

Behavioural Strategies of the Ring-Tailed Lemur (*Lemur catta*) in a
Sub-Desert Spiny Forest Habitat at Berenty Reserve, Madagascar.

by

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ABSTRACT

In an effort to better understand primate behavioural flexibility and responses to low-biomass habitats, behavioural patterns of ring-tailed lemurs (*Lemur catta*) living in a xerophytic spiny forest habitat in southern Madagascar were examined. Behavioural data were collected over two months on two separate groups living in two distinctly different habitats: a sub-desert spiny forest and a riverine gallery forest. Data on the following behavioural categories integral to primate sociality were collected: time allocation, anti-predator vigilance, predator sensitive foraging, feeding competition, and affiliative behaviour. *L. catta* living in the spiny forest habitat differed significantly in many behavioural patterns when compared to *L. catta* living in the gallery forest. I suggest that the ability to successfully alter behavioural strategies to varying ecological conditions allows ring-tailed lemurs to occupy low biomass habitats which are uninhabitable to nearly all other primate species in Madagascar. *Lemur catta* evolution, behavioural flexibility, and conservation will be discussed.

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Dedicated to my parents, Martha and David.

CHAPTER 1: INTRODUCTION

Long-term studies of primate behaviour and ecology have identified that many species have the ability to adjust their behaviour to varying ecological conditions. Moreover, many primate species have shown the ability to withstand environments which are relatively lacking in ample resources (Whiten et al. 1987, Goodman and Langrand 1996, Cowlshaw 1997a, Gould et al. 1999, Nakayama et al. 1999, Umpathy and Kumar 2000, Koenig and Borres 2001, Jolly et al. 2002, Menard 2002) or modified by anthropogenic forces (see Cowlshaw and Dunbar 2002 for review). How do primates cope when living in habitats which are defined by ecological variables which are relatively harsh (e.g. higher ambient temperatures, little to no water, smaller and less nutritional food resources)? Studies of primate behavioural flexibility, especially in habitats relatively lacking in resources, have implications for the advanced understanding of primate biogeography and behavioural ecology. Studies of a single species of primate with separate populations occupying ecologically distinct habitats will aid researchers in understanding if and how primates change the types and rates of behaviours to increase levels of fitness (Melnick and Pearl 1987, Singh and Vinathe 1990, Boinski et al. 2000, Pruettz and Isbell 2000, Henzi and Barrlett 2003).

This thesis aims to investigate the behavioural patterns of the ring-tailed lemur, *Lemur catta*, in two ecologically distinct habitats. *L. catta* is an appropriate species on which to collect data in relation to primate behavioural flexibility between differing ecological contexts. First, *L. catta*, a prosimian native to south and southwest Madagascar, is able to survive in a variety of ecological conditions (Sussman et al. 2003, Goodman et al. 2006, Gould 2006). Additionally, *L. catta* at Berenty Private Reserve,

southern Madagascar, occupy differing habitats, allowing for concurrent data-collection of groups in these differing habitats. The remainder of this chapter will introduce the concept of behavioural flexibility, the theoretical background of the behavioural variables which I have recorded, and a background on the natural history and research history of *L. catta*.

VARIATION IN POPULATIONS, INDIVIDUALS, AND BEHAVIOURAL FLEXIBILITY

Variation has been a leading subject in the study of modern biology. Darwin (1859) was the first to suggest that general biological patterns are defined by variation both within and between groups. Darwin's thorough investigations revealed that organisms vary within populations, and he theorized that variation is the driving force in the selection of biological traits within populations over time. Darwin's theory of natural selection states that a trait which is more beneficial within a specific ecological or social context is more likely to be passed on to future generations, and thus, will become more common within a population over time. Biological variation has also been noted to be a force which allows populations to survive when environmental variables, such as food availability and ambient temperature, suddenly change, causing a shift in genotype and phenotype (Gould and Eldridge 1993). Contemporary biologists still insist that the study of biological variation, not the study of averages, should be the primary method to understand how fauna and flora develop, reproduce, and survive; variation, not the mean, is constant over time (Gould 1996).

Much of the study of biological variation has centered on differences in traits which are determined by genes and passed down from previous generations. Recent

studies in variation in animal behaviour, particularly primates, focus on how individuals rapidly alter the types and frequencies of behaviours as a direct response to environmental variability in space and time (Jones 2005). Behavioural strategies can be defined as decisions made, consciously or unconsciously, by an animal in an environmental or social context (Alexrod and Hamilton 1981). Intra-individual flexibility in behavioural strategies suggests that individuals are highly dynamic entities with the ability to change behavioural strategies depending on the environmental context (Jones 2005). Moreover, behaviour is seen as facultative (i.e. reversible) and condition-dependent, where individuals quickly and frequently alter behaviours in response to stimuli (Goldizen 1987, Hamilton and Bulger 1992, Jones 2005). The ability for an individual to change the types and amount of behaviours in space and time is termed behavioural flexibility (or behavioural plasticity) (Piersma and Drent 2003). Jones (2005) argues that motivation is the key mechanism leading individuals to change behaviours in differing environmental contexts. Motivation is driven by both proximate (e.g. finding food, interacting with social members) and ultimate (e.g. long-term survival and the reproduction of offspring) causes, and individuals are motivated to change behavioural strategies to increase their inclusive fitness when it is warranted by environmental circumstances.

A key to behavioural variation is that animals are able to continuously assess the type and availability of resources (whether ecological or social) and choose (consciously or unconsciously) an appropriate type and amount of behaviour (Jones 2005). Primates are adept at successfully modifying over space and time, as their relatively advanced cognitive abilities allow for them to make beneficial choices using trial and error

learning, insight learning, and social monitoring (Staddon 1983, Lee 1991, Tomasello and Call 1997). There are several benefits afforded by behavioural flexibility. The ability to change behaviours as a reaction to environmental heterogeneity may lessen the negative consequences sudden environmental change may pose to individual fitness (Choe and Crespi 1997, Jones 2005). Behavioural flexibility also allows species to stretch their geographical range by responding to new ecological niches without evolving into a new species via geographic separation or niche specialization (Lee 1991). Finally, individuals may gain a competitive advantage over conspecifics by changing to a more optimal behaviour in times of ecological change (Jones 2005).

Primates are excellent candidates for the investigation of behavioural flexibility. Many primate species have the ability to thrive in a broad range of ecological niches, thus presenting a variety of ecological heterogeneity (e.g. Prosimians: Izard and Rassmmusen 1985, Richard 1978, Sussman et al. 2006, Gould 2006; Neotropical Monkeys: Einsburg 1989, Fragazy et al. 1990; Old World Monkeys: Fooden 1982, Keoning and Borries.2001, Jolly 2007; Apes: Stumpf 2007). Many primates have flexible diets and are able to monitor and change usage of resources as they become available, allowing for survival in variable ecological conditions (see Brockman and van Schiak 2005 for review). Primates also have a relatively high level of cognitive abilities, allowing them to quickly learn the costs and benefits of behaviours in new ecological and social situations (Tomasello and Call 1997). Finally, human beings are perhaps the most behaviourally flexible primate of all, having evolved the ability to create varying behavioural traditions (cultures) via imitation and social transmission of knowledge (Tomasello 1999). Furthermore, studies of behavioural flexibility help to show which behavioural decisions

are beneficial to a primate species when encountering differing ecological elements. My study will compare data on time allocation, anti-predator behaviour, feeding competition, and affiliative behaviour. These variables are a vital part of group living in primates and are reviewed below.

FEEDING COMPETITION AND THE EVOLUTION OF PRIMATE GROUPING PATTERNS

Competition, especially over food, is a key question in primatological research. As primates must acquire adequate resources for survival, in most species, competition occurs over desired ecological resources. Moreover, researchers are interested in how competition over food influences social relationships within groups and how resource competition relates to primate social organization.

Wrangham's (1980) seminal model of ecological influences on primate group formation was the first to examine how resource competition influences the evolution of primate social organization. This model of primate group formation states that when highly-valuable and patchy resources are an important food item for a species, genetically related females are expected to stay in their natal groups and form alliances for acquisition of resources. Wrangham's model is based on the assumption that a female primate's main goal is to increase access to resources which provide for physiological processes, such as lactation and gestation. The cost of living in groups, especially increased foraging competition, is lessened by the creation of alliances between females, allowing individuals enhanced access to high quality food items. Additionally, group formation allows for better resource defense from neighbouring groups. Thus, when food

items are located in randomly spaced patches and must be defended to enable frequent access, females are expected to form the core of social groups.

Wrangham's (1980) model placed an emphasis on foraging competition as a leading cause of group formation and primate sociality, yet many questions were raised about the nature of foraging competition. A major question in the creation of new competition models became—which of the following types of competition is more common in a primate species: contest or scramble? Whereas scramble competition exists when individuals out-compete other group members by exploiting non-usurable food items on a first-come first-serve basis, contest competition occurs when individuals compete over usable and patchy resources (van Schaik 1989, Isbell 1991, van Hooft and van Schaik 1992). Primates which predominantly practice scramble competition more often are believed to live in social groups with weak dominance hierarchies and weak social bonds, while those who practice contest competition more often will form linear dominance hierarchies and will be composed of female matriline and unrelated males. van Schaik (1989) predicted that frugivorous and omnivorous primates would live in social groups characterized by female linear dominance hierarchies because of increased potential contest competition over preferred patchy resources. Predominantly folivorous and insectivorous primates should develop egalitarian social groups with non-linear dominance hierarchies because of their reliance on food items with ubiquitous or unpredictable spatial distributions, which results in decreased agonistic encounters over food items (van Schiak 1989).

While many models of competition are based on the types of food items over which individuals compete (fruit vs. leaves) and the ability for an individual, social

alliance, or group to defend these items (Wrangham 1980, Janson 1988), Isbell's (1991) review of feeding competition in twenty different primate species found that multiple variables can affect agonistic relationships between and within primate groups. Isbell (1991) found that between-group feeding competition is shaped most often by total food abundance, while food distribution within a home range strongly shapes within-group competition. Isbell (1991) also noted that species which feed on multiple types of food items may increase consumption of dispersed food items in order to reduce foraging competition over preferred food items. In a recent review of primate group formation and foraging competition, Overdorff and Praga (2007) stress that foraging competition itself is a flexible behaviour and varies as the availability and distribution of resources changes over time and space.

The introduction of new variables has revealed the complexity of studying feeding competition. Pruettz and Isbell (2000) have suggested that food handling time and site-depletion time are important in understand how individuals compete for food. The authors' comparison of two groups of vervet monkeys (*Cercopithecus aethiops*) in differing habitats showed that the group which predominantly fed on large food items in large patches which were depleted slowly experienced a high rate of foraging agonism. The neighbouring group which overwhelmingly fed on small food items located in small patches which were quickly depleted experienced significantly lower levels of feeding agonism. Further study of feeding competition led Isbell (2001) to propose that food item size and the distance between food items were important indicators of the level of foraging competition in primates.

Finally, Isbell (2004) proposed that the ability for females to disperse from their natal group may be the most important factor in group formation, and the type of dispersal then affects the type of feeding competition a group experiences. Isbell (2004) theorized that mothers should allow their daughters to remain in natal groups if the cost of female dispersal, specifically predation and harassment by females in neighbouring groups, is higher than the cost of increased competition for resources. Females who live in groups which are able to increase their home range as group size increases, even by overlapping home ranges with neighbouring conspecific groups, are most likely to increase resource availability and facilitate the formation of female kin-based social groups (Isbell 2004).

Almost all primates experience feeding competition, and the investigating of how and if competition differs in a single species between habitats may aid in understanding which ecological variables influence the rate of intra-group feeding competition. These ecological variables include the size of food items, the size of food patches, inter-individual spacing while feeding, and the total availability of food resources within a home range. Moreover, the study of feeding competition during a dry season will add to the knowledge of feeding competition during times of low resource abundance.

PREDATION PRESSURE AS AN INFLUENCE ON PRIMATE GROUP FORMATION

The socioecological model produced by Wrangham (1980) did not consider predation as an important variable of social organization, yet other early models of primate group formation cited predation pressure as a key factor in the formation and maintenance of primate social groups (Anderson 1974, van Schiak 1983, van Schiak

1989). Alexander (1974) argued that the ultimate cost of group formation is within-group feeding competition, but this cost is outweighed by the benefits of decreased predation pressure through increased anti-predator vigilance and group dilution. van Schaik (1983) suggested that resource defense and predation pressure are equally important variables in group formation. Later, van Schaik (1989) suggested that predation pressure not only influences the size of groups but also the type of social organization and the amount of feeding competition within the group. Primate groups which experience high levels of predation pressure are more likely to live in highly cohesive groups and compete for food resources with members of the same group at a higher rate than primate groups which experience low predation pressure. Groups which experience low levels of predation pressure are more likely to form egalitarian social groups because of the ability to increase group spread, and therefore, decrease the amount of agonism over food (van Schaik 1989). Isbell (2004), however, has noted that several primate species, including *Eurythrocebus patas* and *Cercopithecus mitis*, have low levels of foraging competition and high levels of predation pressure, yet still form female-based social groups. Thus, Isbell (2004) suggests that food distribution and abundance, not predation pressure, are the main determinates of feeding competition.

Negotiating the impact of foraging competition and predation pressure on primate group formation has proven to be quite complex, yet it is undeniable that predation plays a significant role in the behaviour of most primates. A recent survey of reports on predation of primates shows that multiple species of prosimians, small and medium-sized new world primates, terrestrial and arboreal old world monkeys, and even large-bodied apes experience some form of predation risk (Miller and Treves 2007). Species which

experience potential predation have evolved anti-predator behaviours specific to their potential predators, including vocal warnings (Cheney and Seyfarth 1990, Chapman et al. 1990, Zuberbuehler et al. 1999, Gould and Sauther 2007b), mobbing behaviour (Cowlshaw 1994, Stanford 1995 and 2002), hiding (Gleason and Norconk 2002), and cryptic locomotion (Nekaris et al. 2007).

While observations of predator/prey interactions have been vital in understanding anti-predator behaviour (Cheney and Wrangham 1987), primatologists have recently noted that relying on the observation of predator/prey interactions is not sufficient in understanding the affects predation on the behaviour of primates (Janson 1998, Hill and Dunbar 1998). More specifically, the inability to adequately calculate predation *rate* (the number of deaths caused by a predation attack over a specific period of time) on primate populations makes it an ineffective means of understanding primate behaviour in relation to predation pressure (Janson 1998, Hill and Dunbar 1998). There are several reasons why it is difficult to determine the predation rate in primate populations. The chance of a researcher observing an interaction between predator and prey (either successful or non-successful) is slight (Cheney and Wrangham 1987). Isbell (1994) has also noted that the presence of researchers may deter predators from attacking primates. Furthermore, many accounts of predation are based on indirect evidence, such as assuming that individuals suddenly missing from a group have been killed by a predator or by discovering primate remains in or around prey habitation areas (Miller and Treves 2007). Finally, studies which follow the behaviour of predators are rarely accounted for in reports of primate predation rates (Janson 1998).

Recently, researchers have discussed the need to investigate primate anti-predator behaviour in terms of predation *risk*, which seeks to understand a primate's perception of the chance of being taken by a predator (Hill and Dunbar 1998, Janson 1998, Miller 2002). Janson (1998) states that there is an intrinsic predation risk for all primates which occupy home ranges with potential predators, but the level of risk may change over time and space depending on the level of attacks mounted by predators over a long period of time. Hill and Dunbar (1998) have emphasized that predation risk can be seen as the primate's perception of the likelihood of encountering a predator. This perception is likely to manifest itself in primate anti-predator behaviour, especially vigilance (Hill and Dunbar 1998). Furthermore, perceptions of predation risk most likely involve historical accounts of past predation attempts and present ecological variables, such as canopy cover, refuge availability, detection ability, and the presence of neighbouring primate populations within sight and/or acoustic accessibility (Hill and Dunbar 1998).

The study of predation risk necessitates that researchers collect data on variables other than a primate's response to a successful or unsuccessful predation attempt. Primatologists have studied how differences in habitat structure (Cowlshaw 1997b, Boinski et al. 2003), microhabitat use (Isbell and Enstam 2004), grouping and movement patterns (Boinski et al. 2000, Sauther 2002), foraging tactics (Cowlshaw 1997a, Di Fiore 2002, Treves 2002, Miller 2002), and behavioural context (Cords 1995) influence anti-predator vigilance behaviour.

Recent research on anti-predator behaviour has focused on several variables which possibly lead to differences in predation risk both within and between primate populations. Biological variables, mostly mediated by genetic factors, seem to have a

major influence on predation risk both within and between species. Body size may affect susceptibility to predators of various sizes (Lima and Dill 1990, Overdorff et al. 2002, Sterck 2002), while differing levels of color vision between dichromats and trichromats may affect the ability to spot predators whose colors either stand out against green backgrounds or blend in to the surrounding foliage via camouflage (Caine 2002). Social variables have also accounted for differences in anti-predator behaviour between groups. The most studied social variable is group size. Larger groups are predicted to be less vulnerable than smaller groups (Hamilton 1971, van Schaik and van Noordwijk 1989, Isbell 1994, Miller 2002, Sauther 2002), as increased numbers of individuals within a group enhances group vigilance and dilutes the chances of each individual being taken by a predator. Alternatively, Anderson (1986) found a positive linear relationship between predation rate and group size, while predation risk has also been theorized to increase with primate group size (Dunbar 1988, Hill and Lee 1998). Other studies have found that group composition (Rose and Fedigan 1995, Van Schaik and van Noordwijk 1989), total group size (Isbell and Young 1993, Sauther 2002, Overdorff et al. 2002), and social monitoring within the group (Hirsch 2002) can influence predation risk and anti-predator vigilance behaviour.

Studies of primate anti-predator behaviour have also focused upon how primates alter anti-predator behaviour to proximate ecological variables between both time and space. The predominant ecological variable considered in studies of anti-predator behaviour is the amount of canopy cover provided to a primate group. Areas with heavy vegetation cover tend to provide greater protection against potential predators than do open areas with little cover, and a difference in vegetation cover may lead to differences

in anti-predator vigilance rates between habitat structure (Hill and Cowlshaw 2002, Boinski et al. 2003). However, it has also been argued that animals will exhibit more anti-predator vigilance behaviours when heavy vegetation impedes visibility (Lima and Dill 1990, Goldsmith 1990). Varying vegetation cover may also expose a group of primates to varying modes of predation (i.e. aerial or terrestrial), and primates may change behavioural patterns between ecological conditions to decrease vulnerability posed by specific predators (Miller 2002). Thus, primates that occupy a varying range of habitats, both within and between groups, are likely to alter anti-predator behaviours based on the changing risk of predation between habitat types. Moreover, a single primate species which occupies several habitat types may experience varying levels predation risk, and thus, provides ample opportunity to test predictions of how ecological factors affect anti-predator vigilance behaviour.

Investigators of primate anti-predator behaviour have recently expanded the scope of their studies to include non-vigilance behaviours; specifically, recent studies have focused on how predation risk influences foraging behaviour (see Miller 2002 for review). Foraging is believed to be a relatively risky behaviour, as hand-eye coordination while feeding may distract an individual from potential predators (Cords 1995). Furthermore, food items may be located in exposed, high predation risk areas (Cowlshaw 1997a). Instead of forgoing foraging when predation risk is high, primates must engage in behavioural tactics which simultaneously allow them to forage efficiently while decreasing the chance of being preyed upon (Miller 2002). The study of these foraging tactics has been described as predator sensitive foraging (Miller 2002) or 'threat sensitive foraging' (Helfman 1989).

Studies have shown that primates use predator sensitive foraging tactics in several ways. Primates tend to respond to high-risk foraging areas with appropriate predator-sensitive behaviours. For example, primates which experience risk from terrestrial predators may decrease time spent feeding while on the ground (Lima and Dill 1990, Cowlshaw 1997a, Treves 2002, Cowlshaw and Hill 2002), while primates which experience high levels of predation risk from aerial predators may forage away from the periphery of trees and closer to the central areas of trees or in areas with high-vegetation coverage (Sauther 2002, Sterck 2002, Overdorff et al. 2002, Boinski et al. 2002). Individuals may also choose to forage in greater proximity to neighbours when predation risk is high, as increased proximity to a neighbour may increase the recognition of social cues indicating the presence of predators (Hirsch 2002) and decrease the chances of being taken by a potential predator (Hamilton 1971, Lima and Dill 1990, Treves 1999, Hill and Cowlshaw 2002, Sauther 2002). Finally, primates which experience high levels of predation risk may choose to forage with other primate species which are sensitive to similar predators (Terborgh 1983, Sauther 2002, Garber and Bicca-Marques 2002). Few studies have examined how ecological differences affect primate predator sensitive foraging tactics between conspecific groups (see Hill and Cowlshaw 2002). Studies of this nature will add to the growing body of work on how primates adjust their behaviours to varying ecological patterns and levels of predation risk.

THE INFLUENCE OF AFFILIATIVE BEHAVIOUR

Affiliative behaviour has also been recognized as a key attribute of primate sociality (Smuts 1985, Gould 1992, Gould 1996a, Gould 1997a, Dugatkin 1997, Silk

2002, Sussman and Garber 2004, Fuentes 2004). Early models of primate affiliative behaviour were centered on affiliative behaviour between kin (Hamilton 1964, Wrangham 1980, van Schaik 1983, Silk et al. 1999, Nakamichi and Shizawa 2003). Kin-biased affiliative behaviour theories were based on the concept that individuals are more likely to aid related individuals when defending food items and home ranges. Additionally, affiliative behaviour, including post-agonism grooming and reconciliation, has been suggested as a mechanism to reinforce social bonds after agonistic encounters. Bernstein (2002) argues that because conflict and competition tend to be present in all primate social groups, the management of aggression via affiliative interactions is vital to limiting the potential damage caused by conflict and increasing the chances of group defense of ecological resources. de Waal (2000) has proposed that the proximal benefits of primate affiliation and cooperation are based on the amelioration of the physiological and psychological stress which occurs during and directly after agonistic events.

Recent propositions of the benefits of sociality suggest that affiliative behaviour may not be a direct response to agonistic behaviour but instead may be the key driving force in primate sociality. Sussman and Garber (2004) argue that primate group formation evolved through means of affiliation and group solidarity and that agonistic behaviour is an eventual by-product of group living. While related individuals in certain species tend to exhibit the highest levels of affiliative behaviour towards one another, affiliative bonds also commonly occur between unrelated individuals (Smuts 1985, Gould 1997b, Cords 2002, Silk 2002). Moreover, Pazol and Cords (2005) have stressed that investigations of primate ecology and behaviour should look past ecological variables as a deterministic force on competition and should more often pay closer attention to all behavioural

strategies used by individuals, especially affiliative behaviour, in understanding primate sociality. Many affiliative behaviours appear to be beneficial for all individuals involved. For example, alloparenting, where non-mothers care for infants, benefits the infant, who engages with members of the social group, the non-mother, who gains important experience handling and caring for infants (or in the case of males, increases the survivability of related infants or gains future reproductive opportunities), and mothers, who gain important time away from their infants for feeding and socializing with other group members (Nicholson 1987, Gould 1990, Tardif et al. 1993). Grooming between partners increases social bonds, which may be useful when individuals need to form coalitions (Cords 2002), aids in the removal of potentially harmful parasites (Tanaka and Takefushi 1993), and potentially decreases stress (Kikusui et al. 2006).

Whether serving as the key core to primate sociality or the by-product of unavoidable competition, affiliative behaviour is a key attribute of primate sociality. A comparative study of the amount and types of affiliative behaviours between groups living in different habitat types may provide insight into how affiliative interactions are incorporated into the lives of primates facing varying ecological challenges. Potential differences in activity budgets may increase or decrease the amount of time an individual can afford to engage in affiliative behaviours (Whiten et al. 1987, Dunbar 1992). Differences in predation risk may require individuals to engage in affiliative behaviour more or less often to decrease their chances of being taken by a predator (Gould 1997a).

MADAGASCAR AND LEMUR EVOLUTION

Madagascar, a 587,045 km² island off the eastern coast of Africa, is one of the most biologically diverse locals in the world (Mittermeier et al. 2003). It separated from

the coast of mainland Africa approximately 165 million years ago and from the landmass of present day India eighty-eight million years ago (Yoder et al. 2003). During this period of isolation, mammals evolved in diverse habitats and relatively-open niches throughout the island. Because of such a long period of relative isolation in these diverse ecosystems, the flora and fauna of Madagascar have emerged as one of the most diverse radiations on earth, some of which only recently discovered by scientists (Sussman 2002).

Almost all of the fauna is endemic to the island, and there is no other place in the world with the same amount of species richness and endemism (Goodman et al. 2003). It is suggested that fauna colonized Madagascar by rafting on or swimming from small islands of vegetation, and these species then radiated into the various habitats on the island (Goodman et al. 2003, Yoder 2003, Tattersall 2006). One of the most well represented groups of mammals endemic to Madagascar are the lemurs. Currently, there are five taxonomic families, fourteen genera, fifty-three species, and sixty-four taxa of lemur, all of which are endemic to Madagascar (Ganzhorn, et al. 1999, Mittermeier et al. 2003). Yoder (2003) suggests that all extant species have evolved from one common ancestor, although Tattersall (2004) argues that lemuriformes may have colonized Madagascar in multiple waves. Lemurs range in size, from the pygmy mouse lemur (*Microcebus murinus*), which weighs 30g, to the indri (*Indri indri*), which can weigh up to 6.3 kg (Ganzhorn et al. 1999). Extant lemur species live in marshland, dry deciduous, wet evergreen, riverine, dry spiny forests, and at one site, in tundra-like, high elevation conditions above the tree line at Andringitra Massif (Goodman and Langrand 1996, Ganzhorn et al. 1999). When compared to the earth's other continents, the diversity of

Madagascar's primates is striking. Of all countries, only Brazil and Indonesia contain more primate taxa. In size comparison, Madagascar is only seven percent the size of Brazil and twenty-five percent the size of Indonesia, yet Madagascar's primate diversity rivals both of those countries. In total, Madagascar is home to ten percent of all primate taxa, sixteen percent of all species, twenty-one percent of all genera, and thirty percent of all primate families (Mittermeier et al. 2003).

A key factor in the radiation and speciation of lemurs over time was the diversity of habitats into which they radiated and the lack of large mammals competing for the same niches (Ganzhorn et al. 1999). While many lemur species evolved in different niches within the eastern and northern rainforests, fewer species were able to adapt to the dry habitats of south and southwest Madagascar, most likely due to the low density of food resources (Ganzhorn et al. 1999, Sussman 2002). Much of southern Madagascar is composed of dry spiny forests, which spread throughout the island after it broke off from present-day Africa (Wells 2003). As the island drifted north of the high-pressure desert belt at 30° S, humid forests spread in the north, leaving southern Madagascar as one of the only dry habitats on the island (Wells 2003).

One species which evolved in this unusually dry habitat in southern Madagascar was the ring-tailed lemur, *Lemur catta* (Tattersall 1982, Ganzhorn et al. 1999, Goodman et al. 2006). Most intensive studies of *L. catta* have been conducted in lush gallery forests bordering riverbeds (see, for example, Jolly 1966, Sussman 1974, Budnitz and Danis 1975, Bunditz 1978, Mertl-Millhollen et al. 1979, Gould 1990, Sauther 1992, Gould 1996a, Sauther 1998, Gould et al. 1999, Koyama et al. 2001, Sauther 2002, Jolly et al. 2002, Gould et al. 2003, Pride 2005a, Pride 2005b, Soma 2006), leading many

behavioural and ecological models of *L. catta* evolution to be centered on these ecological parameters. Over the past few years, however, increased population and distribution surveys have shown that *L. catta* groups are widely distributed in a plethora of habitats (Sussman et al. 2003, Goodman et al. 2006, Gould 2006). It has been suggested that *L. catta* show many behavioural and physiological traits which may suggest it evolved in dry habitats. *L. catta* live in more non-forested habitats than any other lemur (Goodman et al. 2006, Sussman et al. 2006, Gould and Sauther 2007a), spend the least amount of time in the trees, and have evolved feet shaped to endure terrestrial ranging patterns (Jolly 1966, Sussman 1974, Goodman et al. 2006, Gould and Sauther 2007a). Moreover, *L. catta* are able to live in areas without groundwater and with few water-based food parts (Goodman et al. 2006), although they are found in smaller populations in these areas than *L. catta* in riverine gallery forests (Goodman and Langrand 1996, Sussman et al. 2003). *L. catta* are characterized as “weed” species because of their ability to live in harsh environments with extremes of heat and frost, exploit a variety of high and low quality food items, ultimately survive periods of intense water scarcity, and the ability for populations to rebound from decreased habitat productivity relatively quickly (Gould et al. 1999, Goodman et al. 2006).

It is the relative lack of resources in these dry habitats which most likely had a direct impact on the evolution of *L. catta* social organization and behaviour. Female *L. catta* are socially dominant to males, and female hierarchies form the foundation of access to high quality food items, which are scarce during the dry season and help to ensure successful reproductive success (Jolly 1966, Jolly 1984, Sauther 1993, Sauther 1998). *L. catta* live in multi-male/multi-female and female philopatric social groups

(Jolly 1966, Sussman 1991). Female philopatric social organization most likely evolved because of a need for related females to defend high quality resource items from other conspecific groups (Jolly 1966, Budnitz 1978, Jolly 1984, Sauther and Sussman 1993, Sauther 1998). Males emigrate from natal groups to look for mates, while females remain in natal groups and form strict dominance hierarchies (Jolly 1966, Koyama et al. 2001, Gould et al. 2003).

THE NATURAL HISTORY OF *LEMUR CATT*A

Ring-tailed lemurs are the only species in the genus *Lemur* and form a phylogenetic clade with the genus *Hapalemur* (Yoder 2003, Delperio et al. 2006). This species is so named because of the black and white rings found on the tails of both males and females. Males and females are monochromic and display white faces, a black crown, black muzzles, and black patches around the eyes (Jolly 1966). Males and females exhibit no sexual dimorphism in body weight, although males tend to have larger upper canine teeth (Kappeler 1996). On average, adults weight 2.2-2.4 kg (Sussman 1991, Ganzhorn et al. 1999, Gould et al. 2003).

Distribution and habitat

Lemur catta are highly adaptable and currently range in several habitat types throughout south and southwest Madagascar (Sussman et al. 2003, Goodman et al. 2006, Sussman et al. 2006, Gould 2006). Groups have been observed in riverine gallery forests (Jolly 1966, Sussman 1974, Sussman 1977, Sauther 1994, Nakamichi and Koyama 1997, Sauther 1998, Jolly et al. 2002, Sussman et al. 2003, Gould et al. 2003), spiny forests

(Sussman et al. 2003), mountainous zones (Goodman and Langrand 1996, Goodman and Rasolonandrasana 2001, Goodman et al. 2006), limestone forests (Sussman et al. 2003), and in areas with anthropomorphic crop production and *Opuntia* fields (Gould 2006). While population density is highest in gallery forests (Sussman et al. 2003), *L. catta* exist in lower-density populations as far north as the Parc National de Kirindy-Mitea, which is characterized by dry forests with associated ecological elements similar to the spiny forests of the south (Goodman et al. 2006). Goodman et al. (2006) suggest that the northern distribution is highly associated with the plant family of Didiereaceae, a taxonomic family found in scrub/spiny forests in Madagascar. The eastern-most distribution of *L. catta* populations is associated with the end of dry deciduous forests and the beginning of eastern humid forests (Goodman et al. 2006). It is able to survive in habitats with extreme ecological variability and a lack of drinking water, which they overcome by consuming water-retaining, dry-adapted succulent desert plants. Because of these ecological characteristics, *L. catta* most likely evolved in dry ecological niches and dispersed into highland areas relatively recently while also taking advantage of gallery forest areas which fall into its extended range (Goodman et al. 2006).

Population densities are highly variable according to rainfall, food availability, and habitat type (Gould et al. 1999, Sussman et al. 2003, Pride 2006). For example, population density can range from 600/km² in areas with introduced fruit trees and a constant supply of water, 250/km² in naturally occurring gallery forests, and less than 100/km² in the scrub and spiny forest at Berenty Reserve (Jolly et al. 2002, Pride 2005a).

Territory use and sympatry

Pride (2003) has shown that territory use by *Lemur catta* is related to food availability, group size, and total population in a forested area. *L. catta* tend to expand home ranges during times of resource scarcity (Gould and Sussman 2001, Jolly et al. 2006b). *L. catta* tend to more often defend resources and win inter-group confrontations while within the group's home range (Jolly et al. 2006b). *L. catta* can use both arboreal and terrestrial niches, and depending upon the month and season, groups may spend between seven and seventy-five percent of the time on the ground (Sussman 1974, Sauther 2002). At Berenty reserve, *L. catta* groups share gallery forest habitats with two other lemur species: *Propithecus verreauxi* (Jolly 1996, Bunditz 1978, Howarth et al. 1986, Simmen et al. 2003) and *Eulemur fulvus* (Jolly et al. 2002, Pinkus et al. 2006). Although *P. verreauxi* are naturally occurring at Berenty, *Eulemur* were introduced in the 1970s (see Jolly 2004). *Eulemur* and *Lemur* overlap in diet and canopy use throughout gallery forests (Sussman 1974, Simmen et al. 2003, Pinkus et al. 2006). In the gallery forest of Berenty Reserve, the two species share eighteen different species of food items (Simmen et al. 2003), but both species can use different habitat niches, theoretically decreasing some resource competition (Simmen et al. 2003). However, *Eulemur fulvus* often displace *L. catta* and have begun pushing *L. catta* groups out of gallery forest habitats in recent years (Jolly pers. comm.), causing more *L. catta* to occupy scrub/spiny forests at the edges of the reserve. *L. catta* share fewer food items with *Propithecus verreauxi* at Berenty Reserve (Simmen et al. 2003) and at Beza Mahafaly Reserve (Yamashita 2002).

Population structure, Group fission, and territory defense

It is theorized that primate groups will increase in size until competition for resources becomes too great, and when maximum carrying capacity is reached, the population will fission into two groups (Wrangham 1980). The *Lemur catta* population at Berenty reserve has almost tripled since 1985 (Jolly et al. 2002). With this population increase, the number of groups has increased from 12 to 33 (Jolly and Pride 1999). Groups only ranged in gallery and open deciduous forests until recently, but as the population has increased, fissioned groups have moved into scrub and spiny forest habitats (Jolly and Pride 1999, Koyama et al. 2001, Ichino 2006).

Atypically large groups experience increased within-group competition compared with relatively normal sized groups, while atypically small groups may also experience more stress because of increased encroachment from neighbouring groups (Pride 2005a). Intense intra-group aggression has been described as targeted agonism (Hood and Jolly 1995, Ichino 2006), and when large groups split, individuals in the newly-formed smaller group are more likely to be the target of aggression from individuals in the larger group (Hood and Jolly 1995). Small groups tend to defend specific resources while larger groups defend a broader range (Hood and Jolly 1995). When inter-group aggression occurs, the group which defends its base territory is more likely to win the encounter (Pride 2005c, Jolly et al. 2006b). During times of low resource availability, groups at Berenty Reserve may not be able to keep neighbouring conspecific groups out of their range (Pride 2005c). Groups living in high quality ranges are more likely to experience inter-group encounters than those in ecologically scarce ranges, most likely because of the greater population density in high quality habitats (Pride 2005c). Ichino (2006) found

that *L. catta* groups fissioned along matrilineal lines, as the ejected mother and daughter were later joined by related females and non-related males.

Social Organization

L. catta form multi-male/multi-female social groups (Jolly 1966, Sussman 1974, Budnitz 1978, Mertl-Millhollen et al. 1979, Sussman 1991). There is no report of variation in this type of social organization. Operational sex ratio is usually close to 1:1 (Koyama et al. 2001, Jolly et al. 2002, Gould et al. 2003). A recent report of *L. catta* at Berenty Reserve shows that groups range in size from nine to twenty-six individuals (Pride 2005a). Groups size may reach as low as three adult individuals at Beza Mahafaly Special Reserve (Gould et al. 2003), and recently, researchers have observed *L. catta* groups at Berenty Reserve that have less than seven or fewer adult and juvenile members (Gould pers. comm.). Groups are female philopatric, with males immigrating from their natal groups close to sexual maturity (Jolly 1966, Jones 1983). Females almost always remain in their natal groups for their entire lives, but groups may fission as group size becomes closer to twenty non-infants (Hood and Jolly 1995, Gould and Sussman 2001, Jolly et al. 2002, Gould et al. 2003). *L. catta*, like many other species of Lemuriformes, exhibit female dominance over males (Jolly 1966, Jolly 1984, Sauther 1993, Wright 1999). Jolly (1984) states that *L. catta* show the most extreme form of female dominance, with females having been observed charging, cuffing, and biting males who eat preferred food items. These observations have been corroborated by all other studies of *L. catta* social behaviour (Sauther 1993, Gould 1996a, Nakamichi and Koyama 1997, Sauther 1998, Gould 1999).

Jolly (1984) and Wright (1999) suggest that female dominance evolved in *L. catta* as a response to intense resource seasonality and female reproductive biology. *L. catta* evolved in low resource seasonal habitats and are synchronic breeders with a period of gestation, birth, and lactation coinciding with the dry season. These three reproductive processes require a high amount of caloric intake for female primates (see Lambert 2007). Female *L. catta* have adapted to seasonal resource scarcity by gaining feeding priority over males in order to have access to greater quality and quantity of food items (Jolly 1984, Sauther 1993, Wright 1999). This form of dominance allows females to gain enough energy for successful reproduction (Jolly 1984, Wright 1999). Preferred food items contain more calories, calcium, and nutrients which increase the chances of infant survival. Such environmental pressures have also created a strict dominance hierarchy between females (Jolly 1966, Nakamichi and Koyama 1997, Wright 1999). Males, however, do not show strict dominance hierarchies over a long period of time, most likely because of the frequency of inter-group male migration (Gould 1997b).

Diet

L. catta is a frugivore/folivore and prefers to feed on ripe fruit, new leaves, and flowers (Sauther 1998). It is also known to eat insects and even chameleons (Jolly 2003). The fruit of *Tamarindus indicus* is their most preferred food item in the gallery forest habitat (Sauther 1998) and has been found to make up as much as 70% of all food items eaten in this habitat (Mertl-Millhollen et al. 2003). As seasons change, *L. catta* change their home ranges and day ranges in order to find food items with a higher nutritional content (Sauther 1998, Mertl-Millhollen et al. 2003). It has been found that individuals in

gallery forests at Berenty Reserve exploit food items with the highest amount of water, protein, and calories (Mertl-Millhollen et al. 2003). Vegetation availability, and thus diet, fluctuates between seasons. The availability of young leaves and fruit are correlated with rainfall, which also correlates with the period of infant weaning (Sauther 1998). During dry seasons, foods which *L. catta* eat are high in tannins, which decrease the ability for primates to digest nutrients (Simmien et al. 2003). *L. catta* groups are also able to exploit low quality foods. The diet of *L. catta* populations in high-altitude regions are composed of the leaf tips of succulent plants, flowers, young fronds, young leaves, herbs, tubers, and seeds (Goodman and Langrand 1996). These food items are believed to be lower in water and nutritional value than foods found in gallery forests (Goodman and Langrand 1996), although no data analysis on nutritional content of these food items at this location has taken place. *Lemur catta* in gallery forests at Berenty Reserve have also been found to feed on introduced fruits and flowers of the genera *Leucaena*, *Cordia*, *Azadirachta*, and *Pithecellobium* during dry seasons, which may buffer the effects of food scarcity and lead to population growth (Soma 2004, 2006).

Social Behaviour

Reproduction

Lemur catta are seasonal breeders (Jolly 1966, Jolly 1984, Sauther 1991, Sauther and Sussman 1993). This reproductive strategy is related to Madagascar's resource seasonality (Jolly 1966, Jolly 1984, Sauther 1991, Sauther and Sussman 1993, Wright 1999). Infants are almost completely weaned from their mothers' milk at sixteen weeks after birth (Gould 1990) and are approximately two months old when food availability is

at its highest (Sauther 1998). This synchronic weaning period allows infants to intake the maximum amount of nutrients during normal phenological conditions. Females at Beza Mahafaly Reserve first give birth between the age of three and four years old (see Gould et al. 2003), although two year old females residing in areas with introduced fruit trees and occasional provisioning by humans at Berenty Reserve have been observed giving birth at lower rates (Koyama et al. 2001). Three year old females successfully give birth significantly more often than do two year old females (Koyama et al. 2001). Females rarely give birth for the first time after the age of five, and birth rates and infant survival rates tend to increase with the age of the female (Koyama et al. 2001, Gould et al. 2003). Infant mortality rates also fluctuate between sites. For example, over a span of fifteen years at Beza Mahafaly Reserve, only fifty percent of infants survived to the age of one, but severe drought in a two year period led to infant mortality rates of eighty percent (Gould et al. 1999, Gould et al. 2003). Infant mortality has been documented at thirty-eight percent as a mean over a ten year period at Berenty Reserve, but annual infant survival rate fluctuates with available food and water (Koyama et al. 2001, Jolly et al. 2002). Birth and survival rate does not correspond directly to water availability but instead is more closely related to food, primarily fruit, availability (Gould et al. 1999, Koyama et al. 2001).

Anti-predator behaviour

Ring-tailed lemurs experience predator pressure from both terrestrial and aerial predators (Sauther 1989, Gould 1996a, Sauther 2002, Goodman 2003b, Gould and Sauther 2007b). Although the high rate of predator responses has been suggested to be a

vestigial behaviour relating to very large extinct raptors (Goodman 1994), extant predators can pose very real threats. Madagascar harrier hawks, buzzards, civets, and feral cats and dogs have been cited as potential predators (Sauther 1989, Gould 1996a, Sauther 2002, Goodman 2003b). *Lemur catta* groups respond to predators with vocalizations, movement into safe areas of trees, or even mobbing (Sauther 1989, Gould 1996a, Sauther 2002). Gould (1996a) observed that alpha females are most vigilant towards potential predators, but there are no differences in rates of anti-predator responses between males and females. Differences in anti-predator behaviour have also been found between *L. catta* groups of different size (Sauther 2002). Compared to larger groups, smaller groups spend significantly less time feeding on the ground during times of high predation pressure. Smaller groups stay closer together than larger groups when entering new high-risk foraging areas (Sauther 2002). These data parallel other studies (Cowlshaw 1997a 1997b, Miller 2002, Overdorff et al. 2002) which show that groups may reduce their use of open spaces when the risk of predation is high. This study will be the first to present data on the rates of vigilance in *L. catta* between habitat types.

Affiliative behaviour

Affiliative behaviour occurs between all individuals in *L. catta* groups (Gould 1994, 1996b, 1997a, 1997b) and occurs more often between related individuals than between non-related individuals (Nakamichi and Koyama, 1997). All individuals partake in alloparenting behaviour, where individuals other than the mother provide care for an infant (Gould 1992). In groups found in gallery forests, mothers with infants have been found to have the highest rate of alloparenting behaviour, followed by young females and

adults without infants (Gould 1992). There have been no studies of *L. catta* alloparenting behaviour across habitat type or group size. Males and females engage in affiliative behaviour together, and preferred social partners have been observed at times (Gould 1996b). In groups with fewer males, males tend to have higher frequencies of affiliative relationships with females and stay in closer proximity to females (Gould 1996b, Sauther 2002). These affiliative behaviours allow males to stay closer to the center of the group, which may increase protection from potential predators, especially in open habitats (Gould 1996b). Males also frequently interact with immature individuals for the same reason (Gould 1997a). Males have affiliative relationships with other males, although they were found to be short-term, rarely lasting over a 12 month period. Males engage in affiliative behaviours with other males most often during lactation periods (Gould 1997b).

There have been no comparative studies of affiliative behaviour in *L. catta* between habitat types.

Agonistic behaviour

As *Lemur catta* groups live in habitats which experience great seasonal differences in resources, there is a high amount of inter- and intra-group resource competition (Jolly 1966, Sauther 1993, Sauther 1998). Agonistic encounters include chasing, cuffing, and displacement (Jolly 1966, Jolly 1984, Gould 1996b, Sauther 1993). Intra-group agonistic encounters occur most often over food items and during the dry season, especially while females are lactating (Sauther 1993, Wright 1999, Jolly et al. 2000). Inter-group aggression is more often directed by larger groups toward smaller

groups (Hood and Jolly 1995, Pride 2005). During inter-group encounters, high ranking females are more likely to lead the defense of home ranges (Jolly et al. 2001, Pride 2005a). Females direct agonistic behaviour toward inter-group and intra-group females during all seasons, but marked aggression occurs more often during lactation seasons just before the rainy season begins (Sauther 1993, Ichino 2006). Males direct agonistic behaviour towards all males during the female estrus periods and towards immigrant males as they attempt to enter groups throughout the year (Jones 1983, Nakamichi and Koyama 1997). Infant wounding and abandonment can result from these agonistic encounters (Hood and Jolly 1995, Jolly et al. 2000). Infants have been observed being killed and wounded by immigrant males, natal females, and resident males (Jolly et al. 2000).

SIGNIFICANCE OF RESEARCH

A study of *L. catta* behaviour in spiny forests, an ecologically sparse habitat, is an ideal research project for several reasons. The lack of data on *L. catta* in ecologically sparse habitats makes proposed models of the evolution of *L. catta* behaviour incomplete (Gould 2006). By collecting data on three major categories of behaviour in a habitat more closely related to that in which *L. catta* evolved may provide additional insights into the evolution of *L. catta* behaviour. Finally, comparisons of behaviour between groups in distinctly different habitats may provide a better understanding of behavioural plasticity in *L. catta*.

One of the best known field sites in which *L. catta* has been studied is Berenty Reserve in southern Madagascar (see for example, Jolly 1966, Budnitz 1978, Gould

1990, 1991; Hood and Jolly 1995, Jolly and Pride 1999, Jolly et al. 2002, Koyama et al. 2001, Pride 2003, Ichino 2006, Jolly et al. 2006a). This reserve contains several habitat types in which *L. catta* groups can be found. They have been intensively studied in riverine gallery forests, yet only one study has focused on *L. catta* in the open and dry scrub forest (Pride 2003, Pride 2005a, 2005b). No published reports have occurred in the spiny forest. Thus, I intend to compare the behaviour of a ring-tailed lemur group in a spiny forest habitat with that of one in a gallery forest habitat in Berenty Reserve, Madagascar, with the intention to investigate behavioural plasticity in *Lemur catta* and the behavioural patterns of *Lemur catta* in an ecologically sparse habitat.

HYPOTHESES

Activity budget between groups

If primates consider time as a limited resource when making decisions throughout the day (Dunbar 1992), we may expect the percentage of time spent in each behaviour to be a function of the percentage of time spent in all other behaviours. *L. catta* in gallery forests have been found to spend the majority of their activity budgets on self-maintenance behaviours, such as resting, sitting, feeding, and moving (Gould 1994). Most studies of primate activity budgets have found that almost all behaviours are self-maintenance behaviours (see Sussman and Garber 2004 for review), but the percentage of time spent in different behaviours may change with respect to various ecological and social conditions. For example, Chacma baboon groups (*Papio cynocephalus ursinus*) in ecologically scarce habitats spent more time foraging, less time socializing, and more time traveling (Whiten et al. 1987). However, there may be a cut-off point of time

appropriated for specific behaviours, which limits variation in activity budget because of equal need for rest and socializing (Whiten et al. 1987, Umapathy and Kumar 2000).

Alternatively, some primates which have diets based on low quality food items tend to increase their time spent resting and decrease their time spent traveling to minimize the energy expended during the day (Milton 1980). Rasamimanana et al. (2006) have described *L. catta* as energy minimalists, as energy expenditure decreases when potential energy in the environment is limited or when female *L. catta* must save energy for lactation and gestation. Thus, *L. catta* in the spiny forest are expected to decrease energy expenditure because of decreased possible energy intake available in the spiny forest.

Based on the existing literature on primate activity budgets in varying habitats, I predict that the *L. catta* group in the spiny forest group will differ from the *L. catta* in the gallery forest group in the following self-maintenance behaviours.

Hypothesis: *Individuals in spiny forest group will spend a greater proportion of time resting and sitting and a lower proportion of time feeding, foraging, traveling, and socializing when compared to individuals in gallery forests. Individuals in the spiny forest will spend a greater proportion of time resting and sitting in order to decrease the amount of energy expended during active hours.*

Vigilance behaviour

It has been argued that one of the main benefits of living in groups is increased predator protection (Alexander 1974, Van Schaik 1983). Sauther (2002) has found that *L. catta* change the rates and types of anti-predator behaviour between groups of different size. Smaller *L. catta* groups remain in close contact when entering new foraging areas

(Sauther 2002), which was also observed in other primates living in open habitats (Cowlshaw 1997a, Overdorff et al. 2002). Moreover, primates have shown the ability to change anti-predator behaviour as their habitat structure changes (Stanford 2002, Boinski et al. 2003, Enstam and Isbell 2004, Enstam 2007, Hill 2007). These studies have found that primates in open habitats are more sensitive to predators than groups in enclosed habitats. Thus, I predict that *Lemur catta* living in the more open spiny forest habitat will exhibit a higher rate of anti-predator vigilance than those living in the gallery forest, outlined in the following hypothesis.

Hypothesis: *Individuals living in the spiny forest habitat will exhibit a higher anti-predator vigilance rate than individuals in the closed gallery forest habitats.*

Hypothesis: *Individuals in the spiny forest will exhibit a higher proportion of anti-predator vigilance events while more than five meters from a nearest neighbour compared to individuals in the gallery forest.*

Hypothesis: *Individuals in the spiny forest will exhibit proportionally more predator vigilance events while on the ground and in the highest vertical levels of the canopy.*

Social Behaviour

Feeding Agonism

Intra-group agonism increases with increased foraging contest competition, and contest competition is expected to occur more often in habitats with clumped valuable resources (Wrangham 1980, Van Schaik 1989, Isbell 1991). Plant reproductive parts, including fruit and flowers, are considered to be energy-rich patchy resources, while leaves are predicted to be spread equally through a home range and lower in energy

content (Wrangham 1980). Moreover, decreased social spacing caused by patchy food resources may lead to increased instances of agonism (Hirsch 2007). Pruett and Isbell (2000) predict that there will be less agonism over small food items which are able to be eaten quickly and cannot be usurped when compared to large food items which take greater handling times and can be stolen by a higher-ranking individual. Thus, individuals living in the gallery forest, which is characterized by fruiting trees with large reproductive parts, should exhibit higher rates of feeding agonism than individuals in the spiny forest, which is characterized by smaller trees with smaller plant reproductive parts.

Hypothesis: *Individuals in gallery forest will exhibit higher rates of intra-group agonistic behaviour compared to individuals in the spiny forest.*

Affiliative behaviour

In a review by Sussman and Garber (2004), these authors found that the majority of primate social behaviour is spent in affiliative behaviour. Thus, I predict that patterns of total percentage of affiliative behaviour in *L. catta* groups will be correlated to the total percentage of time spent in social behaviour. *L. catta* may engage in affiliative behaviour to gain access to the center of a group (Gould 1996a, 1997a) and to decrease space between individuals to protect against inter-group aggression (Hood and Jolly 1995). Gould (1996b) suggests *L. catta* increase contact with conspecifics in order to decrease the chance of being taken by a predator. Thus, *L. catta* which experience a high risk of predation between groups will increase proximity behaviour with conspecifics to decrease the chances of being taken by a predator. If a group increases the time spent resting, there may be a coordinated increase in time spent engaged in affiliative

behaviours such as grooming and sitting in close contact. Time spent in alloparental behaviour should increase due to decreased nearest neighbour distances and heightened need to remain away from the periphery of the group (Gould 1996b). However, because time may be seen as a limited currency (Dunbar 1992), individuals have a limited amount of time to perform specific behaviours which are necessarily for immediate survival. Thus, primates may decrease the amount of time spent in social behaviour in lieu of self-maintenance behaviours. I predict that the proportion of time spent engaged in affiliative behaviours will be correlated with time spent in active behaviours, as outlined in the following hypothesis.

Hypothesis: *Individuals in the gallery forest group will spend a greater proportion of time in affiliative behaviours, such as alloparental care and allogrooming. This will occur because individuals in the spiny forest group will need to spend more time in self-maintenance behaviours, and thus, will have less time to perform affiliative behaviours.*

The next chapter of this thesis will be the research methods chapter. This chapter will describe the research site, methods used to select research subjects, behaviours which were recorded, the data collection methods, and the methods of data analysis. Finally, the research methods chapter will lay out the specific research questions involved, along with hypotheses and predictions which accompany each research question.

CHAPTER 2: METHODOLOGY

RESEARCH SITE: BERENTY RESERVE, MADAGASCAR

Data collection was conducted between September 4 and November 4, 2006. These dates correspond to the end of the dry season in southern Madagascar and to the late gestation and lactation seasons of *L. catta*. Research was carried out at Berenty Private Reserve in southern Madagascar, a 240 km² private ecotourism reserve located on the banks of the Mandare River (Jolly 1966, see Jolly et al. 2006a for review). The reserve is located at the coordinates S 25° 0.5' latitude, E 46° 18.5' longitude and is owned and managed by the de Heaulme family (Jolly 1966, Pride 2003, Jolly et al. 2006a).

The reserve is composed of several ecological zones: closed canopy gallery forest, scrub forest, spiny forest, and hotel plantation garden (Pride 2003, Blumenfeld-Jones et al. 2006). Berenty reserve is, in effect, a small stretch of gallery forest surrounded by open forest, scrub forest, and spiny forest (Pride 2003). The spiny forest of Berenty reserve is found on the Northwestern edge of the reserve. Most of the spiny forests which formerly bordered the reserve have been cleared and replaced by sisal fields, which were planted by French colonialists and used to fabricate rope export (Jolly 2004).

Berenty Reserve experiences seasonal variation in rainfall which is typical of southern Madagascar. Between 400-520mm of rain falls between the months of November and February, which is 70% of the annual rainfall (Pride 2003). The warmest months of the year are between December and February, while the coldest period occurs between July and August. Average temperature ranges from 9° to 33° C. Temperatures may be as high as 50°C during the hot season (Jolly 1966). During this study, daily

temperatures reached between 40^o C and 45^o C during the middle of the day in the spiny forest, while temperatures in the gallery forest were less than five degrees lower.

Data were collected on *L. catta* groups in three separate ecological zones: gallery forest, scrub forest, and spiny forest. The gallery forest, known as “Ankoba”, contained the lemur group which I called “gallery forest group”. The Ankoba forest is a secondary forest which contains both native and introduced plant species. It was cleared by native Tandroy villagers and the reserve owners for crops more than sixty years ago but was quickly abandoned because of infertile soils (Jolly et al. 2006a). Along with native *Tamarindus indica* trees, this forest also contains introduced trees such as *Pithecellobium dulce*, *Azadirachta indica*, and *Leucaena leucocephala* (Soma 2006). Ankoba forest is now a fully mature secondary growth forest with a canopy height of 10-15 meters. The forest borders the Mandare River, which provides ample groundwater for large fruit trees. The river also provides drinking water for *L. catta* groups, even in the middle of the dry season when only small puddles remain in the large riverbed. Along with introduced trees, Ankoba forest contains several other anthropogenic factors. One of the reserve’s main water wells is located in the middle of the forest along with small water troughs, both of which provide easily-accessible drinking water for *L. catta* groups. Several reserve employees live in Ankoba forest and maintain large foot-paths. Finally, Ankoba forest is an attraction for visiting tourists, although the tourists are no longer allowed to feed any lemurs. Finally, village fields with edible anthropogenic food sources are within range of Ankoba forest groups. The gallery forest group used in this study, however, was never observed outside of the forested area.

The second research group during the study will be referred to as the ‘spiny forest’ group. This group inhabited both the scrub and spiny forests of Berenty Reserve. Like the gallery forest, the scrub forest contains large *Tamarindus indica* trees which are supported by groundwater from the ancient bank of the Mandare riverbed. However, unlike gallery forests, the scrub forest does not contain any introduced trees and is highlighted by low-lying xeric vegetation and smaller trees, including the species *Quivisianthe papinae*, *Azima tetracantha*, and *Salvadora angustifolia* (Blumenfeld-Jones et al. 2006). The concentration of *Tamarindus indica* trees is considerably lower here than in the gallery forest. The canopy of the scrub forest is open, with less than fifty percent solar coverage. This differs from the structure of the gallery forest habitat, which is characterized by a canopy with greater than 50 percent solar coverage (Jolly et al. 2006a). Blumenfeld-Jones et al. (2006) argue that the scrub forest contains no true canopy. *Tamarindus indica* trees are farther apart from one another in the scrub forest than in the gallery forest, and *L. catta* in the scrub forest are rarely able to travel through their habitat via the canopy.

The transition from scrub forest into spiny forest is distinct. A nearly seven meter vertical hill segregates the scrub and spiny forests, but this hill does not prevent lemur groups from moving between forests. This seven meter hill was most likely the outer-edge of the Mandare River in the past, and thus, represents the end of the supply of groundwater which supports large fruiting trees. All plant species found in the spiny forest are endemic to this specific forest type and have evolved to survive in areas with low nutrient soils, high temperatures during the summers, and low amounts of rainfall (Grubb 2003, Fenn 2003). The forest is dominated by plant families Didiereaceae,

especially the Genus *Alluaudia*, which is characterized by tall yet slender trees with thorny trunks and branches, and *Euphorbia candelabra*, characterized by low-lying succulent vines (Grubb 2003). All trees have small and exposed canopies and are significantly shorter than trees in the gallery forest at Berenty. Soil in the spiny forest is considered to be dry, sandy, and low in macronutrients when compared to gallery forests, yet high in iron (Grubb 2003, Fenn 2005). Compared to the gallery forests, all spiny forest plants are highly exposed to the solar rays. *Alluaudia* trees have very few branches, which contributes to the lack of a true forest canopy. Because of such intense solar exposure, leaves of *Alluaudia* are small and succulent, which allows the tree to retain water during the dry season. *Alluaudia* trees also have thorns throughout the trunk to protect the leaves. Although canopy height was not measured, Grubb (2003) estimates almost all *Alluaudia* trees in south and southeast Madagascar are no taller than 6m in height. *Gyrocarpus* trees, which are shorter than the species within the Didiereaceae family, contain a small amount of branches forming a small canopy crown (Grubb 2003).

For the final four days of the study, the spiny forest group periodically moved into the surrounding sisal plantations to feed. The sisal plantations were planted by the reserve owners after clearing large tracks of endemic spiny forest (Jolly 2004). The sisal plantations at Berenty Reserve contain only *Agave sisalana* plants. These plants produce no canopy, which allows for no shade, and are highlighted by tall exposed stalks with flowers at the tip.

DATA COLLECTION

Materials

All data were collected by hand via pen and paper and entered into a notebook. Binoculars were used for observation and location of the study group when needed.

Group and Animal Selection

The initial days of the research season were focused on the selection and identification of a spiny forest group. Because groups in the spiny forest have not been systematically studied like those in the gallery forest, group selection and identification took multiple days. The initial study group was chosen because they were the first to be identified on a continual basis as a group which used the spiny forest everyday. Data were collected on the spiny/scrub forest group beginning on September 6th. As data collection of the first spiny forest group continued, it became apparent that the group was spending little time in the spiny forest. On September 25th, a new group which occupied the spiny forest for the majority of its daily activities was chosen as the new spiny forest group. On October 13th, the second spiny forest group relocated to a new section of the reserve and could not be found by multiple researchers studying them. After several days of searching, the original spiny forest group was chosen as the representative spiny forest group. On November 1st, the second spiny forest group was discovered and followed for three consecutive days. In this study, data were analyzed only on the second spiny forest group, as they spent the majority of the daylight hours in the spiny forest. Data collection on the gallery forest group was restricted to one group.

Because *L. catta* group size has been shown to influence both vigilance behaviour (Sauther 2002) and feeding agonism (Sauther 1993), I attempted to select groups with the same number of adult individuals. Because groups occupying the Berenty gallery forest

tend to be larger than scrub/spiny forest groups (Jolly et al. 2002, Pride 2003), the gallery group was chosen because it was the smallest gallery group which could be found.

Focal individuals were restricted to adult males and females. The gallery forest group contained seven adult individuals, while the first spiny forest group contained five adult individuals and the second spiny forest group contained six adult individuals. The study took place during the birth season, but infants were born at two different periods between groups. Four infants in the gallery forest group were born between the dates of September 12th-21st, with all four infants surviving through the study. Three infants were born in the second spiny forest group between September 30th and October 9th and two survived. As research has been conducted on *L. catta* in the gallery forest for 46 years (Jolly 1966), habituation of the gallery forest group was not necessary. Despite the fact that groups in the spiny/scrub forest have never been systematically studied, the groups were well habituated within a few days at the onset of the study.

Ethogram

An ethogram is a list and description of all potential behaviours recorded in a study. The ethogram used during this study included all behaviours deemed relevant to the thesis research (Table 2.1). The ethogram was adapted from Jolly (1966), Gould (1996a), and Gould (1996b).

Table 2.1. Behavioural ethogram. Ethogram was adapted from those used by Jolly (1966), Gould (1996a), and Gould (1996b).

Behaviour	Description	State or Event?
Time Allocation		
Feed	-When the focal individual placed a food item into the mouth and continued to chew.	State
Forage	-When the focal individual moved through a	

Drink	single feeding tree searching for food. This did not include movement between trees. -When the focal individual drank from a water source.	State
Self-groom	-When the individual groomed one's self with their tooth comb.	State
Rest/sleep	-When the individual put the head down and closed their eyes.	State
Sit	-When the individual sat with the head up and eyes open.	State
Locomotion	-When the focal individual moved between trees or on the ground in the environment.	State
Affiliative Behaviour		
Mutual groom	When two individuals simultaneously groomed one another.	State
One-way groom	When only one individual groomed a recipient.	State
Social play	When two or more individuals engaged in active play, especially chasing and 'rough and tumble play'	State
Sit near	When the focal individual sat within one meter of the nearest neighbour.	State
Sit in contact	When the focal individual sat while touching the nearest neighbour.	State
Mate with	When two individuals engaged in copulation	State
Agonistic Behaviour		
Stink fight	-When the focal animal rubbed the tail with scent glands and directed the tail towards the opposing individual with which the agonistic encounter is occurring.	Event
Slap	-When the focal animal hit the partner with their hand.	Event
Fight with	-When the focal animal was engaged in a long-term agonistic encounter their partner.	Event
Chase	-When the focal animal ran towards an evading agonism partner for more than three meters.	Event
Displace	-When the focal animal moved toward the agonism partner and occupied the direct location of that social partner. This was only scored when it was obvious that the agonism partner moved away because of the approach of the focal animal.	Event
Lunge	-When the focal animal moved their body towards the agonism partner and the partner retreated. It did not involve striking the agonism partner.	Event

Submissive chatter to Push	-When the focal animal gave a submissive vocalization to the agonism partner. -When the focal individual pushed the agonism partner with both arms.	Event Event
Spat Call	-When the focal individual gave a short submissive agonistic vocalization	Event
Solitary behaviour Scentmark	-When the individual marked an aspect of the environment with a scent glad.	State
Sunning	-When the focal animal moved into an area with sunlight and opened their arms, allowing solar rays to warm their body.	State
Sniff	-When an individual sniffed an object or ground for more than five seconds.	State
Vocalizations Territorial Call	Given when the focal individual gave a vocalization meant to notify a neighbouring group of their presence.	Event
Alarm Call	Given when the focal individual screams because of a predator.	Event
Lost Call	Given when the focal individual has lost contact with other group members	Event
Contact Call	Given by an individual when the group is in vicinity but cannot be seen.	Event
Vigilance Anti-predator	When the focal individual looked into vacant space or actual predator	Event
Inter-group	When the focal individual looked towards a neighbouring group.	Event

I recorded specific behaviours which occurred directly prior to each predator vigilance event. This provided a more detailed context of whether *L. catta* are more sensitive to predators while engaging in the following behaviours: feeding, locomotion, and sitting. These data were measured by dividing the number of vigilance events after each specific behaviour by the total amount of time spent in that behaviour.

The rate of agonism was determined by dividing the number of agonistic events in which the principle actor (the individual on whom data were being collected) was involved in and dividing that number by the total number of hours of data collected on that individual. The rate of agonism within a specific behavioural context was determined in the same manner, yet using the total number of hours engaged in each specific behavioural context.

Schedule of Sampling

Data were collected six days per week for the entire study period. Data collection began as soon as the group was found and ended when it became necessary to leave to ensure return to the field camp before dark or when it began to rain. Groups were observed on alternating days to avoid major ecological changes both within and between habitats. This alternation of days also helped to ensure that hours of data collected were similar between groups.

Within groups, a sampling record was created to ensure that there was not significantly more data recorded on any one individual when compared to all other individuals. This schedule also ensured that data collected on any individuals were not skewed towards any specific period of the day. The day was separated into five periods (7:00-10:00, 10:00-12:00, 12:00-14:00, 14:00-16:00, 16:00+). After a data collection period, the individual and time period was marked. Thus, this “schedule” allowed me to keep an updated and easily accessible record of the amount of data which had been recorded on each individual.

RECORDING AND COLLECTION METHODS

Data were collected using fifteen minute continuous time focal animal sampling methods (Altmann 1974). All behaviours engaged in by the focal animal were recorded and exact start and stop time of each behaviour was noted. *Ad libitum* sampling was used to collect unusual occurrences, such as predation attempts on *L. catta* and inter-group conflicts between *L. catta* groups. At the beginning of each sample, the individual, date, time, habitat, and group were recorded. The exact time spent in each behaviour was recorded via fifteen minute time periods using a digital wristwatch. Time, to the second, was recorded at the beginning of each new behaviour. At the beginning of all vigilance and feeding behaviour, I recorded the identity of the nearest neighbour, the distance category to the nearest neighbour, and the vertical level which the focal individual occupied. If at any time any of these three variables changed while the behaviour continued, the time was recorded. The following contexts of agonism were recorded: feeding, drinking, social, locomotion, and other. The measurement of distance of nearest neighbour are the same as those used by Sauther (2002): near (0-2m), intermediate (2-5m), and distant (>5m). Vertical level was recorded as a relative height in relation to the highest point in each specific forest which the individual was found. Vertical level was not measured in height because of the significant differences in canopy height between all three habitats. Horizontal level of the canopy was not recorded, as some trees in the gallery forest and most trees in the spiny forest did not contain horizontal branches. Thus, the vertical levels measured were ground, low, middle, and high.

Predation threat was defined as the number of predation attempts observed per month, with a 'high' level equaling four or more predation attempts per month (as per

Sauther 2002). Vigilance was scored as “inter-group” if the individual’s gaze was focused on an observable and separate group of *L. catta*. These data were also corroborated by *L. catta* group calls and chasing of inter-group members. All other vigilance was recorded as anti-predator vigilance, even if a predator was not visible. During all predator vigilance occurrences, the behavioural context was recorded. Three contexts were recognized: while feeding, while sitting, and while traveling. This method provides a more specific context on when vigilance occurred.

If the focal animal was lost for more than ten seconds, the sample was paused while the individual was sought. The behaviour “not visible” was recorded immediately after the individual went out of sight. If the individual was not found after five minutes of searching, the individual was scored as “lost” and a new sample on a separate individual was begun. Data collection samples of the “lost” individual were retained if the sample lasted more than seven minutes.

STATISTICAL ANALYSIS

Data were statistically analyzed using the statistical software program SPSS (version 14.0). Non-parametric tests were used to determine whether or not the null hypothesis could be rejected. Non-parametric statistics were used to test for variance in all behavioural categories between groups, with significance level set at 0.05. Non-parametric statistics were used because the sample sizes of both groups were small, which may have led to a lack of normal distribution caused by outlying data points (Lehner 1996). The Mann-Whitney U-test, which organizes the data into ranks and compares the ranks of each individual between groups, was used to compare variables

between groups. The Kruskal-Wallis ANOVA analysis of ranks test was used to compare multiple variables within groups (For example, significant differences between vertical levels used while feeding).

Dominance hierarchies were established by analyzing the winner and loser of each agonistic interaction. I created a matrix to sum all wins and losses for each individual within their respective sex category. Reversals, where one individual wins an encounter with another who has won the majority of agonistic interactions with the first individual, were resolved by establishing the individual with more wins within the dyad as dominant. Landrau's index of linearity (Bekoff 1977, Lehner 1996) was used to determine the linearity of each dominance hierarchy. This equation uses the number of individuals within the group and the number of individuals each member dominates to equate linearity index. Landrau's index can be determined using the following equation:

$$h = (12/n^3 - n) \sum_{a=1}^n \{V_a - (n-1)/2\}^2$$

where n = number of animals in the group and V_a = number of animals that an individual dominates.

A value of $h \geq 0.9$ was used to indicate a nearly linear dominance hierarchy.

The next chapter in this thesis deals with the data recorded in this study and the statistical results obtained after comparing behavioural variables between the two study groups.

CHAPTER 3: RESULTS

I spent 420 hours in contact with my study groups. Three-hundred and nineteen hours of data were collected, with 147 hours collected on the gallery forest group, 90 hours collected on the scrub forest group, and 82 hours collected of the spiny forest group (Table 3.1). This study will focus on data collected on only the gallery forest and spiny forest groups. This allows for a comparative analysis of groups in habitats with significantly different ecological characteristics, i.e. habitats which share just one floral species and habitat structures which differ significantly in canopy cover, canopy height, ground vegetation cover, horizontal branch size and abundance, and ambient temperature. A mean of 21.02 hours of data were collected per individual in the gallery forest group, with a range of 3.56 hours (Table 3.1). There was only a slight difference in the mean number of hours of data collected between males and females. Within the spiny forest group, a mean of 10.36 hours of data were collected per individual. The range of 2.26 hours (Table 3.1) occurred because the individual with the fewest hours of data collected (SM1) left the group for several days.

Bars in the graphs represent the standard mean. All P values listed in graphs were derived using the Mann-Whitney U Test.

TIME ALLOCATION

L. catta in the spiny forest group spent 51.2% of the daytime behaviours resting, 20.0% sitting, 11.2% feeding, 2.3% foraging (13.5% feeding and foraging), 7.5% locomoting, 3.6% in social behaviours, and 1.3% in vigilance behaviour (Fig. 3.1). In order to determine the amount of time spent in active behaviours, I summed the

proportion of time spent feeding, foraging, locomoting, scent marking, exhibiting vigilance, and in social behaviours. Resting and sitting qualify as inactive behaviours because they are considered energy minimizing behaviours in *L. catta* (Rasamimanana et al. 2006). In the spiny forest group, active behaviours accounted for only 27.0% of daily activities, while 73.0% of the daily activities were devoted to inactive behaviours. The gallery forest group rested for 36.2% of all activities, making it the most prominent behaviour. Individuals spent 24.1% of their time feeding, 14.8% sitting, 9.3% in social behaviours, 6.9% of the time locomoting, 6.5% foraging (30.6% feeding and foraging), 14.8% sitting, 9.3% in social behaviours, and 1.4% in vigilance behaviours (Fig. 3.1). Active behaviours accounted for 49.0% of their daily behaviours and inactive behaviours for 51.0% of daily behaviours.

Table 3.1. Number of hours and sessions of data collected in each habitat by individual focal animal.

Individual	# of Hours	# of Sessions
<u>Spiny Forest</u>		
F1	14.08	56
F2	13.43	53
F3	14.03	56
M1	12	48
M2	14.16	56
M3	14.26	57
Mean	13.66	54.33
<u>Gallery Forest</u>		
F1	18.9	92
F2	22.4	92
F3	21.8	89
F4	22.1	91
M1	21.2	86
M2	20.7	86
M3	19.9	82
Mean	21.02	88.2

Individuals living in the gallery forest group spent a significantly greater proportion of time feeding ($U=0$, $P<0.005$, $N=13$) and foraging ($U=0$, $P<0.005$, $N=13$) when compared with the spiny forest group. Resting occurred significantly more often in the spiny forest group than in the gallery forest group ($U=0$, $P<0.005$, $N=13$), while social behaviours occurred significantly more often in the gallery forest group than in the spiny forest group ($U=3$, $P<0.01$, $N=13$). There was no significant differences in the proportion of time spent locomoting ($U=17$, $P>0.05$, $N=13$) or in vigilance behaviour ($U=20$, $P>0.05$, $N=13$). The gallery forest group spent a greater proportion of time engaged in active behaviours than the spiny forest group ($U=0$, $P<0.005$, $N=13$), while the spiny forest group were inactive for a significantly greater proportion of time than the gallery forest group ($U=0$, $P<0.005$, $N=13$). Summarizing, individuals in the gallery forest group spent a significantly greater proportion of time feeding, foraging, and socializing, while individuals in the spiny forest group spent significantly more time resting and sitting.

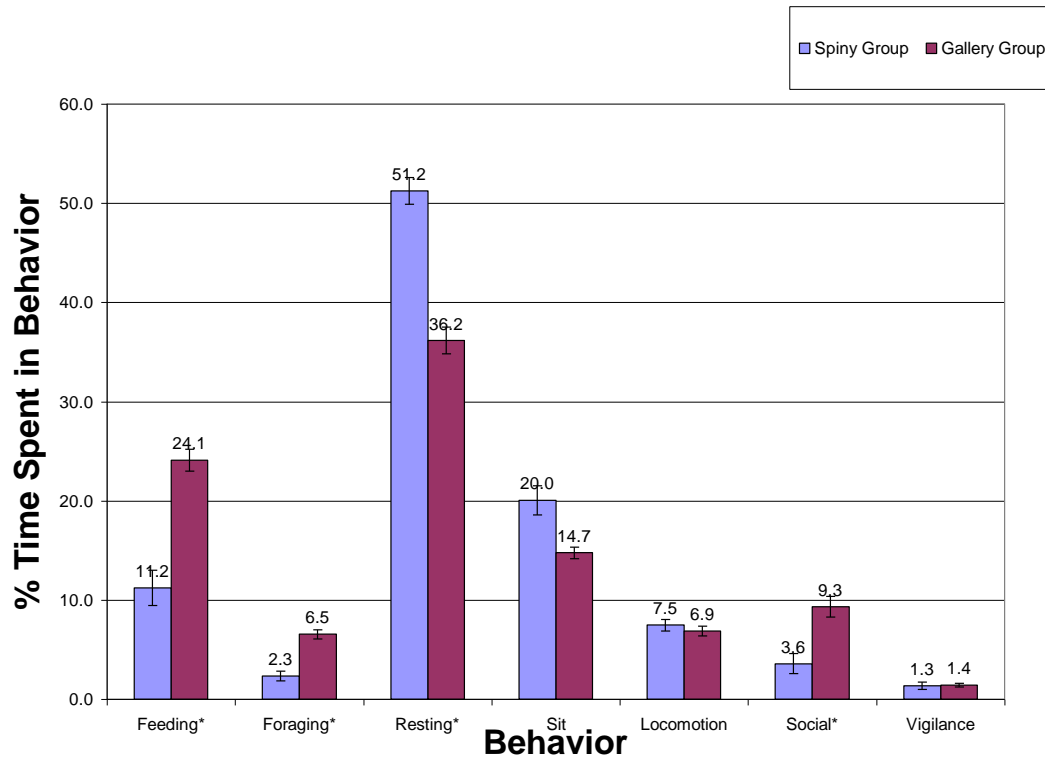


Fig. 3.1. Average activity budget of study groups. Bars indicate one standard error. * indicates $P < .05$.

ANTI-PREDATOR VIGILANCE

Potential predator pressure levels

While predators are rarely seen by primate researchers relative to their actual presence in their habitats, the identification of observed predators is useful for understanding relative predation pressure and a primate's sensitivity to those specific predators. Village dogs prey on *L. catta* at Beza Mahafaly Reserve (Gould 1996a, Sauther 2002, Gould and Sauther 2007b) and were observed to aggressively approach both the gallery forest group and the spiny forest group each once during this study. During these occurrences, both *L. catta* groups responded by moving vertically up the trees and producing ground predator calls for several minutes. Other primate researchers at Berenty

Reserve have communicated that village dogs have attacked individuals in several other *L. catta* groups in the past (Ichino and Soma pers. comm.).

Large aerial predators of *L. catta* include the Madagascar harrier hawk (*Polyboroides radiatus*) and the Madagascar buzzard (*Buteo brachypterus* (Gould 1996b, Sauther 2002, Goodman 2003b, Gould and Sauther 2007b). I observed a single *Buteo brachypterus* once during this study, but there have been no reports of any *Polyboroides radiatus* at Berenty Reserve for several years. A Malagasy primate researcher did report a *Buteo brachypterus* sighting which elicited an anti-predator vocal response by a *L. catta* group living in the scrub forest at Berenty Reserve during this study period (Haja per. comm.). A single *Buteo brachypterus* was observed flying above the spiny forest *L. catta* group, but no individuals in the group elicited a vocal response. Black Kites (*Milvus migrans*), a small raptor, were observed in the scrub forest and frequently made nests in trees which were simultaneously used by *L. catta* groups. Individuals in the spiny forest group were seen to respond to these raptors as they flew close on several occasions, but I estimate that the proportion of *L. catta* anti-predator vigilance events towards these small raptors were very low, many times occurring after the raptors had passed.

Rates of vigilance

The two groups of *L. catta* exhibited similar rates of total vigilance (Spiny forest group: 1.40 events/h, Gallery forest group: 1.01 events/h) which were not significantly different ($U=16.5$, $P=0.83$, $N=13$) (Fig. 3.2). Greater between-group differences were observed in anti-predator and inter-group vigilance rates. Individuals in the spiny forest group exhibited a significantly higher rate of anti-predator vigilance events (0.98/h) than

the gallery forest group (0.27/h) ($U=0$, $P<0.005$, $N=13$), a four-fold difference between groups (Fig. 3.2). The rate of inter-group vigilance events was higher in the gallery forest group (0.21/h) than in the spiny forest group (0.12/h), but this difference was not significant ($U=10$, $P=0.68$, $N=13$). *Ad libitum* data collection on inter-group encounter rate showed that the gallery forest group averaged 1.80 encounters/day and the spiny forest group averaged 0.62 encounters/day, which paralleled data on mean individual inter-group vigilance rates.

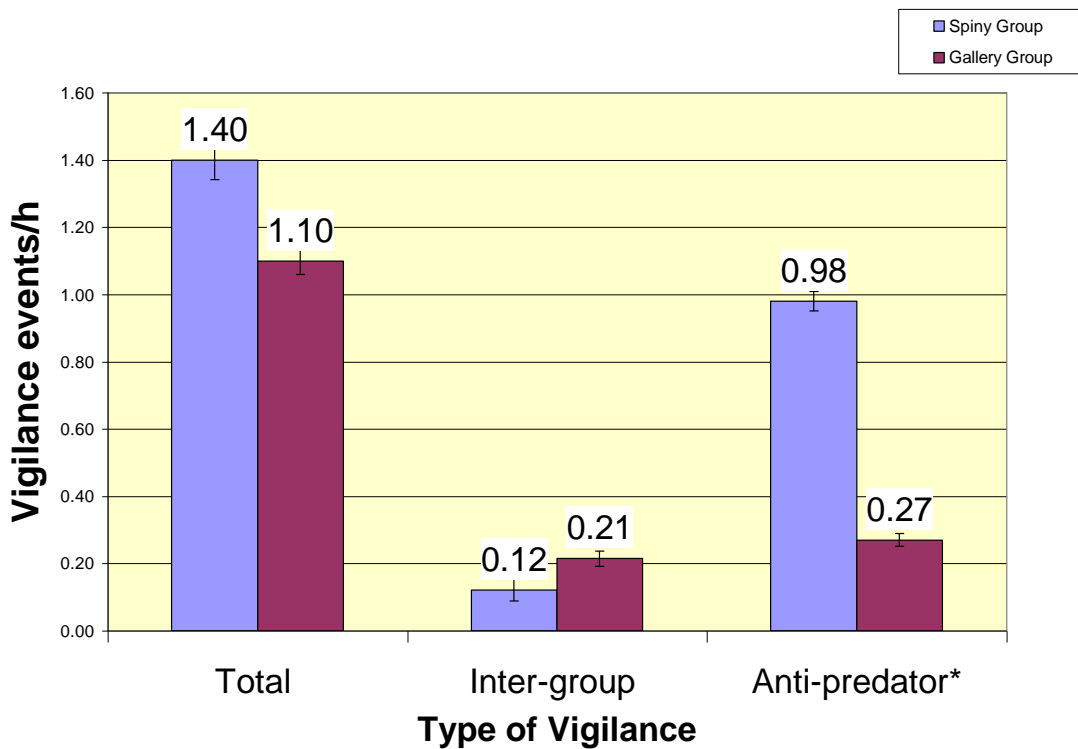


Fig. 3.2. Average rate of total, inter-group, and anti-predator vigilance events per hour. Bars indicate one standard error. * indicates $P<.05$.

Behavioural contexts of anti-predator vigilance

The spiny forest group exhibited more anti-predator vigilance events per feeding hour (.86) than the gallery forest group (0.52) (Fig. 3.3), but these rates did not differ significantly ($U=12.5$, $P>0.05$, $N=13$). Individuals in the spiny forest group were vigilant towards potential predators while sitting at a significantly greater rate (2.80) than those in the gallery forest group (1.27) (Fig. 3) ($U=2$, $P<0.01$, $N=13$). Finally, anti-predator vigilance while locomoting occurred at significantly different rates between groups, with the spiny forest group exhibiting a rate 7.60 times greater than the gallery forest group (spiny forest group: 4.63 events/h, gallery forest group: 0.63 events/h) ($U=0$, $P<0.005$, $N=13$) (Fig. 3.3). Thus, the spiny forest group averaged higher rates of anti-predator vigilance while feeding, sitting, and moving through their habitat when compared with the gallery forest group, with the latter two rates of vigilance being significantly different.

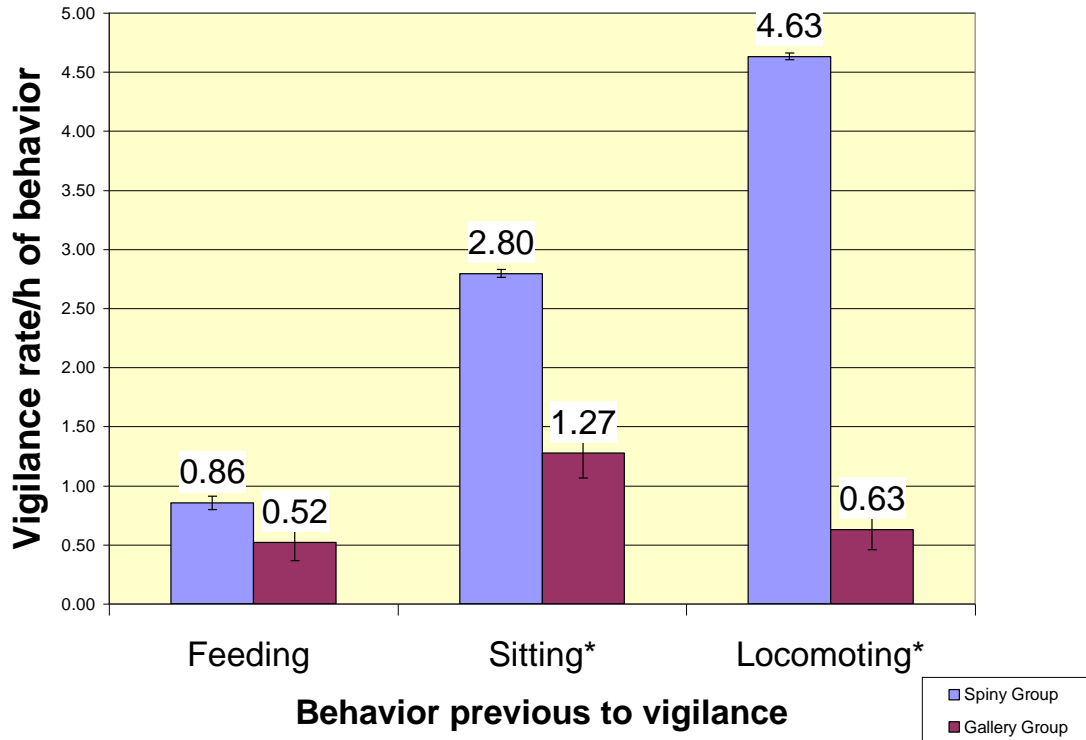


Fig 3.3. Average rate of anti-predator vigilance events while feeding, sitting, and locomoting. Bars indicate one standard error. * indicates $P < 0.05$.

Within the spiny group, anti-predator vigilance while feeding occurred at significantly lower levels than while sitting ($\chi^2=8.33$, $df=1$, $P < 0.05$) and while locomoting ($\chi^2=8.33$, $df=1$, $P < 0.05$). Anti-predator vigilance rates while locomoting and sitting did not differ significantly ($\chi^2=3.10$, $df=1$, $P=0.078$). Thus, individuals in the spiny forest were more vigilant towards potential predators while sitting and moving than while feeding. The gallery forest group were more vigilant while sitting than while feeding ($\chi^2=5.58$, $df=1$, $P < 0.05$). However, no significant differences were found either between anti-predator vigilance while locomoting and sitting ($\chi^2=3.44$, $df=1$, $P=0.06$) or while feeding and locomoting ($\chi^2=.41$, $df=1$, $P=0.521$).

Anti-predator vigilance and canopy level

L. catta in the spiny forest group exhibited a greater proportion of anti-predator vigilant events while on the ground (38.6%) in the middle canopy (34.5%), with a slightly lower percentage of events occurring in the lower arboreal level (24.3%) and a very small proportion occurring while in the highest vertical level (2.5%) (Fig. 3.4). The proportion of anti-predator vigilance events did not differ significantly while on the ground, or in the low, and middle levels of the trees (Kruskal-Wallis ANOVA: $\chi^2=1.98$, $df=2$, $P=0.34$); however, the proportion of anti-predator vigilance events did differ between the high level and the three lowest levels (Kruskal-Wallis ANOVA: $\chi^2=11.53$, $df=3$, $P=0.01$), indicating that individuals were significantly less vigilant towards potential predators while at the highest levels of the trees than at any other vertical level.

The majority of anti-predator vigilance events in the gallery forest group occurred while on the ground (59.7%), followed by the middle level of the trees (25.9%), the highest level (7.3%), and low level (7.1%) (Fig. 3.4). Individuals were significantly more likely to exhibit anti-predator vigilance while on the ground than while in the low canopy level (Kruskal-Wallis ANOVA: $\chi^2=7.12$, $df=1$, $P=0.008$) and highest canopy level (Kruskal-Wallis ANOVA: $\chi^2=6.77$, $df=1$, $P=0.009$), while the differences between vigilance exhibited on the ground and in the middle canopy approached significance (Kruskal-Wallis ANOVA: $\chi^2=3.03$, $df=1$, $P=0.08$).

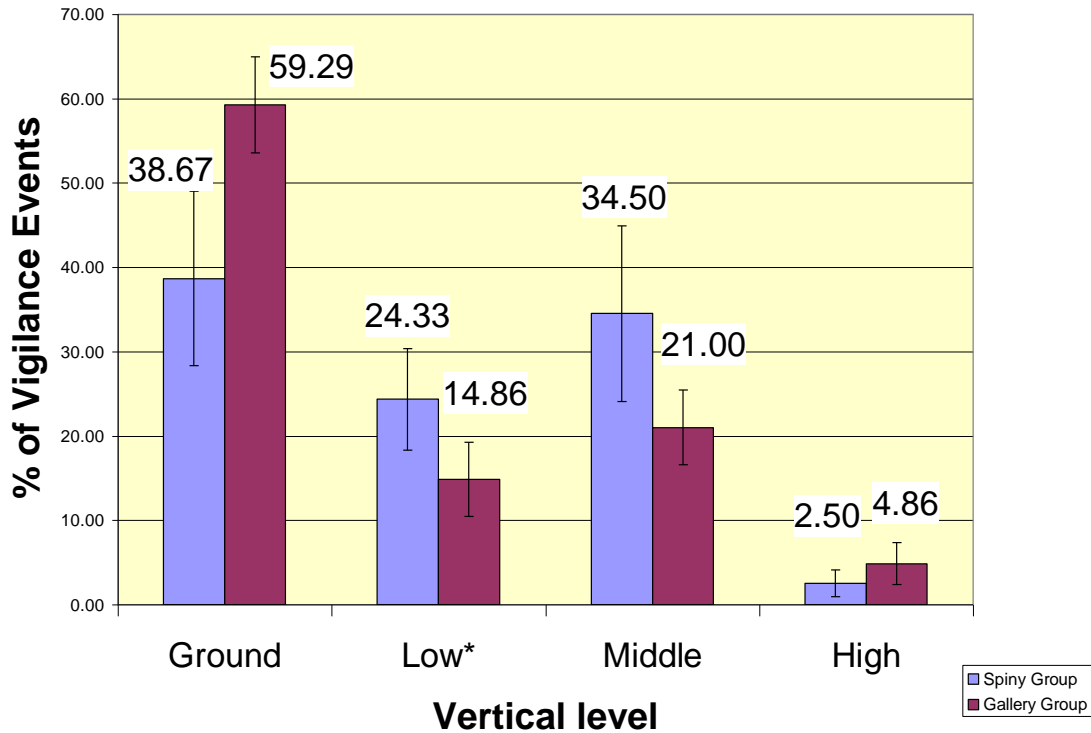


Fig. 3.4. Average proportion of anti-predator vigilance events between vertical levels. Bars indicate one standard error. * indicates $P < 0.05$.

The spiny forest group had a significantly higher proportion of anti-predator vigilance events in the lower level of the trees when compared with the gallery forest group ($U=7$, $P=0.04$, $N=13$). Animals in the gallery forest group exhibited a greater proportion of anti-predator vigilance than those in the spiny forest group while on the ground (59.3% vs. 38.7%, respectively, Fig. 3.4) and while in the highest levels of the trees (4.9% vs. 2.5%, respectively, Fig. 3.4). Anti-predator vigilance was more common in the middle level of the trees in the spiny forest group (34.5%) than in the gallery forest group (14.8%) (Fig. 3.4). There were, however, no significant differences in the proportion of anti-predator vigilance events occurring on the ground ($U=11$, $P=0.15$,

N=13), in the middle of trees (U=16, P=0.47, N=13), or while in the highest vertical levels (U=20, P=0.93, N=13) between groups.

Anti-Predator Vigilance and Nearest Neighbour Distance

Anti-predator vigilance events while between two and five meters from a nearest neighbour took place at a significantly greater proportion in the spiny forest group (49%) than in the gallery forest (36%) (U=7, P<0.05, N=13) (Fig. 3.5). There were no significant differences in the proportion of anti-predator vigilance events which took place while far (>5m) and near (<2m) from a nearest neighbour between groups. Anti-predator vigilance events while in proximity to a nearest neighbour (<2m) occurred more often in the gallery forest group (45.0%) than in the spiny forest group (32.5%) (Fig. 3.5), but this difference was not significant (U=8, P>0.061, N=13). The proportion of anti-predator vigilance while far (>5m) from a nearest neighbour occurred at nearly equivalent amounts in the spiny forest group (18.7%) and the gallery forest group (18.6%) (Fig. 3.5) (U=14, P=0.349, N=13). There were no significant differences in the proportion of anti-predator vigilance events between all three nearest neighbour distances in either the spiny forest group ($\chi^2=5.54$, df=2, P=0.06) or the gallery forest group ($\chi^2=4.52$, df=2, P=0.1).

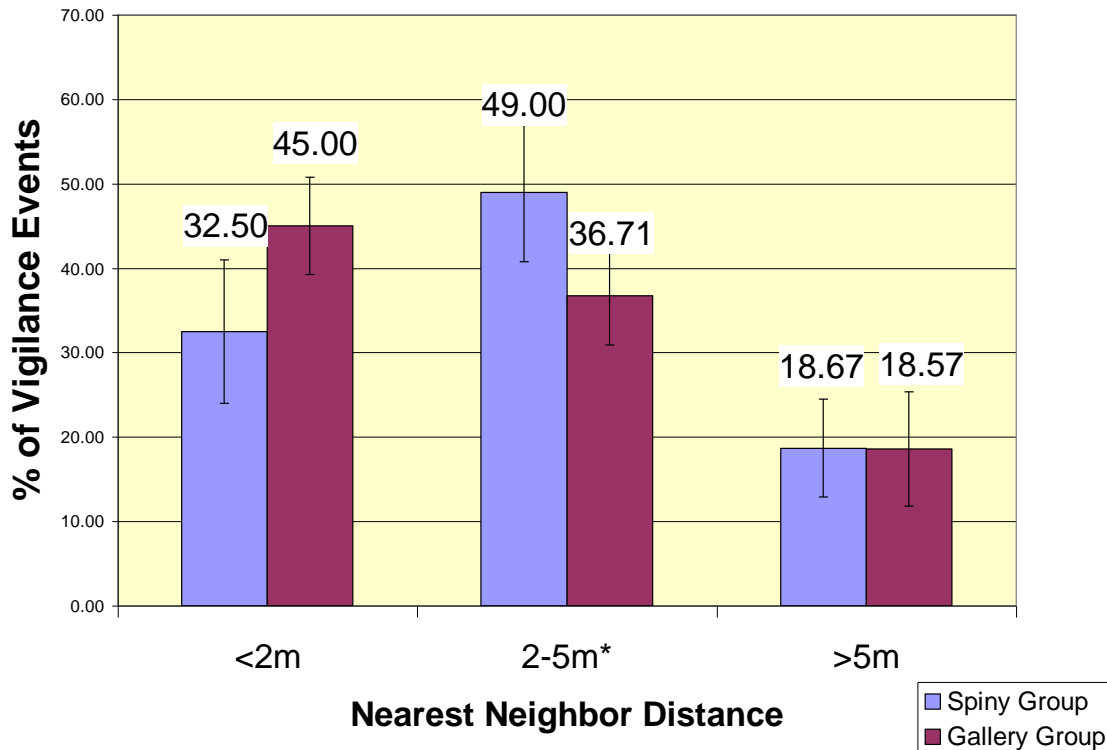


Fig. 3.5. Average proportion of Anti-predator vigilance events while in nearest neighbour distances. Bars indicate one standard error. * indicates $P < .05$.

FEEDING AND FORAGING BEHAVIOUR

Food Species consumed

Table 3.2 lists all plant species and plant parts eaten by both *L. catta* groups. The spiny forest group consumed a total of fourteen plant species, which are composed of thirteen floral families. Two of these species, *Agave sisalana* (sisal) and *Opuntia* (Mexican prickly pear), are not native to the spiny forest ecosystem of Madagascar but are native to semi-desert habitats (Felger 2000). The gallery forest group consumed a total of eleven species representing seven floral families. Unlike those in the spiny forest, the majority (six out of ten) of floral species consumed by the gallery forest were non-native to Madagascar (Fig. 3.2). Although there are no direct data on total minutes

dedicated to the consumption of specific food species, personal observations revealed that many of these species were primary food items for *L. catta* in the gallery forest group, including the leaves of *Azadirachta indica*, *Leucaena leucocephala*, and the fruit of *Pithecellobium dulce*. Combined together, individuals in the gallery and spiny groups shared a total of one food species out of twenty-three (4%). The only shared species, *Tamarindus indica*, is located throughout the gallery forest and the scrub forest, which the spiny forest group occasionally entered, but do not occur in the spiny forest.

Individuals in both groups consumed a variety of food parts, including mature and immature fruits and leaves, stems, leaf buds, flowers, and succulent plants. Individuals in both groups consumed soil, and the gallery forest group consumed termite soil on two separate occasions. The gallery and spiny forest groups predominantly ate a combination of fruit and leaves, at 94.0% and 74.9%, respectively. Thus, both groups fit into the dietary niche of folivore/frugivore ascribed to *L. catta* by several researchers (Jolly 1966, Sussman 1977, Sauther 1994, Soma 2006, Gould and Sauther 2007a). The two groups differed significantly in their consumption of both fruits and flowers. The spiny forest group ate a significantly higher percentage of fruit (57.1%) than the gallery forest group (26.2%) (Fig. 3.6) ($U=0$, $P=0.003$, $N=13$). The gallery forest group spent nearly four times the amount of time consuming leaves (69.1%) than the spiny forest group (17.8%) (Fig. 3.6), and this difference was significant ($U=0$, $P=0.003$, $N=13$). The gallery forest group spent the remaining 5.1% of their time feeding on leaf buds (1.1%), succulent plants (1.4%), soil (1.1%), and flowers (0.8%) (Fig. 3.6). The spiny forest group supplemented their diet with flowers (8.8%), leaf buds (8.4%), vines and stems (1.4%), succulent plants (.7%), and soil (.5%) (Fig. 3.6). The spiny forest group spent a

significantly greater proportion of their time consuming flowers (U=2, P=0.01, N=13) and vines /stems (U=10.5, P=0.04, N=13) than individuals in the gallery forest group.

The volume of plant reproductive parts was measured on major fruiting species consumed by *L. catta* in both groups. While these data are limited, it appears that fruit items are much larger in the gallery forest than in the spiny forest. The two major fruiting species eaten by the gallery forest group were *Tamarindus indica* and *Pithecellobium dulce*. *Tamarindus indica* fruit had a mean size of 3.25 cm² (n=5), while *Pithecellobium dulce* fruit averaged 1.98 cm² (n=10). Conversely, fruit parts eaten by the spiny forest group were much smaller. *Gyocarpus* fruit averaged 0.35 cm² (n=10) and *Tarenna* fruit averaged 0.03 cm² (n=8).

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Table 3.2. Plant Species eaten by research groups. *Indicates a non-native species to Madagascar. †Indicates a species shared between groups.

Taxonomic Family	Genus/Species	Items Eaten
Spiny Forest		
*Agave	<i>Agave sisalana</i>	Succulent leaves
Burseraceae	<i>Commiphora sp</i>	Leaf buds
Boraginaceae	<i>Cordia caffra</i>	Leaves
*Cactaceae	<i>Opuntia sp.</i>	Succulent leaves
†Caesalpinioideae	<i>Tamarindus indica</i>	Fruit, leaves, leaf buds
Capparaceae	<i>Maeura folfimus</i>	Leaves
Didiereaceae	<i>Alluadia procera</i>	Flowers, leaves, fruit
Euphorbia	<i>Euphorbia sp.</i>	Stems
Hernandiaceae	<i>Gyrocarpus americanus</i>	Flowers, leaves, fruit
Liliaceae	<i>Aloe sp</i>	Succulent leaves
Mimosoideae	<i>Acacia sp.</i>	Leaves
Rubiaceae	<i>Tarenna sp.</i>	Fruit
Salvadoraceae	<i>Azima tetracantha</i>	Leaves, flowers
Salvadoraceae	<i>Salvadora augustifolia</i>	Fruit, leaf buds
	.	Soil
Gallery Forest		
*Cactaceae	<i>Opuntia sp.</i>	Succulent leaves
†Caesalpinioideae	<i>Tamarindus indica</i>	Leaves, leaf buds, fruit
*Capparaceae	<i>Cordia sp.</i>	Leaves and fruit
Capparaceae	<i>Craveta excelsa</i>	Flowers
Capparidaceae	<i>Cadaba virgata</i>	Leaves
*Convolvulaceae	<i>Iporea robbars</i>	Flowers
Mimosoideae	<i>Acacia royumae</i>	Leaves
*Mimosoideae	<i>Leucaena lerrocephalla</i>	Leaves
*Mimosoideae	<i>Pithecellobium dulce</i>	Fruit, flowers
*Meleaceae	<i>Azadirachta indica</i>	Leaves
		Soil

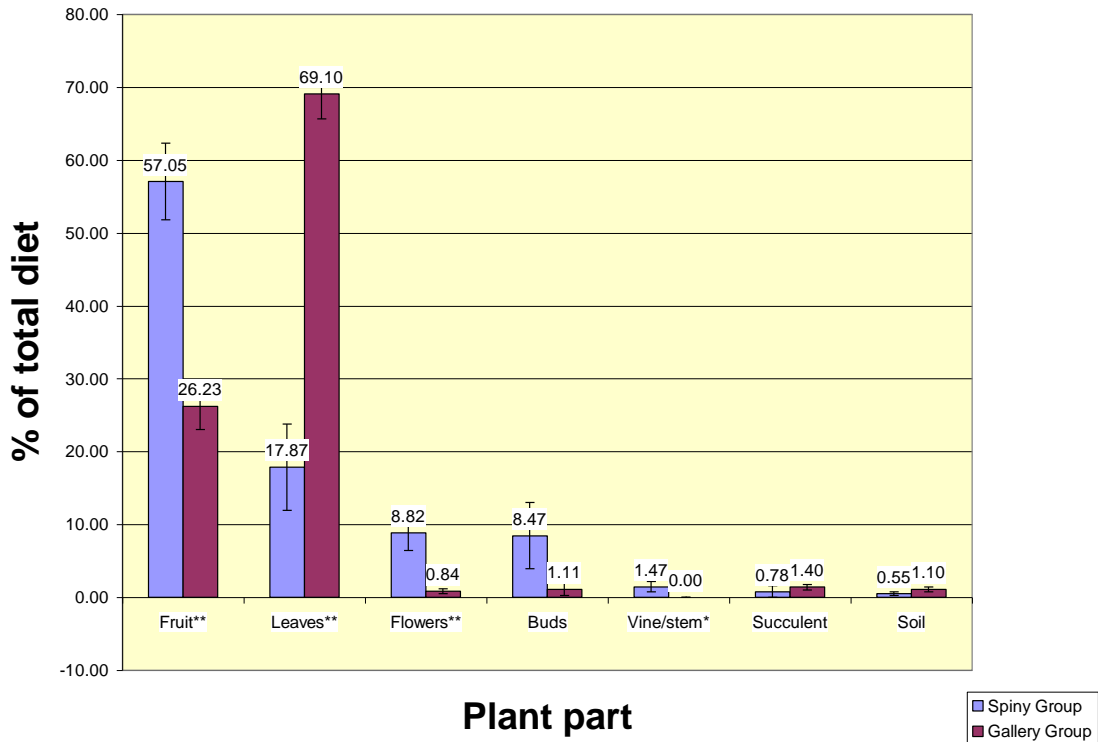


Fig. 3.6. Average proportion of plant part eaten. Bars indicate one standard error. ** indicates $P < 0.005$, * indicates $P < 0.05$.

Feeding Level

There were no significant differences between groups in the proportion of time spent feeding at any of the canopy levels (Fig. 3.7). Both *L. catta* groups preferred to feed in middle and high canopy. The spiny forest group spent a similar proportion of time feeding in the middle canopy (48.1%) compared with individuals in the gallery forest (38.2%) ($U=12$, $P=0.19$, $N=13$) and at the highest vertical levels of the trees (34.2%) than the gallery forest group (33.1%) ($U=16$, $P=0.475$, $N=13$). Feeding in the low canopy occurred slightly more often in the gallery forest group (21.7%) than in the spiny forest group (12.3%) ($U=9$, $P=0.08$, $N=13$), while the two groups fed for similarly low

proportions while on the ground (spiny forest group: 5.1%, gallery forest group: 6.7% (U=15.5, P=0.43, N=13)).

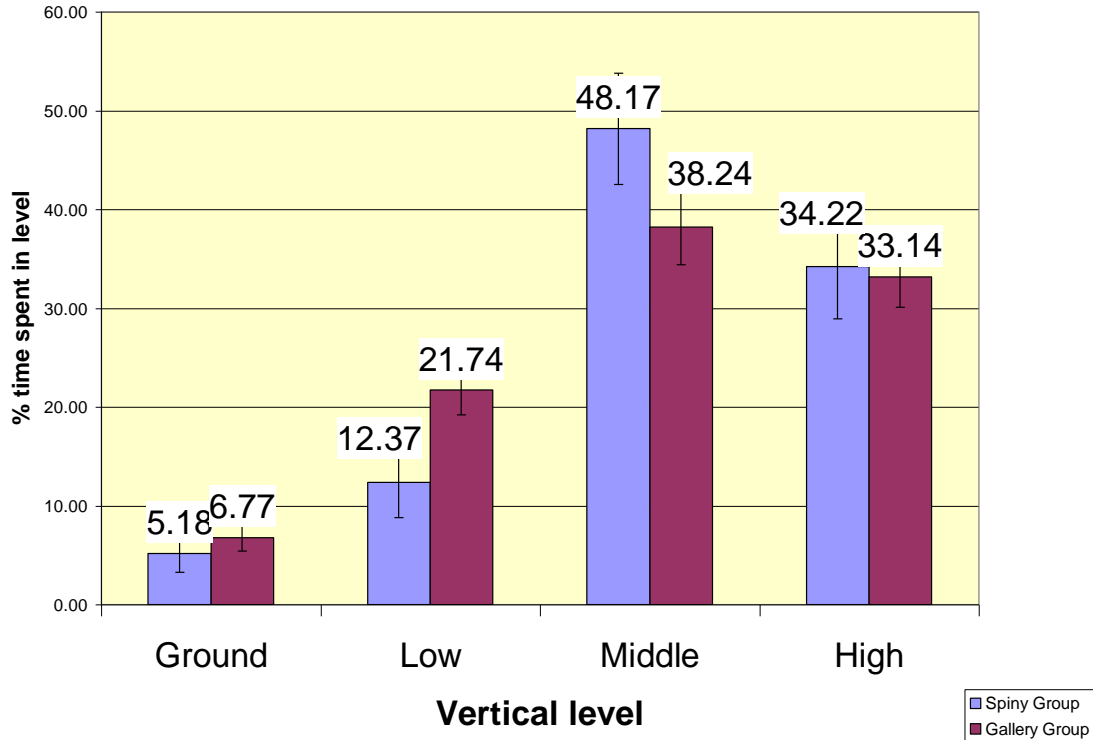


Fig. 3.7. Average proportion of vertical level use while feeding. Bars indicate one standard error.

Nearest Neighbour Feeding Distance

Individuals in the spiny forest group and gallery forest group showed similar percentages of time spent within two meters (30.6% and 28.1%, respectively), between two and five meters (41.7% and 47.1%, respectively), and more than five meters (27.4% and 25.0%) of their nearest neighbour while feeding (Fig. 3.8). There were no significant differences in nearest neighbour distance while feeding when within two meters (U=16.5,

P=.52, N=13), between two and five meters (U=9, P=.08, N=13), and more than five meters (U=20, P=.88, N=13).

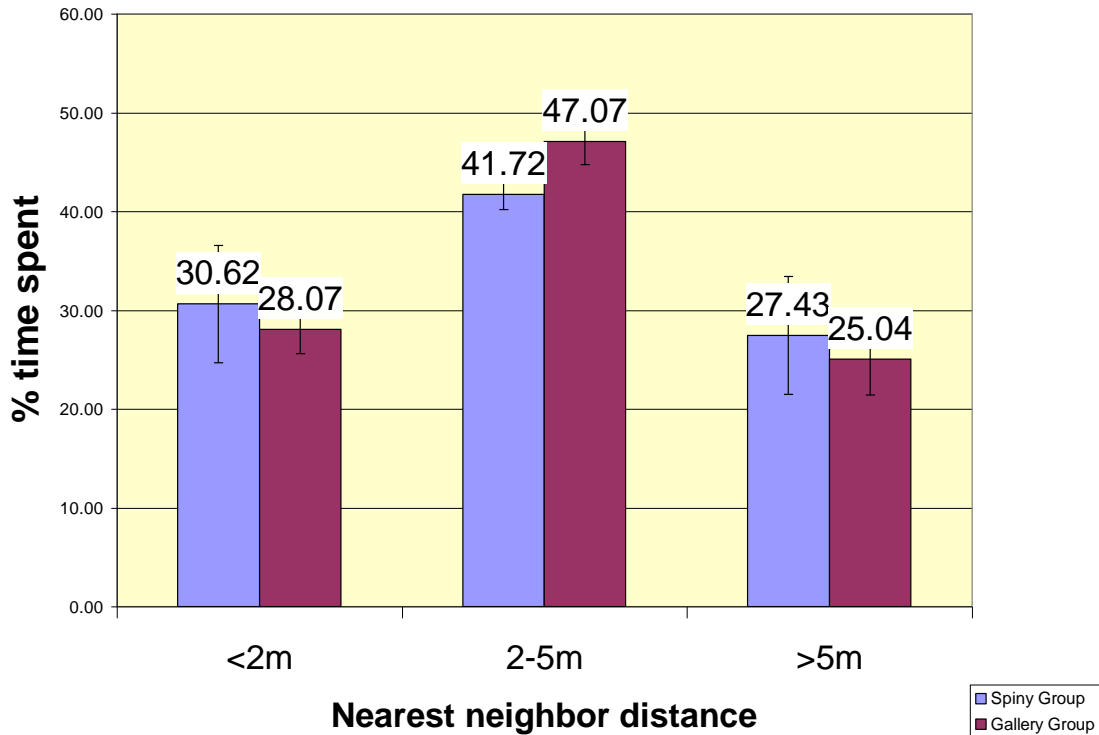


Fig. 3.8. Average nearest neighbour distance while feeding. Bars indicate one standard error.

When the proportion of time spent within specific nearest neighbour categories was compared within both groups, two different patterns emerged. Individuals in the spiny forest group showed no significant differences in the proportion of time spent feeding between all three nearest neighbour distances (Kruskal-Wallis ANOVA Test: $\chi^2=3.86$, $df=2$, $P=0.15$). In the gallery forest group, there were no significant differences in the proportion of time spent feeding while near to (>2m) and far from (<5m) nearest neighbour (Kruskal-Wallis ANOVA Test: $\chi^2=.59$, $df=1$, $P=0.44$). Thus, the gallery forest group preferred to feed between two and five meters from their nearest neighbour.

Data on nearest neighbour distance while feeding on the two major food items, fruit and leaves, show differing patterns of social spacing between food items. While feeding on fruit, the spiny forest group spent a significantly greater proportion of time (36.5%) within two meters of their nearest neighbour than the gallery forest group (12.9%) (Fig. 3.9) ($U=4$, $P=0.015$, $N=15$). The individuals in the gallery forest group were more spread when feeding on fruit, spending a significantly greater proportion of their time more than five meters from a nearest neighbour (47.8%) compared with the spiny forest group (18.4%) ($U=3$, $P<0.05$, $N=13$). The two groups also differed in spacing patterns while feeding on leaves. Animals in the gallery forest group spent a significantly greater proportion of time in close proximity to ($<2m$) a nearest neighbour (31.4%) compared with the spiny forest group (19.7%) (Fig. 3.10) ($U=7$, $P<0.05$, $N=13$), whereas the spiny forest group spent a significantly greater proportion of time far ($>5m$) from a nearest neighbour (39.7%) than the gallery forest group (17.1%) ($U=6$, $P<0.05$, $N=13$) (Fig. 3.10).

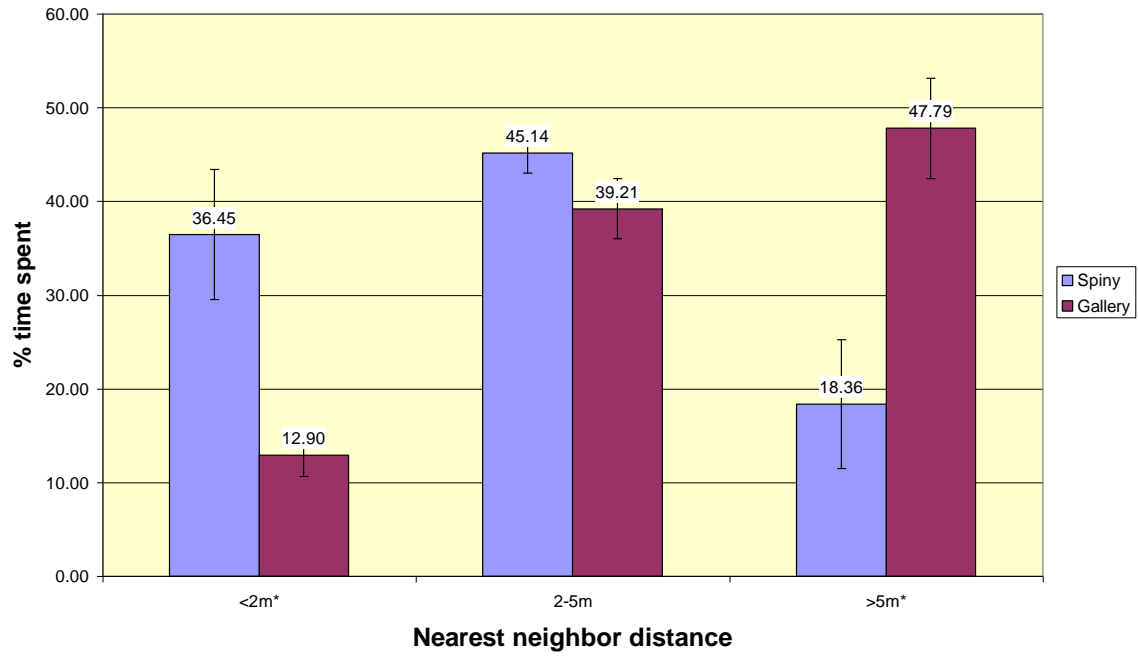


Fig. 3.9. Average proportion of time spent in nearest neighbour distance category while feeding on fruit. Bars indicate one standard error. * indicates $P < .05$.

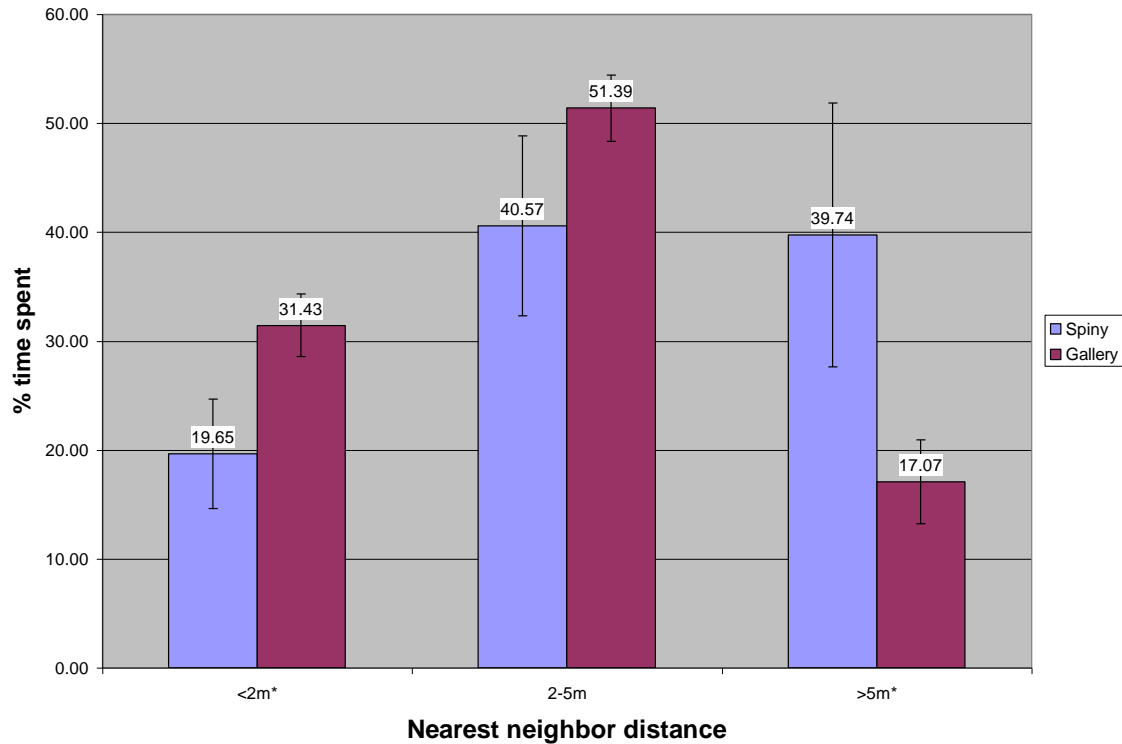


Fig. 3.10. Average proportion of time spent in nearest neighbour distance category while feeding on leaves. Bars indicate one standard error. * indicates $P < .05$.

DOMINANCE AND AGONISTIC BEHAVIOUR

Dominance Hierarchy

Dominance hierarchies were initially analyzed with all males and females together. In the spiny forest and gallery forest groups, no male had a higher amount of wins compared with losses in a dyad with a female. There was only one recorded reversal of dominance relationship between a male and female, where the female GF2 chattered at GM2. GF2, however, won 4 contests against GM2, and thus, is considered to be dominant to GM2. Furthermore, female chattering toward males is related to male friendship advances and not to female-directed agonism (Jolly 1966, Sauther 1993). Thus, as has been found in virtually all studies of ring-tailed lemur social behaviour,

females in both the spiny and gallery forest groups were dominant to males. Gould (1996) has noted that when dominance hierarchies are separated by sex, males and females tend to show differing strengths of linear dominance hierarchies. Female dominance hierarchies were linear in both study groups (Landrau's index of hierarchy linearity: spiny forest group: $h=1.0$, gallery forest group: $h=1.0$). There were a low number of reversals in the female dominance hierarchy in both groups (Gallery forest: 3 out of 37 agonistic interactions (8.1%), Spiny forest: 0 out of 10) (Table 3.3). Male dominance hierarchies, however, differed between groups. The male dominance hierarchy in the spiny forest group was found to be linear (Landrau's index of linearity: $h=1.0$) with no ties or ambiguous dominance relationships. The low linearity value in the gallery forest male hierarchy (Landrau's index of linearity: $h=0.35$), however, reflects a high degree of nonlinearity. The non-linearity found in this study is based on ambiguous dominance relationships between all males. No agonistic encounters with other males were recorded for GM3, while GM1 and GM2 won one encounter each against the other. These dominance hierarchies were based solely on agonistic encounters, yet another behavioural indicator, *ad lib* data on inter-group male chasing, shows that GM1 may have been dominant, as this male was the only individual to chase neighbouring males away from the gallery forest group. It could be possible that a long-term research study would have unveiled more clear dominance relationships between males in the gallery forest group.

Loser

Winner	GF1	GF2	GF3	GF4	Total
GF1	\	3	5	10	18
GF2		\	5	5	10
GF3		1	\	7	8
GF4	1		1	\	2
Total	1	4	11	22	

Gallery forest group females

h=1.0

Loser

Winner	SF1	SF2	SF3	Total
SF1	\	1	7	8
SF2		\	2	2
SF3			\	0
Total	0	1	9	

Spiny forest group females

h=1.0

Loser

Winner	GM1	GM2	GM3	Total
GM1	\	1		1
GM2	1	\		1
GM3			\	0
Total	1	1	0	

Gallery forest group males

h=.35

Loser

Winner	SM1	SM2	SM3	Total
SM1	\	4	1	5
SM2		\	1	1
SM3			\	0
Total	0	4	2	

Spiny forest group males

h=1.0

Table 3.3. Dominance matrices. Dominance matrices for male and females dyads in spiny forest and gallery forest group. Rows indicate number of interactions won in each dyad. Columns indicate number of interactions lost in each dyad. H indicates the linearity value within each hierarchy. Hierarchies are considered linear if $h \geq 0.9$.

Agonism rates

Both groups had similar rates of total agonism per hour (0.88 agonistic events/h) (Fig. 3.11). Feeding agonism occurred at a much higher rate than total agonism. Individuals in the spiny forest group averaged a significantly higher rate of agonistic events per feeding hour (3.98 events/h) than individuals in the gallery forest group (1.55 events/h) ($U=4.5$, $P<0.05$, $N=13$) (Fig. 3.11). Agonism over social events occurred more often in the gallery forest group (2.01 events/h) than in the spiny forest group (0.81 events/h), but these rates were not significantly different ($U=12$, $P=0.18$, $N=13$) (Fig. 3.11). Finally, individuals in the spiny forest group had a higher rate of agonism over sitting spots (0.46 events/h) than did individuals in the gallery forest (0.17 events/h), and these rates were not significantly different ($U=15$, $P=0.35$, $N=13$) (Fig. 3.11).

Sex-directed agonism

The proportion of sex-directed agonism was calculated by counting the number of agonistic interactions occurring between males and females (MF), males and males (MM), and females and females (FF). There were no significant differences between groups in the proportion of agonistic events between males and females (MF) and females and females (FF). The majority of all agonistic interactions in both the spiny and gallery forest groups occurred between males and females (MF) (spiny forest group = 60.3%, gallery forest group = 63.0%) (Fig. 3.12) ($U=18$, $P=.67$, $N=13$). Agonistic interactions between females (FF) accounted for the second-most frequent agonism dyad (spiny forest group = 26%, gallery forest group = 35.4%)

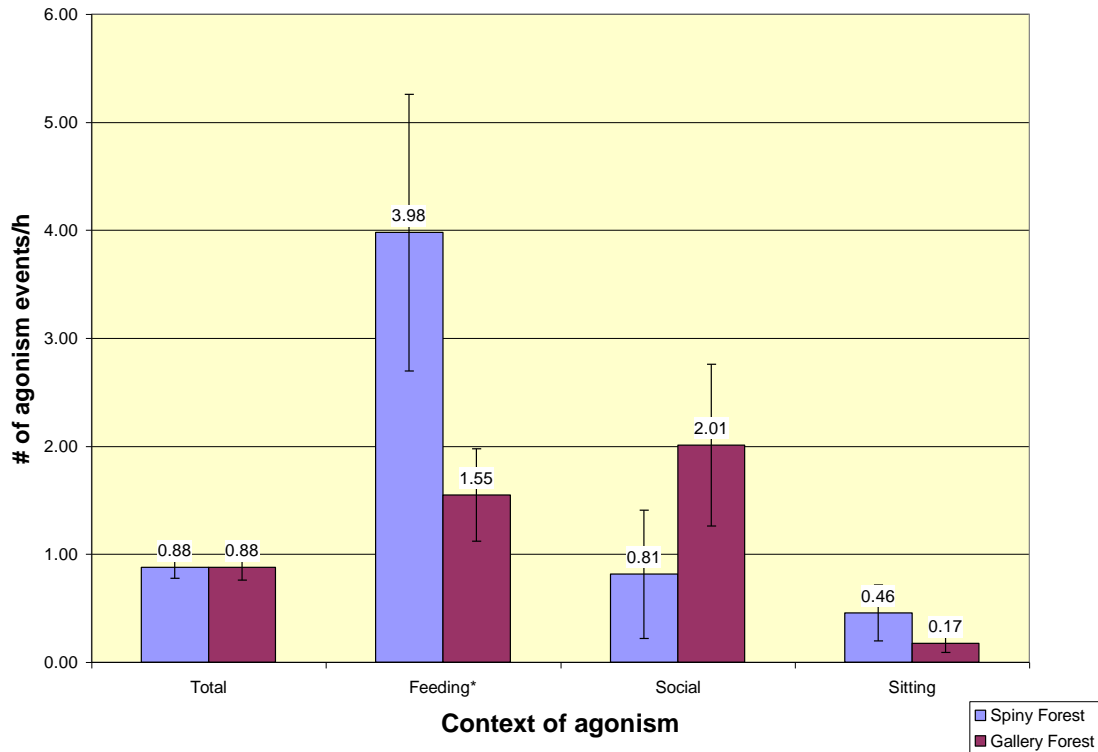


Fig. 3.11. Average rate of agonism per total hour, hour feeding, hour in social behaviour, and hour sitting. Bars indicate one standard error. * indicates $P < .05$.

(Fig. 3.12) ($U=6$, $P=1.0$, $N=7$). Male-male (MM) agonistic interactions made up the smallest percentage of agonistic interactions in both groups (spiny forest group = 13.5%, gallery forest group = 1.6%) (Fig. 3.12), and this difference was significant ($U=0$, $P < .05$, $N=6$). Because all MF agonistic interactions were won by females, 63.0% of agonistic interactions in the gallery forest group and 60.0% of agonistic events in the spiny forest group comprised of agonism by females towards males.

There were no significant differences between groups in the proportion of feeding agonism in any three sex-dyads groups (MM, FF, MF). MF feeding agonism occurred at a greater proportion in the gallery forest group (82.7%) than in the spiny forest group (54.2%) (Fig. 3.13) ($U=12.5$, $P=0.22$, $N=13$). FF feeding agonism occurred more often in

the spiny forest group (41.7%) than in the gallery forest group (26.7%) (Fig. 3.13) (U=4.5, P=0.59, N=7). MM agonism occurred the least often in both groups, accounting for 19.0% of all feeding agonism in the spiny forest group and 4.7% of all feeding agonism in the gallery forest group (Fig. 3.13) (U=4, P=0.80, N=6).

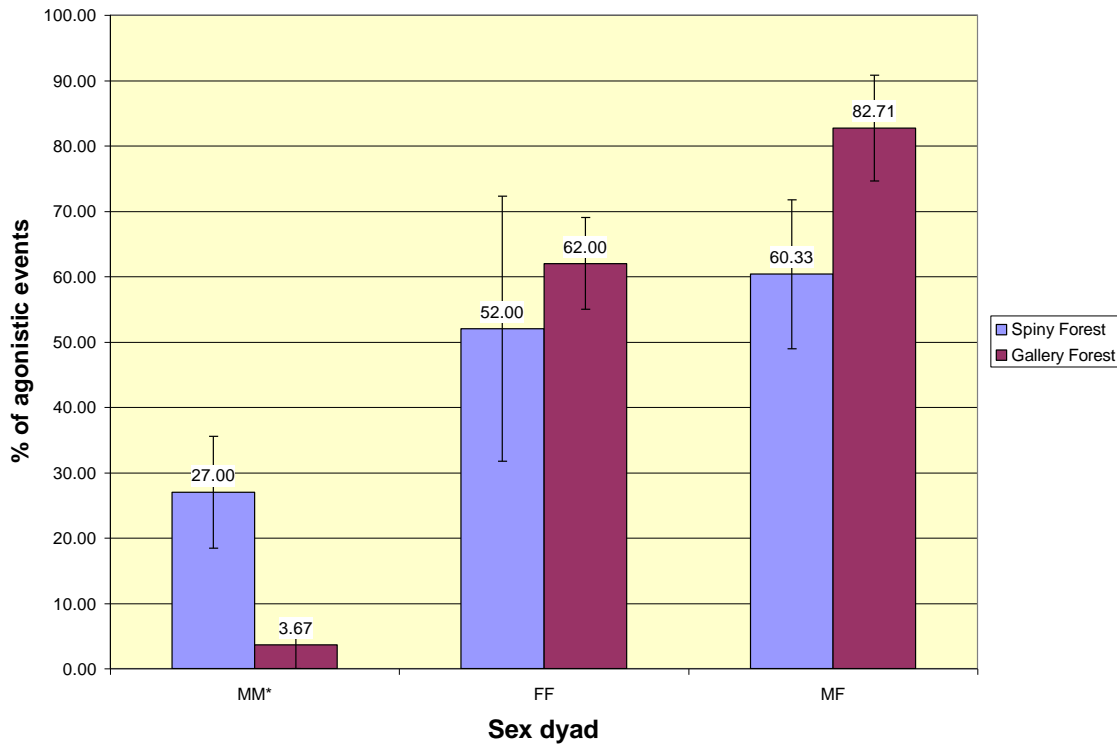


Fig. 3.12. Average proportion of all agonistic events between sex dyads. MM= male-male dyads (n=6), MF= male-female dyads (n=7), FF= female-female (n=13). Bars indicate one standard error. * indicates P<.05.

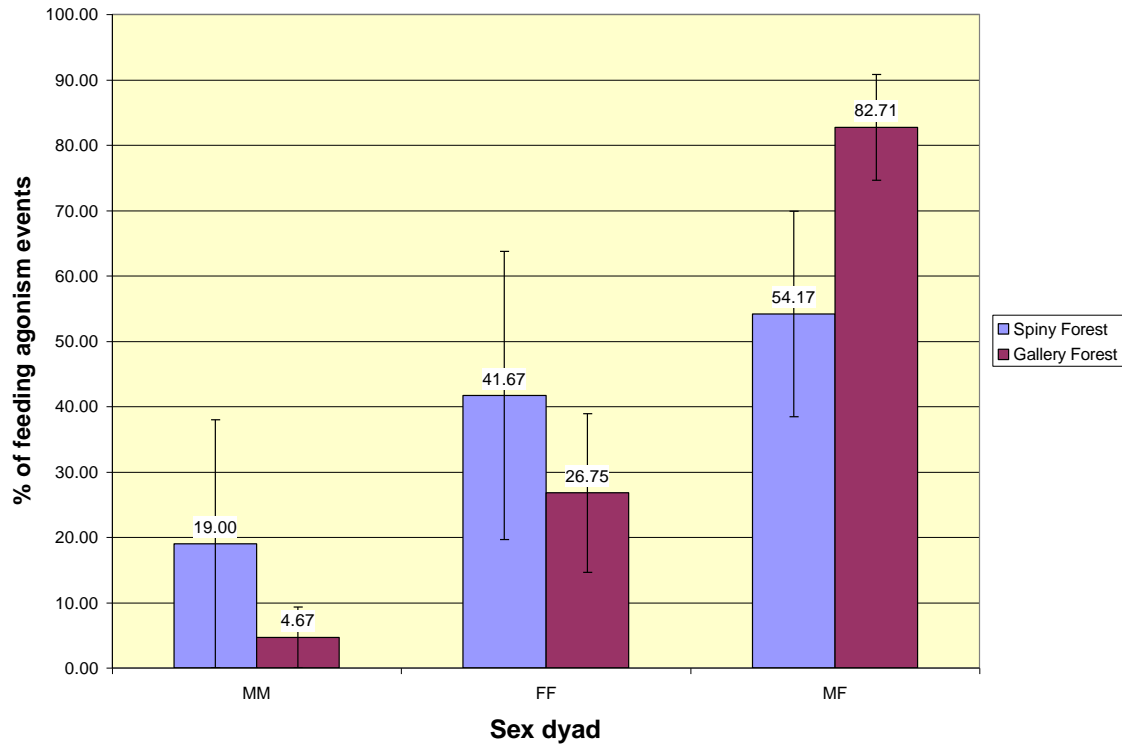


Fig. 3.13. Average proportion of feeding agonism events between sex dyads. MM= male-male dyads (n=6), MF= male-female dyads (n=7), FF= female-female (n=13). Bars indicate one standard error.

AFFILIATIVE BEHAVIOUR

Affiliative behaviour accounted for a small proportion of all daily behaviours- 0.4% in the spiny forest group and 0.19% in the gallery forest group (Fig. 3.14). The difference in proportion between the two groups was significant ($U=2.5$, $P=0.003$, $N=13$). Both groups dedicated similar proportions of time in specific affiliative behaviours, with no significant difference occurring between groups in any affiliative behaviour. Both groups spent a large majority of their affiliative time sitting close (less than one meter) to social partners. The spiny forest animals spent 66.2% of their affiliative time sitting near partners, compared with 78.9% in the gallery forest group (Fig. 3.14) ($U=7.5$, $P=0.053$, $N=13$). Grooming, the second-most frequent social behaviour for both groups, occurred

for more than twice the proportion of time in the spiny forest group (32.0%) compared with the gallery forest group (14.7%) (Fig. 3.14) ($U=7.5$, $P=0.053$, $N=13$), while *L. catta* in the gallery forest group allocated six times the proportion of time towards alloparental behaviour (6.31%) than did those in the spiny forest group (1.1%) (Fig. 3.14) ($U=10.5$, $P=0.122$, $N=13$).

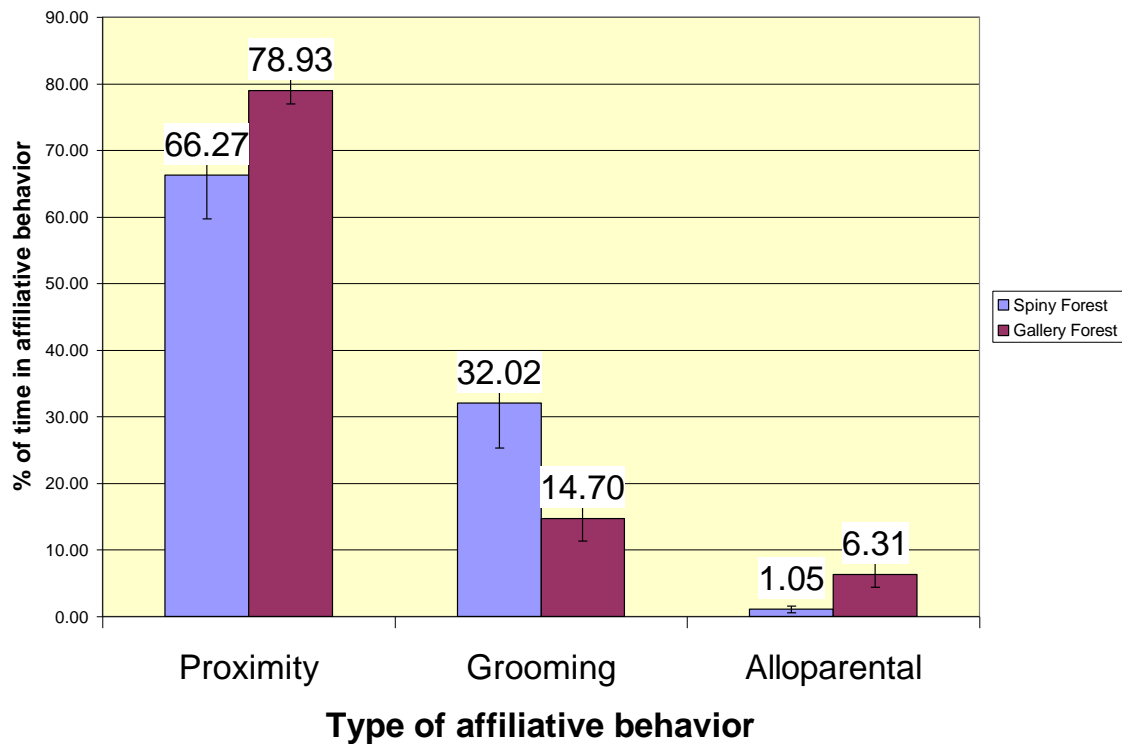


Fig. 3.14. Average proportion of affiliative behaviours. Bars indicate one standard error.

Males in the gallery forest group spent a higher average proportion of affiliative time with other males than did males in the spiny forest group (59.7% versus 40.3%, respectfully) but spent a lower average proportion of affiliative time with females than did males in the spiny forest group (42.7 % versus 59.3%, respectfully) (Fig. 3.15). These differences between groups were not significant (MM: $U=3$, $P=0.51$, $N=6$, MF: $U=3$, $P=0.52$, $N=6$). There were no significant differences in the proportion of affiliative time

spent with females between males of differing rank (spiny forest and gallery forest group: Kruskal-Wallis ANOVA Test: $\chi^2=2$, $df=2$, $P=.37$). Similarly, females of differing rank did not spend significantly different proportions of affiliative time with males in either group (Kruskal-Wallis ANOVA Test: spiny forest group: $\chi^2=2$, $df=2$, $P=.37$; gallery forest group: $\chi^2=3$, $df=3$, $P=.39$). These were no significant differences in the proportion of affiliative time females spent with other females between groups (FF: $U=2$, $P=0.16$, $N=7$, FM: $U=2$, $P=0.16$, $N=7$). Female-female affiliative interactions accounted for a similar average proportion of time in the gallery forest group than in the spiny forest group (84.0% versus 72.3%, respectfully) (Fig. 3.16), and females in the spiny forest group spent only a slightly greater average proportion of affiliative time with males than did females in the gallery forest group (27.7% versus 16.0%, respectfully) (Fig. 3.16).

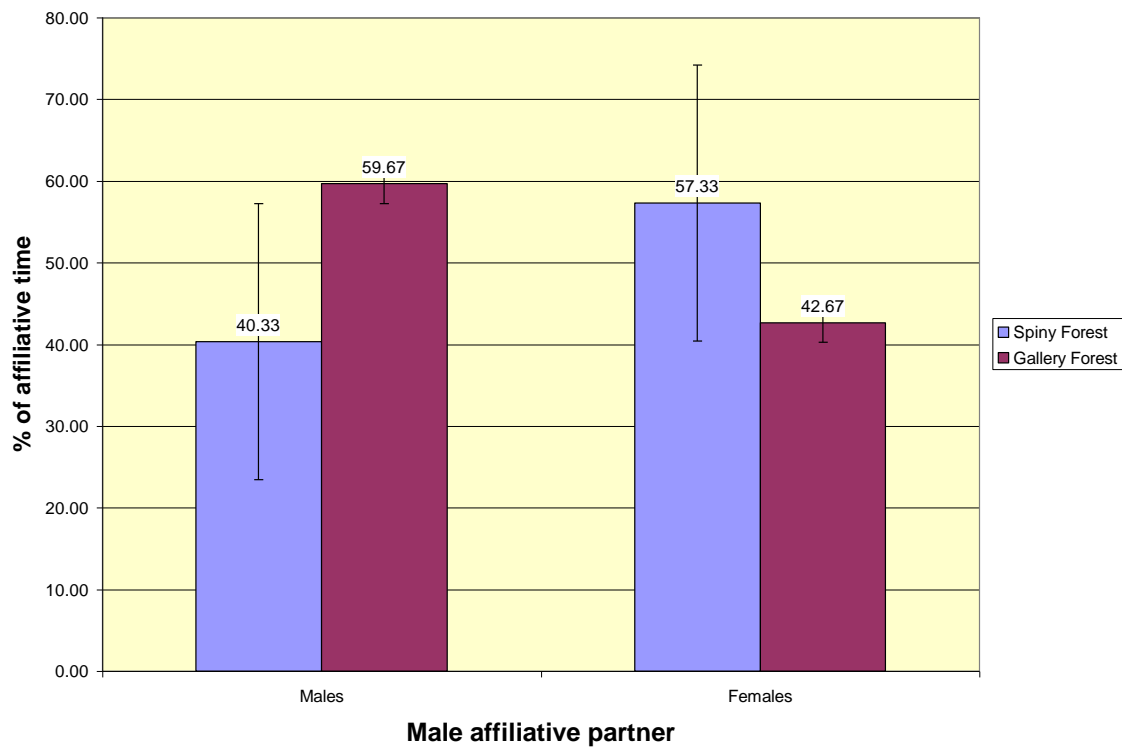


Fig. 3.15. Average proportion of affiliative time spent in sex dyads by males. Bars indicate one standard error.

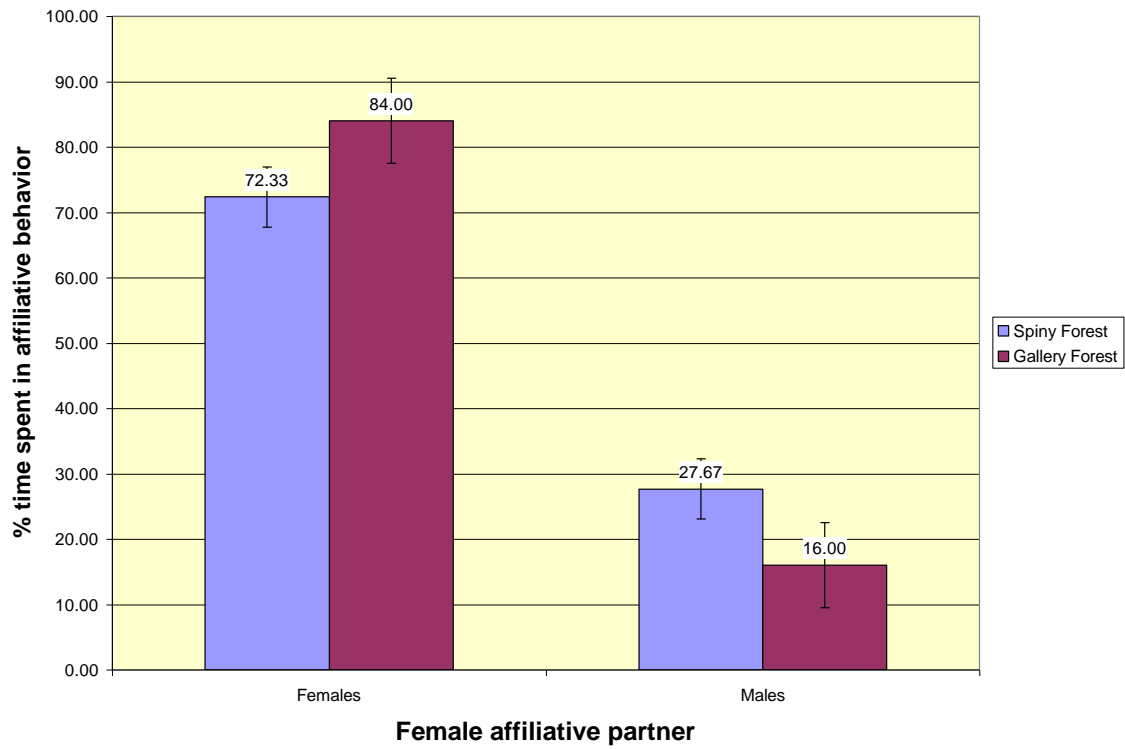


Fig. 3.16. Average proportion of affiliative time spent in sex dyads by females. Bars indicate one standard error.

CHAPTER 4: DISCUSSION

TIME ALLOCATION

Data collected supported the predicted hypothesis *Lemur catta* in the gallery forest group would spend a greater proportion of time in active behaviours. This study showed that *Lemur catta* in the spiny forest habitat spent significantly more time resting and less time feeding, foraging, and socializing. Furthermore, individuals in the spiny forest group spent a significantly greater proportion of cumulative time in “inactive” behaviours, including resting and sitting, whereas individuals living in the riverine gallery forest spent a significantly greater proportion of cumulative time in “active” behaviours, including feeding/foraging and socializing.

Dunbar (1992) suggests that time is a limiting factor in behaviours and individuals should alter the amount of time allotted to specific behaviours based on the surrounding ecological variables. *Lemur catta* living in the spiny forest were found to decrease the time spent feeding and socializing as to increase time spent resting. This inverse relationship between resting and feeding in lemurs parallels previous studies of *Lemur* activity budgets (Sussman 1977). Increased resting behaviour has also been noted for primates living in habitats defined by low quality resources, especially those living in habitats modified by humans (Marsh 1981, Menon and Poirier 1996, Estrada et al. 1999). The remaining parcels of spiny forest habitat, however, have not been modified by humans and should not be considered an inadequate habitat for primate habitation. Ecological, physiological, and behavioural factors must be considered when understanding why ring-tailed lemurs vary in activity levels between habitats.

Patterns of energy usage and acquisition differ between and even within primate species. Energy maximizing strategies denote primate behavioural patterns where individuals increase time spent in food acquisition when resources are limited, whereas energy minimizing behaviours are found in individuals decreasing activity levels when energy availability is low (Schoener 1971, Krebs and McCleery 1984). *Lemur catta* has been categorized as an energy-minimizing primate (Rasamimanana et al. 2006), and both groups in this study seem to use behavioural strategies to minimize energy usage. Both study groups tended towards bimodal activity patterns, with early morning and late afternoon active periods broken up by a long period of midday resting. The significant difference in activity patterns observed between groups seems to be caused by a prolonged resting period by the spiny forest group, which used abbreviated foraging periods during the early and later periods of the day. Energy-conservation strategies are widespread in primates (lemurs: Richard 1978, Wright 1999, Norscia et al. 2006; Atelines: Milton 1980, Estrada et al. 1999 Di Fiore and Rodman, 2001; Colobines: Dasilva 1992, Zhou et al. 2007). Energy conservation strategies (also known as energy-minimizing strategies) allow primates to maintain physiological processes, such as reproductive biology and metabolism, when energy availability is low (Barton et al. 1992, Dasilva 1992, Wright 1999, Di Fiore and Rodman 2001) or when dietary composition is based on low-nutrient food items such as leaves and grasses, by decreasing energy usage (Richard 1978, Milton 1980, Iwamoto and Dunbar 1983, Oates 1987). Energy conservation strategies may have evolved in Malagasy prosimians as a means to combat extreme climatic variability and long-periods of resource scarcity (Wright 1999) and

correspond to relatively low basal metabolic rates in all prosimians (Richard and Nicoll 1987, Snodgrass et al. 2007).

Intra-specific differences in time allocation between populations living in separate habitats or seasons with varying resource availability tend to be due to differences in energy availability (Marsh 1981, Menon and Poitier 1996, Doran 1997, Di Fiore and Rodman 2001, Hanya 2004). Primate species which subsist on leaves tend to spend more time resting than those which spend more time feeding on high-energy food items like insects and fruit, as the digestion of leaves requires high amounts of physiological energy to break down secondary compounds and high amounts of cellulose (Milton 1980, Fleagle 1999). However, *Lemur catta* are not folivorous, and both groups sought out fruit within their habitats. Thus, more specific ecological and physiological variables must be considered to explain the observed results. While this research presents no data on nutritional and caloric content of food items eaten by *L. catta* between habitats, pre-existing reports of spiny and gallery forest ecology can aid our understanding of energy availability between habitats. The floral species in the spiny forest of southern Madagascar have evolved to withstand long periods of drought and high amounts of solar radiation (Grubb 2003, Fenn 2005). Spiny forest trees have adapted to these environmental pressures by producing small and succulent fruit and leaves, which decreases evaporative water loss. Specifically, food items eaten by *L. catta* in the floral families Didiereaceae, Hernandiaceae, and Euphorbia produce small leaves and fruit (Grubb 2003). In contrast, trees on which *Lemur catta* fed in the riverine gallery forest habitat are characterized by having the ability to produce either large leaves or large reproductive parts (Blumenthal-Jones et al. 2006). *Azadirachta indica* produces large

leaves, while *Tamarindus indica* and *Pithecelobium dulce* produce fruits much larger than those in the spiny forest habitat. Moreover, trees in the gallery forest were located adjacent to the Mandare River and presumably had higher water content than those in the spiny forest. Even if water availability from plant parts was not a significant factor in metabolism between groups, individuals in the gallery forest had access to drinking water from small pools in the Mandare River and from man-made wells located in the middle of the Ankoba gallery forest. Other than slight amounts of water moisture via morning dew, no stand alone water sources were available for *Lemur catta* in the spiny forest. While *Lemur* groups in the spiny forest can maintain sufficient hydration by consuming plant parts (see Goodman and Langrand 1996), restricted water intake may serve as a limiting factor in the activity levels of ring-tailed lemurs. If the calorie content, nutritional content, and water availability of each food item in the spiny forest is small, we may expect that *Lemur catta* in the spiny forest would not be able to receive the same amount of energy per food item as *L. catta* in the gallery forest. These theoretical differences in nutritional and water content per food item must be tested and may give an indication as to how differing nutritional factors lead ring-tailed lemurs to alter activity patterns.

Thermal stress has shaped the structure and function of the spiny forest floral community, and the thermal environment must be considered as a factor in *Lemur catta* activity patterns. High ambient temperatures have been considered a significant influence on primate activity cycles (Bernstein 1972, Stelzner 1988, Hill 2006), whereas primates tend to increase their time spent in active behaviours, especially foraging, when temperatures are low (Iwamoto and Dunbar 1983, Moreland 1993, Nakayama et al. 1999). Evaporative water loss in anthropoid primates (i.e. monkeys and apes) increases

when ambient temperature rises over 30°C and rises sharply when temperatures exceed 40°C (Elizondo 1977). Stelzner (1988) has suggested that ambient temperature is a primary constraint to behaviour, as primate physiological abilities to reduce thermal stress are limited. Data from anthropoids living in high thermal environments have corroborated these theories. Pigtailed macaques (*Macaca nemestrina*) increase resting behaviour and decrease the proportion of time spent traveling, feeding, and grooming when ambient temperatures were highest (Berstein 1972). Chacma baboons (*Papio cynocephalus ursinus*) tend to spend the greatest amount of time resting in shade when perceived temperatures (i.e. humidity) are greatest (Hill et al., 2003, Hill 2006). Stelzner (1988) found that yellow baboons (*Papio cynocephalus cynocephalus*) use high-vegetative areas most often when the ambient temperature was highest, while Pochran (2000) also found that high humidity level led yellow baboon groups to increase resting behaviour while seeking shade more often than at any other period of the day. *L. catta* in the spiny forest follow these same trends. This study was conducted during some of the hottest months in southern Madagascar and daily maximum temperatures at Berenty reached over 40° C on many days during the duration of the study. Despite the two habitats being relatively close in distance, differences in canopy size and cover influenced the amount of radiation which reached the study groups, and thus, influenced the ambient temperatures each study group experienced. One day, for example, temperatures in the spiny forest reached more than 46° C, but temperature readings taken in the gallery forest at the same time of day revealed that temperatures did not rise above 40° C. Moreover, *Lemur catta* in the spiny forest had few refuges from the sun, as small tree trunks, branches, and leaves created little shade throughout the forest. The spiny forest group,

therefore, most likely increased time spent resting in the shade to avoid intense solar radiation and to decrease evaporative water loss. Active behaviours, especially locomotion and foraging were most pronounced when temperatures were at their lowest, the early morning and later afternoon, and movement and foraging occurred at a very fast pace during the coolest times of the day.

Lemur catta in the spiny forest may use an extreme energy-minimizing strategy because of a naturally low basal metabolic rate (BMR). The BMR of Stepsherine primates is considerably lower than that of almost all Haplorhine primates (Daniels 1984, Muller 1985, Richard and Nicoll 1987, Snodgass et al. 2007) and is below the predicted values estimated by the Kleiber equation (which predicts a species' BMR according to body size, diet, and locomotion) (Snodgass et al. 2007). The BMR of *Lemur catta* deviates from the predicted value more than any other primate tested, with a BMR 69.22% lower than predicted by the Kleiber equation (Snodgass et al. 2007). A low metabolic rate limits energy processing and usage by lowering the rate of oxidation, which in turn lowers the amount of energy processed by the body. All *Lemur catta* use energy-minimizing behavioural strategies because of this inherent physiological characteristic (Rasamimanana et al. 2006), but differences in energy-availability between habitats may lead those living in the spiny forest to maximize energy retention via increased resting behaviour. Moreover, low metabolic rates may not allow ring-tailed lemurs to increase active behaviours to search for more energy in the home range.

VIGILANCE BEHAVIOUR

Lemur catta in the spiny forest group were predicted to exhibit a greater rate of anti-predator vigilance than those in the gallery forest group due to greater exposure to potential predators because of a lower amount of canopy cover and fewer refuges. The data from my study support this prediction. In fact, the anti-predator vigilance rate was nearly four times greater in the spiny forest group than in the gallery forest group. There were, however, no significant differences between groups with respect to the rate of inter-group vigilance. These results suggest that ring-tailed lemurs in the spiny forest behave as though they are under a greater risk of being preyed upon and react to this increased risk with a higher level of vigilance behaviour. Numerous variables must be taken into account in order to understand why *Lemur catta* in the spiny forest group were at greater predation risk.

Primarily, predation risk may be a result of differing levels predator abundance and/or attempted attacks. Dogs were seen to chase each group once, and both groups responded to these attacks with a long period of vocalizations associated with terrestrial predators (Sauther 1989, Gould and Sauther 2007b). A single Madagascar buzzard (*Buteo brachypterus*) was observed in the spiny forest, but no predator alarm calls were given by *Lemur catta* in response to the raptor. No aerial predators were observed in the gallery forest group. These observations suggest that there were no observable significant differences in predator abundance between habitats. Using Sauther's (2002) scale of predator pressure, both groups of *Lemur catta* observed in this study are considered to be under a low predator pressure, as they experience less than four predation events per month. The categorization of 'low' predation pressure does not imply that *Lemur catta* in

this study were under no risk of predation but rather helps to contextualize predation pressure in both groups.

Group size also tends to affect predator vigilance rates (Clutton-Brock and Harvey 1977, Teaborgh 1983, Sauther 2002, Overdorff et al. 2002), but group size was fairly similar in both groups. The gallery forest group had one more adult individual than did the spiny forest, but it is unlikely the presence of an additional adult led to a significant difference in predator-directed vigilance rates. Operational sex ratios were different between groups, but Gould (1996a) found that *L. catta* in a gallery forest at Beza Mahafaly, a site in southwest Madagascar, show no sex differences in predator vigilance rates. Thus, the slight difference in operational sex ratio most likely did not cause the noted difference in predator-directed vigilance rates.

Assuming that both biological and social variables have equal bearing on anti-predator vigilance rates between groups, environmental factors must be considered as the remaining potential influence on *Lemur catta* predator-directed vigilance behaviour. The gallery forest is characterized by more canopy cover than the spiny forest, and several tree species in the gallery forest, including *Tamarindus indica*, *Pithecelobium dulce*, and *Azedarach indica*, have dense canopies with a large percentage of canopy cover. This increased cover most likely makes it more difficult for potential aerial predators to spot *L. catta*. Trees in the spiny forest, however, are characterized by their small leaves and lack of a continuous canopy, making it easier for predators to maneuver between trees when attempting to capture prey. Sauther (2002) suggests that large raptors in southern Madagascar may be too large to successfully maneuver through the canopy of a gallery forest but may be instead more successful preying upon lemurs in an open environment

(Gould and Sauther 2007b). Most trees in the gallery forest provide locomotive routes between trees, providing protection from potential terrestrial predators by decreasing the amount of travel time which occurs on the ground. Arboreal travel routes, however, are limited in the spiny forest, because trees have few if any horizontal branches. Consequently, the terrestrial predation risk may have been greater in the spiny forest group. However, this suggestion is based on observation only and must be further investigated using data on total vertical level use.

These data parallel primate studies on predation pressure which cite ecological variables as key to predation risk. Boinski et al. (2003) found that despite equal amounts of predator abundance between habitats, the Bolivian squirrel monkey (*Saimiri boliviensis*) and the black crowned Central American squirrel monkey (*Saimiri oerstedii*) living in open habitats experienced a greater number of predator attacks per observed hour and showed a greater rate of preemptive predator vigilance than the common squirrel monkey (*Saimiri sciureus*) living in a closed canopy forest with a dense understory. Moreover, *Saimiri oerstedii* only engaged in preemptive vigilance when occupying habitats characterized by open skies and a small amount of understory cover. Vervet monkeys (*Cercopithecus aethiops*) show a higher rate of anti-predator vigilance events while in an open habitat characterized by short *Acacia* trees than while in a riverine habitat characterized by large trees (Enstam and Isbell 2002). Chacma baboons (*Papio cynocephalus ursinus*) living in open habitats with sparse vegetation in the Namib Desert decrease predation pressure from leopards and lions by using safe refuges during most activities and move quickly through their habitat when away from these refuges (Cowlshaw 1997a). These studies show that primates under varying levels of predation

pressure are able to change their responses to potential predators and are sensitive to changes in predation risk, especially as the structure of the occupied habitats varies. My data suggest that the same is true for *Lemur catta* living in varying habitats, and future data collection in new habitats and varying predator abundance levels could reveal different methods of predator avoidance.

If engaging in specific behaviours increases predation risk, individuals are more likely to exhibit more vigilance during these behaviours than during other low-risk behaviours (Cords 1995). *Lemur catta* in the spiny forest showed substantially greater sensitivity towards predators while sitting and locomoting when compared to *L. catta* in the gallery forest. The difference in vigilance while moving is most likely related to differences in habitat structure. Without a continuous canopy through which to move, *Lemur catta* in the spiny forest were most likely forced to move between trees on the ground. Village dogs are a potential predator and their presence produced the longest state of predator alarm-calling and vigilance observed in the spiny forest during this study, perhaps making individuals more alert towards potential predators while moving on the ground. This increase in potential risk was reduced by increasing the amount of vigilance towards potential predators while moving through their habitat. Additionally, *L. catta* in the spiny forest entered two open and potentially high-risk habitats to forage on high quality food items. The spiny forest group entered a cleared field containing several *Tamarindus indica* trees located next to a parcel of the spiny forest on several days. This empty field contained no refuges except for the few *Tamarindus indica* trees, and individuals always ran through the field, often scanning their environment until they reached the *T. indica* trees. During the final days of the study, individuals in the spiny

forest foraged in the sisal plantations adjacent to the northern-most parcel of spiny forest. To access sisal flowers in the fields, which contain no refuges, individuals ran consistently through the habitat, only stopping under sisal plant for a few seconds before continuing. Although these feeding sites were entered far less often than the spiny forest, individuals balanced the benefit of accessing high quality resources by increasing vigilance while moving through the corridors between the feeding sites. Sauther (2002) also found that small groups of *Lemur catta* tend to move more quickly when entering new habitats than did larger groups under low-risk of predation. However, more specific data may be needed to understand the trade-off between accessing novel and beneficial resources and the predation risk accompanied by the usage of these resources.

L. catta in the spiny forest group had a vigilance rate while sitting of more than double that of those in the gallery forest group. Vigilance while sitting should be expected, as individuals are generally sitting up, alert, and aware of their surrounds. Observed differences in vigilance rates while sitting in this study may have occurred because an open canopy may increase the abilities of individuals to observe a predator. It is possible that ring-tailed lemurs in the spiny forest were aware of the sensitivity towards predators and use their time spent sitting as a way of increasing predator detection. Individuals in the gallery forest, however, may have a decreased reaction time to potential predators, as the amount of foliage may block their visual line of sight and prevent their response to a potential predator. Assuming equal predator abundance, Enstam and Isbell (2002) suggest that habitats with fewer trees and foliage are a potential benefit to vervet monkeys, as their ability to see potential predators at a greater distance would increase their vigilance but also prevent potential attacks. Enstam (2007) suggests that vervet

monkeys take advantage of open habitats by selectively using certain aspects of the microhabitat (i.e. specific trees or branches) to increase the visibility of predators. Few studies of primate predator sensitivity have taken behavioural sensitivity into account, but Cords (1995) found that blue monkeys (*Cercopithecus mitis*) were more vigilant while sitting than while engaged in other behaviours, including social behaviours, and suggests these results emerged because sitting and resting behaviour occur at a greater distance from nearest neighbours. Future studies of *Lemur catta* behaviour in the spiny forest habitats can measure inter-individual distance while sitting. Moreover, future studies may investigate whether ring-tailed lemurs sit in particular areas of their habitat which provide a better view of potential predators.

L. catta in the spiny forest were predicted to have a significantly greater proportion of predator vigilance events while on the ground and at the highest levels of the canopy, as the two vertical strata theoretically place *Lemur catta* at risk of territorial and aerial predators, respectively. The data do not support these predictions. In fact, individuals in the gallery forest had a significantly greater proportion of vigilance events while on the ground than individuals in the spiny forest. The data, however, must be taken with caution, as there were very few predator vigilance events in the gallery forest group. Individuals in the spiny forest group did, however, exhibit a significantly greater proportion of vigilance events while in the lowest proportion of the habitat, which may have occurred because the trees in the spiny forest are much shorter than those in the gallery forest, producing a greater sensitivity to ground predators while in the lowest levels of the trees.

L. catta in the spiny forest were predicted to exhibit a greater proportion of vigilance events while they were more than five meters away from their nearest neighbour. The data do not support this prediction. In fact, vigilance while more than five meters from their nearest neighbour accounted for the lowest percentage of all predator-directed vigilance events. This result was surprising, as individuals far away from neighbouring conspecifics are theorized to be at greater risk to be taken by a predator than individuals near conspecifics (Miller 2002). Increased spatial cohesion, while theoretically beneficial as it can decrease individual predation risk (Hamilton 1971), increases the chance of agonism between conspecifics (Hirsch 2007). Despite facing increased predation pressure, the costs of increased agonism may have led individuals to maintain social spacing distances similar to those of individuals under less predation pressure. While these data are telling, future studies of the influence of predation pressure on social spacing could be more specific. Data on total group spread and the number of individuals within a specific radius distance (Treves 1999), for example, may tell how the geometry of a social group varies as predation risk changes. Patterns of spatial proximity related to predation pressure may be seasonal in nature and could change with varying ecological and social variables. For example, Gould (1996a) suggests that predation pressure is higher in the dry season because new born and weaning infants attract potential predators. Because this study was conducted during the birth and weaning season, both groups may have similar spatial cohesion patterns while vigilance because of an equal need to protect infants. Long-term studies may determine if spatial proximity during vigilance changes between seasons in *L. catta* inhabiting spiny forest habitats.

Predator sensitive foraging theory states that primates should sacrifice foraging in high-risk areas and at great distances from other group members (see review by Miller 2002). *Lemur catta* in the gallery forest were predicted to spend a significantly greater amount of time feeding on the ground and in high-risk areas within the canopy of trees. Sauther (2002) found that *Lemur catta* under high predation risk foraged on the ground significantly less than those under low predation pressure, but data from this study do not support this prediction. Despite differences in anti-predator vigilance rates, there were no significant differences in the proportion of feeding time in any vertical level. *L. catta* in the spiny forest did feed most often in the middle vertical section, where aerial and territorial predators are less likely to access lemurs. However, it not known how much resource availability affected vertical level choice in this group, as these data were not recorded in this study.

L. catta in the spiny forest were predicted to spend a greater proportion of time feeding within two meters and between two and five meters from a nearest neighbour. Increasing group cohesion has been observed while animals are under risk of predation (Lima and Dill 1990, Treves 1999), as individuals far from the center of the group are most exposed to predators. Furthermore, individuals who are farther from other conspecifics are more likely to be taken by a predator (Hamilton 1974). Being close to a conspecific may allow individuals to use social cues of predation risk, such as observing the timing, direction, and severity of vigilance towards potential predators (Hirsch 2002). The data from this study do not support the hypothesis or agree with other studies of primate predator sensitive foraging. While individuals in the spiny forest spent a greater proportion of time feeding within two meters of the nearest conspecific, the difference

between groups was minimal and not statistically significant. In fact, no nearest neighbour category differed significantly between groups or differed by more than six percentage points. Theoretically, if increased predation pressure compels individuals to feed in greater proximity to one another, nearest neighbour distance should stay relatively equal no matter which food items individuals exploit. The data show that individuals in the spiny forest group spent a greater percentage of time within two meters from a neighbour while feeding on fruit than while feeding on leaves. Similarly, individuals spent a greater proportion of time more than five meters from a neighbour while feeding on leaves than while feeding on fruit. It appears as though *L. catta* in the spiny forest adjust their spatial proximity while feeding to the particular food item being eaten and do not maintain a basal nearest neighbour distance to reduce predation risk while feeding.

Despite the observed differences in anti-predator vigilance, and therefore predation risk, the two groups showed no perceivable differences in predator sensitive foraging tactics. While many authors consider foraging a high-risk behaviour (Lima and Daal 1990, Cords 1995, Miller 2002), *Lemur catta* in both groups were less vigilant while feeding than while sitting or moving through their environment. Moreover, there were no statistically significant differences in rates of anti-predator vigilance while feeding between groups. I suggest that predation risk, while greater in the spiny forest, is not strong enough at Berenty Reserve to significantly influence foraging strategies of *L. catta* living in the spiny forest habitat. Foraging and feeding are crucial behaviours, as energy and nutrients must be obtained in sufficient amount to support physiological processes. Because female *Lemur catta* were under increased need for resource acquisition due to the gestation and lactation period, individuals did not reduce time spent feeding in

potentially high-risk areas. While these results contradict proposed predator sensitive foraging theories, they are similar to studies by Isbell and Enstrom (2002) and Di Fiore (2002), both of which found that primate foraging tactics were more affected by resource distribution than by predation pressure. Both reports suggest that individuals are more likely to combat potential predator attacks by increasing vigilance rates instead of compromising potential resource acquisition.

This proposition differs from the study of *L. catta* predator sensitive foraging conducted by Sauther (2002) at Beza Mahafaly in Southwest Madagascar. Differences in utilization of predator sensitive foraging tactics between research sites may be due to varying levels of predation pressure. Gould (1996b) found that *Lemur catta* at Beza Mahafaly Reserve show vigilance rates of between 0.75-3.5 predator vigilance events per fifteen minutes session. Because I used predator rate per hour, the rates reported by Gould (1996b) can be extrapolated to a range of three to fourteen predator vigilance events per hour observed. This compares to a range of 0.66-1.37 predator-directed vigilance events per hour recorded in this study. Moreover, Gould (1996b) found that *L. catta* at Beza Mahafaly Reserve spent between 0.5-17 % of all time observed in vigilance towards predators, while *L. catta* in the spiny forest of Berenty Reserve only ranged between 0.17-0.37% of all time observed in predator-directed vigilance behaviour.

What could be the cause of a potential decreasing predation risk between populations and research sites? Predator abundance is most likely lower at Berenty Reserve compared to Beza Mahafaly Reserve. This proposal is difficult to support, as no data on predator abundance has been carried out at Berenty Reserve. However, indirect evidence can be used. Sauther (2002) reported that *L. catta* groups, which she studied in

the gallery forest at Beza Mahafaly experienced more than three predator encounters per month, but in my study, only one predation attempt was recorded per group over a two month period. A long-term study in the spiny forest of Berenty Reserve may reveal that predator pressure is greater than observed in this study, but for now, comparative observations suggest that predator abundance is lower at Berenty Reserve. Researcher observations have noted that Madagascar Harrier Hawks (*Polyboroides radiata*) do not exist at Berenty Reserve and Madagascar Buzzards have scarcely been observed (Rambelozrivony pers. comm.), but these predators are regularly observed and frequently prey on *L. catta* at Beza Mahafaly (Gould and Sauther 2007b). Furthermore, *L. catta* in all habitats at Berenty tend to show less-heightened awareness of large yet non-lethal raptors (Gould per. comm.). For example, the black kite (*Milvus migrans*), a small raptor, are numerous in the scrub forest, are similar in shape and size to other raptor predators which are known to prey on *L. catta*, and elicit anti-predator responses from *Lemur catta* at Beza Mahafaly (Gould per. comm.). However, *L. catta* in the scrub/spiny forest tend to ignore kites and were often vigilant prior to kites flying past the group. While anecdotal, this example gives an indication that predation risk is significantly lower at Berenty Reserve. Berenty Reserve is a relatively small strip of forest and most of the surrounding forests have been destroyed for agricultural usage. This has greatly reduced the amount of fauna in the larger geographic range, and thus, has most likely led to a sharp decrease in the number of predators occupying the forest. Moreover, the high volume of tourists which visit Berenty Reserve may influence the predation tactics of any remaining predators. These predators avoid human contact, and thus, most likely reduce contact with highly observed lemurs.

Comparative analysis between research sites can be difficult, but I suggest that these seemingly opposing patterns of predator sensitive foraging tactics between Berenty Reserve and Beza Mahafaly Reserve provide a new example of behavioural flexibility in ring-tailed lemurs. I do not suggest that ring-tailed lemurs do not have the ability to change foraging tactics in light of differing predation risk, but instead are able to incorporate less costly behaviours, such as increased vigilance, to maintain adequate resource acquisition when predation pressure relative to other field sites is low. A theoretical all or nothing approach to predator sensitive foraging may be costly to a group living in habitats with low resource availability, and thus, predator sensitive behaviour is more likely to revolve around non-foraging behaviours; in this study, anti-predator vigilance is the only indicator of increased sensitivity to predators. *L. catta* in the spiny forest most likely make the decision to not sacrifice quality feeding sites to avoid predators, as the cost of avoiding quality feeding resources may outweigh the cost of predation risk, which is most likely relatively low compared to other research sites.

AGONISTIC BEHAVIOUR

FEEDING COMPETITION

I hypothesized that *L. catta* in the gallery forest would exhibit higher feeding agonism than those living in the spiny forest. This hypothesis was based on the usurpability theory, which states that primates will contest for food items at a greater rate when those food items are large because of the longer required handling times (Pruetz and Isbell 2000). The predicted feeding agonism hypothesis was not supported by the data in this study. Indeed, the size of fruits, especially the fruits of *Tamarindus* and

Pitheicilobium fruits, were larger in the gallery forest than those in the spiny forest, but this trend did not lead individuals to compete for food more often than individuals in the spiny forest. Alternatively, high rates of feeding competition were associated with the consumption of small fruit items in the spiny forest group. Therefore, alternative variables should be considered when exploring feeding competition between *L. catta* groups.

Primarily, differences in dietary composition could be a major contribution to differing levels of feeding competition between groups or species (Isbell 1991). Fruit, which ring-tailed lemurs seek in times of environmental stress (Mertl-Millhollen et al. 2003), made up a significantly higher proportion of the diet of individuals in the spiny forest group than in the gallery forest group. Fruit tends to be a more clumped and nutritious resource, and primate species which exploit fruit are more likely to compete over these resources. Plant foliage, however, tends to be competed over less often than fruit because it is more spatially ubiquitous within a habitat (Wrangham 1980, van Schiak 1989). Similar to this idea, individuals in the gallery forest group spent a majority of their time feeding on leaves and competed for food less often than individuals in the spiny forest group. Studies of primate feeding agonism have shown that feeding agonism increases with the overall intake of fruit items within a species or a group (Whitten 1983, White and Wrangham 1988, van Schiak and van Noordwijk 1988, Janson 1988, Barton and Whiten 1993, Sterk and Steenbeek 1997, although see Pazol and Cords 2005 for alternative proposal). No data exist on food items competed over during this study, but previous studies have found that *Lemur catta* tend to compete over fruits significantly more often than leaves, especially during the low-yield dry season of southern

Madagascar, most likely because fruit provides a significant amount of calories, micronutrients, and water (Sauther 1993). Thus, it is possible that differences in feeding competition observed in this study may be the result of differential dietary composition.

Social spacing must also be considered as an important variable in feeding competition (Hirsch 2007). In this study, social spacing was significantly different between groups with respect to both fruits and leaves. If plant reproductive parts are clumped in space within a home range, it is expected that individuals reduce spatial proximity to conspecifics while feeding on these items. Moreover, if dietary composition were the only cause of differences in feeding competition, it would be expected inter-individual spacing to be roughly similar between groups when they feed on fruit. Interestingly, individuals in the spiny forest spent significantly more time close to a conspecific while feeding on fruit, potentially indicating that fruit items in the spiny forest are more clumped than those in the gallery forest. Tree canopy size and the number of feeding sites within a tree were not measured in this study, but observations of the two habitats may explain the differences in inter-individual spread. *Lemur catta* in the gallery forest group spent significantly more time feeding on fruit while far from a neighbour than *L. catta* in the spiny forest, and the larger size of tree crowns and distribution of fruit items within these trees may have led to this trend. *Tamarindus indica* and *Pithecellobium dulce* are large fruiting trees which contain fruit throughout the tree crown. While feeding on the fruit of *P. dulce*, individuals frequently made contact calls to ascertain the location of other group members and were the only lemurs visible while data collection occurred. Large crowns may allow individuals to increase inter-individual spread while feeding on high quality resources and, in turn, reduce the rate of agonistic

encounters over these items. Alternatively, fruiting trees in the spiny forest tend to have small crowns with feeding sites in close proximity to one another; small tree crowns may decrease the amount of individuals able to feed within a crown and potentially increase the chance of individuals competing over resources within the tree. On two occasions in the spiny forest, I observed females threatening males who were attempting to enter feeding trees, most likely because space within a single tree crown was limited to those already feeding within the tree. Trees within the gallery forest, however, were too big for any one individual to restrict access of another individual to a feeding tree.

Patch size has been identified as a primarily important variable to feeding agonism by studies of various primates. The influence of the particular size of a feeding site, however, differs between studies. Along with site depletion time, Pruett and Isbell (2000) found that vervet monkeys (*Cercopithecus aethiops*) had more agonistic interactions in larger patches than in smaller patches. Squirrel monkeys (*Saimiri oerstedii* and *S. sciureus*) increased the rate of agonism over food items in large trees, but decrease competition within the smaller trees (Mitchell et al. 1991), although the rate of agonism did decrease when groups fed in the largest trees available, indicating that competition may decrease when individuals are spaced far away from one another. Data from other studies parallel data from this study. White and Wrangham (1988) found that common chimpanzees (*Pan troglodytes*) spent a greater amount of time feeding in small patches and had higher rates of feeding agonism than pygmy chimpanzees (*Pan paniscus*), which tended to feed in large feeding trees and experienced lower rates of feeding agonism. Barton and Whiten (1993) also found that as food biomass within the habitat of olive baboons (*Papio anubis*) decreased, the size of and distance between food patches

decreased, resulting in an increase in feeding agonism. Similarly, Japanese macaques increased competition during the winter time when preferred food items occurred in smaller patches (Saito 1996). Sauther (1993) found that males had a higher rate of feeding competition with other males during the dry season when the decreased size of feeding patches led to an increase in time spent in close proximity to other males.

Many studies of primate feeding competition focus on agonism between females, as many female primates exhibit linear dominance hierarchies and demand access to high quality resources to ensure lactation and gestation. Female *Lemur catta* in the gallery forest habitats tend to direct feeding agonism towards males more often than other females (Jolly 1966 and 1984, Sauther 1993) and are aggressive towards males more often during the dry season when food is limited and females are lactating (Sauther 1993). Do females compete with males differently between habitats? There is no indication that females increased the proportion of aggression towards males because of increased general feeding agonism or *potential* limitations in energy availability. Females in the gallery forest may have had a higher proportion of feeding agonism events with males as a way to compensate for an earlier lactation period than females in the spiny forest. Decreasing the proportion of agonism towards females may be a way to avoid contest competition with related females caring for new-born infants. This explanation, however, should be taken with caution, as the total rate of feeding agonism may be a better indication of how females competed for food with one another.

The study of primate feeding competition is complex and necessitates the inclusion of many other ecological and social variables. In terms of primate feeding ecology, there have been no long-term studies of spiny forest microhabitat structure,

including the size of tree crowns, and the distance between feeding sites, and the amount of feeding sites within trees. Recording food item and species for which individuals compete could help determine if an asymmetrical relationship exists between the amount of time spent feeding on a food item and the amount of competition which occurs over those food items. Nearest neighbour distance, which was recorded in this study, is only one method of discerning how spacing affects competition. The number of individuals within a feeding patch could be recorded, while the number of individuals within certain nearest neighbour distances would provide greater insight into the dynamic of total group spacing while feeding on particular food items. Studies of feeding competition in the spiny forests and other non-gallery forest habitats will provide greater insight into the varying nature of resource acquisition and socioecology in *Lemur catta*.

Finally, the comparison of feeding agonism between the spiny forest and a secondary gallery forest with introduced trees may be different that feeding agonism rates in primary gallery forest in other areas of Berenty and Beza Mahafaly Reserves. Introduced trees may provide fall-back resources for lower ranking group members on which to feed, potentially reducing feeding agonism in Ankoba forest. The leaves of *Azadaracta indica* and *Leuceana sp.* were sought after by *L. catta* in the gallery forest group, but if these introduced species were not available, would feeding agonism rates increased? A more comprehensive review of feeding agonism between forest types may be required in order to fully understand how food selection and availability affect feeding agonism.

AFFILIATIVE BEHAVIOUR

Data from this study supported the proposed hypothesis that differences in time spent in affiliative behaviours would be related to time spent in social behaviours. Why would *L. catta* in the gallery forest group spend significantly more time in affiliative behaviour than those in the spiny forest group? Two main theoretical approaches must be considered. First, differing patterns of time allocation may lead to varying amounts of time spent in social behaviours. As previously proposed, ecological factors, such as decreased energy availability and increased ambient temperature, most likely constrain the time budgets of *L. catta* the spiny forest habitat and limited the amount of time spent in non-essential behaviours. Individuals in the gallery forest group spent more time foraging and engaged in social behaviours more often than those in the spiny forest group. Studies of primate time allocation patterns both between seasons and populations occupying different habitats reveal that several primate species reduce time spent in affiliative behaviours while increasing self-maintenance behaviours. Altmann (1980) found that lactating female savanna baboons (*Papio anubis*) at Amboseli Nature Reserve decreased time spent in social activities during the lean dry season in order to increase time spent foraging. Two comparative meta-analyses of baboon (*Papio spp.*) behaviour and ecology have shown that time spent grooming is a positive function of daylight hours (i.e. total time available for behaviours) and a negative function of time spent feeding and moving (Dunbar 1992, Hill et al. 2003). Isbell and Young (1993) also found that vervet monkeys (*Cercopithecus aethiops*) in Amboseli National Reserve, Kenya reduced time spent in social activities (specifically grooming) during the dry season in order to increase time spent foraging. Many primate species, however, do not alter the amount of time spent in social behaviour between varying ecological conditions. Whiten et al. (1987)

found that the time spent in social behaviour between separate populations of baboons living in different ecological contexts did not differ, and the authors argue that a cut-off point must exist for time dedicated to resting and socializing, as both behaviours are essential for the maintenance of physiology and social relationships. Similarly, Di Fiore and Rodman (2001) found no difference in time spent in social behaviours between wet and dry seasons in lowland woolly monkeys (*Lagothrix lagotricha poeppigii*) and suggest that groups are able to maintain time for socializing by changing foraging tactics. Hanya (2004) also found no significant differences in the amount of time spent in social activities in Japanese Macaques (*Macaca fuscata*) between the summer and winter seasons when food availability and the amount of daylight differ. In my study, an increase in time spent resting may help to maintain social relationships between individuals, as individuals sleep either close or in contact. Rest was not recorded as a social behaviour in this study, as resting individuals and their nearest neighbours could not be seen at all times. Yet if social relationships are strengthened during resting via close proximity, individuals in the spiny forest group may be able to decrease time spent in affiliative behaviour while active while still maintaining social relationships with other group members. The spiny forest group was relatively small, and a small social group may be able to decrease time in active social behaviours while maintaining social relationships. Social behaviour in ring-tailed lemurs does appear to be a positive function of time spent in active behaviours, and the group living in the spiny forest reduced time spent in social behaviour, along with other “active” behaviours, in order to save energy due to high ambient temperatures and low water availability.

Gould (1996b) has suggested that *Lemur catta* (especially males) use affiliative behaviour and spatial proximity as a way to decrease the likelihood of being taken by a predator. If true, *L. catta* under greater predation risk should be expected to increase the time spent in spatial proximity in order to counteract predation risk. Results from this study do not support this suggestion. While time spent in close proximity to conspecifics is lower in the spiny forest group, these individuals could use spatial proximity via resting behaviour to reduce the risk of predation due to increased predation risk, as has been shown in other primates (Day and Elwood 1999, Ramakrishnan and Cross 2001). More specifically, Gould (1996b) has suggested that males use affiliative behaviours to gain spatial proximity to females, who tend to be located towards the center of group. Males in the spiny forest did spend more affiliative time with females than did males in the gallery forest group, but both percentages were close to fifty percent and not significantly different from one another. Male rank in both groups did not affect the amount of time an individual spent in affiliative behaviour with females. Moreover, time dedicated to affiliative behaviour with females was so low (.1% of all behaviours) that it may not play a significant role in the reduction of predation pressure. These results suggest that time allocation may be the only variable which affects affiliative behaviour between ring-tailed lemur groups, with both groups showing similar patterns of types of affiliative behaviours in which individuals engage in affiliative patterns between males and females.

CHAPTER 5: CONCLUSIONS

This study has shown that ring-tailed lemurs (*Lemur catta*) living in different habitats exhibit the ability to change rates of behaviours, most likely in response to varying aspects of ecology within each habitat. Studies of primate behavioural flexibility are extremely important in understanding how primates sustain fitness levels while coping with changes in resource availability and other environmental variables. This study explored the behavioural strategies of two groups of a single species concurrently and attempted to demonstrate that primate species shift behavioural patterns across ecological parameters to increase proximate fitness. Moreover, the study of primates in low-yield habitats increases the knowledge of how these animals expand their geographic range outside of high-yield riverine forests. The alternation of behavioural strategies between habitats should be expected in a species which have evolved to survive in ecologically variable habitats. This study adds to the growing literature of primate behavioural adaptability by identifying how ring-tailed lemurs adjust key group living behaviours when faced with different ecological situations. This study has revealed the following behavioural trends between two groups living in vastly different ecological conditions: 1) The gallery forest group spent a greater proportion of time feeding and searching for food; 2) the spiny forest group spent more time resting than the gallery forest group, perhaps to directly avoid high ambient temperatures and/or to minimize energy usage because of lower biomass within their home range compared to the gallery forest; 3) Less time was spent socializing in the spiny forest group, perhaps because this group spent much of their daily activity budget resting. Ring-tailed lemurs in the spiny forest group may be able to maintain social bonds through resting behaviour, as the

enhanced proximity of resting in contact may serve the same social benefits of other social behaviours, including grooming. Second, small group size (six or seven adults) may allow for a decreased amount of active social enhancement, as fewer individuals have fewer conspecifics with which to interact.

The causes and implications of energy-saving behaviours are well known, but the lack of data on energy and water availability between habitats limits the ability to more deeply understand why individuals living in the spiny forest habitat restrict activity patterns. Moreover, data on time spent feeding and foraging is only a preliminary step in understanding energy acquisition. Gould (in prep) has collected data on feeding rates and micronutrient content of *Lemur catta* diet in the spiny forest, and these data have the potential to reveal trends in foraging strategies untold by this study. Similarly, more detailed data on travel routes and daily path length may provide a better understanding of energy-usage while traveling. Moreover, the observed trends in activity budget may be seasonal in nature and not inherent in those individuals living in the spiny forest. A full-year study of activity patterns of *Lemur catta* living in the spiny forest could reveal surprising trends about flexibility both within and between habitats.

This study also showed that ring-tailed lemur groups exhibit differing rates of predator vigilance between habitat types in the following ways: 1) The spiny forest group exhibited a significantly higher rate of anti-predator vigilance events per total hour, per hour sitting, and per hour locomoting than individuals in the gallery forest group; there was no significant difference in anti-predator vigilance events per hour feeding. Additional variables attributed to varying levels of predation risk were not significantly different between the two groups: 1) The two groups did not differ in the percentage of

anti-vigilance events within two meters or more than five meters from a nearest neighbour; 2) There were no significant differences in the proportion of anti-predator vigilance in three of four vertical levels, including while on the ground and in the high canopy, two theoretically high-risk areas; 3) Despite seemingly clear differences in preemptive predator vigilance, and furthermore predation risk between groups, there is no evidence that the two groups used different predator sensitive foraging behaviours, including inter-individual spacing and vertical level use while feeding.

I suggest that despite few differences in predator abundance between habitats, *Lemur catta* living in the spiny forest habitat experience greater predation risk resulting from increased exposure to potential aerial predators. Increased exposure to both terrestrial and aerial predators results from decreased foliage cover and lower number of arboreal travel routes. The costs involved in increasing proximity to nearest neighbours (i.e. high rates of foraging agonism) and restricting uses of potential foraging areas (i.e. decreased resource acquisition) are high, and the relatively low predation pressure at Berenty Reserve may allow individuals to negate increased predation risk simply by increasing anti-predator vigilance.

Finally, ring-tailed lemurs living in the spiny forest habitat exhibited feeding agonism at a higher rate than those living in the gallery forest habitat. I suggest that such higher rates of feeding agonism are related to increased consumption of plant reproductive part in the diet and smaller feeding sites leading to decreased inter-individual spacing between feeding group members in the spiny forest group. However, the statistical correlation between feeding agonism rate and ecological variables remains untested. Long-term studies of foraging strategies may reveal whether rate of feeding

agonism changes with the aforementioned ecological variables and female reproductive state over time. Investigations into food item nutrition may create insight into how nutritional availability and intake influence rates of agonism in habitats with low-biomass. Feeding competition may vary in other ecologically distinct habitats, including the Andringitra Massif site described by Goodman and Langrand (1996), where no fruiting items exist and individuals feed on fronds, leaf tips, and succulent plants. Once again, the plethora of habitats in which *Lemur catta* inhabit may provide ample data on how varying degrees of resource quality and distribution affect feeding competition within and between groups.

Aside from being an important comparative assessment, this study provides yet another example of how primates, one of the world's most adaptable mammalian orders, are able to successfully live in areas with low biomass. Ecological and behavioural adaptability is fundamental for the geographic expansion of a species, and ring-tailed lemurs would not show the ecological variability without the ability to successfully thrive in low-biomass habitats characteristic of many biomes of Southern Madagascar. Energy-conservation behavioural strategies (Wright 1999) and relatively fast infant growth periods (Gould et al. 1999; 2003) allow this species to endure periods of resource scarcity. The ability to successfully survive in habitats with low food and water abundance was most likely a result of exploitation of and adaptation to available ecological niches in the arid southern portion of the island, while the majority of all diurnal lemur species have evolved in high-biomass rainforests (Sussman 2002).

This study is the first to collect standardized behavioural sampling on a *Lemur catta* group in low-biomass habitat, and it is a small step in a potentially long-term

research effort. Future studies of *L. catta* in habitats of varying biomass levels can provide insight into how ecological variables affects life history and behavioural patterns in primate species. Such cross population data comparisons have been compiled for primate species in Africa (Dunbar 1992, Hill et al. 2003), South America (Panger et al. 2002) and Asia (Fa and Lindburg 1996), and a more comprehensive analysis of inter-population behavioural trends could be used to generate models of ecological influences on lemur decision making, demography, and health (Gould 2006). This study shows that, at least during the dry season, groups adjust their behavioural patterns to the proximate ecological surroundings, suggesting that populations at different research sites would show different patterns to varying types of food availability, predator presence, and temperature.

These results have significant conservation implications. Ring-tailed lemurs clearly have the ability to occupy varying habitat types (Sussman et al. 2003, Gould 2006, Goodman et al. 2006), and based on my study, can successfully negotiate the potential hazards of occupying low-biomass habitats. As seed dispersers, ring-tailed lemurs are vital species for the survival of gallery forests (Blumenthal-Jones et al. 2006) and spiny forests (Bodin et al. 2006). The protection of all habitat types which contain ring-tailed lemurs should be considered for conservation of the ring-tailed lemur populations and the forests in which they inhabit. The concentration of research effort on ring-tailed lemurs in gallery forests, although crucial to future research efforts, has neglected surviving small populations of *Lemur catta* in geographically diverse and ecologically diverse habitats. While population density is relatively low in non-gallery forest habitats (Sussman et al. 2003), these populations are essential in preserving a diverse population gene pool and

retaining the possibility of conserving the species outside of a small number of gallery forests near rivers. Goodman et al. (2006) have noted that ring-tailed lemurs may disperse through low-resource corridors, and the maintenance of primary or secondary forest throughout the greater region may create a population dynamic capable of maintaining a real presence in the future. The endemic spiny forests are vanishing at a rapid pace because of anthropogenic deforestation, and the remaining small patches of this endemic forest should be viewed as essential to maintaining a geographically and genetically variable primate species (Bodin et al. 2006). Thus, conservation considerations should not be focused simply on populations within gallery forests but instead directed towards all habitats which support ring-tailed lemur populations, as successful behavioural flexibility allow this species to flourish in multiple habitats given the opportunity.

Understanding the abilities and limitations of primate behavioural flexibility is key if anthropologists are to more fully understand hominid exploited new ecological settings as they moved from their ancestral range. Furthermore, humans and a variety of non-human primates share the ability to successfully survive in ecologically sparse habitats, and shared behavioural strategies in these habitats between species may reveal how hominids survived in similar ecoregions.

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