Feeding behavior and nutrition of male and late-gestation female gallery forest *Lemur catta* at the Beza Mahafaly Special Reserve, Madagascar

by

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B.Sc., University of Victoria, 2004

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ABSTRACT

Long isolation and the island environment of Madagascar has led to the evolution of a number of unusual traits in the Lemuriformes, including reproductive synchrony, sexual monomorphism, female dominance, and female feeding priority. Though gestation and lactation are costly in all mammals, the unpredictable and often harsh environment of Madagascar may have led to the selection of particular adaptive traits which offset some of the high costs of reproduction in female lemurs. Sex differences in feeding behavior between male and female *Lemur catta*, which have been documented previously, may be a reflection of increased reproductive female nutritional need, although differences in actual nutritional intake has not been examined. In August and September of 2005, I collected 217 hours of focal feeding data on 9 male and 9 gestating female *L. catta* from two social groups, at the Beza Mahafaly Special Reserve in southwestern Madagascar. Additionally, I collected representative samples of all plant foods eaten by the focal animals. Since reproductive females have higher metabolic needs, I predicted that when compared to males, gestating females would consume more, feed for longer periods, and ingest higher relative amounts of crude protein and minerals, and lower relative amounts of fiber. Additionally, since the two focal social groups have similar and over-lapping home ranges, I predicted that no feeding differences (amount consumed, time spent feeding, ingestion of crude protein, minerals and fiber) would be present between social groups. I found no statistically significant differences in feeding behavior between males and females, while nutritional sex differences were limited to females consuming increased phosphorus (P= 0.004) and potassium (P=0.015). Furthermore, although I detected no between group differences nutrient consumption or amount of food consumption, Green Group did spend significantly more time foraging, when compared to Red Group (P=0.004). These data may be explained by the prior activity of cyclone Ernest, which greatly reduced food availability and caused a fruiting failure of *Tamarindus indica*, a keystone resource of gallery forest *L. catta*. Additionally, although both focal groups ventured outside of the forest to forage on agricultural or introduced plant species, Green Group only fed on crop foods on one occasion, while Red Group fed daily on the easily processed crop foods, which may have decreased their foraging time. Ability to exploit novel resources and adapt to environmental extremes may be a key feature enabling *L. catta* to persist alongside humans in the harsh environment of Madagascar.

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CHAPTER ONE

Theory and General Introduction

In this introductory chapter, I will briefly review nutritional studies of primates, selectivity in feeding, food properties, and foraging theories applicable to ringtailed lemurs (*Lemur catta*) feeding, including female-bonded foraging theory (Wrangham, 1980), and contest and scramble competition theory (Isbell, 1991). Furthermore, I will introduce niche partitioning, discuss traits of Madagascar's lemurs, and will explore *L. catta* sociality and ecology. Last, I will discuss how natural disasters affect diet of *L. catta*, and describe the natural disaster that occurred prior to and affected this study. This chapter will introduce the theoretical background for the remainder of this thesis.

NUTRITIONAL STUDIES OF PRIMATES:

Feeding ecology is a central aspect of a species' biology as it relates to survival, reproduction, population dynamics, habitat requirements, and patterns of sociality (Robbins and Homann, 2006). The earliest primate field studies overlooked diet and feeding when examining social behavior (e.g. Carpenter, 1934; Jay, 1968; Washburn and Hamburg, 1965); however, in the 1970s, the importance of feeding ecology in behavioral field studies became more evident, although researchers who investigated primate diet were primarily concerned with describing and quantifying food items (see Milton, 1981; Smith, 1977; Sussman, 1977). In the last three decades there has been a surge of interest and research in primate feeding ecology, with many studies incorporating the nutritional analyses of primate foods. These data allow us to examine variation in nutritional composition of primate diets in light of physiological and ecological variables. Through recent primate nutritional studies such as those by Curtis (2004 (*Eulemur mongoz*)), Remis (2001 (*Gorilla gorilla gorilla*)), and Rode et al. (2006 (*Cercopithecus ascanius*)), we are becoming increasingly aware of the complexities of primate feeding ecology and the importance of these studies in understanding natural history of the Primates.

SELECTIVITY IN FEEDING

Primates are selective feeders. This was noted as early as 1963 when Schaller pointed out that gorillas (*Gorilla gorilla*) did not eat all the plant species available in their environment. Other early studies, such as those by Oates et al. (1980) or Glander (1982) documented that Nilgiri langurs (*Presbytis johnii*) selected young leaves, fruits and flowers even though these foods were far more limited than mature leaves, and that mantled howler monkeys (*Alouatta palliata*) did not feed equally on all available trees, but rather discriminated between tree species and leaves. Additionally, Wrangham and Waterman (1981) reported that when vervet monkeys (*Cercopithecus aethiops*) were foraging in acacia trees, they avoided mature leaves, and only consumed immature leaves, seeds, fruits, and flowers. In his work Leighton (1993) showed that Bornean orangutans (*Pongo pygmaeus pygmaeus*) deliberately sought out and consumed certain rare food items. Furthermore, in his review on primate food selection Ganzhorn (1989) stated that lemurs, monkeys and apes are all selective feeders, and that species have different tolerances and preferences for food chemicals. Which food chemicals primates may be selecting for or against, will be discussed next.

FOOD PROPERTIES

Nutrition can be defined as "the process of providing or receiving nourishing substances" (Merriam-Webster Online Dictionary). However, plant foods contain both nutrients (feedants) and non-nutritive components (antifeedants). Feedants are desired nutrients such as protein and carbohydrates, while antifeedants are non-nutritious and may include fiber or plant secondary compounds. Primate food selection is thus influenced by both nutrients required for survival, but also chemicals and compounds that may interfere with digestion or even be poisonous. Relative levels of feedants and antifeedants (such as protein and fiber) are often used as a measure of dietary quality (Waterman and Kool, 1994), and will be addressed next.

Feedants

Nourishing foods are those that facilitate body development, growth, maintenance and healing. Macronutrients that are nourishing to primates include protein, carbohydrates, fat, and water. Protein is an integral part of the primate diet because it provides the nitrogenous building blocks essential for DNA replication, body growth and maintenance, and regulation of body functions (Ullrey et al., 2003). Protein is found in high concentrations in young leaves, flowers, some fruits and seeds (Waterman and Choo, 1981; Waterman et al., 1981). Carbohydrates (non-structural) are the primary source of energy for most primate species, and do not require digestion in order to be used by the body (Danish et al., 2006; Ullrey et al., 2003). Rather, non-structural carbohydrates are absorbed across the gut lining, where they enter the bloodstream and are a source of quick energy (Danish et al., 2006; Ullrey et al., 2003). Non-structural carbohydrates are found in high concentrations in fruits, nectars, flowers and some young leaves. Fats are also important in the primate diet, as they particularly rich energy source and because fats can be stored for later use (Danish et al., 2006; Ullrey et al., 2003). Fats can be found primarily in seeds, and insect food sources (Ullrey et al., 2003). Water is also an important macronutrient as it carries other nutrients throughout the body and is required for cell regulation (Bosco et al., 2001). Primates require water intake daily, which can be found directly in tree holes or streams, or indirectly in plant parts such as pulpy fruits and succulent leaves (Glander, 1978).

Micronutrients, such as some vitamins and minerals, are also essential for body development, growth, and maintenance and healing (National Research Council, 2003; Windmaier et al., 2004). For example, calcium and magnesium are required for bone growth and maintenance, and for function of muscles and nerves (National Research Council, 2003; Windmaier et al., 2004). Potassium is also necessary for nerve function and is important in maintaining normal body blood pressure (National Research Council, 2003; Windmaier et al., 2004). Similarly, sodium regulates body fluid volume and concentration (National Research Council, 2003; Windmaier et al., 2004). Vitamins, such as niacin, folic acid, and ascorbic acid are also important in body function and are integral to processes ranging from cell division to building fat muscle and bone to oxygen transport and red blood cell generation (National Research Council, 2003; Windmaier et al., 2004). Micronutrients are found in plant foods, but can also be found in earthy deposits such as clay and soil (Mahaney et al.; 1994).

Antifeedants

Antifeedants are components of foods that do not contribute to body nourishment. Fiber, a structural carbohydrate, is the primary antifeedant consumed by most primates as it is present in all plant foods. Since it is inversely related to digestibility (Van Soest, 1994), fiber does not contribute to caloric intake, but in high levels can also interfere with fat and protein digestibility (Ullrey et al., 2003). Mature leaves, unripe fruits, and plants such as bamboos are particularly fibrous, and should be avoided by primates who do not have specializations to ferment or otherwise deal with high fiber content (Milton, 1979; Rogers et al., 1990; Yeager et al., 1990).

Secondary compounds are those produced by plants that are not essential to the plant's life. They are an evolutionary response to plant predation by insects and herbivores, and can be either reduce digestibility of foods or be toxic (Freeland and Janzen, 1974; Glander,1982). Secondary compounds that primates commonly encounter include tannins and alkaloids. Tannins bind to proteins and thereby reduce the digestibility of the protein, while alkaloids act as toxins and disrupt metabolic processes (Lambert, 1998). Although some primates have evolved adaptations to deal with specific secondary compounds (e.g. *Hapelemur* spp. (Tan, 1999, 2000; Glander et al., 1989), many largely avoid ingesting significant quantities through diet diversification or avoiding foods high in secondary compounds (Fashing et al., 2007). Early works, such as those by Glander (1982), McKey (1979), Oates (1977, 1978), Wrangham and Waterman (1981) all found a negative correlation between the presence of plant secondary compound and primate food choice. Similarly, Coley (1983) and Waterman et al. (1983) suggest that by focusing on a diverse array of immature leaves and herbaceous species, primates gain the advantage of lower digestive inhibitors and other secondary compounds.

As outlined, primate foods contain macro- and micronutrients necessary for survival, but also contain compounds that can interfere with metabolizing nutrients. As such, primates must make food choices and feed selectively based on a food contents and a variety of ecological, morphological, and physiological factors (Fashing et al., 2007). Theories related to how and why primates select food resources will be addressed next.

FORAGING THEORIES:

Wrangham's Female-Bonded Foraging Theory

Wrangham's influential 1980 paper on female-bonded primate groups changed the way primatologists view primate group dynamics and foraging. Prior to Wrangham's paper, analyses of the evolution of primate groups focused on both sexes and looked for correlations between group size and ecological variables (Clutton-Brock and Harvey, 1977). These studies, however, did not account for why females in many primate species spend their lives in the groups into which they are born, resulting in female philopatry and a close degree of inter-female relatedness (Wrangham, 1980) and male dispersal (Packer, 1979). Wrangham's model (1980) examines the ecological pressures leading to the evolution of female-bonded primate groups, and suggests that competition for a limited number of high-quality food patches caused female-bonded groups to evolve. This may seem counterintuitive, since more females in a group should lead to more competition over the same limited resources; however, Wrangham (1980) argues that females in a group are able to cooperatively defend food patches against *other* groups, and thus ensure access to larger foraging areas or amounts of food. The same notion applies to males in multi-male multi-female female-bonded groups wherein males aid in defending valuable resources (Wrangham, 1980). Wrangham (1980) further points out that females belonging to female-bonded species are more involved in group movements and inter-group interactions (when compared to females belonging to male-bonded species), and he relates this to an increased need to frequent certain food patches and protect resources. Females are driven to protect food resources much more than males, because female reproduction is energetically expensive and tied to their ability to secure foods (Wrangham 1980). In short, Wrangham (1980) outlines how in many primate species, females live in groups because the benefits of group living (through cooperative resource defense) outweigh the costs of group living (through intraspecific competition).

Isbell's Contest and Scramble Competition

In her 1991 paper, Isbell reviews the importance of food to female mammals, and how food affects overall reproductive success through age at first birth, interbirth interval, total number of births, and survival of offspring. Isbell's (1991) analyses differ from that of Wrangham (1980), Clutton-Brock and Harvey (1977), and Packer (1979) in that she relates ecological conditions to explain female relationships both *within* and *between* groups of primates. Using data largely from the literature, Isbell (1991) examines female aggression along with ranging behavior, in order to better understand the variation in female relationships between and within multi-female groups of primates.

Isbell (1991) notes that groups of female primates are aggressive towards other groups, and that home range size increases with group size in most species. Additionally, in species with strong dominance hierarchies, day-range length increase is proportional to group size, while day-range length is not proportional in species lacking strong dominance hierarchies (Isbell, 1991). From this Isbell (1991) suggests that *intergroup* competition is determined by food abundance, while *intragroup* competition is determined by food distribution. As with Wrangham (1980), Isbell (1991) details the importance of food resources to group living primates.

NICHE PARTITIONING

As outlined above, competition plays an important role in primate foraging theories. Waser (1987) points out that similarity in resource base indicates that sympatric species compete, but further suggests that differences in resource use between sympatric species suggest that competition has been an important force in the past. In other words, sympatric species are either in competition, or they were once in competition but are now free from it because they now occupy different niches. Ganzhorn (1989) argues that different species can only coexist in sympatry when they occupy different niches. Since empirical studies within several groups of primate taxa have documented that differences in food intake and foraging efficiency are associated with differential reproductive success (Altmann, 1991; van Noordwijk and van Schaik, 1987, 1989; Whitten, 1983), we expect that there is strong selective pressure on patterns of primate food choice. Additionally, fundamental intraspecific differences in primates suggest that individuals should use different foraging strategies (Sauther, 1994), in order to not only best meet their needs, but also the needs of their kin. Next, I will address how niche partitioning can occur both between and within species.

Interspecific

At the species level, primate niches can be separated according to habitat utilization, activity patterns and gross categories of food (Ganzhorn, 1989). Habitat utilization can be related to intrinsic species patterns such as body size and locomotion style, but can also be habitat dependant and a result of resource distribution or behavioral mechanisms of predator avoidance (Ganzhorn, 1989). Since both feedants and antifeedants are not equally distributed throughout a habitat, primate species occupying different parts of habitat may encounter feedants and antifeedants at different rates (Ganzhorn, 1989). Activity patterns also influence primate niches, since food, water and space are not equally available during diurnal or nocturnal periods. Nectar and insects are more readily available during the night, while daylight hours aid primates in discerning fruit and leaf ripeness and maturity. Similarly, gross categories of foods (insects, leaves, fruits) consumed may separate sympatric primates into niches, although since most primates have diverse omnivorous diets, niches are more likely separated on a much finer scale, such as ages of leaves and fruits consumed (Bourliere,1985; Terborgh and van Schaik, 1987).

Intraspecific

Within a primate species, niche separation relates to environmental or physiological variables. Environmental variation between habitats can cause obvious differences in primate diet since food availability, species richness and food tree density varies with habitat. Chapman and Fedigan (1990) documented the high degree of habitat variability and its affect on capuchin (*Cebus capucinus*) diet at the Santa Rosa National Park in Costa Rica. In fact, adjacent capuchin groups had such variability in their diet that one group could be classified as insectivorous and the other group as frugivorous (Chapman and Fedigan, 1990). Additionally, in highly seasonal habitats, such as those in southern Madagascar, primate feeding can vary largely with the season. Although considered frugivorous/folivorous primates, ringtailed lemurs can be further classified as frugivores during the hot wet season, and folivores during the cool dry season (Simmen et al., 2006).

Intraspecific niche partitioning within similar environments relates primarily to physiological variables of body size and reproductive state. In dimorphic species, males require more calories to maintain their larger body mass, although they can subsist on a diet of lower quality (Gaulin, 1979). In monomorphic species, male and female nutritional needs may be similar when individuals are not reproductive, but diverge during reproduction, since female reproductive investment is comparatively high (Lee, 1999). Female metabolic need correlates to reproductive state, as gestation and lactation are nutrient expensive processes. In fact, Gautier-Hion (1980) found that feeding differences between reproductive and non-reproductive female guenons were greater than the feeding differences found between guenon species (*Cercopithecus nictitans, C. pogonias,* and *C. cephus*), thus outlining the importance of physiological factors in niche partitioning within species.

In sum, primate niches can be both intra- and interspecific. Since food is essential for both survival and reproduction, food choices and adaptive foraging can provide important insight into primate evolutionary ecology at both the individual and species level.

LEMUR TRAITS AND MADAGASCAR:

Madagascar has an unusual ecology that encompasses nutrient poor soils, low plant productivity, and harsh and often unpredictable environmental conditions (Ganzhorn et al., 1999; Wright, 1999). Severe and possibly cyclical droughts (Gould 1992; Gould et al., 1999; Jolly, 1998), frequent cyclones and storms (Donque, 1975; Ganzhorn 1995), frost and cold (Wright, 1999), and seasonality in rainforests (Hemingway, 1995; Morland, 1991, 1993a, b; Powzyk, 1997) make for difficult conditions which have facilitated the evolution of a number of traits in the Lemuridae that are unusual within the Primate order (Ganzhorn et al., 1999; Wright, 1999). Lemur traits include: female dominance (Jolly, 1966; Richard, 1987) and female feeding priority (Jolly, 1984; Paul 1997); female-female competition and targeted aggression (Hood and Jolly 1995; Jolly, 1998; Koyama, 1991); sexual monomorphism (Kappeler 1991, 1993, 1996a, b, 1997a, b; Pereira and Kappeler, 1997); high infant mortality (Goodman et al., 1993;Gould et al., 1999; Gould et al., 2003; Janson and van Schaik, 1993; Jolly et al., 2002; Wright, 1998, 1999); cathemerality (in some species) (Curtis and Zaramody, 1999; Colquhoun, 1998; Overdorff, 1988; Overdorff and Rasmussen, 1995; Rasmussen, 1999; Sussman and Tattersall, 1976; Tattersall, 1987); and strict seasonal breeding with weaning synchrony (Wright, 1999). This suite of unusual traits may help lemurs increase chances of reproductive success, despite their harsh and unpredictable environment (Ganzhorn et al., 1999; Wright, 1999).

RINGTAILED LEMURS:

Lemur catta are perhaps the most well known Malagasy primate. They have been studied in the wild since the early 1960s (see Gould 1994; Gould et al., 1999, 2003, 2005; Jolly, 1966, 1984, 2003; Pride, 2005; Sauther 1992, 1994, 1998; Sussman, 1972, 1974, 1991, 1992); and because ringtailed lemurs reproduce well in captivity, they have also been extensively studied in zoos, wildlife parks, and primate centres over the past several decades (e.g. Evans and Goy, 1968; Gebo, 1987; Kappeler, 1991; Parga 2001). Ringtailed lemurs are diurnal and less arboreal than other lemur species, spending up to one third of their waking hours on the ground (Sussman 1974, 1977). Due to their sociable nature, ringtailed lemurs have a wide and complex repertoire of communication skills including visual, vocal, and olfactory signals (Gould and Overdorff, 2002; Jolly, 1966; Sauther et al., 1991; Sussman, 1974, 1977). Their communicatory expertise is used in social interactions such as attracting mates, territory defense, group travel, and in "stink fights" wherein rival males use wrist and brachial glands to mark their tails before waving them at each other (Jolly, 1966). As with many lemur species, ringtailed lemurs are strictly female dominant (Jolly, 1966; Jolly, 1984), thus enabling females preferential access in both social and feeding situations.

Habitat and range

Lemur catta are found in localities of Madagascar's south and southwest (Sussman, 1977; Sussman et al., 2003; Tattersall, 1982). They primarily reside in lowland gallery, dominated by *Tamarindus indica,* and xerophytic (spiny) forests, which are characterized by their dominance of *Euphorbia tirucalli,* and *Alluaudia spp.*. (Budnitz and Dainis, 1975; Gould 2006; Jolly 1986; Sussman 1977, 1991, 2003; Sauther, 1998). Ringtailed lemurs are also found in degraded habitats, anthropogenically induced savannah, scrub and brush land, deciduous forests, and the mesic high altitude forests of the Andringitra mountain range (Goodman and Langrand, 1996; Goodman and

Rasolonandrasana, 2001; Goodman et al., 2006; Gould et al 2006; Pride, 2005; Sussman, 1977; Sussman et al., 2003). Ringtailed lemurs are a remarkably flexible species in their ability to subsist in diverse habitats, and as such, they are deemed an "edge" or "weed" species (Sussman, 1977; Gould et al., 1999; Sauther et al., 1999).

Sociality

As noted, ring tailed lemurs are strictly female dominant (Jolly, 1966; 1984), which allows them both social and feeding priority (Jolly, 1984; Sauther 1993, 1994, 1998). Each ringtailed lemur group consists of related females, their infant or juvenile offspring, and a number of immigrant males, and possibly peripheral males who emigrate at sexual maturity (Gould, 1997; Jolly, 1966; Sauther, 1992; Sauther et al., 1999; Sussman, 1992). Males may transfer groups many times throughout their lives (Gould, 2006; Gould et al., 2003; Sussman, 1992) which aids in the avoidance of incest. Both fission and fusion are documented in ring tailed lemurs, and are the result of group size becoming too large (e.g. 15-20 individuals at Berenty Private Reserve (Gould et al., 2003; Jolly et al., 2002), or too small (i.e. 2 to 3 individuals at the Beza Mahafaly Special Reserve (Gould et al., 2003; Sussman, 1991)). Although group size is habitat and resource dependent, Gould et al. (2003) document 11.5 as the average number of *L. catta* individuals in a group at Beza Mahafaly over a 15-year period. Similarly, in their demographic studies of *L. catta* at Berenty Private Reserve Jolly et al. (2002) and Koyama et al. (2002) note 8.9 as the mean number of individuals per group, although this average varies with habitat type of the reserve.

Reproduction

In *L. catta* females, annual estrus cycles are highly synchronized, and triggered by photoreceptivity (Petter-Rousseaux, 1980; van Horn and Resko, 1977). In fact, all breeding within a particular group can take place within two to four weeks (Gould, 1990; Gould et al., 2005; Gould and Ziegler, 2007; Jolly, 1966; Sauther 1991). Since estrus for each female is restricted to a 6-24 hour period (Jolly, 1966; Sauther, 1991; van Horn and Resko, 1977), there is fierce male-male competition for access to fertile females. Ultimately however, females choose with whom they mate, and prefer higher ranked males in their troops (Jolly; 1966; Sauther, 1991). Gestation averages 141 days and although infant mortality is high, surviving infants are nursed for approximately 18 weeks (Gould, 1990; Jolly, 1966; Sauther, 1991, 1998; Sauther et al., 1999).

Lemur catta reproduction is highly tied to seasonal resources (Jolly, 1984; Rasamimanana and Rafidinarivo, 1993; Sauther, 1992, 1993, 1998; Sauther et al., 1999: Yamashita, 2002), and females are in late gestation and early lactation during the driest parts of the year, which has correspondingly low food availability (Sauther, 1994, 1998; Sauther et al., 1999). Late lactation and early weaning occurs at the onset of the wet season and thus females with young exploit increasing food resources (Sauther, 1994, 1998; Sauther et al., 1999). Furthermore, weanlings' chances of autonomous survival are increased through "weaning synchrony" wherein weaning coincides with the time of year with most predictably abundant food resources (i.e. at the onset of the wet season) (Jolly, 1984; Wright, 1999). Reproductive females they rely heavily on a few key species (e.g. *Tamarindus indica, Maeurua filiformis*, and *Quisianthe papinae*), which tend to be either reliably available or likely to produce short bursts of large amounts of foods during critical times (Sauther, 1994, 1998; Sauther et al., 1999). Perhaps the most important resource for gallery forest *L. catta* is the tamarind tree (*T. indica*), which will be discussed further below.

Feeding Ecology and *Tamarindus indica*

Ring tailed lemurs are opportunistic frugivore/folivores that exploit a variety of plant and non-plant based resources, at all levels of the forest, as those resources become available (Sussman, 1974, 1977, 1991; Sauther, 1994, 1999). Their diet is highly variable but may include ripe and unripe fruits, young and mature leaves, leaf stems, flowers, soil, dead wood, and termite casts (Rasamimanana and Rafidinarivo, 1993; Sauther, 1992, 1998; Simmen et al., 2003, 2006; Sussman, 1972).

Tamarindus indica is of particular importance to gallery forest-residing *L. catta* as both young leaves and fruits are produced asynchronously throughout the year (Sauther, 1998), thus making it available year-round for consumption (Simmen et al., 2006). As a member of the family Fabaceae (formerly Legumaceae), tamarind fruits are protein-dense and provide a rich source of energy (Morton, 1987). Young tamarind leaves are also important in *L. catta* diet as they too provide a protein source (Mertl-Milhollen et al., 2003; Sauther, 1993). Furthermore, tamarind fruits and young leaves usually comprises upwards of 35-60% of gallery forest ringtailed lemurs' diet (Koyama et al., 2006; Mertl-Milhollen et al., 2003; Rasamimanana and Rafidinarivo, 1993; Soma, 2004). Fruits are ripe during the driest parts of the year and provide high energy foods to females who are gestating or lactating, and infants as young as two months feed on and lick tamarinds pods (Simmen et al., 2006). Because of the importance and dominance of *T. indica* to *L.*

catta at the Beza Mahafaly Reserve, Yamashita (2002) suggests that all other foods are secondary.

NATURAL DISASTER AND DIET:

Natural disasters, such as cyclones, plague Madagascar's east coast and central plateau, and in the southern regions, these disasters are most often in the form of drought. Droughts are detrimental to both flora and fauna, which depend on seasonal rains to persist. Gould et al. (1999, 2003) documented a two-year drought at Beza Mahafaly, in which 21% of adult females *L. catta* died the first year and another 29% of the remaining females died the second year. Additionally, 1-year infant survival rates following these drought years dropped to ≤20% (Gould et al., 1999). Jolly et al. (2002) also report mortality rates following a drought at Berenty, but note that *L. catta* deaths occurred after rains commenced (as with the second year 29% female mortality at Beza). Certain forest trees (including *T. indica*) respond to drought by fruiting heavily, but once rains return, they produce very little fruit and become vegetative (Jolly et al., 1999). Thus, it appears that fruiting failure may be more to blame than direct water shortage in these *L. catta* deaths (Jolly et al., 1999).

Although of a different nature, severe storms and cyclones may be equally detrimental to lemur survivorship (Wright, 1999). Direct cyclone activity can result in tree defoliation, blow-downs of canopy trees, landslides and flooding (Ganzhorn, 1995; Ratsimbazafy, 1999, 2006). Lemurs could be affected directly by cyclone activity if they sustain physical injury, but are more likely to be adversely affected by resultant food shortages, which can mean little or no fruits or leaves as food sources until the next season or until sufficient forest recovery time has elapsed (Ratsimbazafy, 1999, 2006). As noted, both drought and storm activity can be detrimental to lemur populations.

It is important to note that my study, described in this thesis, took place following a natural disaster. On January 23, 2005 (approximately 5 months before my research began), the tropical cyclone Ernest swept over Madagascar's south, resulting in sustained winds of 100 km/hr (60 m/h) and severe flooding which originated in the southwestern city of Tulear (Stevens, 2005). At the Beza Mahafaly Special Reserve, staff recorded flood waters of over a meter, and noted that winds resulted in significant tree and plant damage and defoliation (Razanajafy and Razandrainy, pers comm). The storm coincided with peak flowering of *Tamarindus indica* at Beza (Razanajafy and Razandrainy, pers comm), which subsequently almost completely failed to fruit (LaFleur, pers obs). In addition to tamarind fruits, herbaceous forest plants and the few young leaves that would normally be present during August and September were absent as a result of the cyclone activity.

The above outlined conditions greatly altered resource availability and resource use by *Lemur catta* during my study. By examining how *L. catta* react to these conditions, we can better understand how natural disasters affect populations and the importance of fallback foods during famine.

SUMMARY:

In this chapter, I reviewed nutritional studies within primatology, selectivity in feeding, food properties, foraging theories applicable to ringtailed lemurs, and niche partitioning. Additionally, I introduced traits common to Malagasy primates, the social and ecological characteristics of ringtailed lemurs, and the affects of natural disaster on ringtailed lemur diet. In the next chapter, I will present my research hypotheses, questions, methods, and results, and will discuss the significance and implications of my findings.

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CHAPTER TWO

Feeding Behavior and Nutrition of Male and Late-term Pregnant Female *Lemur catta*

ABSTRACT

Differential reproductive energetics between sexes has lead to the evolution of sex-based feeding differences in many primate species. While sperm production in males is relatively inexpensive, the cost of gestation and lactation in females is metabolically expensive and requires increased energy through calories and nutrients. Previous studies have shown that male and female (both reproductive and non-reproductive) ringtailed lemurs have sexually divergent diets, although nutritional analyses of foods did not accompany these earlier works. This research focuses on male and pregnant female ringtailed lemur feeding behavior, and includes nutritional analyses of all plant foods consumed. Results show no significant differences in time spent feeding or amounts eaten by males or females. Furthermore, although no significant differences were found in consumption of protein, fiber (NDF and ADF), calcium, magnesium, or sodium, females did ingest significantly more phosphorus ($P= 0.004$) and potassium ($P=0.015$) when compared to males. These data are somewhat unexpected as divergence in diet is minimal. Reduced feeding differences may be due to the prior activity of cyclone Ernest that resulted in low food availability and a near complete fruiting failure of *Tamarindus indica*, which is a very important resource for these gallery forest ringtailed lemurs. This research suggests that ringtailed lemur diet shows less sex divergence in times of resource scarcity.

INTRODUCTION:

Group living primates incur costs and gain benefits in proportion to the number of individuals in their group (Terborgh and Janson, 1986). Benefits of group living fall into three general categories (Gillespie and Chapman, 2001) including: predator avoidance (Boinski et al., 2000; Chapman and Chapman, 1996; Hamilton, 1971; Noe and Bshary, 1997), foraging advantages (Cody, 1971; Garber, 1988; Struhsaker, 1981; Wrangham, 1980), and avoidance of conspecific threat (Janson and Goldsmith, 1995; Treves and Chapman, 1996; van Schiak and Kappeler, 1993). Foraging advantages through increased foraging efficiency, by which an individual's ability to remember locations and phenological patterns of patchily distributed food resources, decreases the time and effort needed to secure resources (Garber, 1987). However, with increased group members comes an increase in within-group feeding competition, which is generally thought to be the primary limiting factor to group size (Janson and Goldsmith, 1995; Terborgh and Janson, 1986; Wrangham et al., 1993). The topics of predator avoidance and conspecific specific threat (e.g. within-group agonism or infanticide) will not be described further, as they do not pertain directly to my research.

Habitat variation can produce important differences in primate feeding (Agetsuma and Nakagawa, 1998). Even seemingly subtle differences in the home ranges of neighboring groups can produce significant differences in the feeding behavior of its members (Chapman and Fedigan, 1990). Furthermore, food availability and quality can vary significantly with a single group's home range as a result of differing food tree densities (Chapman and Fedigan, 1990). Consequently, habitat variation is an important variable in primate feeding ecology.

Sex differences in feeding are generally a reflection of nutritional need, which is influenced by two main factors: body size (Demment, 1983; Demment and Van Soest, 1981; Hladik, 1981) and reproductive state (Clutton-Brock et al. 1989; Sadleir 1969; Sauther and Nash, 1987). Larger body size demands a larger daily caloric requirement; however larger primates can subsist on lower quality foods relative to smaller bodied primates (Gaulin, 1979). Conversely, although smaller bodied primates require less overall nutrients, in order to meet their metabolic needs they require foods of higher quality (Gaulin, 1979). In sexually dimorphic primate species, such the mandrill (*Mandrillus sphinx*), males can reach 31kg while female maximum weight is 13kg (Hill, 1970). Sexual dimorphism would be expected to play a large role in feeding differences between sexes in *M. sphinx* (Hoshino, 1985; Setchell et al., 2005). However, what is the situation with monomorphic primates? Sex based feeding differences found in monomorphic primates relate to reproductive energetics, as males and females incur differential costs related to reproduction (Lee, 1999). While sperm production in males is relatively inexpensive, the cost of gestation and lactation in females is metabolically expensive (Lee, 1999). Furthermore, female metabolic requirements of fat, protein and calcium are elevated during both gestation and lactation, as these nutrients are necessary for growth of developing young and production of milk (Crissey et al., 2003; Dunkel, 1996). Since males do not require energy from specific nutrients in the same way as do females, they may be able to adapt to a more generalist feeding niche with more flexibility in their diet.

Reproduction is costly for female mammals, and in many species reproduction is associated with behavioral or dietary changes (Clutton-Brock et al., 1989; McCabe and

Fedigan, 2007; Pazol and Cords, 2005; Sadleir 1969; Sauther and Nash, 1987; White and Wood, 2007). In her research on *L. catta* feeding behavior and plant use, Sauther (1992, 1994, 1998) found differences in food choices between lactating females, gestating females, non-reproductive females, and males. Lactating females focused on young leaves and select fruits, which are rich in easily digestible protein (Sauther 1992, 1998). Furthermore, lactating females only fed for short periods of time on any one species, and included many herbaceous leaves in their diet (Sauther, 1994). These behaviors are suggested to reduce digestive inhibitors and secondary compounds which are common in mature leaves (Waterman and Choo, 1981; Coley, 1983), but also to yield more accessible protein and micronutrients from young leaves which have thinner cell walls (Waterman and Choo, 1981; Waterman et al., 1983). Sauther (1994) also found that pregnant *L. catta* females consumed more fruits (namely *T. indica*) than males, and that females also exploited the few existing young leaves and flowers as they became available (1998). Although not as extreme as during lactation, pregnant females have elevated metabolic needs (Gittleman and Thompson, 1988). By focusing on available tamarind fruits and flowers, these pregnant females are privy to rich sources of protein and calcium, which are important both for body maintenance and fetal development (Sauther 1994, 1998). Males and non-reproductive females in Sauther's (1998) study tended to consume costly high-quality foods, such as fruits and young leaves when they were available, and relied on low-quality foods when costly foods were not present. Since males and non-reproductive females were not constrained by reproductive energetics in the same way that were gestating or lactating females, they could exist on a more variable resource base, and also subsist on low-quality food when resources were low (Sauther

1994, 1998). As outlined, foraging differences between males and females are likely reflected in nutrient intake, and are a function of an individuals' metabolic need; whether solely maintaining body function or contributing to developing young.

In her research on ringtailed lemur feeding behavior, Sauther (1992, 1994, 1998) found differences *between* males and females, and *within* females of differing reproductive states, and attributed such differences to increased need for protein and minerals (especially calcium) by females who are gestating or lactating. From Sauther's work (1992, 1994, 1998), we thus know that reproductive gallery forest *Lemur catta* females have distinct foraging patterns, and we infer that they are selecting plant foods which best address their metabolic needs. Until the present study, however, this inference had not been directly tested. The goal of my research is to examine the foraging strategies and nutrients consumed specifically by male and late-term pregnant female *L. catta*. Coincidentally, my data collection took place during a post-cyclone dry season and fruiting failure. Of particular interest is how these gallery forest *L. catta* groups cope with a fruiting failure of *Tamarindus indica*, which is normally their primary food source during the dry season. Previous studies of natural disaster in *L. catta* habitat have documented increased to severe female mortality following drought and fruiting failures caused by drought (Gould et al., 1999; Jolly et al., 2002). However, we do not know the effects of cyclone activity on feeding behavior of *L. catta*. As such, I will address differences in feeding and nutrition between males and female, along with effects of a cyclone (which occurred on Jan 23, 2005) on *L. catta* at the Beza Mahafaly Special Reserve.

Significance

The significance of my research on *L. catta* feeding behavior and nutrition is twofold as it relates to a) conservation efforts, and b) evolution of foraging plasticity. Rapid deforestation and loss of habitat are leaving Malagasy primates in small isolated forest fragments (Sussman et al., 1994). Knowledge regarding nutritional needs of female lemurs could aid in identifying particularly important habitats for immediate protection, reforesting degraded habitats, and in caring for displaced or otherwise captive individuals.

A key feature to surviving in a changing environment is having a high degree of ecological plasticity (Gould, 2006; Ménard, 2002). *Lemur catta* exhibit a number of traits which suggest they are ecologically plastic (Gould et al., 1999, 2003; Sauther et al., 1999; Sussman, 1977). For example, as noted in Chapter 1, *L. catta* are found in a wide range of habitats, and many of those habitats experience extreme seasonal changes in resource base and frequent natural disasters (e.g. Gould et al., 1999; Jolly, 1994; Jolly et al., 2002; Mertl-Milhollen et al., 2003; Pride, 2005). To cope with low habitat productivity, seasonal variability and changes in resource availability, *L. catta* persist at different densities, which at Berenty Private Reserve range from 100 to 500 lemurs/km^2 (Jolly et al., 2006), and at Beza Mahafaly Special Reserve (non-drought years) range from 60 to 100 lemurs/km^2 (Gould et al., 2003). *Lemur catta* also show variation in home range size, group size, and group stability in relation to habitat productivity and seasonality (Gould et al., 2003; Jolly et al., 2002; Koyama et al., 2002; Sussman 1991; Whitelaw and Sauther, 2003). Even life history variables such as male to female ratio, fecundity, infant mortality, and age at sexual maturity show differences between populations, which are thought to be primarily due to habitat variation, although this cannot fully explain differences in sex ratio (Gould, 2007; Gould et al., 2003; Jolly et al., 2002; Koyama et al., 2002). The ability to exploit a wide variety of resources and habitats, as seen in *L. catta*, may be an evolutionary trait which is favored in unpredictable environments such as Madagascar (Wright, 1999). Ecological genotypic plasticity can be indirectly measured through phenotypic plasticity by range of foraging ability and intra specific foraging variation (Ménard, 2002). By examining ecological foraging plasticity between sexes, groups or populations of *L. catta,* we can make inferences about evolution and selection of such a trait.

Research Questions and Predictions

A) Is there a significant difference between time spent feeding or amount of food ingested between sexes or social groups?

***Predictions*:** I expect that females will spend more time feeding and will ingest more than males. During the present study, all adult females are (or assumed to be) in late gestation, and thus will have metabolic need that are higher than those of males. I do not expect animals of neighboring social groups to have significant differences in their time spent feeding or overall amounts eaten, as the groups have overlapping home ranges in gallery forest habitat and appear to have access to the same food resources. However, since even seemingly subtle differences in resource base can affect diet, it is important to examine social group as a possible contributing factor to diet divergence.

b) Are there significant differences in nutrient consumption (crude protein, fiber, and minerals including: calcium, phosphorus, magnesium, potassium, and sodium) by sex or group?

***Predictions*:** I expect reproductive females to have elevated consumption of protein, and minerals (especially calcium), while ingesting less fiber when compared to males. The protein and mineral differences will again be due to the females' elevated metabolic needs associated with gestation. Since fiber does not contribute to caloric intake, and plants of higher fiber content tend to be of lower quality, I expect that females will avoid foods that are particularly fibrous, resulting in a decreased intake. For the reason outlined above in *prediction a*, I do not expect there to be differences in nutrient consumption between neighboring groups. Since both groups seemingly have access to the same gallery forest habitat, they are selecting resources from the same base, and I do not expect their diets to vary significantly. However, in order to be sure that any differences found in feeding can be attributed to sex and not social group, I will explore social group differences in nutrient consumption.

METHODS:

Study Site and Conditions

The Beza Mahafaly Special Reserve is located in southwestern Madagascar, and consists of a primary 1km^2 parcel of forest bordering the Sakamena River (**Figure 1**). The reserve was established in 1978 and deemed a Special Government Reserve in 1985 (Sussman, 1991). The climate is highly variant with a cool/dry season (June to August), a hot/wet season (November to March), and transitional periods in between (Sauther, 1992; Sussman, 1991). As noted in Chapter One, on January 23, 2005 (approximately 5 months before my research began), the tropical cyclone Ernest swept over Madagascar's south,

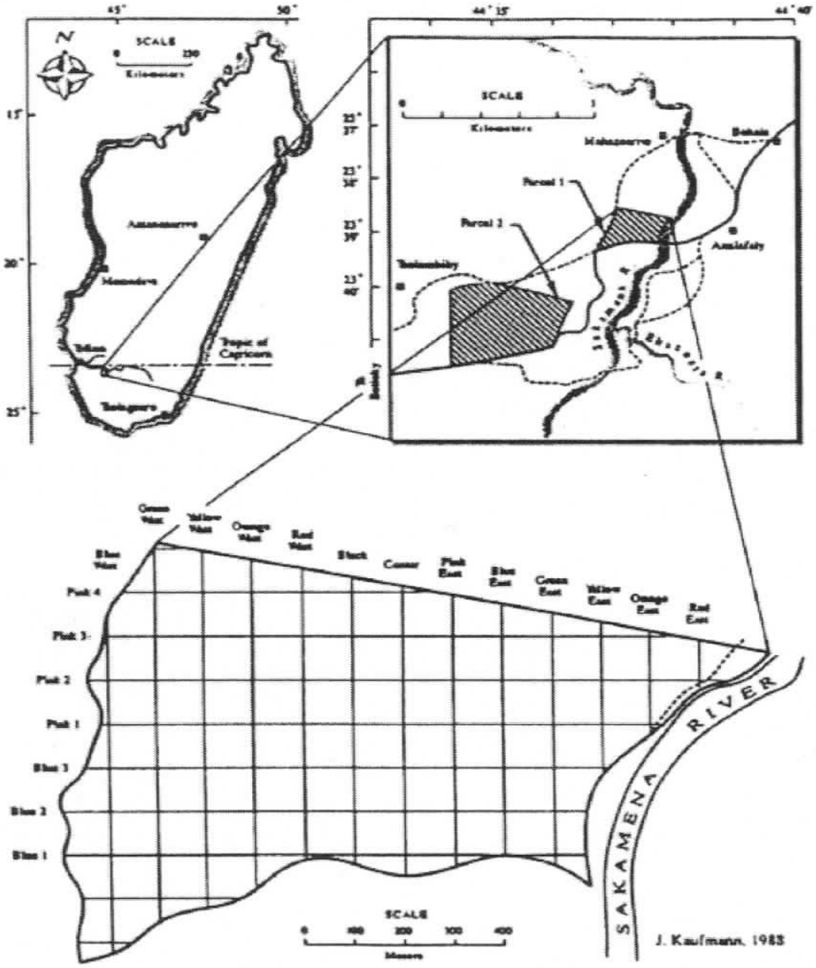


Figure 1. Trail map and location of the Beza Mahafaly Special Reserve, Madagascar. Map from Sussman (1991) after Kaufmann (1988).

resulting in sustained winds of 100 km/hr (60 m/h) and severe flooding which originated in the southwestern city of Tulear (Stevens, 2005). At the Beza Mahafaly Special Reserve, staff recorded flood waters of over a meter, and noted that winds resulted in significant tree and plant damage and defoliation (Razanajafy and Razandrainy, pers comm). The storm coincided with peak

flowering of *Tamarindus indica* at Beza (Razanajafy and Razandrainy, pers comm), which subsequently almost completely failed to fruit (LaFleur, pers obsv).

The western portion of the reserve contains xerophytic forest which is dominated by *Euphorbia tirucalli*, while the eastern portion of the reserve is gallery forest where *Tamarindus indica* dominates the landscape (Sauther, 1998). Both forest types host a plethora of tree species, vines and herbaceous plants. In the dry season, the Sakamena river bed is waterless and becomes quickly populated with the fast growing, drought resistant and invasive weed *Argemone mexicana*.

Data Collection

Over a one month period from August 9 to September 7, 2005, I collected data on all adult animals (n=18) of two distinct neighboring social groups (Red Group and Green Group) residing in the eastern gallery forest at Beza Mahafaly. Home ranges of two groups overlapped extensively, and both ranges bordered the Sakamena River (see **Appendix 1** for group member information). I collected 10 focal sessions (Altmann, 1974), which were each of 15 minute intervals, for each animal[1] in the Red and Green Groups. During focal animal follows, I collected data on the following behavioral states: feeding, foraging, resting, traveling, grooming, and others (see **Appendix 2** for a sample data collection sheet and **Appendix 3** for a complete ethogram). When a focal animal was feeding, I noted the animal's location, amount eaten (number of leaves or bites), and the plant or plant part ingested, and subsequently collected representative food samples (except for *Tamarindus indica* fruits, which were too limited to collect).

All plants collected were dried in the shade, identified by a local Malagasy botanist (Elahavelo), and were later analyzed for the following nutritional content: crude protein, acid detergent fiber, neutral detergent fiber, calcium, phosphorus, magnesium, potassium, and sodium at the Dairy One Forage Laboratory[2]. A complete list of plant foods can be found in **Appendix 4**, and a sample data sheet from the Dairy One Forage Laboratory can be found in **Appendix 5**.

Forest tree phenology

Elahavelo collected phenological data of the Red and Green Groups' gallery forest habitat, once at the onset of and again at the end of my study period. Using line transects, he identified 140 large (greater than 20cm in diameter at breast height) trees (excluding *Tamarindus indica*), by species or local name, and scored trees for presence of flowers. Additionally, if a tree had flowers, Elahavelo scored the abundance on a scale of 1-5 (where 1=few and 5=full bloom). A total of 105 *T. indica* trees were also sampled for presence, abundance (scale 0-5, where 0=none, 1=few, and 5=full fruiting) and ripeness (scale 0-5, where 0=unripe, 1=slightly ripe, and 5=fully ripe) of fruits. Elahavelo did not collect phenological data on flowers in *T. indica* trees, or young leaves and fruits in non-tamarind tree species, because these conditions were not present. A sample data sheet of forest phenology can be found in **Appendix 6**.

From these data, I calculated percentages of trees with flowers or fruits both at the beginning and end of my study period. Furthermore, I calculated average percentages for abundance of flowers or fruits, when possible.

Data Analysis

All data were entered into Microsoft© Excel spreadsheets for editing.

Feeding activity

In order to obtain a percentage of focal time spent feeding, I divided the summed time spent feeding (in minutes) per animal by the total time (in minutes) the animal was observed, and then multiplied that number by 100. This calculation was performed for each animal and then the data were assembled by sex or by group, for comparative purposes.

Amount eaten

In order to estimate the quantity of a plant or plant part eaten (excluding *Tamarindus indica*), I weighed 10 dry samples that were representative of a bite size to find the plant or plant part 'average bite' or average amount and then multiplied the number of leaves or bites an animal took by the average quantity.

Nutrient consumption

The Dairy One Forage Laboratory (see **Appendix 7** for Methods) reported nutritional analyses of each plant as a percent composition (e.g. a sample of *Ipomoea* sp.

leaves contained 20.8% crude protein), however, for ease of comparison, I converted percentages of nutrients to mass of nutrient (e.g. 20.8% crude protein means that for each gram of *Ipomoea* sp. leaves there are 208mg of crude protein). For every focal animal, I created a list of the foods they ate, and amounts eaten of each of those foods. Then, I multiplied the nutritional content of a plant food by quantity of food eaten in order to estimate the amount of nutrient consumed. For example, Red Group female number 234 ingested 14 *Ipomoea* sp. leaves. Since the average mass of a *Ipomoea* sp. leaf is 0.21g, female 234 ate approximately 2.94g (14 leaves x 0.21g/leaf = 2.94g) of *Ipomoea* sp. leaves. Next, since *Ipomoea* sp. leaves have 208mg of protein per gram, female number 234 consumed about 612mg (2.94g x 208mg protein/g= 612mg protein) of crude protein from *Ipomoea* sp. leaves. In other words, I used the following generic formula to calculate each nutrient eaten for each plant a focal animal consumed:

Amount of Nutrient X in Plant Y consumed by Animal Z (grams)	=	# of leaves or bites of Plant Y consumed	**X**	Average weight of one leaf or bite of plant Y (grams)	**X**	Nutrient content of Plant Y (grams/gram)

I continued in this manner and tallied the measured nutrients in each plant food consumed by each focal animal. Last, I summed each specific nutrient (e.g. protein) per focal animal for a total of each nutrient per focal animal over the time observed. It is important to note that due to cost of analyses, not all nutritional elements present in each plant were analyzed, and thus, the percentage of nutrients in a specific plant does not add up to 100 in my analyses.

Top Foods

For each focal animal, I assembled data on the top five foods they consumed. I calculated the total grams consumed for each of the five top foods, along with grams consumed per minute, leaves or bites consumed per minute, and the nutrients (crude protein, fiber, calcium, phosphorus, magnesium, and potassium) ingested from each of the top five foods. Although many animals consumed more than five foods, I used five as the unit of analysis because this limited the inclusion of foods that were consumed in very small quantities (i.e. less than on gram). Once I had the top five foods for each focal animal, I added up the amounts of each plant eaten by a) social group, and b) sex of animal, and then ranked the top five foods based on social group or sex of animal.

Statistics

All data was entered into SPSS 13.0 for Windows©.

I used the Mann-Whitney U-test to compare probability distributions for time spent foraging, feeding rate, and amount eaten between males and females and between Red Group and Green Group. This non-parametric test is used to assess if two samples are from the same distribution.

I performed two-way multivariate analysis of variance (MANOVA) test to see if the differences observed between sexes or groups were statistically significant for each of the measured nutrients (crude protein, acid deterrent fiber, neutral deterrent fiber, non-fiber carbohydrates, calcium, phosphorus, magnesium, potassium, and sodium). MANOVA is an extension of ANOVA methods, and assesses cases with more than one dependant variable and where dependent variables cannot simply be combined. This test may detect whether changes in the independent variables have significant effects on dependent variables, and/or interactions among the independent variables and the association between dependent variables, if any. Furthermore, MANOVA may be able to detect subtle differences between groups, even when univariate analyses fail to do so (Martin and Bateson, 1993). A post hoc test to assess where interactions are occurring in MANOVA, may be necessary. If significant interactions are found in the sex/group model, the Bonferroni post hoc test will be used for to isolate specifically where interactions were occurring. For example, a sex/group interaction could have a number of possible outcomes as the interactions could be from males or females of one or the other social groups. However, if between sex or intergroup interactions are found, post hoc testing will not be necessary, as there are only two subjects being compared at one time (male/female or Red/Green group). The significant alpha level was 0.05 in all tests.

RESULTS:

Forest tree phenology

Of the non-tamarind trees sampled (n=150), 9% (n=12) had flowers at the beginning of my study period, and of these flowering trees, the average floral coverage was 25%. At the end of my study period, 48% (n=67) of these trees were flowering, with an average floral covering of 42%. The increase in flowering was primarily due to *Quisivianthe papionae.* As earlier noted, there were no young leaf blooms or fruits present in any of these trees.

From the *Tamarindus indica* trees sampled, <2% had fruit (n=2), but it is unclear whether these fruits were palatable. The first tree had 3 fruits which appeared to be only casings, without any actual fruit intact. The second tree had a fruit abundance score of 2 (where 0=no fruit and 5=full fruiting) and a ripeness score of 2 (where 0=unripe and 5=ripe) both at the beginning and end of my study period. The fruits present in this tree were unusually small, and may have again only been pod casings without internal fruits.

Feeding activity

There was no significant difference found between time spent feeding by males and females (Mann-Whitney U Test U=30, p=0.38, n1=9, n2=9), however there was a significant difference in time spent feeding between the Red and Green Groups (Mann-Whitney U Test U= 8, p=0.004, n1=11, n2=7), with Green Group feeding longer (**Figure 2**).

Amount eaten

There were no significant differences found between estimates of amount eaten between sexes (Mann-Whitney U Test U =39, p=0.93, n1=9, n2=9) or between groups (Mann-Whitney U Test U=34, p=0.72, n1=11, n2=7). Interestingly, Red Group was able to monopolize the local villager's crop and vigorously defended the territory against Green Group's repeated attempts at access. Green Group was able to forage in the crop once, while Red Group was not present.

Nutrient consumption

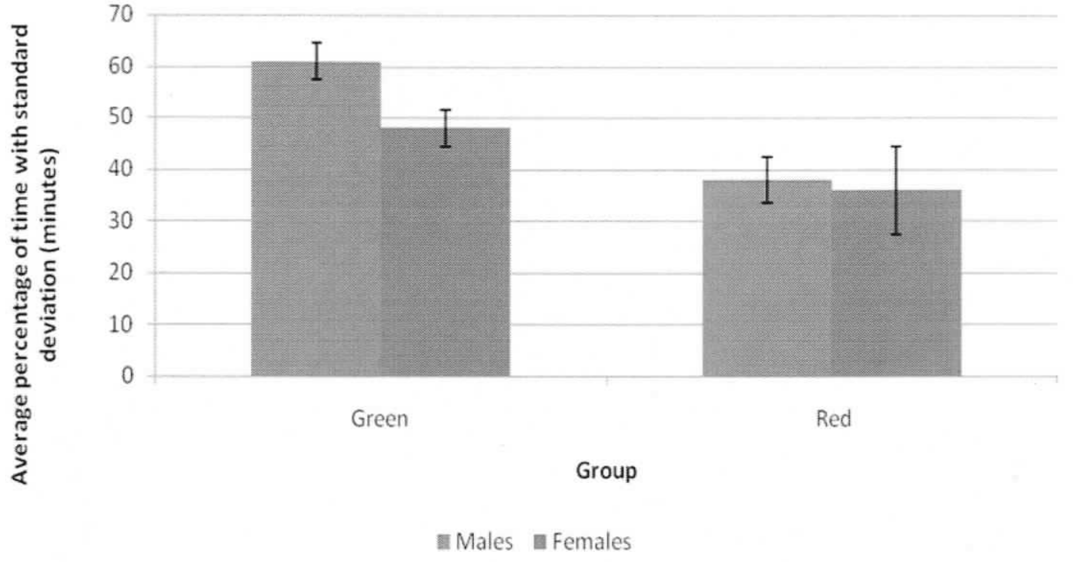
Using the two-way MANOVA, I found significant effects for both Phosphorus ($F_{(1, 18)}$= 12.097, p=0.004) and Potassium ($F_{(1, 18)}$= 7.637, p= 0.015) ingestion between sexes, however no other significance was found (**Appendix 8**, **Figure 3, Figure 4**).

Analyses of Phosphorus and Potassium intake by females and males, show that females ingested higher average levels of the two minerals (see **Figure 3**).

Top foods

Top foods for individual lemurs, along with the associated crude protein, fiber, and select mineral content can be found in **Appendix 9**. Four out of the five top foods were common between Red and Green Groups, although the amounts eaten by group differed (**Table 1**). By sex, three out of the five top foods were common, but again amounts eaten differed (**Table 2**). The top five foods for all focal animals are represented in **Table 3**.

Figure 2. Percentage of average focal time spent feeding by males and females of Green Group (male n=5, female n=6) and Red Group (male n=3, female n=3)



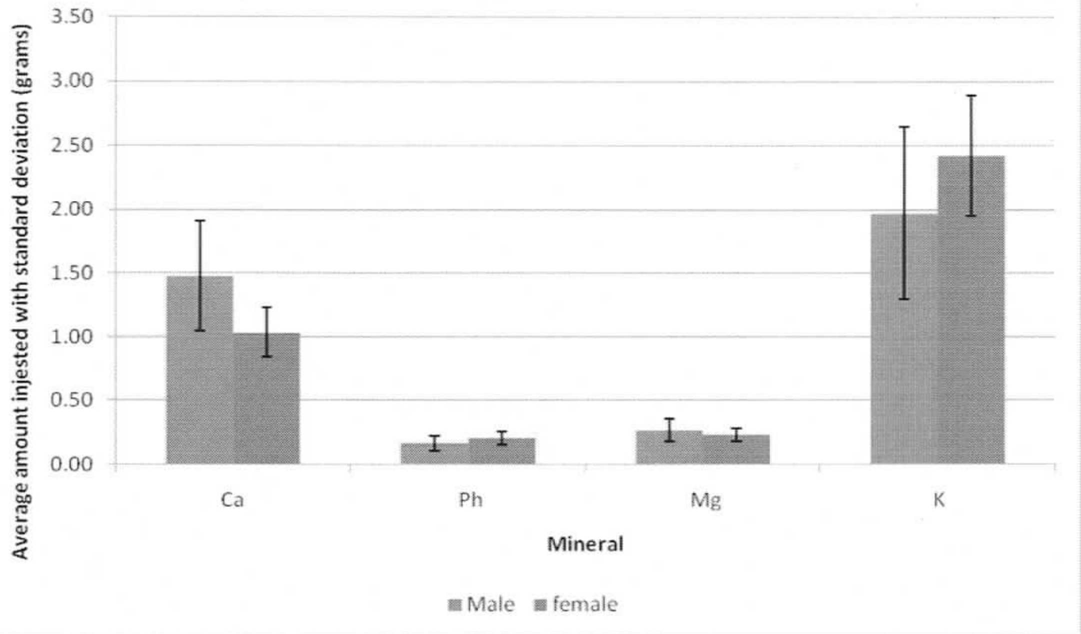


Figure 3. Average amount of Ca, Ph, Mg, and K consumed by males (n=9) and females (n=9)

Figure 4. Average amount of protein, ADF, and NDF consumed by males (n=9) and females (n=9)

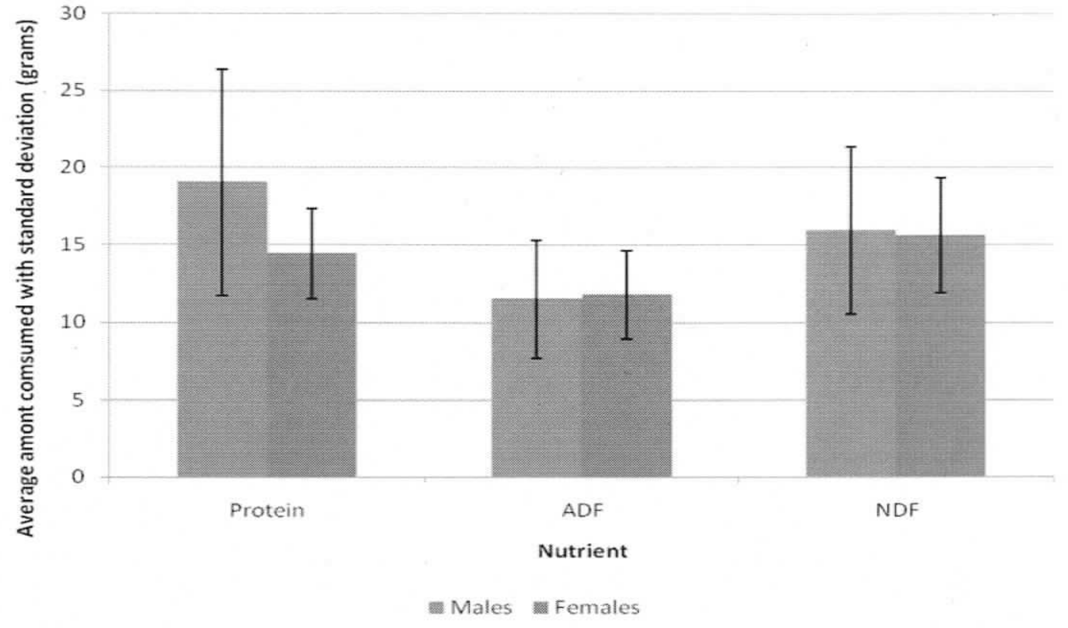


Table 1. Top five foods consumed by Red and Green Group.

Group	**Top food**	**Items (bites/leaves)**
Green	*Quisivianthe papionae*	8371
	Ipomoea sp.	1740
	Maerua filiformes	1553
	Argemone mexicana	858
	Ipomoea sp.	846
Red	*Quisivianthe papionae*	3334
	Ipomoea sp.	1625
	Argemone mexicana	742
	Secamone sp.	324
	Metaporana parvifolia	120

Table 2. Top five foods consumed by males and females.

Sex	**Top food**	**Items (bites/leaves)**
Female	*Quisivianthe papionae*	6486
	Maerua filiformes	1553
	Argemone mexicana	1244
	Ipomoea sp.	798
	Secamone sp.	760
Male	*Quisivianthe papionae*	5219
	Ipomoea sp.	1673
	Secamone sp.	1174
	Argemone mexicana	426
	Gonocrypta grevei	140

Table 3. Top five foods consumed by all focal animals.

Top food	**Items (bites/leaves)**
Quisivianthe papionae	11705
Ipomoea sp.	2471
Secamone sp.	2064
Argemone mexicana	1600
Maerua filiformes	1553

DISCUSSION:

The ability to secure resources is essential to the survival of a species. The Lemuriformes evolved on their island habitat of Madagascar which can be both harsh and unpredictable (Ganzhorn, 1995; Wright, 1999). Frequent natural disasters have shaped many aspects of lemur evolution (Ganzhorn, 1995), including strictly seasonal breeding and female feeding priority (Jolly, 1966; 1984; Young et al., 1990). Annual reproduction (Jolly, 1966; 1984), the availability of particular seasonal food resources (Sauther 1998), and feeding priority allow female lemurs the best possible chances of successfully producing and raising offspring, in their often difficult environment (Jolly, 1966; 1984; Young et al., 1990). Additionally, although female feeding priority may help alleviate *some* of the stress associated with their environment; Cavigelli (1999) found increase fecal cortisol levels in female *Lemur catta* during seasonal times of low food availability and related the cortisol levels to physiological stress associated with extreme seasonality in food resources and reproduction (Jolly, 1974; Pereira et al., 1999). Thus, it appears that female feeding priority may have been selected for, as a means of balancing some of the seasonal stressors of reduction in food availability (Jolly, 1984; Richard, 1987; Young et al., 1990).

As outlined earlier, gallery forest dwelling *Lemur catta* are particularly reliant on food resources from the tamarind tree (Blumenfeld-Jones et.al., 2006; Budnitz and Dainis, 1975; Rasamimanana and Rifidinario, 1993; Sauther, 1998; Sussman and Rakotozafy, 1994; Yamashita, 2002). Flowers, young leaves, and protein-rich fruits of *Tamarindus indica* all play an integral role in gallery forest *L. catta* feeding ecology as they are produced asynchronously and throughout the year (Simmen et al., 2006; Sauther, 1998). During the dry season, *T. indica* fruits are particularly important to ringtailed lemurs at Beza Mahafaly, as there is low overall food availability and females have increased metabolic requirements due to pregnancy (Sauther, 1998; Yamashita, 2002). What then happens to *L. catta* when *T. indica* fails to fruit?

Lemur catta groups at both Berenty and Beza Mahafaly increase their home ranges as a result of food (including tamarind fruit) or water shortages (Jolly and Pride, 1999; Mertl-Millhollen et al., 2006; Sauther, 1998). In their study of ringtailed lemur feeding during a partial tamarind fruiting failure at the Berenty Reserve, Mertl-Millhollen et al. (2006) found that *L. catta* groups had, in fact, lower leaf consumption when compared to fruit in abundant years, and they increased their home range and sought out less abundant fruits, instead of relying on increased foliage (Mertl-Millhollen et al., 2006). Ringtailed lemurs at Beza have also temporarily expanded their home ranges when certain resources are unavailable within existing home ranges (Sauther, 1998; Sauther and Sussman, 1993). However, in both of these cases, *L. catta* ventured out of their normal home range to secure tamarind fruits or rare resources that could be found elsewhere. Such behavior would be advantageous if the energy of the food source being sought out surpassed the energy involved in traveling to get the food, but it would not be worthwhile in cases of extremely low food availability or if travel distance was prohibitive (Stephens and Krebs, 1986). During a drought year, Gould et al. (1999) found that *L. catta* did not increase their home ranges as food was universally limited. Similarly, in the current study, *Tamarindus indica* fruits were absent in the environment and could not be secured even if *L. catta* increased their home range. Nevertheless, focal groups did supplement their diets with plant foods from a local villager's crop and those growing in the dry riverbed (see next chapter). It is difficult to say whether the incorporation of these foods was due to an increase in home range, as I did not directly measure this variable. Furthermore, *L. catta* groups whose home range borders the Sakamena river have been noted to sometimes feed from crops both in the area discussed and in areas across the river bed (Loudon et al., 2006). However, since both of the "supplemental" resources are from outside of the forest, and since the focal animals were spending hours each day foraging in these areas, I suspect both focal *L. catta*, groups were temporarily extending their home range boundaries in order to secure sufficient food resources.

Interestingly, while outside of the forest, Red Group was consuming leaves from *Ipomoea* sp. while Green Group was consuming *Argemone mexicana* plants. Both of these plant foods are known as "critical fallback foods" that are particularly important during the dry season (Simmen et al., 2006). The physical nature of these two plant species is important in explaining why groups had differences in feeding time, while no differences were found in amount eaten or nutrients consumed. *Ipomoea* sp. (a type of sweet potato) leaves are soft and supple, and required no processing prior to eating (personal observation). Conversely, *Argemone mexicana* (mexican thistle) leaves are tough and covered with both sharp spines and thorns. In order to eat the leaves and stems of *A. mexicana*, *Lemur catta* would sever the plant near its base, remove leaves from the stem, and subsequently eat the stem and leaves individually from the base to the apex (personal observation). This procedure was most likely to prevent injury from the plants' sharp spines and thorns, but the technique greatly reduced their foraging efficiency. Despite reduced efficiency, I found no significant differences in the overall amount or nutrients consumed by group, as Green Group foraged for a longer period of time although they did not consume more than Red Group. Additionally, analyses of nutritional components of *Ipomoea* sp. and *A. mexicana*, showed the plants to be very similar in nutritional composition (see chapter 3), and therefore the group's diets were not significantly different in measured nutrients.

Sex differences in feeding behavior and nutrition were limited to an increased ingestion of potassium and phosphorus by females. Potassium is found in many plant food sources and is important sending nerve impulses, muscle contraction, and releasing energy during aerobic respiration, and for maintaining fluid and electrolyte balance in cells (National Research Council, 2003; Somjen, 1979; Windmaier et al., 2004). Since a female's blood volume expands during pregnancy, women are often directed to increase their intake of potassium, especially during late gestation. Phosphorus is also important during pregnancy as it aids in the production of bones and teeth, and is essential for muscle contractions, blood clotting and normal heart rhythm (National Research Council, 2003; Windmaier et al., 2004). Although it is not difficult to explain why *Lemur catta* females in late gestation may have elevated intake of potassium and phosphorus, it is perhaps more difficult to decipher why these same females didn't also show increased intake of protein, calcium, magnesium or total calories, which are also required during pregnancy. However, this may be related to the overall lack of resources and tamarind fruiting failure, which I will explore next.

Tamarind fruits are rich in carbohydrates, protein, calcium, magnesium (Morton, 1987). However, since tamarind fruits were not available at Beza during this study period, *Lemur catta* were left without their most important resource. Under optimal conditions, it is likely that *L. catta* (or any animal) will make food choices that meet their metabolic needs. However, during times of particularly low food ability, individuals may not be able to meet all of their nutritional requirements. With the sudden absence of tamarind fruits in the current study, it is possible that both males and females were not able to meet all of their nutritional requirements associated with body maintenance. Had tamarind foods been available, is it likely that *L. catta* females would have shown increased intake of protein, calcium, magnesium and calories, when compared to males? Sauther (1992) found that during the dry season ingestion of tamarind fruits was not significantly different between males and females, but these pregnant females did eat nearly 10 times more fruits and flowers. This was not the case in the present study, as fruits and flowers were all but absent for the majority of the study period. It is possible that under normal conditions tamarind fruits provide both males and females the carbohydrates, protein, calcium, magnesium needed for body maintenance, while the females' 10 fold increase in fruit and flower consumption provides the additional nutrients and minerals needed for fetal growth and development. Since food resources were limited during the current study, it is highly likely that both males' and females' nutritional intake was reduced, when compared to other non-disaster years. Moreover, metabolic need of females during late pregnancy likely exacerbate any nutritional deficiencies in the present study.

It is important to address consumption of flowers from *Quisivianthe papionae*, as these flowers were the top food consumed by *Lemur catta* in this study. Most notable is that these flowers were only present during the last week (primarily the last 5 days) of data collection. Once bloomed, however, focal animals fed on little else, which resulted in *Q. papionae* contributing a large amount to the diet of these ringtailed lemurs. As outlined by Sauther (1992, 1994, 1998), *L. catta* are opportunistic frugivore/folivores that exploit seasonally available resources, as those resources become available. Additionally, reproduction in *L. catta* is strongly tied to the availability of specific resources. Flowers from *Q. papionae* are annually available for a short period of time when females are in late gestation, thus providing an influx of nutrients at an important time of year (Sauther, 1998; Simmen et al., 2006). The importance of *Q. papionae* was likely magnified during the present study, when tamarind fruits were absent and pregnant females (and males) had little other food resources.

Gallery forests are seasonal and during the dry season, resources are dramatically reduced. However, since tamarind fruit production and ripening is asynchronous, ripe fruits available in the dry season are particularly important to *Lemur catta* residing in gallery forests (Sauther, 1998). That being said, populations of *L. catta* that live in non-gallery forests do not rely on tamarind fruits. Gould (in prep.) found that *L. catta* residing in spiny forest at Berenty only occasionally consume tamarind fruits, and some *L. catta* populations live in areas where tamarind trees are not present (see Goodman and Langrand, 1996). Since tamarind fruits and young leaves are a quality resource that is high in protein and minerals, it is likely that gallery forest groups of *L. catta* have become reliant on tamarind, because it is the most frequently available source of easily digestible protein and minerals. Moreover, as a "weed species" *L. catta* are known for their ability to adapt to unfavorable and difficult conditions (Sussman, 1977; Gould et al., 1999; Sauther et al., 1999), and if tamarind were to be continually missing from the diets of gallery forest populations, it is likely that they would seek and use alternate sources of nourishment, although population densities would likely decrease. Thus, although deemed very important to some populations of *L. catta*, tamarind recourses are not essential at the species level.

Of the foraging theories outlined in Chapter 1, aspects of both the Wrangham (1980) and Isbell (1991) models seems to apply to this study. Wrangham (1980) predicts that diets of female-bonded primates (such as ringtailed lemurs) will have specializations for alternate diets during times of food scarcity. This is highly compatible with feeding behaviors of both Red Group and Green Group, since they each used fallback foods in the absence of tamarind fruits. Ability to survive (and subsequently reproduce) on a fallback diet is one trait that natural selection favors, and may be particularly important to lemurs, since Madagascar is subject to frequent natural disasters. Additionally, Isbell (1991) predicts that female aggression between groups will result in the larger group gaining access to resources at the expense of the smaller group. This seems to be the case here since the larger Red Group was able to hold the villager's crop as part of their home range, while the smaller Green Group was not able to access the crop when Red Group was present, and instead foraged in the nearby riverbed on time-consuming *Argemone mexicana* plants. However, since the crop may be part of Red Groups home range even when the crop is not in season, Red Group may actually have been defending their regular home range boundary rather than defending a valuable, but temporary resource.

Conclusions

In conclusion, it appears that the sexually divergent diets, as found in *Lemur catta* may be minimized during times of resource scarcity. Since food resources were limited during the current study, the diets of both males and pregnant females were likely less complete than when compared to other non-disaster years. Moreover, metabolic need of females during late pregnancy likely exacerbates any nutritional deficiencies in the present study. Further nutritional analyses of gallery forest *Lemur catta* plant foods during reproductive periods are needed to fully understand sex divergence in nutrition.

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Footnotes

1. All methods were approved by the University of Victoria Animal Care Committee.
2. Complete methods from the Dairy One Forage Laboratory available at http://www.dairyone.com/Forage/Procedures/default.htm
3. Total digestible nutrients denotes the sum of the digestible protein, digestible nitrogen-free extract, digestible crude fiber and 2.25X the digestible fat (National Research Council, 1988).

CHAPTER THREE

Feeding Outside the Forest

ABSTRACT

Crop raiding and feeding on introduced species may aid non-human primates in meeting caloric requirements, and increase foraging efficiency, but these behaviors are potentially risky due in part to increased predation pressure and threat from humans. In my study at the Beza Mahafaly Special Reserve in southwestern Madagascar, one of my study groups (Red Group), maintained the crop as part of their home range and were able to increase their foraging efficiency by feeding on the readily available and easily processed *Ipomoea* sp. (sweet potato) leaves. Conversely, Green Group did not have access to crop foods and focused on eating the time-consuming leaves from *Argemone mexicana* (mexican thistle). As such, Red Group was able to satiate themselves more quickly and thus had more time for other behaviors such as resting, or engaging in social activities. In the highly seasonal and unpredictable climate of southern Madagascar, behavioral adaptations allowing *Lemur catta* to persist in times of food scarcity are likely to be selected for.

INTRODUCTION:

Madagascar's unpredictable environment often results in cyclones, droughts, severe storms and other natural disasters (Ganzhorn, 1995; Smith and Ganzhorn, 1996; Wright, 1999). The Beza Mahafaly Special Reserve was hard hit by Cyclone Ernest in January of 2005. Massive defoliation and tree falls occurred, and resulted in an overall reduction in forest food availability in the following reproductive season (Razanajafy and Raznadrainy, pers comm.), which is already a difficult time of year as it is the dry season. Additionally, fruits from gallery forest *Lemur catta*'s most important resource, *Tamarindus indica* (Budnitz and Dainis, 1975; Rasamimanana and Rafidinarivo, 1993; Sauther, 1998; Yamashita, 2002), were absent due to the effects of cyclone Ernest. How the *L. catta* that I studied adapted to this dramatic reduction in food availability will be addressed in this chapter.

Food availability

As outlined in Chapter 2, in times of food scarcity, *Lemur catta* often temporarily increase their home range to secure scarce resources (Jolly and Pride, 1999; Mertl-Millhollen et al., 2006; Sauther, 1998). However, this behavior would not be favorable if the increased distance did not provide an increase in food resources. In times of overall food scarcity, specific plants or "critical fallback" foods that are not normally eaten may prove more crucial in the diets of *L. catta* (Soma, 2006). Additionally, very poor quality foods such as dessicated leaves, dessicated tamarind pods, and *Argemone mexicana* may be incorporated into *L. catta* during food shortages (Gould et al., 1999; Sauther 1992, 1994, 1998).

Crop raiding

Crop raiding is a common occurrence in areas where farming abuts primate habitat (Naughton-Treves et al., 1998). Agricultural products tend to be particularly nutritious and abundant, and thus can be tempting, even in lieu of potential risks associated with obtaining crop foods (Forthman-Quick, 1986; Forthman-Quick and Demment, 1988; Harris, 1970; Knapka and Morin, 1979; Parker, 1984). Predation threat increases once outside of the forest (Sauther, 2002), as aerial predators are more likely to spot crop raiders, and lemurs are more vulnerable to feral dogs (Gould, pers. comm., Sauther, 2002). Additionally, threat from humans is particularly high in crop raiding, as owners' of crops want to protect their agricultural investments (Saj et al., 1999). Thus, consequences of crop raiding may include increased stress, and bodily injury or even death from predation (Saj et al., 1999). These risks are expected to be higher in females who are gestating or who have offspring, since they have both a metabolic investment in their born or unborn offspring, and because they may be weighed down (and not as quick to escape) by their fetus or infant (Cords, 2000, 2002; Pazol and Cords, 2005; Miller, 2002). Conversely, these same females have increased caloric requirements and may be more likely to seek out crop foods, despite increased risks.

Foraging on invasive species

With increasing forest fragmentation and anthropogenic land changes, there is an inevitable increase in the number of invasive plant species present (Chapin et al., 2000) Whether intentional or not, these introduced species may provide important resources if they can in fact be exploited. In her study on introduced flora species at Berenty, Soma

(2006) found that *Lemur catta* allocated a considerable amount of feeding time on introduced species and that such consumption was more prevalent during the dry season, when endemic foods were most limited. However, experimenting with invasive or introduced species may be risky, as harmful secondary metabolites or toxins may be present in the plant. For example, *L. catta* in one area of Berenty exhibit signs of minor to rather extreme alopecia, since they began including the introduced *Leucaena luecocephala* in their diets (Jolly et al., 2006; Crawford et al., 2006; Tew, 2003). *Leucaena luecocephala* contains the compound mimosine, which in addition to alopecia can promote weight loss, infertility, goiter, paralysis and cataracts in mammals (Jones and Hegarty, 1984; Crawford et al., 2006). Clearly, none of these side effects are desirable, and since mimosine is new to their diets, *L. catta* at Berenty are not likely to have adaptations to cope these toxic compounds. However, due to Madagascar's unpredictable climate and rainfall patterns, some lemurs are likely to include experimenting with novel foods in times of severe environmental conditions and variability in food availability.

The diet of *Lemur catta* changes dramatically according to season, as fruiting, flowering, and patterns of leaf growth vary significantly with rainfall and season (Sauther, 1998). Additionally, *L. catta*'s feeding behavior changes over the course of a year, and they make long excursions out of their normal home range to monitor certain seasonal resources (Budnitz, 1978; Gould et al., 1999; Rasamimanana, 1999; Rasamimanana and Rafidinarivo, 1993; Sauther, 1994; Sauther et al., 1999; Sussman, 1991), or expand home ranges during food scarcity (Sauther, 1993; Sussman, 1991). Since, *L. catta* is accustomed to changing feeding behavior in response to frequent fluctuations in plant food availability; it is not surprising that their feeding repertoire includes novel items, such as crop foods or invasive weeds, during times of low food availability (Else, 1991).

Research questions and predictions

Since they are typically intended for humans or other animals, agricultural products can be a rich source of nutrients and calories, and are likely palatable, readily digestible, and more abundant than wild sources in a given area (Forthman-Quick, 1986; Forthman-Quick and Demment, 1988; Harris, 1970; Knapka and Morin, 1979; Parker, 1984). Furthermore, the inclusion of crop foods are likely to increase foraging efficiency, since animals eating these foods would not have to travel between patches as they deplete their immediate food source. Despite this increased efficiency, previous studies of crop raiding in primates (e.g. Altmann and Muruthi, 1988; Brennan et al., 1985) do not show an increase in overall caloric intake. Instead, since crop raiding allows individuals to meet their metabolic needs sooner, animals rest more or engage in other activities, rather than continuing to eat over and above their metabolic requirements (Altmann and Muruthi, 1988; Brennan et al., 1985). In light of such information, I ask the following questions and make the following predictions:

a) Does access to crop foods increase foraging efficiency?

***Prediction*:** The animals in Red Group will spend less time feeding when compared to the animals in Green Group as they include a local villager's crop as part of their home range.

b) Does crop feeding increase the gross amount of food eaten?

***Prediction*:** I do not expect that crop foods will increase the overall amount eaten by Red

Group. Instead, Red Group and Green Group will eat comparable amounts of food, although Red Group will spend less time feeding.

METHODS:

Data Collection

As outlined in chapter 2, I collected focal animal data (Altmann, 1974) on all adults (n=18) from two neighboring social groups of gallery forest dwelling ring-tailed lemurs at the Beza Mahafaly Special Reserve. I collected ten focal animal sessions of 15 minutes in duration, for a total of 150 minutes of focal animal observation per animal. When a focal animal was feeding, I noted the animal's location, amount eaten (number of leaves or bites), and the plant or plant part ingested. Both Red and Green Groups' home ranges bordered the Sakamena River in the eastern part of the reserve. Additionally, Red Group's home range included a local villager's field, where both cultivated crops and weeds grow (*Ipomoea* sp. and *Argemone mexicana*) and Green Group's home range included a portion of the dry riverbed, where *A. mexicana* grows. Using a translator (Youssouf), I asked the local villager how he felt about the crop raiding activities engaged in by the lemurs. Additionally, after gaining permission from the villager who owned the agricultural plot, I collected representative samples of *Ipomoea* sp. leaves. I also collected representative samples of *A. mexicana* from the riverbed. Plant samples were dried in the shade and were later analyzed by the Dairy One Forage Laboratory[1] for the following nutritional content: crude protein, acid detergent fiber, neutral detergent fiber, calcium, phosphorus, magnesium, potassium, and sodium. For the purposes of this chapter only the nutritional content of *Ipomoea* sp. and *Argemone mexicana* will be considered, since those were the two food items upon which Red and Green Group were feeding while outside of the forest.

Plant Phenology

In the villager's crop and the area of the riverbed where Green Group foraged, I estimated the percent of coverage by plant species (i.e. *Colvovulaceae* sp. and *Argemone mexicana* in the crop, and *A. mexicana* in the riverbed).

Data Analyses

Feeding Activity

Foraging efficiency was determined by the amount of time spent feeding for Red and Green Groups. For each group, I summed the time spend feeding by each animal and divided this by the total focal observation time (150 minutes per animal x number of animals in group), and multiplied that number by 100 to obtain a percentage of time spent foraging, which I used as a proxy for foraging efficiency.

Amount eaten

Amount eaten was determined in the same manner outlined in Chapter 2. I weighed 10 leaves or bites from each lemur plant food and took the average weight of a leaf or bite. To specifically determine amount eaten of *Ipomoea* sp. and *Argemone mexicana,* which had large leaves that took a number of bites to consume, I divided the average leaf mass by the median number of bites a lemur took to consume the whole leaf. For example, if an average leaf weighed five grams and the median number of bites to consume the leaf was four, then the average bite would be 1.25grams. I then calculated the total amount of *Ipomoea* sp. or *A. mexicana* eaten by each focal animal by multiplying the number of bites taken or leaves consumed by the average leaf mass or bite mass. Amount eaten by group was determined by adding up the amounts eaten by each group member.

Nutrient consumption

Nutrient consumption was also calculated in the same manner as in Chapter two. To specifically determine the nutrients consumed by each focal animal of from *Ipomoea* sp. or *Argemone mexicana*, I multiplied each of the plant nutrients (as measured by Dairy One Forage Laboratory) by the amount of the plant that an animal ate.

Foraging location

When an animal was foraging, I noted whether they were in the forest, crop, or dry river bed. For each group, I totaled the time spent foraging in the forest, crop, or riverbed by adding up the amount of time each animal spent feeding in these locations. I divided the summed feeding in each location time by the total observation time (and multiplied by 100), in order to obtain a percentage of time spent foraging in the forest, crop, or river bed by Red or Green Group.

Statistics

I used the Mann-Whitney U-test to compare probability distributions of Red and Green Groups overall time spent foraging, amounts of *Ipomoea* sp. and *Argemone* *mexicana* eaten, and to compare the two groups' time spent foraging and grams eaten by location (forest or crop). Since Red Group did not forage in the river bed, no comparisons between groups were made in this habitat.

RESULTS:

Plant phenology

The crop was densely populated by potential lemur plant foods, and consisted of approximately 20% *Argemone mexicana*, and 80% *Ipomoea* plants, which Red Group aggressively defended against Green Group and other neighboring groups' repeated attempts at access. The dry riverbed was sparsely covered with plant life, but of those present the vast majority were *A. mexicana.*

Plant nutrients

Argemone mexicana had higher percentages of crude protein, and all minerals except calcium when compared to *Ipomoea* sp. (**Table 1**). Additionally, *A. mexicana* had lower fiber content when compared to that of *Ipomoea* sp..

Feeding activity

Red Group spent 37% of the total observation time feeding, while Green Group spent significantly more of their observed time feeding- 54% (Mann Whitney U= 8, p=0.004, n1=11, n2=7).

Table 1. Milligrams of crude protein, fiber (ADF and NDF), calcium, phosphorus, magnesium, potassium, and sodium present in one gram of *Argemone mexicana* and *Ipomoea* sp.

	CP	Fiber	Ca	P	Mg	K	Na
A. mexicana	295	306	14.5	3.4	3.8	40.3	0.2
Ipomoea sp.	208	337	17.3	1.9	3.4	20.4	0.1

Amount eaten

Estimates of overall amounts eaten show no significant difference between groups (Mann Whitney U Test U=8, p=0.71, n1=11, n2=7). Red Group consumed 236 grams of Ipomoea sp. leaves and 64 grams of *Argemone mexicana*, while Green Group consumed 130 grams *Ipomoea* sp. leaves and 122 grams of *A. mexicana* (**Figure 1**).

Foraging location

Red Group did not forage in the dry riverbed; rather they spent 47% of their foraging time on the villager's crop and 53% of foraging time in the forest (**Figure 2**). Green Group spent 6% of their foraging time in the crop (which they accessed when Red Group was not present), 17% of their foraging time in the dry riverbed, and 78% in the forest (**Figure 3**). There was no significant difference between the time spent feeding by Red Group and Green Group in the forest habitat, but Red Group spent significantly more time than Green Group feeding in the crop (Mann Whitney U=8, p=0.004, n1=11, n2=7).

Figure 1. Sum of amount consumed by each animal of *Ipomoea* sp. and *Argemone mexicana* for Green Group (n=11) and Red Group (n=7)

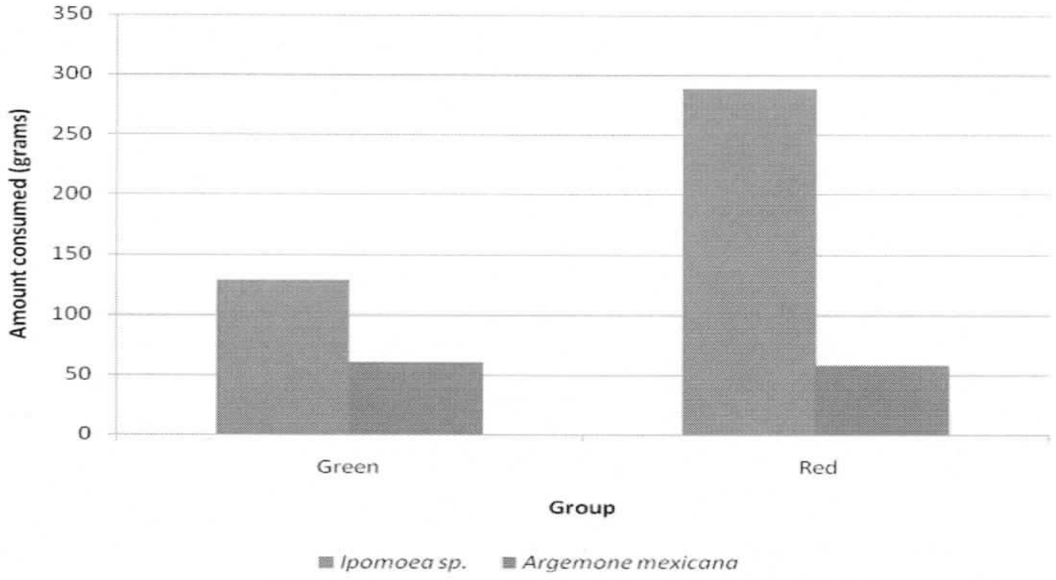


Figure 2. Average percentage of time spent foraging and amount eaten by location for Red Group (n=7)

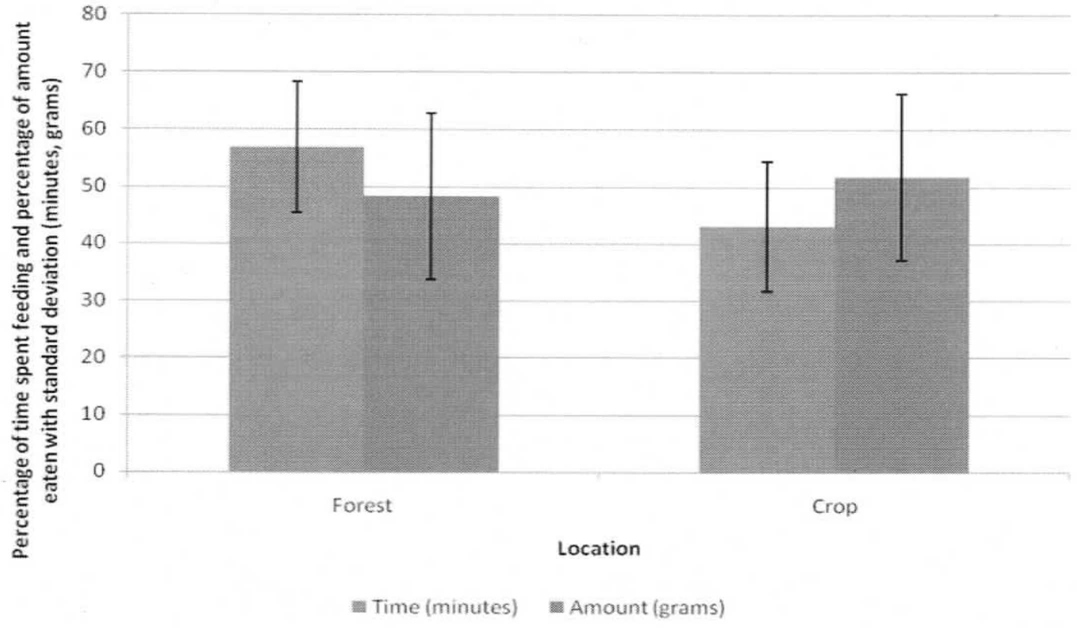
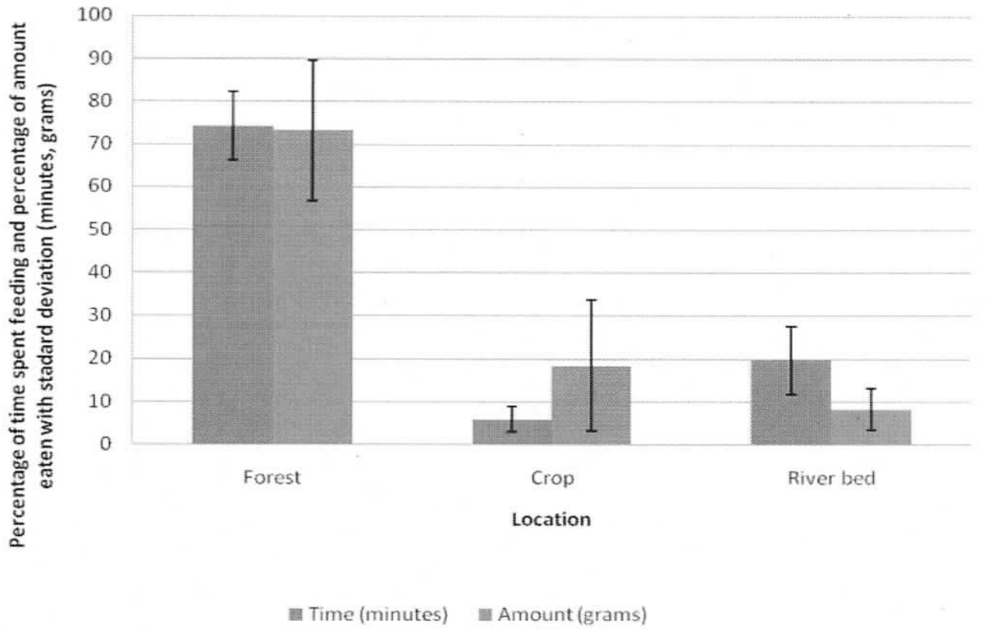


Figure 3. Average percentage of time spent foraging and amount of food consumed by location for Green Group (n=11)



DISCUSSION:

Phenotypic plasticity is a potential mode for a taxon to colonize a broad ecological niche (Ménard, 2002). The ability to exploit a wide variety of resources may be an evolutionary trait which is favored in unpredictable environments, such as those found in Madagascar (Wright, 1999). Dietary plasticity, as found *Lemur catta*, may be a key feature enabling the species to persist amongst environmental change. The variation and limits of *L. catta* ecological plasticity may be exemplified through the wide range of habitat types in which they persist. In addition to the dry forest habitats of southern Madagascar, *L. catta* are found in spiny forests, gallery forests, scrub and brush land, anthropogenically induced savannah, and in high-altitude mountain ranges of Analavelona Massif and Andringitra (Goodman and Langrand, 1996; Goodman and Rasolonandrasana, 2001; Goodman et al., 2007; Gould, 2006; Sussman, 1978; Sussman et al., 2003). Since *L. catta* is thought to have evolved in dry habitats of south and southwest Madagascar (Goodman et al., 2007), ecological plasticity of this species may be best represented by the high altitude populations dwelling in the Andringitra Massif region where plant distribution is described as low ericoid bush and sub-alpine vegetation (Goodman and Langrand, 1996). Both the Andringitra plant distribution and the diversity of plants upon which *L. catta* subsist in other environments, demonstrate the flexibility of this species (Goodman and Langrand, 1996; Gould, 2006; Gould et al., 2003).

Although their resource base is flexible, *Lemur catta* reproduction is highly tied to seasonal resources (Jolly, 1984; Rasamimanana and Rafidinarivo, 1993; Sauther, 1992, 1993, 1998; Yamashita, 2002). Females experience late gestation and early lactation periods during the driest parts of the year (Jolly, 1984; Sauther, 1994, 1998), and gallery forest populations normally depend on the very important resource *Tamarindus indica* as it is a reliable source of protein and other essential nutrients (Mertl-Millhollen et al., 2003; Sauther, 1992, 1994, 1998; Yamashita, 2002). In the current study, the diet of the two *L. catta* groups that I studied was comprised of less than 2% *T. indica* fruits, while Soma (1999) and Sauther (1992) found that *T. indica* made up 35-60% of *L. catta* diet in gallery forests. Tamarind fruits were not incorporated into these lemurs' diets in the current study, because the fruits were not available. Cyclone Ernest swept through the forest on January 23, 2005, and subsequently tamarind trees failed to fruit. As such, *T. indica* fruits and young leaves were all but lacking during the present study, and thus did not play a significant role in *L. catta* diet.

Introduced and cultivated plants appear important in *Lemur catta* diet. During both the wet and dry seasons, gallery forest *L. catta* at Beza have consumed crop and introduced plants for a number of years (Gould, pers. comm.; Loudon et al., 2006). During the current study in which tamarind fruits were absent, it appears that the cultivated and introduced plant foods were of particular importance to the animals I studied. Soma (2004, 2006) found that introduced species at Berenty Reserve reduced the effect of extreme food seasonality in gallery forest (note that these introduced species at Berenty were not part of a crop, but rather invasives that were growing in a plot which was formerly and orchard (Gould, pers. comm.). Additionally, Gould et al. (1999) noted that introduced *Argemone mexicana* was an important *L. catta* food source during a drought at Beza. Other primate species include invasive or agricultural plants into their diets, either because their natural foods are insufficient, or because they have a preference for the non-native foods (Altmann and Muruthi, 1988; Else, 1991; Forthman-Quick, 1986; Forthman-Quick and Demment, 1988; Malik and Southwich, 1988). Although foraging efficiency may vary with introduced plant species, primates who crop raid have an immediate increase in foraging efficiency (Altmann and Muruthi, 1988; Brennan et al., 1985; Fa, 1986; Forthman-Quick, 1986). Crop foods tend to be higher in energy per food unit, densely populated, and easy to exploit, which means crop raiders can meet their metabolic needs sooner (Saj et al., 1999). In fact, primate crop raiding can reduce feeding time by half or more, enabling individuals increased resting or social activity time (Altmann and Muruthi, 1988; Brennan et al., 1985).

In the current study, comparative ease of processing is most likely why Red Group vigorously defended the *Ipomoea* sp. crop plants, instead of concentrating foraging on *Argemone mexicana*, which was more abundant, and nutritionally higher in both crude protein and most measured minerals, and lower in fiber. *Ipomoea* sp. leaves were plump, soft and averages bites weighed 0.21grams. Conversely, extensive processing time required when foraging on *A. mexicana* is most likely why Green Group spent more time foraging, even though they did not eat more than Red Group. This plant is covered in both sharp thorns and spines, and in order to eat it the lemurs would chew the plant through its stem to dislocate it. Then, while holding the stem they would eat from base up, and eat individual leaves from basal to the apical end. This process appeared slow and cumbersome, and bites of *A. mexicana* only averaged 0.07grams. *Argemone mexicana* was regarded by Gould et al. (1999) as a "very poor quality resource", however, in light of the current nutritional data it seems more likely that *A. mexicana* is less desirable because of reduced foraging efficiency, rather than because of nutrient content. Since Red Group had primary access to *Ipomoea* sp. plants, it is somewhat surprising that they also included *A. mexicana* (from the crop) into their diet. This may have been simply because they liked eating small amounts of *A. mexicana.* Although both groups ate *A. mexicana* leaves, they did not consume the plants' flowers or seeds. Seeds are energy rich foods, however, *A. mexicana* seeds are highly toxic (Pahwa and Chatterjee, 1989), which is likely why they were not ingested by *L. catta.* Nonetheless, the seeds often spilled during leaf processing, and were subsequently caught in the lemurs' fur (LaFleur, pers obs). Albeit a widely distributed and successful invasive species, the local proliferation of *A. mexicana* at Beza is likely aided through lemur seed dispersal.

Primates foraging outside of their forest habitat are subject to higher predation risk. Furthermore, crop raiding primates may be harmed by humans (Else, 1991; Newmark et al., 1994; Saj et al., 2001 Strum, 1987), or by conspecifics in trying to defend coveted crop territory (Baskin and Kringe, 1973; Gartlan and Brian, 1968). At Beza, *Lemur catta* who are outside of the forest are subject to increased predation pressure, particularly from feral dogs and cats (Gould, pers. comm.;Sauther, 2002), but also from predatory birds (e.g. *Accipiter madagascariensis*) (Sauther, 2002). However, since humans at Beza do not generally harm crop raiding lemurs, human presence may *actually* offset the risk of predation for these lemurs when they are foraging in the crop. People are often present in the agricultural crops, and by being physically present, they may deter both aerial and terrestrial predators, who might otherwise prey on lemurs. Moreover, the local villager (name unknown) whose crop was raided by lemurs, said that he did not want the lemurs in his field, and that before Beza was protected as a Reserve he and other villagers with agricultural plots would have tried to kill a lemur that was eating crop foods. However, now that the lemurs are protected, he would either ignore lemurs in the crop or perhaps throw a rock at them, with only the intention of scaring them away. That being said, *L. catta* conspecific threat is not reduced by human presence, as I witnessed multiple between group agonistic events on or surrounding crop land. Furthermore, since female lemurs are responsible for the majority of combative territory defense (Jolly et al., 1993; Koyama, 1991; Mertl-Millhollen et al., 1979; Nakamichi and Koyama, 1997), they potentially have more at stake when defending territory, especially if they are pregnant or if they have an infant (Jolly, 1966, 1984; Mertl-Millhollen et al., 2003; Richard, 1987; Sauther, 1992). Although associated with risk, foraging outside the forest (especially on crop foods) can be highly lucrative, and is an important part of lemur feeding in this study, particularly as it was a year following a natural disaster.

Conclusions

Ecological plasticity as an adaptation to living in an unstable environment may enable *Lemur catta* to exploit new and non-native foods during times of food scarcity and following natural disasters (Soma, 2006). Crop foods offer increased foraging efficiency, and invasive species such as *Argemone mexicana* provide calories when other sources (including *Tamarindus indica*) are depleted. However, foraging outside of the forest can elevate risk of predation and conflict, which may be particularly important to reproductive females. At Beza, predation risk may be reduced for *L. catta* when they are foraging in the crop, since humans are often present and may ward off predators. Injury resulting from conspecific combat over crop territory is a risk *L. catta* in this study, but during this season of particularly low food availability, the cost of defending high-yield crop foods are likely outweighed by benefits. Natural selection will favor individuals able to process or persist on critical fallback foods, which is likely why ringtailed lemurs have adapted to a variety of habitats and ecological niches found in south and southwestern Madagascar. Follow-up censuses of *L. catta* at the Beza Mahafaly Special Reserve are planned for summer of 2008, in order to determine the full effects a reproductive season without *T. indica* on the gallery forest ringtailed lemurs.

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Footnotes

1. Complete methods from the Dairy One Forage Laboratory available at http://www.dairyone.com/Forage/Procedures/default.htm

2. Total digestible nutrients denotes the sum of the digestible protein, digestible nitrogen-free extract, digestible crude fiber and 2.25X the digestible fat (National Research Council, 1988).

CHAPTER FOUR

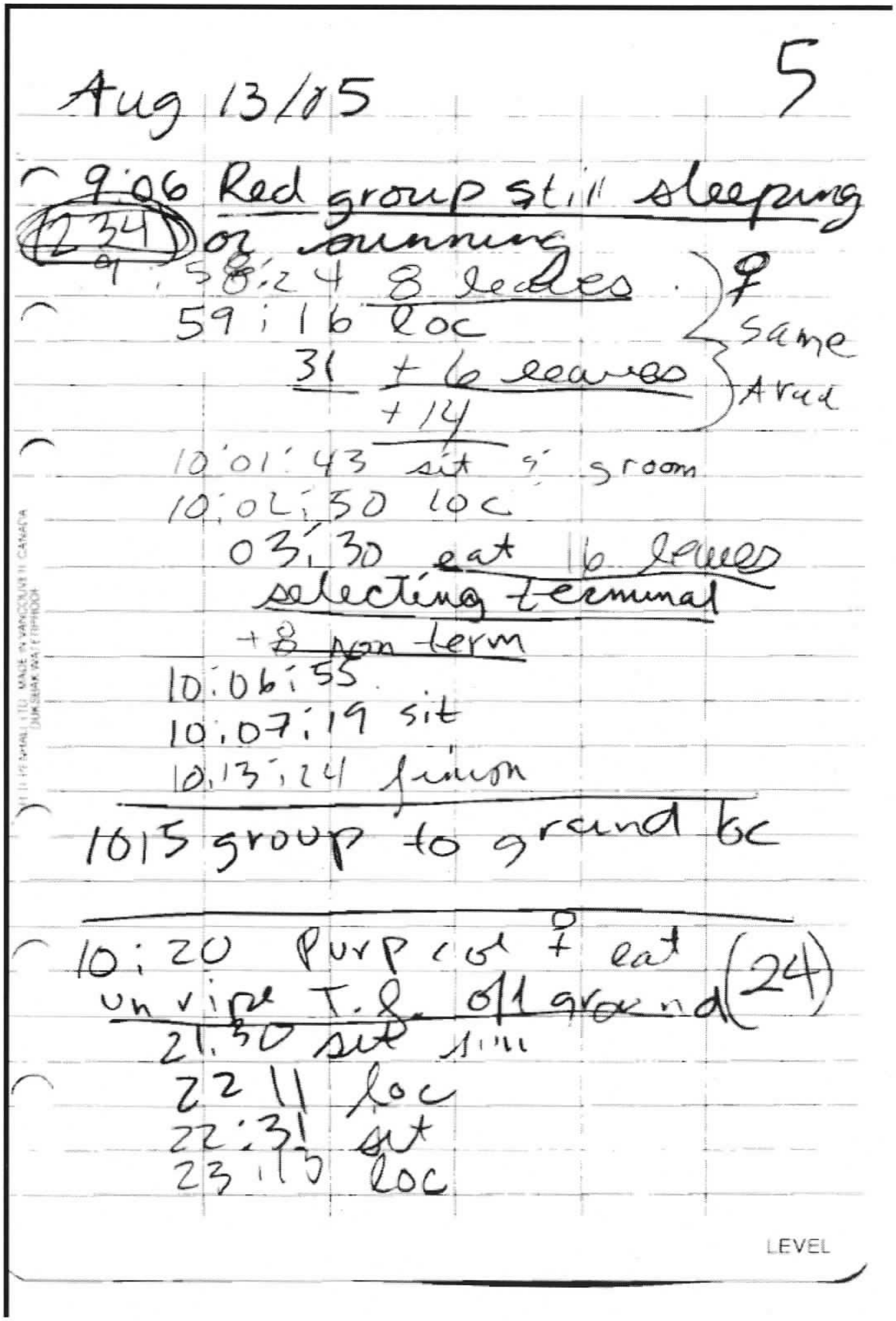
Conclusions

Feeding behavior and nutritional intake have been studied in a plethora of mammalian species. Female mammals incur higher metabolic costs directly related to reproduction than do males, which translates into increased metabolic need. This increased need can be met by foraging for longer periods of time compared to males, or by foraging on foods which are particularly rich in nutrients that are important for reproduction, such as protein, calcium and magnesium. My research showed that during times of food scarcity, the diet of gallery forest *Lemur catta* exhibit some sex divergence (intake of phosphorus and potassium), although male/female divergences are not as extreme as predicted (increased crude protein and calcium, and decreased fiber). Since the previous activity of cyclone Ernest caused a food shortage for *L. catta* at the Beza Mahafaly Special Reserve, it is possible sex differences were minimized because of the lack of resources. It is highly likely that both male and female nutritional intake was reduced, when compared to other non-disaster years. Moreover, metabolic needs of females during late pregnancy likely exacerbate any nutritional deficiencies present. Although not predicted, social groups of *L. catta* did exhibit differences in time spent feeding, a result of Red Group feeding on easy-to-process *Ipomoea* sp., sweet potato leaves, and Green Group feeding on time consuming invasive weeds *Argemone mexicana*, the mexican thistle. Ability to adapt during and after disasters, along with the ability to exploit non-native plant foods are among reasons that *L. catta* have been able to persist in the harsh and unpredictable island of Madagascar, despite recent massive deforestation and anthropogenically altered habitats. Further studies of *L. catta* nutrition during female gestation and lactation, and during years not affected by natural disasters will aid in full understanding sex divergence in feeding behavior and diet of ringtailed lemurs.

Appendix 1: Adult group membership for August 9 to September 7, 2005

Number	Sex	Group
0	male	Green
7	male	Green
9	female	Green
23	female	Green
34	female	Green
37	male	Green
44	female	Red
53	male	Red
167	female	Green
175	male	Green
203	male	Green
210	male	Green
233	male	Red
234	female	Red
235	female	Red
244	male	Red
260	female	Red
459	female	Green

Appendix 2: Sample Data Collection Sheet



Aug 13/05 5

9:06 Red group still sleeping
(234) or sunning
9:58:24 8 leaves) ♀
59:16 loc } same
31 + 6 leaves } Arud
+14
10:01:43 sit ♀ groom
10:02:50 loc
03:30 eat 16 leaves
selecting terminal
+8 non term
10:06:55
10:07:19 sit
10:13:24 fusion
1015 group to ground loc

10:20 Purp c♂ ♀ eat
unripe T.f. off ground (24)
21:30 sit [illegible]
22:11 loc
22:31 sit
23:10 loc

LEVEL

Appendix 3: Ethogram of recorded behaviors

Feeding: actively putting food into mouth, chewing or swallowing.

Foraging: deliberately searching for food items without ingestion. The focal animal may be scanning leaves, sorting through leaf litter, or manipulating food stuffs.

Traveling: group or individual walking or running, without foraging.

Resting: inactive behavior wherein an individual is stationary, sitting, lying. Can be solitary or with other(s).

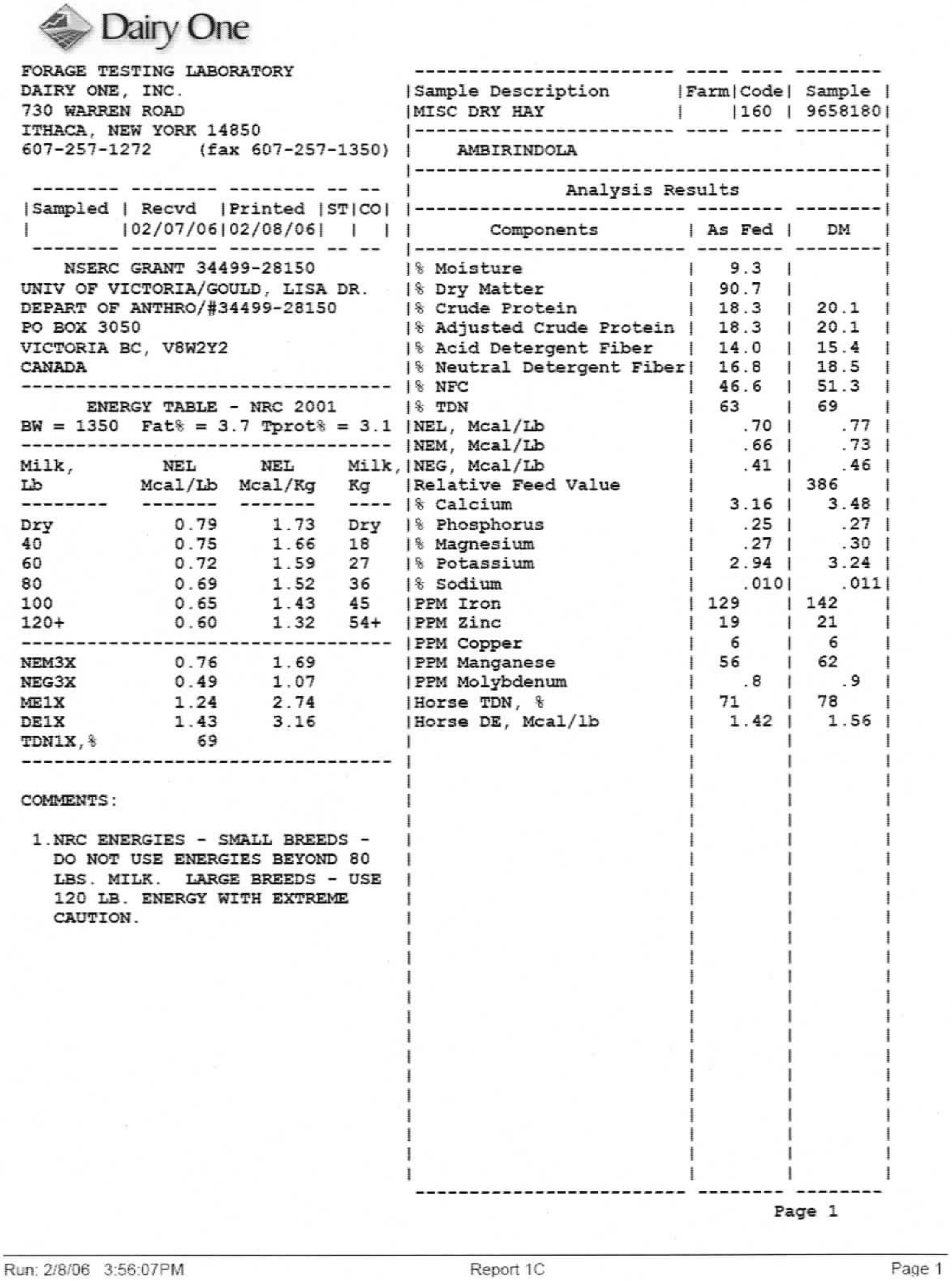
Grooming: Auto- or Allo-grooming where an individual is receiving or delivering physical body inspection alone, or with another lemur.

Other: may include but not limited to aggression, chasing, fighting, displacement, and scent marking. When one of these behaviors was observed, it was recorded as 'other' with a reference to the event context.

Appendix 4: Plant food of *Lemur catta* from August 9 to September 7, 2005.

Vernacular Name	Scientific Name	Family	Part
Ambirindola	N/A	N/A	Leaves
Amelo	N/A	N/A	Leaves
Angalora	*Secamone* sp.	Asclepiadaceae	Leaves
Angamae	*Tridax procumbens*	Asteraceae	flowers, leaves
Atanlsaka	*Dolichos lablalat*	Papilionaceae	Leaves
Bageda	*Convolvulaceae* sp.	Convolvulaceae	Leaves
Bakoa	*Strychnos madagascariensis*	Loganiaceae	Leaves
Beamena	*Boerhavia diffusa*	Nyctaginaceae	Leaves
Filofilo	*Azima tetracantha*	Salvadoraceae	Leaves
Fatiboe	*Argemone Mexicana*	N/A	leaves, stems
Hary	*Bridelia pervileana*	Euphorbiaceae	Leaves
Kijerandolo	N/A	N/A	Leaves
Kililo	*Metaporana parvifolia*	Convolvulaceae	Leaves
Kily	*Tamarindus indica*	Fabaceae	Leaves
Kompiste	*Gonocrypta grevei*	Asclepiadaceae	Leaves
Kongo	N/A	N/A	Leaves
Lamotimboay	*Xerophis* sp.	Flacourtiaceae	Leaves
Lamoty	*Flacourtia ramoutchi*	Flacourtiaceae	Leaves
Lavaenafe	N/A	N/A	Leaves
Lavarave	*Cenecio* sp.	Asteraceae	Leaves
Lobakanjirike	N/A	N/A	Leaves
Mantsake	*Enterospermum pruinosum*	Rubiaceae	fruit, leaves
Reampy	*Plagioscyphys* sp.	Sapindaceae	Leaves
Sagnatry	*Tragia tiverneana*	Legumineuse	Leaves
Salebohoka	*Grewia* sp. 1	Tiliaceae	Leaves
Sarihasy	*Byttneria voulili*	Sterculiaceae	Leaves
Songamy	*Maerua filiformis*	Capparidaceae	leaves, flowers
Taboarandolo	N/A	N/A	leaves, stems
Tamboro	*Temelapsis linearis*	Asclepiadaceae	Leaves
Tamenake	*Combretum* sp.	Combretaceae	Leaves
Tratrioste	*Acacia bellula*	Fabaceae	Leaves
Tsilaitse	*Noronhia* sp. 2	Oleaceae	Leaves
Vihipinde	N/A	N/A	Leaves
Voamae	*Vitex* sp.	Verbenaceae	Leaves
Valiandro	*Quisivianthe pruinosum*	Meliaceae	Flowers

Appendix 5: Sample Dairy One Data Sheet



Dairy One

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FORAGE TESTING LABORATORY           ------------------------ ---- ---- --------
DAIRY ONE, INC.                     |Sample Description      |Farm|Code| Sample |
730 WARREN ROAD                     |MISC DRY HAY            |    |160 | 9658180|
ITHACA, NEW YORK 14850              |------------------------ ---- ---- --------|
607-257-1272    (fax 607-257-1350)  |   AMBIRINDOLA                             |
                                    |-------------------------------------------|
 -------- -------- -------- -- --   |             Analysis Results              |
|Sampled | Recvd  |Printed |ST|CO|  |------------------------ -------- --------|
|        |02/07/06|02/08/06|  |  |  |       Components       | As Fed |   DM   |
 -------- -------- -------- -- --   |------------------------ -------- --------|
   NSERC GRANT 34499-28150          |% Moisture              |  9.3   |        |
UNIV OF VICTORIA/GOULD, LISA DR.    |% Dry Matter            |  90.7  |        |
DEPART OF ANTHRO/#34499-28150       |% Crude Protein         |  18.3  |  20.1  |
PO BOX 3050                         |% Adjusted Crude Protein|  18.3  |  20.1  |
VICTORIA BC, V8W2Y2                 |% Acid Detergent Fiber  |  14.0  |  15.4  |
CANADA                              |% Neutral Detergent Fiber|  16.8 |  18.5  |
----------------------------------- |% NFC                   |  46.6  |  51.3  |
     ENERGY TABLE - NRC 2001        |% TDN                   |  63    |  69    |
BW = 1350  Fat% = 3.7  Tprot% = 3.1 |NEL, Mcal/Lb            |    .70 |    .77 |
----------------------------------- |NEM, Mcal/Lb            |    .66 |    .73 |
Milk,        NEL      NEL     Milk, |NEG, Mcal/Lb            |    .41 |    .46 |
Lb         Mcal/Lb  Mcal/Kg   Kg    |Relative Feed Value     |        | 386    |
--------   -------  -------   ----  |% Calcium               |   3.16 |   3.48 |
Dry           0.79     1.73   Dry   |% Phosphorus            |    .25 |    .27 |
40            0.75     1.66   18    |% Magnesium             |    .27 |    .30 |
60            0.72     1.59   27    |% Potassium             |   2.94 |   3.24 |
80            0.69     1.52   36    |% Sodium                |    .010|    .011|
100           0.65     1.43   45    |PPM Iron                | 129    | 142    |
120+          0.60     1.32   54+   |PPM Zinc                |  19    |  21    |
----------------------------------- |PPM Copper              |   6    |   6    |
NEM3X         0.76     1.69         |PPM Manganese           |  56    |  62    |
NEG3X         0.49     1.07         |PPM Molybdenum          |    .8  |    .9  |
ME1X          1.24     2.74         |Horse TDN, %            |  71    |  78    |
DE1X          1.43     3.16         |Horse DE, Mcal/lb       |   1.42 |   1.56 |
TDN1X,%         69                  |                        |        |        |
----------------------------------- |                        |        |        |
                                    |                        |        |        |
COMMENTS:                           |                        |        |        |
                                    |                        |        |        |
 1.NRC ENERGIES - SMALL BREEDS -    |                        |        |        |
   DO NOT USE ENERGIES BEYOND 80    |                        |        |        |
   LBS. MILK.  LARGE BREEDS - USE   |                        |        |        |
   120 LB. ENERGY WITH EXTREME      |                        |        |        |
   CAUTION.                         |                        |        |        |
                                    |                        |        |        |
                                     ------------------------ -------- --------
                                                                   Page 1

Run: 2/8/06  3:56:07PM                  Report 1C                         Page 1
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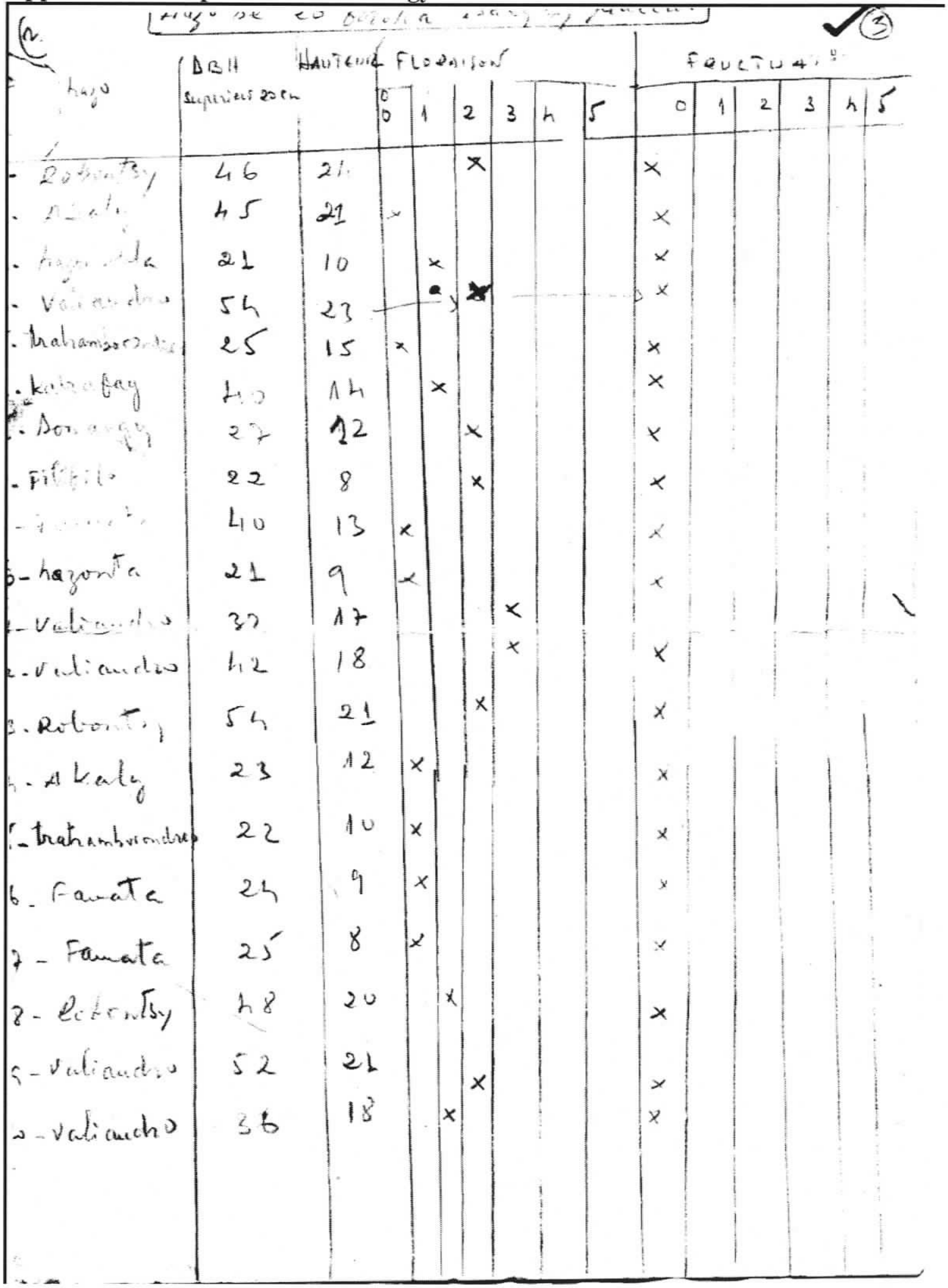
Appendix 6: Sample Forest Phenology Data Sheet



Hazo se eo [illegible]

③

Hazo	DBH supérieur 20 cm	HAUTEUR	FLORAISON 0	1	2	3	4	5	FRUCTUA[illegible] 0	1	2	3	4	5
- Robontsy	46	21			x				x					
- Akaly	45	21	x						x					
- Hazo[illegible]la	21	10		x					x					
- Valiandro	54	23		●	x				x					
. trahambondro	25	15	x						x					
. katrafay	40	14		x					x					
. Donangy	27	12			x				x					
. Fitfilo	22	8			x				x					
- [illegible]	40	13	x						x					
6- hazonta	21	9	x						x					
- Valiandro	37	17				x								
. Valiandro	42	18				x			x					
3. Robontsy	54	21			x				x					
. Akaly	23	12	x						x					
- trahambondro	22	10	x						x					
6_ Famata	24	9	x						x					
7 - Famata	25	8	x						x					
8 - Robontsy	48	20		x					x					
- Valiandro	52	21			x				x					
- Valiandro	36	18		x					x					

Appendix 7: Dairy One Forage Laboratory Methods

I. **Dry Matter**

  A. **Oven** – 60°C for 4 hours (forced air).
  B. **Oven** – 135°C for 2 hours - AOAC 930.15.
  C. **Oven** – 105°C for 3 hours - NFTA Method 2.1.4.
  D. **Near Infrared Reflectance Spectroscopy (NIRS)** – AOAC 991.01.

II. **Protein**

  A. **Crude Protein** (CP)

    1. Kjeldahl – AOAC 984.13. 10.5g of catalyst (ratio of 10g K2SO4 to 0.3g CuS04) is used. A Boric acid receiving solution contains methyl red-methylene blue indicator.
    2. Block Digestion and Tecator Kjeltec 2300 or 2400 Analyzer – Modified Kjeldahl procedure with automatic distillation and titration.
      a. AOAC 2001.11.
      b. FOSS Tecator, Application Note AN 300, pp. 1-12, 1987 "The Determination of Nitrogen according to Kjeldahl using Block Digestion and Steam Distillation".
    3. Leco FP-528 Combustion analyzer.
      a. AOAC 990.03.
      b. Leco Application Note "Nitrogen/Protein in Animal Feeds" Form 203-821-146, 2000.
    4. NIRS – Foss NIR Systems Model 6500 with Win ISI II v1.5 - AOAC 989.03.

      Used for grass, grass-legume mixtures, legume hays, haylages, fresh forages and pastures; corn silage and corn stalks (fresh and fermented); corn silage and haylage mixtures; shelled, ear, and snaplage corn; hays, fresh forages, pastures and silages for barley, wheat, oats, triticale, peavine, soybean and triticale and peas; fresh forages and silages for rye, sorghum, sorghum-sudan and sudangrass; barley, oats, triticale and wheat grains; brewers grains; distillers grains; total mixed rations (TMR's).

  B. **Soluble Protein** (SP)

    1. Cornell Sodium Borate-Sodium Phosphate Buffer Procedure. Soy products incubated at 39°C. All other samples incubated at ambient temperature. Cornell Nutrition Conference Proceedings, 1990, pp. 85-86.
    2. NIRS – Foss NIRSystems Model 6500 with Win ISI II v1.5 - AOAC 989.03.

  C. **Degradable Protein** (Rumen Degradable Protein (RDP))

    1. Cornell Streptomyces griseus (SGP) enzymatic digestion. Enzyme concentration held constant.
      a. Concentrates incubated for 18 hrs. Cornell Nutrition Conference Proceedings, 1990. pp. 81-88.

   b. Forage samples incubated for 2 hrs at higher SGP concentration. J. Dairy Sci. 1999. 82: 343-354.

  2. NIRS – Foss NIRSystems Model 6500 with Win ISI II v1.5 - AOAC 989.03.

D. **Acid Detergent or Neutral Detergent Insoluble Crude Protein** (ADI-CP, NDI-CP)

  1. ADF or NDF residue is subjected to Kjeldahl or Kjeltec analysis to determine the protein fraction bound to the fiber. Sodium Sulfite not used for NDI-CP.

  2. NIRS – Foss NIRSystems Model 6500 with Win ISI II v1.5 - AOAC 989.03.

E. **Non Protein Nitrogen** (NPN; reported as crude protein equivalent – CPE)

  1. Urea and Ammoniacal Nitrogen – AOAC 941.04.
  2. Urea – AOAC 967.07.
  3. NIRS – Ammonia – Foss NIRSystems Model 6500 with Win ISI II v1.5 – AOAC 989.03. Analyzed on corn silage and fermented haycrop forages only.

III. **Fiber**

A. **Acid Detergent Fiber** (ADF)

  1. ANKOM A200 Filter Bag Technique (FBT). ANKOM Application Note 01/02 "Method for Determining Acid Detergent Fiber". Solutions same as AOAC 973.18 (C). Samples individually weighed into filter bags and digested for 75 minutes as a group of 24 in 2L of ADF solution in ANKOM A200 Digestion Unit. FBT eliminates filter steps. Samples are rinsed three times with boiling water in filter bags followed by an acetone rinse and drying at 100°C for 2 hours.

  2. Liquid samples – AOAC 973.18 (C). Whatman 541 filter paper and buchner funnels.

  3. NIRS – Foss NIRSystems Model 6500 with Win ISI II v1.5 – AOAC 989.03.

B. **Neutral Detergent Fiber** (NDF)

  1. ANKOM A200 Filter Bag Technique (FBT). ANKOM Application Note 01/02 "Method for Determining Neutral Detergent Fiber (aNDF)". Solutions same as Journal of Dairy Science 74:3583 - 3597. Samples individually weighed into filter bags and digested for 75 minutes as a group of 24 in 2L of NDF solution in ANKOM A200 Digestion Unit. Four ml of Alpha Amylase and 20g sodium sulfite are added at the start of digestion. FBT eliminates filter steps. Samples are rinsed three times with boiling water. Alpha Amylase is added to the first 2 rinses. Water rinses are followed by an acetone rinse and drying at 100°C for 2 hours.

  2. Liquid samples – Journal of Dairy Science 74:3583 - 3597, 10/91.

  3. NIRS – Foss NIRSystems Model 6500 with Win ISI II v1.5 – AOAC 989.03.

C. **Crude Fiber** – AOAC 962.09

Samples filtered through bingham linen after first boil and through Whatman AH-934 glass membrane filter paper after second boil.

D. **Lignin**

1. ANKOM A200 Filter Bag Technique (FBT). ANKOM Application Note 01/02 "Method for Determining Acid Detergent Lignin in DaisyII Incubator". Solution same as AOAC 973.18(D). ADF performed as in III.A.1. ADF residue digested as a group of 24 in 72% w/w sulfuric acid for 3 hours in ANKOM DaisyII Incubator at ambient temperature.

2. Liquid samples – AOAC 973.18(D). No asbestos.

3. NIRS – Foss NIRSystems Model 6500 with Win ISI II v1.5 – AOAC 989.03.

E. **In-Vitro True Digestibility** (IVTD / NDFD)

1. ANKOM DaisyII Filter Bag Technique (FBT). ANKOM Application Note 11/00 "In Vitro True Digestibility using the DaisyII Incubator". Rumen fluid collected from TMR fed, high producing lactating cow. Feed samples incubated in Van Soest buffer/rumen fluid mixture for 24, 30, or 48 hours under anaerobic conditions at 39°C. After incubation, samples extracted using NDF procedure to remove bacterial contamination. Residue is undigested fibrous material and is used to determine in-vitro true digestibility (IVTD) and neutral detergent fiber digestibility (NDFD).

2. NIRS – Foss NIRSystems Model 6500 with Win ISI II v1.5 – AOAC 989.03.

IV. **Minerals**

A. **Ca, P, Mg, K, Na, Fe, Zn, Cu, Mn, Mo, Co**

Analyzed using a Thermo Jarrell Ash IRIS Advantage HX Inductively Coupled Plasma (ICP) Radial Spectrometer.

1. General Feeds and Forage Types – Thermo Jarrell Ash "The Spectroscopist" Dec. 1994, Vol. 3. No. 1. pp 6-9. Samples ashed in muffle furnace at 500°C for 4 hours. Three ml of 6N HCl are added to ash residue and evaporated to dryness on a 100° - 120°C hot plate. Minerals extracted with acid solution (1.5N HNO3 + 0.5N HCl) and determined using an IRIS Advantage HX.

2. Grain and Mineral Mixes – High Organic Matter (OM) mixes ashed 2 hours at 500°C. Low OM samples not ashed. 10 ml Mineral Mix extracting solution (1.8N HCl + 0.3N HNO3) added to sample and digested on 100° - 120°C hot plate. Filtered through Whatman 4 filter paper into volumetric flasks using 1.5N HNO3 + 0.5N HCl and minerals determined using an IRIS Advantage.

3. NIRS – (Ca, P, Mg, K) – Foss NIRSystems Model 6500 with Win ISI II v1.5 – AOAC 989.03.

B. **Sulfur** (S)

1. Leco Model SC-432. Leco Application Note "Sulfur in Plant Tissue" Form 203-601-229, 08/92. Samples combusted in oxygen rich atmosphere at 1350°C. Sulfur bearing compounds break down freeing sulfur, then oxidized to form SO2. Gases flow through an infrared detection cell which measures the concentration of SO2. The instrument converts that value and reports a percent sulfur.

2. NIRS – Foss NIRSystems Model 6500 with Win ISI II v1.5 – AOAC 989.03.

C. **Chloride Ion** (Cl)

1. Brinkman Metrohm 716 Titrino Titration Unit – 0.5g dried, ground sample extracted in 50ml 0.1N HNO3 followed by potentiometric titration with AgNO3 using Brinkman Metrohm 716 Titrino Titration Unit with silver electrode.

   a. Metrohm Application Bulletin No. 130 by Metrohm Ltd., C-H-9101 Herisau, Switzerland distributed in the US by Brinkmann Instruments Inc., One Cantiaque Road, PO Box 1019, Westbury, NY 11590-0207, phone 1-800-645-30502.

   b. The method by Metrohm is similar to the concepts found in: Cantliffe, D.J., MacDonald, G.E. and Peck, N.H. 1970. The potentiometric determination of nitrate and chloride in plant tissue. New York's Food and Life Sciences Bulletin. No.3, September 1970. Plant Sciences. Vegetable Crops Geneva. No. 1: 5-7.

2. NIRS – Foss NIRSystems Model 6500 with Win ISI II v1.5 – AOAC 989.03.

Appendix 8: Table 1. Results of nutritional elements ingested by males and females of Red and Green Group.

		Red Group		Green Group		Group/Sex			Group			Sex		
		X (g)	SD (g)	X (g)	SD (g)	F	d.f.	p	F	d.f.	P	F	d.f.	P
Protein	♂	26.63	20.58	14.65	6.56	2.685	1, 18	0.124	0.107	1, 18	0.748	2.071	1, 18	.172
	♀	14.09	5.83	12.98	3.36									
ADF	♂	12.45	11.53	11.10	6.58	2.685	1, 18	0.124	0.107	1, 18	0.748	2.071	1, 18	.172
	♀	13.18	3.87	10.78	3.37									
NDF	♂	17.32	16.62	14.70	8.61	2.937	1, 18	0.109	0.037	1, 18	0.851	.902	1, 18	.358
	♀	17.44	5.25	14.83	4.63									
NFC	♂	36.05	37.16	34.23	20.35	0.877	1, 18	0.365	2.685	1, 18	0.124	.423	1, 18	.526
	♀	34.07	14.32	33.34	10.71									
Calcium	♂	1.55	1.37	1.07	0.38	0.011	1, 18	0.919	1.460	1, 18	0.247	2.680	1, 18	.124
	♀	0.96	0.47	1.42	0.31									
Phosphorus	♂	0.17	0.17	0.20	0.11	1.276	1, 18	0.278	0.099	1, 18	0.758	12.097	1, 18	.004
	♀	0.22	0.07	0.16	0.07									
Magnesium	♂	0.29	0.28	0.23	0.10	0.040	1, 18	0.845	2.091	1, 18	0.170	1.097	1, 18	.313
	♀	0.23	0.11	0.25	0.04									
Potassium	♂	2.14	2.08	2.26	0.96	1.255	1, 18	0.281	0.115	1, 18	0.739	7.637	1, 18	.015
	♀	2.75	0.99	1.83	0.56									
Sodium	♂	0.01	0.006	0.029	0.047	0.535	1, 18	0.477	0.867	1, 18	0.368	.385	1, 18	.545
	♀	0.0012	0.007	0.011	0.0016									

Appendix 9: Top foods for each focal lemur

Animal	**Group**	**Sex**	**Plant name-** *Scientific* (Malagasy)	Items (leaves/bites)
9	Green	Female	*Quisivianthe papionae* (Valiandro)	1330
			Metaporana parvifolia (Kilokilo)	295
			Argemone mexicana (Fatiboae)	179
			Tridax procumbens (Angamay)	12
			(Lavarave)	36
			Sum	1852
23	Green	Female	*Quisivianthe papionae* (Valiandro)	730
			Argemone mexicana (Fatiboae)	111
			Secamone sp. (Angalora)	50
			(Lobakanjirike)	41
			Enterospermum pruinosum (Mantsake)	6
			Sum	938
34	Green	Female	*Maerva filiformes*	733
			Secamone sp. (Angalora)	304
			Metaporana parvifolia (Kilokilo)	275
			(Lavarave)	26
			(Lobakanjirike)	16
			Sum	1354
167	Green	Female	*Quisivianthe papionae* (Valiandro)	485
			Maerva filiformes	375
			(Lobakanjirike)	160
			Argemone mexicana (Fatiboae)	51
			Secamone sp. (Angalora)	44
			Sum	1115
235	Green	Female	*Quisivianthe papionae* (Valiandro)	2185
			Maerva filiformes	445
			Secamone sp. (Angalora)	224
			Ipomoea sp. (Bageda)	99
			Argemone mexicana (Fatiboae)	77
			Sum	3030
459	Green	Female	*Ipomoea sp.* (Bageda)	337
			Secamone sp. (Angalora)	64
			Argemone mexicana (Fatiboae)	63
			Byttneria voulili (Sarihasy)	42
			(Lobakanjirike)	33
			Sum	539

Animal	**Group**	**Sex**	**Plant name-** *Scientific* (Malagasy)	Items (leaves/bites)
0	Green	Male	*Quisivianthe papionae* (Valiandro)	1320
			Ipomoea sp. (Bageda)	176
			Secamone sp. (Angalora)	126
			(Kompitse)	29
			Flacourtia ramoutchi (Lamoty)	8
			Sum	1659
7	Green	Male	*Quisivianthe papionae* (Valiandro)	960
			Secamone sp. (Angalora)	206
			(Kompitse)	131
			Ipomoea sp. (Bageda)	93
			(Taboaranandola)	45
			Sum	1435
37	Green	Male	*Secamone* sp. (Angalora)	454
			(Kompitse)	63
			Ipomoea sp. (Bageda)	46
			(Taboaranandola)	38
			Grewia spp. 1 (Selebohoka)	18
			Sum	619
175	Green	Male	*Quisivianthe papionae* (Valiandro)	963
			Dolichos lablalat (Atanlsaka)	153
			Secamone sp. (Angalora)	138
			(Lobakanjirike)	126
			Argemone mexicana (Fatiboae)	76
			Sum	
210	Green	Male	*Quisivianthe papionae* (Valiandro)	398
			Argemone mexicana (Fatiboae)	301
			Secamone sp. (Angalora)	130
			Ipomoea sp. (Bageda)	95
			Sum	924
44	Red	Female	*Cobretum* sp. (Tamenaka)*	1373
			Argemone mexicana (Fatiboae)	644
			Secamone sp. (Angalora)	74
			Ipomoea sp. (Bageda)	14
			(Tamboro)	14
			Sum	2119

Animal	**Group**	**Sex**	**Plant name-** *Scientific* (Malagasy)	Items (leaves/bites)
234	Red	Female	*Quisivianthe papionae* (Valiandro)	983
			Ipomoea sp. (Bageda)	251
			Secamone sp. (Angalora)	130
			Metaporana parvifolia (Kilokilo)	60
			Argemone mexicana (Fatiboae)	49
			Sum	1473
260	Red	Female	*Quisivianthe papionae* (Valiandro)	773
			Ipomoea sp. (Bageda)	97
			Argemone mexicana (Fatiboae)	70
			Azima tetracantha (Filofilo)	55
			NO 5th food	0
			Sum	995
53	Red	Male	*Ipomoea* sp. (Bageda)	870
			Quisivianthe papionae (Valiandro)	185
			Dolichos lablalat (Atanlsaka)	68
			Tamarindus indica (Kily)	10
			Secamone sp. (Angalora)	8
			Sum	1141
203	Red	Male	*Quisivianthe papionae* (Valiandro)	410
			Ipomoea sp. (Bageda)	110
			(Kompitse)	48
			Byttneria voulili (Sarihasy)	33
			(Tamboro)	16
			Sum	617
233	Red	Male	*Secamone* sp. (Angalora)	126
			Enterospermum pruinosum (Mantsake)	61
			Ipomoea sp. (Bageda)	32
			(Reampy)	23
			Grewia spp. 1 (Selebohoka)	10
			Sum	252
244	Red	Male	*Quisivianthe papionae* (Valiandro)	983
			Ipomoea sp. (Bageda)	251
			Secamone sp. (Angalora)	112
			Metaporana parvifolia (Kilokilo)	60
			Argemone mexicana (Fatiboae)	49
			Sum	1455

* Excluded gorging incident.