Adult Female Feeding Competition Within Two Groups of Free-Ranging Ringtailed Lemurs (Lemur catta) in Different Habitats at the Beza Mahafaly Special Reserve, Southwestern Madagascar.

by

Andrea Lynne Gemmill
B.Sc., University of Calgary, 2002

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Abstract

Diet and female feeding competition was examined within two groups of free-ranging ringtailed lemurs (*Lemur catta*) at the Beza Mahafaly Special Reserve in southwestern Madagascar. The first group's home range was located within a protected gallery forest, the second is in a degraded forest and human-occupied area. The diets of the females were found to vary between groups; females fed on different plant species, and those in the unprotected area frequently consumed human food scraps and domestic animal fecal matter. Contest and scramble competition were detected within both groups. Rates of feeding competition were found to increase according to the type of food being consumed; feeding on fruits and leaves correlated with increased competition in the reserve group, and feeding on human foods and animal fecal matter correlated with increased competition with the non-reserve group. These dietary and competitive differences highlight the need for continued, and possibly additional, protection of *L. catta* in this region.

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Chapter 1 – Introduction to the Current Study

This study examines the social relationships amongst adult females in two groups of wild *Lemur catta* occurring in differing habitats in southwestern Madagascar from the months of July to September, 2004. These different habitats contain food resources of varying availability, abundance and distribution. How do these habitats differ? What foods make up the diets of the groups? The effects of these dietary resource differences on the interactions and behaviours of the adult females were monitored. Do factors such as dominance rank, food distribution or type of food being consumed affect agonism levels? These questions are discussed in detail throughout the following pages.

Agonistic and feeding behaviours were carefully observed and are examined in an attempt to relate such behaviour to resource access and feeding competition. Tree phenology and food item data were also collected to contribute to the analysis of the research questions.

The following pages outline the framework for this research project including a brief discussion of group living and female feeding competition, *Lemur catta* natural history, a summary of relevant research conducted on female relationships, feeding competition, foraging, and a brief discussion of the major theories that focus on the ecology of female social relationships and optimal foraging. The objectives, hypotheses, and significance of this study are then presented.

1.1 Introduction: Group Living and Female Feeding Competition

There are many benefits associated with group living for primates. These include improved predator protection and detection, access to food, access to mating partners and affiliative social interactions. Costs can invariably be assigned to group living that are directly associated with the same listed benefits: increased detection by predators and increased competition for food, mates and affiliative social interactions (Isbell, 1991; Koenig *et al*, 1998; Isbell and Young, 2002; Overdorff *et al.*, 2002; Sauther, 2002). Since the majority of primate species live in groups, the benefits must in some way outweigh the costs.

In terms of competition, males and females are expected to be primarily competing for different resources (Trivers, 1972). Males must compete for access to females as mating partners, since receptive mates can be a limited resource due to female selectivity when it comes to choosing a partner. Once mating has occurred, the male's reproductive role has generally been completed. The reproductive role of females, conversely, carries on long after mating has taken place. Pregnancy, birth, lactation and infant carrying are the main physiological costs to a female with respect to reproduction, and these costs can carry over the span of years. These tasks require a great deal of energy - energy that must be supplied through proper diet for both the female and the offspring. The primary motivation for competition between female primates is thus access to food resources.

Living in a group can lead to increased access to food resources with more eyes searching for food within the home range. Living in a group situation with multiple females requiring access to food sources can also lead to various types of relationships between these females, as well as various types of feeding competition. Models of the ecology of female social relationships have attempted to explain these associations in terms of dispersal, the presence, degree of expression and stability of dominance hierarchies, predation, and infanticide (Wrangham, 1980; van Schaik, 1989; Isbell, 1991; Isbell and Van Vuren, 1996; Sterck *et al.*, 1997; Isbell and Pruetz, 1998; Isbell and Young, 2002).

Aside from interactions with other females, female feeding competition is also mediated by the availability of the food resources themselves. Food consumed by primates in their natural habitat varies both temporally and spatially. Many tree and plant species seasonally reproduce (see for example Glander and Teaford, 1995; Janson and Chapman, 1999). Fruit and flowers are not continuously available and can be found at varying degrees of production and ripeness. Leaves also go through reproductive stages and can be more palatable to primates at some specific times more than others, for example, immature leaves versus mature leaves. Furthermore, plants and trees are distributed in various ways - certain species may be plentiful whereas others might be few and far between (Barton, 1993; Isbell *et al.*, 1998).

The temporal and spatial variability of food resources, and in the case of plant resources the stage of their reproductive life cycle, impact primate diets (Glander and Teaford, 1995; Janson and Chapman, 1999). Food resources are typically scarcer during periods with little rain, or the dry season (Gould, 2006; Janson and Chapman, 1999; Rasamimanana and Rafidinarivo, 1993; Sauther, 1992, 1994, 1998; Sauther *et al.*, 1999). It would thus be expected that during a period of food scarcity that competition for available resources would be high. According to optimal foraging theories, individuals base their decisions of feeding site on the benefits versus the potential costs of their selection (Pyke *et al.*, 1977; Manning and Dawkins, 1992; Ahlborn and Rothe, 1999).

Optimal foraging theories suggest that animals make decisions regarding their feeding time, food site depletion and location based on a cost-benefit analysis (Pyke *et al.*, 1977; Manning and Dawkins, 1992; Ahlborn and Rothe, 1999). The decision must be made as to whether it is energetically more efficient for an individual to continue to feed at an increasingly depleted patch, or to begin searching for another source of nourishment. The abundance and distribution of food resources can then presumably affect time spent foraging, feeding competition and, subsequently, female relationships. For instance, if feeding at a particular site is going to result in intense competition from group members, it might be more beneficial for an individual to feed at a less contested location.

1.2 *Lemur catta* Natural History

1.2.1 General Description

Adult *L. catta* have an average body weight of 2.2kg (Sussman, 1991). This applies to both males and females, as there is an absence of sexual dimorphism in the species (Kappeler, 1990; Sauther *et al.*, 2001). Ringtailed lemurs spend over 30% of their time on the ground and have thus been classified as semiterrestrial quadrupeds (Jolly, 1966; Sussman, 1974). *L. catta* are diurnal primates, and at the Beza Mahafaly Special Reserve their daytime activity levels vary depending upon the time of day and the corresponding temperature: activity levels are at their highest during the cooler times of day between 0700 and 1130, and 1400 to 1800 (Sussman, 1974; Gould, 1996a). Activity levels are also affected by season, with less activity in the cold/dry season mornings when temperatures are lower than in the warm/rainy season mornings (Sussman, 1974, Gould, 1994).

1.2.2 Distribution and Habitat

The distribution of *Lemur catta* is in south and southwestern Madagascar, primarily in xerophytic and riverine forests (Jolly, 1966; Sussman, 1977), but they have also been found in low-lying limestone forest and even above the tree line in one mountainous site (Gould *et al.*, 2003; Goodman *et al.*, 2006). Prior to a drought in 1992, the ringtailed lemur density at Beza Mahafaly Special Reserve was 135 animals/km^2 (Sussman, 1991). In the three years following the drought the population did decrease significantly, but began recovering in 1996 (Gould *et al.*, 1999; Gould *et al.*, 2003). This aside, the ringtailed lemur population at Beza Mahafaly remained relatively constant over the fifteen years that the demography of this population was studied (Gould *et al.*, 2003). The home range size of *L. catta* groups vary depending upon their location and habitat (Sussman, 1991; Gould *et al.*, 2003). At Beza Mahafaly, groups inhabiting the more lush eastern riverine portion of the reserve have home ranges averaging 17 ha, whereas groups inhabiting the drier western area of the reserve have home ranges averaging 32 ha (Sussman, 1991). Groups in the area that range primarily or entirely outside of the reserve boundaries had not been adequately monitored before the preparation of this study, therefore home range size estimates for these groups are not available.

1.2.3 Social Organization

Lemur catta live in multifemale-multimale, female philopatric groups (Jolly, 1966; Sussman, 1977). Group size for the species generally ranges from 8 to 25 individuals (Jolly, 1966; Sussman, 1977). The longitudinal study of the groups at Beza

Mahafaly has shown that group size for this population ranges between 2 and 15 adult individuals (Gould *et al.*, 2003). Adult male-to-female sex ratio for ringtailed lemurs is 1:1 (Jolly, 1966; Sussman, 1977), but at Beza Mahafaly it has been calculated at 0.92:1 (Gould *et al.*, 2003). Females within a group are organized into matrilines and adult females and their offspring form the central core of the group (Jolly, 1966; Koyama, 1988; Sauther, 1991; Sauther and Sussman, 1993). Some adult males form close associations with the core females, whereas others remain on the group's periphery: these males can be natal or nonnatal and of various ages (Sussman, 1992; Sauther and Sussman, 1993; Gould, 1994; Gould, 1996b).

1.2.4 Intragroup Relations

Females make up the central core of ringtailed lemur groups (Jolly, 1966; Koyama, 1988; Sauther, 1991; Sauther and Sussman, 1993). They are generally organized into matrilines with friendlier female-female interactions taking place between more closely related individuals and their associated infants and juveniles (Sauther and Sussman, 1993). Male-female nonsexual affiliations also occur, with the males gaining such benefits as predator protection, thermoregulation and increased opportunities for social contact (Gould, 1994, 1996b, 1999). Male-male affiliation depends upon the reproductive season: during the mating period, males who usually associate in a friendly manner can become markedly aggressive towards each other (Gould, 1997a). Affiliation between adult males and immature group members does occur, offering such benefits to the male as the possibility of developing relationships with adult females through affiliation with her juvenile, improved predator protection and thermoregulation (Gould, 1997b). For immature group members, affiliation with adult males can lead to increased predator protection, alloparental care and further opportunities to develop social skills (Gould, 1997b).

Agonism occurs within ringtailed lemur groups in both feeding and nonfeeding contexts (Sauther, 1993). Agonism in ringtailed lemurs is manifested through vocalizations, displacements, chasing and physical contact. The 86% of agonism takes place over food, and females exhibit a higher mean frequency of agonism than males (Sauther, 1993). The sorts of interactions that occur within groups and the associated direction of the behaviours can be used to define the group's dominance hierarchy. It has been demonstrated that in *L. catta*, separate hierarchies exist for males and for females (Jolly, 1966; Taylor, 1987; Sauther, 1992). The highest-ranking male of a group is capable of displacing all other males in his group, but not adult females (Sauther and Sussman, 1993). Male dominance hierarchies are relatively unstable, perhaps due to the constant changing of male group membership (Sauther and Sussman, 1993; Gould, 1997a). Female dominance relationships are quite stable, and females do 'win' the majority of agonistic feeding interactions versus males (Sauther, 1992, 1993, 1998). This is due to the existence of female feeding priority in *L. catta*. Female feeding priority is thought to have evolved in ringtailed lemurs because they are strict seasonal breeders with reproductive synchrony: all females lactate at the same time and thus require access to essential food resources without excessive intragroup, male-female feeding competition (Jolly, 1984).

1.2.5 Intergroup Relations

In some cases, ringtailed lemurs have been described as territorial (Jolly *et al.*, 1993), and in others, nonterritorial (Sauther and Sussman, 1993). At Beza Mahafaly, adjacent home ranges frequently overlap and there are limited areas of exclusive use (Sussman, 1991). The definition of territoriality used by Sauther and Sussman (1993) assumes an exclusive use of an area by a group. Since the groups studied at Beza Mahafaly were found to share most territory equally, they were not considered to be territorial but they do attempt to defend the core area of their home range. Intergroup conflicts still occur frequently and adult females are generally the most active participants in these bouts (Sauther, 1992; Sauther *et al.*, 1999). These encounters can at times be violent, resulting in serious physical injury (Sauther, 1992; Jolly *et al.*, 1993). The possible costs of an intergroup interaction can explain the presence of vigilance behaviour directed towards conspecifics of another group (Gould, 1996a).

Seasonal peaks in intergroup encounters have been noted with marked increases occurring from birth to early lactation, during the weaning period and before the dry season (Sauther, 1992; Sauther *et al.*, 1999). These confrontations seem to occur in order to defend seasonal food resources (Sauther, 1992; Sauther and Sussman, 1993) and to keep other groups away from the core area of a group's home range (Sauther *et al.*, 1999). Group size was found to have little effect on the outcome of intergroup encounters at Beza Mahafaly (Sauther and Sussman, 1993).

1.2.6 Diet and Feeding Ecology

L. catta has been described as frugivorous/folivorous and also as an omnivorous species as they are known to feed on a variety of resources including leaves, leaf stems, buds, flowers, flower stems, fruits, spiders, spider webs, caterpillars, cicadas, insect cocoons and birds (Sauther, 1992, 1994, 1998; Sauther *et al.*, 1999; Gould, 2006). In addition individuals at Beza Mahafaly have often been observed consuming soil from termite mounds (Sauther *et al.*, 1999).

Ringtailed lemur diet is affected by the seasonal nature of their environment, which also coincides with the reproductive state of adult females (Rasamimanana and Rafidinarivo, 1993; Sauther, 1992, 1994, 1998; Sauther *et al.*, 1999). At Beza Mahafaly, food resources are more abundant during the hot/wet season (October-March) than during the cool/dry season (April-September) (Sauther, 1992). The wet season brings about young leaves and many types of fruit; whereas in the dry season, fruit is rare and young and even mature leaves begin to disappear: this can lead to the necessary consumption of dried, brown leaves (Sauther, 1992, 1998). Pregnancy takes place during the dry season, and with the limited resource availability at that time, females feed on rare fruit, leaves and flowers that appear at the very end of the season (Sauther, 1992, 1994, 1998).

Females begin lactating towards the end of the dry season. Those who are lactating have a higher calcium and protein requirement than those who are not lactating and thus feed more on low-cost, predictable, high protein plant resources such as young leaves (Sauther, 1992, 1994, 1998). Feeding differences have also been noted between ringtailed lemurs of varying age, sex and social status (Sauther, 1995). Sauther (1995) notes that younger individuals eat a diet high in protein and sugars, which is also associated with high levels of fibre and tannins. Conversely, the diet of older individuals is low in fibre and tannin content. Females, on average, have a diet higher in protein and sugar than do males. Finally, higher-ranking individuals consume more sugars than lower-ranking individuals (Sauther, 1995).

L. catta has demonstrated dietary flexibility - they can adjust their diets depending upon the season and availability of certain resources (Sauther *et al.*, 1999). At Beza Mahafaly, the ringtailed lemurs have been found to concentrate on resources provided by *Tamarindus indica* throughout the year: this tree species has thus been termed a keystone species (Sauther, 1998). *T. indica* produces resources year-round and is valuable to the lemurs during times of food scarcity (Sauther, 1998). Its importance was demonstrated following the drought of the 1991-1992 season at Beza Mahafaly: the decline of *T. indica* contributed to the malnourishment and high mortality of the ringtailed lemur population at the site (Gould *et al.*, 1999).

1.2.7 Reproductive Ecology

Female emigration in *Lemur catta* is rare (Sussman, 1992; Gould *et al.*, 2003). Males disperse from their natal group usually between the ages of 3 and 5, and after their first dispersal, migrate approximately every 3.5 years (Sussman, 1992). At Beza Mahafaly, male migrations occur from October to March (Sussman, 1992; Gould, 1994; Gould, 2006).

Free-ranging adult female ringtailed lemurs experience estrus once a year for a period of only 6 to 24 hours, and individuals exhibit breeding synchrony (Jolly, 1966; van Horn and Resko, 1977; Sauther, 1991). Mating takes place within a time period of three to four weeks (Sauther, 1991; Gould, 1994). Females exhibit selectivity in their choice of mates; they do not accept mating attempts made by all males (Sauther, 1991; Sauther and

Sussman, 1993). Females also commonly mate with extra-group males, resulting in low or even absent paternity certainty (Sauther and Sussman, 1993).

As females are receptive within the same narrow time frame, they also give birth at the same general time. Gestation in *Lemur catta* averages 141 days, and females generally give birth to a single offspring (Sauther, 1991). The birth season at Beza Mahafaly occurs over a period of a few weeks from late September until early October (Sauther, 1991). The majority of adult females (80% to 85%) bear infants on a yearly basis (Sussman, 1991), but infant mortality rates are high - 30% to 51% of infants die during their first year under normal seasonal conditions (Sussman, 1974, 1991, 1992). During drought years, infant mortality has reached as high as 80% (Gould *et al.*, 1999).

Females begin lactating during the dry season (Gould, 1990, 1999; Sauther, 1992, 1993) and ringtailed lemur infants are weaned between 4 and 5 months of age (Gould, 1990) which demonstrates the rapid development of *L. catta* infants (Sauther, 1992, 1998). At the age of 16 weeks, suckling and dorsal riding is seldomly observed as infants at this stage locomote and forage independently (Gould, 1990).

1.2.8 Predation

Ringtailed lemurs are subject to threat from both arboreal and terrestrial predators in their natural habitat (Sauther, 1989, 2002; Gould, 1996a; Goodman, 2003). Although encounters with predators at Beza Mahafaly have rarely been observed (Sauther, 2002), increased group size and multi-male membership in ringtailed lemur groups might be features in place to improve predator detection and defense (Sauther, 1993, 2002). The occurrence of vigilance behaviour towards potential predators demonstrates that predation on *Lemur catta* at Beza Mahafaly does take place (Gould, 1996a).

1.3 Female Relationships in Nonhuman Primates

1.3.1 Intragroup Relations

Agonism

When observing agonistic behaviours in primates, as with any behaviour, it is essential to consider the context of the situation in which the behaviour is occurring. Male-male agonism has been found to take place over competition for females (Walters and Seyfarth, 1987), such as in *Cercopithecus aethiops* (vervets) (Whitten, 1984), *Macaca fuscata* (Japanese macaques) (Soltis *et al.*, 1997), *Propithecus verreauxi* (Verreaux's sifaka) (Brockman *et* al., 1998), *Papio hamadryas* (Hamadryas baboon) (Colmenares and Anaya-Huertas, 2001), *Mandrillus sphinx* (mandrills) (Setchell and Dixson, 2002), *Pan troglodytes* (chimpanzees) (Boesch *et al.*, 2006) and *Lemur catta* (Sauther, 1993). A great deal of aggression seems to involve the establishment and maintenance of dominance relationships, which might actually be an indirect form of resource competition (Walters and Seyfarth, 1987). Female-female agonistic behaviour is commonly related to resource competition, but to food resource competition, not competition for mates. These ideas stem from Trivers' theory of sexual selection and parental investment (Trivers, 1972). Trivers suggested that females are a limited resource for males and thus do not need to compete to be fertilized. Females are responsible for the carrying, birthing and raising of offspring and to successfully do so must be able to access necessary food resources for their own survival and the survival of the offspring.

Competition in nonhuman primates relates to dominance hierarchies, which are in place in primate groups to regulate social behaviour and to maintain some form of social order. An individual's rank in the hierarchy can be achieved through inheritance from the mother, as in *Macaca fuscata* (Japanese macaques) (Takahata *et al.*, 1993) or sometimes with advancing age and increased time in the group, as with *Semnopithecus entellus* (Hanuman langurs) (Hrdy, 1977). Knowledge of an individual's social rank is vital in order to properly contextualize within-group agonism. For example, agonism observed between adult female vervets was related to access to food resources: low-ranking females were more likely to be chased away from food sites (Whitten, 1984), Japanese macaques have been observed dispersing while feeding in order to avoid aggression (Takahata *et al.*, 1993), and in *Alouatta palliata* (mantled howlers), rank was significantly correlated with rate of agonism in adult females (Zucker and Clarke, 1998).

Females are involved in more agonistic behaviour than males within ringtailed lemur groups (Sauther and Sussman, 1993). These interactions occur over access to food resources, drinking sites, resting and sunning spots. Agonistic encounters over food tend to vary depending upon the type of food in question - agonism seems to occur more frequently over access to fruit than to leaves (Sauther, 1992). It has also been found that there is an increase in the occurrence of spatial related agonism (feeding, resting in proximity) during the dry season with ringtailed lemurs (Sauther, 1992). Lower food availability results in increased competition between females. Feeding too close together could result in lower food consumption rates (Sauther, 1992).

In order to characterize the aggressiveness of a social relationship, the frequency of agonism relative to other kinds of interactions, as well as the absolute frequency of agonistic behaviour must be considered (Walters and Seyfarth, 1987). Another factor to consider is the intensity of the agonistic behaviour. Primate agonistic behaviour ranges along a spectrum from subtle stares to actual killing. To prevent constant aggression, and the costly loss of energy associated with these behaviours, dominance relationships and ritualized displays are in place so that most disputes can be resolved without resorting to physical aggression (Walters and Seyfarth, 1987). In a study of semi-captive ringtailed lemurs, Taylor (1987) separated agonistic behaviours into categories of mild, moderate and severe. Mild included visual threats, lunges and slaps, moderate agonism included baring teeth, biting and chasing and severe agonism was any behaviour with injurious physical contact (Taylor, 1987).

Affiliation

Affiliative behaviours, such as grooming and sitting/resting in close proximity or in contact, serve many possible functions in primate societies. Proximally, affiliation can be used to reconcile after agonism, to gain access to resources (mates or food), to gain access to infants, betterment of rank, or perhaps as a means of easing tension (Aureli and van Schaik, 1991; Dunbar, 1991; Overdorff, 1998). Ultimately, goals could be to secure future mating opportunities or increased chance of offspring survivorship (Strum, 1984; Smuts, 1985; Borries *et al.*, 1999). Factors that must be taken into consideration when observing affiliative behaviour in females include rank and kinship (Seyfarth, 1977; Manson *et al.*, 1999).

The most frequently discussed and studied affiliative behaviour is grooming (Schino, 2001). In 1977, Seyfarth proposed a model to attempt to explain the possible cause and function of female grooming behaviour in primates. The model outlines that high-ranking females interact with other high-ranking females, middle-ranking females with other middle-ranking females and low-ranking females with other low-ranking females, due to the following factors: dominance, individual differences in attractiveness, time available for grooming, preference among close genetic relatives and changes in reproductive state (Seyfarth, 1977).

Schino (2001) imparts that one difficulty with Seyfarth's grooming model is that it does not take into account that an individual's behaviour can be mediated by the behaviours of others. Other aspects of the grooming model were examined in a meta-analysis of studies on female-female grooming (Schino, 2001). Amount of grooming received and social rank were compared with the amount of grooming that was directed toward higher and lower-ranking individuals. Females were found to direct more grooming towards higher-ranked females, therefore the results support that there is a social attraction to high rank. Results also suggested a strong preference for grooming kin over nonkin. It was determined that the effects of attraction to rank and to kin were not additive, but group size may be a confounding factor (Schino, 2001).

It has been suggested that female primates will groom other females of adjacent rank. The fact that kin commonly share similar ranks made this difficult to examine, so all grooming dyads composed of kin were excluded from this particular analysis (Schino, 2001). Without kinship, there was no significant difference between grooming directed towards similarly ranked and differently ranked individuals. Finally, however, significance was found between rank and the amount of grooming performed, suggesting that competition may affect access to grooming partners (Schino, 2001).

Through their work with Rhesus macaques (*Macaca mulatta*), de Waal and Luttrell (1986) proposed an alternative model to Seyfarth's 1977 model: the "similarity principle" is intended to explain social attraction between females within a group. According to this principle, females will engage in affiliative interactions with those females with whom they most resemble: if females have many characteristics in common (kinship, age, rank, social class) they are likely to have common goals and could benefit from forming a relationship (de Waal and Luttrell, 1986). These characteristics were found to have a cumulative effect on affiliative behaviour within the Rhesus macaque study group, and age was demonstrated as being of particular influence in social interactions. Competition for grooming access to matriarchs was higher than for any other age group, and females of similar age tended to form close, affiliative relationships irrespective of kin or social class (de Waal and Luttrell, 1986).

A meta-analysis by Dunbar (1991) examined the function of grooming, with the intention of determining whether it has a purely hygienic function or a purely social function. It would appear that many species spend more time involved in grooming behaviour than would seem necessary for a strictly hygienic function. It is also evident that grooming has a relaxing effect and so part of its function may be related to tension reduction (Schino *et al.*, 1988). Grooming may also be a method for certain animals to spend a period of time in close proximity to each other. There could be ulterior motives on the part of one or both individuals with the hopes of monopolizing the others' time for the purpose of forming an alliance (Dunbar, 1991).

It has been concluded that grooming appears to serve primarily a social function, at least in catarrhine primates (see Tanaka and Takefushi (1993) for an opposing view with *Macaca fuscata*). Dunbar admits that there was no testing for the possibility that ectoparasite infestation might also increase with group size (Dunbar, 1991), but if more grooming was to occur (i.e., due to the availability of more grooming partners), a prediction of a drop in ectoparasite infestation could be made. This could be accomplished by determining if there is a positive correlation between group size and time spent autogrooming.

Lemur catta females form the core of each group (Sauther and Sussman, 1993). Groups are further subdivided into matrilines, within which females have been found to exhibit a higher level of affiliation (preference for kin over nonkin) (Taylor, 1987; Sauther and Sussman, 1993; Sauther *et al.*, 1999). Close kin form mutual grooming pairs significantly more than unrelated individuals, with little seasonal variation (Taylor, 1987). Related individuals are more likely to be resting partners, to huddle in groups and to approach each other more often for affiliative interactions than unrelated group members (Taylor, 1987).

1.3.2 Intergroup Relations

Whether an intergroup encounter between primate groups is peaceful or aggressive depends on numerous factors. One of these is the territoriality of the species. Cheney defines a territory as "...the area that a group consistently attempts to defend against incursion by others (Cheney, 1987; 268)". Groups that range over a large territory are usually not overtly territorial. Intergroup spacing through vocalizations is more common than actual physical encounters (Cheney, 1987). If a group's home range is small relative to its daily foraging route, intergroup encounters are generally concerned with access to specific feeding resources and defense of the entire range (Cheney, 1987). Groups that defend all or part of their range are likely to have intergroup interactions that are characterized by aggression rather than mutual avoidance. Territorial groups are typically male dispersed species (Cheney, 1987): it is in a male's interest to defend his mates and food from extra-group males attempting to takeover his resources.

Another factor influencing the relative aggressiveness or peacefulness of an intergroup encounter is the number of members in the group (Cheney, 1987). Intergroup encounters can often be mediated by dominance (between the groups in the area). This is usually a function of group size, with larger groups generally being able to displace groups with fewer members. The frequency and intensity of intergroup encounters may also depend upon resource availability and the seasonality of the environment. Groups may need to seek out food resources in times of scarcity, and this could involve leaving the home territory and encountering another group in their territory.

Vervets have territorial overlaps, and females are generally aggressive when intergroup interactions take place (Whitten, 1984). Japanese macaque groups also have areas of home range overlap, and encounters are frequent in these regions (Takahata *et al.*, 1993). Intergroup dominance is not always clear as it partly depends upon where the encounter takes place. Dominant troops may interfere with feeding of subordinate troops by occupying food patches, disrupting time budgets, forcing changes in course of travel and raising stress levels. Conversely, in Chacma baboons (*Papio ursinus*), female-female aggression is almost nonexistent (Cowlishaw, 1995). Intergroup encounter rates are low, even with changes in resource availability. When encounters do occur, they are generally peaceful events (Cowlishaw, 1995).

In ringtailed lemurs, intergroup encounters involve females defending seasonal food resources (Sauther and Sussman, 1993; Sauther *et al.*, 1999). Females appear to attempt to keep others away from the core areas of the home range (usually containing key resources) during intergroup interactions (Sauther *et al.*, 1999). Intergroup encounters tend to peak in ringtailed lemurs during the weaning period, before the dry period, and during the birth and early lactation periods (Sauther *et al.*, 1999) - times when food resources have decreased in availability or when they are strongly needed for offspring survivorship. Interestingly, group size has been found to have little effect on the outcome of these intergroup encounters (Sauther and Sussman, 1993).

1.4 Ecological Theories of Female Social Relationships

Over the past twenty-five years there have been many models proposed in an attempt to explain the diverse relationships that exist between female primates. Four of the most influential are discussed below.

1.4.1 Wrangham (1980)

The first key distinction made in Wrangham's argument is that between what he terms female-bonded and non-female-bonded. Groups made up of females who remain in their natal group are referred to as female-bonded. Groups composed of females who did not remain in their natal group but dispersed to a neighbouring group are in turn categorized as non-female-bonded. Wrangham suggested the term "female-bonded" in order to avoid confusion with "established anthropological concepts", such as the terms "matrilineal" and "matrilocal" (Wrangham, 1980: 263).

The occurrence of this type of social organization was expected to be correlated with the distribution of food in the group's habitat. If food is found in spatially separated discrete clumps and is of high quality (e.g. fruit), it is argued that females would be philopatric. Intergroup aggression would take place as groups compete for access to spatially clumped (spread-out), desirable resources. Since clumped foods are more easily defended than more evenly dispersed foods, a dominance hierarchy should develop between groups in the area. Wrangham also suggests that if high quality food clumps vary in quality, differentiated relationships would form between females within the social group. Females live with kin in female-bonded groups and form stable relationships with their relatives in order to compete with other females more effectively. Individuals ultimately improve their inclusive fitness through supporting genetic relations. Female offspring inherit the rank of their mother and band together with their kin in aggressive interactions, competition and searching for resources. These matrilines in turn form linear hierarchies within the group, each occupying various ranks in relation to each other. It is presumably beneficial for females to remain in their natal group and be able to form coalitions with kin members and compete for high quality food (Wrangham, 1980).

Non-female-bonded groups form under different ecological conditions. If food is evenly distributed, for example leaves, or is in tiny, high quality clumps, such as insects, females should disperse from their natal group. These forms of food distribution would not be easily defended; therefore the formation of dominance hierarchies would not take place. Low levels of aggression would occur between groups, as there would presumably be sufficient resources to accommodate multiple groups. Since females within a social group would not be related, the inclusive fitness benefits of associating with and aiding kin would be absent. Relationships between females within a group would be egalitarian or only weakly affected by dominance (Wrangham, 1980).

Males living in female-bonded primate groups, irrespective of number, are expected to play a less integral role in group activities, such as group movement, interactions and foraging. The opposite is true for males inhabiting non-female-bonded groups. As females are the dispersing sex, there is a greater chance that males are interacting with male kin frequently in multi-male groups. As female relationships are not cohesive, males direct more activities within and between groups (Wrangham, 1980).

1.4.2 van Schaik (1989)

van Schaik made two "extensions" to the model proposed by Wrangham in 1980. Food competition was still held as being an important component of social structure in group living primates. Wrangham had stressed that this was due mainly to competition that occurs between groups living in a given area. Inter-group competition remained an important point in the new model, but what was taken as being of even greater importance was the competition that occurred between individuals within the same group.

Intra-group competition could vary categorically depending on quality and density of the available food supply (van Schaik, 1989). When all animals share the same food supply and each is able to access similar amounts, the situation is labeled scramble competition. In this case, food sources are fairly evenly distributed or they come in tiny packages. Monopolizability of these sources is not possible, leading to a more egalitarian social structure. Conversely, if food is randomly distributed in high quality, small patches, contest competition is the result. These resources are more readily defendable and usurpable, resulting in hierarchical relationships (van Schaik, 1989).

Scramble and contest competition, both within and between groups, were used to categorize female social relationships into four possible groups; within group scramble, within group contest, within group scramble in addition to within group contest and between group contest (types A, B, C and D respectively) (van Schaik, 1989). The key points of each category are outlined in the following:

Type A (within group scramble): females or males dispersing; egalitarian; individualistic
Type B (within group contest): male dispersal; despotic; nepotistic
Type C (within group scramble and within group contest): male dispersal; egalitarian; individualistic
Type D (between group contest): male dispersal; egalitarian; nepotistic

A second extension to female socioecological theory by van Schaik is the consideration that within group competition might reflect a need for predator protection (van Schaik, 1989). Safety of females may be increased by being surrounded by many other individuals or by being close to those who are able to deter predators. This model views predation as having a substantial effect on primate groups (van Schaik, 1989).

1.4.3 Isbell and colleagues (1991 - 2002)

Isbell and Young (2002) discuss their theory as having arisen from the fusion of three separate, but not unrelated, research projects; (Isbell, 1991; Isbell and Van Vuren, 1996; Isbell and Pruetz; 1998). Isbell has formulated three 'syndromes', or categories, to group female primate social organization. The terminology is similar to that used by van Schaik (1989), but there are some fundamental differences between Isbell and colleagues' theory and previous theories. The first 'syndrome' is contest and scramble competition, both within and between groups. It is comparable to Wrangham's female-bonded category and differs from van Schaik's type B and Sterck *et al.*'s resident-nepotistic category (discussed in more detail in the following subsection) in that it does not include predation as a factor in the formation of female social structure. The following designation is between group scramble and contest competition, with little or no within group scramble or contest competition - similar to type C and resident-egalitarian, except that predation is once again excluded. The final category is little or no between or within group scramble or contest competition. It corresponds to Wrangham's non-female-bonded classification, and is similar to van Schaik's type A and Sterck *et al.*'s dispersal-egalitarian, but excludes predation as a factor (Isbell and Young, 2002).

Wrangham's female-bonded primate model discusses the distribution of resources and the influence that has on between and within group competition. Isbell (1991) suggests that food distribution will affect competition within groups, but it is food abundance that affects between group competition. Isbell's theory also dismisses the influence that predation has on primate groups (Isbell, 1991; Isbell and Young, 2002). They propose that feeding competition, both within and between groups, and how it varies within and between populations and species, is sufficient to determine the characteristics of female social relationships.

1.4.4 Sterck and colleagues (1997)

These researchers introduced new terminology for the categorization of female primate relationships, "to distinguish them from two earlier, influential models (Wrangham, 1980; van Schaik, 1989)" (Sterck *et al.*, 1997; 294). An attempt was made to move away from the term female-bonded, as it did not distinguish between individualistic and kin based female dominance hierarchies - a variation that warrants separate classification. See Table 1.1 for a comparison between the Sterck *et al.* (1997), Wrangham (1980) and van Schaik (1989) models. 'Resident' signifies that females stay in their natal group. Nepotistic or egalitarian refers to the form of ranking hierarchy found within the observed group.

Table 1.1 – Comparison of three ecological theories of female social relationships.

Sterck and colleagues (1997)	*Wrangham (1980)*	*van Schaik (1989)*
Resident-nepotistic	Female-bonded	Type B
Resident-nepotistic-tolerant	No equivalent	Similar to Type D
Dispersal-egalitarian	Non-female-bonded	Type A
Resident-egalitarian	Similar to female-bonded	Type C

Besides the presentation of new terminology, this model incorporated another competitive factor into the existing list of rank, kinship, predation and resources - infanticide (Sterck *et al.*, 1997). It is suggested that the risk of infanticide by incoming males or even by other females from within the group is influential in the formation of female groups. Females can reduce the potential risk of infanticide by associating with group males and sharing their protection along with other females in the group. Infanticide is expected to be of the highest significance in dispersal-egalitarian groups. Females in these social groups are not related and therefore do not have the coalitionary support of kin in the defense of infanticidal males or females as do the other three female philopatric categories (Isbell and Young, 2002; Sterck *et al.*, 1997).

1.5 Feeding Competition

1.5.1 Food Distribution

Competition for food is suggested by all of the proposed ecological models as being an integral part in the determination of social structure and of female relationships. These statements are based on the assumption that food distribution affects primate social behaviour. The terms 'patchy' and 'clumped' have been introduced to the literature in order to categorize forms of food distribution and the resultant form of feeding competition. Unfortunately, these terms have no set parameters and vary from study to study (Isbell and Young, 2002). What categorizes an area of food as patchy and what categorizes it as clumped? These factors undoubtedly vary from population to population, in different environments and degrees of food abundance. Measures have been conceived to calculate resource abundance by the measurement of tree crown size and leaf, flower and fruit count estimations (Janson, 1988). Such measures might aid in the comparison of relative food abundance and distribution, but does not lend credence to the theoretical generalizations and assumptions of 'patchy' and 'clumped'.

Foods that are patchy are thought to be indefensible, and evenly spread out over a given distance. Clumped foods are more randomly spaced and take up a small enough area that one or more animals can defend the resources it offers; resulting in scramble and contest competition respectively (Isbell *et al.*, 1999; van Schaik, 1989). In addition to the distribution of food, food quality and the primates' diet are also relevant to feeding competition. These models assume food quality to be either high or low; high quality food being more desirable and thus more readily defended. Again, exceptions exist when attempting to generalize behaviour based on an uncontrollable ecological element.

Perhaps due to climatic variations, the usual desired, high quality foods might not be available forcing primates to subsist on lower quality resources. Could this force a population to modify its social behaviour in order to ensure survival? Another related assumption is that primate species have characteristic diets and search out resources of a particular quality (Strier, 1994). This assumption has been correlated with body size and other morphological traits (Kay, 1984), but again could vary in the event of resource depletion due to natural or unnatural environmental forces affecting food type, quality and abundance.

1.5.2 Food Packaging

If an item of food can be taken from an individual that item is said to be usurpable (Isbell and Pruetz, 1998; Isbell *et al.*, 1999). Such behaviour would generally take place between group members of differing rank, with the individual of higher rank taking the item from the individual of lower rank. Usurpability may be a function of food abundance and the amount of time needed to deplete a food site (Isbell and Pruetz, 1998). Foods with long depletion times can include seeds, fruits and gums. Foods with typically short depletion times include arthropods that can be ingested quickly (and are thus difficult to usurp). Other foods, such as leaves, are ubiquitous and may not be worth usurping (Isbell and Pruetz, 1998).

1.5.3 Feeding Proximity

Another factor that can affect feeding competition other than the qualities of the food source itself is the distribution of group members while feeding. Having neighbours while feeding induces greater feeding competition - they can limit resource availability and affect feeding efficiency (Sauther, 1993). The rank of feeding neighbours can also contribute to feeding competition. With high rank comes the ability to displace lower-ranking individuals from desirable resources, such as feeding sites. Low-ranking individuals may then be forced to devise alternate feeding strategies in order to obtain their required resources (Soumah and Yokota, 1991). The size of a feeding site in relation to group size can also have an effect on feeding competition. If a patch or site is crowded, low-ranking individuals may be forced to feed elsewhere, wait until others have finished feeding or avoid the site completely (Whitten, 1984; Saito, 1996).

1.5.4 Cross-Specific Examples

Macaques (Macaca sp.)

The degree of observed feeding competition is dependent upon the type of food consumed by Japanese macaques (*Macaca fuscata*) (Aureli *et al.*, 1992; Saito, 1996). More aggression is witnessed in the presence of novel foods (Aureli *et al.*, 1992) and at crowded sites (Saito, 1996). Rank becomes more apparent when large feeding patches are not available and low-ranking females must either avoid the site (Saito, 1996) or devise a feeding strategy to avoid encounters with high-ranking females (Soumah and Yokota, 1991). The need to create different feeding strategies is evidenced by the fact that food diversity is higher for low-ranking females than for higher-ranking females (Saito, 1996).

In Taiwanese macaques (*Macaca cyclopis*), a linear female dominance hierarchy was determined, as well as the presence of contest feeding competition (Su, 2002).

Agonism was present more often in feeding patches than outside feeding patches only in the Spring season - likely an interim period in food production and availability. Aggressive threats were concluded as being a more effective method of feeding-related competition than displacements: aggression led to the aggressed being deprived of food more often than when the subject of a displacement. High rank in these groups means less time spent foraging, and less time spent feeding on resources with large crown sizes than with females of lower rank.

Baboons (Papio sp.)

Barton and Whiten (1993) found, in their study of female olive baboons (*Papio anubis*), that rank had an effect on feeding competition, and that this effect was more significant when foods became less abundant in the dry season (Barton and Whiten, 1993). Foods that indicated high levels of feeding competition based on social behavioural observations demonstrated differences in feeding rates relative to rank - those with higher rank had increased access to the more desirable foods (Barton and Whiten, 1993). Within group, contest feeding competition was found to create a stable dominance hierarchy in this group.

After studying four groups of Chacma baboons (*Papio ursinus*) whose group sizes and compositions differed and whose home ranges overlapped extensively, results indicated that contest competition for food was low both within and between groups (Cowlishaw, 1994). Even though food availability was high, scramble competition took place (Cowlishaw, 1994). These findings could be indicative of an egalitarian social structure or perhaps of nonusurpable food sources.

Ringtailed Lemurs (Lemur catta)

Wrangham (1980) predicted that large groups of females should have high reproductive success since they would have higher competitive foraging success over smaller groups. This was found to be the case with the ringtailed lemurs at Beza Mahafaly Special Reserve, when there were 5 or fewer females in a group (Gould *et al.*, 2003). More than 5 adult females may create too much within-group feeding competition, negatively affecting births. Group fissioning was documented when group size became too large and during periods of extreme drought. However, fissioning could result in difficulties for the smaller, fissioned group, as they would be more easily displaced at feeding sites if their home ranges significantly overlapped (Gould *et al.*, 2003).

Again at Beza Mahafaly, and focusing on feeding behaviour, 86% of the total agonistic events documented occurred over access to food (Sauther, 1993). The level of agonism displayed varied by sex: females showed higher mean frequencies of agonism than did males (for most months). In the wet season, females exhibited more feeding agonism than would be expected by chance alone. In the dry season females in a large sized group demonstrated the expected level of female-female agonism, but the amount of female-female agonism in a smaller sized group was greater than anticipated (Sauther, 1993). Females showed higher mean frequencies of aggressive agonism than did males in the wet season and greater nonfood agonism in the dry season. In all seasons, the frequency of female-female feeding agonism was greater than what was expected by chance based on the number of potential adult female partners in each group.

Nonaggressive feeding agonism was almost as expected in the wet season but more frequent than expected in the dry season (Sauther, 1993). Having neighbours while feeding induces greater feeding competition - they can limit resource availability and affect feeding efficiency. Males tended to feed at a greater distance from others than did females (Sauther, 1993). During the dry season males and females had similar numbers of nearest neighbours but males continued to have a greater number of more distant neighbours. Males fed most often near low-ranking females (Sauther, 1993).

1.6 Optimal Foraging Theories

Natural selection theory discusses at its core the fitness of animals; essentially their ability to survive and reproduce. Fitness is dependent upon a number of factors, one being sufficient food intake (Pyke *et al.*, 1977). Optimal foraging explains the consumption of food through an energetic cost-benefit analysis – individuals should be looking to maximize their net rate of energy intake – in terms of behavioural decision making (Pyke *et al.*, 1977; Manning and Dawkins, 1992; Ahlborn and Rothe, 1999). Again, once an animal has consumed the majority of the food in a patch, is it energetically more worthwhile for them to travel to a less depleted patch? There are presumably many factors involved in this decision: Which food patch should be the next destination? How far away from the current patch is the other food source? Would more energy be expended traveling than remains in the current patch? Is there a risk of encountering a predator if a move is made?

Optimal foraging theories assume that knowledge of resources located elsewhere exists within animals. This has been documented in primates through longitudinal studies which have demonstrated consistent feeding paths (e.g., black-chested moustached tamarins (*Saguinus mystax*) and saddleback tamarins (*Saguinus fuscicollis*) in Garber, 1989; brown capuchins (*Cebus paella*) in Janson, 1998; yellow baboons (*Papio hamadryas cynocephalus*) in Pochron, 2005). Primates learn the locations of food resources and are able to travel efficiently between them. Optimal foraging also assumes that individuals should be searching for their optimal diet; the foods available at that time that will provide the best quality diet, energetically speaking (Pyke *et al.*, 1977; Pochron, 2005). Searching and handling time of food items must be considered as these are time consuming, and thus energy consuming, activities. The best foods are rich in nutrients and calories and are easily handled (Ahlborn and Rothe, 1999). These factors are weighed when deciding if a food will be eaten or if it will be ignored (Pyke *et al.*, 1977).

As foods are commonly seasonal and are thus scarce during certain times of the year, individuals respond by widening their food choices, or diet. Resources can be added or dropped from a forager's diet depending upon their availability (Jones, 2004). This can lead to the formation of a preferred-ranking of foods that can vary depending upon selection: certain foods may have greater value during specific periods (Pochron, 2005). Foods may become scarce due to reasons other than seasonal changes. Foragers may encounter certain food resources less often due to human impact, causing landscape or climate change (Jones, 2004). If a food that may have been ranked highly on a diet is simply encountered less frequently it will naturally be consumed less.

1.7 Questions and Hypotheses

This project will examine numerous questions and hypotheses and their relationship to free-ranging adult female *Lemur catta* in their natural habitat at the Beza Mahafaly Special Reserve, Madagascar. Two groups were observed, one whose territory is within the forest reserve boundary, the other whose range is in degraded forest outside of the reserve. Although some questions will be examined at the individual level, most of the analysis will take place between the two study groups and the differences between their habitats. These questions include:

1) How do the habitats of the two groups differ?
2) a. How do the diets of the adult females within the reserve differ from the diets of those outside of the reserve?
   b. What foods are available to the different groups?
3) What effect does rank have on the sorts of foods being consumed?
4) a. Does the rate or degree of agonism exhibited by females vary depending upon the type of food being consumed?
   b. Does the rate or degree of agonism vary between habitats?
5) Does the size and species of food being consumed affect female feeding competition?
6) Does the distribution and scarcity of food resources have an effect on female interactions related to feeding competition?

Based on these questions, the following hypotheses were generated and will be analyzed and discussed in this thesis:

In order to develop a valid understanding of the interactions and feeding competition that occurs between adult females, it is first necessary to document the actual composition of their diets. The eastern, riverine portion of the Beza Mahafaly Special

Reserve is composed of dense, lush vegetation (Sauther, 1992; Gould, 1996a). Outside of the reserve towards the south, the vegetation, and subsequently the available plant food resources for the lemurs, becomes sparse due to human influence.

Hypothesis 1: Females within the reserve with home ranges in the dense vegetative areas will have a diet with more numerous food resources that have a high level of distribution; females outside of the reserve will have a diet composed of fewer types of food resources that have a lower level of distribution.

The dominance ranking of an individual has been shown to be positively correlated with their access to such resources as resting sites, grooming partners and feeding resources (e.g. Japanese macaques, Aureli *et al.*, 1992; Hanuman langurs, Borries, 1993; olive baboons, Barton and Whiten, 1993; ringtailed lemurs, Gould, 1996b; vervets, Isbell *et al.*, 1999).

Hypothesis 2: In both groups, high-ranking females will have increased access to more desirable foods over low-ranking females.

In lush areas, primates would presumably need to travel shorter distances in order to obtain sufficient nutrients than those in sparsely vegetated areas. If more time must be devoted to searching for food sources and traveling to these sources then there would be less time available to partake in socially cohesive activities, such as grooming. In a situation where nourishment is scarce, less time is devoted to affiliative social behaviours and competition for available resources is high, it is thought that the frequency and degree of observed agonism will also be elevated.

Hypothesis 3: The nonreserve group will have a higher frequency and a higher degree of within group agonistic interactions between adult females than will the reserve group.

Certain foods are considered to be of higher quality than others, such as ripe fruit over mature leaves (Janson, 1988; Janson and Chapman, 1999). High quality foods, such as ripe fruit, can be patchily dispersed and are seasonally and temporally variable. These highly desirable foods can result in an increased level of competition between females for their acquisition (Glander and Teaford, 1995; Sauther *et al.*, 1999). Foods that are readily available spatially and temporally may be of good quality, but they are also generally produced in amounts that can accommodate all members of the group, thus lessening the need for a high level of competition. Levels of agonistic feeding competition between adult females can therefore vary depending upon the sought-after food type.

Hypothesis 4: The amount and degree of agonistic feeding competition between adult females will increase in situations involving sparsely distributed, highly desirable foods compared to feeding situations with foods that are widely dispersed over space and time.

Foods consumed by primates come in various sizes. Some require the animal to hold the food, biting off one piece at a time. Others can be placed in the mouth in their entirety in a single bite. With the latter, it is difficult for another individual to remove the food from the individual feeding, short of taking the item out of the individual's mouth (Isbell, 1991; Isbell *et al.*, 1998). Conversely, larger foods that require more processing time can be more easily usurped. This general idea can also be applied to feeding sites. If a feeding site is composed of bite sized food items, individuals can move through a patch more rapidly, feeding as they go. Patches containing larger foods that necessitate more than a single pick-and-eat for consumption can be more easily monopolized by more dominant individuals (Isbell, 1991; Isbell and Pruetz, 1998; Isbell *et al.*, 1999; Isbell *et al.*, 1998).

Hypothesis 5: Feeding on foods that come in small, bite sized pieces will result in less feeding competition between adult female *Lemur catta.*

1.8 Summary

The goal of this research is to examine the behaviour and diets of adult female ringtailed lemurs living in different habitats, and to discuss the findings in terms of resource competition and optimal feeding strategies. This section was meant to serve as an introduction to the research goals, the study species and some of the theories relevant to this area of primatological study. Chapter 2 discusses the methods used in this project. Chapter 3 presents the main findings after data analysis. Chapter 4 discusses the results in terms of previous work on female feeding competition, resource scarcity and optimal foraging. The fifth and final chapter is a summary and conclusion for this thesis.

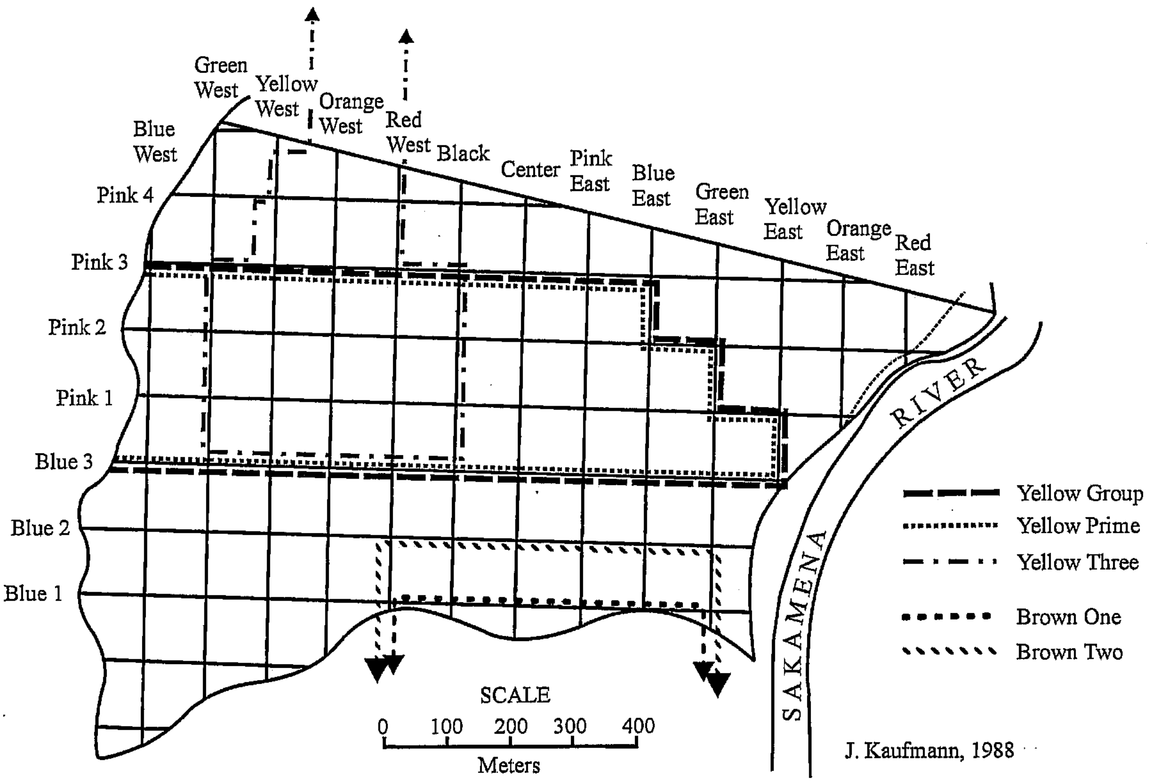
Chapter 2 – Research Methodology

2.1 Study Site

My study took place from July to September, 2004 at the Beza Mahafaly Special Reserve. The site is located in southwestern Madagascar at 23°30' S latitude and 44°40' E longitude (Sussman, 1991). Declared a Special Government reserve in 1986 after its establishment in 1978 (Sauther, 1992, Gould, 1997a), Beza Mahafaly was managed by the School of Agronomy at the University of Antananarivo, Madagascar at the inception of this research. However, by August 2004 the governing body of the research site had become ANGAP, the National Association for the Management of Protected Areas. ANGAP is a national government run organization, and was created in 1990.

Beza Mahafaly has a seasonal climate; the cool/dry season occurs from April to September and the hot/wet season extends from October to March (Sauther, 1992). Annual rainfall values have been recorded at 750 mm (Sussman, 1991) and 522 mm (Sauther, 1992), with only approximately 5% of the precipitation falling in the austral winter (Sauther, 1992). The mean high temperature for the region during the austral summer ranges from 34°C to 37°C and from 23°C to 32°C in the austral winter (Sussman, 1991; Sauther, 1992).

The research site is divided into two parcels. Parcel 2 is composed of 500 ha of dry adapted, desert-like Didierea forest (Sussman, 1991; Gould *et al.*, 1999). Parcel 1, where this study was conducted, contains 80 ha of gallery forest and is completely enclosed by a barbed fence (Sussman, 1991). The fencing does not limit the ringtailed lemurs to the reserve itself, nor does it keep out groups from outside the reserve's boundaries - the lemurs are free to travel within and outside of the reserve. The eastern portion of the study site is composed of riverine forest, which borders the Sakamena River. The forest becomes drier and xerophytic moving towards the west (Sussman, 1991). A trail system of one squared hectare paths, colour coded with marked trees, has been created to facilitate the mapping of the protected site area, as well as the locating of the lemur groups (Sussman, 1991). Figure 2.1 represents the trail system within Parcel 1.



J. Kaufmann, 1988

Figure 2.1 – Trail Map of Parcel 1, Beza Mahafaly Special Reserve.

Outside the fenced 1 km^2 area of the reserve, the forest continues along the template of the reserve; riverine forest remains closest to the banks of the Sakamena and the forest becomes more xerophytic moving westwards from the banks. The non-reserve forest is used by local people for multiple purposes. Trees are harvested for firewood and building materials, foot and ox-cart paths have been worn into the terrain due to repeated use, and livestock such as goats and zebus are allowed to graze relatively freely (Figure 2.2). These factors have caused the unprotected forest to become degraded: larger trees are more widely spaced than those within the reserve, scrub brush is more common than within the reserve and with the increased amount of space between vegetative groups there are more patches of exposed earth with no signs of growth.

Figure 2.2 – Zebus in the unprotected forest. (photo by A. Gemmill)

Human traffic in the region is quite frequent with approximately eight villages situated within a two hour walking distance (Ratsirarson *et al.*, 2001). Figure 2.3 provides an approximation as to the demography of the immediate area. A census conducted in 1993 found that there were approximately 2310 people consistently inhabiting the area around Beza Mahafaly (Ratsirarson *et al.*, 2001). This figure includes the Malagasy people who are employed by ANGAP to work at the Beza Mahafaly camp.

In the research period of 2004 there were six paid employees working and living at the site. Along with their associated family members, the total Malagasy population of the camp was approximately twenty individuals. Beza Mahafaly is also used by various national and international researchers and scientists throughout the year.

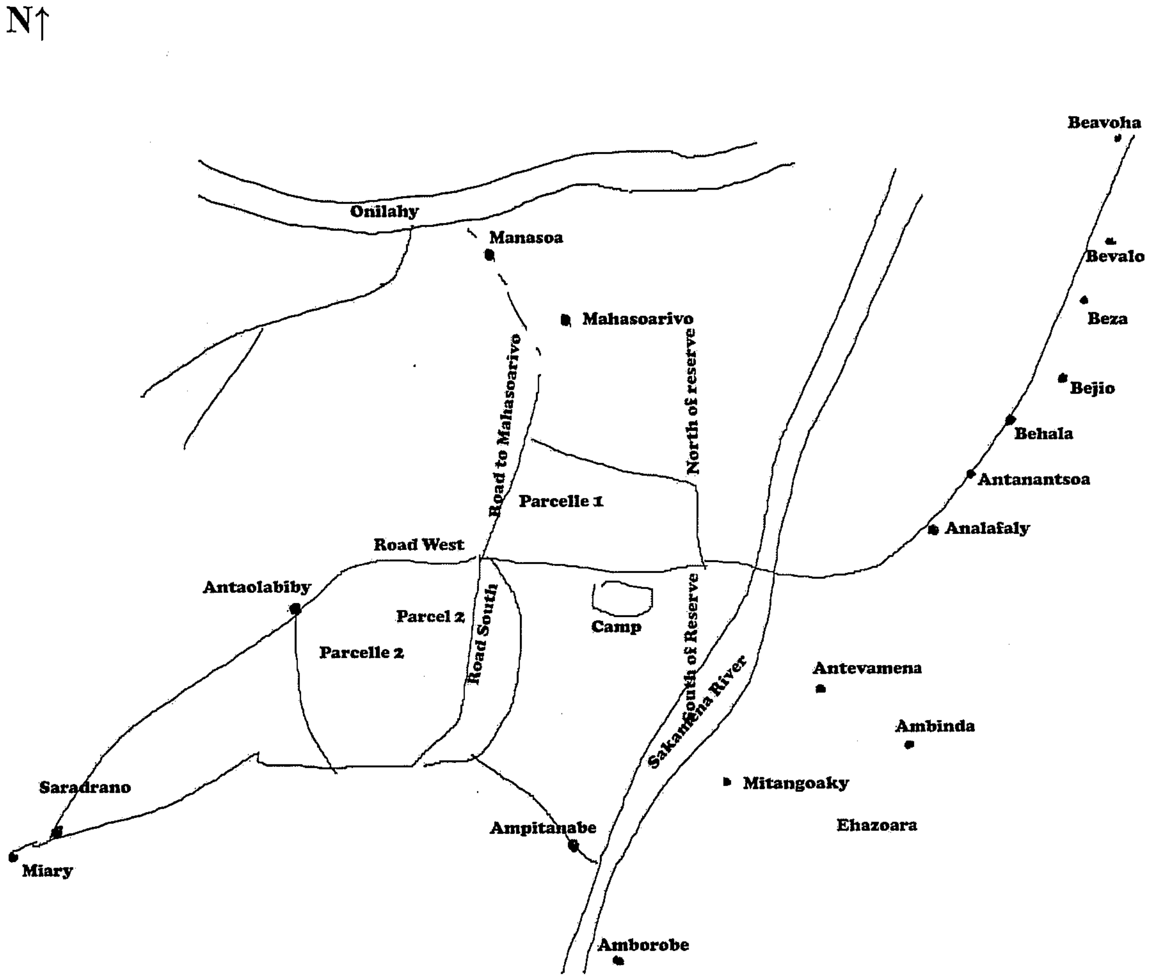


Figure 2.3 – Organization of villages surrounding Beza Mahafaly. (courtesy of Sauther, 2003)

2.2 Subjects of Study

2.2.1 Groups

There are approximately nine *Lemur catta* groups residing within the boundaries of the Beza Mahafaly Special Reserve (Sussman, 1991; Gould *et al.*, 1999). These groups have been monitored for numerous studies (i.e. Sussman, 1991, 1992; Sauther, 1991, 1992, 1998, 2002; Gould, 1994, 1996a, 1996a, 1997a, 1997b, 1999, 2000; Gould and Overdorff, 2002) and were the subjects of a longitudinal study that occurred from 1987 to 2003 (Sussman, 1991, Gould *et al.*, 2003). There are also ringtailed lemur groups that reside outside the reserve boundaries. The majority of these lemurs have not been well studied, and only within the past few years have certain external groups been collared for study (Cuozzo and Sauther, 2004, 2005).

For the purpose of this study, two groups with differing home ranges and habitats were selected. Groups were chosen after the collection of preliminary data during time spent as a field assistant for Dr. L. Gould from May to June 2004. Green group, a fairly well studied group located in the eastern, lush portion of the reserve was selected (see Figure 2.4). The group ranged from the Sakamena River to about 400 m west within the reserve. At times, Green group ranged to the opposite side of the river to raid the field of a local farmer.

The second group chosen for study was Black group, which resides to the south, outside of the western portion of the reserve (see Figure 2.5). Black group ranged from the western bank of the Sakamena River westwards to the research camp – a distance of approximately 500 m. Their home range included the area of the research camp, which they entered at least once daily.

Table 2.1 outlines the composition of each of the study groups. Age class was determined based on the primate's relative size within their cohort; body size distinctively varies between infants (0-6 months), juveniles (6 months – 1 year), subadults (1-2 years) and adults (>2 years) (Gould, 1996a). My study was conducted

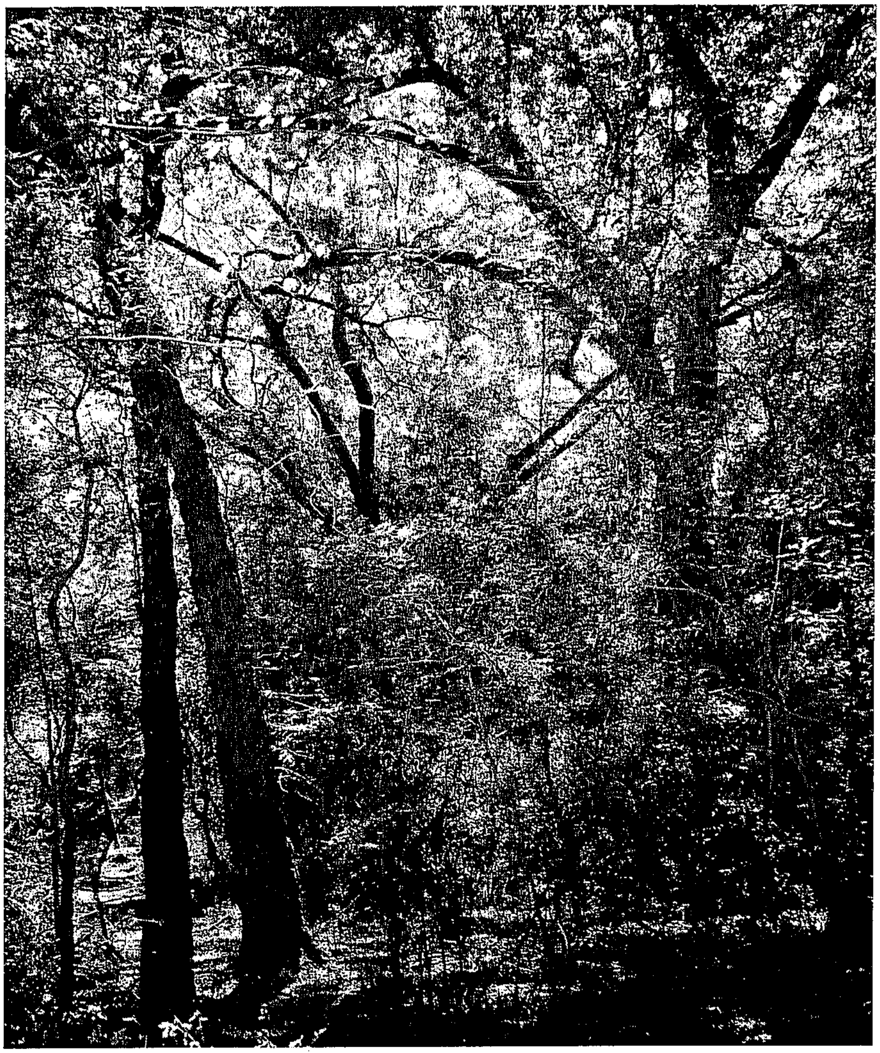


Figure 2.4 – Reserve forest within Green group's home range. (photo by A. Gemmill)

during late gestation; adult females had yet to give birth and were still in close contact with their ten-month-old juvenile offspring. Therefore there were no infants present, only juveniles, subadults and adults. Both Black group and Green group were composed of six adult females, the focus of this study, and had similar total group membership at sixteen and seventeen respectively, therefore, the variables group size and group composition did not affect the analysis (Table 2.1).

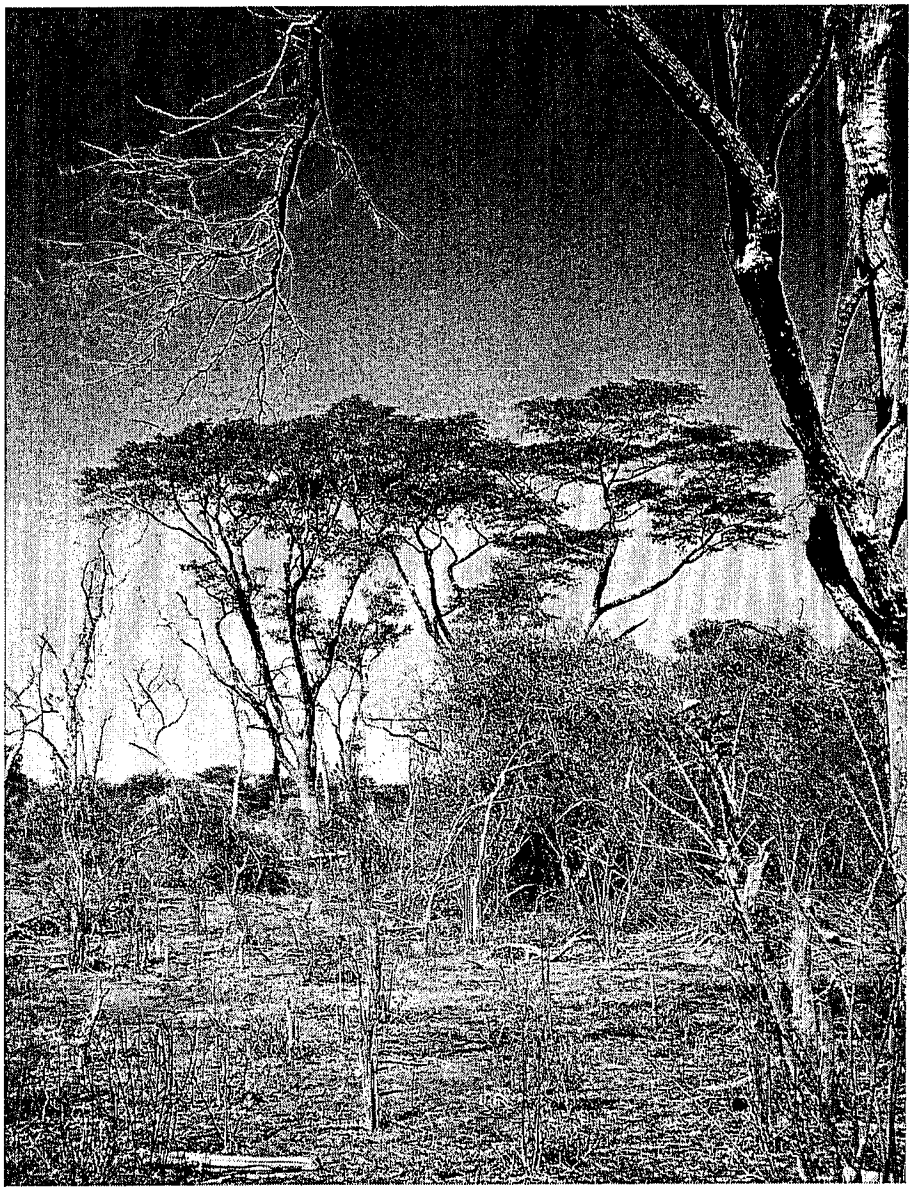


Figure 2.5 – Nonreserve forest in Black group's home range. (photo by A. Gemmill)

Table 2.1 – Study group composition.

Age/Sex Class	***Green Group***	***Black Group***	***Total***
Adult Female	6	6	12
Adult Male	5	5	10
Subadult	4	3	7
Juvenile	2	2	4
Total	17	16	33

2.2.2 Individuals

Adult female focal animals were individually identified based on their associated coloured nylon collars and diversely shaped and numbered tags. These collars have been used for identification purposes of Green group during prior research at the site (Sussman, 1991; Sauther, 1992, Gould *et al.*, 2005), whereas Black group was collared during field seasons in 2003 and 2004 (Cuozzo and Sauther, 2004, 2005). After preliminary research was conducted and I was familiar with the subjects, individuals could also be identified through distinguishing visual markings including facial features, unique pelage patterns or colourations, or any other distinctive visual cues. This was essential since at times tag numbers were not immediately visible. Adult males are also collared, but were not individually monitored and thus will be referred to collectively by their age/sex class. Immature ringtailed lemurs (subadults and juveniles) are not fitted with collars and will also be identified solely according to their age-sex class for the purpose of this study.

The six Green group females had all been fitted with green nylon collars with tags of differing shapes, colours and inscribed numbers from previous studies. They had been assigned names in past research years, which are listed in Table 2.2. Black group females wore black nylon collars with circular yellow tags that were each inscribed with a different number. These females had not been assigned proper names and therefore they will be referred to by their associated tag number (see Table 2.2). Black group adult female 110 can be seen in Figure 2.6 with her collar and tag.

Table 2.2 – Collared adult females within the study groups and their associated tag numbers.

Green Group Females	***Black Group Females***
Anise (Ani)	110
Cinnamon (Cin)	111
Clove (Clo)	112
Ginger (Gin)	116
Madeline (Mad)	121
Nutmeg (Nut)	432

Figure 2.6 – Black group female 110 sitting near camp. (photo by A. Gemmill)

As these groups have been the subjects of various studies over the past twenty years the lemurs are habituated to the presence of researchers, making it possible to unobtrusively observe the lemurs from a distance of approximately 1-2 metres.

2.3 Scheduling of Sample Sessions and Focal Selection

Research was conducted from July to September 2004 with the assistance of Ben Temple, a recent graduate of the University of Victoria Anthropology B.A. program. This time frame encompassed the middle and late gestation periods of adult female *Lemur catta* at Beza Mahafaly Special Reserve. Data were collected on a four-day schedule: one day with Green group, the next day with Black group, etcetera. Upon the completion of four days of data collection, a "non-forest" day was taken to evaluate the status of the research and to rest. Data were gathered, on average, during the morning and afternoon periods of lemur activity (0800 to 1130 and 1400 to 1800 respectively) (Gould, 1996b). On some workdays the lemurs were not easily located, thus collection began as soon as the correct group was in sight. As the study progressed, the groups would at times settle into their sleeping trees as early as 1600h: timing of data collection followed the activity patterns of the study groups.

Data collection for this study followed a widely used random sampling schedule, a method first proposed by Altmann (1974). My assistant and I chose a different adult female to follow in the group at the onset of the data collection day. At the end of the prescribed focal animal data collection session of fifteen minutes, another adult female was selected. Each chosen female could not be one of the two who had been followed in the prior data collection session. With a limited time period for this study, it was found to be too difficult to impose any further restrictions on focal animal selection as each group had only six females. On each non-forest day, tallies were taken of the follows conducted on each female, including the time of day that they took place. This method was undertaken to ensure that the focal animal samples were distributed evenly throughout the different times of the day, and to attempt to prevent individuals from being over-represented in the data set. Necessary allowances for observer rest periods, climatic conditions and the time required to locate the focal individuals were assessed daily.

2.4 Data Collection

2.4.1 Data Collectors

In addition to my assistant and I, two local people from the region also assisted with this project. One local assistant, Delaprairie, collected data on the form, direction and outcome of interactions between adult females. The other, Dada, maintained a record of plant species consumed by the lemurs. Both Malagasy assistants helped identify the plants consumed by adult females as well as plants censused during phenological sampling. Phenological analysis involves examining biological phenomena in terms of climatic conditions (Janson and Chapman, 1999) – this involved the estimation of the percentage of a plant that was covered by leaves, fruit, and/or buds during my study, therefore in the dry season. All three assistants helped locate the lemur groups first thing in the morning and were involved in the collection of phenological data.

2.4.2 Behavioural Recording

Continuous focal animal and *ad libitum* sampling techniques were used in this study (Altmann, 1974; Martin and Bateson, 1993). Continuous time focal animal samples were timed by a stopwatch for a duration of 15 minutes. All focal animal behaviours were recorded during this time including interactions that occurred involving any other individuals, group or non-group members (See Appendix A for a sample data collection sheet). The identities of individuals involved in interactions with the focal animal were recorded. The time of the occurrence of behavioural changes during the focal session was noted. If the focal animal was out of the observer's sight for a period exceeding 10 seconds, the stopwatch was paused in an attempt to re-establish visual contact (Lehner, 1996; Paterson, 2001). If the focal animal was not relocated after a period of 5 minutes, the sample was discarded and a new focal individual was selected. If visual contact with the focal animal was renewed, the stopwatch was restarted (noting the duration of the pause) and the data recording session continued. A total of 14,355 minutes or 239.25 hours of usable focal animal data was collected. The number of sessions per animal varied from 79 to 81 (Table 2.3).

Table 2.3 – Total number of focal animal observations and observation minutes per adult female.

Female	***# Sessions***	***# Minutes***
110	79	1185
111	79	1185
112	79	1185
116	80	1200
121	80	1200
432	80	1200
Ani	80	1200
Cin	81	1215
Clo	79	1185
Gin	80	1200
Mad	80	1200
Nut	80	1200

Ad libitum techniques were used to keep track of any noteworthy interactions of non-focal individuals that were observed by the researcher while conducting the focal sample. This information will be utilized as anecdotal and will not be statistically analysed.

2.4.3 Ethogram

Ethograms have been compiled based on observations of *L. catta* behaviour in past research projects (Jolly, 1966; Taylor, 1987; Gould, 1992). An ethogram is a listing of the observed behavioural repertoire specific to a species, and includes appropriate definitions and explanations of these behaviours (Jolly, 1966). Preliminary observations made while working as a research assistant from May to June 2004 were used to make adjustments to these accepted ethograms to better suit this particular study. The updated ethogram, or listing of behaviours and behavioural categories used in this study is located in Appendix B.

2.4.4 Feeding Behaviour

Following Sauther (2002), the scoring of feeding behaviour in this study was restricted to the actual ingestion of food items. This definition does not include the acts of searching for and handling of food items - these behaviours will be recorded as foraging. Type of food being eaten in terms of part and species was documented. Upon observing feeding behaviour it was noted that only plant material necessitated specificity of part being ingested. Plant parts were identified as leaves, buds, fruit and flowers. The following are the food categories used in this study: leaves, buds, flowers, fruit, wood, insects, dirt, feces (dog and zebu), human food, bird's nest and spider web. If the plant species was not identifiable by the researcher or the local field assistants the food item was described in as much detail as possible for future identification by another local flora expert (Isbell *et al.*, 1998). Wood includes both sticks and bark found on the ground and that which had been pulled off of a living plant. Insects were rarely consumed and it was done rapidly therefore identification was impossible. Human food included fruits and vegetables not attainable by the ringtails within their forest habitat as well as peelings from human cooking areas in the camp. The lemurs in Black group were observed feeding on the following human food scraps: sugar cane, banana, carrot and sweet potato.

Leaves, buds, flowers and most fruit were picked up one at a time by the lemur's mouth. *Tamarindus indica* fruit, locally known as kily, come in the form of seeds within a long pod. They require more processing time and are commonly held to the mouth by the forelimbs. These fruit are also at times licked as the juice can escape to the outside of the pod if it has already been broken in to. When lemurs were observed licking kily fruit it was not recorded as a feeding bout as the fruit was not being chewed and swallowed.

A feeding bout was said to commence once the animal began to feed and terminated when feeding, chewing and swallowing had not occurred for more than 10 seconds (Isbell *et al.*, 1998). A new feeding bout was recorded when the focal animal moved two body lengths between foods or when the food type being fed upon had changed (Isbell *et al.*, 1998). The relative size of the food item being consumed was recorded as either usurpable or nonusurpable (large or small respectively) (Isbell and Young, 2002).

A food site or patch is defined as any location where the focal individual stops to eat (Isbell *et al.*, 1999). For this study the path taken by a group or female to reach food resources was not considered. A group or individual could presumably travel through one food patch without feeding to reach another, but details were recorded only for areas in which feeding was actively taking place. Food patches were classified as small, medium or large in size, based upon the relative size of the patch in comparison to other resource patches at the site (Barton and Whiten, 1993; Overdorff *et al.*, 2002). Food patches were also described as either isolated or contiguous, based on the description provided in Saito (1996) for interspecies distance. A food type was considered isolated if there were no conspecifics within a 30 m radius from the trunk. The food was considered contiguous if there were conspecifics within a 30 m radius from the trunk.

2.4.5 Social Behaviour

Recorded ringtail social behaviours, affiliative and agonistic, are listed in Table 2.4. These behaviours are listed in the ethogram in Appendix B.

Table 2.4 – Recorded social behaviours.

Affiliative	***Agonistic***
one-way groom	subchit
mutual groom	displace
sit near	hit/cuff
feed near	push
Huddle	lunge/charge
Nuzzle	chase
Play	bite

The behaviours in Table 2.4 are interactional and thus required the participation of at least one individual other than the focal animal. The initiator and the recipient of the behaviour were noted. This is referred to as the direction of the behaviour. In order for a lemur to be considered near the focal animal they had to be at a distance of one metre or less. For agonistic behaviours the context of the interaction was also recorded. These were labeled as one of the following: feeding, social, drinking, resting, intergroup and unknown. If an agonistic encounter occurred while one of the participants was engaged in one of these forms of behaviour the interaction context was so categorized.

2.4.6 Determination of Rank

The dominance rank and subsequent hierarchy of the adult females in each study group was decided based on the recording of the following behavioural interactions: approach/retreat interactions, displacements, directions of agonistic and submissive signals and initiation and reception of affiliative interactions (Whitten, 1984; Gould, 1996a, 1996b; Saito, 1996; Zucker and Clarke, 1998; Manson *et al.*, 1999). In order to establish the relative ranks between the adult females, a dominance matrix has been constructed for each group (Martin and Bateson, 1993; Paterson, 2001). From these data, it is possible to discuss the prevalence of the dominance ranking system within each group as being either strong, weak or absent (Isbell, 1991).

2.4.7 Habitat Diversity – Quadrat Sampling

In order to determine the prevalence of tree species within the study area, and to facilitate comparison between the distribution and availability of tree species within the ranges of the ringtailed lemur study groups, quadrat samples or sample plots were taken. Eight 25 m^2 areas were selected in the home ranges of each of the study groups. Quadrats were measured with a premeasured piece of string, and the corners of the square were flagged (Paterson, 2001). The species within the quadrat were identified and counted, and all trees with a trunk circumference greater than 4 cm were subject to the following botanical measurements: diametre at breast height, crown diametre, height, crop coverage, and degree of crop ripeness (Koenig *et al.*, 1998; Janson and Chapman, 1999). For each completed quadrat census, the following ecological variables were calculated:

a) Relative Abundance: calculated by dividing the number of individuals of species 'x' by the number of individuals of all species.

b) Basal Area (BA): total area of species 'x'. The area of each tree was calculated by following these equations:

    i. circumference/π = diameter;

    ii. diameter/2 = radius (r);

    iii. πr^2 = area occupied by the tree.

c) Relative Basal Area: total basal area of species 'x' divided by the total basal area of all trees in the sampled area.

d) Dominance (Dom): calculated by dividing the total basal area of species 'x' by the total area sampled – for this study, 200 m^2.

e) Relative Dominance: dominance value of species 'x' divided by the sum of the dominance of all species.

The percentage of the 25 m^2 area that was covered by growth was recorded and the presence and relative amount of any non-plant objects such as human garbage or zebu feces was noted.

2.5 Data Analysis

2.5.1 Data Storage

In the field, data were recorded into spiral-bound notebooks. Data recording followed the method outlined in the sample data collection sheet found in Appendix A. Upon return from Madagascar, data were entered into Microsoft Excel (Microsoft, 2002) and were subsequently transferred to SPSS version 12.0 (SPSS, 2004) for statistical analysis.

2.5.2 Statistical Data Analysis

The following chapter presents a statistical analysis of the data collected for this study. Phenological records were evaluated using descriptive statistics, and by qualitative analysis. Adult female behaviour was also subject to descriptive analysis, such as converting observational frequencies to hourly rates, in order to facilitate within group and between group comparisons due to variability in total observation times per animal.

With the small sample sizes in this study (limited number of adult female subjects – six per group), nonparametric statistics were used to analyse the data. Nonparametric statistics, although slightly less powerful than parametric statistics, are free from the assumptions that accompany parametric measurements making them more robust for the type of data collected in this study (Martin and Bateson, 1993).

Through nonparametric analysis the aforementioned hypotheses presented in Chapter 1 were tested. For all tests, the minimum acceptable level of significance (α) was set at 0.05. As the questions asked seek to examine the possible existence of a difference between different sets of data and do not suggest a specific direction that the difference should take (i.e. smaller than or greater than), analyses were two-tailed for all tests. Pearson's Chi-Square test for independence is used to discuss whether a relationship exists between two variables. This test is useful for nominal data (Evans, 1998). To determine if there is a significant difference between the scores, such as rate of feeding behaviour of two unrelated samples (for example between adult females in Green group and adult females in Black group) the Mann-Whitney U tests was employed. The Mann-Whitney U test is the nonparametric equivalent to the parametric Two Sample t Test (Martin and Bateson, 1993). To determine whether there is a significant difference between more than two unrelated, unmatched samples, Kruskal-Wallis one-way analysis of variance was used. This test is the nonparametric equivalent to the parametric analysis of variance (ANOVA) (Martin and Bateson, 1993).

Chapter 3 – Results

3.1 Study Group Habitat Variation

3.1.1 Plant Species

The habitats of the two study groups are very different in appearance. Green group's home range within the reserve boundaries is lush, dense forest with few areas of visible sky through the canopy. Black group's home range outside the reserve consists of sparse patches of trees, scrub brush, areas grazed by livestock, and includes the Beza Mahafaly camp. In order to quantitatively analyse and compare the two habitats, eight 25 m^2 plots were randomly sampled from within the home range of each group. Table 3.1 lists the recorded species from each area, providing the plants' vernacular (Mahafaly) name, scientific name and family, and indicates whether the plant species is found in Green group's range, Black group's range, or in both ranges.

Table 3.1 – Recorded Plant Species by Group Range.

Mahafaly Name	**Scientific Name**	**Family**	**Green Group**	**Black Group**
Ahibe	*Panicum maximum*	Poaceae	*	*
Akaly	*Crateva excelssa*	Capparidaceae	*	*
Akata			*	*
Alimboro	*Albizzia polyphylla*	Mimosaceae	*	
Angamay	*Tridax procumbens*	Asteraceae	*	
Angarafke				*
Atapiso				*
Bakoa	*Strychnos madagascariensis*	Loganiaceae	*	*
Basy	*Capparis spinosa*	Capparidaceae	*	
Basy (2)	*Cesalpinia bonduc*	Cesalpinaceae		*
Bea			*	*
Bokabe	*Marsdemia sp.*	Apocynaceae	*	*
Daro	*Commiphora aprevalii*	Burseraceae		*
Engesty				*
Famata	*Euphorbia tirucallii*	Euphorbiaceae		*
Fandriandambo	*Physena sessiliflora*	Flacourtiaceae	*	*
Farehitra	*Uncarina grandidieri*	Pedaliaceae	*	
Farihosy				*

Fatinboay	*Cirsium sp.*	Asteraceae	*	
Fofotse	*Pentarhopalopilia sp.*	Opiliaceae		*
Folimbity				*
Foribitike				*
Hadravala				*
Hazombalala	*Syregada chauvetiae*	Euphorbiaceae	*	*
Ipomaea	*Ipomoea sp.*	Convolvulaceae	*	
Karimbola	*Dialium madagascariense*	Fabaceae	*	*
Katrafay	*Cedrelopsis grevei*	Ptaeroxylaceae		*
Kililo	*Metaporana parvifolia*	Convolvulaceae	*	*
Kily	*Tamarindus indica*	Cesalpinaceae	*	*
Kotipoke	*Grewia grevei*	Tiliaceae		*
Kotika	*Leptolaena sp.*	Sarolaenaceae		*
Lahiriky	*Flacourtia ramontchi*	Flacourtiaceae		*
Lamotimboay	*Xeromphis sp.*	Rubiaceae	*	*
Maintifototse	*Grewis sp.*	Tiliaceae	*	*
Mantsaka	*Tarenna pruinosum*	Rubiaceae	*	*
Roihavitse	*Acacia sp.*	Mimosaceae		*
Raketa	*Opuntia sp.*	Cactaceae		*
Robontsy	*Acacia polyphylla*	Mimosaceae	*	
Roy	*Acacia minutifolia*	Mimosaceae		*
Sakoan'akoho			*	
Sangira	*Neotina coursii*	Sapindaceae		*
Sasavy	*Salvadora angustifolia*	Salvadoraceae	*	*
Sele	*Grewia triflora*	Tiliaceae	*	*
Somontsy	*Kigelianthe madagascariensis*	Bignoniaceae		*
Tamboro	*Bakerella sp.*	Loganiaceae	*	*
Tamenaka	*Combretum sp.*	Combretaceae	*	*
Tangatanga		Euphorbiaceae		*
Tarasoampoa			*	
Taritarike	*Combretum albiflorum*	Combretaceae		*
Tombokapa				*
Totonga	*Aristolochia bernieri*	Aristolochiaceae		*
Tratramborondreo	*Grewia leucophylla*	Tiliaceae		*
Tratriotse	*Acacia bellula*	Mimosaceae	*	
Tsarihosy			*	
Tsingilifilo			*	*
Tsiratsira	*Pluchea bojeri*	Asteraceae	*	
Tsompia	*Pentopetio sp.*	Apocynaceae	*	*
Vahimasy	*Cynanchum compactum compactum*	Asclepiadaceae		*
Vahipinde	*Hippocratea angustifolia*	Hippocrateaceae		*
Valiandro	*Quisivianthe papionae*	Meliaceae	*	*
Velai		Convolvulaceae		*
Voamena	*Abrus precatorus*	Papilionaceae	*	*
Vory			*	
Votapose				*

Species diversity in this study is defined as the total number of different plant species within the sampled area. Sampling conducted in Green group's range yielded a species diversity of 35; species diversity in Black group's range totaled 51. Of those plants included in species counts within quadrats, those with a trunk circumference equal to or greater than 4 cm were recorded for further analysis (Paterson, 2001). Features of the sampled habitats were also documented for discussion.

3.1.2 Green Group Territory

Within the eight 25 m^2 quadrats surveyed in Green group's home range a total of 21 trees with a circumference equal to or greater than 6 cm were measured. Table 3.2 presents the results from the phenological calculations.

The most abundant measurable tree in these quadrats was Kily (*Tamarindus indica*) with five specimens, followed by Maintifototse (*Grewis sp.*) with three. Kily were also the largest trees as they have the highest relative basal area at 0.75 m^2. Although there were only two Tsingilifilo (Scientific name not available) as opposed to the second most abundant Maintifototse with three, the Tsingilifilo trees measured occupied the second greatest relative basal area at 0.22 m^2 (Maintifototse had one of the smaller relative basal areas at 9×10^{-4} m^2). The tree species with the lowest relative basal area and dominance value was the Mantsaka (*Tarenna pruinosum*) (BA= 2×10^{-4} m^2, Dom=3×10^{-6}). The Kily specimens measured had 75% dominance relative to the other measured species; Tsingilifilo had a relative dominance of 22%; all other species had less than 1.5% relative dominance.

Average height was calculated for each measured species. The height of each specimen was estimated between the four researchers. The tallest of the measured trees was Kily with an average height of 18 m in the gallery forest. This is double the average height of the second tallest species, Akaly (*Crateva excelssa*) at 9 m. The shortest species are Tsingilifilo and Tratriotse (*Acacia bellula*) both at a measured height of 2 m.

All measured trees were subjected to an estimation of crown coverage. This was recorded as a percentage – the estimated portion of the crown that was covered by leaves, fruit, and/or flowers. Specimens with< 35% leaf crown coverage were: Lamotimboay (*Xeromphis sp.*), Sele (*Grewia triflora*) and Mantsaka. Specimens with a leaf crown coverage of <70% were: Maintifototse, Akaly, Valiandro (*Quisivianthe papionae*), Vory (Scientific name not available), Hazombalala (*Syregada chauvetiae*). The highest leaf crown coverage was observed in Kily with an average of 76% and Tsingilifilo with 73%. The only species that was observed fruiting was Kily with an average fruit crown coverage of 23%. No specimens were documented at a flowering phase.

The 200 m² sampled area within Green group's home range included many plant species that were too small to be included in the measurements, observable in the discrepancy between the total species recorded and total species measured listed in Tables 3.1 and 3.2 (35 and 11 respectively). The quadrat samples taken within the reserve boundaries provided various species of vine covering portions of the area. Low-level vine coverage, < 5%, was found for the following species: Tamboro (*Bakerella sp.*), Tsarihosy (Scientific name not available), Tsompia (*Pentopetio sp.*), and Ipomaea (*Ipomoea sp.*). Only one species of vine, Basy (*Capparis spinosa*), was observed within the given area as having a higher level of coverage (> 5%).

Species (Mahafaly Name)	Abundance	Relative Abundance	Average Height (m)	Total Basal Area (m^2)	Relative Basal Area (m^2)	Dominance ($x 10^{-5}$)	Relative Dominance (%)
Kily	5	0.24	18	2.6	0.75	1000	75
Maintifototse	3	0.14	4	$3.0 x 10^{-3}$	$9.0 x 10^{-4}$	2	0.09
Akaly	2	0.10	9	$1.0 x 10^{-2}$	$3.0 x 10^{-3}$	5	0.29
Hazombalala	2	0.10	7	$5.0 x 10^{-3}$	$1.0 x 10^{-3}$	3	0.14
Sele	2	0.10	6	$5.0 x 10^{-2}$	$1.0 x 10^{-2}$	30	1.4
Tsingilifilo	2	0.10	2	0.76	0.22	400	22
Lamotimboay	1	0.05	6	$1.0 x 10^{-3}$	$3.0 x 10^{-4}$	0.5	0.03
Mantsaka	1	0.05	3	$6.0 x 10^{-4}$	$2.0 x 10^{-4}$	0.3	0.02
Tratriotse	1	0.05	2	$4.0 x 10^{-2}$	$1.0 x 10^{-2}$	20	1.1
Valiandro	1	0.05	5	$9.0 x 10^{-4}$	$3.0 x 10^{-4}$	0.5	0.03
Vory	1	0.05	8	$1.0 x 10^{-3}$	$3.0 x 10^{-4}$	0.5	0.03

Table 3.2 – Phenological characteristics of 11 species of tree found in quadrats sampled in Green group's territory.

Green group spent a significant amount of feeding time in the dry riverbed consuming Fatinboay (*Cirsium sp.*) leaves. A quadrat was thus conducted in 25 m^2 of this area. Counts yielded 137 Fatinboay, two Tsiratsira (*Pluchea bojeri*) and one Akata (Scientific name not available). There were also five piles of zebu feces. Green group was viewed on a number of occasions in the farmer's field on the opposite side of the Sakamena River from the reserve forest. Sampling in this 25 m^2 area provided 15 Angamay (*Tridax procumbens*), one Fatinboay and one Bea (Scientific name not available). Green group also frequented the farmer's field south of the reserve on the same side of the Sakamena. This quadrat yielded 36 Fatinboay plants. Approximately 10% of these plants were flowering at the time the sample was taken.

3.1.3 Black Group Territory

An area totaling 200 m^2 was surveyed within Black group's home range. A greater number of trees compared with Green group's range had a circumference of more than 6 cm, and were suitable for measurement: 38 as opposed to 21 specimens. Table 3.3 presents the calculations derived from the measurements taken in the field.

The most abundant measurable tree in these quadrats was Tsingilifilo with six specimens, followed by Bakoa (*Strychnos madagascariensis*) with five, and both Kily and Valiandro with four. As found in Green group's measurements, Kily were the largest trees as they have the highest relative basal area at 0.81 m^2. Although there were only two Famata (*Euphorbia tirucallii*), these measured trees occupied the second greatest relative basal area at 0.21 m^2. The six Tsingilifilo represent the third highest relative basal area at 0.13 m^2. Even with five measured specimens, Bakoa measured one of the smaller relative basal area values at 5×10^{-3} m^2.

As found in Green group territory, Kily and Tsingilifilo trees were the most dominant of the trees measured. Kily trees demonstrated a dominance of 81% relative to the other measured specimens in Black group's range; Tsingilifilo relative dominance was 13%, 9% lower than in Green group's range. The tree species with the lowest relative basal area and dominance value were Tratamborodreo (*Grewia leucophylla*) and Somontsy (*Kigelianthe madagascariensis*) (BA= 4×10^{-4} m², Dom=6×10^{-6}).

The tallest of the measured trees outside of the reserve in Black group's range were the Valiandro and Maintifototse with an average height of 12 m. This is 6 m shorter than the tallest species in Green group's range (Kily, 18 m). The measured Kily in Black group's quadrats averaged 10 m in height. The shortest species were found to be Mantsaka, Tangatanga (member of the Euphorbiaceae family) and Daro (*Commiphora aprevalii*), all with a measured height of 3 m.

The 200 m² sampled area within Black group's home range included many plant species that were too small to be included in the measurements, observable with the discrepancy between the total species recorded and total species measured listed in Tables 3.1 and 3.3 (51 and 16 respectively). Thirty-five species recorded were not robust enough to be included in the sampling. The quadrat samples taken in the non-reserve forest showed various species of vine covering portions of the area. Low level vine coverage, < 5%, was not found in this area. Moderate coverage, > 5% was recorded with the following species: Karimbola (*Dialium madagascariense*), Vahipinde (*Hippocratea angustifolia*), Tsompia (*Pentopetio sp.*), and Velai (member of the Convolvulaceae family). A high level of vine coverage, > 50%, was found with Tamboro (*Bakerella sp.*). There were three observed mounds of zebu fecal matter and one quadrat exhibited 10%

Species (Mahafaly Name)	**Abundance**	**Relative Abundance**	**Average Height (m)**	**Total Basal Area (m^2)**	**Relative Basal Area (m^2)**	**Dominance ($x 10^{-5}$)**	**Relative Dominance (%)**
Tsingilifilo	6	0.16	5	0.34	0.13	200	13
Bakoa	5	0.13	5	1.3×10^{-2}	5.0×10^{-3}	7.0	0.5
Kily	4	0.11	10	2.2	0.81	1000	81
Valiandro	4	0.11	12	4.0×10^{-2}	1.6×10^{-2}	20	2.0
Lamotimboay	3	0.08	6	6.0×10^{-3}	2.0×10^{-3}	3.0	0.2
Mantsaka	3	0.08	3	5.0×10^{-3}	2.0×10^{-3}	2.0	0.2
Maintifototse	2	0.05	12	3.0×10^{-2}	1.0×10^{-2}	10	1.0
Sele	2	0.05	4	3.0×10^{-3}	1.0×10^{-3}	2.0	0.1
Famata	2	0.05	6	6.0×10^{-2}	0.21	30	2.0
Tratamborodreo	1	0.03	7	1.0×10^{-3}	4.0×10^{-4}	0.6	0.04
Basy (2)	1	0.03	8	5.0×10^{-3}	2.0×10^{-3}	3.0	0.2
Tangatanga	1	0.03	3	3.0×10^{-3}	1.0×10^{-3}	2.0	0.1
Voamena	1	0.03	6	2.0×10^{-3}	7.0×10^{-4}	0.9	0.07
Kotipoke	1	0.03	4	2.0×10^{-3}	6.0×10^{-4}	0.8	0.06
Somontsy	1	0.03	4	1.0×10^{-3}	4.0×10^{-4}	0.6	0.04
Daro	1	0.03	3	2.0×10^{-3}	6.0×10^{-4}	0.8	0.06

Table 3.3 – Phenological characteristics of 16 species of tree found in quadrats sampled in Black group's territory.

coverage of rotting, dead wood.

A 25 m^2 plot was also sampled near the riverbed – an area commonly used by Black group during the first two weeks of this study. This area had low vine coverage with Engesty (Scientific name not available), Totonga (*Aristolochia bernieri*), Atapiso (Scientific name not available), and Lahiriky (*Flacourtia ramontchi*). Moderate levels of Tamboro, Bea, Tamenaka (*Combretum sp.*) and Hadravalala (Scientific name not available) vines were recorded. Eighty percent of the ground in this small area was covered with dead and burned wood fragments. A plot taken south of the Beza Mahafaly campsite included the only cactus censused, Raketa (*Opuntia sp.*), as well as a bird's nest and one mound of zebu feces. There was low coverage of Tsompia and Tamboro vines, and 5% grass coverage, Ahibe (*Panicum maximum*).

Black group ranged into the research camp at least once daily for a minimum duration of thirty minutes. At the mid-way point of the study the members of Black group were spending most of their active hours in the camp. Two quadrat samples were thus recorded in the camp. The first plot, taken close to the researcher sleeping quarters, exhibited much scrub brush too small to measure, as well as approximately 10 L of water in plastic buckets. The second was taken at the extreme north end of the camp behind buildings inhabited by the Malagasy support staff. This area contained low coverage of Votapose vine, two mounds of zebu fecal matter, seven corncobs, and two corn husks. There was also a burn pit with a great deal of ash, paper garbage, chewed sugar cane and human fecal matter. The lemurs were observed feeding in all of the areas described above.

3.1.4 Group Habitat Comparison

A total of 35 plant species were identified in Green group's territory and a total of 51 plant species were identified in Black group's territory – a difference of 16 species. The ecological count data amassed for the two home ranges were analysed using an index of comparison for different communities or sample sets, Morista's Index of Similarity (Paterson, 2001; from Morista, 1959). The following formula was used:

$$C_\lambda = 2 * \Sigma X_{i1} X_{i2} / (\lambda_1 + \lambda_2) N_1 + N_2$$

where:
X_{i1} = number of individuals of species i in sample one
X_{i2} = number of individuals of species i in sample two
N_1 = total number of individuals (all species) in sample one
N_2 = total number of individuals (all species) in sample two
C_λ = measurement of similarity

$\lambda_1 = \sum(X_{i1} * (X_{i1}-1)) / N_1(N_1 - 1)$
and
$\lambda_2 = \sum(X_{i2} * (X_{i2} - 1)) / N_2(N_2 - 1)$

Counts of all recorded species were compared between the two study groups. This index can be interpreted as a calculation of probability: the probability that one species will be drawn from one sample and that same species will be drawn from the other sample, divided by the probability that two specimens drawn from either sample one or two will be of the same species. The index is scaled from 0.0 to 1.0; a result of 0.0 signifying no similarity and 1.0 implying complete similarity. Applying this formula to the data collected from the two groups provided a C_λ value of 0.32. This figure indicates the existence of a low degree of similarity between the two habitats.

3.2 Within Group Dominance Structures

3.2.1 Rank Determinants and Dominance Matrices for Females in the Study Groups

Dominance matrices (Paterson, 2001) were constructed based on the results of all observed dyadic agonistic encounters (Whitten, 1984; Gould, 1996a, 1996b; Saito, 1996; Zucker and Clarke, 1998; Manson *et al.*, 1999). These included submissive vocalizations (subchitting), displacements, lunging, hitting and chasing. The dominance matrices for Green and Black group females respectively are presented in Table 3.4 and 3.5. These dominance matrices are constructed such that the table columns represent the aggressors and the rows the submissive individuals, or those receiving the agonistic acts. The relative dominance order of females within each group are listed from most to least dominant from left to right in the columns of Table 3.4 and 3.5.

Table 3.4 – Green group adult female dominance matrix, July 15-September 3, 2004 (the names in the top row are read as those having demonstrated dominance in an agonistic interaction; the names in the first column represent those being dominated).

	Ginger	**Madeline**	**Nutmeg**	**Cinnamon**	**Clove**	**Anise**
Ginger	----------	0	0	6	0	0
Madeline	7	----------	3	5	0	1
Nutmeg	4	18	----------	6	0	0
Cinnamon	6	36	26	----------	1	1
Clove	26	40	26	20	----------	0
Anise	17	25	13	16	17	----------

Table 3.5 – Black group adult female dominance matrix, July 15-September 3, 2004 (the names in the top row are read as those having demonstrated dominance in an agonistic interaction; the names in the first column represent those being dominated).

	F111	**F110**	**F116**	**F112**	**F432**	**F121**
F111	----------	3	0	0	0	0
F110	35	----------	4	3	1	1
F116	13	20	----------	0	2	2
F112	21	21	18	----------	3	2
F432	8	13	9	8	----------	0
F121	11	20	16	2	9	----------

3.3 Activity Budgets

The hourly rates of general behavioural categories were calculated for each study group and provided in Figure 3.1. These behavioural categories are listed in the ethogram found in Appendix B. The category "social behaviour" stands for all forms of behaviour with an interaction taking place between animals, excluding agonistic interactions: grooming, sitting near or in contact, feeding near or in contact, and play.

The activity budgets of the two groups are quite similar in most categories. There is a slight difference between groups in percentage of time spent engaged in some of the behaviours: Green group females spent 3% more time engaged in agonistic behaviours than females in Black group, and Black group females spent 4% more time foraging than Green group females.

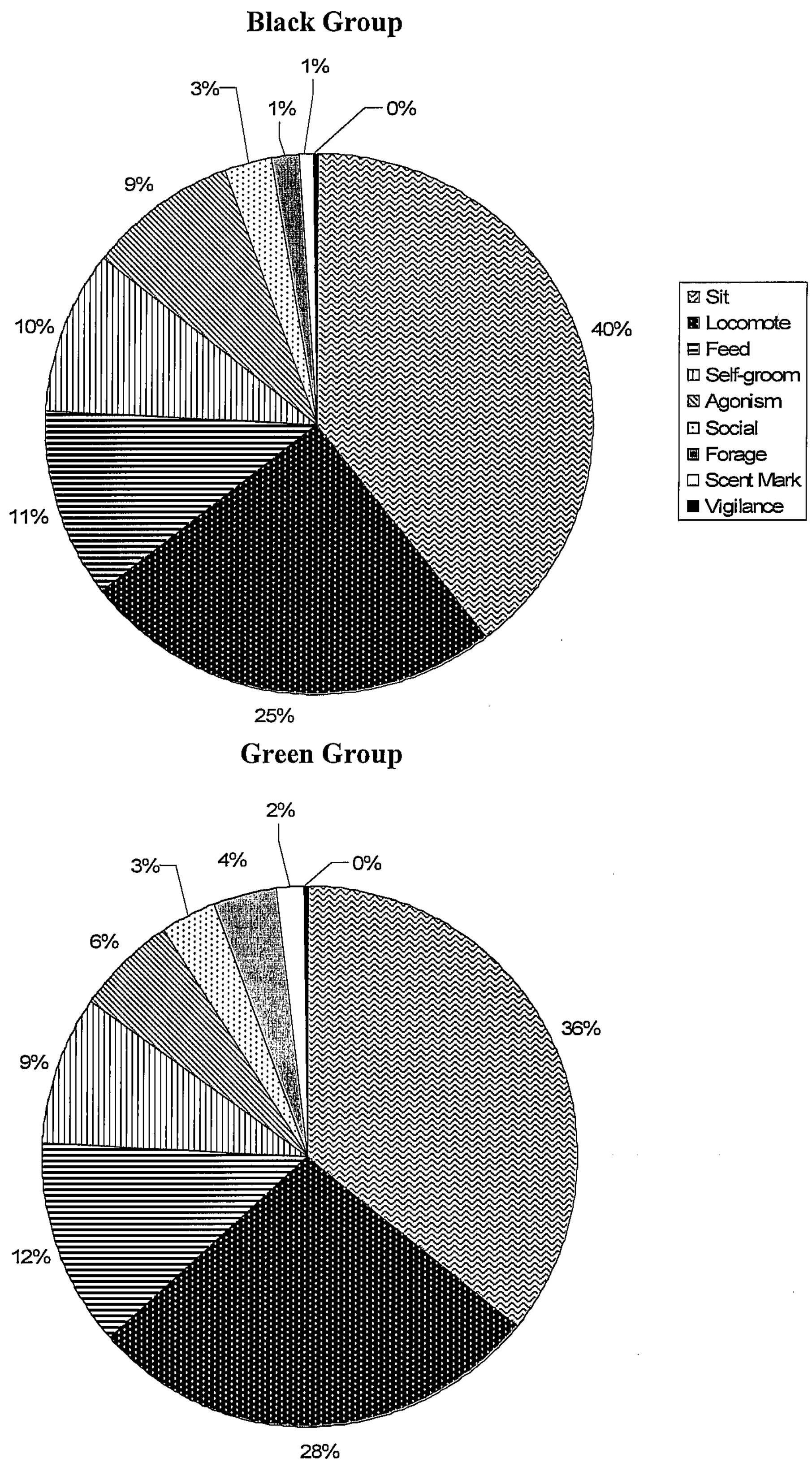


Figure 3.1 – General activity budgets of adult females within Black group and Green group

3.4 Feeding Patterns

3.4.1 Dietary Composition

Plant species consumed by focal females, as well as the plant part being consumed, were recorded for each feeding bout (Tables 3.6 and 3.7). Green group females fed on a total of 24 plant species. Of those 24 species, leaves were eaten from 20 different species, buds from five species, three types of flowers and fruit (Figure 3.2), and wood from one species. Black group females fed on a total of 25 plants species: 20 species of leaves, eight species of buds, four types of flowers and fruit, and two wood species. It was unclear with both groups what exactly was being consumed with the wood. It appeared as though the animals were eating the bark on some occasions, and as though they were licking and consuming a substance off of the wood itself, possibly termite leavings.

Table 3.6 – Plant species and plant parts consumed by Green group.

	Plant Part Consumed				
Plant Species	Leaves	Buds	Flowers	Fruit	Wood
Panicum maximum (Ahibe)	*				
Crateva excelssa (Akaly)	*				
Tridax procumbens (Angamay)	*				
(Angarafke)	*				
(Atapiso)	*				
Marsdemia sp. (Bokabe)	*				
Cirsium sp. (Fatinboay)	*				
(Fitarasoampoa)	*				
Ipomaea sp. (Ipomaea)	*	*	*		
Metaporana parvifolia (Kililo)	*				
Tamarindus indica (Kily)	*			*	*
Grewia grevei (Kotipoke)				*	
Xeromphis sp. (Lamotimboay)	*			*	
Cryptostegia madagascariensis (Lombiry)	*				
Tarenna pruinosum (Mantsaka)	*				
Salvadora angustifolia (Sasavy)		*			
Maerua filiformis (Somangy)	*	*			
Bakerella sp. (Tamboro)	*				

Combretum sp. (Tamenaka)	*				
(Tarasoampoa)	*	*			
Cynanchum mahafalense (Try)		*	*		
(Tsingilifilo)	*				
Pentopetio sp. (Tsompia)	*				
(Velai)			*		

Table 3.7 – Plant species and plant parts consumed by Black group.

	Plant Part Consumed				
Plant Species	***Leaves***	***Buds***	***Flowers***	***Fruit***	***Wood***
Panicum maximum (Ahibe)	*				
Aloe divaricata (Aloe)	*				
Tridax procumbens (Angamay)	*				
(Angarafke)	*				
(Bea)	*				
Marsdemia sp. (Bokabe)					*
(Dalitse)	*				
Gyrocarpus americanus (Kapaipoty)		*			
Metaporana parvifolia (Kililo)	*			*	
Tamarindus indica (Kily)	*	*		*	
Grewia grevei (Kotipoke)	*			*	
Xeromphis sp. (Lamotimboay)			*	*	
Cryptostegia madagascariensis (Lombiry)	*				
Gouania sp. (Masokara)		*			
Opuntia sp. (Raketa)	*				
Salvadora angustifolia (Sasavy)	*	*	*		*
Maerua filiformis (Somangy)	*	*			
Bakerella sp. (Tamboro)	*				
Acacia bellula (Tratriotse)	*	*			
Cyanchum mahafalense (Try)		*	*		
(Tsingilifilo)	*				
Pentopetio sp. (Tsompia)	*				
(Vadrianoa)	*				
Quisivianthe papionae (Valiandro)	*	*	*		
(Votapose)	*				

Figure 3.2 – Green group adult female feeding on Kotipoke (*Grewia grevei*) fruit. (photo by A. Gemmill)

Of the plant species observed being consumed by adult females, 15 were common to both groups; these are listed in Table 3.8. Green group females fed upon nine plant species that Black group females did not, and Black group females fed upon ten plant species that were not documented as part of the diet of Green group females.

Non-plant food resources were also consumed by the lemurs during this study; these are listed for both groups in Table 3.9. Black group females were observed feeding on numerous food types aside from plants. The category of human food scraps includes foods intended for human consumption, and any waste product associated with the preparation of human foods. On many occasions, Black group was observed feeding on human food scraps in the form of sweet potatoes (vegetable and peel), bananas (fruit and peel), fresh and chewed sugar cane, and unidentifiable bits consumed from waste piles. Figure 3.3 shows an adult female feeding in a waste pile in camp. Individuals from Black group were also observed consuming the fecal matter of dogs and cattle on multiple

Table 3.8 – Listing of plant species fed upon by adult females in both Green group and Black group.

Plant Species
Panicum maximum (Ahibe)
Tridax procumbens (Angamay)
(Angarafke)
Marsdemia sp. (Bokabe)
Metaporana parvifolia (Kililo)
Tamarindus indica (Kily)
Grewia grevei (Kotipoke)
Xeromphis sp. (Lamotimboay)
Cryptostegia madagascariensis (Lombiry)
Salvadora angustifolia (Sasavy)
Maerua filiformis (Somangy)
Bakerella sp. (Tamboro)
Cyanchum mahafalense (Try)
(Tsingilifilo)
Pentopetio sp. (Tsompia)

occasions, whereas only one individual in Green group was seen consuming cattle feces on one occasion. Black group frequently accessed water intended for human use at the camp (Figure 3.4). Green group was not observed drinking water on any occasion during the research period. It is possible that drinking occurred out of sight of observations, or the members could have been receiving sufficient water from their dry-season diet.

Both groups were observed eating what appeared to be soil, although it is possible that tiny seeds or insects were the actual targeted food source. Geophagy, the active consumption of soil, will be briefly discussed in Chapter 4. Members of Black group were witnessed consuming pieces of spider web, remnants of old bird's nests, and insects. Insects were caught and eaten too rapidly to allow for species identification.

Figure 3.3 – Adult female from Black group feeding on organic waste from a pile in camp.
(photo by A. Gemmill)

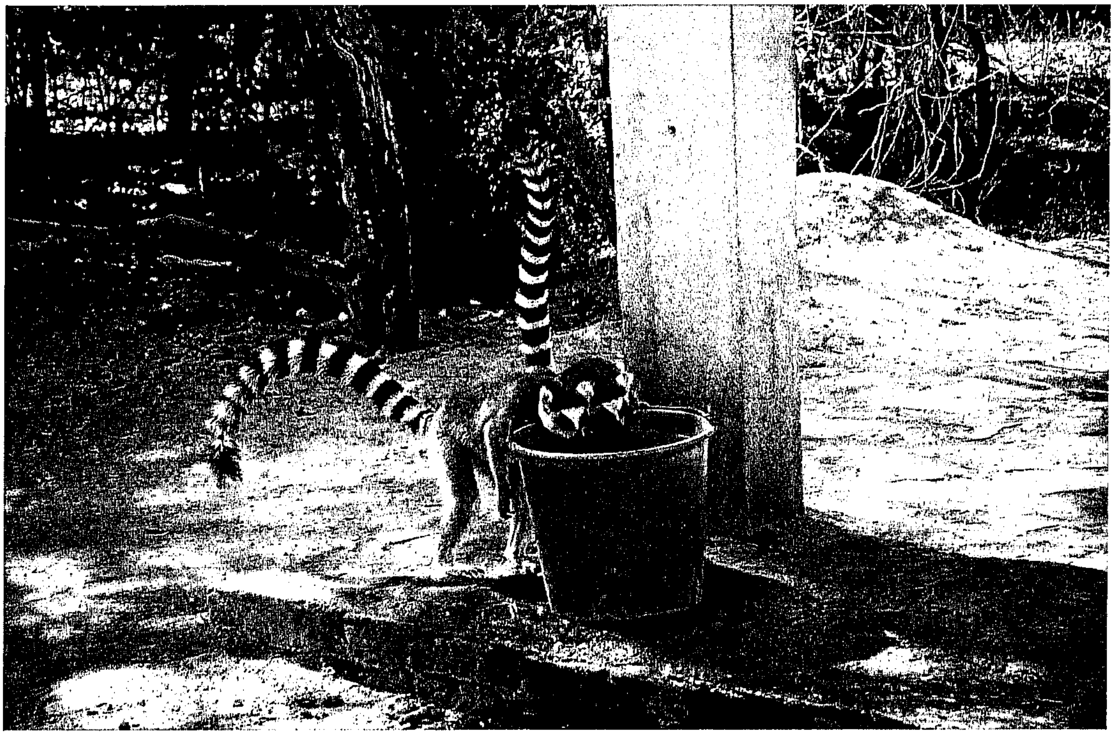


Figure 3.4 – Two Black group subadult females drinking water from the Beza camp well.
(photo by A. Gemmill)

Table 3.9 – Non-plant foods consumed by Green group and Black group.

Food Type	*Green Group*	*Black Group*
Human Food Scraps		*
Feces	*	*
Soil	*	*
Spider web		*
Birds nest		*
Insect		*

3.4.2 Feeding Frequency by Food Species and Type

Following Powzyk and Mowry (2003), the top ten food items for the adult females of Green group and Black group were tabulated (Tables 3.10 and 3.11). The importance of Fatinboay to the diets of Green group females is evident, as it comprised nearly 50% of their total recorded diet (Figure 3.5). Kily represents nearly one quarter of the diets of adult females in both groups (Figure 3.6). These results suggest greater variation in the diets of females in Black group, as the top ten foods comprised 86% of their diets: the top ten foods for Green group represent 93% of their total diet. Some effect of the degraded and human influenced habitat of Black group is obvious in Table 3.12: human food scraps is the third highest diet component and domestic animal fecal matter (Figure 3.7) is the sixth.

Figure 3.5 – Green group adult female feeding on Fatinboay (*Cirsium sp.*) leaves in the Sakamena river bed. (photo by A. Gemmill)

Figure 3.6 – Ripe and partially consumed *Tamarindus indica* (Kily) fruit. (photo by A. Gemmill)

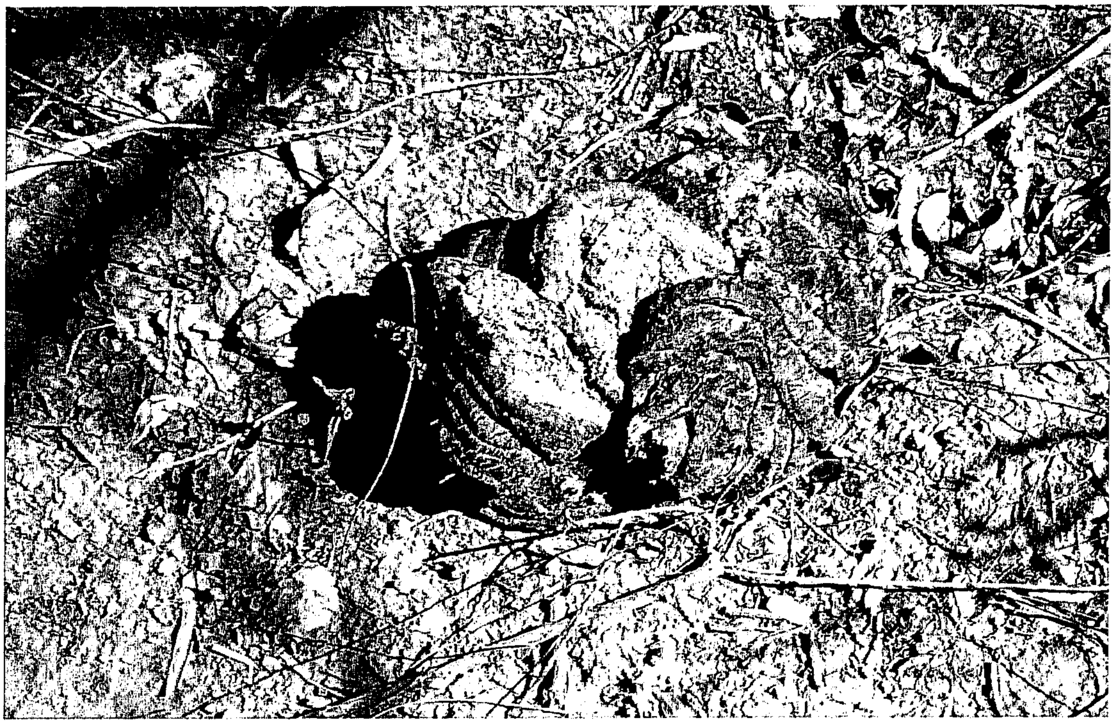


Figure 3.7 – Zebu fecal matter found within Black group's home range. (photo by A. Gemmill)

Table 3.10 – Ten most popular food items consumed by Green group adult females.

Top 10 Green Group Food Items	*Percentage of Diet Represented*
Cirsium sp. (Fatinboay)	44.8
Tamarindus indica (Kily)	21.9
Ipomaea sp. (Ipomaea)	5.2
Tridax procumbens (Angamay)	5.1
Pentopetio sp. (Tsompia)	5.0
Metaporana parvifolia (Kililo)	2.9
Bakerella sp. (Tamboro)	2.4
Marsdemia sp. (Bokabe)	2.2
(Tarasoampoa)	1.8
Soil	1.2
Total	92.5

Table 3.11 – Ten most popular food items consumed by Black group adult females.

Top 10 Black Group Food Items	***Percentage of Diet Represented***
Tamarindus indica (Kily)	24.2
Salvadora angustifolia (Sasavy)	16.9
Human food scraps	11.6
Quisivianthe papionae (Valiandro)	8.8
(Bea)	5.8
Fecal Matter (dog and cattle)	4.9
Tridax procumbens (Angamay)	3.7
Bakerella sp. (Tamboro)	3.7
Soil	3.3
Metaporana parvifolia (Kililo)	3.0
Total	85.9

The proportion of plant and non-plant foods identified for each group is provided in Table 3.12. Diets of Green group females included a lower percentage of non-plant items than did the diets of the females from Black group, expected due to Black group's access to a greater variety of foods at the Beza Mahafaly camp.

Table 3.12 – Amount of diets that are plant and non-plant items.

	Green Group	**Black Group**
Plant Parts	99%	79%
Non-Plant Parts	1%	21%

A significant relationship exists between the consumption of plant and non-plant foods and group membership ($\chi^2 = 201.3$, df = 1, $\rho < 0.001$) with Black group animals consuming far more non-plant foods.

3.4.3 Within Group Feeding Comparison: Food Type

Feeding was further broken down into hourly rate of consumption of specific plant parts (Figure 3.8 and Figure 3.9). As buds represented, at the time of this study, immature flowers, the two categories were combined for analysis purposes. No significant difference was found to exist between Green group females and hourly feeding rates on specific plant parts (Kruskal-Wallis, $\chi^2 = 1.222$, $\rho > 0.05$). For comparison of feeding rates within Black group, human food scraps and fecal matter were included in the analysis as these food types represent a significant portion of the diets of Black group females. Figure 3.9 presents the hourly feeding rates for leaves, flowers/buds, fruit, human food scraps, and feces for all six adult females of Black group. No significant difference was found when comparing feeding rates between females in Black group (Kruskal-Wallis, $\chi^2 = 1.828$ $\rho > 0.05$).

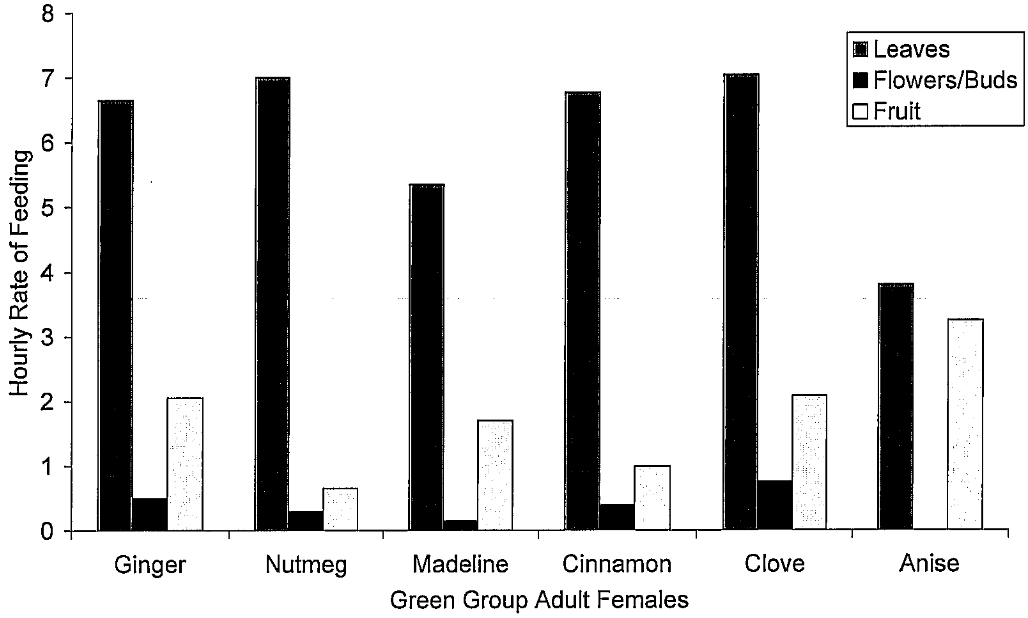


Figure 3.8 – Hourly feeding rates by food type within Green group.

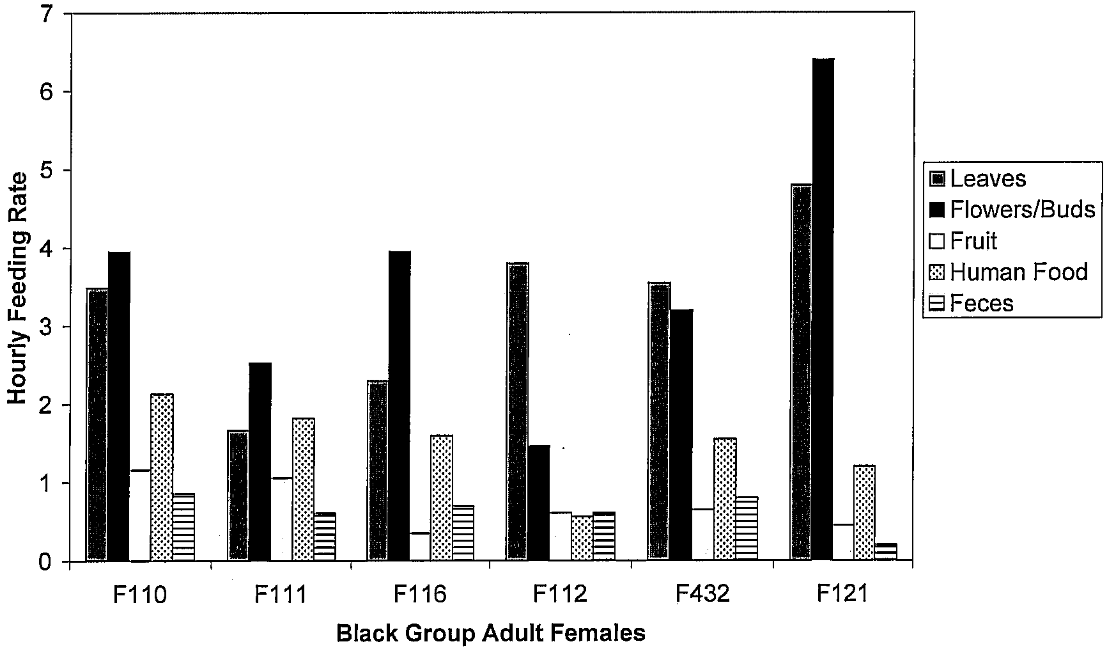


Figure 3.9 – Hourly feeding rates by food type within Black group.

3.4.4 Between Group Feeding Comparison: Food Type

Total hourly rate of feeding by food type was compared between adult females in Green group and Black group (Figure 3.10). This comparison was made for only the following food types: leaves, flowers/buds, and fruit (Green group females did not consume any human food scraps and were observed feeding on fecal matter on only one occasion). Green group females ate significantly more leaves than did Black group females (Mann-Whitney, $U = 1.5$, $\rho = 0.008$). Black group females ate flowers/buds at a significantly higher rate than Green group females (Mann-Whitney, $U = 0.0$, $\rho = 0.004$). Finally, Green group females consumed fruit at a significantly greater rate than Black group females (Mann-Whitney, $U = 4.5$, $\rho = 0.030$).

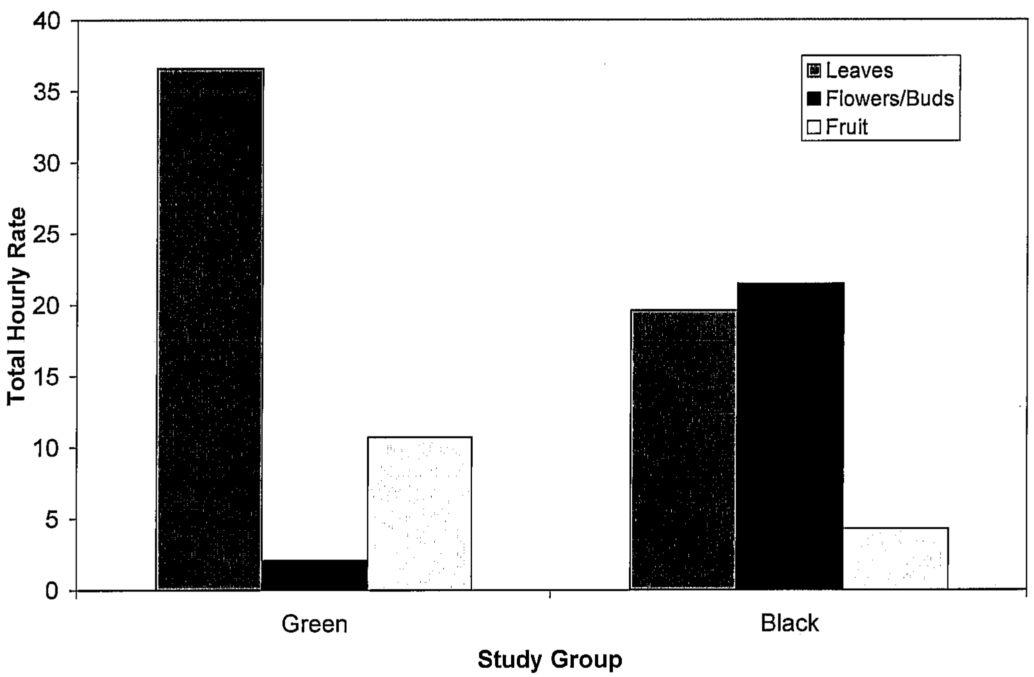


Figure 3.10 – Total hourly feeding rate of plant parts by Green group and Black group.

3.4.5 Feeding and Rank: Within Groups

Based on the results of the dominance matrices discussed in section 3.2, adult females have been divided into one of two categories within their group: higher rank and lower rank. As there is an equal number of adult females in each group, six, this allows for a valid comparison of rank effects with three individuals in each category within each group (Table 3.13).

Table 3.13 – Within group rank classification.

	Higher Rank	**Lower Rank**
Green Group	Ginger, Madeline, Nutmeg	Cinnamon, Clove, Anise
Black Group	F111, F110, F116	F112, F432, F121

Within group rank classifications were applied to food items eaten in each group (Figures 3.11 and 3.12). The types of foods consumed by females, as outlined in section 3.4.3, were analysed in terms of female dominance ranking category (higher or lower) within each group. Within Green group there is no significant difference between higher and lower ranking females in hourly rates of leaf consumption (Mann-Whitney U, $U = 4.0$, $\rho = 0.827$), flower/bud consumption (Mann-Whitney U, $U = 4.0$, $\rho = 0.827$), or fruit consumption (Mann-Whitney U, $U = 2.0$, $\rho = 0.275$). Within Black group, the food categories human food scraps and dog/cattle fecal matter were also analysed. There is no significant difference between higher and lower ranking adult females in Black group when hourly feeding rates are compared for flowers/buds (Mann-Whitney U, $U = 4.0$, $\rho = 0.724$), fruit (Mann-Whitney U, $U = 3.0$, $\rho = 0.376$), or feces (Mann-Whitney U, $U = 3.0$, $\rho = 0.376$). A significant difference does exist between higher and lower-ranked females in hourly feeding rates for leaves; lower ranking females in Black group fed on leaves significantly more often than did higher ranking females (Mann-Whitney U, $U = 0.0$, $\rho = 0.050$). There is also a significant difference between rank categories and human food scraps consumption; higher ranking females in Black group consumed human food scraps at a significantly higher rate than lower ranking females in Black group (Mann-Whitney U, $U = 0.0$, $\rho = 0.050$).

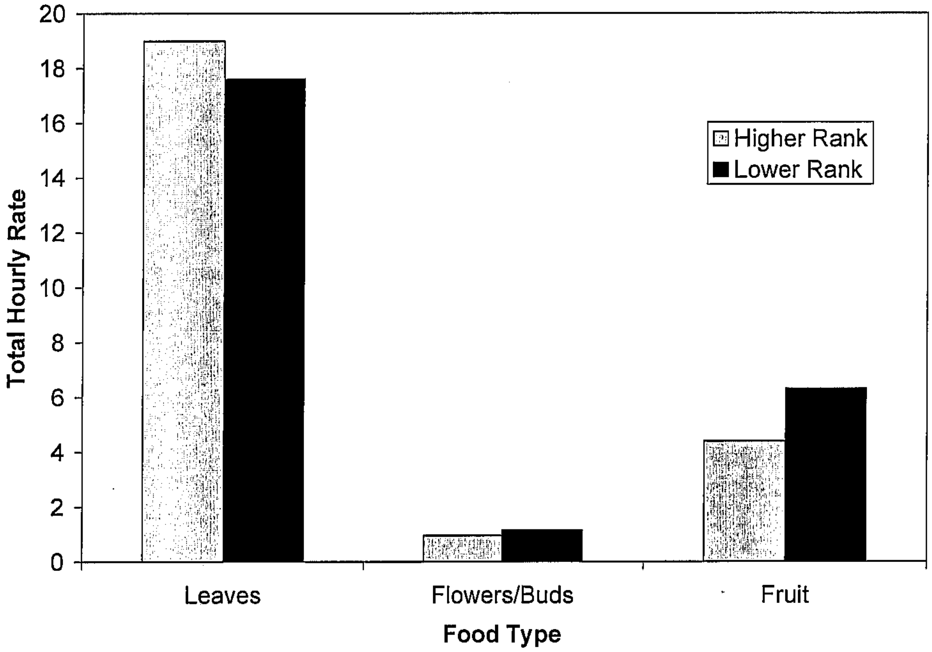


Figure 3.11 – Comparison of total hourly feeding rate by food type between ranks within Green group.

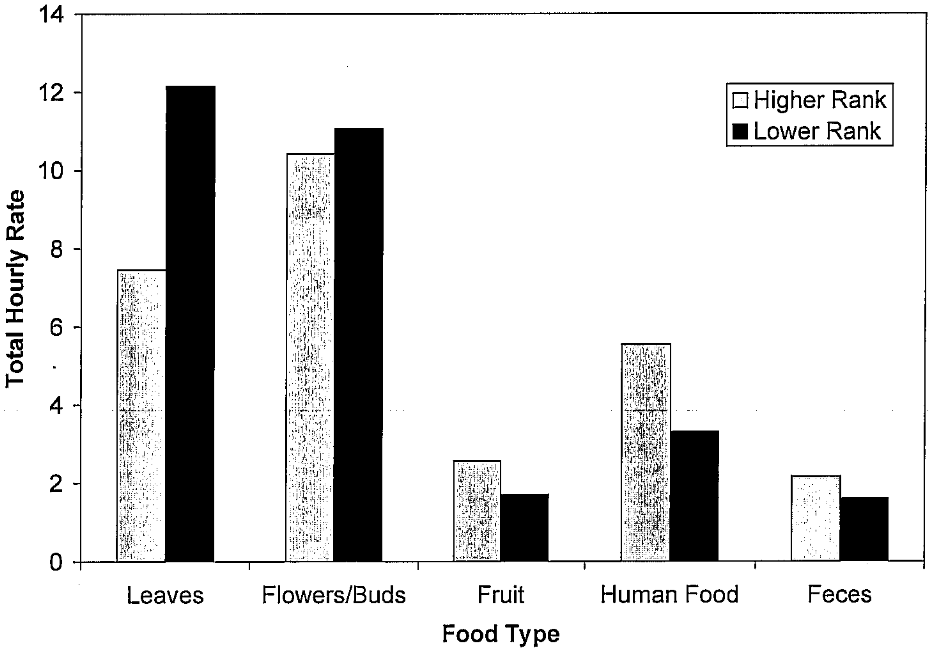


Figure 3.12 – Comparison of total hourly feeding rate by food type between ranks within Black group.

3.4.6 Feeding and Rank: Between Groups

Hourly feeding rate for leaves, flowers/buds, and fruit were compared between groups and rank. Higher ranking female between group comparisons are shown in Figure 3.13 and lower ranking female between group comparisons are presented in Figure 3.14. There was no significance between group difference in leaf feeding rates for lower ranking females (Mann-Whitney U, $U = 1.5$, $\rho = 0.184$); however higher ranking females in Green group consumed leaves significantly more often than those in Black group (Mann-Whitney U, $U = 0.0$, $\rho = 0.050$). Black group females of all ranks consumed flowers/buds significantly more often than all females in Green group (higher rank: Mann-Whitney U, $U = 0.0$, $\rho = 0.046$; lower rank: Mann-Whitney U, $U = 0.0$, $\rho = 0.050$). Finally, when examining fruit consumption, there is no significant difference between higher ranking Green group females versus higher ranking females in Black group (Mann-Whitney U, $U = 2.0$, $\rho = 0.275$). Lower ranking Green group females ate fruit significantly more often than did lower ranking Black group females (Mann-Whitney U, $U = 0.0$, $\rho = 0.050$).

3.5 Adult Female Agonism

Agonism has been divided into four levels (Table 3.14). Each level represents an increasingly elevated degree of agonism – a greater risk and expenditure of energy is required in order for the individual to carry out a higher level of agonistic behaviour. Ag1 includes submissive chitter – vocalizations made from a submissive animal to a dominant animal. Ag2 represents displacements – with the approach of another, an

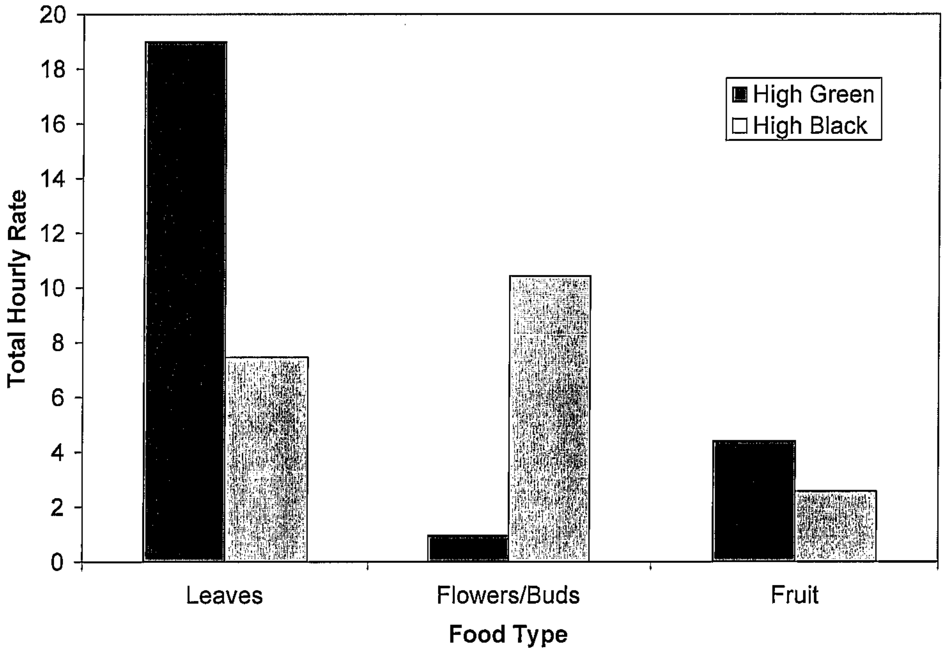


Figure 3.13 – Total hourly feeding rates of plant parts for higher-ranked females from Green group and Black group.

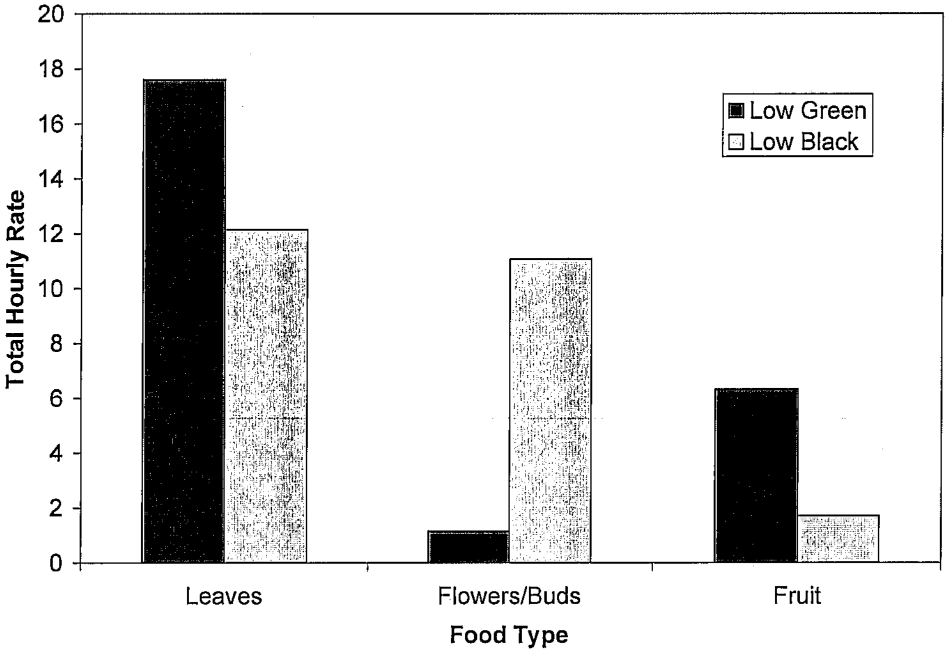


Figure 3.14 – Total hourly feeding rates of plant parts for lower-ranked females from Green group and Black group.

individual stops their current behaviour and changes location. Ag3 includes lunging and charging. Lunging involves a sudden, brisk movement towards another individual without leaving the occupied space. Charging is very similar but includes a rapid movement towards an individual, away from the previously occupied space. The final category, Ag4, includes hitting, slapping, cuffing, pushing and chasing. The final behaviour of this list, chasing - the pursuit of another individual, requires the expenditure of a great deal of energy. The other behaviours in the category Ag4 are all forms of aggressive physical contact and could thus bring a risk of physical and/or social conflict to the actor, making them potentially energetically costly.

Table 3.14 – Agonism categories and associated behaviours.

Agonism Level	*Behaviours*
Ag1	submissive chitter
Ag2	displacement
Ag3	lunge, charge
Ag4	hit, cuff, slap, push, chase

3.5.1 Agonism and Habitat

Proportions of agonistic versus nonagonistic behaviours (any behaviour recorded that is not a form of agonism) are listed in Table 3.15. Proportion of time engaged in agonistic behaviour is similar between both groups: 6% for Black group and 9% for Green group. Both groups also demonstrated very similar rates of agonism when examining overall activity budgets: Black group 7.1/hour and Green group 7.05/hour. Analysis suggests that there is no significant relationship between rate of agonism and group membership, and thus between overall agonism rate and habitat in which each group lives ($\chi^2 = 0.513$, df = 1, $\rho > 0.05$).

Table 3.15 – Proportion of observed behaviours that are agonistic and affiliative.

	Green Group	**Black Group**
Agonistic	9%	6%
Affiliative	91%	94%

All instances of adult female social behaviours were isolated from other behavioural occurrences. Social behaviours are any interactions between individuals including any level of agonism, one-way grooming, mutual grooming, play, nuzzling, and the act of sitting, foraging, feeding and drinking near another individual. Behaviours were then separated into two categories: agonistic and affiliative. Agonistic behaviours refer to all levels of agonism, and affiliative behaviours are all other social behaviours. The proportions of affiliative and agonistic behaviours within Green group are presented in Figure 3.15, and for Black group in Figure 3.16. Agonistic and affiliative behaviours represent a nearly equal proportion of social interactions in both groups – a ratio of 3:1 for affiliative behaviours over agonistic behaviours.

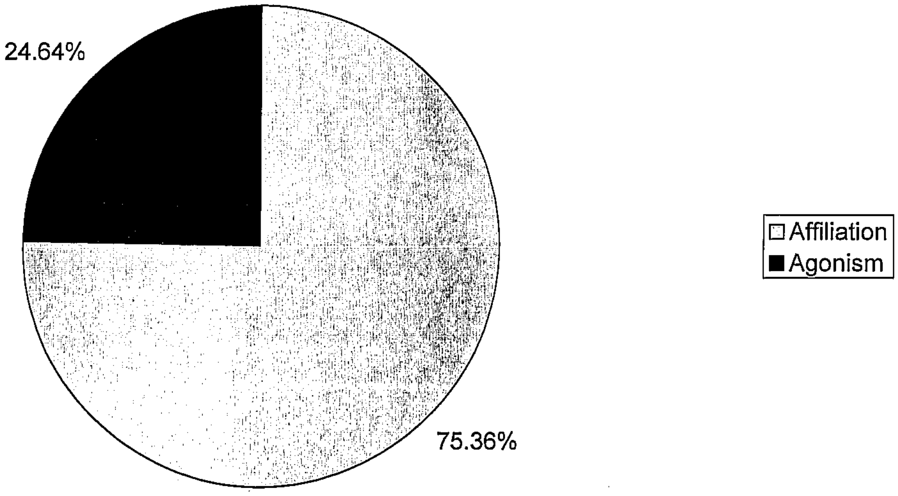


Figure 3.15 – Proportions of affiliative and agonistic interactions within Green group.

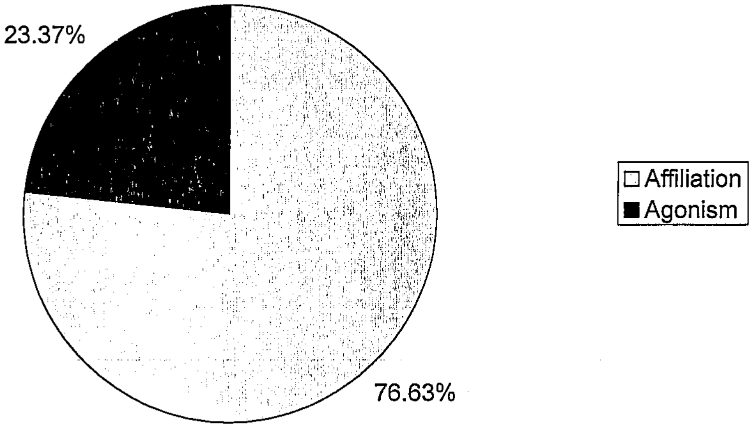


Figure 3.16 – Proportions of affiliative and agonistic interactions within Black group.

When frequency of observed agonism is divided into the four levels of increasing agonistic severity and compared between groups, Black group females engaged in severe

agonism more frequently than Green group females. Lower levels of agonism are quite similar for both groups, as demonstrated in Table 3.16. For the higher levels of agonism, Ag3 and Ag4, Black group's rates are nearly twice that of Green group's rates. But when analysed no significant difference was detected between groups for overall agonism (Mann-Whitney U, $U = 17.5$, $\rho = 0.94$), rate of Ag1 (Mann-Whitney U, $U = 17.5$, $\rho = 0.94$), rate of Ag2 (Mann-Whitney U, $U = 15.5$, $\rho = 0.69$), rate of Ag3 (Mann-Whitney U, $U = 10.0$, $\rho = 0.20$), or for rate of Ag4 (Mann-Whitney U, $U = 14.5$, $\rho = 0.57$). Proportions of agonistic behaviour assigned to each level of agonism within Green group and within Black group are shown in Figure 3.17 and Figure 3.18.

Table 3.16 – Hourly rates of agonism by level for Green and Black groups.

Group	*Ag1*	*Ag2*	*Ag3*	*Ag4*
Green	24.05	15.15	0.95	2.15
Black	22.33	15.70	1.72	3.14

3.5.2 Agonism and Rank

Amongst Green group females there was a relationship between rank and rate of agonistic versus other behaviours (Pearson's Chi-Square, $\chi^2 = 17.36$, $df = 1$, $\rho < 0.001$) (see Table 3.17).

Table 3.17 – Hourly rates of agonistic and nonagonistic behaviour by rank in Green group.

	Higher Rank	**Lower Rank**
Agonistic	18.45	23.80
Nonagonistic	214.50	204.55

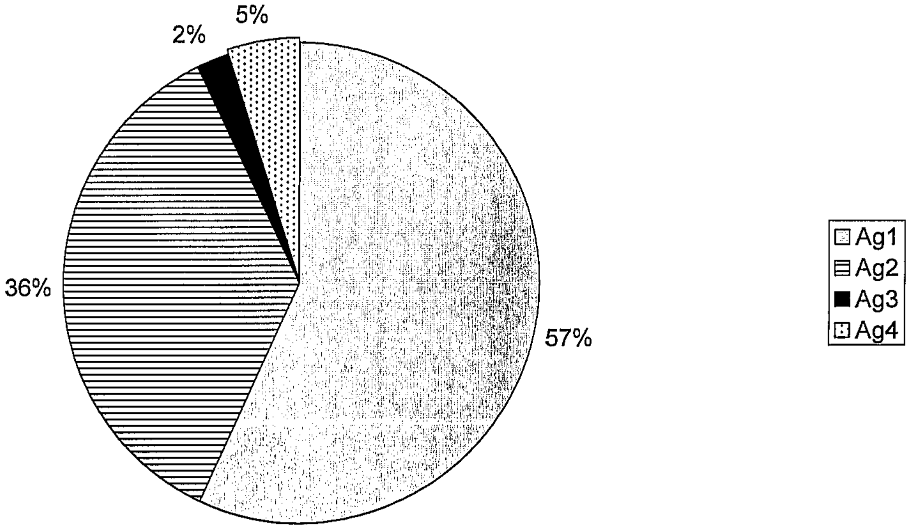


Figure 3.17 – Proportions of agonism by level within Green group.

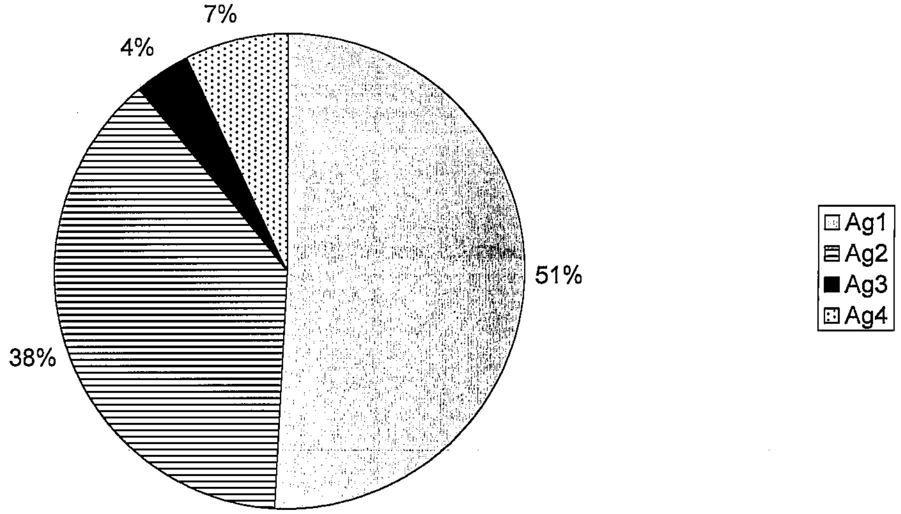


Figure 3.18 – Proportions of agonism by level within Black group.

Amongst Black group females, there was a highly significant relationship between rank and rate of agonism versus other behaviours (Pearson's Chi-Square, $\chi^2 = 31.07$, df = 1, $\rho < 0.001$) (see Table 3.18).

Table 3.18 – Hourly rates of agonistic and nonagonistic behaviour by rank in Black group.

	Higher Rank	**Lower Rank**
Agonistic	25.01	17.82
Nonagonistic	310.28	329.52

No between group differences were detected when comparing rates of agonistic and nonagonistic behaviours in high-ranking females (Pearson's Chi-Square, $\chi^2 = 0.82$, df = 1, $\rho = 0.37$). However, a relationship was found between groups in rate of agonistic versus nonagonistic behaviour in low-ranking individuals (Pearson's Chi-Square, $\chi^2 = 114.2$, df = 1, $\rho < 0.001$): lower-ranked females in Green group are engaging in significantly more agonistic behaviour than are lower-ranked females in Black group.

3.5.3 Level of Agonism and Rank

Both high-ranking and low-ranking individuals in both groups engaged in a similar amount of each level of agonism (Figure 3.19). High-ranking Green group females engaged in a higher rate of Ag3 than their lower ranking counterparts, and lower-ranked females exhibited higher rates of Ag1, Ag2 and Ag4 than high-ranking females. High-ranking Black group females were more frequently observed engaging in all four agonistic levels when compared to the low-ranking females of that group.

Rates of agonism levels displayed by higher-ranked and lower-ranked adult females in Green group were not statistically significant (Ag1: Mann-Whitney U, U = 3.0, ρ = 0.51; Ag2: Mann-Whitney U, U = 2.0, ρ = 0.28; Ag3: Mann-Whitney U, U = 3.5, ρ = 0.66; Ag4: Mann-Whitney U, U = 3.0, ρ = 0.51). No relationship was found between agonism level and rank (higher or lower) in Black group for Ag1 (Mann-Whitney U, U = 1.0, ρ = 0.13), Ag2 (Mann-Whitney U, U = 3.0, ρ = 0.51), or Ag3 (Mann-Whitney U, U = 0.5, ρ = 0.07).

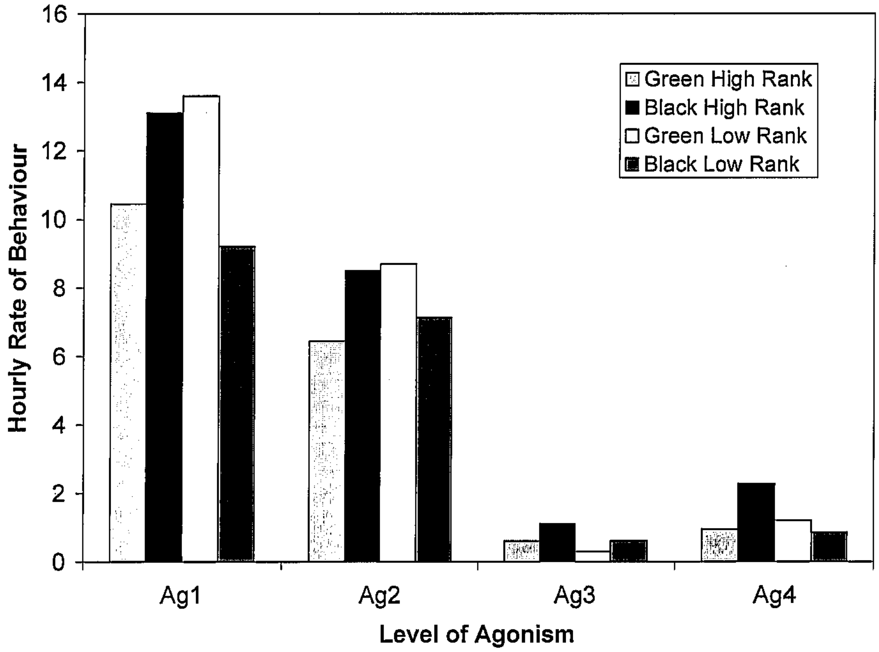


Figure 3.19 – Hourly rates of agonism by level in Green and Black groups, designated by rank.

But higher-ranked adult females in Black group exhibited a significantly higher rate of Ag4 compared with lower-ranked females (Mann-Whitney U, U = 0.0, ρ = 0.046).

3.5.4 Context of Agonism

As discussed in Chapter 2, the context of each agonistic encounter was noted when decipherable. If the observer was unable to assign a context to an agonistic situation, possibly due to an obstructed viewpoint or commencing the session in the midst of an encounter, the context was scored as unknown. Upon tabulation 30% of contexts for both Green group and Black group were recorded as unknown. These figures will be excluded from the following discussion.

Figure 3.20 displays the mean hourly rate of each context scored for the study groups. The highest rates for both groups occur in the context of feeding, followed by social situations and resting spots. No members of Green group were observed drinking at any time, therefore their context rate for drinking is zero. "Intergroup" refers to agonistic encounters that occurred between two neighbouring groups, and is included for interest in Figure 3.20. This category will not be included in the discussion of the context of within group agonism.

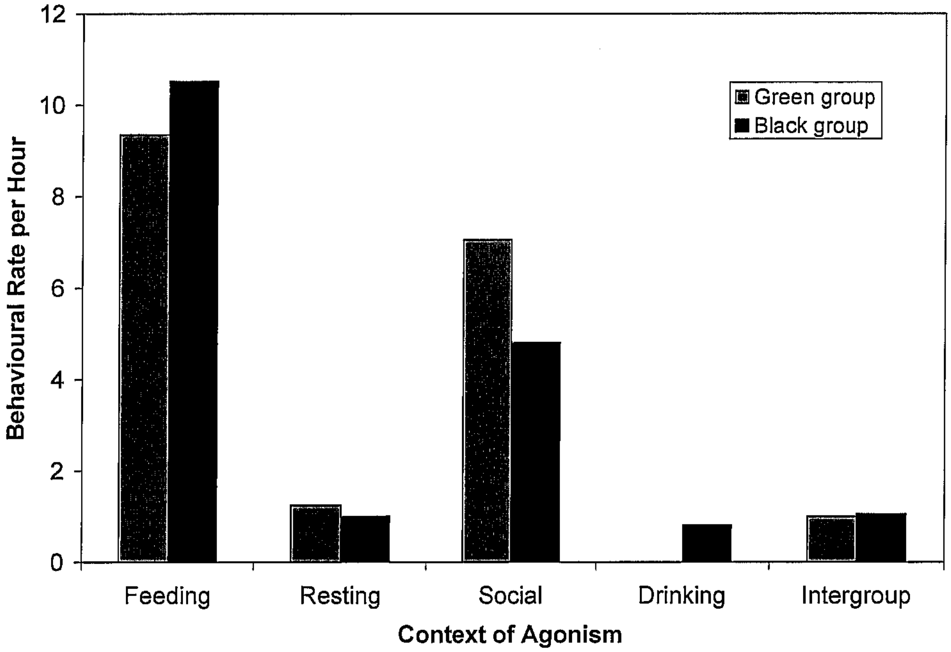


Figure 3.20 – Hourly rates of agonism contexts for Green group and Black group.

Black group females exhibited a higher rate of agonism related to feeding than did Green group females, and Green group females displayed a higher rate of agonism occurring in social situations than females in Black group; there is strong evidence against the hypothesis of no association between context of agonism and group membership (Black group or Green group) (Pearson Chi-Square, $\chi^2 = 26.46$, df = 5, $p < 0.001$). That said, the differences detected between groups related to context of agonism were not substantial enough to be statistically significant (feeding: Mann-Whitney U, U = 15.0, $\rho = 0.63$; resting: Mann-Whitney U, U = 12.5, $\rho = 0.37$; social: Mann-Whitney U, U = 8.0, $\rho = 0.11$).

Hourly rates of agonism context by rank for each group are listed in Tables 3.19 and 3.20. In both groups, high-ranking females exhibit higher rates of agonism in feeding contexts than all other contexts. Low-ranking females in both groups also demonstrate agonism in feeding contexts more often than all other contexts.

Table 3.19 – Average hourly rates of agonism context by rank in Green group.

	Feeding	Social	Resting
Higher Rank	3.90	2.35	0.85
Lower Rank	5.40	4.70	0.40

Table 3.20 – Average hourly rates of agonism context by rank in Black group.

	Feeding	Social	Resting	Drinking
Higher Rank	6.08	2.94	0.46	0.51
Lower Rank	4.46	1.87	0.56	0.30

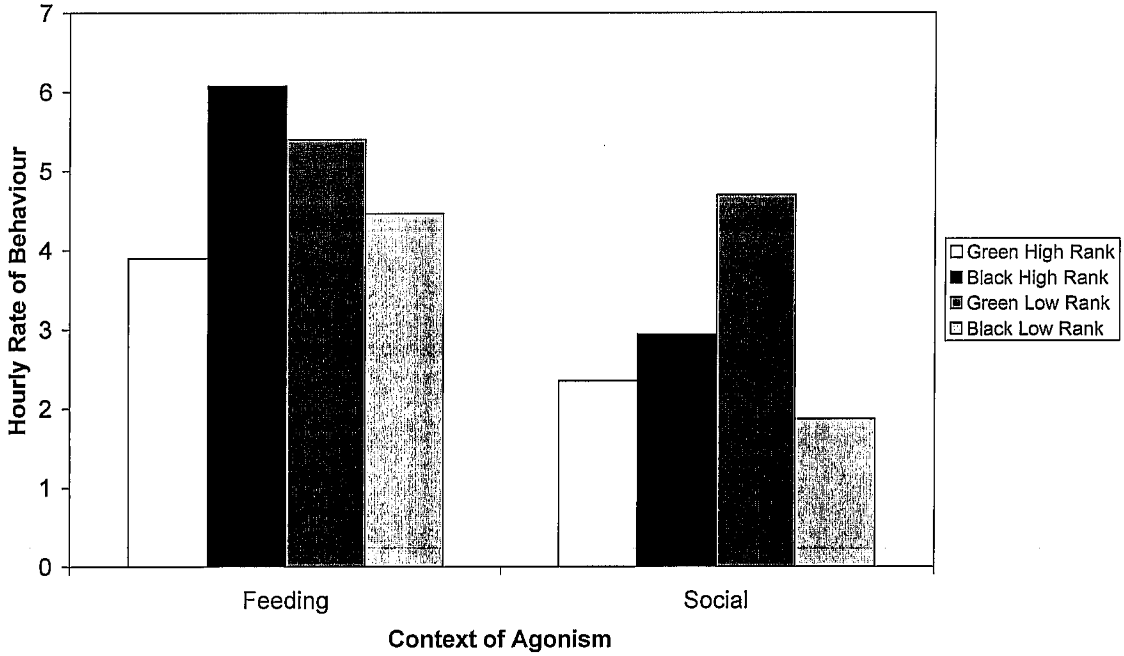


Figure 3.21 – Average hourly rates of most frequent agonism contexts (feeding and social) by group and rank.

Within Green group low-ranking females are involved in feeding and social agonism at a higher rate than are high-ranking females. Within Black group high-ranking females are involved in feeding and social agonism at a higher rate than are low-ranking females. When analysed statistically, of the six possible combinations of between group rank and context groupings, only one demonstrated significance: lower-ranked adult females in Green group have significantly higher average hourly rates of social agonistic interactions than lower-ranked adult females in Black group (Mann-Whitney U, $U = 0.0$, $\rho = 0.046$). All other comparisons were not significant (higher rank and feeding: Mann-Whitney U, $U = 1.0$, $\rho = 0.12$, social: Mann-Whitney U, $U = 2.0$, $\rho = 0.28$, resting: Mann-Whitney U, $U = 0.5$, $\rho = 0.07$; lower rank and feeding: Mann-Whitney U, $U = 3.0$, $\rho = 0.51$, resting: Mann-Whitney U, $U = 2.0$, $\rho = 0.24$). Figure 3.21 shows average rates for the two most frequent contexts of agonism, feeding and social situations by rank.

A highly significant relationship exists between the agonism level AG2 and feeding for both groups (Green group females: Kruskal-Wallis, $\chi^2 = 15.26$, $p < 0.001$, df = 2, and Black group females: Kruskal-Wallis, $\chi^2 = 17.03$, $p < 0.001$, df = 3). The hourly rates of agonism level by agonism context are shown for Green group in Table 3.21 and for Black group in Table 3.22.

Table 3.21 – Average hourly rates of agonism level by agonism context in Green group.

	Agonism Level				
Agonism Context	**Ag1**	**Ag2**	**Ag3**	**Ag4**	**Total**
Feeding	4.05	4.70	0.25	0.35	9.35
Social	5.00	1.60	0.05	0.40	7.05
Resting	0.40	0.65	0.00	0.20	1.25
Total	9.45	6.95	0.30	0.95	17.65

Table 3.22 – Average hourly rates of agonism level by agonism context in Black group.

	Agonism Level				
Agonism Context	**Ag1**	**Ag2**	**Ag3**	**Ag4**	**Total**
Feeding	4.15	4.91	0.91	0.56	10.53
Social	3.85	0.71	0.05	0.20	4.81
Resting	0.10	0.86	0.00	0.05	1.01
Drinking	0.20	0.56	0.05	0.00	0.81
Total	8.30	7.04	1.01	0.81	17.16

3.6 Feeding Agonism

The overall most frequent context in which agonistic interactions were observed for both groups was feeding, as indicated in Table 3.21 and 3.22. The following tables further examine the occurrence of feeding agonism within each group. Table 3.23 and Table 3.24 list the types of food that were related to feeding agonism in Green group and Black group respectively.

Table 3.23 – Percentage of agonism by food type in Green group (found by dividing the number of bouts of food type agonism by the total number of observed feeding bouts of that food type) and average hourly rate of agonism by food type.

Food Type	***Percentage of Feeding Bouts Related to Agonism***	***Average Hourly Rate of Agonism***
Soil	25.00	0.15
Leaves	17.90	6.55
Fruit	12.10	1.30
Wood	8.25	1.20
Buds	9.10	0.10
Flowers	0.00	0.00

Table 3.24 – Percentage of agonism by food type in Black group (found by dividing observed agonism of food type by total number of observed feeding bouts of that food type) and hourly rate of agonism by food type.

Food Type	*Percentage of Feeding Bouts Related to Agonism*	*Average Hourly Rate of Agonism*
Wood	66.7	0.51
Spider Web	50.0	0.15
Birds Nest	40.0	0.10
Human	21.0	1.87
Feces	17.3	0.66
Fruit	12.6	2.43
Soil	11.8	0.30
Leaves	11.0	2.18
Buds	7.90	1.37
Flowers	7.10	0.30
Insects	0.00	0.00

Figures 3.22 and 3.23 present the proportion of feeding agonism represented by food types consumed amongst adult females in Green group and adult females in Black group respectively.

A large portion of feeding agonism is associated with plant part food items. The five plant species that were associated with high rates of feeding agonism, based on their frequency of consumption, amongst Green group adult females are: Bokabe, 23% of feeds; Angamay, 22% of feeds; Tamboro, 21% of feeds, Fatinboay, 20% of feeds; Tsompia, 14% of feeds. The five plant species most frequently associated with high rates of feeding agonism, based on their frequency of consumption, amongst adult females of Black group are: Votopose, 100% of feeds; Bea, 15.73% of feeds; Kily, 12.67% of feeds; Angamay, 10.71% of feeds; Tamboro, 10.71% of feeds.

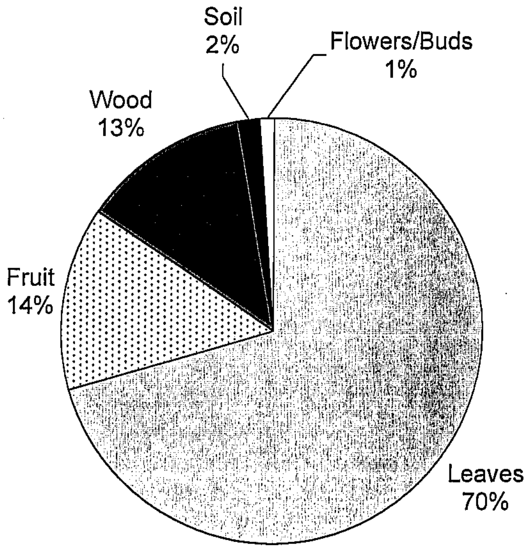


Figure 3.22 – Proportion of feeding agonism related to food type within Green group

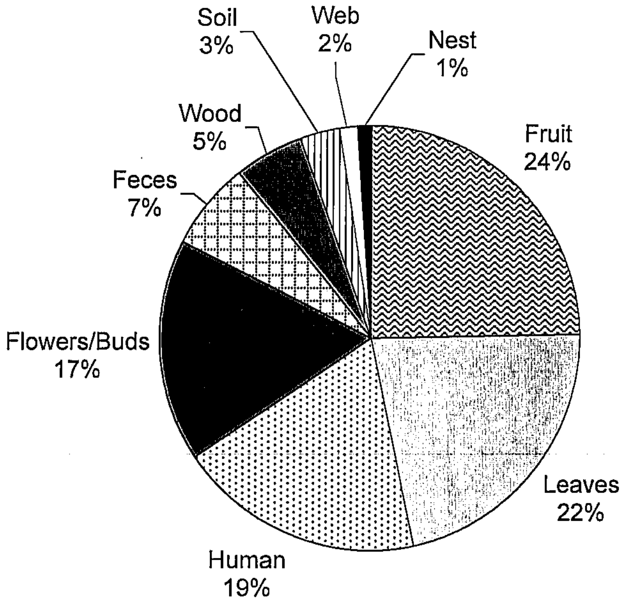


Figure 3.23 – Proportion of feeding agonism related to food type within Black group

Level of feeding agonism varies according to food type, as seen in Figures 3.24 and 3.25 for Green and Black groups respectively.

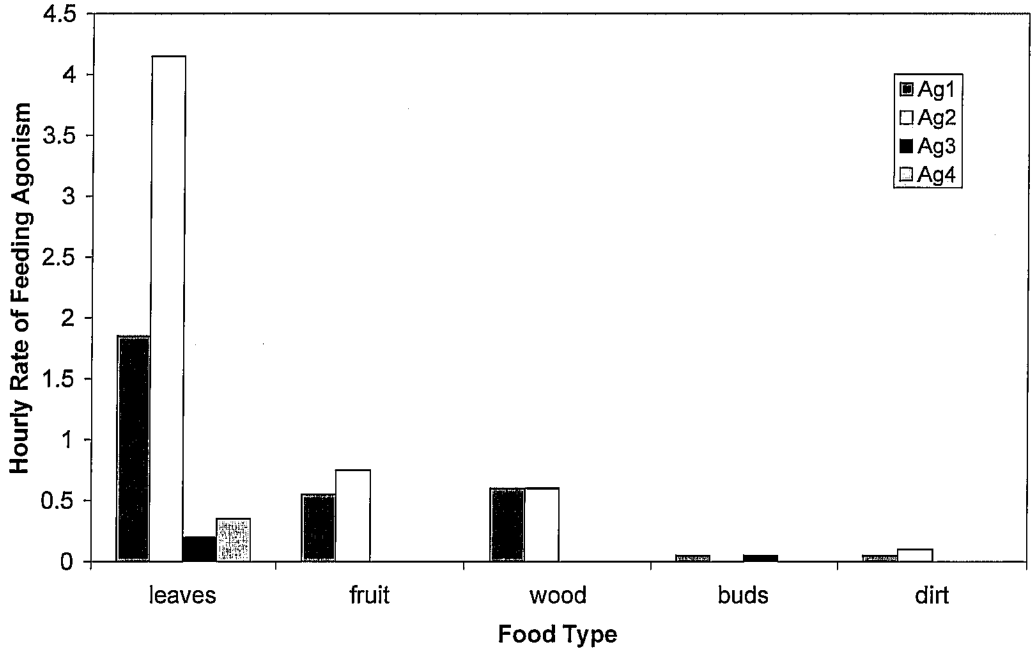


Figure 3.24 – Average hourly rates of feeding agonism levels by food type in Green group.

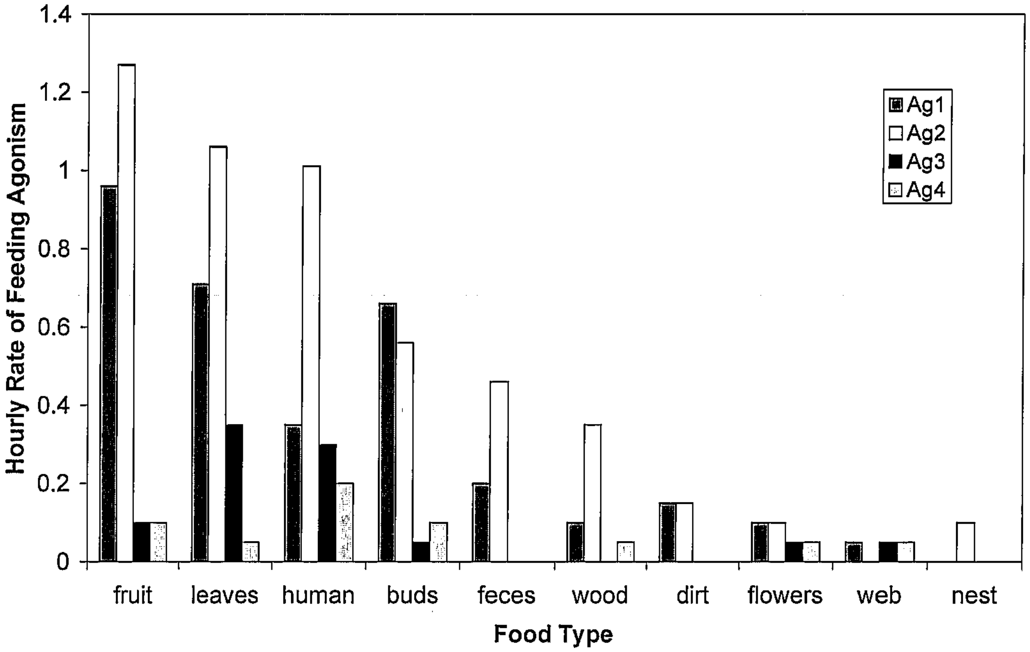


Figure 3.25 – Average hourly rates of feeding agonism levels by food type in Black group.

In neither Green group nor Black group was there a significant association between level of agonism and food type (Green group females: Kruskal-Wallis, $\chi^2 = 7.56$, $\rho = 0.11$, $df = 4$; Black group females: Kruskal-Wallis, $\chi^2 = 13.01$, $\rho = 0.16$, $df = 9$).

Chapter 4 – Discussion

4.1 Introduction

The goal of this chapter is to synthesize the results produced by this study, and relate them to relevant theory and literature, including past studies on *Lemur catta* at the Beza Mahafaly Special Reserve and elsewhere. The hypotheses for this work, put forth in Chapter 1, will first be examined in terms of the findings of this project. The research questions, also previously stated in Chapter 1, will then be addressed.

4.2 Habitat Variability and Resource Availability

The first hypothesis predicted that differences in habitat would result in notable dietary differences. Adult female ringtailed lemurs with home ranges within the dense vegetation of the reserve were expected to have a varied diet with a large amount of abundantly distributed resources. It was anticipated that adult female ringtailed lemurs with home ranges outside of the reserve, in habitat degraded due to anthropogenic factors, would have a restricted diet composed of fewer, sparsely distributed resources. To examine this hypothesis, habitat variation was measured between Green group, a troop within the reserve, and Black group, a troop outside the reserve in the degraded forest and in the research camp. Dietary composition was carefully recorded and analysed in terms of plant species and food type consumed. Food types included leaves, fruit, flowers/buds, soil, wood, human foods, feces (dog and cattle), birds' nest, and spiders' web.

4.2.1 Habitat Comparison

It was expected that there would be a marked contrast between the habitats of Green group and Black group. Since 1978, the forest within the boundaries of the reserve has been protected and allowed to flourish (Gould, 1997a; Sauther, 1992; Sussman, 1991). Over the same time period the forest outside the reserve has been subjected to various forms of human-induced disturbance: the removal of trees for building materials, fuel and agricultural space; grazing of domestic animals such as cattle and goats; expansion of neighbouring villages and of the Beza Mahafaly camp, leading to a need for waste disposal areas (both biological and organic) (Ratsirarson *et al.*, 2001; Sussman *et al.*, 2003). In many areas, trees are separated by substantial expanses of dry, sandy earth. The growth of thick, spiny scrub brush limits travel, lemur or human, in some non-reserve forest segments.

There was a measurable difference between the two habitats. Unexpectedly, the non-reserve habitat contained a greater number of species than the reserve habitat, determined through quadrat sampling methods. The non-reserve samples yielded nearly twice the number of trees deemed robust enough for additional measurements than did the reserve samples. The reserve trees were found to be on average taller than those outside of the reserve with the tallest species, Kily (*Tamarindus indicus*), averaging 18m. The tallest trees outside the reserve were two-thirds of this height.

There was a low level of phenological similarity between the two habitats: few plant species were common to both forests. This could be explained by the following:

1) Quadrat samples taken were not sufficiently representative of the reserve, nor the non-reserve, habitat;
2) Plant species were misidentified;
3) Phenological samples were mismeasured or were incorrectly approximated;
4) The different habitats have contrasting levels of soil richness, shade, and amounts of solar radiation; therefore the need of an environment suitable to the growth and distribution of certain plant species could be a limiting factor.

Option 1) is possible, as the samples were taken from territory used by the reserve and non-reserve groups studied. These groups used only a fraction of the reserve forest, and the forest and camp south of the reserve. Since phenology is only being discussed in terms of Green group and Black group home ranges, this should not pose a problem. Options 2) and 3) are both unlikely explanations for the phenological deviation detected. The Mahafaly research assistants have a great deal of experience in working with the flora and fauna in the area. Multiple opinions were sought for any uncertainties in associating a vernacular term with scientific nomenclature. Those that could not be resolved were left as "species unknown" in order to avoid any erroneous conclusions.

Option 4) is a likely and plausible explanation, but cannot be verified without detailed knowledge of the developmental requirements of the particular plant species, or without soil analysis. Quantitative observations demonstrate that there is markedly more canopy coverage within Green group's range, which occurs within the reserve. The soil in the home range of Green group is darker and moister. These might be the conditions necessary for certain trees to reach their growth potential – both in basal area and in height (Hubbell, 1979; Kraaij and Ward, 2006). The dense, protected forest could also limit the deposition and growth of any seeds from outside species through carriers such as natural forces, i.e. wind, and human influence, i.e. cattle feces (Seidler and Plotkin, 2006). The unprotected, sparse, non-reserve forest used by Black group had numerous areas with little canopy cover and many open spaces with no coverage at all with very dry, sandy earth (Hubbell *et al.*, 1999). A lot of the forest has been eroded over time due to consistent traffic of humans and herds of grazing livestock. The feeding patterns of these animals may have contributed to the disappearance of plant species that are still found within the reserve. The waste material that cattle and goats necessarily leave behind, coupled with the more sparsely distributed trees, could allow for the propagation of plant species that would not have usually grown in the forest as it once was (Cosyns *et al.*, 2005; Olff and Ritchie, 1998). Cosyns and colleagues (2006) found that endozoochony, the dispersal of plant seeds through animal fecal matter, was more successful in terms of seed germination when deposits were made in areas with many gaps in vegetative growth. The details of such a scenario could only be verifiable through a closer examination of what the domestic animals surrounding Beza Mahafaly are eating, and if their fecal deposits are aiding in the transport and development of any plant species.

Further phenological measurements showed that more than twice as many trees censused in the non-reserve forest as compared to the reserve forest had less than one third total leaf crown coverage. No sampled reserve trees were in a recognizable phase of flowering during the study, and the only fruiting species was Kily with an average of 23% fruit crown coverage. Of the non-reserve trees, the only species observed to be in a flowering phase was Sasavy (*Salvadora angustifolia*) with approximately 30% bud crown coverage. Kily was again the only sampled fruiting species, but with only 1% fruit crown coverage.

It was expected that there would be an overall lack of types of crown coverage as this was the end of the lengthy dry season at Beza Mahafaly. There are few species that produce buds/flowers or fruit during the months of July and August (Sauther, 1992, 1998). Kily has been appointed the title of keystone species, or species essential to survival, for ringtailed lemurs at Beza Mahafaly in many past studies (such as Gould *et al.*, 1999; O'Connor, 1987; Rasamimanana and Rafidinarivo, 1993; Sauther, 1998; Sauther *et al.*, 1999), due to its nature of producing new leaves and fruit throughout the seasons: individual trees are on different cycles such that different individuals could be at variable reproductive phases at any given time (Simmen *et al.*, 2006). Ringtailed lemurs have been found to take advantage of these temporally diverse life cycles, depending upon the Kily for food throughout the seasons (Gould *et al.*, 1999; O'Connor, 1987; Sauther, 1998). It was thus anticipated that there would be a range of foods being produced by the Kily trees available to the lemurs for consumption.

Kily trees were well represented in the phenological samples. In Green group's habitat, Kily were the tallest, the most robust, and the most abundant tree species that met standards for measurability. To provide a better idea of relative tree size: the second tallest tree measured was half the averaged height of the Kily, and the second largest species in terms of total basal area was one third of that maintained by the Kily trees. In Black group's habitat, Kily was again dominant when looking at total basal area, and was among the top three species in terms of average height. In both habitats the Kily trees had the highest percentage of leaf crown coverage – useful as coverage for afternoon rests and bedding down for the night, or as a potential food source. Kily was indeed an important component of adult females' diets in both Green group and Black group (the species was responsible for 25% of the total food consumed in both groups), but to a lesser degree than has been documented in other studies in gallery forests: between 35 and 60% (from Gould, 2006: Koyama *et al.*, 2006; Mertl-Millhollen *et al.*, 2003). This is expected as Kily fruit and leaves have high concentrations of protein and water (Mertl-Millhollen *et al.*, 2003) – essential nourishment for females during the dry gestation period.

4.2.2 Diet Variation

Contrary to the assumption that the reserve group would have a more varied diet than the non-reserve group, both groups had nearly equal totals of food species consumed: 24 for Green group, 25 for Black group. Fifteen of these plants were common to both groups. The top ten foods fed on by Green group females made up more of their diet than did the top ten foods fed on by Black group females: the non-reserve lemur diet was more varied than the reserve lemur diet. Black group females consumed a greater, more evenly distributed quantity of their varied food resourced. Green group females focused mainly on two food sources, for 75% of their diet: Kily (tamarind) and Fatinboay (thistle).

Fatinboay was definitely in season, as Green group spent long periods of time feeding on its leaves in the dry Sakamena riverbed on the outskirts of the reserve. Green group females ate significantly more leaves than Black group females, likely due to the abundance of Fatinboay leaves within Green group's home range. Many of the Kily trees within Green group's range were fruiting readily during the period of this study. Those within Black group's range were not: crown fruit coverage was significantly higher for Kily in Green group's range than in Black group's range. The varied cycles of the Kily trees between the two ranges directly contributed to the fact that Green group females were found to consume significantly more fruit than Black group females. A similar instance is responsible for significantly more buds/flowers having been consumed by Black group females: Sasavy trees within Black group's home range were providing the lemurs with what seemed to be an endless supply of buds over many days.

Feeding rates on resources from *T. indica* were relatively equal between groups at Beza. During the gestation period at Berenty Reserve, southern Madagascar (July/August) when there were few available species of fruit, *T. indica* was a significant part (90%) of the diets of the nonprovisioned females within the reserve (Rasamimanana and Rafidinarivo, 1993). Females in a provisioned group had a more varied diet than the nonprovisioned group. Kily seems to be of less importance during these months to females at Beza than at Berenty. Like the Berenty provisioned group, the non-reserve group from this study, with access to human foods, had a more varied diet.

There was no significant difference found overall between groups and rates of feeding on plant parts, but a significant difference in rates of feeding on non-plant items was found between groups. Adult females in both groups were on occasion witnessed feeding on what appeared to be wood. This is discussed as a nonplant food item as it likely that they were not actually consuming the wood or bark for its properties, but for what was on top or within it: termite leavings, rich in protein and minerals. This type of feeding has been documented in past studies on ringtailed lemurs (Gould, 1994; Sauther, 1992). Feeding on termite leavings was not very common in this study, perhaps again due to the extremely dry conditions.

4.2.3 Geophagy

Both groups were found to consume soil, a behaviour termed geophagy. Theories suggest many potential adaptive explanations for the occurrence of the behaviour. A review by Krishnamani and Mahaney (2000) assessed six nonexclusive hypotheses which could contribute to geophagy. Four of these hypotheses deal with relieving gastrointestinal disorder: 1) Soil absorbs toxins; 2) Soil adjusts the pH of the gut; 3) Soil acts as an antidiarrhoeal; 4) Soil offsets the effects of endoparasites. The remaining two hypotheses deal with geophagy supplementing nutrients and/or minerals: 5) Soil acts as a supplement to nutrient-poor diets; 6) Soil is a source of extra iron at high altitudes. Soil was the tenth most frequently consumed item for Green group, and the ninth for Black group. It is not possible based on the data collected in this study to determine conclusively why *L. catta* at Beza Mahafaly practice geophagy. The sixth hypothesis is not relevant in this case. No cases of diarrhea were observed within the study period; therefore hypothesis 3) seems unlikely for this data set. Hypotheses 1) and 5) seem the most plausible for Green group. Green group females consumed many leaves potentially requiring soil to absorb the excessive secondary compounds. Also, soil may have been contributing nutrients to a low quality, dry season diet. These options are all possible explanations for soil consumption within Black group. Hypothesis 2) should also be considered for this group as they were ingesting a large amount of various types of human food which could have served to upset the pH balance of their intestinal systems. Parasitic analyses of Beza Mahafaly *L. catta* are currently being conducted by Loudon and colleagues (in preparation), and it is plausible that hypothesis 4) can also be applied to this site.

Dew (2005) suggested the possibility of soil counteracting toxins in fruit eaten by spider monkeys (*Ateles belzebuth belzebuth*). Hsu and colleagues (2001), in a study of geophagy in Taiwanese macaques (*Macaca cyclopis*), suggest the possible importance of soil consumption for mineral absorption, particularly iron, by pregnant females. This may be an additional benefit of geophagy for the adult females of this study as the dry season at Beza Mahafaly coincides with the gestation period.

4.2.4 Coprophagy

Further comparison of the diets and resource availability of both groups demonstrates considerable differences in terms of access to non-plant food sources. The sixth most consumed food by Black group females was fecal matter (cattle and dog), and the third most frequently consumed item was human food.

Coprophagy, the consumption of fecal matter, has been observed in relatively few primate species (chimpanzees, *Pan troglodytes*: Goodall, 1986; lowland gorillas, *Gorilla gorilla*: Collet *et al.*, 1984; Sportive lemur, *Lepilemur mustelinus*: Napier and Napier, 1985; Redtailed Sportive lemur, *Lepilemur ruficandatus*: Hladik, 1978). It is a common behaviour with apes in the wild and in captivity (Hoff *et al.*, 1994; pers. obs.). Theories explaining its function in natural settings have hypothesized coprophagy could highlight insufficient roughage (Fritz *et al.*, 1992) or food scarcity (Goodall, 1986). Internally, it could contribute to the upkeep of the system to digest cellulose (Collet *et al.*, 1984) and can aid with the assimilation of vitamins (Oxnard, 1966). Hladik (1978) found that coprophagy improved the nutrient uptake of the Lepilemur (*L. ruficandatus*). All of these possibilities are plausible benefits for the ingestion of fecal matter by Black group females: increased roughage, food during scarcity, nutrient supplement, digestive aid, and vitamin absorption. There are potential costs associated with this type of feeding. Uncovering these costs is one goal of a current longitudinal study on the health of ringtailed lemurs that range into the camp at Beza Mahafaly (Loudon and Sauther, 2007; Sauther *et al.*, 2006). Early results of that study have shown ringtailed lemurs exhibit behaviour associated with health issues and parasite loads: lemurs in the camp have been found to have a more elevated endoparasite load than those not in consistent contact with humans and their associated waste products (Loudon *et al.*, 2005; Loudon and Sauther, 2007).

4.2.5 Human Food

Nonhuman primates feeding on human food in a non-provisioned sense has been documented numerous times in various species of primates. Living in close proximity to human habitations, either due to direct human encroachment on space or due to primates' search for supplemental food resources has provided many primate groups the opportunity to sample foods not traditionally part of their diets. Some examples include Olive baboons (*Papio anubis*: Strum, 1984), long-tailed macaques (*Macaca fascicularis*: Fuentes *et al.*, 2002), Rhesus macaques (*Macaca mulatta*: Ghimire, 2000), Tibetan macaques (*Macaca thibetana*: Zhao, 1999), red colobus (*Procolobus badius*: Siex and Struhsaker, 1998), and vervets (*Cercopithecus aethiops*: Saj *et al.*, 1999).

Saj and colleagues (1999) discuss the impact of feeding on human foods on vervet activity budgets. They argue that human foods are usually of higher quality than wild food; therefore animals can meet their nutritional needs more rapidly. This leads to improved foraging efficiency, leaving extra time to spend resting or engaged in social behaviour.

According to optimal foraging theory, animals should be seeking to maximize their net rate of energy intake – high benefits and low costs (Pyke *et al.*, 1977). In times of scarcity, such as the dry season, and in times when benefit need is elevated, such as pregnancy, the costs of not finding additional food resources could be great. Human foods are usually higher in calories and, in the case of human waste produced at the Beza Mahafaly camp, could be more abundant than wild foods (Saj *et al.*, 1999). That said, it is difficult to decipher whether feeding on alternate foods, such as human foods as seen in Black group, reflects optimal foraging requirements due to resource scarcity, or is an example of animals developing a preference for human foods (Altmann and Muruthi, 1988).

4.3 Rank and Food Access

In various primate species, dominance rank has been positively correlated with improved access to desirable, high quality resources (see sections 1.3.1 and 1.7 for examples). Individual rank is expected to have a direct effect on the dynamics of within group, adult female feeding competition. The second hypothesis of this study suggested that there would be differential access to feeding resources between ranks within both groups. It was predicted that there would be a more pronounced difference between feeding patterns of higher-ranking and lower-ranking females within Black group than Green group, due to Black group's expected lower availability of food resources. Scarce resources would presumably intensify within group competition for access to those resources, thus making rank disparity more pronounced.

A dominance hierarchy was detected in both groups through directional monitoring of submissive and agonistic behaviours. The second hypothesis failed to be accepted in relation to Green group females: there was no significant difference between high and low rank and the consumption of leaves, buds/flowers, or fruit. There was no significant difference between high and low ranked females within Black group when feeding on buds/flowers, fruit, or feces. There was, however, a significant association between rank category and feeding on leaves and human foods: lower-ranking females fed significantly more often on leaves than did higher-ranking females; higher-ranking females fed significantly more often on human foods than did lower-ranking Black group females.

Green group females were organized hierarchically, yet this did not have an effect on feeding in terms of food types. Higher-ranking females did not feed on higher quality foods, such as fruit, more often than their lower-ranking counterparts. This is in contrast to Sauther's 2002 findings that higher ranking ringtailed lemurs consumed significantly more fruit than lower ranking ringtailed lemurs. The lower availability of such food types during the dry season could be confounded, but then it would be expected that high rank would entitle the individual to the few fruit that were found. This was not the case for Green group in this study. Dominance ranking could serve a purpose in the access to other resources, such as grooming partners or resting sites (Sauther, 1992).

What makes one food source more desirable than another? In a study on Japanese macaques, Aureli *et al.* (1992) defined desirable foods as being temporary and of small quantity. Desirable foods are also described as high quality foods, which Vogel (2005) discusses in terms of energy gain rate (KJ/min). If desirability for a food item is defined by the attraction and drive of individuals to obtain that food item, then human foods are a desirable option for females within Black group. Feeding agonism surrounding human food scraps could be interpreted as drive or motivation of Black group females to obtain that type of food. As data were collected during the dry season, foods were presumably scarcer than at other times of the year, so it would be of value to monitor human food consumption and associated differences of this type of feeding between ranks during the wet season.

4.4 Within Group Interactions

4.4.1 Activity Budgets

It has been postulated that distance between food patches can affect within group feeding competition (Isbell *et al.*, 1999; van Schaik, 1989; Vogel, 2005). In this study, it was expected that Green group females within the reserve would require less travel time from food source to food source, than would Black group females outside the reserve. Less time would also need to be devoted to foraging for food, freeing up time to spend in other activities, including resting, and affiliative, socially cohesive behaviours, such as grooming. Activity budgets of primates have been studied in numerous species, as they can serve to demonstrate constraints on time-energy balances, such as food scarcity (Bercovitch, 1983; Clutton-Brock, 1974; Li and Rogers, 2004). Particularly in the dry season when food resources are scarce and competition for those resources is presumably high, it was anticipated that Black group females would devote less time to affiliative, social behaviours and would spend a greater proportion of time foraging and competing for nourishment. This led to the hypothesis that there would be a higher frequency, and a more elevated level, of within group agonism amongst non-reserve females than amongst females living in the reserve.

The results of this study did not fully support this hypothesis. As found in the group activity budgets, Green group females did exhibit more instances of sitting than Black group females, but they also exhibited slightly more agonism than Black group females. Black group females were observed locomoting and foraging somewhat more often than Green group females. After statistical analysis it was shown that these results did not differ enough to be significant. Although time spent resting and moving around is relevant, interactional behaviours were isolated to take a better look at affiliation and agonism and how they might relate to intragroup feeding competition.

4.4.2 Affiliation and Agonism

Proportions of affiliative and agonistic behaviours were basically equal between groups. There was no significant difference in agonism between groups, and no significant difference between groups when agonism rates were broken down into four levels of increasing agonistic severity. The rate of the lowest level of agonism, Ag1 (submissive vocalization), was higher in Green group than in Black group. The rates of the three more severe forms of agonism, Ag2 (displacement), Ag3 (lunging), and Ag4 (chasing/physical contact) showed no significant difference between study groups. When the factor of rank category was applied to within group level of agonism, the only combination that resulted in a significant association was within Black group: higher ranking females in Black group engaged in more Ag4 activity than lower ranking females in Black group.

When examining interactions between animals, it is essential to look at not only the event itself, but also the context of the situation in which the behaviour occurred. The context of agonistic interactions could indicate particular areas of concern, or even stress, amongst individuals in a group (Sauther, 1992). Context could provide insight into areas that are associated with within group competition.

The contexts in which agonistic encounters took place in each group included feeding, social and resting situations. When analysed, none of these agonistic contexts had significantly different average agonism rates between groups. When the factor of ranking category is considered along with agonism context and level, feeding agonism rates are higher than the other contexts for both higher ranking and lower ranking females. There was a significant difference in average agonism rates between groups for agonism in a social context for lower ranked females: lower ranking Green group females exhibited more social agonism than lower ranking females in Black group. This might suggest that at the time of this study, feeding was of greater concern to Black group than to Green group, and social situations were of greater concern to Green group than to Black group.

There are four possible options to explain the lack of support for this hypothesis:

1) The scope of this study included only adult females. With additional information on within-group interactions between all age and sex classes, a more complete picture of within-group dynamics could be drawn.
2) 30% of interaction context were scored as "unknown" – the observer could not detect a context, or the observation session was commenced once an interaction had already been initiated.
3) The hypothesis can be outright rejected – there is no difference between groups in frequency or intensity of agonistic interactions.
4) Sample sizes were too small in order to detect a significant difference between populations.

Options 1) and 4) would necessitate a longer investigation of the ringtailed lemurs through adding age and sex classes for study, and likely additional groups from each of the habitats in order to increase the sample size. The effects of option 2) could also be reduced with a longer study – proportions of in and out of sight might remain the same, but there would be a greater number of observable interactions from which to draw conclusions. The results of this study indicate option 3), although the findings could have been affected by the other listed factors. These results suggest that habitat differences are not associated with agonism rates for these groups of ringtailed lemurs. Female feeding ecology theories and studies stress the relevance of agonism to intragroup competition (Aureli *et al.*, 1992; Barton and Whiten, 1993; Isbell, 1991; Isbell and Young, 2002; Koenig *et al.*, 1998; Saito, 1996; Sterck *et al.*, 1997; Takahata *et al.*, 1993; van Schaik, 1989). Within-group agonism can produce a detectable, stable dominance hierarchy when contest feeding competition occurs (Barton and Whiten, 1993; Koenig *et al.*, 1998;

van Schaik, 1989) and in some cases agonism related to feeding significantly outweighs agonism in any other context (Aureli *et al.*, 1992; Saito, 1996; Takahata *et al.*, 1993).

As females in Green group and Black group are competing amongst themselves for access to food resources, perhaps the effects of the differing habitats are not manifested in overall affiliative and agonistic behaviours, but in the direction of these behaviours, particularly agonism, surrounding particular food species.

4.5 Food Type and Feeding Competition

All primates, humans included, demonstrate preferences when it comes to foods selected for consumption. Foods that are desirable can in some senses be considered of high quality. Of course, food quality should also be determined scientifically through the chemical analysis of nutrients and toxins found within any given item, as has been done in numerous studies (langurs: Li and Rogers, 2004; baboons: Dunbar *et al.*, 2002; chimpanzees and bonobos: Hohmann *et al.*, 2006; lemurs: Curtis, 2004; Mertl-Millhollen *et al.*, 2003; Simmen *et al*, 2006; Soma, 2006). In times of scarcity preferences for specific food species or food types may have to be set aside and foods of lower quality, in terms of preferential value and nutritional analysis, may become the primary dietary component (Stephens and Krebs, 1986; Wrangham, 1980).

Wrangham (1980) proposed that a lesser degree of feeding competition should be evident during times of food scarcity than in times of abundance. When foods are scarce females should feed on lower quality foods, thus decreasing energetic costs associated with feeding competition.

Typically high quality foods, such as fruit, tend to be patchily dispersed - fruiting trees are not generally organized in large, lined groves within a forest. They are also seasonally and temporally variable (Janson, 1988). The period of availability of these foods is finite; therefore feeding competition between females for their acquisition is high (Borries, 1993). Foods that are readily available spatially and temporally, such as leaves, may also be of good nutritional quality and a preferred selection amongst a primate group. These sorts of food are generally produced in large amounts that can accommodate and satisfy an entire group. For example, a lone tree branch could have 100 edible leaves, but only a single piece of fruit. Such a situation would not be problematic for a solitary primate, or even a very small group. In this study group size was 15 animals total per group, six adult females per group. More individuals vying for the limited selection of desirable, high quality food would expectedly lead to high levels of intragroup feeding competition surrounding especially those high quality food types (Barton and Whiten, 1993; Glander and Teaford, 1995; Pazol and Cords, 2005; Sauther *et al.*, 1999). Again, as these data were collected during the dry season, higher quality food, such as fruit, was not readily available, but preferential foods were detected for females of both groups.

The fourth hypothesis proposed that there would be a difference in the amount and degree of female feeding competition depending upon the food in question. It was expected that levels of feeding competition would be more elevated for foods that were sparsely distributed, temporally limited, and of high quality than for foods that were more widely dispersed over space and time. This hypothesis was evaluated by examining the amount and degree of agonistic interactions in terms of the food type and the food species involved in the encounter. It could be assumed that a food source was valuable to the animals in terms of benefit if individuals are engaging in energetically costly agonistic behaviours in order to obtain it (Aureli *et al.*, 1992; Pyke *et al.*, 1977).

4.5.1 Within the Reserve

Within Green group the food type that had the highest associated proportion of agonism was soil, followed by leaves and fruit. Soil feeding was recorded only 12 times for Green group, and 25% of those observations involved agonism. As soil is fairly readily accessible, agonism in this case might have been associated with another factor undetectable to the observer, such as a social cue. Soil compositions can also vary depending upon region (Krishnamani and Mahaney, 2000); therefore areas of feeding on soil would need to be pinpointed and sampled in order to determine any particular nutritional benefits of a specific area. It is also possible that there was a concentration of insects in the patch of soil being consumed.

There were four tree species for which proportion of agonistic encounters was greater than 20%. As plant parts made up the majority of food ingested by Green group females, these data are more open for interpretation. The food most commonly consumed by Green group females throughout this study, Fatinboay leaves, had an associated proportion of feeding agonism of 20%. Their second most frequently consumed food source, Kily, had an associated agonism percentage of only 12%. Kily is known to be available in differing reproductive phases between specimens to ringtailed lemurs throughout all seasons. *T. indica* were somewhat randomly distributed throughout the reserve, not growing in clumps. Kily trees were also measured with extremely tall and wide dimensions, and were found to have large, full crowns. An entire group can feed within a Kily crown without requiring a great deal of interaction between members due to space restrictions. This served to lessen the opportunity for an individual to monopolize an area over another. Also, if one tree has stopped reproducing another will likely already be in the process, therefore contributing to the lower and less intense competition for the resources.

The leaves and fruit of Kily trees are an important resource to *L. catta* throughout the year, and essential in times of scarcity, but its consistency in availability and large average size seem to incite less competition between females than more seasonally restricted resources. Another factor worthy of mention for Kily selectivity is that Kily in different areas within a range have varying nutritional values (Mertl-Millhollen *et al.*, 2003). Mertl-Millhollen *et al.* (2003) uncovered an association between river proximity, leaf protein and water content, fruit availability, canopy density, and Kily food choice by *L. catta* at Berenty Reserve, Madagascar. Moving away from the river and the closed canopy forest into more open canopy, leaf protein and water content decreased, and fruit availability increased. Ringtailed lemurs chose to feed on leaves in the closed canopy, and fruit in the open canopy. Mertl-Millhollen *et al.* (2003) demonstrated nutritional variation within a tree species, within a habitat. A similar evaluation of Kily tree nutritional value and associated feeding patterns of ringtailed lemur groups between reserve and non-reserve habitats could shed more light on the importance of this food source at Beza Mahafaly.

The higher rate of agonism in Green group that was associated with Fatinboay could be correlated with a number of factors. Without a doubt, this plant species is a seasonal resource. It was found growing in the dry riverbed of the Sakamena: the riverbed is submerged between the months of October through March (Gould *et al.*, 1999; Sauther, 1992; Ratsirarson *et al.*, 2001), therefore Fatinboay is a confirmed seasonal and temporal food source. Fatinboay plants were spread out over a large area of the river bed, under the shade of the reserve trees. The plants were in fairly concentrated clumps spread over an area of approximately100m along the reserve and 20m in width; a relatively large area, but the only plant type growing within it. An individual would usually sit at one plant, picking off leaves one by one. Individual plants were therefore monopolizable, but an entire area was not. Isbell (1991) suggests that if clumped monopolizable foods are present, then a hierarchical priority of access should be evident. A clear distinction between adult female rank was not observed while feeding on this food source. It is likely that priority of access was based on sex of the animal and not rank.

Fatinboay plants are a novel, clumped, seasonal, and temporally distributed food resource for Green group. Agonism was dependent upon food type within a group of Japanese macaques: more aggression was displayed over temporarily available foods than permanent food sources (Aureli *et al.*, 1992). For Wrangham's prediction to hold true in Green group, female feeding competition rates would need to be higher during the wet season, a time of relative abundance, than the rates calculated in this study during the dry season (Wrangham, 1980). On the contrary, Sauther (1993) found that female-female feeding agonism was higher in the dry season than the wet season amongst *L. catta* at Beza Mahafaly.

4.5.2 Outside the Reserve

Within Black group, the food types that resulted in the highest proportion of agonism were wood, spider webs, and bird's nests. The frequency of feeding on these items by Black group females was extremely low over the course of the study, and thus they are considered truly novel. Webs and nest in particular are discovered purely by chance. Curiosity or past feeding experience could spur others to compete for the resource.

Feeding agonism on resources that were a substantial portion of Black group's diet was highest for human food, followed by fecal matter, fruit, soil, leaves, and buds and flowers. The two highest agonism inducing, regular components of the diets of females in Black group were related to the group's more frequent contact with human habitation. Fecal matter encounters can be somewhat likened to the chance encounters of webs and nests: random and sporadic. But, it was encountered much more often and thus fed upon more frequently than the sole fecal encounter of the reserve group. The clumped distribution of fecal matter, and the longer processing time at the food site could correlate with the higher rates of agonism associated with its feeding (Isbell, 1991; Isbell and Pruetz, 1998; Isbell *et al.*, 1999). An individual must pick up a piece of the material and take multiple bites while holding it between the hands, increasing the chance that it could be usurped by another animal. Commonly more than one piece would be available at a clump; therefore the opportunity for the entire clump to be usurped was also high as its depletion time would be great.

Human food was being consumed by Black group within the Beza Mahafaly camp – in a sense, the camp is analogous to one large clump. More precisely, food within the camp was organized in discrete patches: food peeling areas beside each residence and garbage pits behind each residence. These areas were small enough for only one or two females to monopolize at a time.

These patches are not spatially or temporally dependent, as there are people residing at the site year-round. There are more international travelers and researchers during the dry months however, coinciding with typical North American and European research and travel time. This is perfect timing for the ringtails that frequent the camp, as their forest habitat is scarce on resources when there is an abundance of human food and refuse at the camp. This is one possible explanation for the frequent consumption of human foods, as well as the feeding agonism that surrounds it. The concept of novelty could also be related. Quantity of human foods available is also somewhat seasonal based on influx of travelers and researchers, thus the scavenging of the ringtails could vary between visits to the camp.

When more traditional ringtailed lemur dietary components (plant parts) are examined, only a small proportion of related agonism is found, with one exception. The plant Votopose (Scientific name not available) was associated with feeding agonism 100% of the time it was fed upon; however, it was observed being eaten only a total of six times, on only one occasion. This is not a representative sample of feeding behaviour associated with this specific species, and it is thus difficult to extrapolate from those few instances. All six occurrences of feeding on Votopose were on leaves. This plant may have had new leaves at this time that had become palatable to the lemurs. Another possible explanation is that this plant was not a regular part of the day range of Black group and that it was located and eaten through happenstance.

No other plant species had greater than 20% associated feeding agonism. The proportion of Kily feeds that were agonistic was 12.67%. A species that is present year round in various reproductive phases, in various locations, and that is of substantial height, width, and crown area is not conducive to feeding agonism and competition according to theories of female feeding ecology (Isbell, 1991; Isbell and Pruetz, 1998; Isbell *et al.*, 1999). Competition should not be intense at a feeding site that is not rapidly depleted and has a fairly even distribution of resources throughout – an entire group can spread out and feed without needing to contest for resources.

4.6 Food Size and Feeding Competition

The correlation between size of a food item and feeding competition has been an area of focus in some research studies that examined primate feeding ecology (Isbell *et al.*, 1999; Pruetz and Isbell, 2000). Primates naturally tailor how they eat a food item depending upon its size. Some are small enough that the entire item can be placed in the mouth at once; others are too large and thus require pieces to be bitten off one at a time. In the first option it is difficult for one animal to remove the food item from the possession of another. In the second option, a large food item would require more processing time and could theoretically be more easily usurped. The final hypothesis examined in this study suggests that there would be an observable difference in feeding competition between different sized food items: feeding on bite-sized food items should result in less feeding competition between females than feeding on larger, multiple bite items.

When applied to the diets and feeding agonism recorded for adult females in Green group (discussed more fully in section 4.5), this hypothesis holds true. If desirable soil is considered to come in high quality patches, then it would require multiple bites or licks to deplete the patch. This would allow an individual, presumably of higher rank, to usurp the item or patch from the animal already using it. Fatinboay leaves made up a large portion of the diets of females in Green group. These leaves were usually large enough that they required the animal to remove the leaf from the stalk of the plant, hold it between their hands, and take several bites. A large proportion of feeding on Fatinboay leaves was associated with agonism. The leaves were usurpable and thus a competition inducing food item. Finally, the fruit consumed most often by Green group females were Kily pods. These pods are upwards of 10cm long. Ringtailed lemurs hold Kily fruit with their hands in order to break open the pod with their teeth and feed on the fruit inside. There was also a fairly high degree of agonism associated with Kily fruit feeding amongst Green group females.

Lower amounts of feeding agonism found with feeding of other leaf species could possibly be explained by the small size of the leaves themselves. These leaves can be consumed in a single bite, making competition for the individual food items very difficult. The same argument could be applied to low levels of feeding agonism surrounding leaf and flower buds.

The correlation between food item size and feeding competition is also discernable within Black group. The food items with an associated greater proportion of feeding agonism, e.g. spiders' web, birds nest, human food, and fecal matter, are all larger items that require longer processing times. For instance, human foods included corn cobs, sugar cane and sweet potato peels. These were all large enough, in comparison with the body size of ringtailed lemurs, that it was necessary for an animal to hold the pieces of food and take bites. Fecal matter was picked up in dried pieces from larger piles, but the pieces removed were habitually too large to be placed in the mouth whole.

As discussed in Chapter 3, adult females in Black group ate a large amount of Sasavy buds during this study. Sasavy had the lowest proportion of associated feeding agonism than any other plant species consumed by Black group: 7%. Buds are food items small enough to be eaten in one bite while moving quickly around the tree. These findings are supportive of Pruetz and Isbell's (2000) usurpability theory. There is a relationship between size of a food item and amount of feeding competition.

4.7 Female Social Relationships and Feeding Competition

Socioecological theories of female feeding ecology suggest the distribution and availability of resources determine the type of competition that will be observable within a population, and will in turn shape the social relationships within a group (Wrangham, 1980; Isbell, 1991; Isbell and Young, 2002; Sterck *et al.*, 1997; van Schaik, 1989). When food resources are limited and are found in high quality patches that can be monopolized or usurped, within group contest competition is expected (Isbell *et al.*, 1998; van Schaik, 1989). Agonism is expected to be frequent, and a stable dominance hierarchy should determine priority of access to resources. Affiliation should be directed towards individuals who would make beneficial allies. When food resources are limited and are readily available, low quality, or are quickly consumable and thus not usurpable, within-group scramble competition is expected (Isbell *et al.*, 1998; van Schaik, 1989). Agonism should be infrequent, and a dominance hierarchy absent or unstable. Affiliation rates should be low – there would be no coalitions and thus no need to cultivate relationships (Pazol and Cords, 2005).

The dry season is a time of limited resources, both within and outside of the Beza Mahafaly Reserve. The monopolizability, level of quality, and size of food resources dictated the type of competition that was recorded for both study groups. Competition type was directly influenced by the type of food being consumed. In both groups, high quality, highly desirable foods incited contest competition. When Green group females fed on Fatinboay leaves, agonism rates were elevated and a dominance hierarchy was discernable. Fatinboay leaves are usurpable. When Black group females fed on human foods at the Beza camp, more agonism was observed than with other food sources. Higher ranking females took priority of access of this resource over lower ranking females. Human foods were found in monopolizable patches.

Scramble competition was also found in both groups. When feeding on Kily leaves or leaves of many other species, associated agonism was low. Sasavy buds were plentiful in large crowned trees. Feeding on this resource had a very low proportion of agonism amongst Black group females. All of these food sources were in patches too large to be monopolized, and the food items were too small to be usurped. Elevated dominance rank incurred no feeding priority over these resources.

4.8 Research Questions

Research questions were outlined in section 1.7. These questions will be revisited and briefly discussed in light of the findings of this study.

1) How do the habitats of the two groups differ?

There is a low degree of similarity between the habitats of Green group and Black group. The sampled areas yielded a total of 35 species within Green group's habitat and 51 species within Black group's habitat. It was expected that a higher number of species would be found within the reserve, but this discrepancy could be indicative of a greater number of scrub, vine and liana species outside of the reserve: two thirds of the species recorded within Black group territory were not robust enough for additional measuring.

The specimens within the reserve were on average taller and had a greater trunk diameter at breast height (DBH) than did specimens outside the reserve. Reserve trees also had greater percentages of leaf and fruit crown coverage, factors that contribute to the ample canopy cover and moister soil that is found within the reserve, as opposed to the lack of canopy cover and dry, sandy soil that is found outside of the reserve.

2)a. How do the diets of the adult females within the reserve differ from the diets of those outside the reserve? and b. What foods are available to the different groups?

Because this study took place during the dry season at Beza Mahafaly, foods were likely more scarce than at other times of the year. The diets of both groups indicate that they are indeed opportunistic folivore/frugivores. Females within the reserve fed on 24 plant species, and females outside of the reserve fed on 25: there were 15 common plant food species between the groups. Plant parts fed upon included primarily leaves, followed by fruit and buds/flowers. The reserve group females ate significantly more leaves and fruit than the non-reserve females. As the reserve trees had more crown coverage they subsequently had more food to offer.

Females in both groups were observed engaging in geophagy, feeding on wood/termite leavings and engaging in coprophagy (once for the reserve group, multiple occasions with the non-reserve group). These could be indicative of certain health requirements or potentially mineral deficiency of some sort. These factors would require chemical analysis of all dietary components to determine the nutritional content of the food resources. The reasoning for these food selections may also be as simple as food availability and food preferences. If Green group had encountered fecal matter on more than one observed occasion, they might have fed on feces more often, as did Black group.

Non-reserve females ranged into the research camp multiple times each day, feeding on human food refuse. Whether human food is a preferred food choice or is consumed out of scarcity of resources is an important question that could only be answered with careful nutritional analysis of consumed food. Examining non-reserve feeding patterns during the wet season would also eliminate the factor of extreme resource scarcity during the dry season. The effects of water availability and water content in foods should also be examined. Reserve group females were not ever observed drinking water; non-reserve females were frequently observed drinking water from buckets and spilt well water at the camp.

3) What effect does rank have on the sorts of foods being consumed?

Within the reserve group, rank did not have a significant effect on food that was consumed. Within the non-reserve group, lower-ranked females ate more leaves than higher-ranked females, and higher-ranked females ate more human food than lower ranked females. The fact that rank differences in food type consumed in the reserve group were insignificant could be related to their more resource abundant environment. Although there was a fair amount of feeding agonism recorded for various food types and species, rank does not factor into the equation for this group.

The fact that higher-ranked non-reserve females ate more human foods than did lower-ranked females could be related to a preference for human foods over leaves, as lower ranked females consumed more leaves than higher ranked females. This could also be evidence of within group feeding competition during a time of scarcity. High ranked females won more competitions with lower ranked females over access to a high quality food source.

4)a. Does the rate or degree of agonism exhibited by females vary depending upon the type of food being consumed?, b. Does it vary between habitats? and 5) Does the size and species of food consumed affect female feeding competition?

Rates of agonism were dependent upon the type of food being consumed within each group, and the types of foods inducing higher rates of agonism differed significantly between groups. Of the food types that were consumed frequently by the reserve group throughout the study, a higher proportion of feeding agonism surrounded leaves and fruit. The large size of the most common type of leaf eaten, Fatinboay, and the large size of the most common type of fruit eaten, Kily, required the food to be held in the hands of the lemur and that multiple bites be taken. This creates a situation where another lemur can attempt to usurp the food item being held by the individual, therefore opening additional opportunities for feeding agonism, and competition, to take place.

A large proportion of Black group's feeding agonism was associated with feeding on human foods and fecal matter. These items were large enough in size to necessitate holding between the hands and taking more than one bite. Foods that could be eaten in only one bite, such as buds, had a lower proportion of associated feeding agonism in both study groups. Type and size of food affected female feeding competition.

6) Does the distribution and scarcity of food resources have an effect on female interactions related to feeding competition?

The Fatinboay leaves consumed often by the reserve group were found for a limited time, in a limited area, and were organized in smaller groupings of plants with up to 5m between each plant grouping. This food type was associated with feeding agonism within Green group, likely exacerbated by the fact that it is in season during a period of relative low abundance of food sources. Its distribution allowed for attempted monopolization of the clumps, potentially leading to increased amounts of feeding competition (as per van Schaik, 1989). The relatively numerous, large, spacious crowns of the Kily trees used by the reserve group provide resources year-round for the reserve group. Although Kily was used often by Green group, little feeding agonism was associated with the species: there are enough resources in one space and group members can spread out.

The scarcity of resources for Black group, either due to anthropogenic factors or seasonal factors, could have contributed to their increased use of food at and in the immediate vicinity of the human encampment. Human foods and fecal matter were found in small clumps within the area, therefore allowing individuals to monopolize a feeding site. Foods were desired or required badly enough that others would attempt to usurp the sites, leading to greater feeding agonism for these food types.

Overall, the distribution and scarcity of resources has an effect on feeding competition within both the reserve group and the non-reserve group. The presence of both contest and scramble competition was detected within both groups (Sterck *et al.*, 1997; van Schaik, 1989).

Chapter 5 – Conclusion and Directions for Future Work

Competition for food in primates can occur both at the inter-group and the intra-group levels. Groups with intersecting or overlapping territories might compete over shared sources of nourishment. Within a group rates of feeding competition are likely heightened when there are multiple reproductive females, as several females will be simultaneously seeking food resources. Female primates charged with the energetically taxing processes of gestation, development and rearing of infants must ensure they have access to food resources that are sufficiently abundant in numbers and energy for both the female and her offspring. Feeding competition is also mediated by the food resources themselves; their type, size and distribution.

This study examined feeding competition amongst adult female ringtailed lemurs within two non-intersecting groups. Questions were formulated in an attempt to examine potential behavioural differences related to feeding between two groups living at the same site, but in different habitats and with access to different food resources. The varied habitats occupied by Green group and Black group at the Beza Mahafaly Special Reserve provide a significant opportunity for examining the effects of human encroachment in southwestern Madagascar. These findings could serve to highlight the need for protecting additional forested area in Madagascar for the continued survival of ringtailed lemurs.

As previously documented in ringtailed lemur females by Sauther (1993), the majority of agonism corresponded to situations involving feeding. The results of this study suggest that type and size of an item of food are associated with rates of feeding competition. Items that required more than a single bite and that are held in the individuals' hands lead to an increased frequency of food usurpation and associated agonism, as Isbell and colleagues have discussed (Isbell, 1991; Isbell *et al.*, 1998; Isbell and Young, 2002). Foods distributed in monopolizable clumps also had higher associated rates of feeding competition. These findings are indicative of contest competition, and were observed in both study groups (van Schaik, 1989; Sterck *et al.*, 1997). In studies involving vervets (*Chlorocebus aethiops*) and patas (*Erythrocebus patas*), the same conclusion was reached; clumped foods resulted in contest competition in both species (Isbell *et al.*, 1998; Pruetz and Isbell, 1999). Fashing (2001) found that feeding agonism in guerza (*Colobus guerza*) occurred most often in small monopolizable food patches. The same results have been documented for Japanese macaques (*Macaca fuscata*) (Saito, 1996), and within two groups of ringtailed lemurs at Berenty Reserve, another ringtailed lemur research site in southern Madagascar (Rasamimanana and Rafidinarivo, 1993).

Food items requiring only a single bite or mouthful are not easily usurped and thus generated low rates of competition. Also, foods that are widely dispersed in an area making monopolization difficult have low associated rates of feeding agonism. These findings are indicative of scramble competition (van Schaik, 1989; Sterck *et al.*, 1997), and were documented in both Green group and Black group. Both forms of within-group feeding competition (scramble and contest) have been documented within a single species in other cases, such as brown capuchins (*Cebus apella*) (Janson, 1988) and Hanuman langurs (*Semnopithecus entellus*) (Borries *et al.*, 1991).

Rates of feeding competition were found to increase depending upon the type of food being consumed, and food types associated with agonism differed between the two study groups. Reserve group females displayed higher rates of intra-female agonism while feeding on leaves and fruit as compared to other food types. Non-reserve group females engaged in more intra-female agonism when consuming human food scraps and animal fecal matter as compared to other food types eaten by the group. These agonism-inducing foods were fed upon frequently within the respective groups. Comparatively, female blue monkeys (*Cercopithecus mitis stuhlmanni*) in the Kakamenga Forest, Kenya were observed competing agonistically for buds and flowers more frequently than for other foods in their diet (Pazol and Cords, 2005). Frequent feeding on a food type, as well as a high degree of feeding agonism associated with that food type, suggests that the food is desirable to the group.

With regard to the habitats of the study groups, results from this study demonstrate the existence of substantially more dense and lush forest within the reserve than outside. Detailed descriptions of habitat and dietary compositions for each group facilitated between-group comparisons. Females within the reserve ate significantly more plant products than did females outside of the reserve, whose diets were largely composed of human food scraps and domestic animal feces. These findings are undoubtedly the most poignant of this study. It is unclear whether non-reserve females are consuming large amounts of human food and feces out of necessity or due to opportunity. This could potentially be measured in future research projects by analysing the nutritional content of the foods consumed by reserve and non-reserve groups. Furthermore, this study was limited to the dry season. Documenting the diets and nutrition of these groups over the course of entire year would serve to eliminate any seasonal factors in dietary composition and analysis. However, the advent of a dry season does not guarantee differential food availability. Bayart and Simmen (2005) found seasonal food scarcity to be non-existent in a black lemur (*Eulemur macaco macaco*) population in northwestern Madagascar.

Sauther (1994) did examine *L. catta* groups within the reserve at Beza Mahafaly over the course of one year. Dietary composition was recorded, but nutritional analysis was not carried out. Sauther's project was also restricted to groups found within the reserve boundaries. Another valuable expansion to such research would be the addition of other study groups within and outside the reserve, thus increasing the sample size, and allowing for more robust statistical analyses.

A longitudinal study of ringtailed lemurs in contrasting habitats would also permit examination of the ultimate result of adult female feeding competition: the successful birth and survival of offspring. It would be of interest to document and compare the survivorship of infants born to females from the reserve and to those outside. Over time this focus would be pertinent in uncovering whether the incorporation of human foods into some ringtailed lemur diets is beneficial or detrimental to reproductive success. Research conducted with vervets in contact with humans and human food in Uganda demonstrated that by consuming human foods vervets were foraging optimally: metabolic needs were potentially attained more quickly by eating human foods (Saj *et al.*, 1999). Saj and colleagues (1999) also determined that adult females in this population consumed human food significantly less often than did other group members. This suggests the possibility of risk associated with obtaining or consuming this type of food, and that females could be increasing their reproductive success by choosing to consume it less often.

For now what is indisputable is that the ringtailed lemurs outside the boundaries of the Beza Mahafaly reserve are dramatically impacted by their human neighbours, as is the plight of the majority of free-ranging primates world-wide (see Fuentes and Wolfe, 2002 as an example of an entire volume dealing with primate-human interactions). The forest inhabited by the non-reserve lemurs is degraded. They are in close proximity to humans and domestic animals numerous times each day. Their diets include the scraps and feces of these animals. A longitudinal health survey of the ringtailed lemurs in this area (initiated by Sauther and colleagues) has already documented higher weights and greater intestinal parasites in the animals who venture into the research camp (Sauther *et al.*, 2006). With studies such as this, and the continued protection of forest in the area and the continued involvement of local residents, it is hoped the ringtailed lemurs both within and outside of the reserve at Beza Mahafaly will be ensured a successful, healthy future.

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Appendix A. Data Collection Sheet Template

Day______Month______Year______ Time__________

Group___________

Focal ID________ Weather/Temperature____________________

Location_____________________________

Time	Behaviour	Direction	ID	Tree	Comments

Appendix B. Ethogram for *Lemur catta*, developed by Jolly (1966), Taylor (1987), Gould (1992) and modified to apply to the current study by A. Gemmill.

Affiliative Behaviors
1. mutual groom
2. one-way groom
3. social play
4. feed near
5. rest near
6. rest/contact with
7. sit near
8. sit/contact with
9. huddle with
10. mate with
11. lick wood near

Agonistic behaviors
12. stink fight
13. tail wave
14. slap
15. fight with
16. chase
17. cuff
18. displace
19. lunge
20. submissive chitter

Self-maintenance behaviors
21. feed
22. forage
23. drink
24. self-groom
25. rest/sleep
26. lick wood

Solitary behaviors
27. spur mark
28. anomark
29. sunning
30. sniff
31 lick (an object)

Vocalizations
32. vocalize

Locomotor behaviors
33. locomote
34. sit
35. walk bipedally
36. out of sight

Vigilance
37. vigilant