistic capacity" (Nakamichi and Koyama, 1997: 89). From the available cross-sectional data, females are may achieve their highest lifetime rank in the old adult stage, although longitudinal information is necessary to confirm this suggestion. Once a female reaches the 'very old' stage (i.e. ≥ 18 years), she rapidly falls in rank (Table 5). Despite the fact that my data set includes only one such individual, the extremely low ranks exhibited by very old females has been witnessed on previous occasions at Beza (L. Gould, *pers. comm.*). Such a sharp decline in rank of very old females may be attributed to age-related decline in cognitive capacities (Toxopeus, et al., 2004), sensory senescence (Nusbaum, N.J., 1999; Aujard and Némoz-Bertholet, 2004) or an ultimate deterioration in physical condition (Roth et al., 2004), as I observed very old females repeatedly lagging behind during group processions and struggling to relocate their respective groups (R. Bauer, *pers. obs.*; L. Gould; *pers. comm.*).

While the proximate mechanisms of age-related dominance rank in female *L. catta* are only beginning to unfold, several possibilities are apparent. In ring-tailed lemur social groups, age is expected to be linked to a female's length of tenure in the group owing to the fact that females usually remain in their natal troops (Jolly, 1966; Sussman, 1974, 1992; Budnitz and Dainis, 1975; Jones, 1983) and only rarely are evicted (Taylor and Sussman, 1985; Taylor, 1986; Vic and Pereira, 1989; Sussman, 1991; Gould et al., 2003). Older group members are likely to have more in-depth experiences in locating and exploiting key food resources within their respective home ranges and utilizing efficient techniques to extract them (Chapais, 1991). Indeed, early research into the patterns of group movement in this species reveals that the top-ranking female is highly influential in directing intra-troop activities, and she often initiates the direction of group travel (Jolly, 1966; Budnitz and Dainis, 1975; Sauther, 1992). In addition, the experiences gained by older individuals through multiple exposures to predators may award them the advantage of predicting predators' behavior (Gartlan, 1968); a hypothesis which is partially supported by the research of Gould (1996) who found that higher-ranking females are more vigilant of predators and potential predators than lower-ranking females. Taken together, it is plausible that sub-adult individuals defer to older, more experienced group members who, in turn, share this knowledge.

Other factors, namely demography and kinship, may influence the results of the age-rank analysis and will be discussed briefly here. As Dunbar (1984: 516) aptly describes, "we will never fully understand behavior if we fail to take demographic processes into account." In fact, there are a number of explanations as to how the age composition of a sample population can strongly affect the outcome of statistical correlations (Sprague, 1992). With this in mind, one possible reason why statistical significance was lost upon removing sub-adults from my analysis is that demographic parameters may be confounding the effects of age on rank. The removal of the sub-adult age category from my analysis narrows the age ranges in the ANOVA analysis. In effect this underscores the rank-effects within each age-class while underestimating the rank-effects between different age-classes (Sprague, 1998). In addition, the presence of a large cohort of females assigned to the prime-adult age-class acts to reduce the correlation between age and rank because similar aged individuals are assigned differing ranks within a linear rank-order.

Patterns in the structure of female-relatedness within groups may likewise impact the results of female rank in relation to age. Although I assumed that there are limited kinship effects based upon the fact that *L. catta* do not exhibit matrilineal rank inheritance (Pereira, 1995, Nakamichi and Koyama, 1997), and that kin-based alliances are extremely rare (Sauther, 1992; Kappeler, 1993b; Nakamichi and Koyama, 1997; Pereira and Kappeler, 1997), there are other ways in which kinship can modify age-rank relations. For example, several authors have noted that, in *L. catta*, mothers consistently hold dominant positions over their daughters (Sauther, 1992; Pereira, 1993; Nakamichi et al., 1997). The existence of strong social bonds between mothers and their offspring may act to reduce the aggressive tendencies of daughters directed towards their mothers in this species, as such patterns have previously been reported in Japanese macaques (Nakamichi, 1984; 1991). In addition, studies of free-ranging populations of ring-tailed lemurs have shown that all members of one matriline typically dominate another (Taylor, 1986), which – if also true in wild populations – would act to diminish the effects of age on rank. My lack of detailed knowledge of mother-daughter relationships in the current study precludes the separation of kinship effects on rank, and solving such dilemmas should be a priority in future research involving this species.

While short-term studies such as mine are useful in elucidating the influences of physical attributes on rank, only a limited number of long-term studies have comprehensively addressed the effect of maturational status on rank (i.e. van Noordwijk and van Schaik, 1999; Takahashi, 2002). Such longitudinal studies are crucial not only to delineate the extent to which the variability in age-related dominance relationships is altered by demographic processes over multiple years (Hausfater et al., 1987), but also to elucidate how female dominance relationships are affected by changes in relational measures – such as age, weight, and state of pregnancy – relative to such changes in other group members (Bernstein, 1981).

Weight in relation to social rank of females

Thus far, published accounts examining the effect of weight on dominance rank acquisition in *L. catta* are limited to pre-pubescent age groups: authors have found that mass is strongly correlated to dominance rank in juvenile cohorts (Pereira, 1993). To my knowledge, the current study is the first of its kind to examine such correlations in mature individuals of this species, and is instrumental in elucidating how biological and ontogenetic parameters shape female rank-relations.

I found that high-ranking females were almost 10% heavier than those females occupying lower ranks in the dominance hierarchy, and these differences were statistically significant (Fig. 5), and only marginally influenced by female age (Fig. 6). Moreover, the effects of weight on rank were even more pronounced upon removing the outlier 'lightweight' value from teal group (Fig. 5). These data add to the growing body of literature that has found similar rank-related differences in body mass or condition in females of other primate taxa (Small, 1981; Whitten, 1983; Dittus, 1998; Koenig, 2000), and may refute the assumption that the effect of size/strength on dominance rank is more pronounced in male than female nonhuman primates (Walters and Seyfarth, 1987).

Although the weight of females appears to be related to dominance rank position, whether such variation is a cause or consequence of female rank is not fully understood. One argument would suggest that increased weight leads to high rank (i.e. the 'cause' argument). According to this view, heavier individuals may utilize their increased strength-for-weight advantage in fights (Rowell, 1974, 1988) which would promote a greater proportion of wins, and hence a correspondingly higher rank.

Another plausible, but not mutually exclusive explanation for the weight-rank relationship is that higher ranking females are heavier as a consequence of priority of access to resources (i.e. the 'consequence' argument). Sauther (1992) found that higher-ranking female ring-tailed lemurs employed less active forms of movement, had greater access to scarce water resources, and consumed a larger proportion of energy-rich fruit in their diet, in comparison to lower-ranking females. Such priority of access to resources may lead to superior nutritional status which would confer advantages in coping with food shortages, while allowing for weight increases and a surplus in their energy budget to engage in - and possibly win - contests.

Resolution of the cause or consequence argument will require: (1) determining the extent to which body mass is influenced by genetics; a topic that is beyond the scope of the current study (but see Jaquish et al., 1997; and Cheverud et al., 1994 for an analysis of the heritability of body mass in hamadryas baboons and cotton-top tamarins respectively); and (2) examining the potential of such physical attributes to confer long-term reproductive success in females. Among my study population, I found no direct evidence that body weight affected a female's ability to conceive nor the survival rate of her infant of $\leq$ 8 months of age (unpub. data). In light of the relatively small sample sizes for weight in the current study ($n = 18$), I maintain that the ability of dominance rank to modulate female body mass, and subsequent fecundity and infant survivorship merits further study.

Careful inspection of extreme values in one's dataset is often useful to provide insights into factors responsible for such anomalies. Such an exceedingly low value for weight (1.89 kg) for the top-ranking female in teal group (Fig. 5) prompted me to examine alternate factors contributing to her uncharacteristically high-rank. A closer look at the mean rates of agonism revealed that this particular individual was not only the most aggressive member of her group, but also the most aggressive individual in the entire study population. Thus it is apparent that while weight is one potential factor influencing a female's rank, other attributes - such as agonistic tendencies - are likely acting in concert.

Aggressiveness in relation to social rank of females:

The present analysis suggests that the rate of agonism initiated by females was a good indicator of dominance rank in four of the six groups studied (Fig. 7). Such findings are consistent with those reported in a host of other nonhuman primate females (e.g. talapoin monkeys: Batty et al., 1986; white-fronted capuchins: Robinson and Janson, 1987; proboscis monkeys: Suryana, 1992). In identifying the proximate factors that enable more aggressive females to attain higher status positions, I will consider the effects of learning from previous experiences, the importance of status awareness, the confounding influence of age on aggression, and the concomitant role of non-contact threats.

The importance of prior conditioning and experience in predicting the outcome of conflict has been well documented in nonhuman primates (e.g. Parker, 1974; Rowell, 1974; Bernstein, 1981; Dunbar, 1988; Mason, 1993). Repeated victories by higher-ranking individuals are argued to be a "power reinforcing agent" (Scott, 1962: 168) that provokes successful and more experienced individuals to engage in subsequent aggressive interactions with subordinates. This phenomenon has been reported in mice and rhesus monkeys, by which consistent wins in dyadic contests raises the likelihood of engaging in – and winning – future contests (Emlen, 1973; van Doorn et al., 2003; Dugatkin and Earley, 2004). This phenomenon may be applicable to female *L. catta* as well, given that females likely spend the majority of their lives in regular social contact with conspecific females of the same group (Budnitz and Dainis, 1975; Jones, 1983;

Sussman, 1992; Gould et al., 1999). The role of subordinates in such interactions may also be influential, because they too learn the fighting capabilities of dominant individuals through prior outcomes, and are perhaps more likely to infer – and perhaps avoid – the consequences (Dunbar, 1988).

One prerequisite to the role of learning is that individuals are capable of recognizing and remembering their respective positions in the dominance hierarchy. While this phenomenon, termed "status awareness" (de Waal, 1986: 465) exists in a number of anthropoid primates (reviewed in Seyfarth and Cheney, 2000; Bergman et al., 2003), lower vertebrates (white-throated sparrows: Wiley et al., 1999; chickens: d'Eath and Keeling, 2003) and even invertebrates (crayfish: Gherardi and Daniels, 2003), comparable studies in prosimians are relatively scarce. Preliminary evidence for the knowledge of status awareness in ring-tailed lemurs is demonstrated by the remarkably unidirectional, stereotypical submissive chatters elicited by subordinates in response to a glance by a dominant individual, or by simply walking past a dominant group member (Taylor, 1986; *pers. obs.*). However, the existence of rank-awareness in this species to the complex level of that reported in anthropoid primates remains controversial (Nakamichi and Koyama, 1997; Pereira, 1995), and to date it is unclear whether *L. catta* has the capacity to recognize and adhere to transitive relations among other group members, or whether they simply comprehend who is dominant and who is subordinate to themselves (Seyfarth and Cheney, 2000).

Age and kinship are two additional factors likely to affect the relationship between female aggressiveness and rank. For example, age and experience are crucial parameters in determining the probability of winning disputes I many mammals (Wilson, 1975; Thouless and Guiness, 1986; Pochron and Wright, 2003). My data reveal that females of prime adult age were 1.3 – 2.5 times more aggressive than younger individuals, and although these results were not statistically significant, they nevertheless indicate that the interaction between age and differential agonistic experiences may influence rank determination. Perhaps older and more experienced group members have had ample opportunity to develop strength, agility and fighting skills in comparison to younger individuals (Thouless and Guinness, 1986). However, such descriptive qualities of an individual are difficult to quantify in wild populations, and despite the extensive use of the term "fighting ability" in the literature (e.g. Parker, 1974: 225; Dunbar, 1988: 212; Chapais, 1991: 197; Noë, 1994: 211), I was unable to uncover a precise methodology of how to accurately measure this parameter. Until a standardized means of quantifying and comparing relative fighting ability is established, the interaction between fighting ability and experience on female rank in ring-tailed lemurs remains unknown.

The degree of relatedness of females affected the expression of agonism in two semifree-ranging troops of *L. catta*, as Taylor (1986) found that severe forms of agonistic interactions occurred more frequently among distant and unrelated individuals. Thus, it may be that the influence of female rank on intragroup aggressive patterns may be overshadowed by the number of kin and their degree of relatedness. In other words, those females residing in social groups with few closely related female kin may be expected to act more aggressively.

In my study population, not all rank-related agonistic interactions resulted in contact between the actor and the recipient, and the percentage of contact aggression (i.e. attack, bite, cuff; 45%) was lower than those involving near-contact (i.e. lunge, chase; 55%), although both types of aggression are strongly correlated to female rank (Fig. 9). The results of this analysis support the assertion that individuals achieve dominance status not only through overt aggression, but also through more "subtle behaviors that convey confidence, power, or threat" (Dabbs and Hargrove, 1997: 447). The pervasiveness of threats - without actual physical contact - may be understood from an evolutionary perspective, as such threats may function to resolve conflict and establish dominance relationships without risking injuries by engaging in physical contact.

In ring-tailed lemurs at Beza-Mahafaly, the highest-ranking female demonstrates the highest frequency of aggressive encounters overall (Sauther, 1992; Sauther and Sussman, 1993). My findings support their observations, as the top-ranking female was responsible for the highest rate of aggressive interactions in five out of the six groups studied (Table 6). The exception occurred in red group, in which the second-ranking female was most aggressive, a result which is similar to Gould (*pers. comm.*) who reports that the second ranking female of her study troop in 1994 was far more aggressive than the alpha female. Such anomalous findings are not unique among non-human primates, as Yamada (1963) reports that an alpha female in a group of macaques maintained a high dominance rank while only rarely being aggressive to others. These results, in conjunction with the data that the relationship between rank and rates of aggression are not invariably linearly correlated (Fig. 7), suggest that the degree of aggressiveness is not the only predictor of female rank in this species.

In comparing the correlates of rank in social insects and lower vertebrates to that of the more complex social systems of nonhuman primates, Wilson (1975: 290) posits that "...the greater the size of the brain and the more flexible the behavior, the more numerous are the determinants of rank." The data presented here provides some support for the theory that dominance orders of females are characterized by age, size and aggressiveness. However, the findings that these parameters are not perfectly correlated to female rank across all groups suggest that attainment and expression of female social rank in this species is exceedingly complex. Such complexity is reflected in the multitude of factors which have been cited to influence dominance related behavior in other species of nonhuman primates, which include personality or temperament (Goodall, 1986; Mondragon-Ceballos and Santillan-Doherty, 1992; Welker et al., 1992) cognitive abilities (Welker, 1986), agility (Walters and Seyfarth, 1987) and early rearing experience (Berman, 1980; Coelho Jr., 1981; Higley et al., 2000).

Although the full scope of biological and behavioral attributes of female rank in ring-tailed lemurs is not yet fully understood, the current research strengthens our understanding of the intricacies of female social interactions in this species, while providing key insights into how female rank-relations govern several aspects of social organization, including feeding ecology and possibly infant survivorship. Future studies should examine how cognition, personality, agility and early rearing experience may likewise contribute to our overall understanding of the determinants of dominance rank in female *L. catta*

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CHAPTER THREE

The social, behavioural, and biological correlates of testosterone levels in two troops of wild, female ring-tailed lemurs at the Beza Mahafaly Special Reserve, Madagascar.

ABSTRACT

Testosterone is a hormone of particular interest to behavioural endocrinologists due to its capacity to influence a wide range of social behaviors in non-human primates, including rank-related aggression and dominance. The goal of the current research is to investigate how a number of social and behavioral traits (i.e. female rank, frequency of aggression, and dietary choices) and biological parameters (i.e. age, gestational stage and diurnal patterns of hormone secretions) influence testosterone concentrations in 10 females residing in two social troops of ring-tailed lemurs (*Lemur catta*) at the Beza Mahafaly Special Reserve, Madagascar. I used continuous-time focal animal sampling methods to calculate rates of agonism and delineate female rank-order, and I non-invasively collected 120 fecal samples which were preserved in the field and sent to the Wisconsin National Primate Center for enzyme immunoassay. My results indicated that: (1) stage of reproduction appeared to be the best predictor of testosterone levels, as the data show significantly higher mean fecal testosterone (fT) titers during late gestation in comparison to early lactation; (2) there was a trend for older females to exhibit correspondingly higher fT levels in comparison to prime-aged or young females; (3) fT concentrations were not significantly affected by dietary differences nor the timing of fecal sample collection; (4) no clear patterns emerged with respect to testosterone levels in relation to rates of female-initiated agonism; and finally (5) the top-ranking female in red group, and two top-ranking females in green group exhibited the lowest mean fT levels. The preliminary evidence suggests that testosterone levels are not an underlying mechanism mediating social rank and frequency of aggression in female *L. catta*, and these findings are discussed in light of the challenge hypothesis, the aromatization hypothesis, the suppression of testosterone by stress-induced cortisol production, and the long-term effects of prenatal androgen exposure. This study is significant as it establishes appropriate methodologies and sampling protocols to monitor female androgen levels, while providing key information to help to disentangle complexity of endocrine responses during reproduction in female ring-tailed lemurs.

INTRODUCTION

In the past two decades there has been a heightened interest in the field of socioendocrinology, in which researchers aim to elucidate the reciprocal influences of hormones and behavior, and how this intricate relationship is affected by the social environment (Bercovitch and Ziegler, 1990). Androgens, including testosterone, which is reported to be the most potent of the androgenic steroid hormones (Rose et al., 1974), are of particular interest due to their capacity to influence a wide range of social behaviors in both male and female mammals, including rank-related aggression and dominance (Rose et al., 1974; Dixson, 1980; Floody, 1983; Nelson, 2000). Testosterone is not exclusively secreted by the Leydig cells in the testis of males (Nelson, 2000), but it is also produced in the adrenal cortex of both sexes, and in the stroma and thecal cells of ovaries (Bulun and Adashi, 2003). Indeed, in a few mammalian species testosterone levels outside the breeding season are reported to be as high or higher in females than in males (spotted hyena: Racey and Skinner, 1979; Verreauxi's sifaka: Brockman et al., 1998a; European mole: Whitworth et al., 1999).

Although the overwhelming majority of research on rank-related aggression and testosterone in nonhuman primates has focused on males (i.e. Bernstein et al., 1979; Sheffield et al., 1989; Brockman et al., 1998b; Aujard and Perret, 1998; Strier et al., 1999; Cavigelli and Pereira, 2000; Barrett et al., 2002; Ostner et al., 2002), there is evidence that androgens influence social status (Batty et al., 1986), sexual responses (Everitt et al., 1972; Dixson et al., 1973) and normal development (Staub and De Beer, 1997) in females as well. For example, in female talapoin monkeys (Batty et al., 1986), and female chimpanzees (Birch and Clark, 1946) social status is closely linked to circulating testosterone levels: subordinate individuals exhibit significantly lower serum testosterone compared to dominant or intermediate-ranking females. Moreover, a rise in testosterone levels through the administration of exogenous androgens in females, including ovarioectomized rhesus monkeys (Trimble and Herbert, 1968), young rhesus monkeys (Joslyn, 1973), and infant marmosets (Abbott and Hearn, 1978), led to parallel increases in aggressive behaviour which, in turn, enhanced dominance status.

In contrast to the above-mentioned findings testosterone concentrations in females residing in two captive troops of ring-tailed lemurs were not significantly correlated to either rank or rates of aggression (von Engelhardt et al., 2000). It is important to consider, however, that results derived from captive studies may be confounded by a number of variables, including artificial social groupings, cage size, reduced potential for maneuvering and escape, and the influence of provisioning on intraspecific feeding competition (Singh, 1966; Southwick, 1967; Mason, 1993; Hill and Okayasu, 1996; Isbell et al., 1999). These human-imposed factors, in turn, have the capacity to influence stress levels (Gartlan, 1968), patterns of dominance formation (Rowell, 1966; Richards, 1974), and frequency and intensity of agonistic behaviors (Singh, 1966, Hill and Okayasu, 1996; Isbell et al., 1999). Thus results from studies on captive animals should be supported by studies from free-ranging animals. The current study, which focused on wild, female ring-tailed lemurs at the Beza Mahafaly Special Reserve (BMSR) in southwestern Madagascar (Fig. 1), permitted an assessment of behavioral and physiological correlates of testosterone levels in the natural environment while avoiding the potential confounds of captivity. By comparing my findings to those found in captive, female *L. catta* (von Englehardt et al., 2000) I will determine to what extent results from captive animals be reconciled with those derived from a wild troops. The comparison of

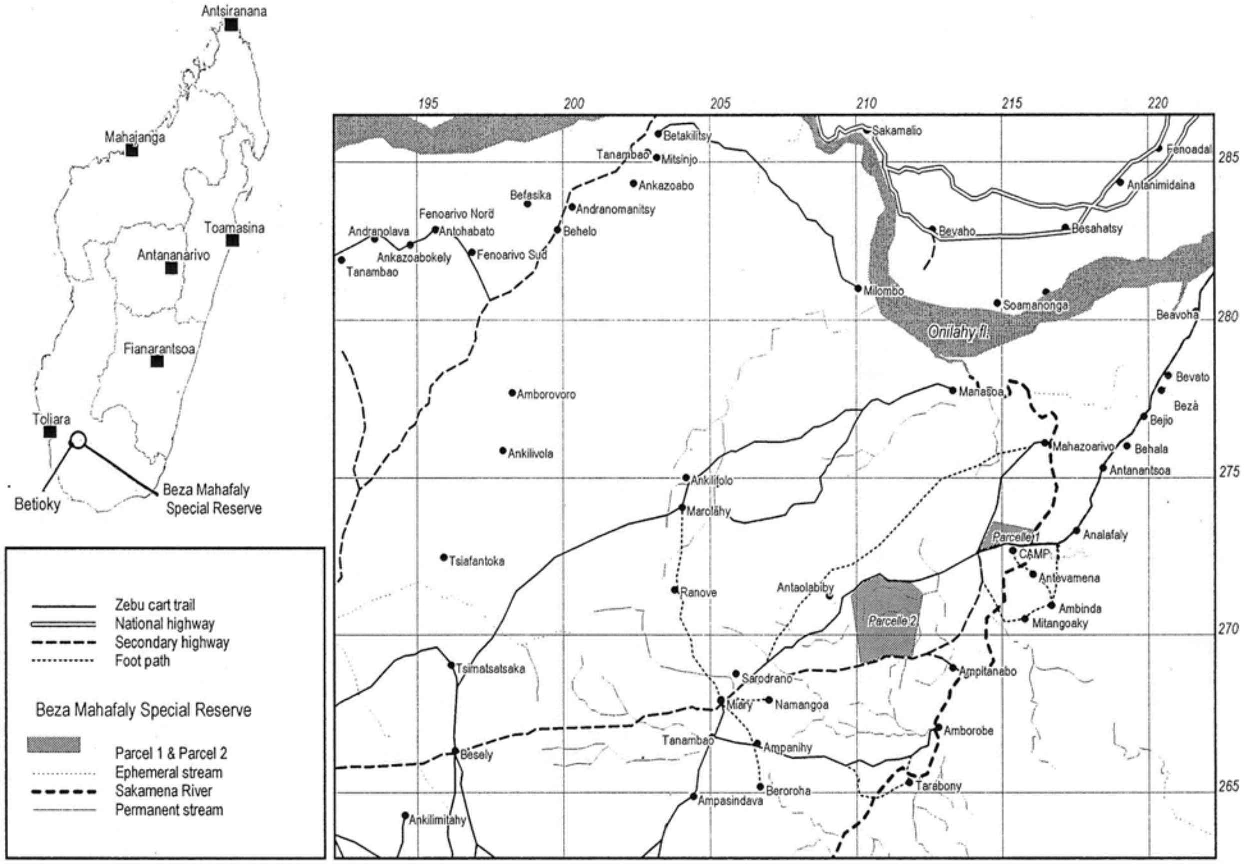


Figure 1. Location of the Beza Mahafaly Special Reserve in southwestern Madagascar produced by the ESSA/FORETS lab. The map on the right shows an enlargement of the reserve and surrounding area.

complementary data from both sources may be useful in piecing together the dynamics of hormone-behavior interactions.

The first goal of the current study was to utilize non-invasive techniques to monitor fecal testosterone levels (herein denoted fT) in relation to rank, reproductive status, and rates of aggression among wild, female ring-tailed lemurs. The second goal was to monitor how variable amounts of undigested fiber in fecal samples (Wasser et al., 1993; Ostner and Heistermann, 2003) and diurnal patterns of hormone secretion (van Horn et al., 1976; Rose et al., 1978a; Enomoto, 1980; Castracane et al., 1981; Wiebe et al., 1984; Kholkute, 1984; Perret, 1985; Coe and Levine, 1995; Stoinski et al., 2002) influence testosterone concentrations.

Female ring-tailed lemurs provide a unique opportunity to examine the behavioral and physiological correlates of testosterone in females, as they form clear intragroup dominance hierarchies which are relatively stable in wild troops (Budnitz and Dainis, 1975; Sussman, 1977; Sauther, 1992). In addition, they are one of the few group-living primate species to exhibit unambiguous female dominance (Jolly, 1966, 1984; Budnitz and Dainis, 1975; Taylor, 1986; Pereira et al., 1990; Kappeler, 1990a, 1993a; Sauther, 1992), accompanied by a lack of sexual size dimorphism (Kappeler, 1990b, 1991; Sauther et al., 2001). This unique combination of traits prevents the actions of larger, dominant males from constraining the behavior of females, as such has been seen in many sexually dimorphic anthropoids (Kappeler, 1993b).

The current study took place during the peak birth and lactation season in this highly seasonally breeding species (Jolly, 1966; van Horn and Resko, 1977; Sauther, 1991; Pereira, 1991). Females typically give birth to a single offspring, and rarely twins

(Sussman, 1991; Koyama et al., 2001; Gould et al., 2003; *pers. obs.*). The high energetic demands placed on female *L. catta* during reproduction are exacerbated by the fact that females gestate and lactate during the dry season, during which resources are scarce (Sauther, 1992, 1993; Rasamimanana and Rafidinarivo, 1993). Possibly because of these stringent conditions, female ring-tailed lemurs exhibit a relatively high degree of agonistic interactions in comparison to females of other primate species (Sauther and Sussman, 1993; Pereira, 1995). Sauther (1992, 1993) reports that while the birth season coincides to a peak in the incidence of intergroup encounters at Beza, it is during lactation that females initiate the greatest frequencies of severe agonism - such as chasing, cuffing, and biting - towards group members of both sexes.

Technological advances in immunoassay protocols to analyze fecal samples provide new opportunities to reliably and non-invasively monitor the endocrine status of wild animals (Whitten et al., 1998; Bercovitch and Ziegler, 2002; Ziegler and Strier, 2004). To my knowledge, this study is the first to examine the proximate mechanisms underlying behavioural and physiological variation in testosterone levels in wild female ring-tailed lemurs. Increasing our understanding of the role of testosterone in female *L. catta* will provide insights into the potential costs and benefits of producing this hormone, and its consequential influences on behaviour. In addition, results from this study will provide a more comprehensive perspective of the endocrine changes associated with aging and reproduction in female *L. catta*, for which little information is available to date.

METHODS

Study site and focal animals

I studied 10 female, ring-tailed lemurs (≥ 2 years) residing in two social groups ("red" and "green" group) with adjacent home ranges in parcel one at the Beza Mahafaly

Special Reserve (Fig. 1), located in southwestern Madagascar (23°30'S lat., 44°40'E long). A detailed description ecological conditions and climactic patterns of this site can be found elsewhere (Sussman, 1991; Sauther, 1991, 1992, 1993; Gould 1994, Gould et al., 1999, 2003). At the beginning of the study period, green group contained 14 individuals (6 adult females, 6 adult males, and 2 juveniles), and red group contained 11 individuals (4 adult females, 4 adult males, 1 sub-adult female, and 2 juveniles). All individuals were thoroughly habituated to human observers and easily distinguished by different colored collars and uniquely shaped and numbered tags that were placed on all focal animals prior to the onset of the study.

Two Malagasy field assistants and I conducted behavioural observations (inter-observer reliability $R > 0.95$) for five to six consecutive days per group for the duration of the 12-week study period from August to November, 2003. Using continuous-time focal animal sampling methods (Altmann, 1974), I collected 886 focal animal sessions of 12-minutes in duration (mean 88.6 ± 6.9 sessions/animal) for a total of 193.2 hours of focal animal observation and 226 hours of *ad libitum* notes. Observations commenced in the early morning (0600-0730 hours) and continued until dusk (1630-1800 hours) with a 2-3 hour break in the afternoon which coincided with the lemurs' extended siesta. The order of focal animal observation was determined randomly at the onset of each observation day, and the number of focal samples for each individual was distributed approximately evenly between the morning and afternoon sessions. All methods were approved by the Animal Care Committee at the University of Victoria.

Determination of rank and frequency of aggression

I used an ethogram with behavioral elements previously described by Jolly (1966), Gould (1994), and Pereira and Kappeler (1997) to record the occurrence of all agonistic behaviors - 'chase', 'lunge', 'bite', 'grab', 'cuff' and 'attack', and submissive responses - 'flee', 'cower', 'jump away' and 'spat call' or 'submissive chatter' – involving the focal animal during each 12-minute sample session. I then measured the relative aggressiveness of each female by computing a rate of agonism (i.e. the number of bouts of agonism per hour initiated by females towards adult group members, wherein a 'bout' is defined as a dyadic agonistic conflict lasting ≤ 10 seconds in duration).

The criterion I used to determine female dominance rank was the direction and outcome of approach-retreat and agonistic interactions among females which had clear, decided outcomes. Such interactions were considered 'decided' (Bernstein, 1981) when one animal (i.e. the "loser") exhibited only submissive signals in response to an approach or other agonistic behaviour by its opponent (i.e. the "winner") thus implying that that both parties recognize their respective dominance positions (Vervaecke et al.2000). The methodology I used to delineate female rank order is one commonly employed by animal behaviorists (Martin and Bateson, 1993). First, I arranged all females in a matrix which permitted the minimum number of reversals while maintaining the maximum degree of linearity (Martin and Bateson, 1993). Then, I plotted "winners" along the rows and "losers" and along the columns, and determined a female's rank on the basis of the number of same-sexed individuals which she dominated.

Determination of age and reproductive status of females

As a part of a three-year study investigating the effects of reproductive season and social interactions on the endocrine profiles on a subset of the ring-tailed lemur population at Beza Mahafaly, LG and RB (see page 12) captured all females (≥ 2 years) from two study troops using a Telinject blowpipe and 0.25 – 0.30cc of Tiletamine

(Telazol). While the animals were immobilized, I fit all animals with colored, nylon collars (denoting red and green group) and numbered tags for individual identification. In addition, I compiled detailed information on patterns of dental attrition, tooth loss, nipple length, and body weight (using a digital scale accurate to 0.01g). Based on this information, I assigned all females ($n = 10$) to one of four age-classes: old ($9 \leq x < 19$ years), prime ($5 \leq x < 9$), young ($3 \leq x < 5$ years), or sub-adult ($2 \leq x < 3$ years; see Sauther *et al.*, (2002) for a more detailed description age assignments).

As reproductive condition is likely to influence endocrine events of females, I conducted daily group censuses of all focal females to determine the precise dates of parturition and hence, their reproductive status. If a female was seen with an infant in September – October, it was assumed that she was pregnant at the onset of the study in August. Only one female ("F34") was not seen with an infant during the birth season, and I coined her "non-pregnant." However, whether this female was anovulatory, ovulated but failed to get pregnant (as I did not witness her to mate in the spring), or experienced an early abortion cannot be confirmed in the current analysis. The infant of female, "F24", died on the second day postpartum and I examined her testosterone levels separately from the remaining lactating females.

Fecal sample collection, preservation, and the effects of time and diet on fT concentrations:

One fecal sample was collected weekly from each adult female from both red ($n = 4$) and green groups ($n = 6$), for a total of 120 fecal samples across the 12-week study period. I ensured the correct identification of fecal samples by restricting collection to only those samples that could be reliably matched to clearly identified individuals.

I controlled for potential diurnal fluctuations in testosterone concentration (Strier et al., 1999) by limiting sample collection to before 9:30am. In addition, I examined the influence of small time differences on steroid concentration by collecting 10 pairs of fecal samples from the same individuals in the early (between 6:00 - 7:30 am) and late (between 7:30 - 9:30 am) morning, and subsequently analyzed for mean differences in fT levels between these two time categories.

In order to minimize the effects of the break-down of steroids by fecal bacteria (Khan et al., 2002) I preserved samples within the first two hours of collection by drying the sample in a Coleman camp stove at 55-70°C for 20-40 minutes (depending on the ambient temperature) until thoroughly dried (Whitten et al., 1998). This technique results in a high recovery (76-86%) and stability (100%) of testosterone over a 3 week period (Whitten et al., 1998), and yields measurable hormone profiles even $\geq$ 3 years after collection (Brockman and Whitten, 1996).

I recorded detailed data on individual feeding patterns and types of plant foods consumed, and used this information to assess the level and type of undigested vegetable matter in their feces (Goldin et al., 1982; Wasser et al., 1993). Although females excreted variable types of undigested plant matter, likely as a result of their omnivorous dietary regime (Sauther, 1992, 1994), I found that all undigested matter was readily identifiable in their feces.

After drying the fecal samples, I used a mortar and pestle to grind the fecal samples for 2-3 minutes until they reached a consistency of a fine powder. I removed the majority of seed coats and large fibrous material from fecal powder prior to analysis (Curtis et al., 2000), then I visually inspected the fecal powder for undigested contents and indexed each sample according one of three categories based on the predominant type of material present: (1) plant fibre, (2) seed coat, or (3) absence of plant matter (herein termed 'absent') for subsequent statistical comparisons. Finally, samples were wrapped twice in aluminium foil, labelled, and prepared for shipment.

Extraction, separation and enzyme immunoassay (EIA) procedures:

All fecal samples were analyzed for testosterone within five months of collection via enzyme immunoassay at the Wisconsin National Primate Research Center. For the preliminary extraction procedure, 2.5 mls of distilled water and 2.5 mls of 100% ethanol were added to 0.2g to 0.3g of dried feces. The mixture was vortexed and particulate matter was separated from the slurry by centrifugation (3000 rpm x 10 min). The supernatant was extracted by adding 4.5 mls of ethyl acetate to 1ml extract which was further vortexed and centrifuged (1000 rpm x 3 min). Next, the ethyl acetate was pipetted off, dried and rehydrated in 1 ml ethanol. Finally, 200 μl of the extract was transferred to a culture tube, evaporated and resuspended in the celite chromatography solvent which is a 96:4 ratio of iso-octane, ethyl acetate (Iso:EA).

Prior to assay, we used the System I celite chromatography technique (Abraham et al., 1972) to separate testosterone (T) from its metabolite dihydrotestosterone (DHT, which has a high cross-reactivity with the T antibody). Briefly, glass disposable serological pipettes (5ml) were packed with 2:1 (weight:volume) celite:glycol, wherein the glycol mixture was 50% ethylene glycol and 50% propylene glycol. Columns were rinsed with two 3.5 ml aliquots of 100% iso-octane. The extracted steroid samples were vortexed for 1 min, followed by sonication to ensure homogeneity with the Iso:EA. 1ml of the sample and 1ml 96:4 Iso:EA were loaded into the column, and forced into the column under nitrogen. Meanwhile, 0.5 mls of 96:4 Iso:EA was added to the sample tube and placed in the sonicator. This rinse was then pushed into the column. Next, 3.5 mls of 100% iso-octane was pushed into the column. The DHT was eluted with 4.0 mls of 90:10 (Iso:EA), and the T was eluted into a culture tube using 4.0 mls of 80:20 (Iso:EA). Finally, the T fraction was dried, resuspended in 200 μl ethanol, and stored in the refrigerator until assay. The recovery of T was 85% ± 1.35 SEM.

For the EIA procedure, we followed Munro and Stabenfeldt (1984). The T antibody (R4859) was obtained from C. Munro, Clinical Endocrinology laboratory at UC Davis. The cross-reactivity of this antibody (50% binding) with other substances are: 92.4% with DHT, 11.2% with 4-androsten 3β,17β-diol, 5.4% dehydroandrosterone, 3.4% androstanediol, 2.1% androstenedione, 0.5% dehydorepiandrosterone, and less than 0.07% with hydrocortisone, cortisone, corticosterone, desoxycorticosterone, oestrone, oestradiol, progesterone 17-alpha-hydroxy-progesterone, cholesterol and pregnenalone (Ginther et al., 2001).

Before coating the plates (Nunc 439454) with the T antibody, the plates were stored overnight at room temperature in a humidity chamber. 100 μl of the T antibody, which was mixed in a 1:27,000 carbonate-bicarbonate was then added to the plate. The plates were then returned to the humidity chamber for 5-6 hours and transferred to a fridge overnight. The next day, the plates were washed twice and each well was filled with 150 μl EIA buffer and stored in the freezer. On the day of the assay, the plate was brought to room temperature, along with the standards (Sigma T-1500), samples and buffer. 75 μl of the T extract was evaporated under air, resuspended in 300 μl of testosterone: horseradish-peroxidase (T:HRP), and then vortexed and transferred to the

EIA tubes. Next, the buffer was emptied from the plate and 100 µl of the T:HRP is added per well. After a 2 hour incubation at room temperature the unbound testosterone was removed by washing the plates 5 times and adding 100 µl of an 2,2'-azino-bis-(3-benzthiazoline-6-sulfonic acid) solution (ABTS). After 30 minutes to 1 hour (i.e. once the absorbance approached one), 100 µl of a .15 M hydrofluoric acid solution was added to terminate the reaction. The plate was then read on a Spectramax 340. The fecal sample pools had an intra-assay coefficient of variation of 4.6% (n = 5) and an inter-assay coefficient of variation of 11.6% (n = 5), and the minimum sensitivity of the assay at 90% bound was 0.68pg/well. T values are expressed as nanograms per gram (ng/g) of dry feces.

Previous research on free-ranging *L. catta* by Cavigelli and Pereira (2000), revealed that testosterone levels obtained via extraction and analysis of fecal material accurately reflects circulating levels in this species, thus providing validation for the endocrinological analysis of fecal samples in this species.

Statistical analysis

Unless otherwise noted, data for each social group - red and green - were considered separately in all of the following statistical procedures. Visual inspection of the data revealed that the distributions of fT values for both groups were positively skewed, with many low values and few high values. In addition, for red group I detected two significant outliers for testosterone at the right end of the distribution, and these anomalous values could not be readily explained by dietary differences, behavioural patterns, preservation techniques, or immunoassay procedures (D. Wittwer, *pers. comm.*). In order reduce the influence of these outliers and to satisfy the assumption of normal distributions for the parametric analyses (Quinn and Keough, 2002), testosterone values for both groups were $\log_{10}$-transformed which resulted in normal distributions (green group: Shapiro-Wilk $W_{72} = .981$; $P = .352$; red group: Shapiro-Wilk $W_{48} = .961$; $P = .109$). Next, I calculated a mean $\log_{10}$ testosterone value based on four samples per reproductively active female during each four-week period: late gestation, early lactation, mid-lactation. Finally, I examined the effect of reproductive season on androgen excretion by one-way repeated measures analysis of variance (ANOVA) with planned comparisons using the $\log_{10}$ fT data as the dependent variable and reproductive season as the within-subjects variable.

To determine whether mean differences in $\log_{10}$fT values were significantly different among pregnant ($n = 5$) versus non-pregnant ($n = 1$) females in green group, I computed a one-sample t-test. In addition, I calculated Kendall's correlation coefficients to analyze the relationship between monthly rates of female-initiated aggression to their corresponding mean fT values. To examine the effects of dietary differences (fibre, seed coat, and absence) on the $\log_{10}$ fT values across the entire study period, I used a three factor univariate ANOVA with a Tukey's post-hoc multiple comparisons test. As there were no significant two- or three-way interaction effects among the independent variables (i.e. $P > 0.05$ for diet x age, diet x rank, rank x age, and diet x rank x age), I dropped the interaction terms from the model. I examined the influence of sample collection time on fT concentrations by applying a paired samples t-test to detect significant differences between samples collected from the same individuals in the early versus late morning. Small sample sizes for both age ($n = 2$ females for each age class) and rank ($n = 2$

females for each rank) precluded meaningful statistical analysis, therefore the relationships between these variables are presented descriptively.

All data were analyzed using the SPSS (version 11.5) statistical software package. The significance level was set at $\alpha = 0.05$ for all analyses and all data are presented as means ± SE unless otherwise noted.

RESULTS:

Dominance relations among females

All focal females in the six groups could be arranged in a linear rank-order (Table 1 and Fig. 2) with the exception of green group in which a non-transitive relationship existed between F459 and F34. In addition, rank reversals were rare as they occurred in $\leq 5\%$ of all female-female agonistic and approach-retreat interactions (see Chapter 2). Finally, female rank-order and the female component of troop composition remained stable throughout the duration of the 12-week study.

Temporal patterns of fT excretion

The paired samples t-tests revealed an absence of statistically significant difference mean $\log_{10}$ fT concentrations for samples collected from the same females in the early vs. mid-morning for red group ($t_{.05(2)6} = -1.115$; $P = .307$), and green group ($t_{.05(2)9} = -.015$; $P = .988$), which suggests that fecal sample collection time does not significantly influence testosterone levels if sampling is restricted to the morning hours only (Fig 3).

The effects of diet on testosterone levels

The percentages of undigested plant matter for each category are as follows: in green group 32% (n = 23) of samples contained primarily undigested fiber, 25% (n = 18)

Table 1. Summary of the mean rates of female-initiated aggression and mean testosterone concentrations over the three-month study period with respect to different ranks, ages, and the presence or absence of infants in the birth season

group	**female**	**age**	**infant**	**rank**	**mean rate of aggression** [b]	**mean testosterone concentration** [c] **(± SE)**	**number of fecal samples/female**
green	#9	prime	yes	1	1.58	18.57 ± 1.70	10
green	#34	young	no	2	1.03	15.57 ± 2.55	10
green	#23	prime	yes	3	1.17	39.11 ± 6.00	9
green	#459	old	yes	4	0.42	35.15 ± 5.73	10
green	#24	young	died [a]	5	0.44	24.22 ± 4.65	10
green	#46	prime	yes	6	0.44	23.57 ± 2.69	10
red	#114	old	yes	1	0.89	31.28 ± 8.21	10
red	#55	prime	yes	2	1.02	31.50 ± 6.91	10
red	#44	prime	yes	3	0.98	33.97 ± 9.64	10
red	#59	old	yes	4	0.20	38.09 ± 16.11	10

[a] infant diet two-days post-partum

[b] mean rate of aggression refers to the number of bouts of aggression per hour that females initiated towards adult group members (i.e. excluding infants and juvenilles).

[c] testosterone values are expressed as ng/g dry fecal weight

Figure 2. Agonistic dominance matrices for female ring-tailed lemurs in green and red group. Female rank-order was determined by the direction and outcome of decided agonistic interactions (i.e. chase, lunge, bite, grab, cuff and attack) between female-female dyads. Each number represents instances of agonistic interactions recorded during focal animal observations.

GREEN GROUP

dominant → **subordinate**

recipient actor	**F9**	**F34**	**F23**	**F459**	**F24**	**F46**	**TOTAL**
F9		13	4	1	4	2	**24**
F34	0		14	0	3	2	**19**
F23	0	0		10	14	14	**38**
F459	0	3	0		3	3	**9**
F24	0	0	0	0		4	**4**
F46	0	0	1	0	0		**1**
TOTAL	**0**	**16**	**19**	**11**	**24**	**25**	**95**

RED GROUP

dominant → **subordinate**

recipient actor	**F114**	**F55**	**F44**	**F59**	**TOTAL**
F114		2	13	2	**17**
F55	0		6	11	**17**
F44	0	0		13	**13**
F59	0	0	0		**0**
TOTAL	**0**	**2**	**19**	**26**	**47**

Figure 3. Differences in fecal testosterone levels (mean ± 2 S.E.) between fecal samples collected between 6:00 to 7:30am and those collected between 7:30 to 9:30am from 10 females of two troops of ring-tailed lemurs at the Beza Mahafaly Special Reserve, Madagascar.

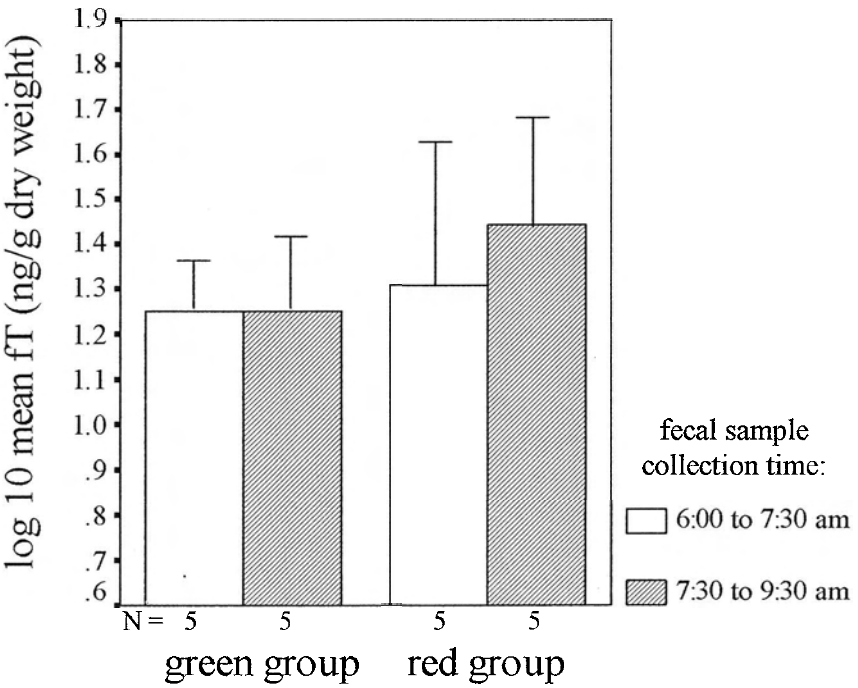
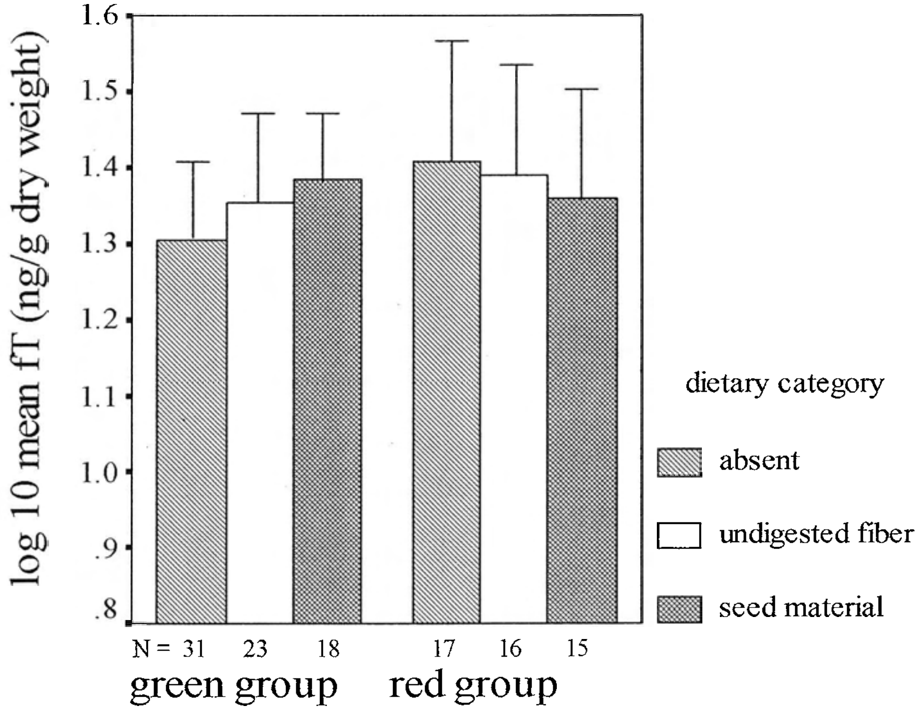


Figure 4. Differences in fecal testosterone levels (mean ± 2 S.E.) of samples from three dietary categories: undigested plant material, seed material, or the absence of plant material (termed 'absent').



contained seed material, and 43% (n = 31) were free of undigested plant matter. In red group, the number of samples containing predominantly undigested fiber and seed material were 33%; (n = 16) and 31% (n = 15) respectively, while the percentage of samples that contained no undigested plant matter was 36% (n = 17). Dietary differences did not significantly affect mean fT levels in green group ($F_{2,69}$ = .603, P = .550), and in red group ($F_{2,45}$= .083, P = .921; Fig. 4).

The effect of age on testosterone levels

Table 1 presents the overall mean fT concentration for the entire study period in relation to rank, age, reproductive state, and rates of aggression for all females in both study troops. In green group, individuals of the old age-class had mean fT levels that were 1.3 times greater than prime-aged individuals, and 1.8 times greater than those of the young adult age-classes (Fig. 5). In red group, there was very little difference in the mean fT levels of prime-aged versus old adults (Fig. 5).

The effect of rank on testosterone levels

Mean fT concentrations were lowest in the top-ranking females of both red and green groups (Fig. 6). However, these differences were most pronounced in green group, as the two high-ranking females had a mean fT concentration that more than twice as low as the two mid-ranking females (17.1 ± 3.06 vs. 37.3 ± 8.16 ng/g).

Seasonal variation in fT levels

I found a significant effect of reproductive season (i.e. late gestation, early lactation, mid-lactation) on the mean fT levels for pregnant females in both green group (repeated measures ANOVA: $F_{2,60}$ = 10.878, P = 0.000) and red group (repeated measures ANOVA $F_{2,60}$ = 8.432, P = 0.001). Post-hoc tests revealed that these significant

Figure 5. Mean fecal testosterone levels (± 2 S.E.) in females of differing age-classes in two troops of ring-tailed lemurs at the Beza Mahafaly Special Reserve, Madagascar.

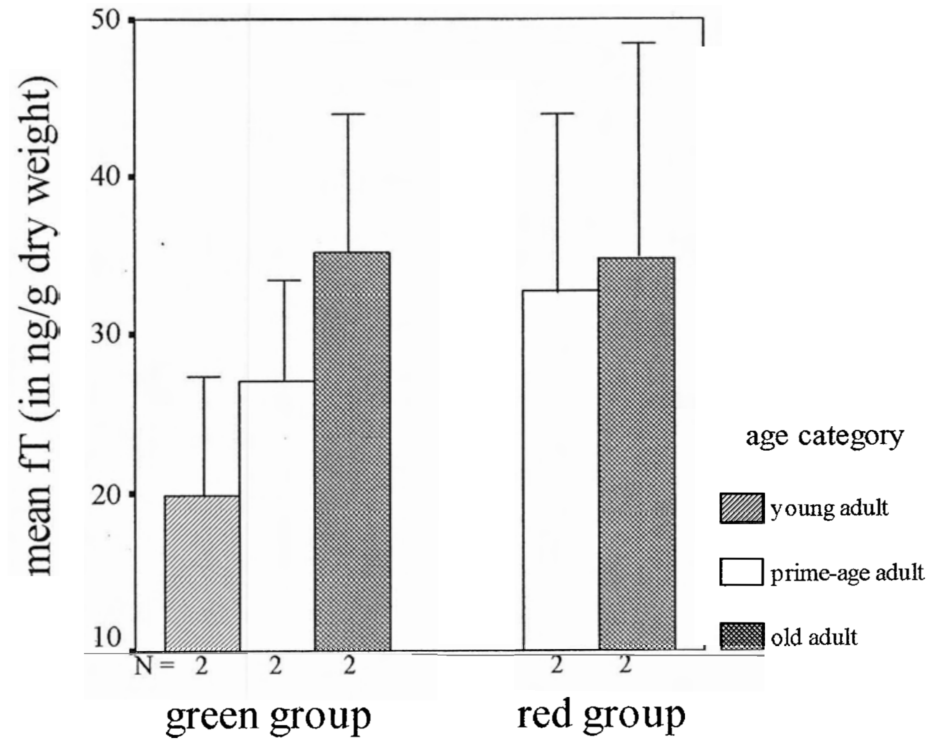
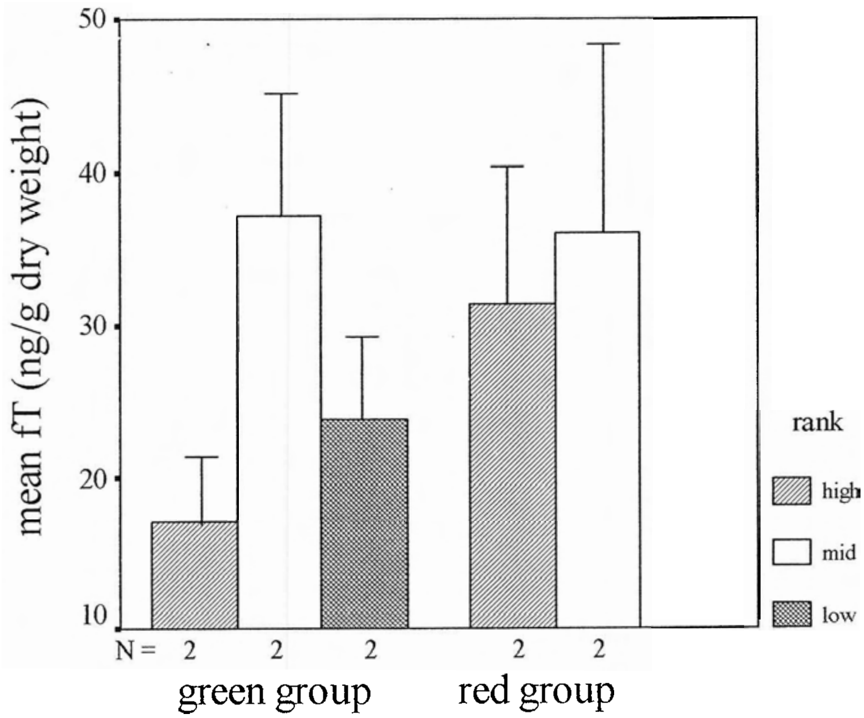


Figure 6. Mean fecal testosterone levels (± 2 S.E.) in females of differing social ranks in two troops of ring-tailed lemurs at the Beza Mahafaly Special Reserve, Madagascar.



differences occurred between late gestation and both early and mid-lactation in green and red groups (Tukey's HSD $P < .05$). The pattern of mean fT excretion for all reproductively active females followed a similar course from late gestation to early lactation in both groups (Fig. 7). Highest mean fT concentrations were observed at four weeks pre-parturition (green group: 36.38 ± 8.04 ng/g; red group 66.86 ± 25.03 ng/g), and these values markedly declined in the week encompassing parturition, reaching a low of 12.53 ± 1.99 ng/g and 14.58 ± 2.07 ng/g at four weeks postpartum for green and red groups respectively (Fig. 7).

By comparing mean fT levels of F34 (the green group female who did not bear an infant) to that of reproductively active females, I found that unique hormone profiles emerged between them (Fig. 8). The most striking differences occurred during late gestation in which mean fT of F34 was significantly lower than the mean for pregnant females (independent samples t-test: $t_{.05(2)38} = 4.035$; $P = 0.00$). In addition F24, whose infant died two days post-parturition, exhibited similarly low fT excretion patterns throughout lactation (Fig. 8).

Rates of aggression in relation to fecal testosterone levels:

The only statistically significant correlations between bi-monthly mean rates of female-initiated aggression and mean fT levels occurred in red group during the birth season, for which a significant, negative correlation was found (Fig. 9). For the remaining seasons, early lactation (Fig. 10) and mid-lactation (Fig. 11), Spearman's rank order correlations revealed no statistically significant results.

Figure 7. Profiles of fecal testosterone levels from late gestation to early and mid-lactation (parturition is marked by an arrow). Each point represents the bi-monthly mean testosterone value obtained from samples of all reproductively active females from green group (n = 5) and red group (n = 4).

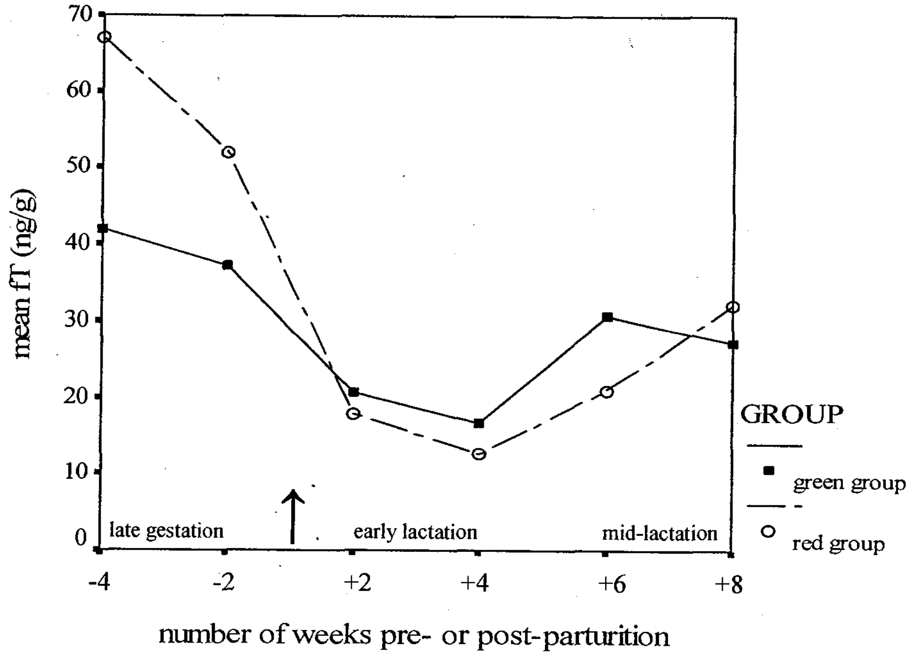


Figure 8. Profiles of fecal testosterone levels from late gestation to early and mid-lactation (parturition is marked by an arrow). Each point represents the bi-monthly mean testosterone value obtained from samples of all reproductively active females (n = 8) from both red and green group in comparison to two non-reproductively active females

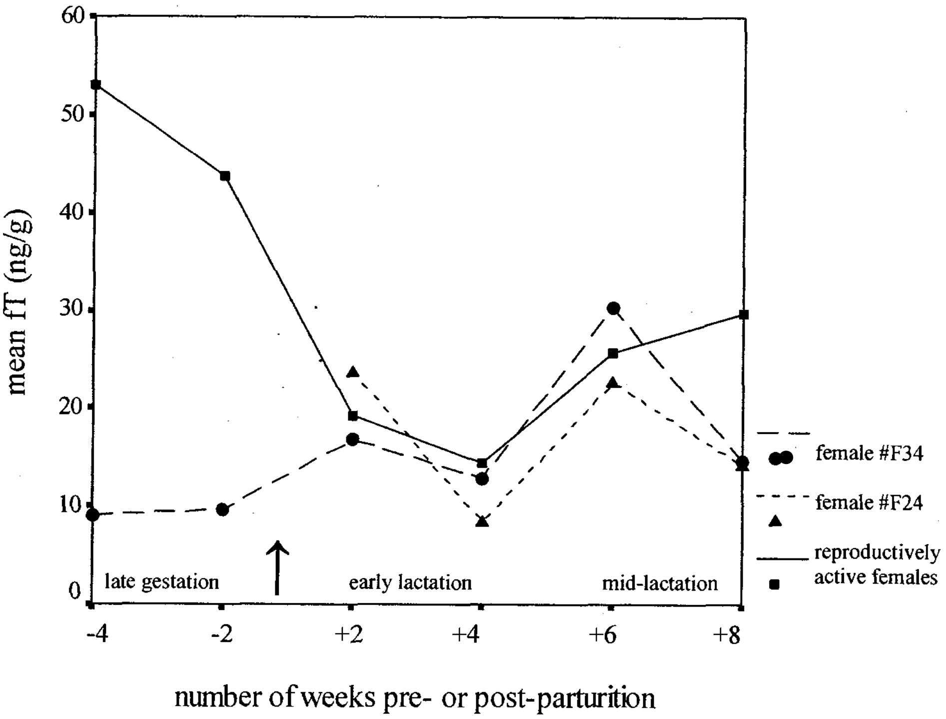


Figure 9. Scatterplot showing the relationship between individual mean rates of female-initiated aggression and individual mean fecal testosterone levels during late gestation for all adult female ring-tailed lemurs in green group (n = 5) and red group (n = 4).

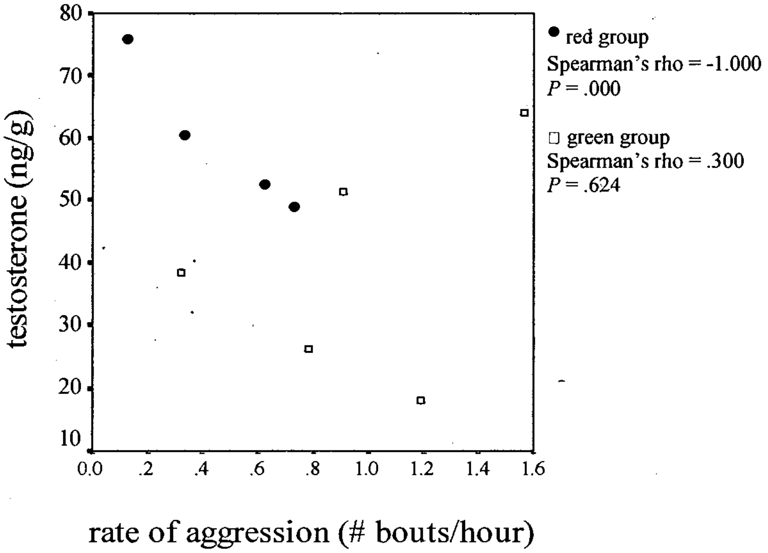


Figure 10. Scatterplot showing the relationship between individual mean rates of female-initiated aggression and individual mean fecal testosterone levels during early lactation for all adult female ring-tailed lemurs in green group (n = 5) and red group (n

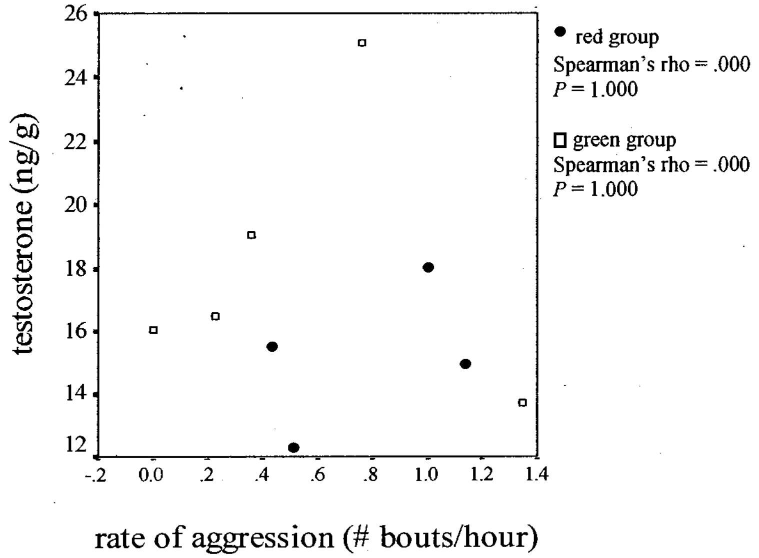
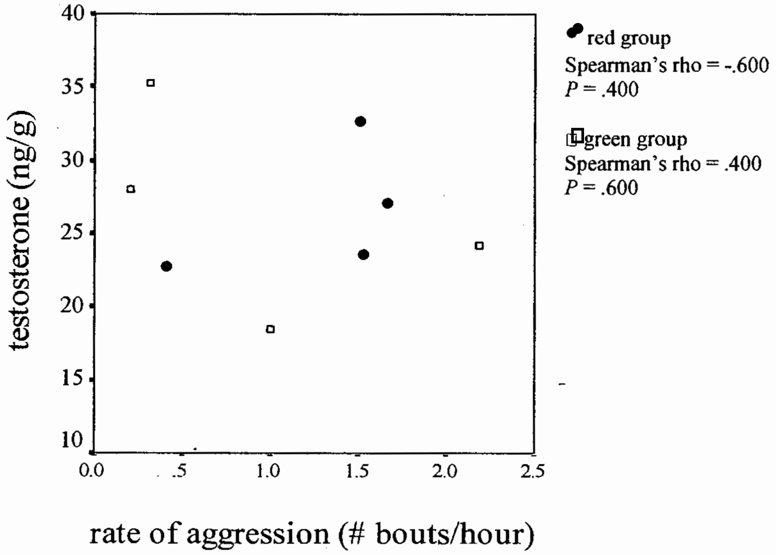


Figure 11. Scatterplot showing the relationship between individual mean rates of female-initiated aggression and individual mean fecal testosterone levels during mid lactation for all adult female ring-tailed lemurs in green group (n = 5) and red group (n = 4).



DISCUSSION

In contrast to my expectations, clear relationships between testosterone, female rank, and female-initiated aggression did not occur. The lack of a clear pattern among these three parameters was not confounded by either dietary differences or diurnal patterns of fT excretion. In reconciling these results, I will discuss the potential role of physiological, social, and environmental factors in influencing these relationships.

The effect of fecal sample collection time on fT values

Biological rhythms, such as circadian patterns, are key regulators of both the physiology and behavior of living organisms (Krieger, 1978; Pittendrigh, 1981; Morin and Dark, 1992). In light of the importance of time differences on steroid hormone concentrations, surprisingly few studies of hormone-behaviour interactions have indicated whether or not they controlled for these circadian effects (Sapolsky, 1993). In the current research, I controlled for potential diurnal fluctuations in testosterone in female ring-tailed lemurs by limiting my sample collection to consistent time periods (i.e. in the morning hours; Sousa and Ziegler, 1998). Furthermore, by partitioning sample collection times into two categories (early vs. mid-morning) I found that fT levels in early morning samples did not differ significantly from those collected from the same individuals in the mid-morning (Fig 4). This lack of a statistically significant difference may be related to the fact that steroid hormones measured in feces are representative of the accumulation of secreted and excreted hormones over several hours (Whitten et al., 1998), and are therefore less likely to be affected by small differences in the timing of collection. This is in stark contrast to the measurement of plasma hormone titers in blood in which values fluctuate widely in a matter of minutes due to the pulsating nature of steroid secretion (Suttie et al., 1992).

As it is often difficult in a field setting to collect fecal samples at the exact same time each day, and the data presented here are useful for future studies as it provides a guideline for the timing the collection of feces for monitoring fecal testosterone profiles in this species. However, these findings do not negate the importance of controlling for potential diurnal variations (i.e. morning vs. afternoon or evening samples) of testosterone in future studies, as such differences were previously reported to be significant in male ring-tailed lemurs (van Horn et al., 1976) and male lesser mouse lemurs (Perret, 1985), as well a number of anthropoids (Rose et al., 1978a; Enomoto, 1980; Castracane et al., 1981; Wiebe et al., 1984; Kholkute, 1984; Coe and Levine, 1995; Stoinski et al., 2002).

Aside from diurnal fluctuations in fT levels, it is also important to consider the time-lag between the secretion of steroids hormones into the blood and subsequent excretion in the feces (Wasser et al., 1994; Whitten et al., 1998). While the peak excretion of labeled estradiol in *L. catta* is occurs between 24-48 hours following injection (Perez et al., 1988), to my knowledge the time course of excretion of testosterone has yet to be determined in this species. However, given that the passage time of radio-labeled testosterone ranges from 4 hours in common marmosets to 26 hours in long-tailed macaques (Möhle et al., 2002), time-lags for ring-tailed lemurs are likely to fall between these two values. My study design accounted for these time-lags by (1) commencing fecal sample collection *after* the first day of each week for which behavioral observations began, and (2) computing monthly means for fT to decrease the impact of particularly stressful or aggressive events on fT profiles. Further analysis needs to be performed to enhance our understanding of the time lags between the occurrence of the physiological events and the subsequent detection of these hormones in the feces (Wasser, 1994).

Dietary effects on testosterone measures

The need to account for the potential effects of dietary variations is underscored in wild populations with omnivorous diets (Shideler et al., 1993) such as ring-tailed lemurs who incorporate a wide variety of fruits, leaves, flowers, and insects in their diet (Jolly, 1966; Sussman, 1977; Sauther, 1992, 1994). This fluctuating dietary regime was reflected in their fecal samples, as the amount and type of undigested plant matter excreted was variable but easily determined through visual inspection. Higher proportions of dietary fiber may result in increased fecal bulk - due to increases in both water and dry material (Wasser et al., 1993) - and a subsequent dilution of fecal hormone concentrations (Cavigelli, 1999). I controlled for the effects of increased water by expressing samples as g/dry weight (Wasser et al., 1993), and accounted for the differences in the amount and type of dry, fibrous material by comparing the mean variation in fT concentrations across three categories: (1) fiber, (2) seed coat, (3) and absence of plant material. In contrast to my expectations the effect of diet on the mean variation in fT levels was not significant. In red group, mean fT concentrations in samples containing undigested fiber and seed coats were slightly lower than in samples where fibrous material was absent, and in green group the reverse was true. Taken together, these results support those of Shideler et al., (1993) and Curtis et al., (2000), and suggest that dietary differences may not confound fecal steroid concentrations.

However, other means of elucidating such effects could be explored (i.e. indexing fecal steroid excretion, Wasser et al., 1993; or monitoring fecal weight, Cavigelli, 1999).

Testosterone in relation to female age

In both males and females, the neuroendocrine system plays a key role in regulating the aging process, as this system is capable of influencing the function of "every organ and tissue in the body" (Meites and Lu, 1994: 14). While age-related endocrine profiles in females have perhaps been most intensely studied in humans (Hiort, 2002; Copeland et al., 2004), such patterns have also been examined in females of a number of nonhuman primate species (Copeland et al., 1985; Tardif and Ziegler, 1992; Youssefzadeh and Raleigh, 1995; Bellino and Wise, 2003; Goncharova and Lapin, 2004).

Age-related patterns of testosterone secretion in both human and nonhuman primates appear to be dependent upon life history stage considered (i.e. pre-reproductive, adult, and late life-history stages). Puberty is associated with an increase in the production of androgens in human females (Hiort, 2002; Parker, 1991), and similarly in nonhuman primates, testosterone levels are significantly lower in pre-pubescent/adolescent females in comparison to older cohorts (chimpanzees: Copeland et al., 1985; vervet monkeys: Youssefzadeh and Raleigh, 1995; bonobos: Sannen et al., 2004). My findings, although limited by a small sample size of pre-reproductive females (n = 1), corroborate with the data presented above as the mean fT titers across the first four weeks of the study were significantly lower in this pre-reproductive female (F34) compared to her reproductively active adult cohorts (Fig. 8). While testosterone is suggested to play a critical role in female reproductive development (Staub and De Beer, 1997), significant rises in androgens at this time may not be essential for the expression of aggressive behaviour. For example, F34, who was the second most aggressive female in her group, exhibited a very low mean fT concentration, and this pattern has also been seen in female golden hamsters (Takahashi and Lisk, 1983) and male rhesus monkeys (Rose et al., 1978b).

Young individuals exhibited the lowest mean fT levels, with higher levels in prime-aged females, and the highest levels in old females. These findings are similar to the age-related rise in testosterone that occurs in adult female vervet monkeys (Youssefzadeh and Raleigh, 1995), but differ from the age-related declines in adrenal and gonadal testosterone that have been linked to the onset of menopause in human females (Guay, 2004, Dabbs and Hargrove, 1997). These differences may be reconciled by the fact that ring-tailed lemurs, unlike humans, do not invariably undergo reproductive senescence (Gould et al., 2003), and therefore may not exhibit the same hormone profiles associated with menopause. Examining the changes in steroid hormones during the process of aging is promising area for future research in this species, and would improve our understanding of the diversity of neuroendocrine mechanisms that regulate aging.

Patterns of testosterone excretion and reproductive state

Much attention has focused on the androgenic hormone profiles of females during the periovulatory phase of the reproductive cycle, and many studies indicate that elevated female androgens coincide with the mid-cycle (i.e. ovulatory) phase in nonhuman primates (chimpanzees: Nadler et al., 1985; baboons: Stavisky et al., 1995) and humans (Epstein et al., 1975; Campbell and Ellison, 1992). Such elevations in T are responsible for cyclic fluctuations in sexual interest in human females (Sherwin, 1988), and the regulation of copulatory behaviour in female nonhuman primates (Everitt et al., 1972; Dixson et al., 1973)

In contrast, information on the patterns of testosterone excretion during the periparturition in nonhuman primate females is available from only a few studies (i.e. yellow baboons: Castracane and Goldzieher, 1983; olive baboons: Hodges et al., 1984; Verreauxi's sifaka: Brockman et al., 1998a; and redfronted lemurs: Ostner and Heistermann., 2003). To my knowledge, the current study is the first to monitor testosterone profiles during gestation and lactation in wild, female *L. catta.*

Results from the present study indicate that reproductive status strongly influences levels of testosterone in female ring-tailed lemurs. The young, non-reproductive female (F34) showed levels of testosterone which were significantly lower that that of gestating females, and paralleled that of female F24 whose infant died two days post-parturition (Fig 8). Furthermore, mean fT titers were significantly higher during late gestation in comparison to early lactation for females of both groups (Fig. 7). Similar findings have been reported in redfronted lemurs, in which a 4 - 8 fold elevation in fT levels occurred during late gestation (Ostner and Heistermann, 2003), and in human females, in which testosterone increases steadily during pregnancy, and declines sharply post-parturition (Schubring et al., 1998). Taken together, these patterns may be indicative of the potential importance of testosterone during fetal development in late pregnancy, however, evidence for the functional significance of testosterone during pregnancy remains largely enigmatic. Given that the aromatization of testostosterone is the final step in the biosynthesis of estrogens from cholesterol (Kragie, 2002), increased testosterone secretion during late pregnancy may function as an important estrogen precursor (F. Bercovitch, *pers. comm.*). In primates, the tissues of the skin, connective, adipose and placental tissues are all capable of T aromatization (Simpson et al., 1994).

Irrespective of its function, the ability to non-invasively monitor testosterone profiles during gestation may prove to be useful to distinguish amenorrhea from early pregnancy (Brockman, 1998b) as other steroid hormones (i.e. estrogen and progesterone) have previously been employed to detect pregnancy in a variety of species of anthropoid primates (pig-tailed macaque: Risler et al., 1987; cynomolgus monkey: Wasser et al., 1991; yellow baboon: Shideler et al., 1993; squirrel monkey: Moorman et al., 2002), and prosimians within the lemuridae family (ruffed lemur: Shideler et al., 1983; mongoose lemur: Curtis et al., 2000). If proven successful, testosterone could be another tool for reproductive endocrinologists and captive breeders to non-invasively monitor reproductive status in wild primates.

Testosterone and rates of aggression

Testosterone levels were not clearly linked to frequencies of female-initiated agonism in the current study, and this finding corroborates the data collected during the mating season in captive female *L. catta* (von Engelhardt et al., 2000). The consistency of these two studies may reinforce the utility of fecal sample analysis to monitor hormone-behavior interactions in females of this species. These results were surprising given that much of the literature reveals positive relationships between testosterone and aggression in nonhuman primate males (Rose et al., 1971; Sapolsky, 1983; Stelkis et al., 1985; Cavigelli and Pereira, 2000) and females (Trimble and Herbert, 1968; Joslyn, 1973; Abbott and Hearn, 1978). In reconciling these results, it may be essential to examining the role that social factors play in mediating the relationship between rank and fT (Sapolsky, 1993).

In order to explain apparent inconsistencies in the relationship between androgens and aggression in a host of vertebrates, Wingfield et al., (1990) proposed the "challenge hypothesis." This theory, which is applicable to fish (Pankurst and Barnett, 1993), reptiles (Klukowski and Nelson, 1998), birds (Johnsen, 1998), and mammals (Cavigelli and Pereira, 2000), posits that elevated testosterone levels are expected to correspond to high rank or increasing aggression during periods of social instability (i.e. during the formation of dominance relationships, establishment of territorial boundaries, or changes in group membership). Under stable conditions, however, these parameters are often not correlated (Gordon et al., 1976; Sapolsky, 1982; Steklis et al., 1985; Nieuwenhuijsen et al., 1987; Cavigelli and Pereira, 2000). Due to the high costs of sustained, elevated testosterone levels, which include a rise in energy consumption, suppression of immune function, and increased risk of injury (Folstad and Karter, 1992; Wingfield et al., 2001), this mechanism ensures that substantial rise in testosterone occurs only in the appropriate social context (Wingfield et al., 1990).

In examining the potential role of the challenge hypothesis in ring-tailed lemurs, it is important to consider a few salient aspects of their social structure. While both male and female ring-tailed lemurs form clear, intra-troop dominance hierarchies (Jolly, 1966; Sussman, 1977; Sauther, 1992), dominance relationships of females can remain relatively stable in wild troops (Budnitz and Dainis, 1975; Sauther, 1992) although social instability in females may arise in response to changes in the female component of group membership through death or recruitment (Koyama, 1996; Nakamichi et al., 1997; Ichino and Koyama, 2004). In contrast to females, rank-relationships among male *L. catta* are often unstable, especially during the brief mating season during which extreme male-male competition and male migration takes place (Budnitz and Dainis, 1975; Taylor, 1986; Sussman, 1992; Sauther, 1992; Sauther and Sussman, 1993; Pereira, 1993; Gould, 1994; 1997). Indeed, a recent study of semifree-ranging ring-tailed lemurs, Cavigelli and Pereira, 2000) have provided support for the challenge hypothesis in males, as testosterone and aggression were significantly and positively correlated only during the period of social instability that took place during the mating season, and not during the socially stable period encompassing pre-mating.

The challenge hypothesis, though traditionally applied to males, also applies to females (Langmore et al., 2002; but see Elekonich and Wingfield, 2000), and a closer look at the applicability of this hypothesis in female *L. catta* is warranted. Testosterone may be related to aggression in female ring-tailed lemurs, but the expression of this relationship may be contingent upon the degree of social stability. In the current study, testosterone was not correlated to rates of aggression for either red or green group, but this is perhaps not surprising given the female rank-order was stable for the duration of the study. Future studies should monitor testosterone levels during periods of female social instability to determine how these two parameters are correlated. This type of research would take us one step further in elucidating how social factors may modulate hormone-behaviour interactions in females of this species.

Another theory which might account for the lack of a clear relationship between testosterone and female-initiated aggression is the "aromatization hypothesis" (MacLusky and Naftolin, 1981). It is well known that T is neurally converted to an estrogen form -

estradiol (E_2) - in the CNS by the enzyme aromatase (Rucklidge, 1995). E_2 then binds to estrogen receptors which activate a totally different array of genes from the androgen receptor. According to this theory, testosterone's ability to "masculinize" behavior occurs only after T is aromatized to E_2 (Feder, 1981; Naftolin and MacLusky, 1984). As many regions in the brain contain varying amounts of aromatase (MacLusky and Naftolin, 1981), the activational effect of T may be attributable to the effects of E_2, or to the proportion of enzymes available for the conversion of testosterone to estradiol, as opposed to the concentration of T itself. Support for the aromatization hypothesis is derived from research which has demonstrated that estrogens produced by the aromatization of T regulate the expression of aggressive behavior in a number of vertebrate taxa (birds: Schlinger and Callard, 1990; Wingfield et al., 2001; reptiles: Woodley and Moore, 1999). In addition, there is strong evidence to suggest that E_2 influences female rank-related aggressive behaviour in chimpanzees (Birch and Clark, 1946) and rhesus monkeys (Michael and Zumpe, 1970).

Given the paucity of research which has examined the applicability of the aromatization hypothesis in female nonhuman primates (but see Michael et al., 1986; Wallen and Baum, 2002; Kragie, 2002), systematic studies which scrutinize the effectiveness of aromatizable versus non-aromatizable androgens, and/or aromatase inhibitors in restoring aggressive behaviour in gonadectomized individuals are essential to our understanding of the complexity of hormonal interactions and their subsequent behavioral influences in nonhuman primates.

An alternative model to explain the lack of significant correlations between aggression and testosterone in adult female *L. catta* is that the expression of aggressive behavior in females may be sensitive to the organizational effects of androgens via prenatal exposure. The presence of androgens during crucial periods of prenatal brain development exert a permanent organizational effect upon the central nervous system which acts to increase the likelihood that certain behaviours will by activated by exposure to particular hormones later in life (Monaghan and Glickman, 1992). In a few mammalian taxa (i.e. guinea pigs: Grady et al., 1965; rhesus monkeys: Eaton et al., 1973; Pomerantz and Goy, 1988) evidence suggests that exposure to prenatal androgens has important behavioural consequences, and are linked to higher frequencies of threats and agonism in response to T secretion in adulthood. Conclusions about the effects of prenatal androgen exposure on subsequent agonistic behavior in adult female *L. catta* can only be reached through long-term research which examines the levels of prenatal androgen exposure in relation to the propensity to express aggressive behaviors in adulthood.

Testosterone concentrations in relation to female social status:

The relationship between rank and fT levels in female ring-tailed lemurs was unexpected, as it was the top-ranking female in red group and two top ranking females in green group who exhibited the lowest mean fT levels (Table 1 & Fig. 6). To better understand the interrelationships between testosterone, rank, and aggression in the current study, a consideration of the concurrent effects of cortisol (the principle steroid hormone secreted by the adrenal cortex in response to stress) warrants further attention.

In a number of vertebrate species, including squirrel monkeys, olive baboons, hamadryas baboons; rhesus macaques, and human males (Rose et al., 1972; Coe et al., 1978; Goncharova et al., 1979; Cumming et al., 1983; Bernstein et al., 1983; Sapolsky, 1983, 1985; Hayashi and Mobreg, 1987) stress-induced secretion of cortisol suppresses gonadal testosterone production (Deviche, 1983; Tokarz, 1987). The existence of multiple regulators within the hypothalamic-pituitary-gonadal (HPG) axis are reported to be responsible for reciprocal relationships between these two hormones (Sapolsky, 1985; Wingfield and Silverin, 1986; Moore and Deviche, 1988).

The highly seasonal environment at Beza imposes unique challenges to female ring-tailed lemurs, as the energetically demanding stages of gestation and early lactation occur during the dry season, in which food resources are extremely scarce (Sauther, 1992, 1993, 1998). However, it appears that the stress imposed on females does not fall equally onto high-ranking and low-ranking individuals. In a study of the relationship between cortisol and dominance rank in female ring-tailed lemurs during birth and lactation - which included two troops residing at BMSR - higher ranking females exhibited significantly higher mean fecal cortisol concentrations in comparison to females of lower-ranks (Cavigelli et al., 2003). The authors suggest that "two different sets of challenges [exist] for these two classes of females," and they provide three possible explanations for this imbalance: (1) sustained, elevated levels of cortisol in higher ranking females may be due to an increase in the activity of their adrenal glands or HPA axis; (2) increased glucocorticoids may be required if higher ranking females produce more energy-rich milk for their offspring; or (3) higher rates of aggression displayed by higher-ranking females may stimulate corticoid production. My results support the latter explanation, as higher ranking females in the current study initiated a rate of severe aggression (i.e. cuff, lunge, bite, chase, attack), which was 1.87 times higher than that of lower ranks. Also, while Cavigelli et al., (2003) reported that either the first-or second-ranking female in each group exhibited significantly higher mean cortisol levels in comparison to lower-ranked females, data from the current study indicated that the inverse was true for testosterone (i.e. the first or second-ranking female that exhibited the *lowest* mean fT values). In considering these results together, I hypothesize that the heightened degree of stress experienced by higher-ranking females at Beza, may lead to the suppression of testosterone production in these individuals. Such reciprocal relationships have been demonstrated in a number of studies (cited above). As I was unable to concurrently monitor cortisol titers, evidence for the theory that testosterone is suppressed by cortisol in female ring-tailed lemurs is inconclusive, but remains a promising area for future research. These above-mentioned examples emphasize the importance of considering not only the effects of a single hormone, but how a complex array of hormones and enzymes may interact to produce dynamic responses in the behavior and physiology of organisms.

Concluding arguments:

This study contributes to the emerging field of behavioural endocrinology by elucidating the interrelationships between social, behavioral, and physiological factors in relation to testosterone concentrations in females of a wild, prosimian primate, for which only a few studies exist to date (i.e. Brockman et al., 1998a; von Engelhardt et al., 2000). Evidence suggests that endocrine responses (i.e. testosterone levels) are not an underlying mechanism mediating social rank and frequency of aggression in female *L. catta*, but conclusions about the influences of androgens should be considered preliminary. The capacity to express aggression and dominance may be hormonally based, but the strength of this relationship could be contingent upon the stability of the social environment and the confounding influences of additional hormones and enzymes. My data points to directions for future research on the behavior and physiology of female ring-tailed lemurs, as other intriguing research questions emerge. For example: (1) To what extent is the "challenge hypothesis" applicable to female *L. catta*? (2) How does the presence of the aromatase enzyme influence fT levels in female *L. catta*? (3) Do the organizational effects of prenatal androgens influence the expression of agonistic behavior in adulthood? (4) Given that cortisol has been demonstrated to suppress gonadal testosterone production in males, how do levels of cortisol affect T titers in females?

The results obtained from the current study will aid future researchers in establishing appropriate methodologies and sampling protocols to account for the potential confounding effects of diet and diurnal variation on female androgen levels. In addition, by monitoring fT levels from early gestation through to mid-lactation, I provided key information on distinct fluctuations in androgen profiles that will help to disentangle complexity of endocrine responses during reproduction, and may eventually prove to be useful in detecting pregnancy and early abortion in female prosimians (Brockman et al., 1998). Finally, the current study illuminates the challenges experienced by females differing in social status during key stages of reproduction. The ability to cope with these challenges may influence subsequent infant survivorship and ultimate reproductive success of females in this species.

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CHAPTER FOUR

Summary of chapter one:

1. Female alliances only occurred on behalf of other females - and not males - and the overall percentage of female-female alliances was low: less that 3% of agonistic interactions were characterized by third-party support.

2. Preliminary evidence for the validity of the dominance hierarchy in female ring-tailed lemurs was derived from the data that female rank-order was predicted – to varying degrees – by both biological parameters (age and weight) and behavioural correlates (agonistic and approach retreat interactions in both feeding and non-feeding contexts).

3. The mean weight of high-ranking females (i.e. those occupying the alpha, beta, and gamma positions in the dominance hierarchy) were significantly greater than that of lower-ranking females.

4. The relationship of age in relation to rank followed an inverted J-shaped pattern, with old adults attaining the highest average rank, followed by prime adults, young adults, and very old adults.

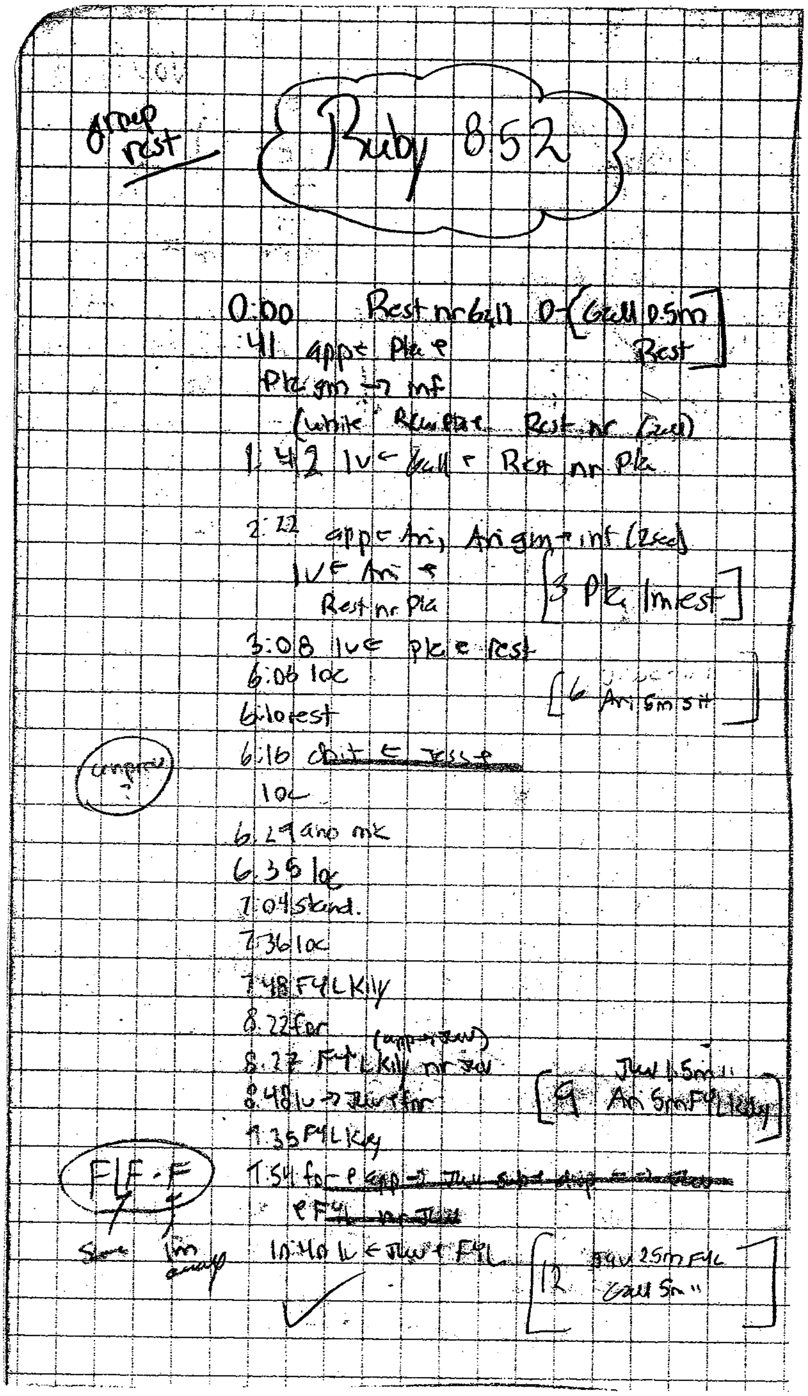
5. Significant, positive correlations between female rank and female-initiated rates of agonism existed in four of the six study groups.

Summary of chapter two:.

1. There were no statistically significant differences in mean fecal testosterone levels in relation to the timing of fecal sample collection (i.e. early vs. late morning) or dietary differences (i.e. undigested fibre, undigested seeds, and absence of undigested material); however these data do not negate the importance of controlling for these variables in future studies, as numerous authors report that diurnal and dietary differences significantly influence fecal endocrine profiles in other nonhuman primate species.
2. There was a trend for older females to exhibit correspondingly higher fT levels in comparison to prime-aged or young females. Age-related declines in testosterone, which have clearly been linked to the onset of menopause in human females, were not seen in the current study.
3. Stage of reproduction appeared to be the best predictor of fecal testosterone levels in females of red and green group: fT titers were significantly higher during late gestation than early lactation. Elevated levels of testosterone during late gestation may function as an important estrogen precursor.
4. No clear patterns emerged with respect to testosterone levels in relation to rates of female-initiated agonism. Three possible explanations for these findings include the challenge hypothesis, the aromatization hypothesis, and the influences of prenatal testosterone exposure.
5. The top-ranking female in red group, and two top-ranking females in green group exhibited the lowest mean fT levels. Elevated levels of cortisol in higher-ranking individuals may act as an important suppressor of testosterone in these individuals.

APPENDIX

Sample data collection sheet recorded during focal animal observation:



group rest

Ruby 852

0:00 Rest nr Gull 0 [Gull 0.5m Rest]
:41 app c Pla c
Pla gm → inf
(while Rewplat Rest nr Gull)
1:42 lv c Gull c Rest nr Pla

2:22 app c Ari, Ari gm + inf (2sec)
lv c Ari c
Rest nr Pla [3 Pla 1m rest]
3:08 lv c Pla c rest
6:06 loc [6 Ari 5m sit]
6:10 rest
6:16 ~~chit c Jess c~~
loc
(unprov ?)
6:29 app mk
6:35 loc
7:04 stand.
7:36 loc
7:48 F4L Kily
8:22 for
8:27 F4L Kily nr Jkw (app → Jkw)
8:48 lv → Jkw + for [9 Jkw 1.5m " An 5m F4L Kily]
9:35 F4L Kily
9:54 for c ~~app → Jkw subt disp [illegible]~~
c F4L ~~nr Jkw~~
FLF·F
5m 1m away
10:40 lv c Jkw + F4L [12 Jkw 25m F4L Gall 5m "]
✓