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Lemur catta in the Region of Cap Sainte-Marie, Madagascar: Introduced cacti, xerophytic Didiereaceae-Euphorbia bush, and tombs

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Lemur catta in the Region of Cap Sainte-Marie, Madagascar: Introduced cacti, xerophytic Didiereaceae-*Euphorbia* bush, and tombs

by

Elizabeth Ann Kelley

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Acknowledgements

This monograph is the product of hard work, critical thinking, and support from numerous people. I would like to take the time to thank everyone here.

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The employees of ANGAP Cap Sainte-Marie were instrumental in ensuring that I was cared for and safe at the campsite. In addition, they kindly lent me the on-sight ANGAP building to weigh and measure plant samples in a suitable environment at the expense of their own comfort. Their kindness and friendship, especially among the wives, made me truly feel at home.

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My dad, Richard Torkelson, drove five hours in the rain and spent two days with me to provide invaluable insight on the content and presentation of this work for the public talk. In addition, he was a great field assistant and companion when he came to the site March and April of 2008. He was especially helpful with the collection and drying process of the plant samples, each of which he weighed and dried with the methodical and meticulous care of someone with the soul of a scientist. Most importantly, although we didn't know it then, he gave up two precious months with his wife and my mother at her insistence to make sure I was ok. She died two years after his visit, and that time they had after he retired was donated to my welfare and the completion of this project. Thank you.

Brad Kelley, my husband, was instrumental in the execution of this project from start to finish. From setting up my campsite with an in-depth solar panel system to maximize my comfort, to reading drafts of grants and chapters in their roughest forms, to spending endless hours with me working on Access, to taking time away from his own career to work with me in the field, spreading his charm and generosity among the villagers to ensure that, by proxy, I would be accepted as a member of the community. His participation in this project was comprehensive, and no amount of words with give justice to the credit he deserves. He truly should be a coauthor of this dissertation.

During this final phase of the dissertation, I experienced both the loss of a close loved one and the birth of two beautiful children. The adaptability and strength that exuded all life in the CSM region is what encouraged me to continue to work on this project even when it seemed that life would direct me to do the opposite. I still carry the place’s strength with me, and I hope that I can pass that strength on to my children.

Last, I would like to recognize the ring-tailed lemurs that inhabit this region. Out of all the observations, there is one that best summarizes their character:

> A female infant in the Tsankalamanga troop was observed one day with what appeared to be a broken back. All who observed the incident were certain she would die. Her crying, which persisted all day, was unbearable. The temperature that day was 95º+F, and she kept dragging herself out of the shade in an attempt to follow the troop. Her mother was the oldest female in the study; a scraggly female who appeared to be the mother of at least two other females in the troop. The mother continuously approached the infant to move her to the shade, while the rest of the troop ceased all activity and watched through an *O. ficus-indica* hedge. The next day, the troop had left for a long excursion to the other end of their home range. We were certain +that the infant had died. Then we saw the drag marks. This female had dragged her infant from one end of the troop's habitat to the other, and the infant had clung on her back with her hands, dangling her feet all the way. The following weeks, we watched as this female would be "parked" on a branch, hanging by her hands meters from the ground. We were always certain she wouldn't survive. Except that she did. In fact, she recovered completely from the incident and became an active, well-nourished central troop member. We named her Oops. The moral of the story: Oops happens, but the strength derived from sociality is the network from which improbable accomplishments by the individual become possible through the group. It is observations such as this that make the field of primatology such a worthy endeavor.

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CHAPTER 1

Introduction

This is the first study to document the natural history of *Lemur catta*, ring-tailed lemurs, outside of gallery forest environments: in xerophytic Didiereaceae-*Euphorbia* bush habitat that represents over 90% of this species' potential range. Moreover, this study is the first to document ring-tailed lemurs, or any primate species for that matter, as cactus dwellers. The objective of this study is to offer, through quantitative means, a completely new perspective on *L. catta* ecology, behavior, and adaptability.

Data were collected for 15 consecutive months on two different troops in the Cap Sainte-Marie (CSM) area, which is Madagascar's southernmost region. All-day follows, nutritional analyses, and health assessments were the methods used to test hypotheses on the following themes: a) behavioral flexibility, b) ecology, health, and nutrition, c) the shared use of space with humans, and d) the utilization of nonnative species.

The Importance of Natural History Research

The study of natural history, when viewed in its narrowest sense as "descriptive ecology and ethology" (Greene, 2005), has for decades been considered by some to be an outdated and even non-scientific approach towards understanding the behavior and ecology of extant organisms (see Futuyama, 1998; Greene, 2005). The merit of natural history research *sensu stricto* is debated (see Futuyama, 1998, Arnold, 2003; Greene, 2005). Nonetheless, my description of this project as rooted in natural history is based on the following premises. First, while the design of this project is centered on a conceptual framework complete with hypotheses, in my view the most important element of this project is that it is a focused study on how a seemingly well-studied organism lives in a range of habitats that include a) the habitat most typical for this species, b) a habitat dramatically different than the tamarind forests in which it has been so thoroughly researched, and c) a habitat that has not been well investigated by scientists in its own right. Second, while several methodologies were used to collect the data needed for hypothesis testing, the all-day follows allowed for over a thousand of hours of observations in which new adaptations of this species were revealed. These observations will later be the foundation from which future hypothesis driven research on this population will be based (see also Greene, 2005).

Finally, while many of the methods and research questions of this project originate from the fields of ecology and zoology, my interpretation of the data is based on training in biological anthropology. The advantage of having this project interpreted from an anthropological background is twofold. First, every square km of Madagascar is inhabited by humans, and even many of the national parks are frequented by the neighboring villagers' zebu, goat and sheep herds (CIESIN, 2000). Therefore, it is becoming increasingly important to recognize human impact as an integrated and significant part of Madagascar's ecosystems. The viewpoint is especially relevant for south and southwest Madagascar (Seddon et al., 2000; Fenn, 2003; Elmqvist et al., 2007).

Second, as has been emphasized by Martin (2002), primate field research is an essential component for understanding human evolutionary biology. Decades of research on many taxa of non-human primates have provided much comparative data from which general valid principles in primate and human evolution can be deduced (Martin, 2002). Specific to this study, research on *L. catta* at Cap Sainte Marie will be used as a comparative example of how behavioral response to environmental variance is a key evolutionary strategy in primate evolution. *L. catta* is unique in that it has the following combination of characteristics: 1) it is the most terrestrial of the extant prosimian species, 2) in contrast to its perceived simian counterparts (e.g., macaques and baboons), *L. catta* is a monotypic species (but see Tattersall 2007), and 3) *L. catta* is from a lineage that from around 62 Ma until around 2,000 years ago evolved in an environment free of humans (Burney et al., 2004; Yoder and Yang, 2004; Muldoon, 2010). Thus, based on these qualities, *L. catta* is an ideal model for studying the basal characteristics of behavioral flexibility in primates as expressed in a relatively recently changed landscape. If the introduction of *Opuntia* is accounted for in this model, then the timeline for the changed landscape is as recent as two centuries, since that late 18th century (see Middleton, 2002, Larsson, 2004).

Behavioral Flexibility

Behavioral flexibility is a loosely defined term that is used to describe the extent to which a species is able to adapt to a new or changing environment (Sol et al., 2002; Jones, 2005). Although this quality has been identified through the isolation of single behaviors in animals as simple as fruit flies (Heisenberg et al., 2001), behavioral flexibility is most richly expressed in mammals that have a large neocortex and in birds that have a large hyperstriatum ventrale and neostriatum (Heisenberg et al., 2001; Sol et al., 2002; Jones, 2005). In previous ethological studies on birds, counts of different and new feeding behaviors have been used to index behavioral flexibility across taxa (Sol et al., 2002). However, a single measurement for behavioral flexibility undermines the complexity and importance of this characteristic.

Ranges in behavioral flexibility among the Malagasy lemurs can be predicted by several behavioral and ecological characteristics. At one extreme is *Varecia variegata*, the ruffed lemur. Ruffed lemurs have a fission-fusion social structure, which appears to change in size and composition with resource availability (Ratsimbazafy, 2002). However, this species is highly frugivorous and relatively inflexible in its ecological requirements (Vasey, 1997). In consequence, ruffed lemurs do very poorly in disturbed environments such as logged forests (Balko, 1998; Ratsimbazafy, 2002; Balko and Underwood, 2005). Conversely, *Propithecus verreauxi* (Verreaux's sifaka) adapt relatively well to variable ecological conditions (Richard, 1978; Richard et al., 2002). In contrast to ruffed lemurs, Verreaux's sifaka can live in human altered forests (to an extent) and they will diversify their diets during seasons of resource scarcity (Richard, 1978; Smith, 1997). The behavioral flexibility of ring-tailed lemurs is even more extreme and appears to more closely typify terrestrial anthropoid primates in this characteristic. In fact, ring-tailed lemurs (*L. catta*) are grouped with vervet monkeys, baboons, certain macaque species, and the Hanuman langur as among the most adaptable of the non-human primate species (Gould et al., 1999; Sussman et al., 2003; Hart and Sussman, 2005; Goodman et al., 2006; Sussman et al., 2006).

The Effects of Human Impact

Within the last 40 years, forests around the world have shrunk considerably and the extent of cultivated land has expanded (Hill, 1997; Sprague and Iwasaki, 2006; Parker et al., 2008). It therefore seems intuitive that the primate species most adaptable to anthropogenic changes in the environment would be the species least at risk of extinction. However, highly adaptable primates often become the most vulnerable in human altered landscapes because they incorporate anthropogenic foods and habitat in their daily activity cycles (Strum, 1994; Hill, 1997; Siex and Struhsaker, 1999; Hill, 2000; Saj et al., 2001; Fuentes, 2002; Wheatley et al., 2002; Tweheyo et al., 2005; Wieczkowski, 2005; Sprague and Iwasaki, 2006). For the ring-tailed lemurs of CSM, all of their available land has been modified by humans. These lemurs have access to two major anthropogenic habitats: agricultural fields that are bordered by *Opuntia monacantha* (prickly pear) hedges, and sacred forests.

Crop raiding

Several nonhuman primate species have learned to incorporate agricultural products in their diet, which has resulted in increased conflict between humans and nonhuman primates in such situations (Hill, 1997; Parker et al. 2008). This trend appears to be especially true in Asia and Africa (Hill, 1997; Estrada, 2006). In Africa, researchers have demonstrated baboons are a major cause of crop loss (Hill, 1997; Hill, 2000). Conversely, in other studies, the damages caused by crop raiding were shown to be grossly exaggerated (Siex and Struhsaker, 2006). In Madagascar, crop raiding behaviors have been reported for *Eulemur macaco* (black lemurs) and *L. catta*. However, estimates have mostly been qualitative. For example, Loudon et al. (2006) observed ring-tailed lemurs eating cassava leaves on “several occasions of observations” (p. 64). At CSM, ring-tailed lemurs sleep, sun and feed from the *Opuntia monacantha* hedges that surround and connect fields (discussed in chapter three). Thus, these troops spend much of their time in close proximity to fields, and in close proximity to the watchful eyes of villagers who tend the crops. This combination places these lemurs at extreme risk of retribution. The alternative habitat for these troops is the numerous small sacred forests that spot the landscape.

Sacred forests

The Malagasy people have a deep-rooted reverence for the dead, and one of the major expressions of this reverence are the sacred stone tombs of the Antandroy (Drury, 1729 [1969]; Parker Pearson, 1997; Brown, 2000; Dietz et al., 2003). Almost without exception, the older tombs in the CSM region of Madagascar are sheltered by forests (Tengö et al., 2007). These forests are called *ala faly* (taboo forests) or *ala kibory* (burial forests) by the Antandroy, but are known as "sacred forests" by Westerners (Parker Pearson et al., 1996; Tengö et al., 2007). Nearly all of the remaining forests in this region are sacred forests (Tengö et al., 2007). Typically, these sacred forests are roughly circular and 300 to 400 meters in diameter (Clark et al., 1998). Most of these forests are only five to 13 ha in size (Clark et al., 1998; Tengö et al., 2007). However, one researcher identified, through satellite imagery, more than 1,400 of these forests along the coasts of south and southeastern Madagascar (Engström, 2002 in Dietz et al., 2003). Sussman et al. (2003) found that the boundaries of these forests have remained largely unchanged for at least the past 50 years. This is largely because landscape-altering activities such as burning, wood collection, defecation, and the collection of plants are prohibited within these forests. Yet sacred forests are not pristine environments, as domestic hoofstock species (i.e. zebu, goats and sheep) frequently roam and graze within these forests unattended.

Sacred forests may be an integral component of the habitat for the CSM *L. catta* (see chapter six), and ecologists have recently discovered that *L. catta* may be key seed dispersers in the sacred forests (Bodin et al., 2006). However, sacred forests are usually spaced kilometers apart from one another (Clark et al., 1998), and as noted earlier, they are extremely small. My observations demonstrated that ring-tailed lemurs at CSM therefore never inhabited a single sacred forest site for more than a day. In fact, they never spent the night in a sacred forest unless it contained an *Opuntia monacantha* hedge. *Opuntia* has been referred to as the archetypical invasive species (Elton, 1958), a characterization certainly supported by its behavior in Madagascar.

Opuntia

An invasive species is defined as “an alien plant spreading naturally (without the direct assistance of people) in natural or semi-natural habitats, to produce a significant change in terms of composition, structure or ecosystem processes” (Cronk and Fuller, 1995). The idea that certain plants can invade a landscape and replace native vegetation dates to the 1800s (Gray, 1879), but Charles Elton’s 1958 book titled *The Ecology of Invasions* is the foundation on which modern studies of this subject are based (Simberloff, 2004; Mooney, 2005). Known as Invasion Biology, rigorous research on the effects of invasive species has been on-going since the publication of Elton’s book, and many journals, such as *Biological Invasions,* are dedicated to the topic (Enserink, 1999). A primary concept of invasion biology is that island environments are more susceptible to invasive species than are mainland environments. There are two major hypotheses for why this is the case. First, there is the hypothesis that island species are less resistant to outside pressure because they have evolved in less competitive environments (Atkinson, 1989; Lodge, 1993; reviewed in Sol, 2000). Second, there is the hypothesis that island environments as a whole are relatively unstable because their communities generally contain fewer species (Elton, 1958; Lodge, 1993; Simberloff, 1995; but see MacArthur, 1972; Levine and D'Antonio, 1999). Extensive research on these two hypotheses has led to contradictory conclusions (e.g., Hedgpeth, 1993; Simberloff and Von Holle, 1999; Kaiser, 2000; Levine, 2000; Knight, 2001; Grotkopp et al., 2002; Kennedy et al., 2002; Wolfe, 2002; Rouget and Richardson, 2003; Zavaleta and Hulvey, 2004; Parker et al., 2006), although they are not mutually exclusive. Yet all of the above cited ecologists share the common premise that invasive species are harmful to natural ecosystems.

Some biologists have challenged this premise. These biologists argue that 50 years of research have failed to prove that invading species either necessarily out-compete native species or destroy natural ecosystems (e.g. Burdick, 2005; Sagoff, 2005). In addition, these biologists argue that eradication of invasive species should proceed with caution as there are plant species that directly benefit human society (Garibaldi and Turner, 2004; Sagoff, 2005; but see Simberloff, 2005). A possible example of such a situation is posed by the widespread presence of *Opuntia* in Madagascar's arid south.

Opuntia monacantha[1], known in Madagascar as *raketasonjo*, has been a crucial resource for the Antandroy since its introduction to the region in the late 1700s (Drury, 1729 [1969]; Decary, 1925; Francois, 1938; Decary, 1947; Jolly, 1966; Brown, 2000; Kaufman, 2001; Middleton, 2002; Bingelli, 2003; Larsson, 2004). Since its appearance in southeast Madagascar, the Antandroy have planted *O. monacantha* as a means to connect and delineate ownership of their crop fields (Drury, 1729 [1969]; Decary, 1925; Francois, 1938; Decary, 1947; Jolly, 1966; Parker Pearson, 1997; Brown, 2000; Kaufman, 2001; Middleton, 2003). In addition, its fruits have been essential food and water resources, and

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[1] Some of the literature reference *O. monacantha* hedges as *O. ficus-indica* (e.g., Larsson, 2004). However, photographs of the cactus hedges from this study have been identified as *O. monacantha* by Dr. Juan Antonio Reyes Agüero at the The Autonomous University of San Luis Potosí, Dr. Héctor Hérnandez at the Institute of Biology at the National Autonomous University of Mexico, and Dr. Peter Raven, President Emeritus, at the Missouri Botanical Garden, St. Louis.

its pads have been essential sources of food for the livestock (Drury, 1729 [1969]; Decourse, 1901; Decary, 1925; Binggeli, 2003; Middleton, 2003; Larsson, 2004). In fact, when the stands of *O. monacantha* were wiped out in the 1920s by the cochineal insect, over 30,000 local inhabitants of the Tsiombe district alone (the town closest to CSM) were either displaced or starved as a result of the lack of cacti for forage for their livestock (see Decary, 1925; Kaufman, 2001; and unpubl. documents in Middleton, 2003; Deschamps, 1959 in Larsson, 2004). The *O. monacantha* present in the region today either survived the near eradication of the 1920s or was reintroduced to the region fewer than 10 years after its initial eradication (Kaufman, 2001; but se Larsson, 2004). Although *O. monacantha* used to pervade the southern landscape of Madagascar, this species now exists primarily in the form of planted hedges[2].

Opuntia monacantha is thought of as a "tree pear" as it tends to grow into dense hedges that can be 3 - 6 m high with a trunk 30 - 45 cm in diameter. In addition, these hedges support lianas and bushes, most notably, *Flacourtia ramontchi*, *Leptadenia*, *Paederia*, *Phyllanthus amanu,* and *Strychnos decussata*. It is reported that ground boas live within the hedges, although I never saw any. In fact, *L. catta* was the only vertebrate animal species that I ever saw inside the hedges. The fruits of *O. monacantha* mature in January and February (Larsson, 2004). At Cap Sainte-Marie, the villagers consumed large quantities of this fruit from January through September (pers obs). Shoots of *O. monacantha* are also found in the brush and scrub habitat and in some of the sacred forests.

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[2] It is not clear why *O. monacantha* does not spread widely over southern Madagascar today. Two theories have been suggested by Dr. Peter Raven, President Emeritus of the Missouri Botanical Garden. The first theory is that the cochineal insect, which may persist locally, forms a kind of biological control. The second theory is that *O. monacantha* is being outcompeted by *O. stricta*.

While *Opuntia monacantha* is planted as hedges around fields in home gardens, there is a second species of *Opuntia* that spreads over the arid landscape as *O. monacantha* did until the 1920s. *O. stricta,* known locally as *raketamena,* is a low spreading bush up to 0.8 m tall, without a distinct trunk, and is a naturalized aggressive weed that has spread throughout the world (Raven, pers comm).The introduction of *O. stricta* is undocumented, but it seems to have been introduced sometime after the famine of the 1930s, perhaps as late as the 1950s, reaching the Cap Sainte-Marie landscape around 1970 (Larsson, 2004). Unlike *O.monacantha, O. stricta* covers huge areas of open lands, and the Antandroy consider it a major environmental problem (Larsson, 2004). In contrast to *O. monacantha,* the fruits of *O. stricta* are tart rather than sweet and are only occasionally eaten by humans, mainly in extreme drought conditions (Larsson, 2004). There is widespread belief among the Antandroy that the fruits of *O. stricta* kill livestock and make people sick, that the spines of *O. stricta* cause serious infections, and that the very presence of the plant in the region inhibits crop production and destroys native flora (Larsson, 2004).

Although botanists and biologists have long believed that *Opuntia monacantha* and *O. stricta* have decimated Madagascar's arid ecosystem (Decary, 1921; Perrier de la Bâthie, 1927; Decary, 1930; Francois, 1938), not enough is known about the native plants or animals that occupied southern Madagascar before *O. monacantha* was introduced to enable us to test this hypothesis (see also Ferguson, 2002; Middleton, 2002; Middleton, 2003). The only quantitative study that has measured the effects of *Opuntia* on the non-human vertebrates of southern Madagascar is the recent study on *Geochelone radiata,* radiated tortoises, by Leuteritz et al. (2005) at Cap Sainte-Marie. These researchers found that radiated tortoises feed upon *Opuntia* (primarily *O. stricta*) 7.6% of the time, and that nearly a third of this population's nests depend on *Opuntia* for shelter (see also Leuteritz, 2003; Leuteritz and Ravolanaivo, 2005; Lingard et al., unpubl. manuscript). The ecological role of *Opuntia* spp. for the CSM *L. catta* is a central component of this study.

Dissertation Plan

Questions and hypotheses

Prior to the research that is presented here, I conducted a short pilot study in the CSM region in October of 2005. The following questions and hypotheses are based upon the combined observations of that preliminary study and published background material. Data to test the following questions and hypotheses were collected from May 2007 through July 2008.

Q1: How does the behavioral ecology of the cactus-adapted *L. catta* compare with gallery forest *L. catta*?

- H_{1a}: Home range patterns will follow predictions made at gallery forest sites that home ranges of *L. catta* are larger in brush and scrub habitats than they are in gallery forest habitats (Mertl-Millhollen et al., 2003). However, since it is theorized to be less costly for troops to fission than to expand home range area (Jolly et al., 2002; see also Gould, 2006), range sizes in arid areas will be markedly larger than gallery forest sites. Day range sizes will be smaller than that which has been recorded at gallery forest sites.
- H_{1b} : Since *L. catta* troops at CSM are largely isolated units, migration opportunities for individuals will be scarce. In consequence, dyadic relationships within the troop will be more established, which will be reflected through the kind of social behaviors

that are expressed among troop members. For example, there will be less “active” social behaviors (e.g., social grooming; approach/retreat sequences) and instead more “passive” social behaviors (e.g., huddling) when compared with gallery forest troops. In addition, since current socioecological models predict that the primary function for living in groups is to either 1) compete with other groups over food resources (Wrangham, 1980), or for protection against predation (vanSchaik, 1983), CSM troops will be only loosely cohesive. Socially intense events, such as the mating season, the arrival of new infants, and feeding bouts, will be examined to test this theory.

Q2. Are there any indications that the CSM *L. catta* suffer from chronic health issues or nutritional deficiencies?

- H_{2a}: In general, the CSM population of *L. catta* will have more restricted diets than the gallery-adapted *L. catta*. Moreover, the smaller troop, the Tsankalamanga troop, will have a less diverse diet than the larger troop, the Bevaro Moravato troop (Pride et al., 2006).
- H_{2b}: Health assessment and nutritional analyses will indicate significant deficiencies in essential mineral concentrations (e.g., phosphorus, nitrogen, and iron) and fat-soluble vitamins (Dierenfeld and McCann, 1999; Crawford, 2004). In addition, CSM *L. catta* will on average weigh less and will be more dehydrated than gallery forest populations.

Q3: How important is *Opuntia* for CSM *L. catta*?

- H_{3a}: Resting, social activity, and thermoregulatory behaviors will be concentrated within the *Opuntia monacantha* hedges. Time spent within these hedges will positively correlate with wind speed, temperature and rain bouts.
- H_{3b}: *Opuntia* will be the primary fruit consumed by the CSM population during the austral winter months.
- H_{3c}: *Opuntia monacantha* and *O. stricta* will be nutritionally very different than the native foods consumed by *L. catta* in the CSM region.

Q4: How does the behavioral ecology of CSM *L. catta* affect the local villagers' awareness of this population?

- H_{4a}: CSM *L. catta* will spend significantly more time within the *Opuntia monacantha* hedges, which surround fields, than at the sacred forest sites.
- H_{4b}: Moreover, because these hedges surround the villagers' crops, CSM *L. catta* are more subjected to human distrust and potential harm when they are in the *Opuntia monacantha* hedges than when they are in sacred forest habitat.

Outline of dissertation by chapter

To avoid unnecessary duplication of methodological and theoretical descriptions, I have arranged the chapters by subject as a monograph rather than by research question as separate journal articles. A summary of the results of each research question will be directly addressed in the concluding chapter.

In chapter two, I describe the setting of this study, the group structure of the two focal troops, the *L. catta* population structure of the CSM region, and a general description of the methods that were used to collect the data for testing the hypotheses.

The focus of chapter three is ranging behavior, habitat use, and feeding ecology. In this chapter, I begin with a review on the ranging behaviors of comparable anthropoid primates and discuss the definition of primate migration. I then use ArcGIS 9.2 mapping software to analyze yearly and monthly ranging and feeding activity. Movement behaviors (e.g., day length, home range size and ground travel frequency) of the focal troops are compared with that found among gallery forest *L. catta.*

In chapter four, I focus on the topics of behavioral flexibility and social organization in *L. catta,* including intra troop cohesion patterns, activity budgets, and dyadic relationships. These data are put in the theoretical context of intrasexual and intersexual affiliative bonds, context aggression, and male/infant relationships (from infanticide to parental care).

Chapter five is an overview on the general health and nutrition of the CSM study troops. A primary question I address in this chapter is whether the lemurs' habitation in and consumption of *Opuntia* has led to any negative health consequences in this population. In addition, I examine overall health and nutrition profiles of the focal troops for insight that may help explain (1) why there were so many deaths in the Tsankalamanga troop specifically and (2) whether health and nutrition is a factor for why *L. catta* density is so low in the CSM area generally. In this chapter, I present the results of the veterinary health assessments of the CSM troops and compare these findings with data from previous health assessments on gallery forest and semi-free ranging North American populations. Water and nutrient profiles of the plant species that were eaten by the CSM *L. catta* are also presented here.

Chapter six is an addendum on the subject of behavioral thermoregulation.

Activity, ranging patterns, and health data are reexamined to determine whether and to what extent *L. catta* alter their postures and daily activity to adjust to daily climatic and seasonal weather conditions. Moreover, because deaths among members of the Tsankalamanga troop appear to have been seasonal, seasonal differences in behavior between the two troops are compared for clues as to why the Tsankalamanga troop suffered from mass mortality during the austral winter months while the Bevaro Moravato troop seemed largely unaffected.

Finally, in chapter seven I review the observations that I believe most impact our current understanding of *L. catta* behavioral ecology, and I synthesize the results from the analysis chapters to answer the four major research questions presented in this chapter. I also review the very premise of this dissertation: why lemurs in the CSM region are less successful than their gallery forest conspecifics.

CHAPTER 2

Field Site, Study Population and Methods

The Androy region of Madagascar, also known as the “southern domain”, extends from the Mandrare River in the east to the Strictandroy River in the west, and from the sea to 150 km inland (**Fig. 1a**; Drury, 1729 [1969]; Rauh, 1995; Clark et al., 1998). Cap Sainte-Marie (CSM) is the southernmost area of this region. The two focal troops of this study, the Bevaro Moravato troop and the Tsankalamanga/Andafambola troop, were both located in the CSM area and were far from the rivers that mark the region’s boundaries. In fact, neither troop was within 33 km of the region’s three river systems (**Fig. 1b**).

Climate

The average yearly rainfall at CSM is less than 500 mm a year (Rauh, 1995; Tengö et al., 2007), which is a defining characteristic of semiarid deserts (Noy-Meir, 1973). However, it rained a total of 685.95 mm from the months of August 2007 through July 2008, the primary months of this study (**Fig. 2)**. Rainfall conditions in southern Madagascar are markedly erratic compared to most other regions of the world (Dewar and Wallis, 1999; Jolly et al., 2006; see also Rauh, 1995), and the rainfall pattern in the CSM area is no exception (Leuteritz and Ravolanaivo, 2005). During my study period, it rained only 57 days (**Fig. 2a**), which is just slightly more than that which is typical of arid desert environments (Noy-Meir, 1973). Moreover, 247.40 mm of the total yearly rainfall occurred within February; 150 mm of this rain fell within one day alone (**Fig. 2b**). Finally, while it rained a total of 36.1 mm in July 2007, it only rained 0.9 mm in July 2008.

Fig. 2.1a. Androy region. Reprinted from Clark et al., 1998.

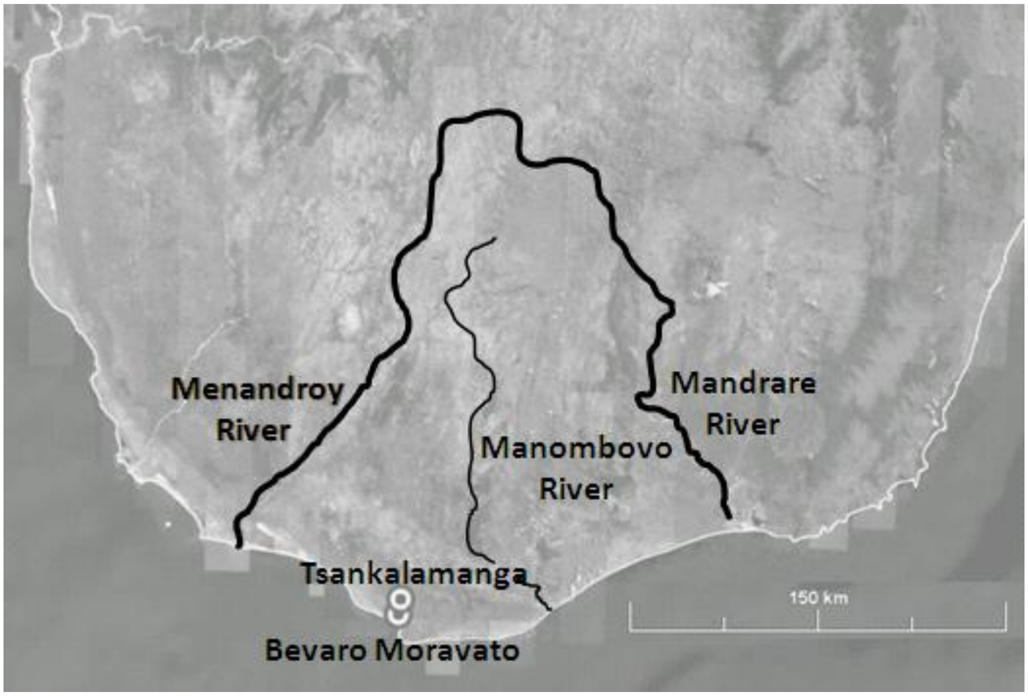

Fig. 2.1b. Close-up of Androy region and CSM area. Map adapted from Google Earth, version 4.3.7284. Google Inc., Mountain View California.

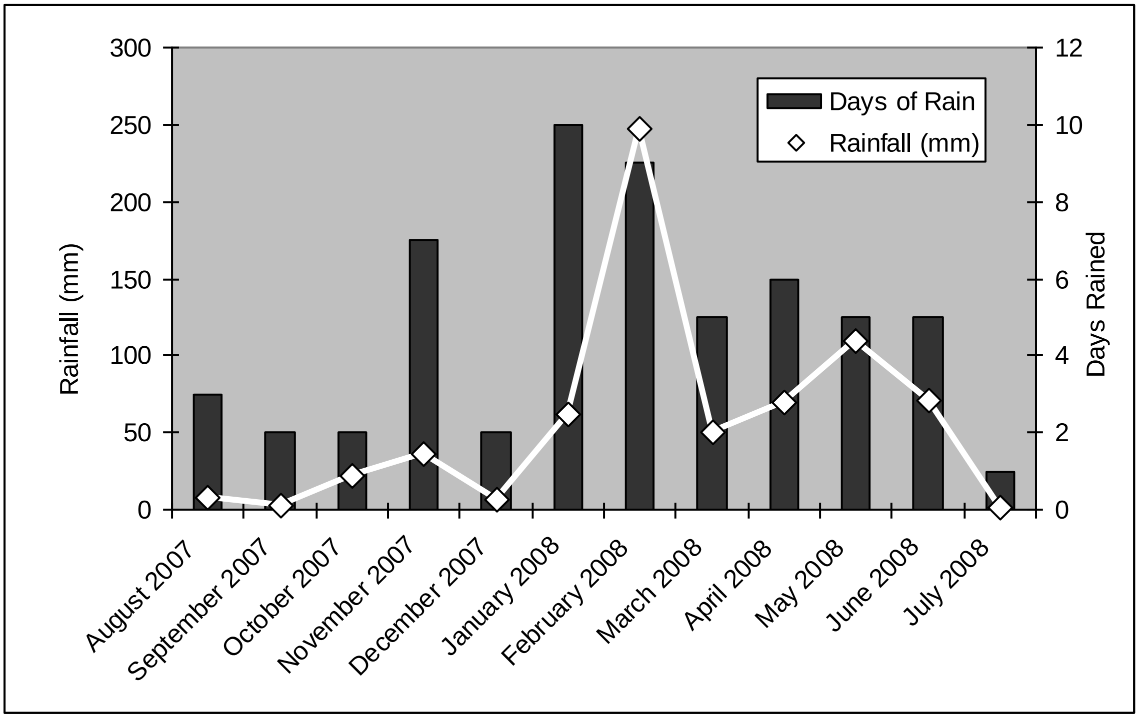

Fig 2.2a. Monthly rainfall and days rained at CSM from August 2007 through July 2008.

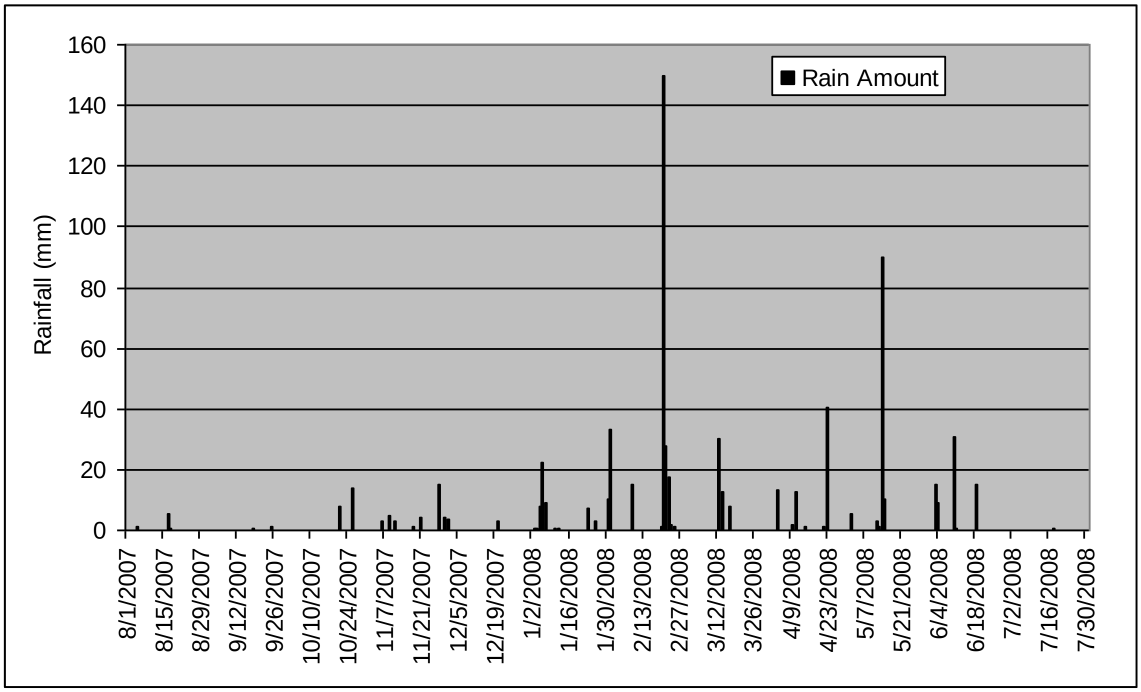

Fig. 2.2b. Daily rainfall at CSM from August 2007 through July 2008.

The temperature ranges of the CSM area are most similar to that of semiarid desert biomes. At Bevaro Moravato, I recorded temperatures as high as 46.7º C (116º F) during the summer months, which is comparable to both hot and dry and semiarid deserts (**Table 2.1**). However, temperatures never fell below 12.8º C (55º F), which is uncharacteristic of most desert biomes (UCMP, 2011).

The median monthly high temperatures at Tsankalamanga were normally higher than that of Bevaro Moravato (**Fig. 2.3a**). This variation in median daytime high temperatures ranged as much as 10F. Conversely, there were no consistent differences in daytime low temperatures between the two sites (**Fig. 2.3b**).

Table 2.1. Temperature comparisons between desert biomes and Cap Sainte-Marie. Desert biome data was accessed from: http://www.ucmp.berkeley.edu/exhibits/biomes/deserts.php

Type of Desert	**Temperature Characteristics in Celsius**	**Fahrenheit Conversion**
Hot and Dry Desert	Maximum Annual Temperature: 43.5º - 49º Minimum Annual Temperature: -18º	110.3º - 120.2º -.4º
Semiarid Desert	Maximum Annual Temperature: 38º Evening Temperatures: 10º	100.4º 50º
Coastal Desert	Maximum Annual Temperature: 35º Minimum Annual Temperature: -4º	95º 24.8º
Cold Desert	Mean Summer Temperature: 21º - 26º Mean Winter Temperature: -2º - 4º	69.8º - 79.8º 28.4º - 39.2º
Cap Saint-Marie	Maximum Annual Temperature: 46.7º Minimum Annual Temperature: 12.8º Median Daytime High Temperature: 32.2º Median Waking Temperature: 20.6º	116º 55º 90º 69º

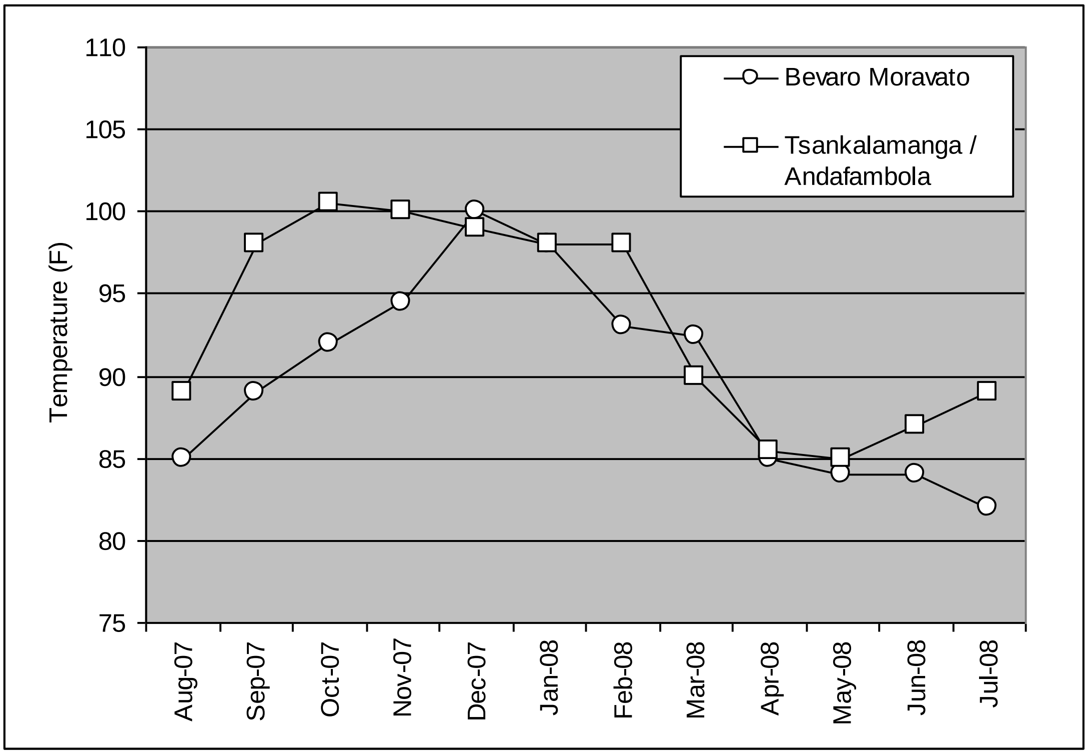

Fig. 2.3a. Median monthly high temperature comparisons between the two sites.

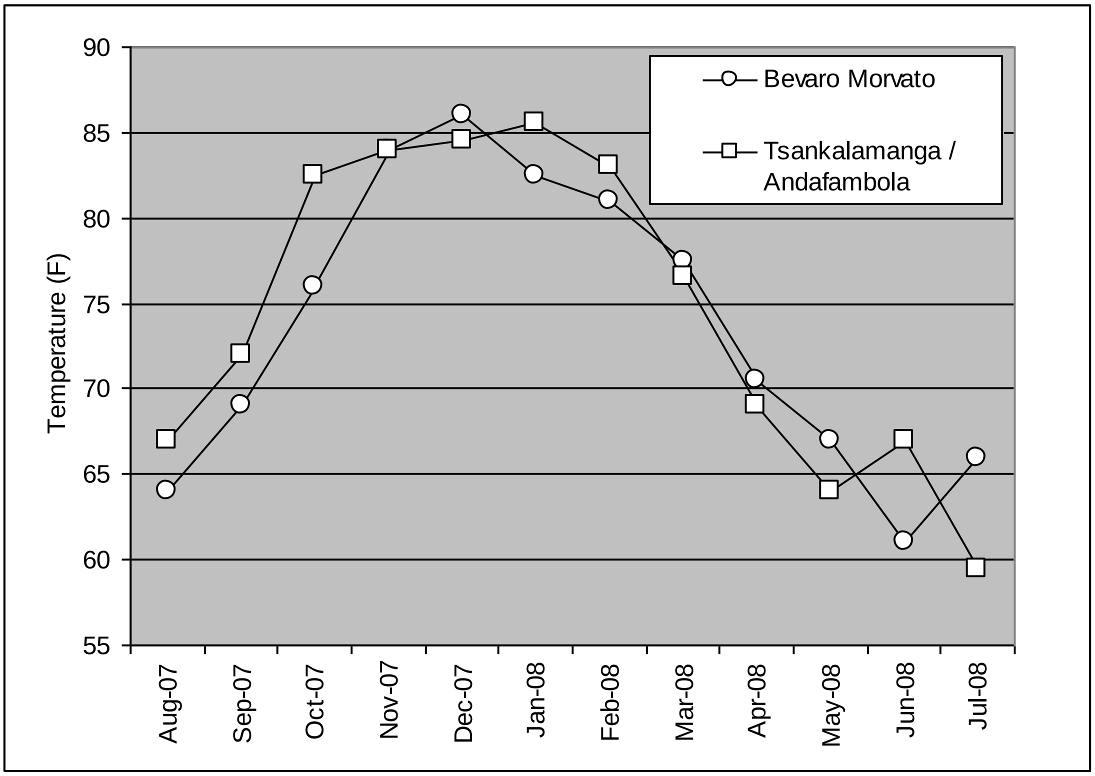

Fig. 2.3b. Median monthly morning temperature comparisons between the two sites. Temperatures recorded were taken between 7:00 a.m. and 8:00 a.m.

Study Site

Vegetation

Despite the widespread presence of *Opuntia stricta*, 95% of the plant species in the Androy region are endemic (Humbert, 1959; Koechlin, 1972); in fact this region is considered to be one of the earth's most distinctive ecoregions (Olson and Dinerstein, 1998). The habitat type is scrub vegetation known as Didiereaceae-*Euphorbia* bush forest (Rauh, 1995). Categorized as xerophytes, these plants are adapted to survive long periods of drought through specialized physical characteristics that slow the processes of evaporation and transpiration (Rauh, 1995). Examples of such characteristics include succulent leaves (e.g., Crassulaceae *Kalanchoe integrifolia*), which may hang vertically (e.g., Didiereaceae *Alluaudia dumosa*); with very small leaves (e.g., Zygophyllaceae *Zygophyllum madecassum*); seasonal shedding of leaves (e.g., Didiereaceae *Alluaudia procera*); and spines (e.g., Euphorbiaceae *Flueggea virosa*), the function of which is to collect morning dew and thereby moisten the plant’s surface roots (Rauh, 1995; Schatz, 2001). Many endemic Androy plant species have more than one of these characteristics.

At Cap Sainte-Marie, the coastal winds are an important variable in shaping the landscape, as the winds have dwarfed the area’s vegetation (Erdmann, 2003). In consequence, all of the vegetation in the reserve is dwarfed to less than 3 m in height. Further inland outside of the reserve, only the *Opuntia monacantha* hedges, one aloe species (*Aloe vahombe*), and a few tree species (e.g., *Euphorbia laroo, Alluaudia dumosa, A. procera*) ever grow above 3 m in height, and virtually no plant attains heights greater than 6 m.

The home ranges of the two focal groups extended over the same mosaic of vegetation: brush and scrub habitat, sacred forest, and fields surrounded by *Opuntia monacantha* hedges (**Fig. 2.4**). The dominant plant in the brush and scrub habitat was *O. stricta*. Although many endemic plants, including the endangered *Aloe vahombe*, were present in this habitat, the landscape was sparsely vegetated and there were few trees. In contrast, the sacred forests contained very few plants of *O. stricta*, and they had a denser canopy (**Fig. 2.4**). Nearly all of the sacred forests contained tombs made from limestone. Some of these tombs can even be seen in satellite images (**Fig. 2.4**). In addition, sacred forests were the only places where *Alluaudia procera* was found. However, very few other plant species consumed by the lemurs were unique to the sacred forests (see chapter five), and forest canopy density (FCD) in the sacred forests was only 35% to 50% (Sussman et al., 2003).

The majority of both troops' home ranges were comprised of the brush and scrub habitat, but the percentages of habitat composition differed between the two areas. Maps that depict the percentages of each habitat type are presented in chapter three.

Fig. 2.4a. Satellite image of the Bevaro Moravato field site (7/16/2003). Image is from Google Earth, version 6.0.1.2032 (beta). Google, Inc. Mountain View California.

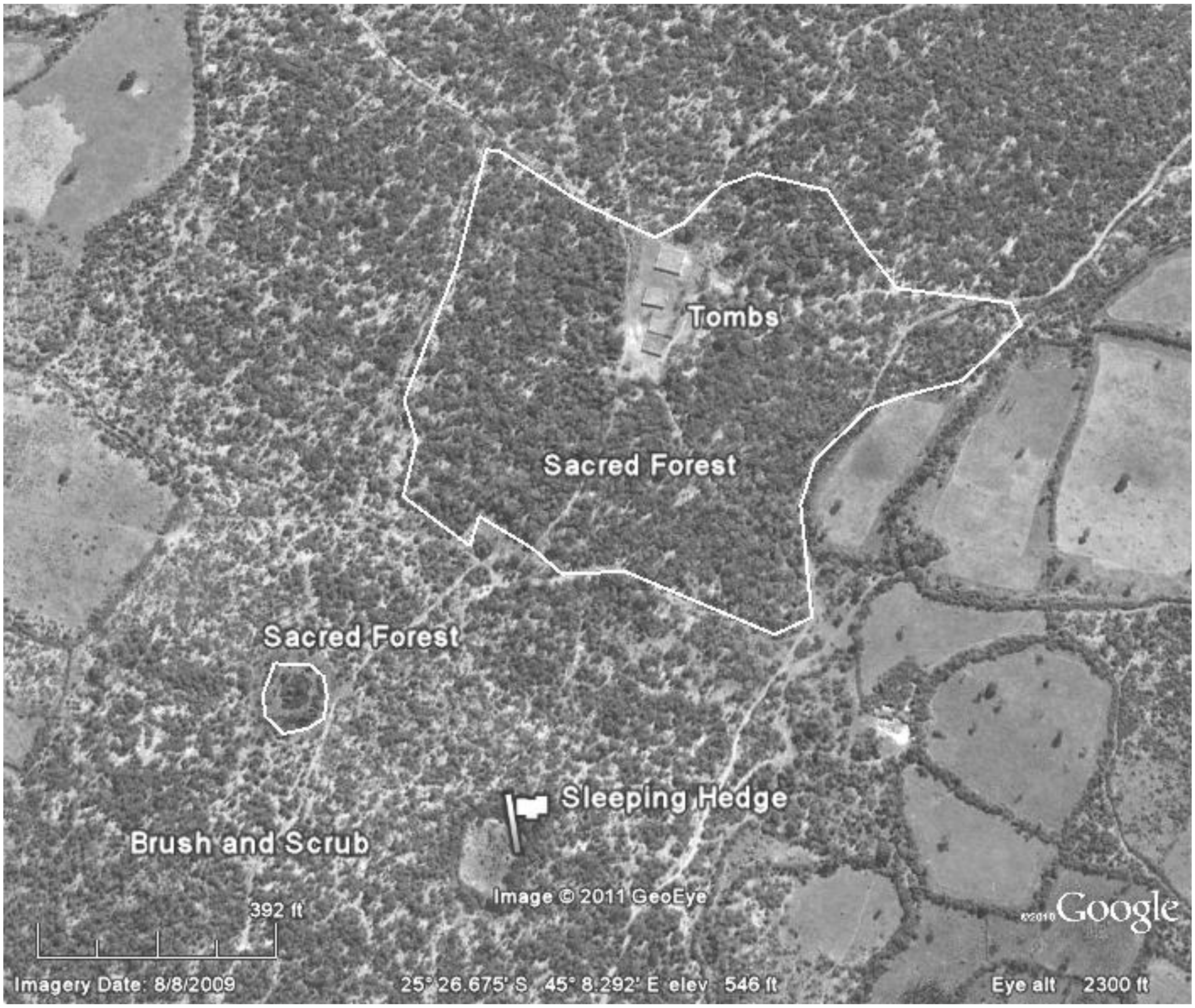

Fig. 2.4.b. Satellite image of the Tsankalamanga field site (7/16/2003). Image is from Google Earth, version 6.0.1.2032 (beta). Google, Inc. Mountain View California.

Other animals and people

Perhaps because there was an absence of water and shade in the region, there were very few nonhuman mammalian predators of CSM *Lemur catta*. There was no evidence of fossa, *Cryptoprocta ferox*, and even domestic dogs and cats were few. Conversely, the Madagascar buzzard, *Buteo brachypterus*, was common, as were snake species such as *Acrantophis dumerili*, Dumeril's ground boa (Raxworthy, 2003). The lack of threat to predation by other fauna is discussed in the following three chapters.

Most of the villagers in the Androy region are Antandroy (Sharp, 1996; Ferguson, 2002). The Antandroy have a reputation among other Malagasy tribes and expatriates as being fierce and independent. Much of this reputation is supported by history, as the Antandroy were able to resist Merina (the most influential tribal sect of Madagascar), French, Portuguese, English, and Dutch conquests throughout the entire course of the 19th century (Parker Pearson, 1997; Brown, 2000). Even after the Androy region was pacified through aid of Senegalese troops in 1900, during the period of French colonization (1895-1960), southern Madagascar was still considered a treacherous place for foreigners (Parker Pearson, 1997). As a result, the Antandroy were largely left alone during the colonial period (Brown, 2000); even today the CSM area remains largely isolated from the country's national politics.

In traditional Antandroy culture, it is *fady* (taboo) to eat *Lemur catta* or *Geochelone radiata,* the radiated tortoise (Decary, 1930). In the CSM region, I saw indirect evidence that strongly suggests one of my study animals was butchered by humans early in the study (but see chapter six). Moreover, I saw several hollowed tortoise shells. In general, however, it appears that the tradition not to eat these species has largely been maintained in the CSM region. In fact, I regularly saw radiated tortoises throughout the day, and this area appears to be the last refuge for this critically endangered species (Lingard et al.,unpubl). Conversely, I was told that it is not considered *fady* to consume *Microcebus,* the only nocturnal primate at CSM. Finally, the status of *fady* is differentiated from *sacred* in traditional Malagasy religions (Harpet, 2000; Lingard et al., unpubl). This may partly explain why I saw numerous tortoises (in one instance as many as 5 in a week) that were either killed or wounded via oxcarts, cars, or the throwing of stones. Stone throwing was also directed towards the sifaka and ring-tailed lemurs in the area, but it is not clear whether any of the ring-tailed lemur mortalities were a direct cause of this behavior. The relationship between the local villagers and ring-tailed lemurs will be discussed in detail in chapter five.

Children in the CSM region go to either public or private Christian primary schools, but they do not attend regularly, and it is not uncommon for the teacher to cancel class. Most of the region's villagers are pastoralists and males learn to herd zebu, goats, and sheep before puberty (Mahr et al., 2005). The primary role of females is to conduct daily household chores such as washing laundry, collecting water, and caring for younger siblings (Mahr et al., 2005). However, both sexes tend to the crops, often with children in tow. At the villages where I conducted my research, males tend to stay in the community where they were born while females move after marriage. However, it is not uncommon for men of the Antandroy tribe to migrate from the region to seek better economic opportunity (Jarosz, 1993; Sharp, 1996; Casse et al., 2004). Migration into the Antandroy region is minimal to nonexistent (CIESIN et al., 2000; Kelley, unpubl data).

The Study Species

General information

Ring-tailed lemurs are the most terrestrial of the Madagascar primates and will spend up to a third of their time on the ground in their natural environment (Shaw, 1879; Hill, 1953: Sussman, 1972; see also Sussman, in press). As is typical among the Lemuriformes, this species is monomorphic, weighs around 2.19-2.70 kg and measures 399-423 mm in body length (Tattersall, 1982; Sussman, in press). The first ecological description of *L. catta* was written in 1879 by George A. Shaw, in which he noted that this species feeds on wild figs, *Opuntia,* and plantain cultivars (see also Elliot, 1913). However, in 1935, Austin Loomer Rand reported that *L. catta* inhabit the “most densely wooded areas and the gallery forests” of Madagascar (Rand, 1935:96). Since Rand’s statement, nearly every subsequent study on this species has been conducted in the habitat type he described.

In 1963, Alison Jolly began the first detailed ethological study on *L. catta* in a 100 ha gallery forest site, Berenty Private Reserve (Jolly, 1966; **Fig. 2.5**). Her study has continued intermittently since this time, and data have been collected on some of these troops for over 40 years (Jolly and Pride, 1999; see also Jolly et al., 2006). In 1970, Robert Sussman conducted the second systematic study on *L. catta* in a 10 ha gallery forest, Antserananomby (Sussman, 1972; **Fig. 2.5**). This is the only study that has been conducted on this species outside of a protected reserve. Unfortunately, this forest has recently been cleared and there is only a relict population of *L. catta* that still inhabits the area (Kelley et al., 2007). In the mid 1970s, Sussman and others (e.g., Alison Richard and Joelisoa Ratsirarson) participated in the establishment of the second ongoing research site, Beza Mahafaly (Richard and O’Connor, 1997; Sussman and Ratsirarson, 2006; **Fig. 2.5**). Beza Mahafaly, which became a Special Reserve in the 1980s, is comprised of two different forests 10 km apart, parcel no.1 and parcel no. 2 (Sussman and Ratsirarson, 2006). It is in parcel no.1, which is comprised of 80 ha of fenced gallery forest plus another 200 ha of unprotected gallery forest, where ring-tailed lemurs have been systematically studied for over two decades (Sussman, 1991; Sauther et al., 1999; Sussman and Ratsirarson, 2006). Finally, a graduate student is currently conducting research on *L. catta* in Tsimanampetsotsa National Park (**Fig. 2.5**).

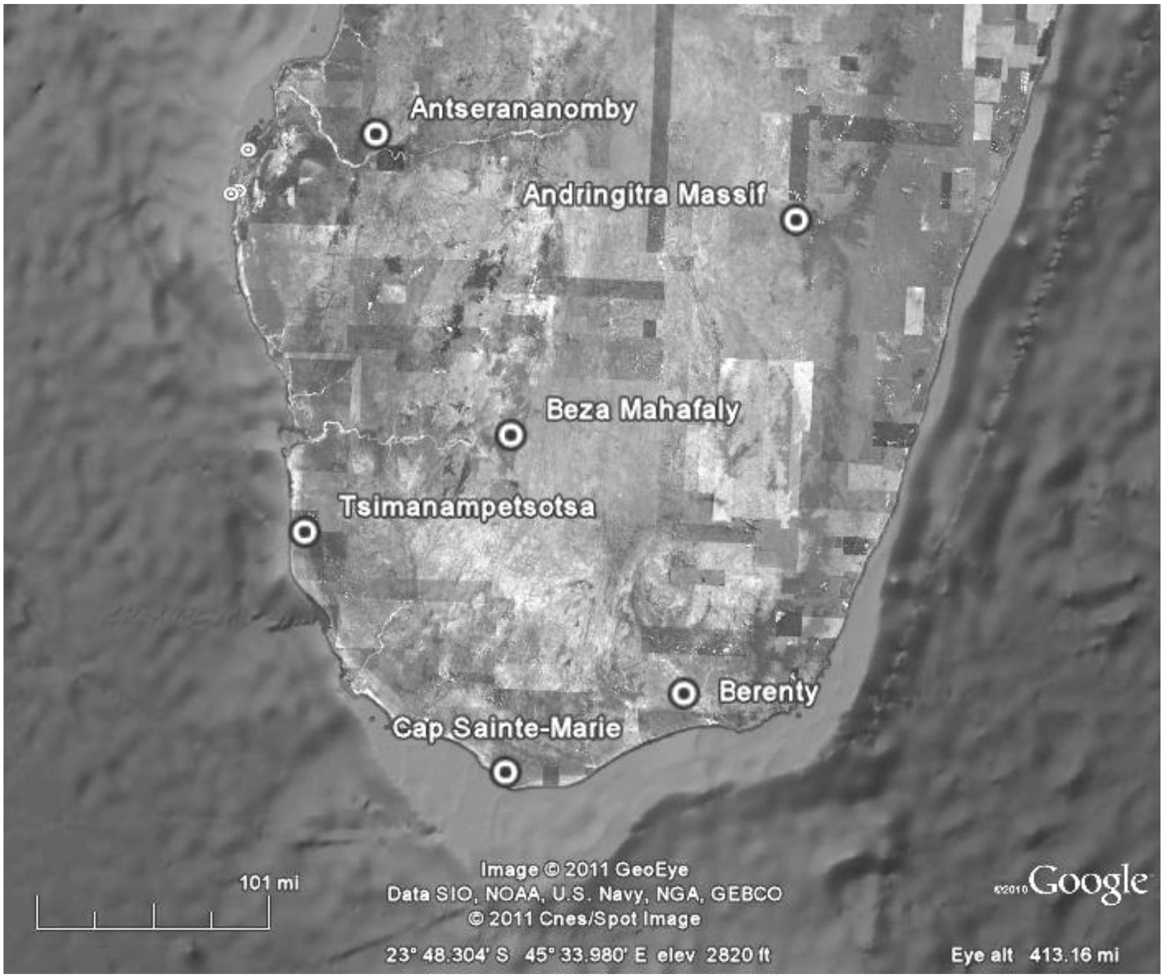

Fig. 2.5. Location map of major *L. catta* research sites. Image is from Google Earth, version 6.0.1.2032 (beta). Google, Inc. Mountain View California.

Decades of nearly continuous research on ring-tailed lemurs at both Berenty and Beza Mahafaly has made this species the most intensively studied of the Malagasy primates (Pastorini et al., 2005; Goodman et al., 2006; Mittermeier et al., 2006). Based on these studies, ring-tailed lemurs are stated to have the following patterns of behavior.

Ring-tailed lemurs form multimale-multifemale troops. The typical troop size is 11.5-14 individuals at Beza Mahafaly and 16 ± 7 individuals at Berenty (Sussman, 1991; Koyama et al., 2002; Gould et al., 2003). However, troop sizes of more than 25 have been reported at both sites (Sussman, 1991; Koyama et al., 2002). The species is female dominant, and troops are comprised of hierarchical matrilines with male migration (Jolly and Pride, 1999; Sauther et al., 1999). In the wild, female ring-tailed lemurs can live to their late teens and oldest known wild female lived to be 21 (Cuozzo et al., 2010; Sauther, pers comm). Less is known about the longevity of the males in the wild (Gould et al., 2003), but recent data indicate that they only live to their mid-teens (Cuozzo et al., 2010; Gould, pers comm). Densities depend upon habitat quality, ranging from 1.0 lemur/ha to 5.8 lemurs/ha (Koyama et al., 2002). Troop range boundaries are remarkably consistent year to year and vary in size from 7.97 ha at Berenty to 25 ha at Beza Mahafaly (Mertl-Millhollen et al., 1979; Sussman, 1991; Jolly and Pride, 1999). Day range lengths average from 1,000 m to 1,377 m (Jolly et al., 1993; Sussman, in press). There are inter-troop conflicts at contested boundaries where troop ranges overlap, with females as the primary defenders (Jolly et al., 1993; Sauther and Sussman, 1993; Gould, 1996).

The mating season of ring-tailed lemurs is highly seasonal and coincides with Madagascar’s wet season (Jolly, 1966; Sauther, 1992). Females are receptive only six to 24 hours a year within a one to three week period (Jolly, 1966; Koyama, 1988; Sauther, 1992). Although resident males with dominant status have greater mating success, females also mate with non-resident males (Koyama, 1988; Sussman, in press). The birth season falls within a two to three week period in September through November (Sussman, 1991; Pride, 2005), with births occurring later in the scrubbier habitats (Jolly et al., 2002). Females typically conceive every year (Budnitz and Dainis, 1975; Sussman, 1991; Koyama et al., 2001). Singletons are the most common, but twinning also occurs (Sussman, 1991; Koyama et al., 2001). The infant mortality rate within the first year of birth averages close to 35% (Koyama et al., 2001). However, a study at Beza Mahafaly during a drought year recorded an 80% infant mortality (Gould et al., 1999).

The diet of ring-tailed lemurs is primarily frugivorous and secondarily folivorous (Jolly, 1966; Sussman, 1972; but see Oda, 1996). Although *L. catta* feed from as many as 114 different species of plants at one site (Sussman, in press), most of its feeding time is concentrated on only a few of these species, and most notably *Tamarindus indica* (Jolly, 1966; Sussman, 1972; Sauther, 1992; Rasamimanana and Rafidinarivo, 1993). At both Berenty and Beza Mahafaly, *L. catta* suffer marked increases in mortality following droughts. This affects all age classes, and is hypothesized to be more closely linked to decline in the availability of these few key resources than to decline in water sources during the actual drought period (Sauther, 1998; Jolly et al., 2002).

The only research on ring-tailed lemurs that has been conducted in Madagascar outside of a gallery forest environment occurred in 1995, when Goodman and Landgrand (1996) conducted a behavioral study on a troop of ring-tailed lemurs on the Andringitra Massif in Andringitra National Park (**Fig. 2.5**). Through their research, they found that this troop migrates to adjust to seasonal changes, and that the pelage of these individuals is woolly and dark (Goodman and Landgrand, 1996; Yoder et al., 2000; Goodman et al., 2006). In fact, the behaviors and appearance of these individuals are so distinctive that genetic tests were conducted to evaluate whether the Andringitra ring-tailed lemur might better be considered distinct subspecies of the gallery forest ring-tailed lemur. However, the results of the analysis showed no significant molecular differences between the two populations (Yoder et al., 2000).

Focal groups

All of the behavioral data for this study were collected from two troops in the CSM area. The range of the first troop was primarily limited to the land of Bevaro Moravato village, the home of the (former) regional President (S° -25 29.682, E° 45 7.688) (**Fig. 2.6**). The range of the second troop spanned two villages, Tsankalamanga and Andafambola (S 25 26.7777; E 045 08.264; S 25 27.060; E 045 07.825). These three villages are the closest known *L. catta* habitats to Cap Sainte-Marie Reserve. Bevaro Moravato, the closer site, is over 10.7 km from the reserve. The minimum distance between the two focal troops' ranges is 5.5 km (**Fig. 2.6**).

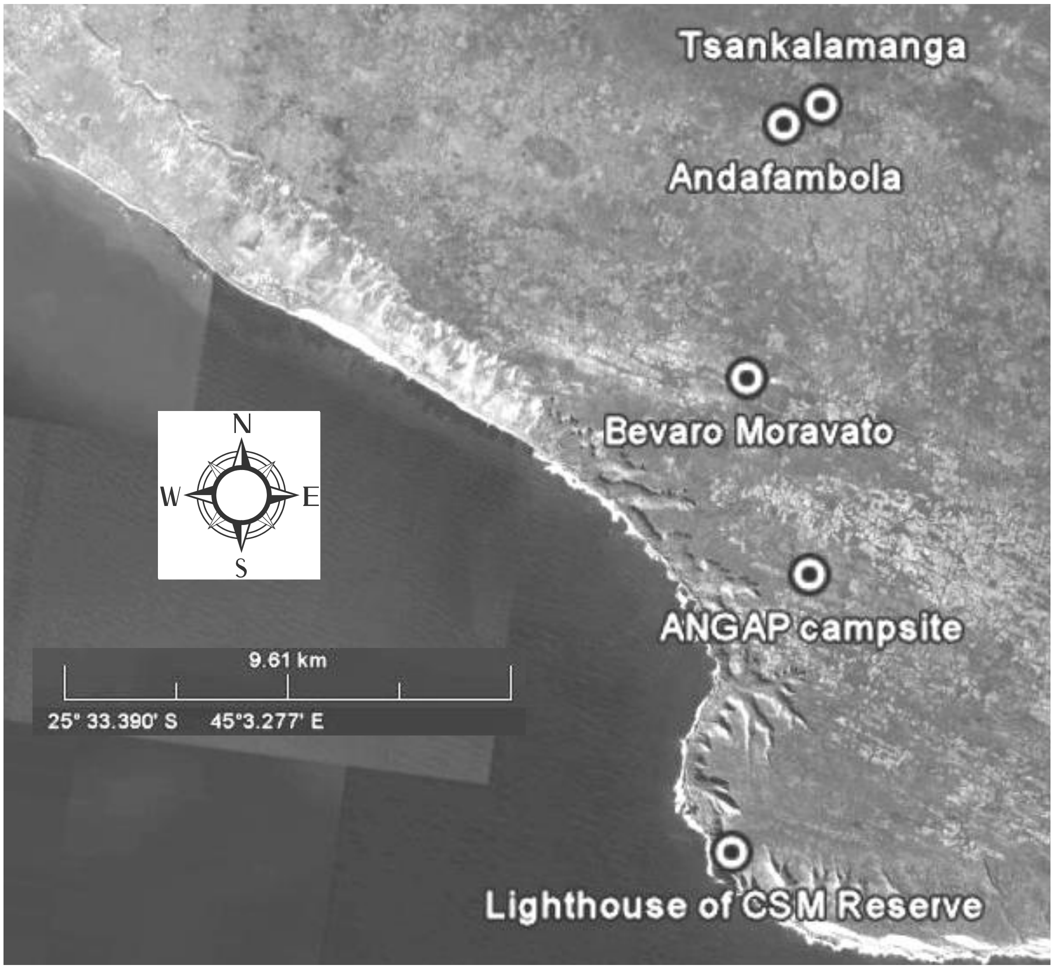

Fig. 2.6. Key sites of CSM *L. catta* study. Map adapted from Google Earth, version 4.3.7284.

At the commencement of the study in May 2007, the Bevaro Moravato troop consisted of three adult males, five adult females, one subadult male[1], one infant male[2], and two infant females. To assess the relative age classes of the adult troop members, we attempted to use the criteria of Sauther et al., 2002 and Gould et al., 2003 (see also Gould, 1994; Richard et al., 2002). Yet it soon became evident that not all of the conditions used to assess relative ages of gallery forest *L. catta* apply to the lemurs of CSM. For example, female nipple length is always less than 0.5 cm, even when the females have infants. Similarly, weight appears to be an unreliable indicator of relative age among adults (**Table 2.2**). Therefore, we assessed relative ages on only two criteria: 1) ranges of variation in tooth wear (notably molars and to a lesser extent canine status), and among males, 2) testicle descent (**Table 2.2**).

Based on this revised method, we deduced that the Bevaro Moravato troop was comprised of two prime age males, one young adult male, and one infant (see Gould, 1994; **Table 2.2** for definitions of relative adult age categories). Among the females, we assessed that one female was old prime, two were prime, one was young prime, one was young, and two were infants.

Throughout the study, I documented the changes in the troop's social structure. In mid August 2007, one prime adult female was found dead. Two infants were born in September, one of which, a female, survived. Twins were born in October. One of the infant twins, a male, survived. Two adult males, who were seen weeks earlier in and

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[1] As per Sauther et al. (2002) and Gould et al. (2003), a subadult ring-tailed lemur is an individual who is between one to two years of age. However, the use of the word "subadult" is used interchangeably with "juvenile" in the literature (see Sauther, 1992; Gould et al., 2003).

[2] As per Sauther (1992) and Gould et al., (2003), an infant ring-tailed lemur is defined as an individual who is less than one year old.

around Cap Sainte-Marie Reserve (see chapter three), were observed for the first time interacting with the troop in early November, 2007. These two males became fully integrated into the troop by May, 2008 (see chapter four). At the end of the study, the troop consisted of six adult males, four adult females, two subadult females, one subadult male, one infant female, and one infant male. In sum, the troop size increased from 11 to 15 individuals.

In May 2007, the structure of the Tsankalamanga/Andafambola troop was comprised of three resident adult males, four adult females, one visiting adult male[3], and two juveniles. Among the adult males, one male was old prime, one male was young prime, and one male was young (**Table 2.2**). Among the adult females, one female was old prime, two females were young, and one female was never immobilized but was clearly younger than the female who was assessed as old prime (see chapter four). When the darting team was in the main sleeping hedge at Tsankalamanga to conduct the initial immobilizations, the decomposing bodies of two young females were found.

In addition to these dead two females, the following deaths occurred early in the study: one young adult female died early June 2007, the young adult male died early July, the old prime male died late July 2007, and the second young adult female died in mid August 2007. As for births, one female was born in September 2007, and one male was born in October 2007. However, the infant male later died in mid May 2008. In mid April 2008, a new male was first observed interacting with the troop. This male was a fully integrated troop member by May 2008 (see chapter three). The juvenile male died mid April 2008. At the end of April 2008, the only surviving adult male who was a part of the

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[3] One male was considered a visiting male as he first appeared in June 2007, stayed through January 2008, disappeared from February 2008 through May 2008, reappeared through June 2008, and then disappeared again in July 2008.

troop in 2007, the male assessed as young prime, disappeared. In sum, the size of this troop decreased from nine individuals plus a visiting male to five individuals plus a visiting male. The high mortality rate of this troop is further discussed in chapter five.

Table 2.2. Criteria used to assess relative ages of adult focal individuals. Criteria have been modified from those of Sauther et al. (2002). As per Gould (1994), Old is defined as 12+ years, Old prime as 9-12 years, Prime as 6-9 years, Young prime as 4-6 years, Young as 3-4 years, and Subadult as 2-3 years.

Estimated age grade	**Troop Membership**	**Adult Animal ID**	**Weight**	**Testicle Descent**	**Status of Upper Canine Eruption**	**Status of Molar Cusps**	**Status of tooth comb**	**Status of caniniform P2**
Old	Tsankalamanga	R3	2.1 kg	Descended and large	Full	Heavily worn and stained, upper and lower	Mostly gone	Worn, Right maxillary canine tip is heavily stained
Old prime	Bevaro Moravato	G4 (Mena)	1.9 kg	N/A - ♀	Full	Very flat molars to the gum	Good	Worn
Old prime	Tsankalamanga	G10	1.6 kg	N/A - ♀	Full	Worn, upper and lower	Slightly worn	Worn left maxillary canine tip
Old prime	Tsankalamanga	SF*	2.3 kg		Full	Worn	Worn	Worn
Prime (?)	Bevaro Moravato	G2	1.8 kg	N/A - ♀	Full	Worn and stained, upper and lower	Good	Good
Prime	Bevaro Moravato	G14	2.1 kg	N/A - ♀	Full	Upper molars stained and worn	Good	Good
Prime	Bevaro Moravato	B1	1.7 kg	Descended and large	Full	Stains	Good	Worn left maxillary canine tip
Prime	Bevaro Moravato	WS	1.9 kg	Descended and (very) large	Full	Slight stains and mild wear	Good	Good
Young prime	Bevaro Moravato	R1	1.8 kg	N/A - ♀	Full	Good	Good	Good
Young prime	Tsankalamanga	B7	1.9 kg	Descended and medium to large	Full	Good	Good	Missing right maxillary canine tip
Young	Bevaro Moravato	G12	2.1 kg	N/A - ♀	Full	Mild stains	Good	Missing right maxillary canine tip
Young	Bevaro Moravato	R9	2.0 kg	Descended but small	Full	Stains	Good	Good
Young	Tsankalamanga	B5	1.5 kg	Descended but small	Full	Good	Good	Good
Young	Tsankalamanga	G8	1.2 kg	N/A - ♀	Full	Mild stains	Good	Good
Young	Tsankalamanga	R6	1.6 kg	N/A - ♀	Full	Good	Good	Missing left maxillary canine tip
Subadult	Bevaro Moravato	ST	1.5 kg	Descended but small	No Data	No Data	No Data	No Data

*Age estimate of SF is based on final health assessment, which occurred on 7/28/2008

Population structure of *L. catta* at CSM

In addition to the two focal troops, two or possibly three other troops were known to be within 10 km of the Cap Sainte Marie ANGAP camp. The main sleeping hedge of the first troop was about 400 meters from the village Tsikotake (S 25 27.123; E 045 06.316; **Fig. 2.7**). Six individuals were observed in this troop. However, since these individuals were not habituated and I went to this site only once, it is possible that this troop was even larger. A second troop was observed 13 times. The main sleeping hedge of this troop surrounded a *raketambazaha* crop, a cultivated "spineless" variant of *Opuntia, O. ficus-indica* var. *inermis (*Zarasoa, 2011*).* The *raketambazaha* sleeping hedge was 5.9 km from a Bevaro Moravato sleeping hedge and 0.2 km from the Tsankalamanga sleeping hedge (**Fig. 2.7**). In fact, the *raketambazaha* troop was twice observed within the Tsankalamanga sleeping hedge when the Tsankalamanga troop was not there. The *raketambazaha* troop was comprised of a minimum of five adults, one juvenile and two infants. One of the males of this troop could be easily identified by a scar on his cheek that had healed to look like a mole. This troop was observed approximately once a month from May 2007 through March 2008. Although we revisited this site several times after March 2008, we never again found this troop. Since March demarcates the end of the fruiting season of *raketambazaha* (Larsson, 2004), it is possible that this troop relocated to another hedge for the austral winter. This scenario is plausible since the observations of this troop from May 2007 through October 2007 were not near the *raketambazaha* field. Finally, since I could not confirm that the southernmost observation was the *raketambazaha* troop, it is possible that this was a sighting of a fifth troop in the area (**Fig. 2.7**).

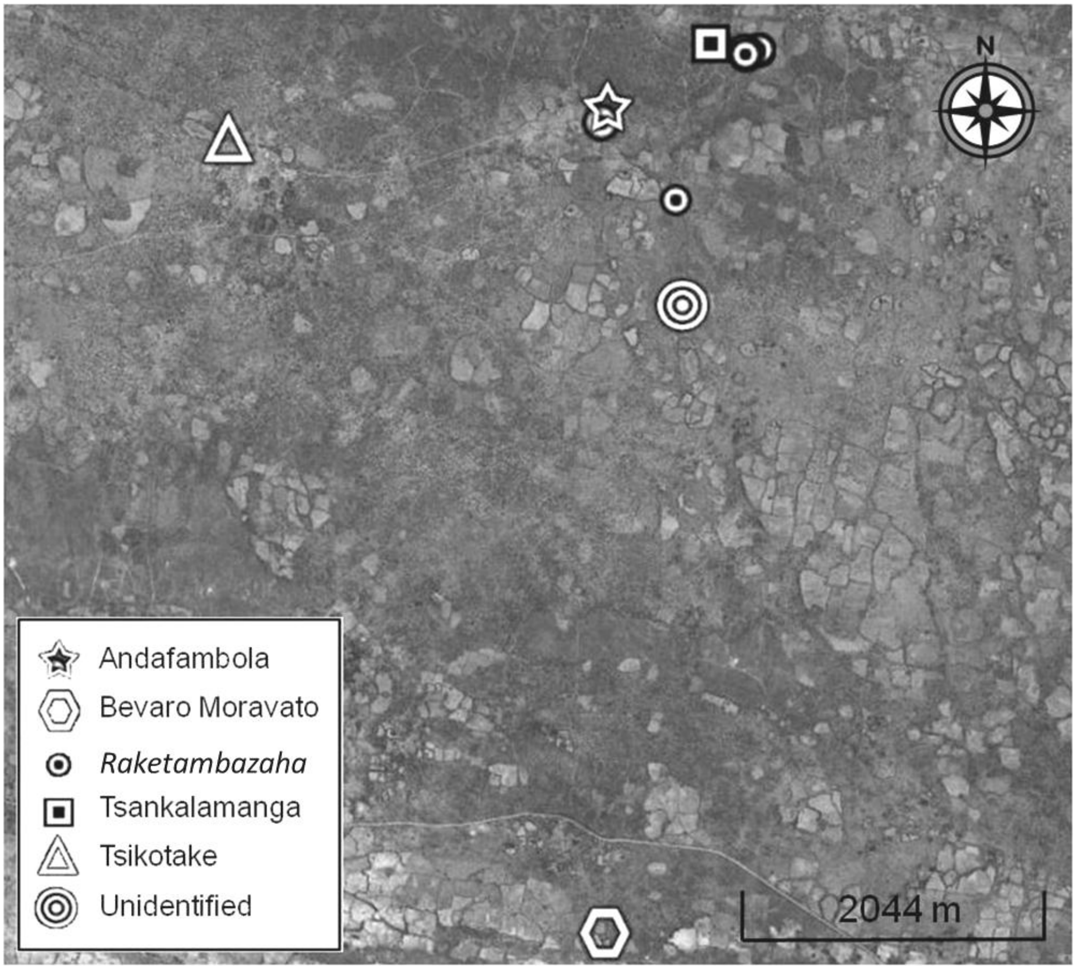

Fig 2.7. Observed troops within 10 km of the CSM ANGAP camp. Data were collected from May 2007-July 2008. Map adapted from Google Earth, version 4.3.7284

General Methods: Data Collection, Storage and Analysis

Health assessments

On May 17 and May 18 2007, a total of 14 adults were immobilized for veterinary health assessments. In addition, these same adults were fitted with either radio collars or nylon “safe-cat” collars. Darting started around 6:30 a.m., at daybreak. All individuals were darted within *Opuntia monacantha* hedges, and no individual was higher than 3 meters from the ground. Each individual was injected with 50 mg of Telazol® (Fort Dodge Laboratories, Fort Dodge, IA) through the use of a blow-pipe (Telinject USA, Inc.). The veterinary crew included the Director of Animal Health at the St. Louis Zoo (Dr. Randall Junge), a Malagasy wildlife veterinarian (Dr. Fidy Rasamainarivo), and a Malagasy darter. After each lemur was anesthetized, it was brought to a clean and shaded tarp. An electrolyte solution equal to the volume of blood collected was given to each individual subcutaneously. Saline drops were placed in each individual's eyes to prevent the corneas from drying (see also Miller et al., 2007). The following data were obtained from each individual by Junge and Rasamainarivo: weight, blood glucose level, heart rate, respiratory rate, presence/absence data on wounds, broken bones, and ectoparasites, and general dental health assessments. Moreover, $\leq$ 12 ml of blood, 22 cc of feces, and ectoparasites were collected from each individual (see also Miller et al., 2007). Blood smears and total white cell counts (WBCs) were conducted in the field. The remaining blood was centrifuged in the evening to preserve the samples for shipment to the United States, and serum was separated from cells before the samples were frozen in liquid nitrogen. Fecal samples were also frozen in liquid nitrogen. Parasite samples were preserved in a 70% ethyl alcohol mixture (see also Miller et al., 2007). Final health assessments and the removal of collars took place on July 28 and July 29, 2008.

Biological samples shipped to the United States were submitted by Junge to several reference laboratories (see Miller et al., 2007; chapter five) for measurements of 1) serum biochemical profiles, 2) fat-soluble vitamin levels, 3) trace mineral levels, 4) viral serology, and 5-7) endo-, ecto-, and hemoparasite loads. Health assessment data were then entered into the Normal Physiological Values database by Randy Junge. This database is a sub-unit of the International Species Inventory System (ISIS). Comparisons between the two CSM troops were analyzed using Mann-Whitney U tests. Comparisons between the two capture periods were analyzed using Wilcoxon signed ranks tests. In addition, health values of the CSM groups were compared with the physiological values of *L. catta* collected from other sites in Madagascar (e.g., Berenty n = 11 [spiny forest], Beza Mahafaly n = 161, Tsimanampetsotsa n = 25), and with semi-free ranging individuals from St. Catherines Island, GA USA n = 13. These results are presented in the chapter on health and nutrition, chapter five.

All day follows

Following the health assessments, I spent the rest of May and all of June 2007 habituating the two troops to my presence (Hall, 1965; Williamson and Feistner, 2003). Although the lemurs were never fully habituated to the guides, they stopped reacting to my presence by the end of June. However, to ensure that all of the data are truly representative of habituated animals, I analyzed behavioral data only from August 2007-July 2008. A total of 1,019 hours and 49 minutes were included in the behavioral data analyses.

Since the Bevaro Moravato site was 6 km from camp and the Tsankalamanga troop was 13 km from camp, we would bike from camp at approximately 5:20 a.m. and arrive at the closest field site before 6:30, well before the lemurs were awake. We often arrived at Tsankalamanga just before 7:30. I was the only person who collected behavioral and ranging data.

Behavioral data were collected for 10 hours a day four days a week. I used one-minute instantaneous focal animal sampling (as per Gould, pers comm) to record activity (sleep, rest, self groom, mutual groom, feeding, drinking, movement, travel, sunning, play, huddle) and substrate (*Opuntia monacantha* hedge, ground, ground/shade, tree [e.g., *Euphorbia laroo, Alluaudia dumosa*], field, foliage/shrubs, sisal mix) (Hall, 1965; Sussman, 1972; Altmann, 1974; Gould, 1994; Kelley, 2001; Sussman et al., 2005). In addition, I recorded all occurrences of social behaviors of the focal individual, which included: approach; overt aggression (fight, bite, chase, pounce); maintenance aggression (stink fight, tail wave, cuff, lunge, displacement); submission (flee, submissive chatter; sequenced avoidance as defined in approach/leave); and copulation (Gould, 1994; Kelley, 2001). Binoculars were never needed as I was typically less than 3 meters from the focal individual. Focal individuals were rotated every hour (Gould, pers comm). To obtain ranging data, I took GPS readings when I switched focal individuals and during major travel bouts (see also Pimley et al., 2005). Temperature was recorded throughout the day, typically at the change of the focal individual. Group scans were taken every 15 minutes. Every two to three days, handwritten data were entered into Excel for future transfer to Access and SPSS databases.

Activity budget data were analyzed and compared with gallery forest studies using descriptive and nonparametric statistics (e.g., Pearson's chi-squared tests) (Dytham, 1999; Kelley and Mayor, 2001; Sussman et al., 2005). To analyze spatial cohesion data, I first analyzed nearest neighbor data using an association index (Lehner, 1998; Kelley, 2001). Results were then illustrated through spatial group cohesion patterns (Altmann, 1968; Lehner, 1998; Kelley, 2001). Moreover, I also used nonparametric statistics (e.g., Spearman's rank-order correlations) to assess whether time spent in *O. monacantha* hedges were significantly correlated with the seasonality of *O. monacantha*, environmental conditions, or the presence of villagers (Dytham, 1999), and to determine the relationship between thermoregulatory behaviors and the environment (see chapters four and six).

To measure the home-ranges of the CSM study troops, I used the Home Range Tools package in ArcGIS 9.2 (http://blue.lakeheadu.ca/hre/). I generated home-ranges using both Minimum Convex Polygons and Kernel Polygons (see chapter three). To measure the spatial distribution of sacred forests and *Opuntia,* I recorded all GPS readings of vegetation points for display on ArcGIS. I then measured the daily path lengths of the troops by tracing consecutive GPS readings. Last, I created maps of high use feeding sites by month and combined these maps with the ranging data to test for significant correlations between ranging behavior and phenology.

Nutrition data

For the nutrition component of the study, the two Malagasy guides collected a minimum of 150 grams of each plant part and taxa that the lemurs consumed each month. Within 24 hours, I weighed each sample to obtain wet weight. Immediately afterwards, I would hang these samples in paper sacks under a makeshift roof to begin the process of shade drying (Hladik, 1977; Silver et al., 2000; Wakibara et al., 2001; Curtis, 2004). However, since much of the vegetation consumed by the *L. catta* of CSM is 70-90% water content (see chapter five), shade drying alone often proved inadequate and mold would be the result. Therefore, I spent three days a week using a modified Coleman camp oven to fully dehydrate a majority of the samples. When possible, I preserved a minimum of 50-100 grams of each sample per taxa per month consumed (Dierenfeld and McCann, 1999; Silver et al., 2000). After the samples were dried, I stored each sample in a new paper bag and sealed each one with masking tape for export and future chemical assay (Dierenfeld and McCann, 1999; Silver et al., 2000; Curtis, 2004; Gould, pers comm). A total of 70 different plant species, a nearly complete sample of the lemurs' yearly diet, were collected throughout the study season. The scientific names of the plant species were provided on site by Balzac Mbola, a Malagasy botanist who works for the national forestry department (ANGAP).

To assess the relative diversity of the study troops' diets, I compared the diets of the CSM *L. catta* with the diets of *L. catta* at Andringitra, Antserananomby, Berenty, and Beza Mahafaly (Goodman and Landgrand, 1996; Simmen et al., 2006). To estimate how much each plant species was consumed, I created hierarchical lists in descending order on the plant species consumed. Separate lists were made for the two troops to compare the diversity of diets within CSM *L. catta* troops. Plant parts consumed (i.e., fruit/seeds, leaf, flower) were noted in a separate column, as were months of consumption.

To obtain nutrition values, 41 samples, representing the top 75% of each CSM troop's monthly diets, were first ground into 1 mm particles or less. No less than 20g of each sample was then placed into separate zip-lock bags and was shipped to Dairy One for the following analyses: crude protein (to determine nitrogen content); macromineral concentrations (Ca, Mg, Na, P), trace elements (Cu, Fe, Mn, Zn); percentages of neutral detergent fiber (NDF), water soluble carbohydrates (WSC), alkaloids, and tannins (Dierenfeld and McCann, 1999; Dutton et al., 2003). The mean nutrient values were compared with the recommended values of nutrient requirements for non-human primates (NRC, 1978; Dierenfeld and McCann, 1999; CAM et al., 2003).

CHAPTER 3

Ranging Behavior and Substrate Use in Relation to Feeding Ecology, Migration and Terrestriality

Lemur catta occupies a habitat that is comparable to that of the most adaptable of anthropoid primates e.g., *Papio,* some *Macaca* species, *Chlorocebus, Erythrocebus* (Sussman, 1991; Gould et al., 1999; Sussman et al., 2003; Hart and Sussman, 2005; Goodman et al., 2006). Three key characteristics that this prosimian species shares with these anthropoid primates include 1) relatively large multimale, multifemale groups, 2) a habitat range that includes marginal scrub habitat, and 3) quadrupedal, terrestrial locomotion, defined as "a movement in which all four limbs move in a regular pattern above a horizontal support or on the ground" (Gebo, 1987:273). All three of these characteristics influence ranging distance. While large group size is hypothesized to necessitate larger ranging distances due to ecological constraints (Chapman and Chapman, 2000), the latter two characteristics enable the flexibility to exploit different habitat types across a landscape.

Background

For the Cap Sainte-Marie (CSM) *L. catta* population specifically, the question of what drives ranging behavior is especially intriguing. Ring-tailed lemurs in this region have been observed traveling within the CSM Reserve from unknown locations during the month of October. Since no one knows where these troops come from or go to afterwards, there is the question of whether ring-tailed lemurs in this region are transient, or migratory in the primatological sense (Sussman et al., 2003).

The most common theoretical significance of migration in the biological and ecological literature is that organisms (mainly bird species) travel long distances, often across widely separated latitudes and on an annual cycle, to adapt to either inhospitable changes in climate and/or suboptimal breeding conditions (e.g., Huntley and Webb, 1989; see Alerstam and Hedenström, 1998). Within the literature on primate behavior, however, the word migration is typically used to refer to the intergroup movements of the dispersing sex rather than the long distance travel of an entire group (e.g., Pereira and Weiss, 1991; Sussman, 1991; Sprague et al., 1998; Sugiyama, 1999). The closest documentation of migratory-like behavior in a primate species has been that of a fragmented population of *Gorilla gorilla diehli* in Takamanda Forest Reserve, Cameroon (Bergl and Vigilant, 2007). In this population, both males and females have been observed to travel as far as 10 km to reach another group. Moreover, the travel is unidirectional; some groups only have emigrants, while other groups only have immigrants (Bergl and Vigilant, 2007). The authors theorize that environmental constraints, such as roads and disturbed forest, are the reason for this pattern of travel.

In the CSM region, unidirectional travel patterns similar to the gorilla example above were observed. Specifically, no individuals were observed leaving the Bevaro Moravato troop throughout the 15 months of observations. However, two male immigrants arrived from an unknown location over 6 km away from this group in the month of October. The reason for this unidirectional travel is still not known. Among gallery forest troops, ranging behavior is closely tied to the animals' proximity to rivers (Sussman and Rakotozafy, 1994). However, rivers and lakes are absent in the CSM region (see Chapter two). Therefore, other environmental resources, such as perhaps vegetation with high water content, may be correlated with the animals' ranging behaviors. The focus of this chapter is to determine to what extent the desert-like environment of the CSM region uniquely affects the ranging behavior and habitat use of *L. catta*.

Intraspecific variation in ranging distances: environmental and social constraints

Over 90% of the remaining potential habitat for *L. catta* is composed of Didiereaceae-*Euphorbia* bush (Goodman et al., 2006; Sussman et al., 2006), and it has been suggested that this habitat type is a component of this species' ancestral range (Goodman et al., 2006). Yet despite the prevalence of bush forest habitats, it is the fragmented gallery forest that supports the densest populations (Sussman, 1991; Koyama et al., 2002; Sussman et al., 2003; Pride, 2005; Gould, 2006; Jolly et al., 2006; Sussman et al., 2006). Relative to the troops that live in adjacent spiny forest habitat, gallery forest troops have small home ranges and greater overall density (Budnitz and Dainis, 1975; Mertl-Millhollen, 1988; Sussman, 1991; Jolly et al., 1993; Gould, 2006; but see Koyama et al., 2006). Moreover, the ranging areas of these troops have been found to be (inversely) correlated with the number of trees with Diameter Breast Heights (DBH) $\geq$25 cm (Sussman and Rakotozafy, 1994). Thus, in gallery forest environments, small home ranges likely indicate microenvironments that are rich and varied enough ecologically to support the needs of a troop within a small area. In fact, home range areas appear to be inversely correlated to the productivity of the landscape for other ecologically similar primates, such as *Chlorocebus aethiops* (vervet monkeys), and at least two baboon species, *Papio anubis* and *P. hamadrayas* (anubis baboons and Ethiopian hamadrayas baboons) (Struhsaker, 1967; Nagel, 1973; but see Swedell, 2002).

Yet home range areas are not fixed throughout the year and have been found to be cyclical among gallery forest *L. catta*. For example, Sussman (1991) and Sauther (1998) have found that numerous troops in the Beza Mahafaly region, some of which have the smallest home ranges by the river for most of the year, have larger home ranges in October and November to feed on the fruit of *Salvadora augustifolia*, a tree species that grows only in drier environments of the region. Moreover, although a characteristic of gallery forest *L. catta* is that troops have relatively stable ranging areas; female troop members (the philopatric sex) at both Beza Mahafaly and Berenty will often lead their troops on daily excursions outside of home range boundaries periodically throughout the year (Jones, 1983; Sussman, 1992; Jolly and Pride, 1999; Koyama et al., 2006). These excursions are likely executed for the purpose of inspecting the availability of seasonal resources that extend beyond their core and home range areas (Jolly and Pride, 1999). Therefore, while small home range is a characteristic of gallery forest *L. catta*, long daily ranging distances appear to be an indication of seasonal resource abundance. This ranging pattern has also been observed among other primate species. For example, Swedell (2002) found that hamadryas baboons travel longer distances during the wet season, the season of resource abundance, than during the dry season, the season of resource scarcity.

Last, ranging distances can also be influenced by social variables. At Berenty Private Reserve for example, newly fissioned troops of *L. catta* have been found to limit their ranging distances to avoid intertroop encounters (Jolly and Pride, 1999; Koyama et al., 2002). At CSM, intertroop encounters were rare among troops, and the ranges of the two focal troops were kilometers apart. However, the ranging behaviors of the CSM troops may have been influenced by male dispersal. The effects of these variables on ranging distance, as well as the ecological variables mentioned above, will be tested and reviewed in the first set of analyses in this chapter.

Interspecific variation in ranging distances: physiological constraints

At gallery forest sites, ring-tailed lemurs spend approximately one third of their total activity time on the ground (Shaw, 1879; Hill, 1953: Sussman, 1972; see Sussman, in press). In comparison, rhesus macaques (*Macaca mulatta*) at Cayo Santiago spend over half of their activity time on the ground (Wells and Turnquist, 2001), and most baboon species are predominantly terrestrial (Altmann and Samuels, 1992). Therefore, although *L. catta* is the most terrestrial of the extant prosimians, this species is still often classified as an arboreal primate. In fact, the locomotor classification of *L. catta* as an arboreal primate has been used to test morphological and behaviorial theories on the evolution of *Homo*. For example, Tasuku Kimura and his colleagues spent decades researching differences in locomotor characteristics between what they classified as arboreal primates (e.g., *Pan troglodytes*, *Cebus apella*, and *L. catta*) with terrestrial primates (e.g., *Macacca mulatta*) to better understand possible preadaptations to human bipedalism (e.g., Kimura et al., 1979; Kimura, 1992).

Yet an accurate account of a species' locomotive repertoire is important for reasons that extend beyond academic curiosity. From a conservationist's view, it is important to understand a species' true locomotive flexibility when creating action plans for conserving a threatened species, especially in regard to corridor design and metapopulation potential (see Cowlishaw and Dunbar, 2000). In Africa, Anderson et al., (2006) discovered that the primarily arboreal primate species, the Angola black-and-white colobus (*Colobus angolensis palliatus*), will travel short distances on the ground between areas of viable forest habitat. Similarly, through a study conducted on black howler monkeys (*Alouatta pigra*) in Mexico, Pozo-Montuy and Serio-Silva (2007) found that this largely arboreal primate used ground travel and foraging as a means to obtain adequate resources in a highly fragmented forest when necessary. In both studies, the authors concluded that there should be efforts to minimize ground use through landscape management as ground use was an indicator of stress and increased predation risk. Similarly, Tabacow et al. (2009) documented a 20-fold increase in ground activity within a group of the almost exclusively arboreal species *Brachyteles hypoxanthus* (muriqui monkeys). However, in contrast to the aforementioned studies, these researchers suggest that the muriquis' increase in ground use has been driven by the transmission of social learning rather than by ecological necessity (Tabacow et al., 2009). For *L. catta*, Sauther (2002) found that gallery forest troops at Beza Mahafaly may spend as much as 75% of their activity time on the ground during some months of the year. Moreover, this increase in ground use appears to have been driven by seasonal dietary needs (Sauther, 2002). However, these troops will also avoid the ground when predation pressure is high (Sauther, 2002).

In the CSM region, vast areas of landscape are covered by *Opuntia stricta.* While this habitat may ideal for the avoidance of some predator species, there are no opportunities for arboreal locomotion. Whether this habitat is beneficial to the CSM *L. catta* population depends upon the extent to which *L. catta* is a terrestrial primate, and to what extent arboreal habitats are needed to further protect this species from predators.

The topic of ground use, especially in relation to terrestrial locomotion, will be the focus of this chapter’s second set of analyses.

Analysis 1: ArcGIS-Finding Ranging Patterns

In 1943, William Henry Burt defined home range as the “area traversed by the individual in its normal activities of food gathering, mating, and caring for young” (p. 351). This is the definition that is still commonly used today. However, this definition is too diffuse to be of value when attempting to make quantitative comparisons within and across animal populations. A more practicable term for quantitative analyses has been defined by White and Garrot (1990), who state that an animal’s (or group’s) home range is the smallest area in which it spends 95% of its time. Moreover, they define an animal’s (or group’s) core range as the area where 50% of the group’s concentrated activity occurs (see Downs and Horner, 2007). These are the definitions I have used for the following home range analyses.

Methods

Home ranges of the study troops were obtained using Home Range Tools (Rodgers et al., 2007), which is the ArcGIS® version of the Home Range Extension program for ArcView 3x (Rodgers and Carr, 1998). To obtain home range results, I generated both Minimum Convex Polygons (MCPs) and Kernel Density Estimates (KDEs). Data used for these analyses were taken by a Garmin GPS unit approximately every hour throughout the day. Data were taken on nonconsecutive days so that morning sleeping site points were independent of evening sleeping site points. To obtain missing sleeping site data, I plotted known sleeping sites on Google Earth® (2008) and used the sleeping site point closest to the last recorded GPS point of the day to complete the daily travel route. Since all troop members traveled as a cohesive group during travel bouts (see chapter four), animal id was treated as synonymous with troop id. In total, 937 GPS points were used to obtain home range estimates for the Bevaro Moravato troop, and 608 GPS points were used to obtain home range estimates for the Tsankalmanga troop.

Both data sets were found to be significantly autocorrelated when tested against the Swihart and Slade index (1985). Autocorrelation occurs when 1) data are taken at too frequent intervals (Swihart and Slade, 1985) and/or when 2) animals move in a non-random fashion (DE Solla et al., 1999). Yet whether autocorrelation should be corrected for in home range analyses is debatable. Swihart and Slade (1985) believe that autocorrelation is a problem as it violates the statistical assumption of data independence (see Rodgers and Carr, 1998). Conversely, DE Solla et al. (1999) argue that reducing the intervals of data collection reduces statistical power as well as biologically relevant information. To determine whether autocorrelation should be corrected for in this study, I created surface maps and ran exploratory runs on reduced two hour interval data sets. The surface maps indicate that both troops had habitual “nesting” hedges throughout the year, which accounts for the multitude of duplicate data points (**Fig. 3.1**). In addition, the exploratory runs on the reduced data sets still failed to eliminate significant autocorrelation. Therefore, I did not correct for autocorrelation, and both MCP and KDE analyses are based on the one hour data collection intervals (see DE Solla et al., 1999).

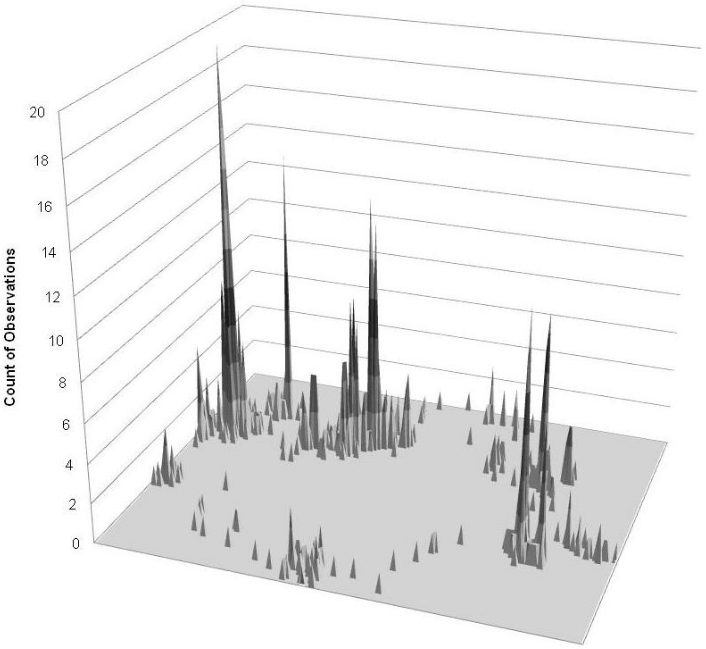

Fig. 3.1a. 3D surface map of the Bevaro Moravato troop's ranging patterns throughout the study. The grid is divided into 156 by 128 cells. Each cell is 10 meters^2. The z axis indicates the number of GPS points that were recorded within each cell. Note the perforated (hollowed circular) distribution of the points (Downs and Horner, 2007).

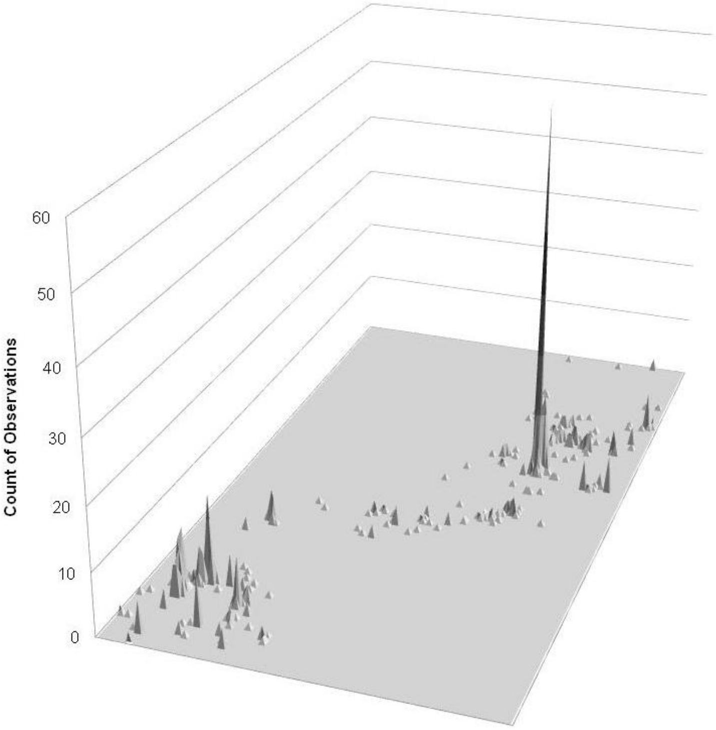

Fig 3.1b. 3D surface map of the Tskankalmanga troop's ranging patterns throughout the study. The grid is divided into 109 by 207 cells. Each cell is 10 meters^2. The z axis indicates the number of GPS points that were recorded within each cell. Note the linear distribution of the points (Downs and Horner, 2007).

MCPs are generated by connecting the outermost points of a group's home range using the smallest number of possible sides (Coates and Downs, 2005). This method is essentially a simulation of the grid analyses that have been used at Berenty Private Reserve and Beza Mahafaly Special Reserve (Mertl-Millhollen et al., 1979; Sussman, 1991; Jolly and Pride, 1999; Koyama et al., 2006; but see Grueter et al., 2009). I chose the MCP method because the dispersion of fixes for the CSM troops was too spread out to make a 25 m x 25 m grid analysis meaningful, and differences in grid size also inhibit the ability to directly compare results (Mohr, 1947; Grueter et al., 2009). The MCP analyses were generated using a fixed mean (Rodgers and Carr, 1998).

For KDEs, data were rescaled using Unit Variance (Seaman and Powell, 1996; Rodgers and Carr, 1998). I used an adaptive smoothing method (Rodgers and Carr, 1998) to account for the fact that there are several low density outer points in the data sets (**Fig. 3.1**). Since both troops had preferred hedges that they regularly frequented as well as multiple centers of activity, finding the appropriate bandwidths for the analyses was especially problematic [i.e., least-squares cross-validation and h_{ref} bandwidths are not appropriate choices in these instances (Rodgers and Carr, 1998; DE Solla et al., 1999]. Therefore, as per Rodgers (pers comm.), I experimented with proportions of reference bandwidths. With this method, one decreases the bandwidth size in increments until the data are broken into island segments. The ideal bandwidth is the increment one larger than this occurrence. For both data sets, I first decreased bandwidth size by increments of 20% and then refined the bandwidth search by increments of 5%. I used 10 m^2 raster cell sizes for resolution, a scaling factor of 1,000,000 m (the default), and a buffer of 5,000 m.

I chose polygons to demarcate home range and core range areas of the CSM troops. These steps were repeated for monthly KDE analyses.

To determine monthly activity in the troops' core areas, I added five layers on each of the monthly KDE home range maps. The first layer was monthly sleeping hedge sites. All of the sleeping hedge sites are *Opuntia monacantha* hedges. These hedges are typically contiguous around a field and are usually at least 3 m wide and 3-5 m high. The second layer was the top-quartile food(s) that each troop fed upon that month[1]. These foods have been classified by the names assigned to them by Balzac V.A. Mbola[2]. The third layer was sacred forest locations. The fourth layer was all other feeding site locations. The fifth and final layer was general troop movements. This last layer represents all of the points that were recorded during the hourly intervals that did not fall within any of the aforementioned categories.

Finally, to obtain rough estimates of the habitat composition of the troops' home ranges, I first layered georeferenced images from Google Earth® (2008) over the KDE maps. Next, I traced polygons over the fields and sacred forests and obtained the area measurements of the shapes, after which, I estimated hedge area by multiplying the lengths of the hedges by 3m. Last, I labeled the remaining area as brush and scrub forest.

Final notes on the methodology

I have chosen to conduct KDE analyses in addition to MCP analyses because multiple simulation studies have concluded that KDE analyses are more accurate estimators of home range area than MCP analyses (Worton, 1987; Nilsen et al., 2008; but

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[1] A top-quartile food is a food item or items that comprised 25% or more of a troop's total monthly feeding time.

[2] Mbola is currently working with ANGAP at Andohahela National Park. He is a botanist, and his specialty is Madagascar's southern flora. In addition, Soafara Niaina Andrianarivelo from the Missouri Botanical Gardens has helped with refining some these species identifications.

see Downs and Horner, 2008). Yet MCP analyses are still useful for comparative studies because more ecological studies have used MCP analyses (Nilsen et al., 2008), and many ecological studies use both methods to compare results (e.g., Pavey et al., 2003; Coates and Downs, 2005; Pimley et al., 2005).

The KDE method also has its limitations. For example, Downs and Horner (2007) have found through simulation studies that the accuracy of KDE analyses depends on the point pattern shape of the data set, which is perforated and linear for the Bevaro Moravato and Tsankalamanga troop respectively (see **Fig. 3.1**). These patterns performed poorly in their simulation tests although the standard error decreased substantially with increasing sample size (Downs and Horner, 2007, Table 2). Moreover, Arthur Rodgers, the primary author of the Home Range Tools program and its predecessor, Home Range Extension, states that the real problem with using KDE analysis is that his programs were created to demarcate utilization distributions and not home range boundaries. Utilization distributions are areas or features of the landscape that the animals use most frequently and are rarely continuous segments of the landscape (**Fig. 3.2**). Largely because KDEs depict these fragments as one continuous shape, Rodgers (pers comm.) emphasizes that the results of KDE analyses should be interpreted as an index and not an absolute measure of home range area. Yet since other home range estimation alternatives to MCP and KDE analyses have not undergone the same scrutiny as have these methods, I have chosen to conduct both MCP and KDE analyses, the current home range estimation standard in the field of ecology, with the knowledge that these results will require revision when better methods are developed.

Fig. 3.2. Utilization distributions of the Bevaro Moravato troop and Tsankalamanga troop respectively. The GPS fixes are outlined in black. A grey scale demarcates the utilization intensity of the troops' ranging habits, with the blackest areas representing the most frequently used areas.

Results

Although the yearly home range of the Bevaro Moravato troop is larger than that of the Tsankalmanga troop (**Fig. 3.3**), the home ranges of both CSM troops are over twice as large as gallery forest troops. In fact, average home range estimates from gallery forest sites are closer in size to CSM core ranges than they are to CSM home ranges (**Table 3.1**).

Table 3.1 Comparison of range areas among the study sites using Minimum Convex Polygons (MCP) and Kernel Density Estimates (KDE). Home range is defined as the area where a troop will spend 95% of its activity time. Core range is defined as the area where a troop will spend 50% of its activity time. Core Ranges were generated using KDE analyses. *Home range numbers for Berenty and Beza Mahafaly are population averages and were estimated using 25 x 25 m grid quadrants (Sussman, 1991; Jolly and Pride, 1999; Koyama et al., 2006). In contrast, MCP estimates are based on connecting the outermost points and is similar to the practice of enlarging grid cells until corresponding fixes connect (Worton, 1987; Coates and Downs, 2005).

Study Site	**Home Range (95%)**		**Core Range (50% KDE)**
	MCP Analysis	**KDE Analysis**	
CSM Bevaro Moravato troop	132 ha	154 ha	14 ha
CSM Tsankalamanga troop	87 ha	95 ha	6 ha
Berenty	8 ha*	N/A	N/A
Beza Mahafaly	25 ha*	N/A	N/A

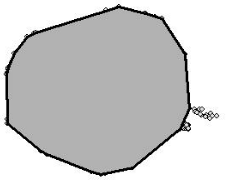


Fig. 3.3a. Minimum Convex Polygon (MCP) of the Bevaro Moravato troop's home range (defined as the area utilized 95% of the time [White and Garrott, 1990]). The MCP was generated using a fixed mean in Home Range Tools for ArcGIS®.

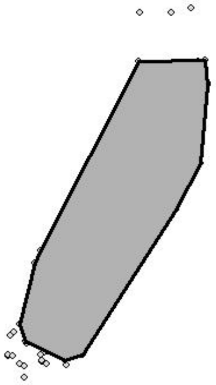


Fig. 3.3b. Minimum Convex Polygon (MCP) of the Tsankalamanga troop's home range (defined as the area utilized 95% of the time [White and Garrott, 1990]). The MCP was generated using a fixed mean in Home Range Tools for ArcGIS®.

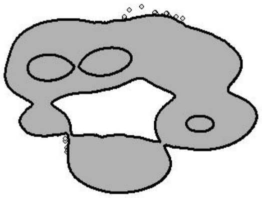


Fig. 3.3c. Kernel Density Estimate Analysis (KDE) of the Bevaro Moravato troop's home range (defined as the area utilized 95% of the time [White and Garrott, 1990]). The KDE was generated using an adaptive smoothing method and a reference bandwidth of 85% of the recommended bandwidth. The ellipses outlined in black demarcate the troop's core range (defined as the area utilized 50% of the time [White and Garrott, 1990]). Map was generated using Home Range Tools for ArcGIS®.

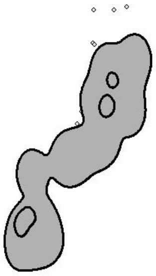


Fig. 3.3d. Kernel Density Estimate Analysis (KDE) of the Tsankalamanga troop's home range (defined as the area utilized 95% of the time [White and Garrott, 1990]). The KDE was generated using an adaptive smoothing method and a reference bandwidth of 35% of the recommended bandwidth. The ellipses outlined in black demarcate the troop's core range (defined as the area utilized 50% of the time [White and Garrott, 1990]). Map was generated using Home Range Tools for ArcGIS®.

The habitat composition of the troops' home ranges is presented in **Table 3.2** and **Fig. 3.4.** The primary difference between the two sites was that the Bevaro Moravato troop had over three times the amount of sacred forest habitat and almost twice the area of brush and scrub habitat as the Tsankalamanga troop. In fact, one-fourth of the Tsankalmanga troop's home range consisted of fields.

Table 3.2. Main habitat type compositions of the focal groups' home ranges.

	Bevaro Moravato	**Tsankalamanga**
Brush and scrub vegetation	110.81 ha (72%)	64.02 ha (67.4%)
Fields	29.29 ha (19%)	24.1 ha (25.4%)
Sacred forest	10.08 ha (6.5%)	3.15 ha (3.3%)
Opuntia monacantha hedges	3.83 ha (2.5%)	3.73 ha (3.9%)

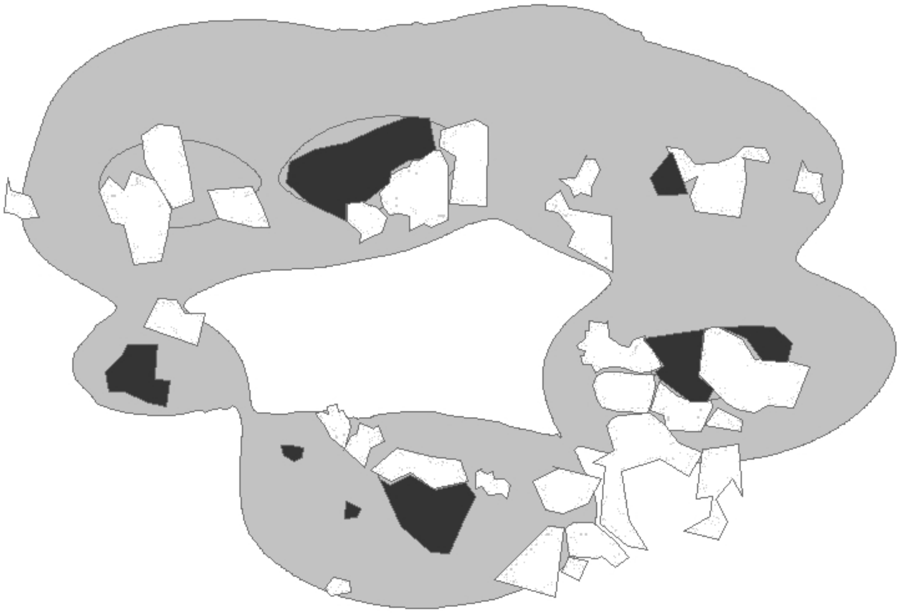


Fig. 3.4a. Habitat composition of the Bevaro Moravato troop. Map was generated using a Kernel Density Estimate Analysis in Home Range Tools for ArcGIS® and Google Earth® 2008. Core areas are demarcated by black ellipses. The white irregularly shaped polygons are fields and encompassing *Opuntia monacantha* hedges. The irregularly shaped black polygons are sacred forests. The remaining grey area is brush and scrub habitat.

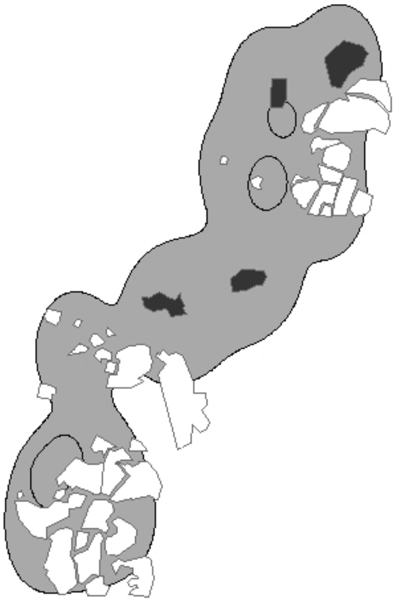
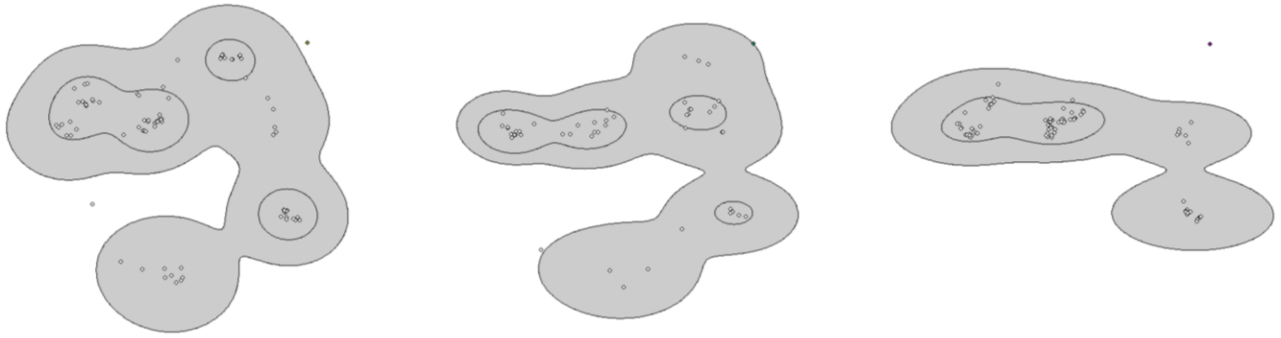


Fig. 3.4b. Habitat composition of the Tsankalamanga troop. Map was generated using a Kernel Density Estimate Analysis in Home Range Tools for ArcGIS® and Google Earth® 2008. Core areas are demarcated by black ellipses. The white irregularly shaped polygons are fields and encompassing *Opuntia monacantha* hedges. The irregularly shaped black polygons are sacred forests. The remaining grey area is brush and scrub habitat.

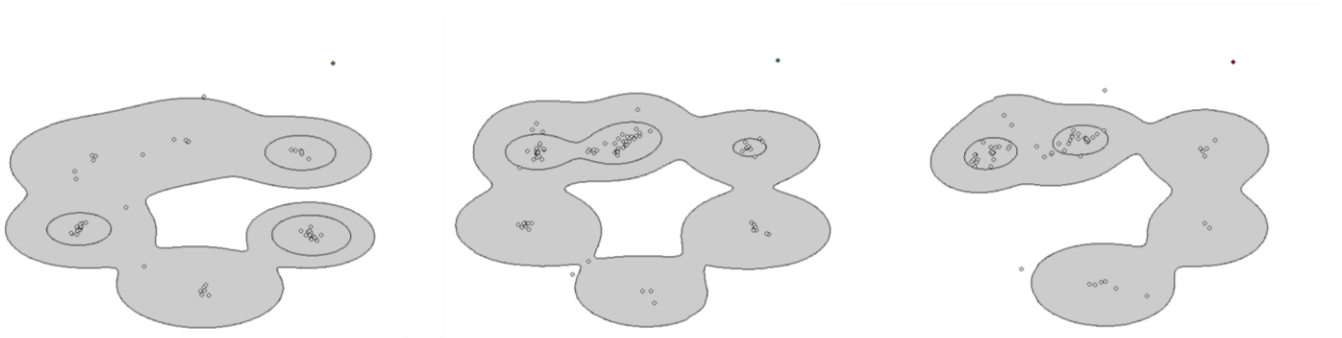
The median size of the troops' home range areas were in the months of September and October (**Fig. 3.5.a; Fig. 3.5.b**). These estimates are similar to that of the yearly MCP home range estimates of the troops (**Table 3.1**). Both troops had the smallest home ranges in August. The largest home range was the austral summer month of January for the Bevaro Moravato troop (**Fig. 3.5.a**) and the austral summer month of December for the Tsankalamanga troop (**Fig. 3.5. b**). Yet despite these similarities, the variance in the monthly home ranges of the Tsankalamanga troop was over 100 ha greater than that of the Bevaro Moravato troop and exceeded both the minimum and maximum values of the Bevaro Moravato troop's home range estimates. In addition, trends in monthly home range patterns between the two troops diverged markedly in the months of July and December.



January Home Range: 180.5 ha

February Home Range: 147.2 ha

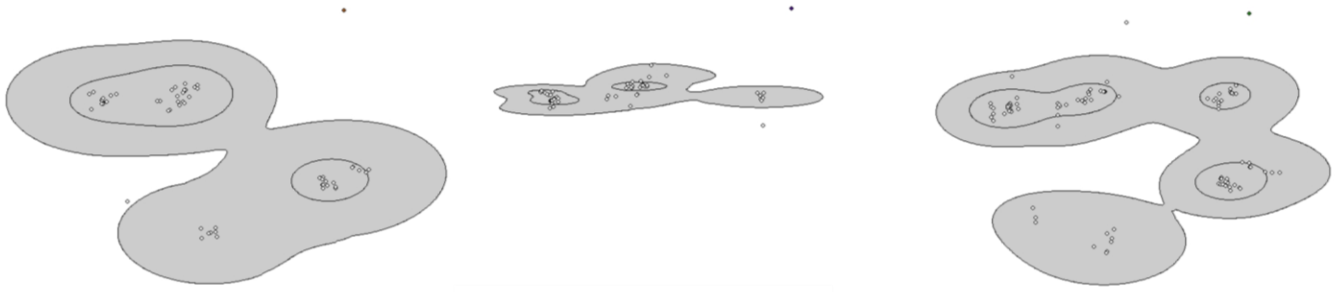
March Home Range: 101.2 ha



April Home Range 154 ha

May Home Range: 146.1ha

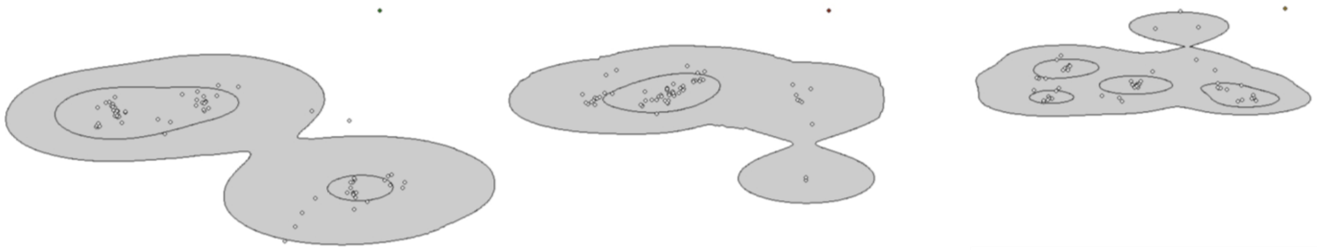
June Home Range: 115.2 ha



July Home Range: 169.9 ha

August Home Range: 26.0 ha

September Home Range: 143.2 ha

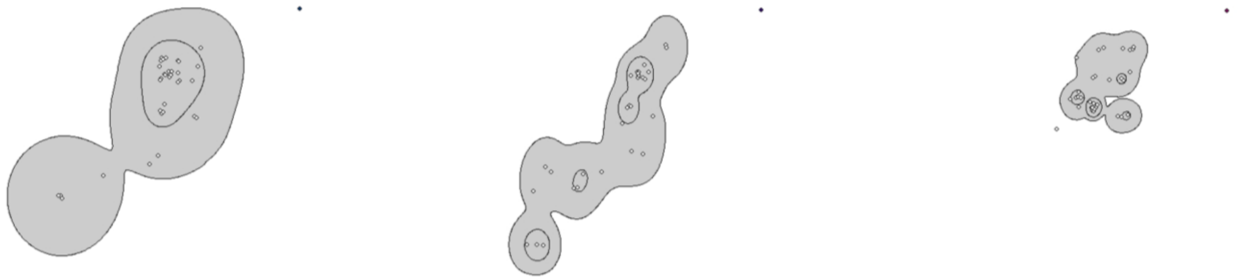


October Home Range: 117.5 ha

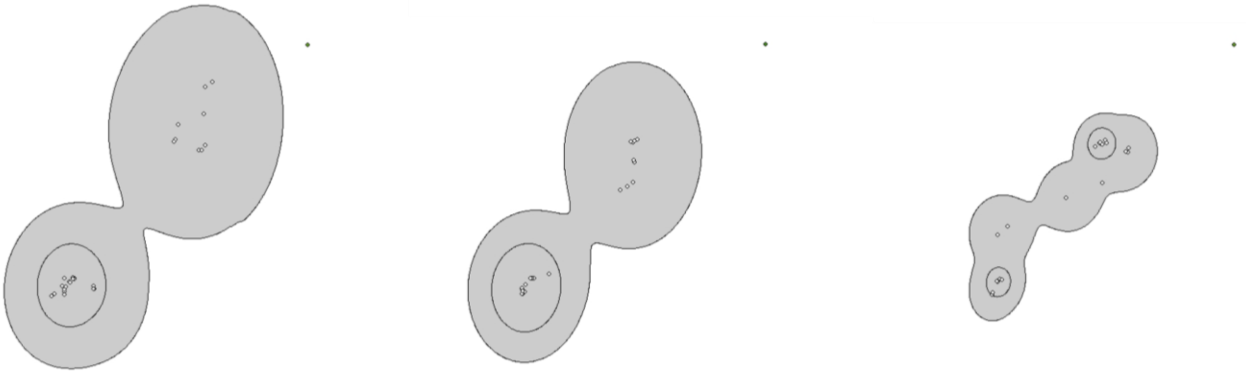
November Home Range: 92.8 ha

December Home Range: 59.5 ha

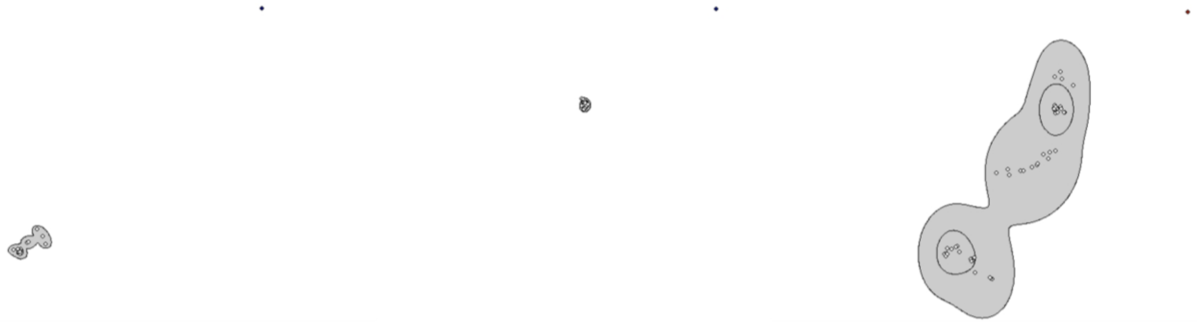
Fig. 3.5a. Kernel Density Estimate analyses of the Bevaro Moravato troop by month. Maps have been generated using the program Home Range Tools for ArcGIS®. Core ranges are demarcated by elipses within each home range. Dots are locations of lemur presence. ha is hectares. Scale is 11:124,000 meters.



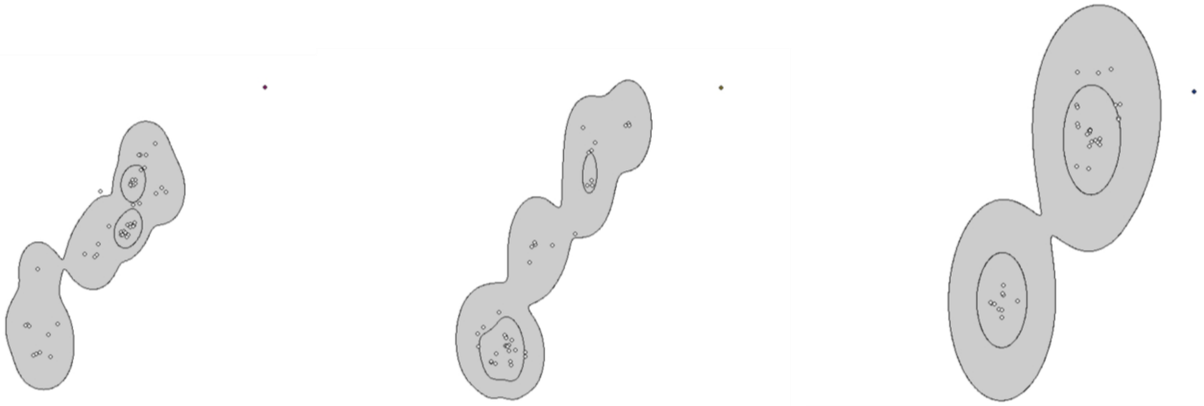
January Home Range: 115.3 ha **February** Home Range: 75.5 ha **March** Home Range: 26.0 ha



April Home Range: 224.7 ha **May** Home Range: 152.7 ha **June** Home Range: 66.3 ha



July Home Range: 2.8 ha **August** Home Range: 0.5 ha **September** Home Range: 92.6 ha



October Home Range: 76.9 ha **November** Home Range: 97.4 ha **December** Home Range: 291.9 ha

Fig. 3.5b. Kernel Density Estimate analyses of the Tsankalamanga troop by month. Maps have been generated using the program Home Range Tools for ArcGIS®. Core ranges are demarcated by ellipses within each home range. Dots are locations of lemur presence. ha is hectares. Scale is 11:124,000 meters.

Analysis 2: Diet in Relation to Ranging Patterns

The Bevaro Moravato troop had a more varied monthly diet than the Tsankalamanga troop (**Table 3.3;** see also **Table 5.10; Table 5.11**). However, whereas only 11 different species composed the top 75% of the Bevaro Moravato troop's diet for more than one month of the year, 12 plant species composed the top 75% of the Tsankalamanga troop's diet during the same period.

Table 3.3. Food species of the CSM troops listed in receding order of observed monthly consumption. FR = fruit and seeds, LV = leaves, FL = flowers, IN = insect, OT = other.

	Bevaro Movravato			Tsankalamanga		
Month	**Name**	**Type**	**Percent**	**Name**	**Type**	**Percent**
January	*Strychnos decussata*[3]	FR	26.9%	*Grewia punctata*	FR	15.3%
	Mimosa sp.	FL	17.4%	*Grewia cyclea*	LV	12.7%
	Zygophyllum madecassum	LV	12.2%	*Psiadia restita*	FR	10.8%
	Metaporana sp.	LV	8.6%	*Terminalia fatrae*	FR	10.2%
	Opuntia stricta	FR	7.4%	*Adenia* sp.	LV	10.2%
	Commiphora simplicifolia	LV	5.5%	*Poupartia junior*	FR	8.3%
	Leptadenia sp.	FL	5.2%	*Opuntia stricta*	FR	8.3%
	Phyllanthus amanu	FR	3.1%	*Opuntia monacantha*	FR	3.8%
	Strychnos madagascariensis	FR	2.2%	*Marsdenia* sp.	LV	3.2%
	Poupartia junior	FR	1.7%	*Metaporana* sp.	LV	2.5%
	Rinorea sp.	LV	1.0%	"indet. plant"	LV	2.5%
	Cedrelopsis grevei	LV	1.0%	*Opuntia ficus-indica* var. *inermis*	FR	2.5%
	Ficus marmonata	FR	1.0%	*Bulkophylum* sp.	LV	2.5%
	unidentified insect nest	IN	0.7%	*Albizzia* sp.	FL	1.9%
	Flacourtia ramontchi	FR	0.7%	*Zygophyllum madecassum*	LV	1.3%
	"kolovy"	OT	0.7%	*Mimosa* sp.	FL	1.3%
	Abutilon asiaticum	LV	0.7%	*Cissus quadrangularis*	LV	1.3%
	Grewia cyclea	LV	0.5%	*Paederia* sp.	LV	0.6%
	Fabaceae	FL	0.5%	*Terminalia ulexioides*	FR	0.6%

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[3] Originally identified as *Canthium* sp. "haze" in the field by Mbola VA Balzac, this species was identified through photographs as *Strychnos decussata* by Soafara Niaina Andrianarivelo and colleagues at the Missouri Botanical Garden, St. Louis MO.

	Bevaro Movravato			Tsankalamanga		
Month	**Name**	**Type**	**Percent**	**Name**	**Type**	**Percent**
	“indet. plant”	LV	0.5%			
	Croton sp.	LV	0.5%			
	Terminalia fatrae	FR	0.5%			
	Opuntia monacantha	FR	0.3%			
	Psiadia restita	FR	0.3%			
	Flueggea virosa	LV	0.2%			
	Aloe vahombe	FL	0.2%			
	Adenia sp.	LV	0.2%			
February	*Phyllanthus amanu*	FR	48.6%	*Terminalia fatrae*	FR	28.8%
	Strychnos decussata	FR	19.1%	*Opuntia monacantha*	FR	14.4%
	Poupartia junior	FR	7.1%	*Adenia* sp.	LV	9.0%
	Mimosa sp.	FL	4.3%	*Poupartia junior*	FR	6.3%
	Opuntia monacantha	FR	2.5%	*Zygophyllum madecassum*	LV	6.3%
	Poupartia sp.	FR	2.5%	*Diospyros* sp.	FR	5.4%
	Opuntia stricta	FR	1.8%	*Aloe divaricta*	FL	4.5%
	Opuntia ficus-indica var. *inermis*	FR	1.8%	*Buxus madagascariensis*	FR	4.5%
	Metaporana sp.	LV	1.4%	*Opuntia stricta*	FR	3.6%
	Rinorea sp.	LV	1.4%	cicadas	IN	3.6%
	Psiadia altissima[4]	FL	1.4%	*Grewia cyclea*	LV	2.7%
	Psiadia restita	FR	1.1%	termites	IN	2.7%
	Acanthaceae	LV	1.1%	“indet. plant”	LV	1.8%
	termites	IN	1.1%	*Opuntia ficus indica* var. *inermis*	FR	1.8%
	Zygophyllum madecassum	LV	0.7%	*Mimosa* sp.	FL	1.8%
	Leptadenia sp.	FL	0.7%	*Marsdenia* sp.	LV	0.9%
	“indet. plant”	LV	0.7%	*Metaporana* sp.	LV	0.9%
	Flueggea virosa	LV	0.7%	*Zygophyllum depauperatum*	FR	0.9%
	Tabernaemontana modesta	FR	0.7%			
	Adenia sp.	LV	0.4%			
	"fatikekolahy"	LV	0.4%			
	Diospyros sp.	FR	0.4%			
	cicadas	IN	0.4%			
March	*Phyllanthus amanu*	FR	27.1%	*Opuntia monacantha*	FR	28.4%
	Buxus madagascariensis	FR	14.9%	*Terminalia fatrae*	FR	14.7%

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[4] Identified through research by Soafara Niaina Andrianarivelo, Missouri Botanical Garden, St. Louis.

	Bevaro Movravato			Tsankalamanga		
Month	**Name**	**Type**	**Percent**	**Name**	**Type**	**Percent**
	Opuntia monacantha	FR	14.0%	*Metaporana* sp.	LV	10.3%
	Rinorea sp.	LV	12.4%	*Grewia* sp.	LV	10.3%
	Metaporana sp.	LV	9.3%	*Zygophyllum madecassum*	LV	5.4%
	Zygophyllum madecassum	LV	5.5%	*Diospyros* sp.	FR	5.4%
	Fabaceae	FL	2.6%	*Adenia* sp.	LV	3.4%
	termites	IN	1.6%	*Terminalia mantaly*	FR	3.4%
	Leptadenia sp.	LV	1.5%	*Grewia cyclea*	LV	2.9%
	Mimosa sp.	FL	1.3%	*Tarenna* sp.	FR	2.9%
	cicadas	IN	1.1%	termites	IN	1.5%
	Diospyros sp.	FR	0.7%	*Opuntia ficus-indica* var. *inermis*	FR	1.5%
	Croton sp.	LV	0.7%	*Marsdenia* sp.	LV	1.5%
	Paederia sp.	LV	0.7%	*Rinorea* sp.	LV	1.5%
	Aloe divaricta	FL	0.7%	*Phyllanthus* sp.	FR	1.5%
	Terminalia ulexioides	FR	0.7%	*Commiphora simplicifolia*	LV	1.5%
	Adenia sp.	LV	0.5%	“indet. plant”	LV	1.0%
	Commiphora simplicifolia	LV	0.5%	*Terminalia ulexioides*	FR	1.0%
	Euphorbia hirta	LV	0.5%	*Aloe divaricta*	FL	0.5%
	Grewia sp.	LV	0.5%	*Mimosa* sp.	FL	0.5%
	Terminalia mantaly	FR	0.5%	Fabaceae	FL	0.5%
	“indet. plant”	LV	0.4%	*Stereospermum variabile*	LV	0.5%
	Grewia punctata	FL	0.4%			
	Marsdenia sp.	LV	0.4%			
	Opuntia stricta	FR	0.2%			
	Flueggea virosa	LV	0.2%			
	“indet. insect nest”	IN	0.2%			
	Terminalia fatrae	FR	0.2%			
	Zygophyllum depauperatum	FR	0.2%			
	ants	IN	0.2%			
	Alluadia dumosa	FR	0.2%			
April	*Terminalia fatrae*	FR	*39.6%*	*Phyllanthus amanu*	FR	26.6%
	Terminalia ulexioides	FR	*23.7%*	*Opuntia monacantha*	FR	12.9%
	Metaporana sp.	FL	*11.3%*	*Metaporana* sp.	FL	12.1%
	Terminalia sp.	FR	*4.7%*	*Paederia* sp.	LV	9.7%
	Opuntia monacantha	FR	*3.2%*	*Zygophyllum madecassum*	LV	7.3%

	Bevaro Movravato			Tsankalamanga		
Month	**Name**	**Type**	**Percent**	**Name**	**Type**	**Percent**
	Tabernaemontana modesta	FR	*2.1%*	*Adenia* sp.	LV	6.5%
	Adenia sp.	LV	1.8%	*Flacourtia ramontchi*	FR	6.5%
	Commiphora simplicifolia	FR	1.8%	*Phyllanthus* sp.	FR	4.8%
	Flacourtia ramontchi	FR	1.8%	*Aloe divaricta*	FL	4.0%
	Zygophyllum madecassum	LV	1.6%	*Mimosa* sp.	LV	3.2%
	Leptadenia sp.	LV	1.6%	*Grewia cyclea*	LV	1.6%
	Paederia sp.	LV	1.3%	*Grewia punctata*	FL	1.6%
	Kalanchoe integrifolia	LV	1.1%	*Leptadenia* sp.	LV	1.6%
	Diospyros sp.	FR	0.8%	*Terminalia mantaly*	FR	0.8%
	“Rothmannia” sp.	FR	0.8%	*Zygophyllum depauperatum*	FR	0.8%
	Phyllanthus amanu	FR	0.5%			
	ants	IN	0.5%			
	Poupartia sp.	FR	0.5%			
	Citrullus lanatus	FR	0.5%			
	“indet. plant”	LV	0.3%			
	Phyllanthus sp.	FR	0.3%			
May	*Commiphora* sp.	FR	*31.0%*	*Opuntia monacantha*	FR	*17.1%*
	Terminalia fatrae	FR	*20.0%*	*Canthium* sp.	FR	*14.8%*
	Terminalia ulexioides	FR	*12.4%*	*Metaporana* sp.	LV	*13.9%*
	Metaporana sp.	LV	*8.2%*	*Flacourtia ramontchi*	FR	*13.9%*
	Opuntia monacantha	FR	*7.6%*	*Terminalia fatrae*	FR	*8.8%*
	Rinorea sp.	FR	6.1%	"matiake"	FR	*8.3%*
	Tabernaemontana modesta	FR	4.5%	*Grewia cyclea*	FR	7.4%
	Vepris sp.	FR	1.8%	*Zygophyllum madecassum*	LV	5.6%
	Acanthaceae	LV	1.5%	*Paederia* sp.	FR	2.8%
	Zygophyllum madecassum	LV	1.2%	*Adenia* sp.	LV	1.4%
	Leptadenia sp.	LV	1.1%	*Zygophyllum depauperatum*	FR	1.4%
	Paederia sp.	FR	0.8%	*Rinorea* sp.	FR	1.4%
	Diospyros sp.	FR	0.8%	“indet. insect”	IN	1.4%
	Grewia cyclea	FR	0.8%	“indet. plant”	LV	0.9%
	Flueggea virosa	LV	0.6%	*Mimosa* sp.	LV	0.5%
	Rhigozum madagascariensis	FR	0.6%	termites	IN	0.5%
	Zygophyllum	FR	0.5%			

	Bevaro Movravato			Tsankalamanga		
Month	**Name**	**Type**	**Percent**	**Name**	**Type**	**Percent**
	depauperatum					
	“indet. plant”	LV	0.3%			
	Grewia punctata	FR	0.3%			
	“indet. insect nest”	IN	0.2%			
June	*Opuntia monacantha*	FR	*25.0%*	*Metaporana* sp.	LV	*40.5%*
	Metaporana sp.	LV	*15.4%*	*Opuntia monacantha*	FR	*32.9%*
	Rinorea sp.	FR	*14.7%*	“matiake”	FR	6.3%
	Paederia sp.	LV	*8.5%*	*Paederia* sp.	LV	6.3%
	Zygophyllum depauperatum	FR	*6.6%*	*Flacourtia ramontchi*	FR	5.1%
	Flacourtia ramontchi	FR	4.4%	*Zygophyllum depauperatum*	FR	3.8%
	Acanthaceae	LV	4.0%	*Rinorea* sp.	FR	3.8%
	Grewia punctata	FR	4.0%	*Grewia punctata*	FR	1.3%
	Grewia cyclea	FR	3.7%			
	Flueggea virosa	LV	2.9%			
	Opuntia stricta	FR	2.6%			
	Aloe divaricta	LV	2.2%			
	Terminalia fatrae	FR	1.5%			
	Cucums sp.	LV	1.5%			
	Zygophyllum madecassum	LV	0.7%			
	Leptadenia sp.	LV	0.7%			
	“indet. plant”	LV	0.7%			
	“indet. insect”	IN	0.4%			
	ants	IN	0.4%			
July	*Opuntia stricta*	FR	34.6%	*Opuntia monacantha*	FR	*54.2%*
	Paederia sp.	LV	19.3%	*Paederia* sp.	LV	*18.1%*
	Grewia cyclea	FR	10.0%	*Metaporana* sp.	LV	15.3%
	Opuntia monacantha	FR	9.7%	*Grewia cyclea*	FR	4.2%
	Metaporana sp.	LV	9.0%	*Flacourtia ramontchi*	FR	2.8%
	Zygophyllum madecassum	FL	5.6%	*Zygophyllum depauperatum*	FR	1.4%
	Euphorbia sp.	FR	2.8%	*Zygophyllum madecassum*	FL	1.4%
	Flueggea virosa	LV	2.5%	dirt	OT	1.4%
	Zygophyllum depauperatum	FR	2.2%	*Kalanchoe beharensis*	LV	1.4%
	Leptadenia sp.	LV	1.2%			
	Mimosa sp.	LV	1.2%			
	Kalanchoe integrifolia	LV	0.9%			

	Bevaro Movravato			Tsankalamanga		
Month	**Name**	**Type**	**Percent**	**Name**	**Type**	**Percent**
	Aloe divaricta	LV	0.3%			
	"fatikekolahy"	LV	0.3%			
	Aloe vahombe	FL	0.3%			
August	*Leptadenia* sp.	LV	17.7%	*Opuntia monacantha*	FR	*69.7%*
	Opuntia stricta	FR	13.6%	*Psiadia restita*	FR	14.7%
	Mimosa sp.	LV	12.9%	*Metaporana* sp.	LV	4.6%
	Opuntia monacantha	FR	9.5%	“indet. plant”	LV	3.7%
	Aloe vahombe	FL	9.5%	*Zygophyllum madecassum*	LV	2.8%
	Grewia punctata	FL	9.5%	*Grewia punctata*	FL	1.8%
	Zygophyllum madecassum	LV	6.8%	*Opuntia stricta*	FR	1.8%
	Pouzolzia mandrarensis	LV	6.8%	*Aloe vahombe*	FL	0.9%
	Grewia cyclea	LV	4.1%			
	Metaporana sp.	LV	4.1%			
	Azima tetracantha	FR	2.7%			
	Flueggea virosa	LV	0.7%			
	Terminalia sp.	LV	0.7%			
	Phyllanthus amanu	LV	0.7%			
	Croton sp.	LV	0.7%			
September	*Opuntia stricta*	FR	28.2%	*Opuntia monacantha*	FR	48.7%
	Aloe vahombe	FL	20.3%	*Zygophyllum madecassum*	LV	15.4%
	Gymnosporia linearis	LV	11.9%	*Aloe vahombe*	FL	12.8%
	Opuntia monacantha	FR	6.2%	*Opuntia stricta*	FR	11.1%
	Flueggea virosa	LV	5.7%	*Alluaudia dumosa*	LV	5.1%
	Phyllanthus amanu	LV	4.4%	*Leptadenia* sp.	LV	3.4%
	Acanthaceae	LV	4.0%	*Cynanchum perrieri*	LV	2.6%
	Metaporana sp.	LV	2.6%	“indet. plant”	LV	0.9%
	Grewia cyclea	LV	2.2%			
	Terminalia sp.	LV	2.2%			
	Flueggea virosa	LV	2.2%			
	Grewia punctata	LV	1.8%			
	“fatikekolahy”	LV	1.8%			
	Leptadenia sp.	LV	0.9%			
	Zygophyllum madecassum	LV	0.9%			
	Paederia sp.	LV	0.9%			
	Zygophyllum	FR	0.9%			

	Bevaro Movravato			Tsankalamanga		
Month	**Name**	**Type**	**Percent**	**Name**	**Type**	**Percent**
	depauperatum					
	Achyrocalyx decaryi	LV	0.9%			
	Croton sp.	LV	0.4%			
	unidentified sp.	LV	0.4%			
	unidentified insect	IN	0.4%			
	Psiadia restita	LV	0.4%			
	Xerosicyos danguyi	LV	0.4%			
October	*Opuntia stricta*	FR	23.4%	*Opuntia stricta*	FR	34.0%
	Phyllanthus amanu	FR	14.0%	*Opuntia monacantha*	FR	31.4%
	Alluadia procera	LV	13.6%	*Zygophyllum madecassum*	LV	9.0%
	Aloe vahombe	FL	9.8%	*Aloe vahombe*	FL	9.0%
	Metaporana sp.	LV	7.9%	*Croton* sp.	LV	6.9%
	Leptadenia sp.	LV	5.7%	*Leptadenia* sp.	LV	2.1%
	Euphorbia hirta	LV	4.9%	*Metaporana* sp.	LV	1.6%
	Flueggea virosa	LV	4.2%	*Cynanchum perrieri*	LV	1.1%
	Opuntia monacantha	FR	3.0%	*Zygophyllum depauperatum*	FR	1.1%
	Zygophyllum madecassum	LV	3.0%	*Alluaudia dumosa*	LV	0.5%
	Strychnos decussata	FR	3.0%	“indet. plant”	LV	0.5%
	Euphorbiaceae	LV	3.0%	*Aloe divaricta*	LV	0.5%
	Mimosa sp.	LV	1.5%	*Cissus quadrangularis*	LV	0.5%
	Zygophyllum depauperatum	FR	0.8%	*Azima tetracantha*	FR	0.5%
	Croton sp.	LV	0.8%	*Geochelone radiata* feces	OT	0.5%
	“indet. plant”	LV	0.8%	*Xerosicyos danguyi*	LV	0.5%
	Aloe divaricta	LV	0.8%			
November	*Strychnos decussata*	FR	35.8%	*Azima tetracantha*	FR	19.9%
	Azima tetracantha	FR	21.9%	*Opuntia stricta*	FR	18.1%
	Metaporana sp.	LV	5.2%	*Mimosa* sp.	FL	10.2%
	Leptadenia sp.	LV	5.2%	*Cedrelopsis grevei*	LV	10.2%
	Opuntia stricta	FR	5.00%	*Operculicarya decaryi*	FR	8.8%
	Alluadia procera	LV	5.0%	*Maerua filiformis*	FR	8.4%
	Fabaceae	FL	3.4%	*Opuntia monacantha*	FR	7.5%
	Euphorbia hirta	LV	3.1%	*Leptadenia* sp.	LV	5.8%
	Mimosa sp.	FL	2.9%	*Grewia punctata*	LV	3.1%
	Paederia sp.	LV	2.3%	*Metaporana* sp.	LV	2.2%
	Maerua filiformis	FR	2.3%	*Psiadia restita*	LV	2.2%
	Phyllanthus amanu	FR	1.8%	*Gymnosporia linearis*	LV	1.3%

	Bevaro Movravato			Tsankalamanga		
Month	**Name**	**Type**	**Percent**	**Name**	**Type**	**Percent**
	Flueggea virosa	LV	0.8%	*Manihot utilissima*	LV	1.3%
	“indet. plant”	LV	0.8%	*Zygophyllum madecassum*	LV	0.9%
	Pouzolzia mandrarensis	LV	0.8%			
	Kalanchoe integrifolia	LV	0.8%			
	Zygophyllum madecassum	LV	0.5%			
	Grewia cyclea	LV	0.5%			
	“indet. insect nest”	IN	0.5%			
	Cynanchum perrieri	LV	0.5%			
	Ipomoea batatas	LV	0.5%			
	water	OT	0.3%			
December	*Strychnos decussata*	FR	47.2%	*Boscia* sp.	FR	*32.3%*
	Azima tetracantha	FR	20.7%	*Azima tetracantha*	FR	*27.5%*
	Phyllanthus amanu	FR	11.4%	*Metaporana* sp.	LV	*16.2%*
	Leptadenia sp.	LV	6.3%	*Ficus marmonata*	FR	7.8%
	Metaporana sp.	LV	4.3%	*Opuntia monacantha*	FR	5.4%
	Opuntia stricta	FR	2.8%	*Operculicarya decaryi*	FR	4.8%
	Opuntia monacantha	FR	1.7%	*Opuntia stricta*	FR	2.4%
	Mimosa sp.	FL	0.9%	*Grewia punctata*	LV	2.4%
	Paederia sp.	LV	0.9%	*Psiadia restita*	LV	0.6%
	Zygophyllum madecassum	LV	0.9%	*Stereospermum variabile*	LV	0.6%
	"fatikekolahy"	LV	0.9%			
	Opuntia vazaha	FR	0.9%			
	Rhigozum madagascariensis	LV	0.6%			
	Flueggea virosa	LV	0.3%			
	Grewia cyclea	LV	0.3%			
	spiders	IN	0.3%			

Core areas in relation to major foods

All core areas of the Bevaro Moravato troop contained a top-quartile food location except for the months of January and April, in which two-thirds of the months’ core areas contained a top-quartile food item. From the months of November through May, this top-quartile food item was a native fruit species. *Phyllanthus amanu,* an abundant and native bush species, was the top-quartile food consumed for the months of February and March. Similarly, the fruit of *Strychnos decussata*, a native and abundant tree species, was the top-quartile food consumed from the months of November through January. The top-quartile food items for the months of June through October were the fruits of *Opuntia stricta* and *O. monacantha.* June was the only month in which *O. monacantha* was consumed as the top-quartile species. *O. stricta* was the top species for the other three austral winter months. August and October were the only months in which two food plants composed the top 25% of the troop's monthly feeding time. While the fruit of *O. stricta* was one of these food items, the second and most frequently consumed food for the month of August was a native vine, *Leptadenia* sp. (nonosora). This vine is abundant in the area and grows in the hedges. The second food species that was consumed in October was once again the fruit of *Phyllanthus amanu* (**Fig. 3.6a**).

In contrast to the Bevaro Moravato troop, the Tsankalamanga troop's monthly core area use is much less coupled with top-quartile food consumption. In December, January and April, all core areas contained a top-quartile native species. The fruit species consumed in December was *Boscia* sp. (sasavy),[4] an abundant native tree species that is not found within the ranging distance of the Bevaro Moravato troop. Conversely, the top-quartile fruit species consumed in April was *Phyllanthus amanu*. In January, the Tsankalamanga troop ate a mix of fruit and leaves from different *Grewia* spp. In February, the fruit of the abundant native tree species *Terminalia fatra* was consumed in one of the three core areas that month. This fruit species was also the top-quartile food species of the Bevaro Moravato troop in the month of April (**Fig. 3.6a**). In June, the top food item consumed by the Tsankalamanga troop was a native leafy vine, *Metaporana* sp. (kilio) and this species was fed upon in only one of the two core areas. For seven months of the year, *Opuntia* fruit was a top-quartile food item. While *O. monacantha* was the species consumed the most often for five of these months, *O. stricta* was the top-quartile food item consumed in October and November. In May and November, the top-quartile food items were split between the native fruit species *Canthium* sp. (la jandsy) and *Azima tetracantha,* and the cactus species *O. monacantha* and *O. stricta* respectively. However, only the *Opuntia* was consumed within the core areas for these months (**Fig. 3.6b**).

Last, while sacred forest habitat was a regular component of the Bevaro Moravato's monthly core range area, this was not the case with the Tsanakalamanaga troop. For the Bevaro Moravato troop, sacred forests were a component of every core area seven months of the year. For the remaining five months, sacred forests were included in a minimum of half of the core areas (**Fig. 3.6.a**). In contrast, there was no presence of a sacred forest in any core area of the Tsankalamanga troop for four months of the year. In fact, January and October were the only months in which all core areas were composed of sacred forest habitat (**Fig. 3**).

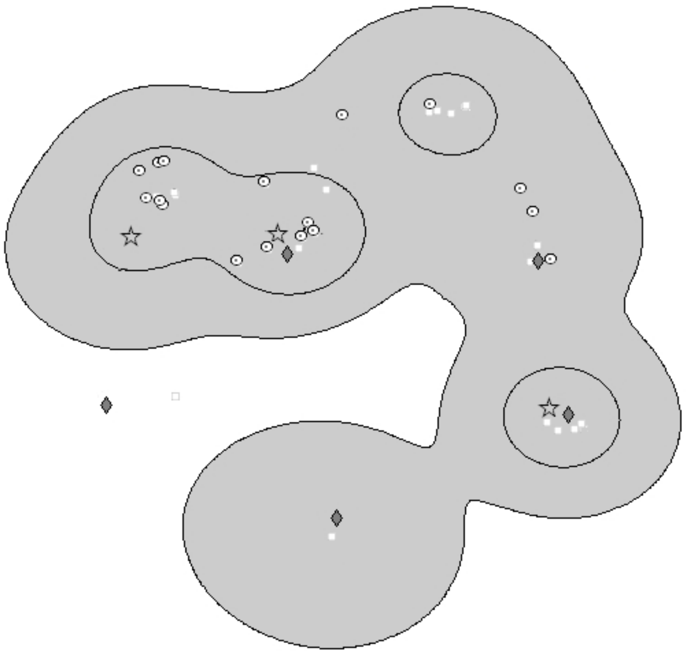


Fig. 3.6a. Home range and core areas of the Bevaro Moravato troop in the month of **January**. Map was generated using a Kernel Density Estimate Analysis in Home Range Tools for ArcGIS® but was modified in Windows® Paint by Brad Kelley to enhance image clarity. Core areas are demarcated by black ellipses. ◆ = Sacred Forest, ⊙ = Native Fruit sp., ▫ = Other Feeding, ☆= Sleeping Site. The top-quartile food for this month (26.9% of total feeding time) was the fruit of *Strychnos decussata*, an abundant and native tree species. Map is not to scale.

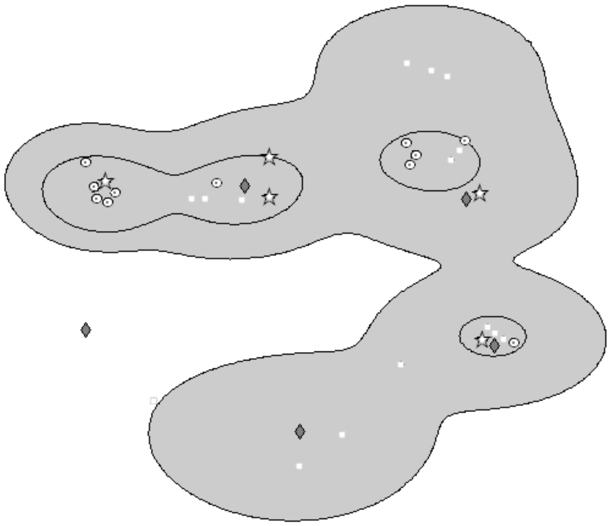


Fig. 3.6a. Home range and core areas of the Bevaro Moravato troop in the month of **February**. Map was generated using a Kernel Density Estimate Analysis in Home Range Tools for ArcGIS® but was modified in Windows® Paint by Brad Kelley to enhance image clarity. Core areas are demarcated by black ellipses. ◆ = Sacred Forest, ⊙ = Native Fruit, ▫ = Other Feeding, ☆= Sleeping Site. The top-quartile food for this month (48.6% of total feeding time) was the fruit of *Phyllanthus amanu*, an abundant and native bush species. Map is not to scale.

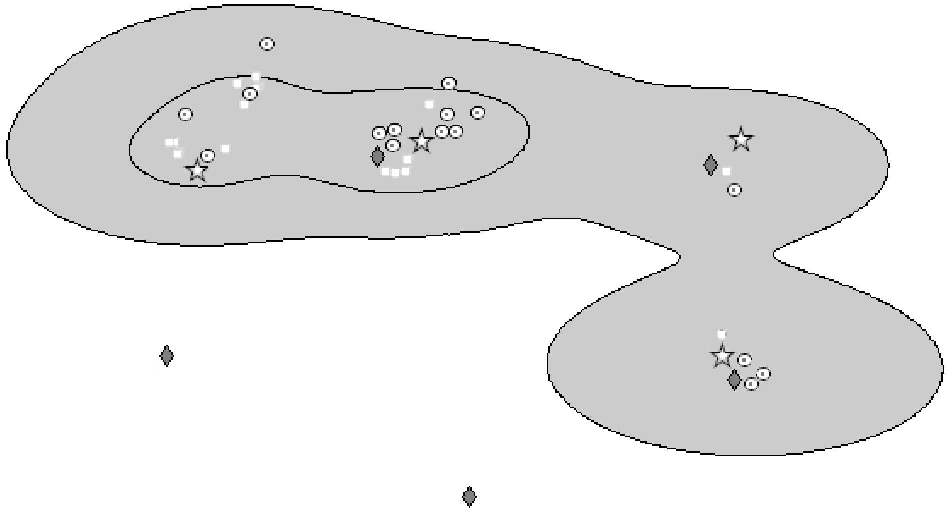


Fig. 3.6a. Home range and core areas of the Bevaro Moravato troop in the month of **March**. Map was generated using a Kernel Density Estimate Analysis in Home Range Tools for ArcGIS® but was modified in Windows® Paint by Brad Kelley to enhance image clarity. Core areas are demarcated by black ellipses. ◆ = Sacred Forest, ⊙ = Native Fruit, ▫ = Other Feeding, ☆ = Sleeping Site. The top-quartile food for this month (27.1% of total feeding time) was the fruit of *Phyllanthus amanu*, an abundant and native bush species. Map is not to scale.

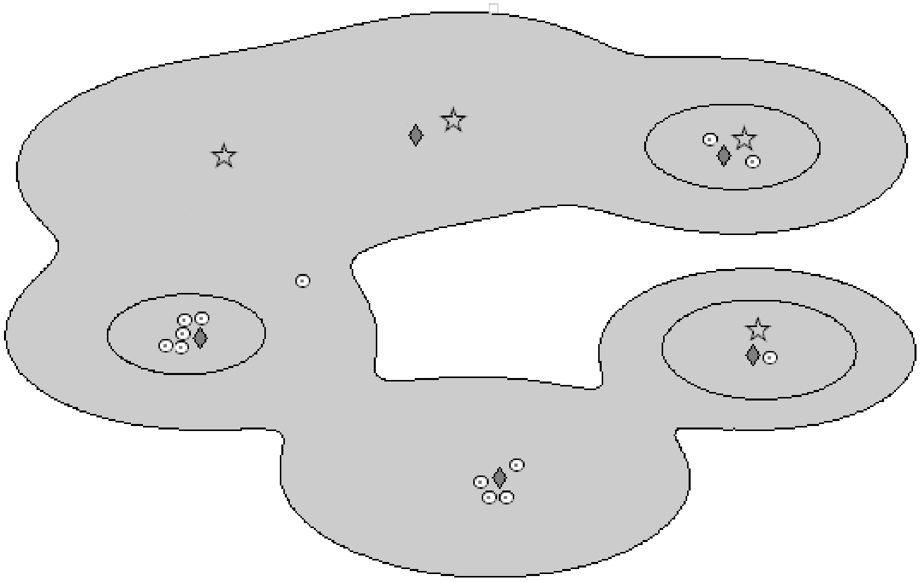


Fig. 3.6a. Home range and core areas of the Bevaro Moravato troop in the month of **April**. Map was generated using a Kernel Density Estimate Analysis in Home Range Tools for ArcGIS® but was modified in Windows® Paint by Brad Kelley to enhance image clarity. Core areas are demarcated by black ellipses. ◆ = Sacred Forest, ⊙ = Native Fruit, ▫ = Other Feeding, ☆ = Sleeping Site. The top-quartile food for this month (39.6% of total feeding time) was the fruit of *Terminalia fatrae*, an abundant and native bush species. Map is not to scale.

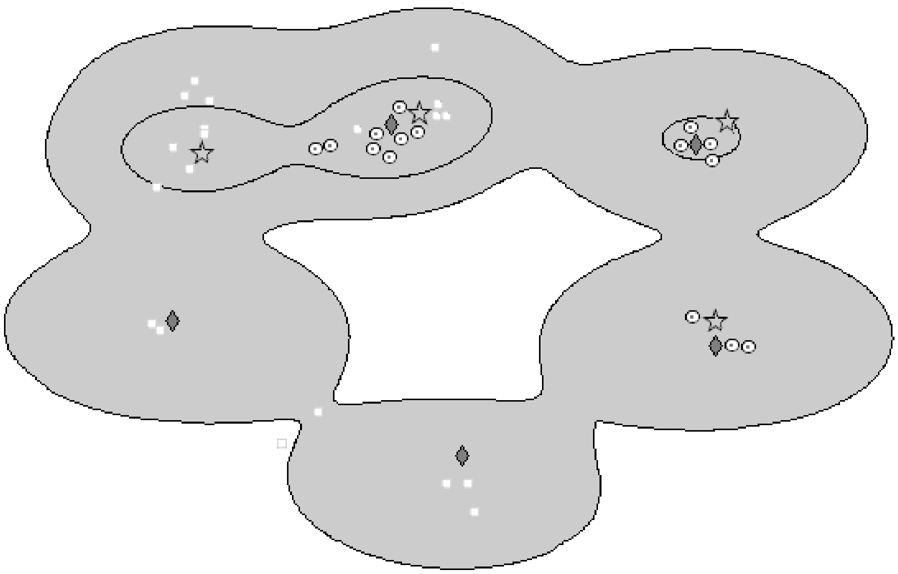


Fig. 3.6a. Home range and core areas of the Bevaro Moravato troop in the month of **May.** Map was generated using a Kernel Density Estimate Analysis in Home Range Tools for ArcGIS® but was modified in Windows® Paint by Brad Kelley to enhance image clarity. Core areas are demarcated by black ellipses. ⧫ = Sacred Forest, ⊙ = Native Fruit, ▫ = Other Feeding, ☆ = Sleeping Site. The top-quartile food for this month (31.0% of total feeding time) was the fruit of *Commiphora* sp. (voampike), an abundant and native bush species. Map is not to scale.

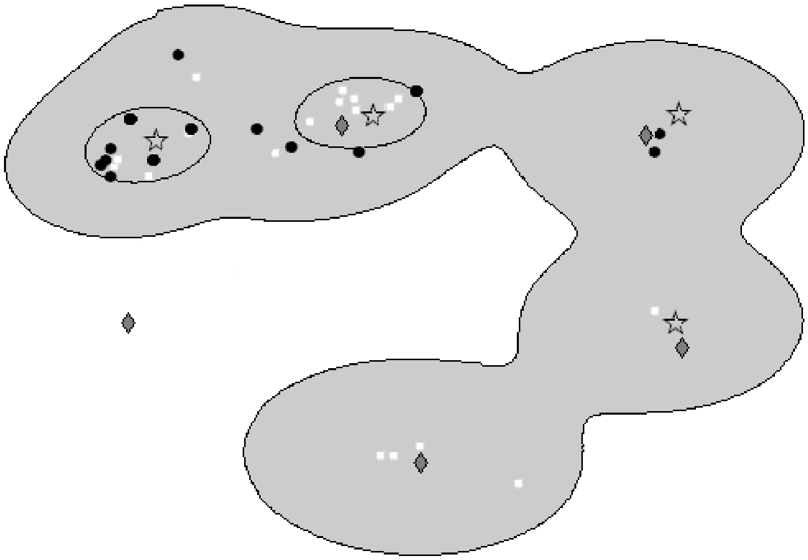


Fig. 3.6a. Home range and core areas of the Bevaro Moravato troop in the month of **June**. Map was generated using a Kernel Density Estimate Analysis in Home Range Tools for ArcGIS® but was modified in Windows® Paint by Brad Kelley to enhance image clarity. Core areas are demarcated by black ellipses. ⧫ = Sacred Forest, ▫ = Other Feeding, ☆ = Sleeping Site, ● = *Opuntia* . Core areas are demarcated by black circles. The top-quartile food for this month (25.0% of total feeding time) was the fruit of *Opuntia monacantha*, an invasive cactus species. Map is not to scale.

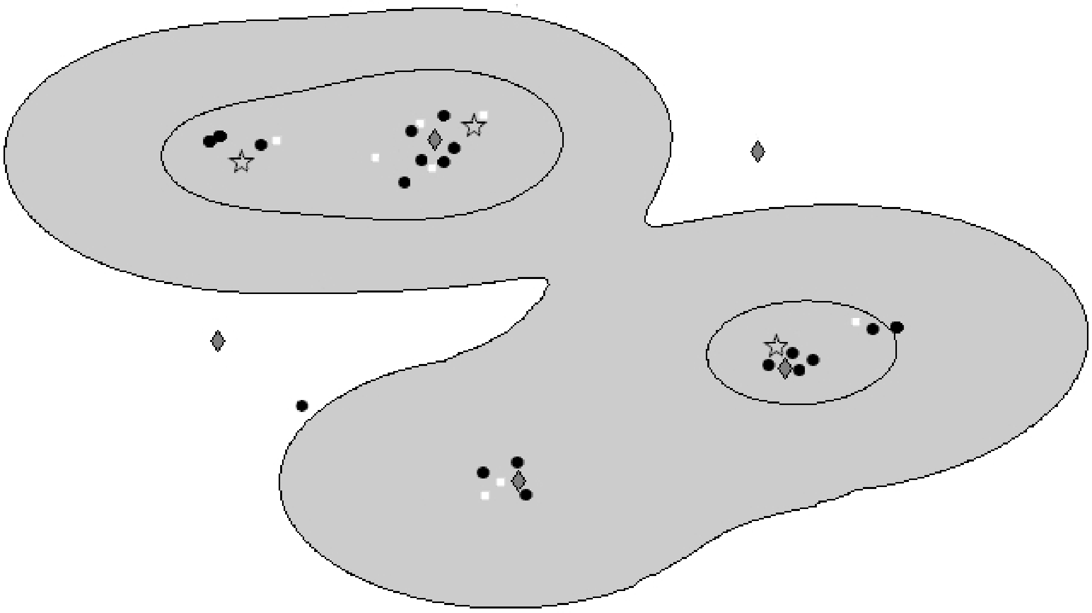


Fig. 3.6a. Home range and core areas of the Bevaro Moravato troop in the month of **July**. Map was generated using a Kernel Density Estimate Analysis in Home Range Tools for ArcGIS® but was modified in Windows® Paint by Brad Kelley to enhance image clarity. Core areas are demarcated by black ellipses. ◆ = Sacred Forest, □ = Other Feeding, ☆= Sleeping Site, ● = *Opuntia* . The top-quartile food for this month (34.6% of total feeding time) was the fruit of *Opuntia stricta*, an invasive cactus species. Map is not to scale.

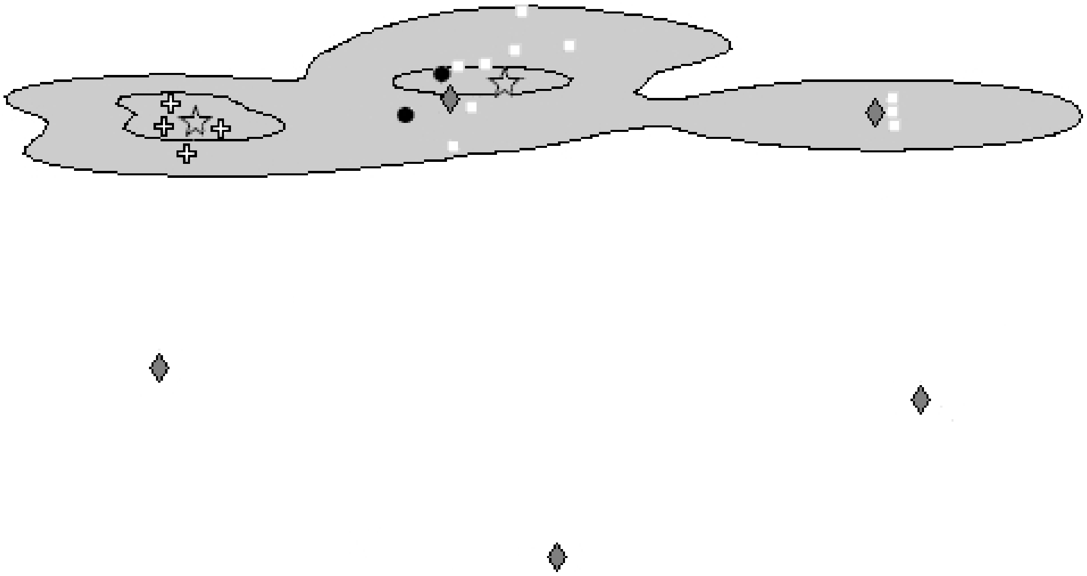


Fig. 3.6a. Home range and core areas of the Bevaro Moravato troop in the month of **August**. Map was generated using a Kernel Density Estimate Analysis in Home Range Tools for ArcGIS® ® but was modified in Windows® Paint by Brad Kelley to enhance image clarity. Core areas are demarcated by black ellipses. ◆ = Sacred Forest, ✚ = Native Leaf, □ = Other Feeding, ☆= Sleeping Site, ● = *Opuntia*.. The top-quartile foods for this month (17.7% and 13.6% of total feeding time) were the leaves of *Leptadenia* sp., an abundant and native vine species, and the fruit of *Opuntia stricta*, an invasive cactus species. Map is not to scale.

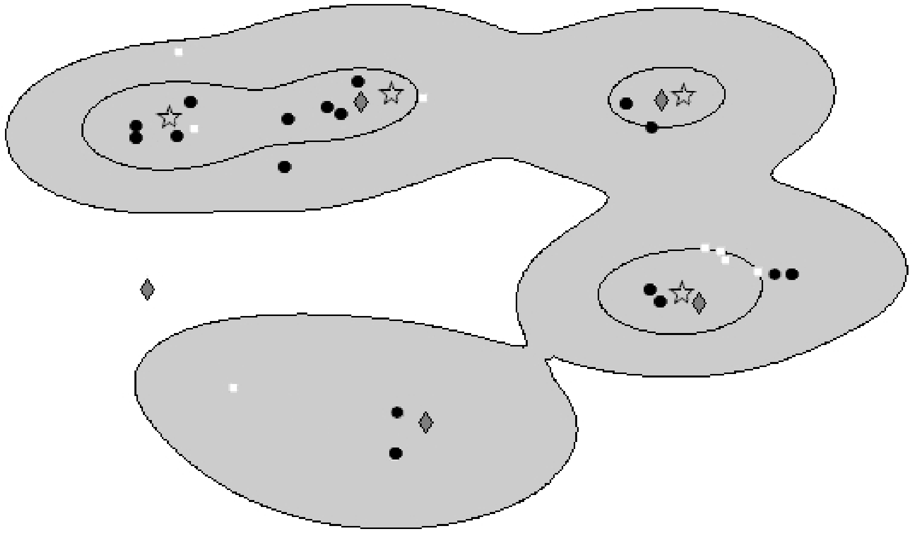


Fig. 3.6a. Home range and core areas of the Bevaro Moravato troop in the month of **September**. Map was generated using a Kernel Density Estimate Analysis in Home Range Tools for ArcGIS® but was modified in Windows® Paint by Brad Kelley to enhance image clarity. Core areas are demarcated by black ellipses. ◆ = Sacred Forest, ▫ = Other Feeding, ☆ = Sleeping Site, ● = *Opuntia*.. The top-quartile food for this month (28.2% of total feeding time) was the fruit of *Opuntia stricta*, an invasive cactus species. Map is not to scale.

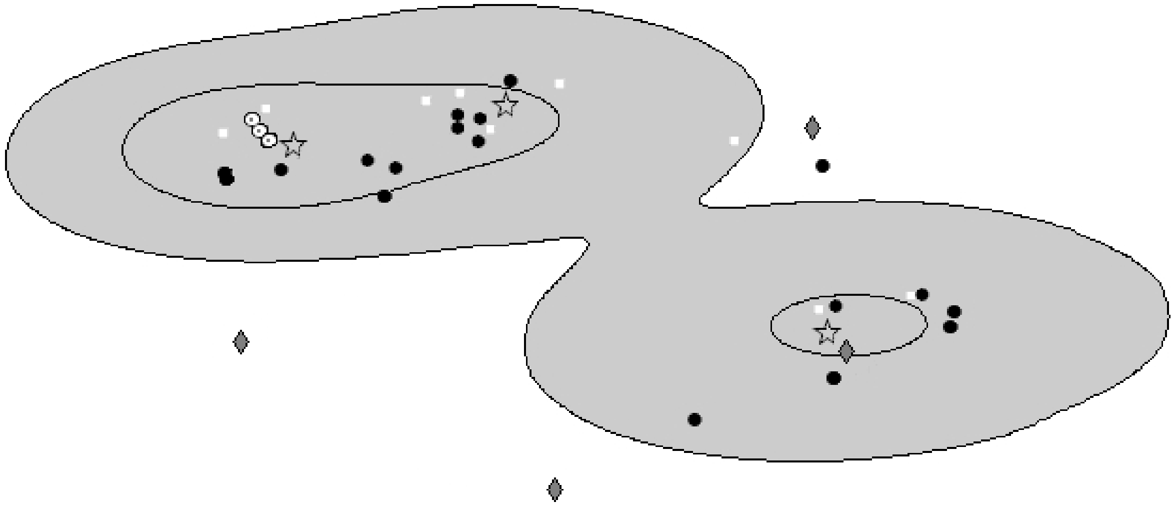


Fig. 3.6a. Home range and core areas of the Bevaro Moravato troop in the month of **October**. Map was generated using a Kernel Density Estimate Analysis in Home Range Tools for ArcGIS® but was modified in Windows® Paint by Brad Kelley to enhance image clarity. Core areas are demarcated by black ellipses. ◆ = Sacred Forest, ⊙ = Native Fruit, ▫ = Other Feeding, ☆ = Sleeping Site, ● = *Opuntia*. The top-quartile foods for this month (23.4% and 14.0% of total feeding time) were the fruit of *Opuntia stricta*, an invasive cactus species, and the fruit of *Phyllanthus amanu*, an abundant and native bush species. Map is not to scale.

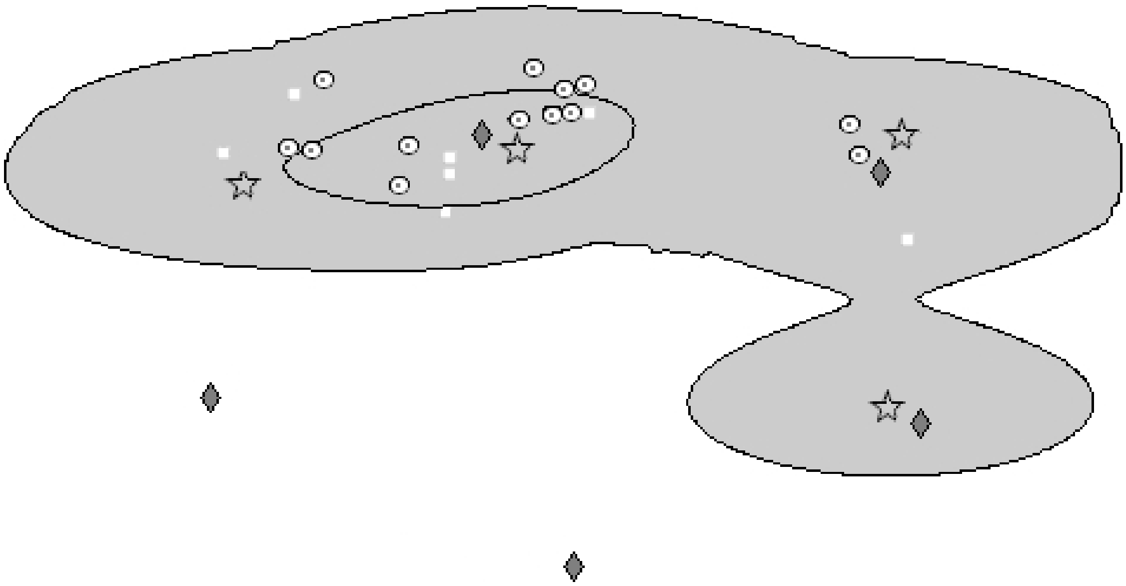


Fig. 3.6a. Home range and core areas of the Bevaro Moravato troop in the month of **November**. Map was generated using a Kernel Density Estimate Analysis in Home Range Tools for ArcGIS® but was modified in Windows® Paint by Brad Kelley to enhance image clarity. Core areas are demarcated by black ellipses. ♦ = Sacred Forest, ⊙ = Native Fruit, ▫ = Other Feeding, ☆ = Sleeping Site. The top-quartile food for this month (35.8% of total feeding time) was the fruit of *Strychnos decussata,* an abundant and native tree species an abundant and native bush species. Map is not to scale.

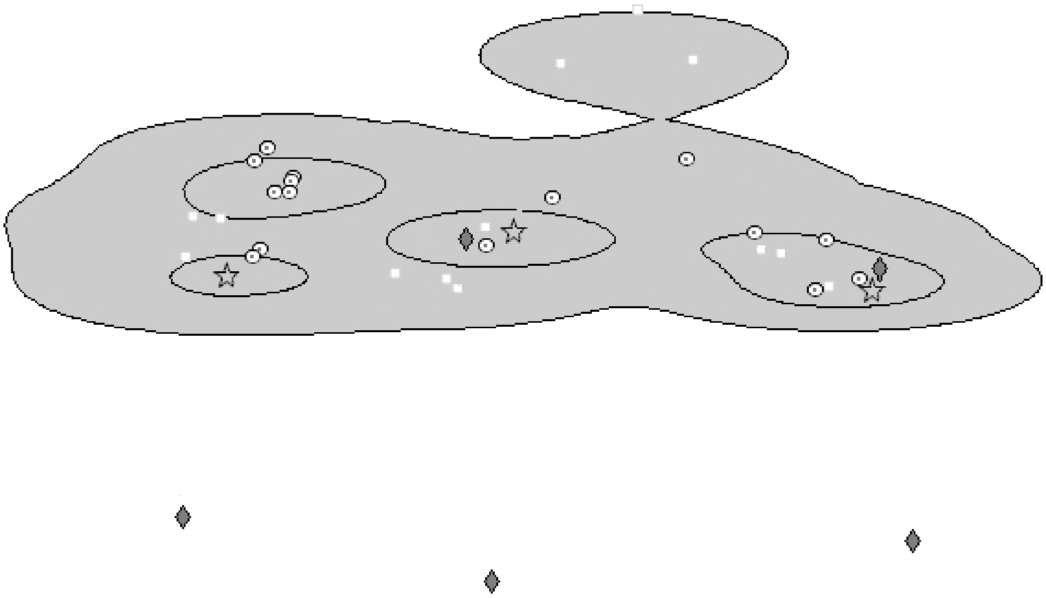


Fig. 3.6a. Home range and core areas of the Bevaro Moravato troop in the month of **December**. Map was generated using a Kernel Density Estimate Analysis in Home Range Tools for ArcGIS® but was modified in Windows® Paint by Brad Kelley to enhance image clarity. Core areas are demarcated by black ellipses. ♦ = Sacred Forest, ⊙ = Native Fruit, ▫ = Other Feeding, ☆ = Sleeping Site. The top-quartile food for this month (47.2% of total feeding time) was the fruit of *Strychnos decussata,* an abundant and native tree species. Map is not to scale.

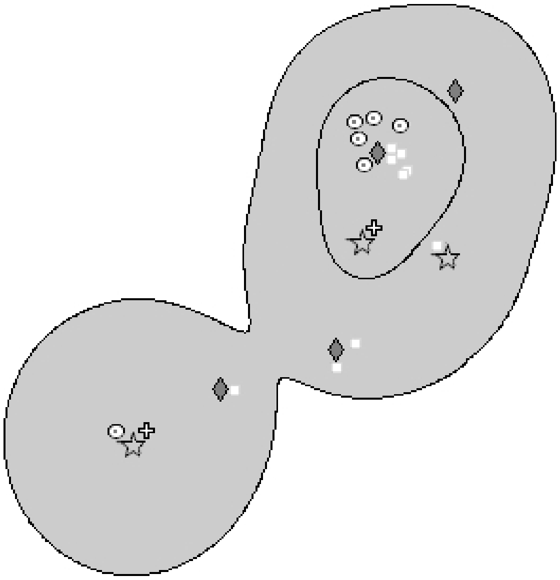


Fig. 3.6b. Home range and core areas of the Tsankalamanga troop in the month of **January**. Map was generated using a Kernel Density Estimate Analysis in Home Range Tools for ArcGIS® but was modified in Windows® Paint by Brad Kelley to enhance image clarity. Core areas are demarcated by black ellipses. ♦ = Sacred Forest, ⊙ = Native Fruit, ✚ = Native Leaf ▫ = Other Feeding, ☆ = Sleeping Site. The top-quartile foods for this month (15.3% and 12.7% of total feeding time) were the fruit of Grewia *punctata*, and native and endangered tree species, and the leaves of Grewia *cyclea*, a native and abundant bush species. Map is not to scale.

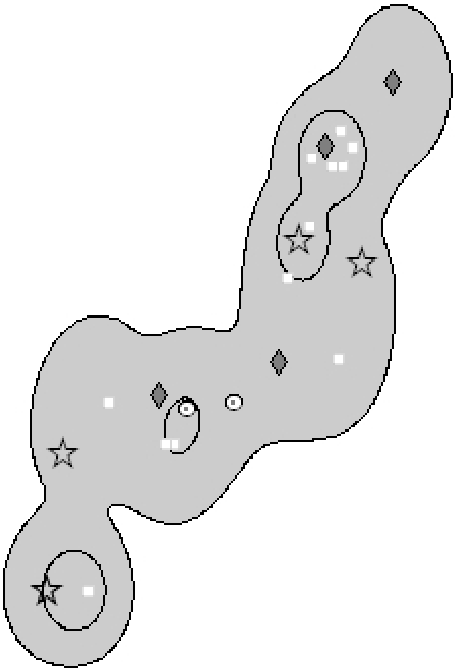


Fig. 3.6b. Home range and core areas of the Tsankalamanga troop in the month of **February**. Map was generated using a Kernel Density Estimate Analysis in Home Range Tools for ArcGIS® but was modified in Windows® Paint by Brad Kelley to enhance image clarity. Core areas are demarcated by black ellipses. ♦ = Sacred Forest, ⊙ = Native Fruit, ▫ = Other Feeding, ☆ = Sleeping Site. The top-quartile food for this month (29.6% of total feeding time) was the fruit of *Terminalia fatrae*, a native and abundant tree bush species. Map is not to scale.

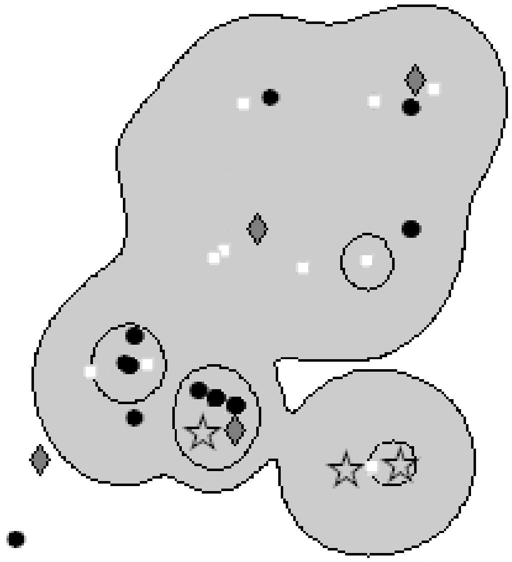


Fig. 3.6b. Home range and core areas of the Tsankalamanga troop in the month of **March**. Map was generated using a Kernel Density Estimate Analysis in Home Range Tools for ArcGIS® but was modified in Windows® Paint by Brad Kelley to enhance image clarity. Core areas are demarcated by black ellipses. ◆ = Sacred Forest, ▫ = Other Feeding, ☆ = Sleeping Site, ● = *Opuntia*. The top-quartile food for this month (29.3% of total feeding time) was the fruit of *Opuntia monacantha*, an invasive cactus species. Map is not to scale.

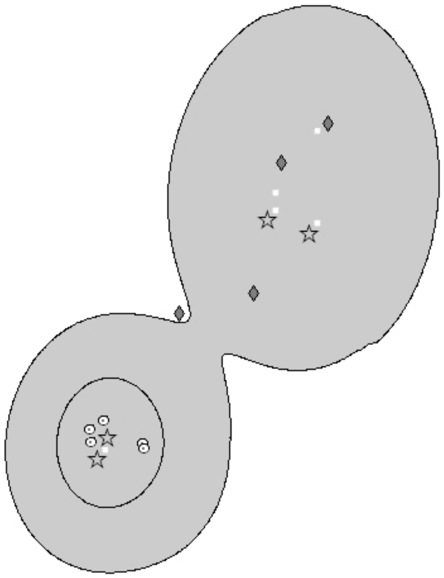


Fig. 3.6b. Home range and core areas of the Tsankalamanga troop in the month of **April**. Map was generated using a Kernel Density Estimate Analysis in Home Range Tools for ArcGIS® but was modified in Windows® Paint by Brad Kelley to enhance image clarity. Core areas are demarcated by black ellipses. ◆ = Sacred Forest, , ⊙ = Native Fruit, ▫ = Other Feeding, ☆ = Sleeping Site. The top-quartile food for this month (26.6% of total feeding time) was the fruit of *Phyllanthus amanu*, an abundant and native bush species. Map is not to scale.

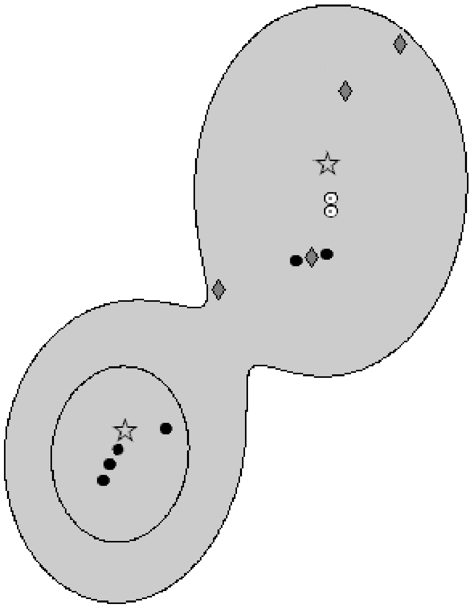


Fig. 3.6b. Home range and core areas of the Tsankalamanga troop in the month of **May**. Map was generated using a Kernel Density Estimate Analysis in Home Range Tools for ArcGIS® but was modified in Windows® Paint by Brad Kelley to enhance image clarity. Core areas are demarcated by black ellipses. ◆ = Sacred Forest, ⊙ = Native Fruit, ▫ = Other Feeding, ☆ = Sleeping Site, ● = *Opuntia.* The top-quartile foods for this month (17.1% and 14.8% of total feeding time) were the fruit of *Opuntia monacantha,* an invasive cactus species, and the fruit of *Canthium,* sp. (la jandsy), an abundant and native tree species. Map is not to scale.

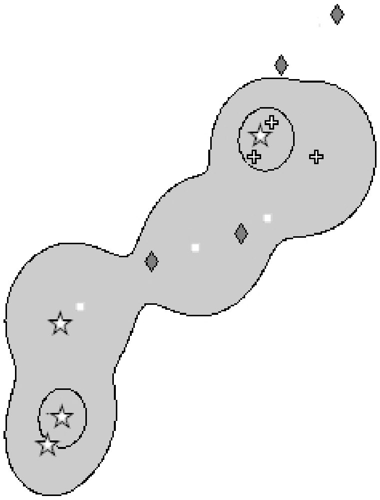


Fig. 3.6b. Home range and core areas of the Tsankalamanga troop in the month of **June**. Map was generated using a Kernel Density Estimate Analysis in Home Range Tools for ArcGIS® but was modified in Windows® Paint by Brad Kelley to enhance image clarity. Core areas are demarcated by black ellipses. ◆ = Sacred Forest, ✚ = Native Leaf, ▫ = Other Feeding, ☆ = Sleeping Site. The top-quartile food for this month (40.5% of total feeding time) was the leaves of *Metaporana* sp. (kililo), a native and abundant vine species. Map is not to scale.

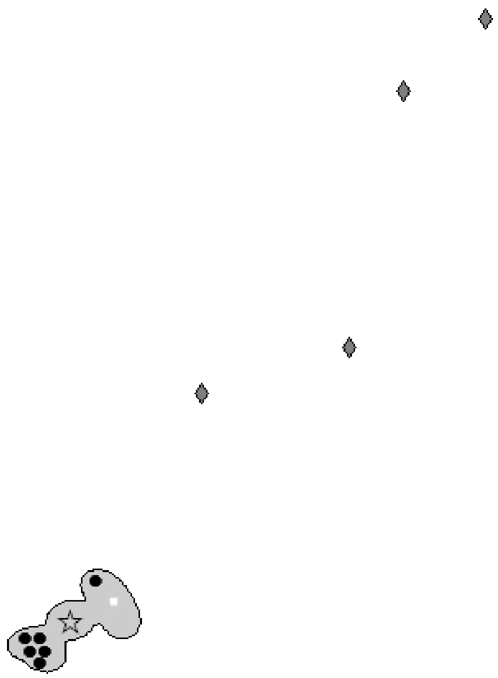


Fig. 3.6b. Home range and core areas of the Tsankalamanga troop in the month of **July**. Map was generated using a Kernel Density Estimate Analysis in Home Range Tools for ArcGIS® but was modified in Windows® Paint by Brad Kelley to enhance image clarity. Core areas are demarcated by black ellipses. ◆ = Sacred Forest, ▫ = Other Feeding, ☆ = Sleeping Site, ● = *Opuntia*. The top-quartile food for this month (55.4% of total feeding time) was the fruit of *Opuntia monacantha*, an invasive cactus species. Map is not to scale.

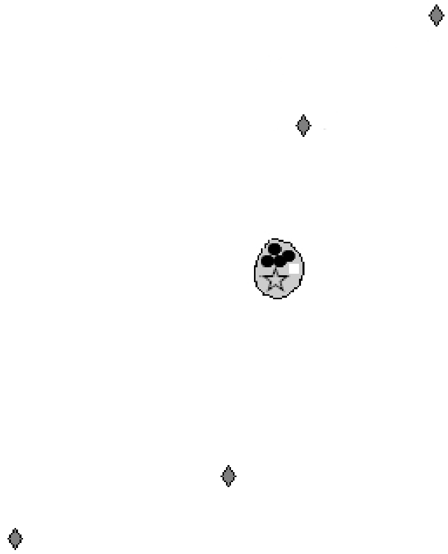


Fig. 3.6b. Home range and core areas of the Tsankalamanga troop in the month of **August**. Map was generated using a Kernel Density Estimate Analysis in Home Range Tools for ArcGIS® but was modified in Windows® Paint by Brad Kelley to enhance image clarity. Core areas are demarcated by black ellipses. ◆ = Sacred Forest, ▫ = Other Feeding, ☆ = Sleeping Site, ● = *Opuntia*. The top-quartile food for this month (72.4% of total feeding time) was the fruit of *Opuntia monacantha*, an invasive cactus species. Map is not to scale.

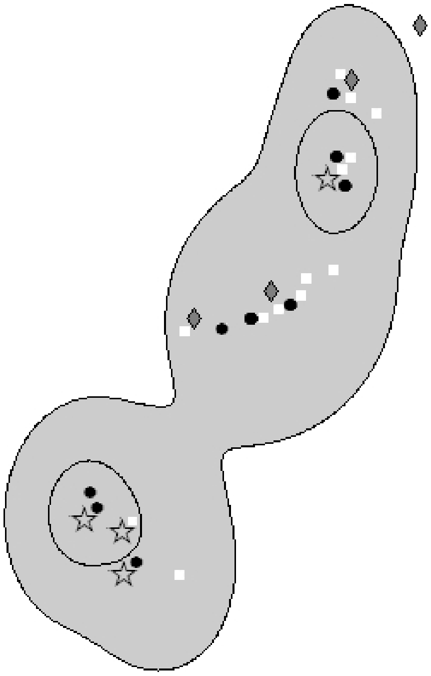


Fig. 3.6b. Home range and core areas of the Tsankalamanga troop in the month of **September**. Map was generated using a Kernel Density Estimate Analysis in Home Range Tools for ArcGIS® but was modified in Windows® Paint by Brad Kelley to enhance image clarity. Core areas are demarcated by black ellipses. ◆ = Sacred Forest, ▫ = Other Feeding, ☆ = Sleeping Site, ● = *Opuntia*. The top-quartile food for this month (49.1% of total feeding time) was the fruit of *Opuntia monacantha*, an invasive cactus species. Map is not to scale.

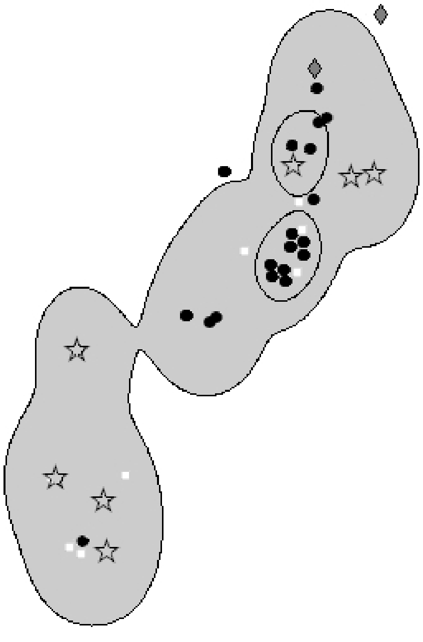


Fig. 3.6b. Home range and core areas of the Tsankalamanga troop in the month of **October**. Map was generated using a Kernel Density Estimate Analysis in Home Range Tools for ArcGIS® but was modified in Windows® Paint by Brad Kelley to enhance image clarity. Core areas are demarcated by black ellipses. ◆ = Sacred Forest, ▫ = Other Feeding, ☆ = Sleeping Site, ● = *Opuntia.* The top-quartile food for this month (33.3% of total feeding time) was the fruit of *Opuntia stricta*, an invasive cactus species. Map is not to scale.

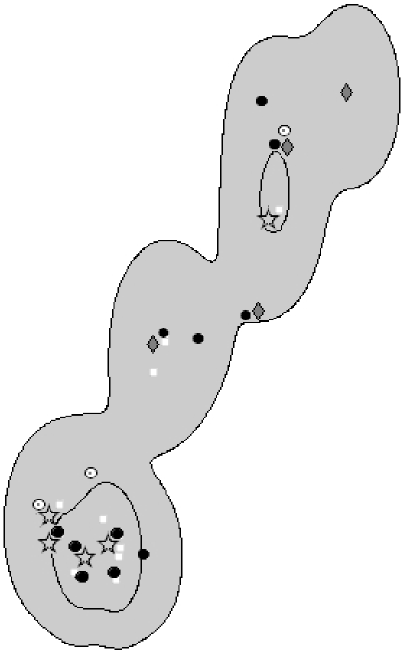


Fig. 3.6b. Home range and core areas of the Tsankalamanga troop in the month of **November**. Map was generated using a Kernel Density Estimate Analysis in Home Range Tools for ArcGIS® but was modified in Windows® Paint by Brad Kelley to enhance image clarity. Core areas are demarcated by black ellipses. ⧫ = Sacred Forest, ⊙ = Native Fruit, ▫ = Other Feeding, ☆ = Sleeping Site, ● = *Opuntia*. The top-quartile foods for this month (19.9% and 18.1% of total feeding time) were the fruit of *Azima tetracantha*, a native and abundant bush species, and the fruit of *Opuntia stricta,* an invasive cactus species. Map is not to scale.

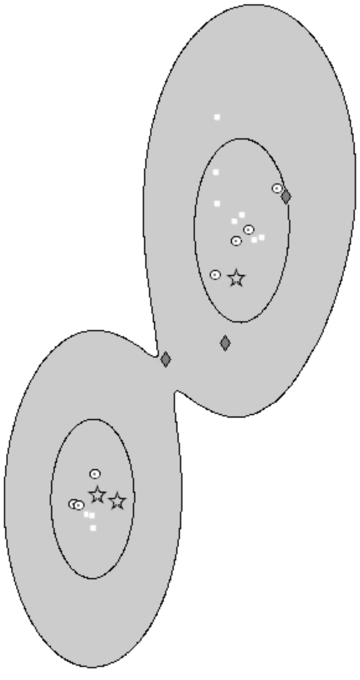


Fig. 3.6b. Home range and core areas of the Tsankalamanga troop in the month of **December**. Map was generated using a Kernel Density Estimate Analysis in Home Range Tools for ArcGIS® but was modified in Windows® Paint by Brad Kelley to enhance image clarity. Core areas are demarcated by black ellipses. ⧫ = Sacred Forest, ⊙ = Native Fruit, ▫ = Other Feeding, ☆ = Sleeping Site. The top-quartile food for this month (35.6% of total feeding time) was the fruit of *Boscia* sp. (sasavy), a native and abundant tree species. Map is not to scale.

Analysis 3: Day Ranges

Boyle et al. (2009) have defined day range as an area that consists of a day's ranging points. However, I have calculated day range (also known as daily path length) as a linear distance calculation, which is the same method that has been used in studies on gallery forest *L. catta* (e.g., Jolly et al., 1993; Strier, 2000). Day ranges were calculated using the distance calculation function in Home Range Tools for ArcGIS®. Spearman rank order correlation tests were conducted to determine whether the troops' daily activities were affected by day range length. The activity budget categories that were tested were a) general movement and travel, b) feeding, c) resting and sleeping (which included huddling), d) social behaviors (i.e., mutual grooming and play), e) sunning, and f) scent marking.

Results

The average length of daily travel for the Bevaro Moravato troop was 1,097 m with a range of 265 m - 2,721 m (**Fig. 3.7.a**). The average length of daily travel for the Tsankalamanga troop was 726 m with a range of 59 m-1,989 m (**Fig. 3.7.b**). When day length averages were calculated by month, two different travel patterns emerged between the CSM troops. The Bevaro Moravato troop traveled the least distance in March ($\bar{X}$ = 670m) and the greatest distance in June ($\bar{X}$ =1,503m) (**Fig. 3.7.a**.). In contrast, the Tsankalamanga troop traveled the least distance in August ($\bar{X}$ = 199m) and the greatest distance in December ($\bar{X}$ = 1,076m) (**Fig. 3.7.b**). Yet the most distinctive difference between the troops' day ranges was the Tsankalamanga troop's notably smaller day ranges the months of May through August.

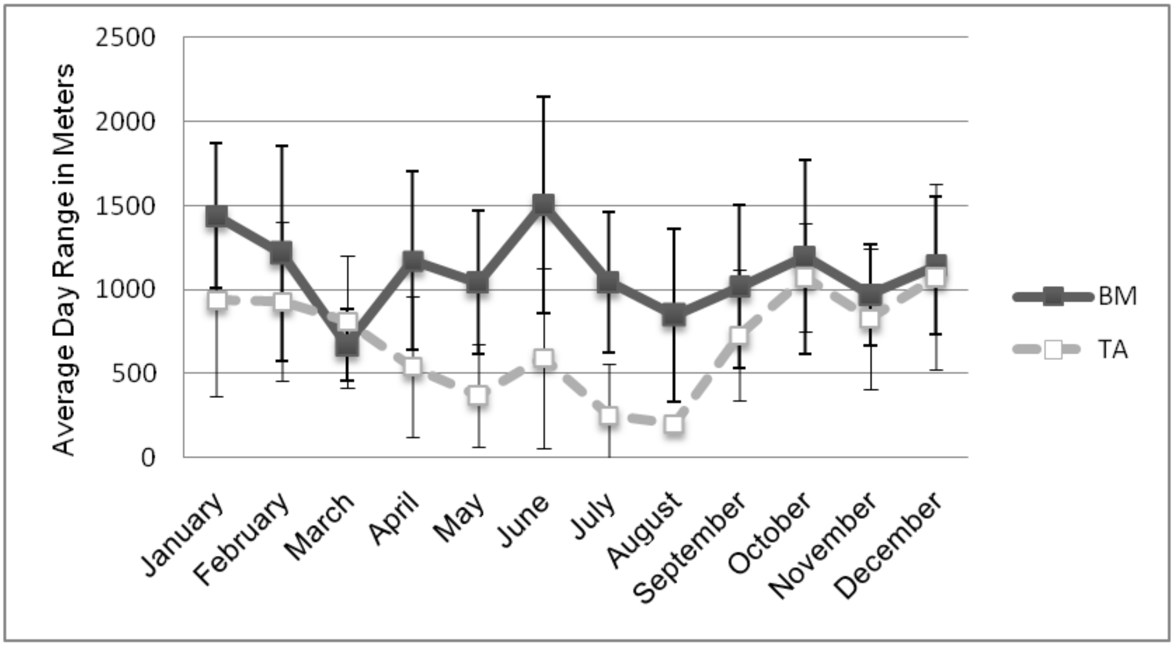
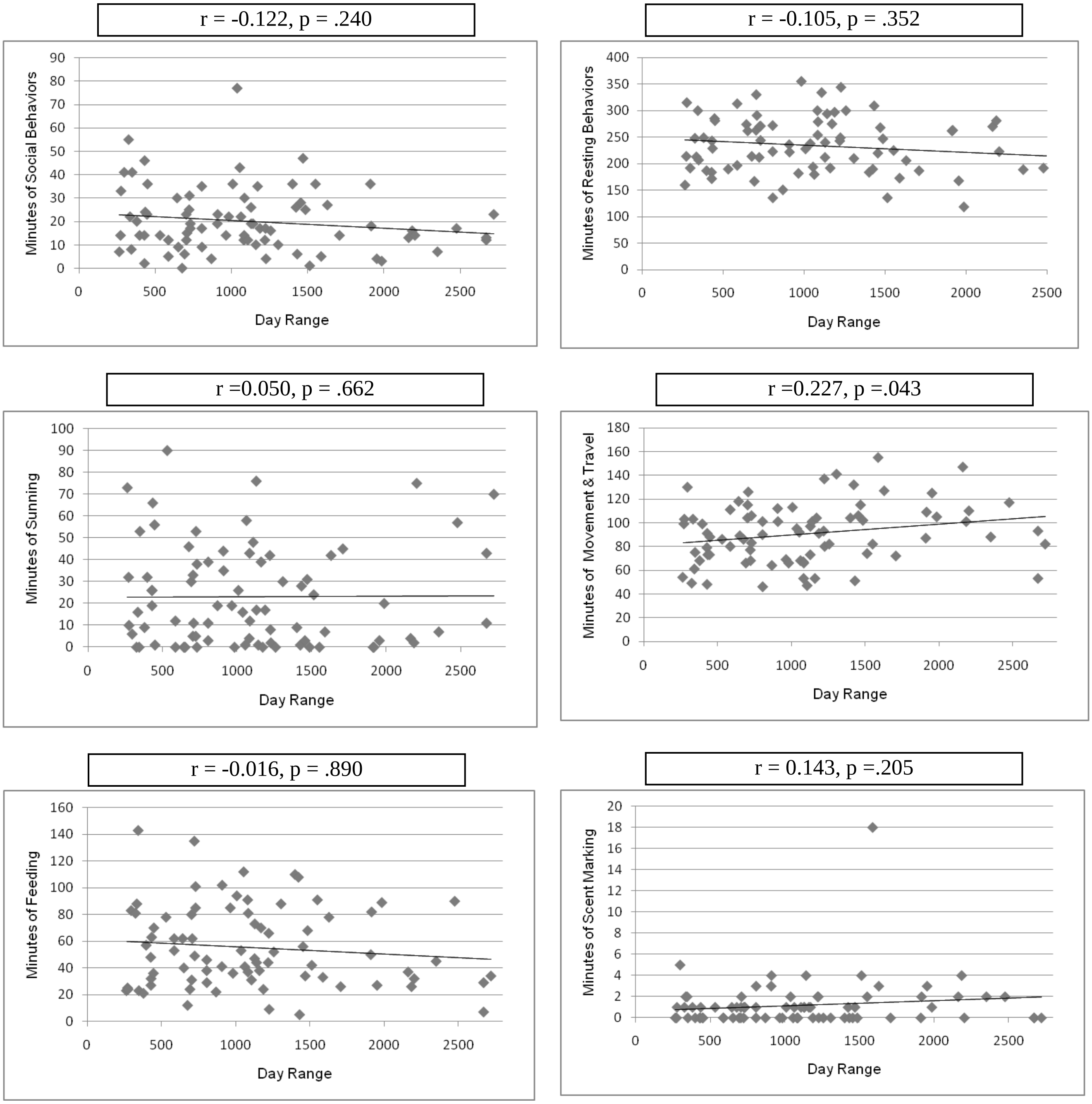


Fig. 3.7. Monthly average day range of the focal troops in meters. BM = Bevaro Moravato. TA = Tsankalamanga. Error bars depict 95% CI.

As expected, there was a significant positive association between day range length and the amount of time troop members spent moving/traveling throughout the day for both troops (BM: $r = 0.240$, $n = 80$, $p \leq .05$; TA: $r = 0.659$, $n = 56$, $p \leq .001$; two-tailed). For the Bevaro Moravato troop, no other daily activity correlated with daily travel length (**Fig. 3.8.a.**). For the Tsankalamanga troop, sunning ($r = -0.497$, $p \leq .001$) and social activity ($r = -0.315$, $p \leq .05$) were negatively correlated with day range, while feeding ($r = 0.286$, $p \leq .05$) and scentmarking ($r = 0.500$, $p \leq 0.001$) were positively correlated (**Fig. 3.8.b**). In fact, resting/sleeping was the only activity category that did not correlate with daily travel length for this troop.

Of the 7,260 minutes of travel and movement recorded for the Bevaro Moravato troop, 175 (2.4%) were noted as fleeing behavior. The causes of the animals’ rapid flight were: people (n = 63; 36 of the data were noted as associated with the field team, 27 of the data were noted as associated with villagers), the lone sifaka that resided in a frequented sacred forest (n = 38), an unknown source (n = 37), other troop members (n = 15), birds of prey and ravens (n = 10), wind (n = 6), zebu (n = 4), a tortoise (n = 1), and cicadas (n = 1). Of the 4,049 minutes of travel and movement data recorded for the Tsankalamanga troop, 27 (0.7%) were noted as fleeing behavior. Within the fleeing category, most were from an unknown source (n = 11), followed by people (n = 9; 7 were associated with a member of the field team, while the remaining two minutes were associated with villagers), other lemurs (n = 5), a tortoise (n = 1), and birds (n = 1).


r = -0.122, p = .240

r = -0.105, p = .352

r =0.050, p = .662

r =0.227, p =.043

r = -0.016, p = .890

r = 0.143, p =.205

Fig. 3.8a. Day range correlations to activity budget data for the Bevaro Moravato troop. Activity budget data were collected during all day follows. Social behavior is composed of mutual grooming and play. Resting behaviors include daytime sleeping, self grooming, and huddling. N = 80 days. Tests are two-tailed.

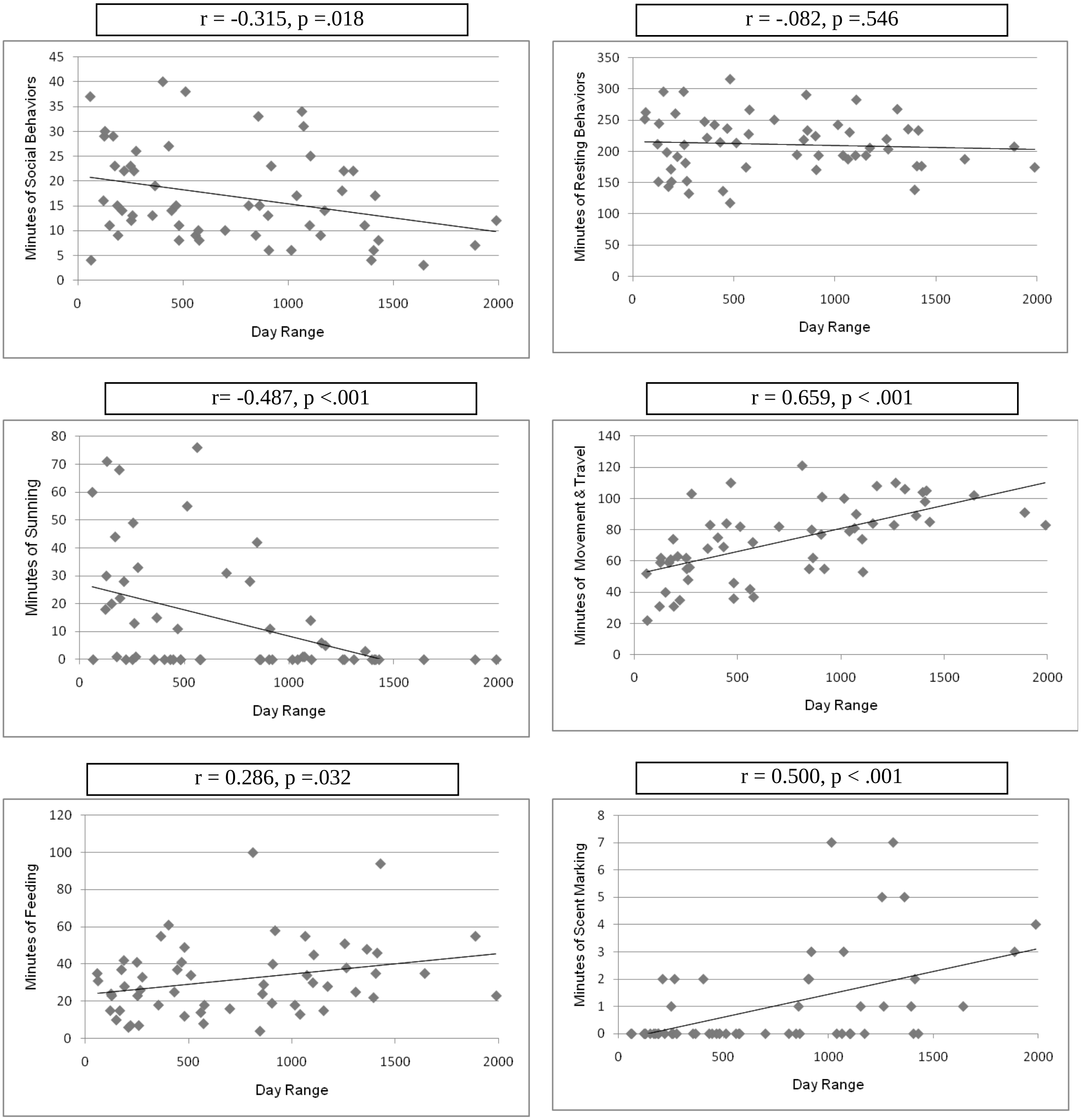


Fig. 3.8b. Day range correlations to activity budget data for the Tsankalamanga troop. Activity budget data were collected during all day follows. Social behavior is composed of mutual grooming and play. Resting behaviors consists of daytime sleeping, self grooming, and huddling. N = 56 days. Tests are two-tailed.

Analysis 4: Habitat Use

There was noticeable similarity in the percentage of time the troops spent in the CSM substrates throughout the year. While just over 35% of the troops' total daily activities were spent in the *Opuntia monacantha* hedges (BM = 36.3%; TA = 38.6%), a little less than 35% of their time was spent on the ground (BM = 34.3%; TA = 31.0%), and a little more than 25% of their time was spent in trees and shrubs (BM = 28.2%; TA = 27.0%) (**Fig. 3.9**).

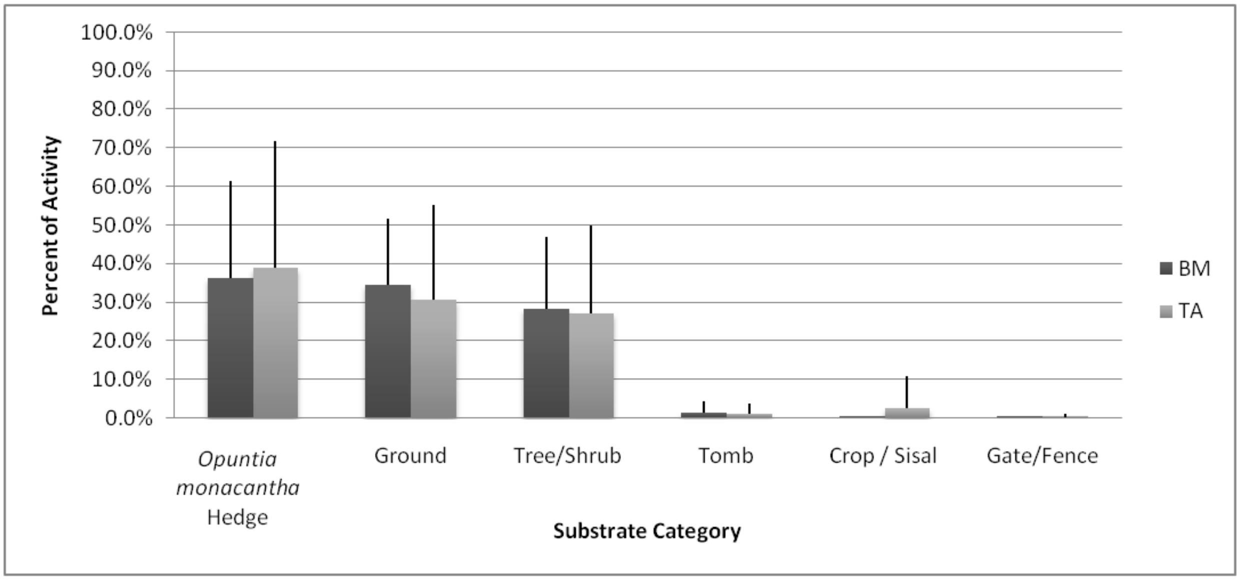


Fig. 3.9. Percent daily activity troops spent in substrate type throughout the year. Error bars signify SD.

When analyzed on a monthly scale, the Bevaro Moravato troop spent over 30% of its total activity time on the ground for every month except March and May. In January, 51.2% of this troop's daily activity was spent on the ground. In comparison, the Tsankalamanga troop spent less than 15% of the time on the ground during the months of June and July (13%, 12.2%), and less than 30% of their total activity time on the ground from the months of February through August. However, the Tsankalamanga troop spent 72.0% of its activity time on the ground in October (**Fig. 3.10**).

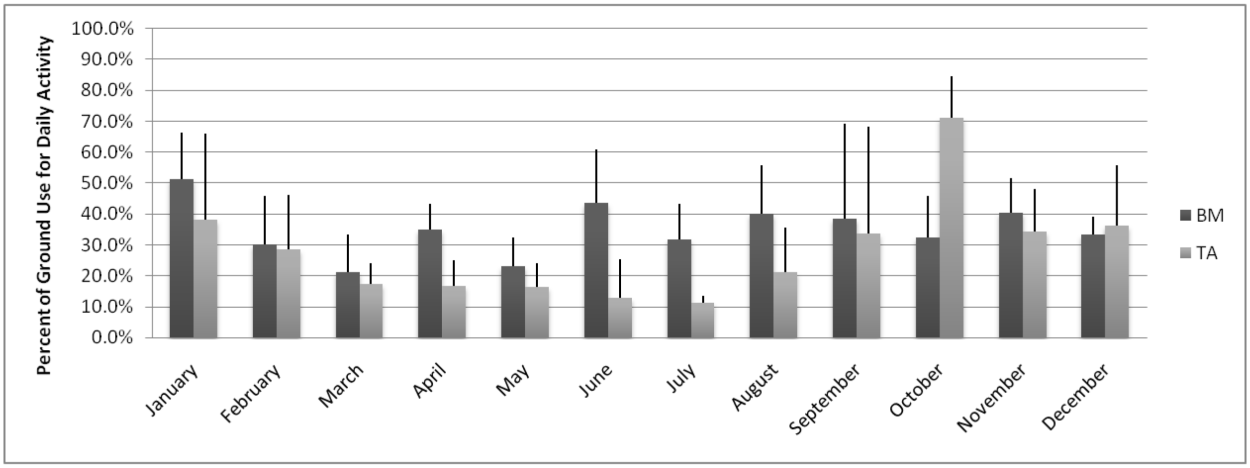


Fig. 3.10. Percent daily activity troops spent on the ground each month. Error bars signify SD.

All day follows on the Tsankalamanga troop typically began long after sunrise, and *Opuntia monacantha* hedges were the troops' sole nightly sleeping sites (see chapter two). Therefore, troop to troop comparisons of hedge use should be interpreted with caution as the Tsankalamanga troop was often awake before I started recording their activity. Yet even with this difference in methodology, the Tsankalamanga troop was observed within the *O. monacantha* hedges more often than the Bevaro Moravato troop for every month except February, October and December. In fact, almost two-thirds of the Tsankalamanga troop's daily activity data were recorded within the *O. monacantha* hedges from the months of June through August. In general, there appears to be no monthly pattern that the two troops shared in *O. monacantha* hedge use. While daily *O. monacantha* hedge use by the Bevaro Moravato troop ranged from only 3.9% in April to 54.3% in October, the Tsankalamanga troop spent nearly half of its time in the *O. monacantha* hedges in April (44.8%) but only 14% of its time in the *O. monacantha* hedges in October. Moreover in contrast to the Tsanakalamanga troop, there were only three months in which the daily activity time of the Bevaro Moravato troop diverged from 30%-48%. October was the only month in which the Bevaro Moravato troop spent over half of its activity time within the *O. monacantha* hedges. Conversely, the troop spent less than 10% of its daily activity time within the *O. monacantha* hedges in the months of January and April (**Fig. 3.11**).

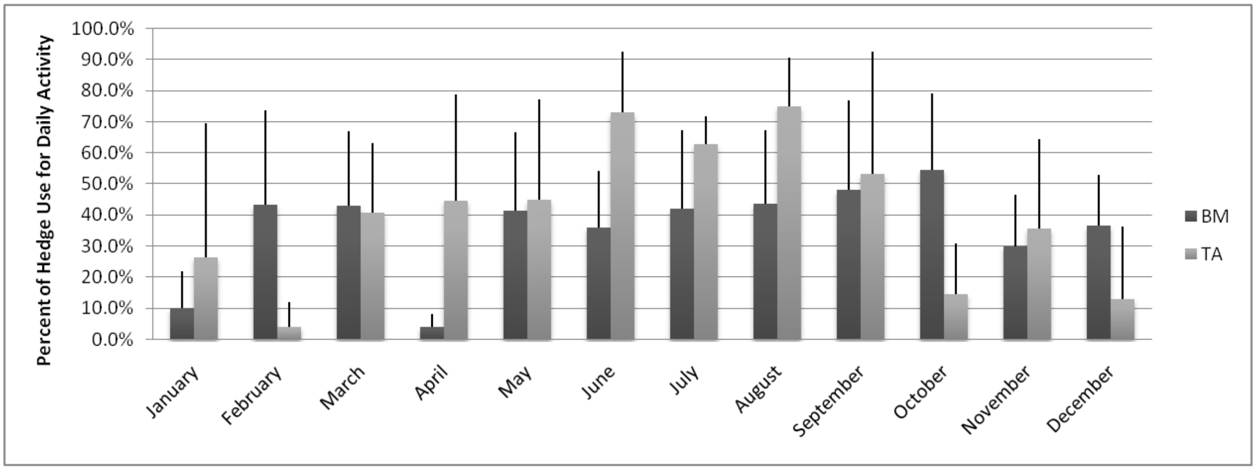


Fig. 3.11. Percent daily activity troops spent within *O. monacantha* hedges each month. Error bars signify SD.

In contrast to hedge use, trees and shrub use followed a seasonal pattern for both troops, with tree and shrub use declining appreciably from the months of June through October. April and February were the months in which the Bevaro Moravato troop and the Tsanakalamanga troop respectively spent the most amount of time in the trees and shrubs (BM =57.7%, TA = 56.6%). Conversely, the two troops spent the least amount of activity time in the trees and shrubs during the months of October and August (BM = 12.1%, TA = 3.5%). The lack of tree and shrub use in the month of August for the Tsankalamanga troop is exceptional when compared with the rest of the data (**Fig. 3.12**).

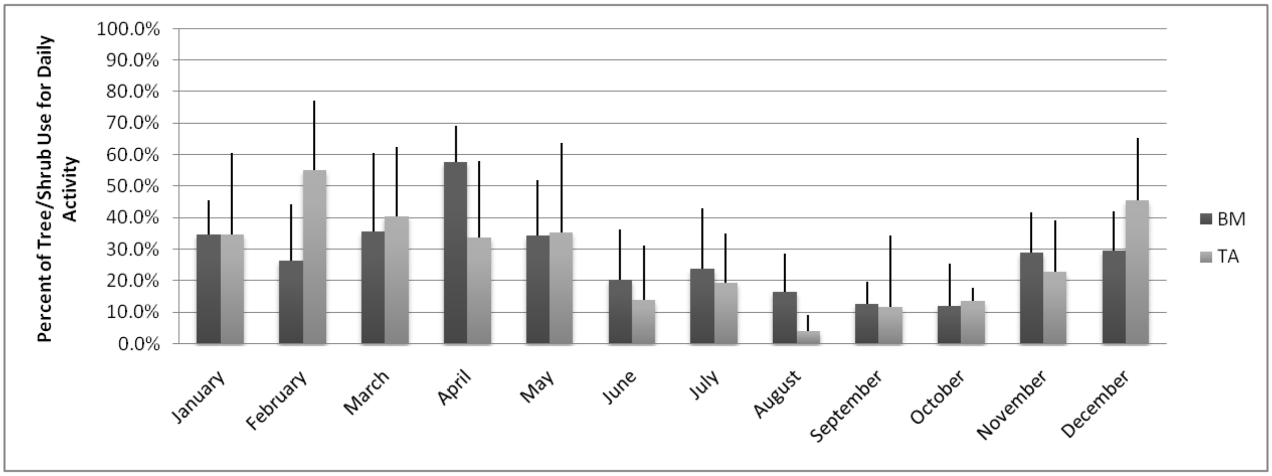


Fig. 3.12. Percent daily activity time troops spent in trees/shrubs each month. Error bars signify SD.

When substrate use was categorized by feeding activity, both troops spent a majority of their feeding time in the trees and shrubs (BM = 60.9%; TA = 48.0%). This behavior was most pronounced with the Bevaro Moravato troop; the Tsankalamanga troop spent more time feeding on the ground (BM = 24.5%; TA = 34.8%). The *Opuntia monacantha* hedges were the third most frequently used feeding substrate (BM = 14.1%; TA = 16.6%). A negligible amount of time was spent feeding on any other substrate (**Fig. 3.13**).

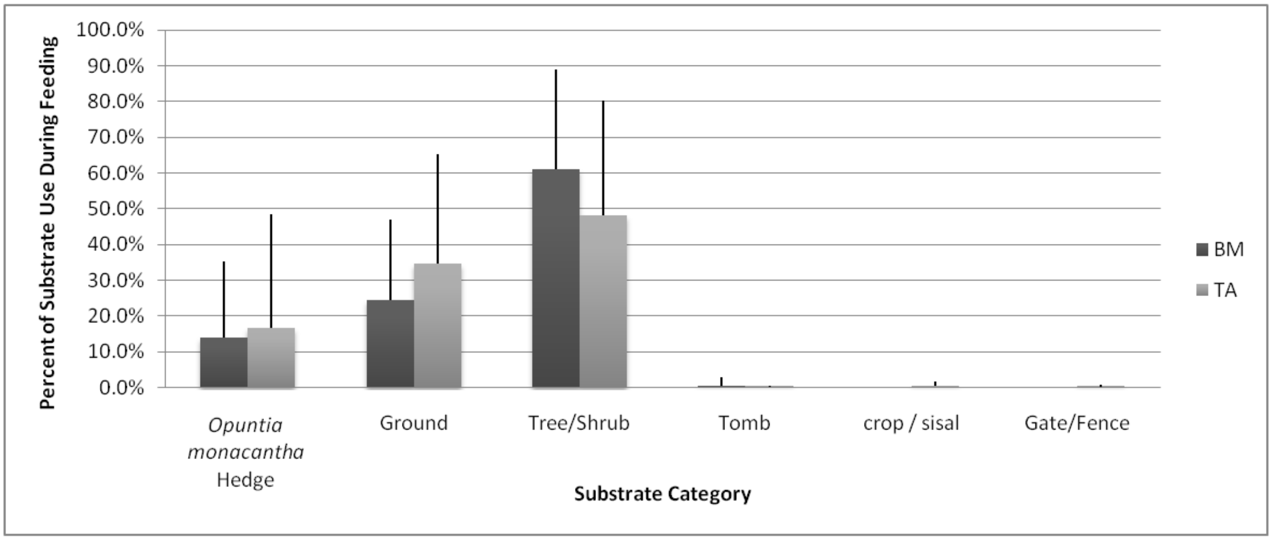


Fig. 3.13. Percent daily feeding activity troops spent in/on substrate type throughout the year. Error bars signify SD.

For both troops, a majority of travel time occurred on the ground (BM = 60.7%, TA = 62.1%). Almost all other travel activity was spent equally divided between the *Opuntia monacantha* hedges (BM = 19.4%; TA = 16.8%) and trees/shrubs (BM = 18.9%; TA = 18.3%). Tombs (BM = 1.0%; TA = 0.2%) and sisal (BM = 0%; TA = 2.2%) were the only other substrates that constituted over 1% of travel bout activity (**Fig. 3.14**).

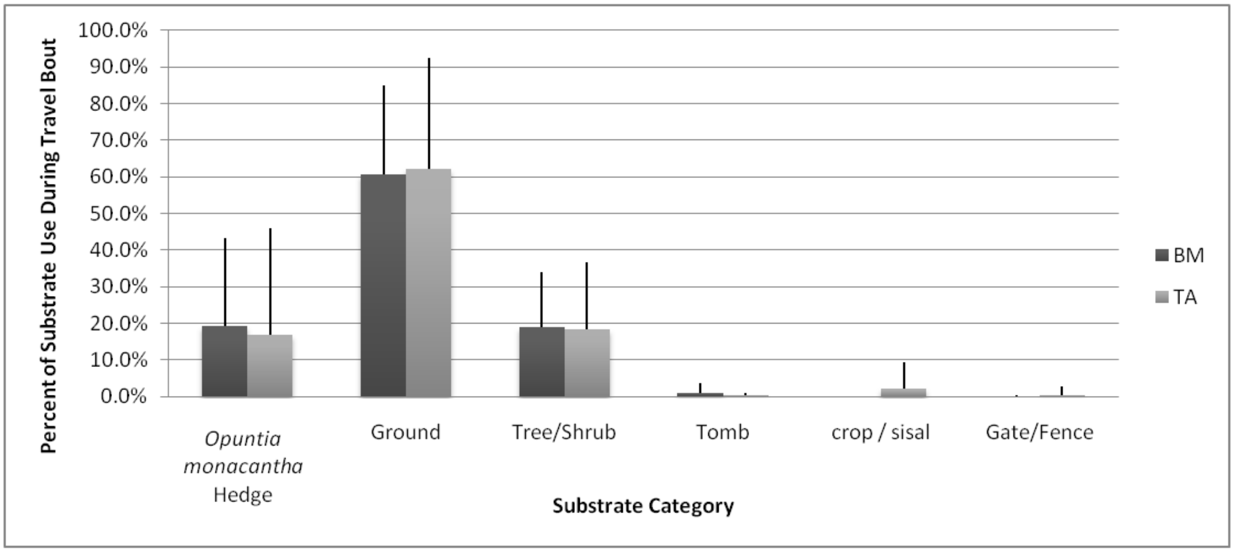


Fig. 3.14. Percent of time each troop spent in/on a substrate type during travel activity throughout the year.

Discussion Part 1: Ranging Patterns in Relation to Current Ranging Theory

The results of the home range analyses support the prediction that primate species in richer habitats have smaller home ranges than do their conspecifics that live in resource-stressed environments (**Table 3.1**). Yet as is evident through the more detailed analyses of this study, there appears to be little synchrony in ranging patterns between the two CSM troops despite the fact that 1) both troops use the same general substrates in their environment (**Fig. 3.9**) and that 2) both troops spend most of their feeding time on some of the same plant species (i.e., *Opuntia monacantha, O. stricta, Phylanthus amanu, Terminalia fatrae*) (**Fig. 3.6**).

Moreover, the results of ranging pattern analyses can vary depending upon whether one defines "ranging" as an area or a linear distance. For example, although the average home range areas of the CSM troops are much larger than that of their gallery forest conspecifics, the average day range distances of the Bevaro Moravato troop ($\overline{X}$ =1,097 m) and the Tsankalamanga troop ($\overline{X}$ = 726 m) are comparable to or smaller than the average day range distances of gallery forest troops; 1,000 -1,377 m (**Fig. 3.8.**; Jolly et al., 1993; Sussman, in press). This finding contradicts preliminary findings of *L. catta* ranging behavior in the scrub forest habitats that neighbor the gallery forest reserve of Berenty (Jolly and Pride, 1999).

The fruit of *Opuntia monacantha* was fed upon, albeit sometimes only to a very limited extent, by both troops throughout the year (**Table 3.3**). Similarly, there were only two months in which neither troop fed on the fruits of *O. stricta* at all, April and May. As discussed in chapter one, the fruits of *Opuntia* (specifically *O. monacantha*) are ripe and abundant enough for mass human consumption January through September. However, the Bevaro Moravato troop spent most of its time feeding on native fruit species until June, at the onset of the austral winter, and *O. monacantha* was only a top-quartile food for this troop in June despite the availability of the fruit in subsequent months (**Table 3.3; Fig. 3.6**). Similarly, since this troop resumed heavy consumption of native fruit in November, there appears to be a trend between the feeding on native fruit species and seasonality with this troop (**Fig. 3.6**). In contrast, *O. monacantha* was a major component of the Tsankalamanga troop's diet February through September (**Table 3.3**). Hence, while it appears that the Bevaro Moravato troop consumed *O. monacantha* fruits only when more favored native fruit species were not readily available; the feeding behavior of the Tsankalamanga troop seems to indicate that *O. monacantha* was a preferred fruit. Conversely, since native fruit was also a major component of the Tsankalamanga troop's diet November through May, there may be another reason why *Opuntia* was such a major component of the Tsankalamanga troop's diet throughout much of the year.

With the Tsankalamanga troop only, day range length was positively and significantly associated with feeding time (**Fig. 3.8.b**). However, the upper limit of this troop's day range length often fell below the average range (**Fig. 3.7**), and this troop spent very little time eating on days that they were largely sedentary (**Fig. 3.8.b**). Therefore, it is likely that these animals exercised a survival strategy in which the objective was to conserve energy within a safe environment during certain times of the year rather than risk travel excursions to seek native foods that may or may not have been available (see Pontzer and Kamilar, 2009). Thus when they did eat, they ate *Opuntia* (see also **Fig. 3.6.b**). It is noteworthy, however, that there was no association between day range length and resting time (**Fig. 3.8**). Therefore, although the Tsankalamanga troop ate very little on days when it was largely sedentary, this sedentary time was not necessarily spent resting. Instead, these animals spent time in social activities or sunning (**Fig. 3.8. b).** Finally, it is of note this sedentary strategy may have only been possible because there is an abundance of both *O. stricta* and *O. monacantha* fruit available near and within their sleeping hedges to sustain them.

Conversely, the widespread availability of *Opuntia stricta* specifically may have been the primary facilitator for the successful immigration of two males to the Bevaro Moravato troop. These two males, one of which was missing an eye, were first observed feeding on *O. stricta* in the CSM Reserve in October.[5]A week later, these same two males were observed within an *O. monacantha* hedge near the ANGAP campsite. By November 4th, they encountered the Bevaro Moravato troop, more than six km away from the ANGAP campsite. Based on these sightings, I suspect that these males relied on both *O. stricta* and *O. monacantha* for sustenance and shelter throughout their passage to Bevaro Moravato.

Moreover, I believe that the CSM reserve may be a potential dispersal route for *L.catta* from currently unidentified locations, but that travel within the reserve is inhibited by a lack of available food. The fruits of *Opuntia stricta* are an exception, and this fruit is the top food item consumed for both focal troops during the month of October. Thus, the seasonality of this fruit may be a major reason why *L. catta* have been observed within the reserve during the month of October. Alternatively, male *L. catta* studied elsewhere have been observed transferring to other troops during the months of October and November when females are lactating [reviewed in Pereira and Weiss (1991)]. Although male *L. catta* don't disperse exclusively during these months (Sussman, pers com), even at CSM (pers obs), the seasonality of *Opuntia stricta* coupled with this tendency may explain the timing of the migratory-like behavior.

In marked contrast to the Bevaro Moravato troop, the primary sleeping hedge of the Tsankalamanga troop (**Fig 3.1.b**) was only 200 m from another, equal sized troop. This troop was known as the *raketambazaha* troop because its primary sleeping hedge surrounded this cultivated variety of *Opuntia, O. ficus-indica* var. *inermis.* Despite the

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[5] I also believe that these males used this vegetation for shelter during this time as there are neither *Opuntia monacantha* hedges nor any other type of vegetation that can offer comparable shelter within the reserve (Rauh, 1995; Erdmann, 2003). Although I only observed *L. catta* use *O. monacantha* hedges for shelter during this study, I did observe *L. catta* within *O. stricta* thickets when the troop was not habituated and there were no alternative shelters nearby.

close proximity of the two troops, I only recorded three instances when the two troops were in visual contact with one another. Two of these dates were in January; the third date was mid-May. During these months, the troops have very different home range areas and day range size. However, I did occasionally hear vocalizations from the *raketambazaha* troop, and the troops may have communicated with one another more regularly through auditory and/or olfactory (see **Fig. 3.8.b**) cues. It is therefore difficult to ascertain the extent to which the close proximity of the *raketambazaha* troop influenced the ranging behavior of Tsankalamanga troop.

Finally, while it is also difficult to ascertain to what extent the threat of predation had on either troop's range use, it is notable that for the Tsankalamanga troop especially, very little of the troop's movement and travel behavior involved flight from a potentially threatening source. Since the Tsankalamanga troop's main sleeping hedge surrounded an abandoned field far from a village, the lemurs encountered relatively few villagers. It is notable, however, that there was also almost no fleeing behavior from raptors for this troop (see Sauther, 1989; Sauther, 2002). For the Bevaro Moravato troop, the two seemingly greatest threats were humans and the sifaka. Yet with the sifaka, fleeing may have been instigated by irritation rather than by fear. For although at times interaction between troop members and the sifaka seemed agonistic, a juvenile troop member was once observed pulling the tail of the sifaka to initiate play. Similarly, the sifaka was once observed sleeping close to a juvenile and infant *L. catta*, who were sleeping in a huddle on the ground. Finally, regardless of the perceived threat of the sifaka, it was the troop that traveled to the sifaka's territory. Thus, predation threat did not appear to have a major influence on range use for either troop. The actual threat of predators to CSM *L. catta* will be further discussed in the following two chapters.

Discussion Part 2: Comparisons in Substrate Use and Terrestriality

In general, CSM *L. catta* spent on average about one-third of their daily activity time on the ground **(Fig. 3.9.)**. This finding is comparable to that which has been found among troops of gallery forest *L. catta* (Sussman, 1977; Sauther, 2002; Sussman, in press). Moreover, monthly analyses of substrate use indicate that CSM *L. catta* were actually less inclined than their gallery forest conspecifics to use the ground as a primary substrate during certain times of the year (**Fig. 3.10**; see Sauther, 2002). This is of interest as most of troops' habitats were comprised of open scrub forest and fields (**Fig. 3.4**), and neither troop appeared to be especially alert when they used the ground as a substrate. This likely reflects that vigilance occurred within the safety of hedges, trees and shrubs and that travel only occurred after the area was perceived to be safe. Indeed, hedges were the substrate of choice during some months, especially among members of the Tsankalamanga troop (**Fig. 3.11**). The only exception was the month of October, which is also the only month when this troop consumed a considerable amount of *Opuntia stricta* (**Table 3.3**). In addition, the day range was relatively larger that month (**Fig. 3.7.b)** even though home range and core areas were relatively smaller that month (**Fig. 3.5**). Since *O. stricta* is dispersed but abundant in the environment, this increase in ground use and day range but decrease in home range and core areas may be partly explained by this shift in diet to *O. stricta*. Notably, this is also the month when both adult females in the Tsankalamanga troop had new infants.

Conversely, the month of June was the only month in which the Bevaro Moravato troop spent more than one third of its daily activity time on the ground, and this is the only month in which the troop's top-quartile food was the hedge fruit, *Opuntia monacantha*. In this case, the troop's increase in ground use was likely a direct reflection of the villagers' behavior. During the austral winter months, June through September, the local Antandroy fed upon large quantities of this fruit while working in the fields that are encompassed by the lemurs' sleeping hedges. During the month of June alone, 57.4% of the Bevaro Moravato troop's consumption of this fruit was of the scraps left on the ground by the local villagers. The Tsankalamanga troop also fed upon the scraps of *O. monacantha* when they were available. However, because this troop's primary sleeping hedge surrounds an abandoned field, this troop did not have as much access to the *O. monacantha* scraps (when they weren't inadvertently provided by my guides).

Chapter Summary

- The home ranges of the CSM troops were in general much larger than those of gallery forest *L. catta*. However, home range area for the Tsankalamanga troop was exceptionally small during the austral winter months relative to all other recorded home range areas for *L. catta*.
- While the mean day range of the Bevaro Moravato troop is similar to the day range average of gallery forest troops, the mean day range of the Tsankalamanga troop is smaller, especially through the months of May through August. Moreover, while day range length for the Tsankalamanga troop positively correlated with feeding time, social activity negatively correlated, and ranging distance had no significant effect on resting time. In contrast, daily activities of the Bevaro Moravato troop were in general

not associated with day range length. Thus, while the results from day range data are consistent with findings that species in general do not have fixed energy budgets (Pontzer and Kamilar, 2009; Pontzer, pers comm), it appears that CSM *L. catta* may at times reduce ranging activity as a strategy to cope with periods of food scarcity. Furthermore, the lack of association between feeding time and day range length with the Bevaro Moravato troop likely reflects the fact that this troop never suffered from the extreme food scarcity as did its more inland neighbors.

- Sacred forests were consistent components of the Bevaro Moravato troop's monthly core range. Similarly, sacred forests were almost always a feeding site for a top-ranked food. Yet the evident disassociation between feeding behavior and travel pattern with this troop indicates that the troop's habitual use of sacred forest habitat likely fulfilled other essential functions such as shade and relative distance from human activity[6]. Conversely, core areas of the Tsankalamanga troop did not consist primarily of top-quartile food species. Moreover, sacred forests weren't even a component of this troop's home range during some months of the year**.** The relationship between sacred forests and the behavioral ecology of CSM *L. catta* will be further investigated in chapters five through seven.
- CSM *L. catta* spent either equal or less time on the ground throughout the year than their gallery forest conspecifics despite the fact that CSM *L. catta* live in more open habitat. In fact, ground use was largely restricted to travel. However, individuals did not appear to be especially fearful when traveling. This likely reflects that vigilance

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[6] Since sacred forests are a place of reverence for the Antandroy and activity within these sites are restricted, it is tempting to also suggest that sacred forests offered a place of refuge from human harassment and predation. However, the most aggressive incident I witnessed from humans towards the focal troop occurred within a sacred forest before they observed my presence.

occurred within the safety of hedges. Moreover, since humans appeared to be the biggest threat to the CSM *L. catta*, it is likely that the lemurs were rarely wrong in their assessments of whether there was human presence because indicators of human activity in the area (e.g., working in the fields, herding zebu, singing and talking) were rarely subtle.

- A fundamental similarity among the CSM *L. catta* was the extensive and consistent use of the cactus hedges for shelter. The use of the cultivated cactus hedges as a primary substrate has never before been recorded in *L. catta* studies and is a very rare behavior among Primates; probably because terrestrial cacti are all from the New World, while terrestrial monkeys and prosimians inhabit Africa and Asia. However, although other primate taxa such as *Loris tardigradus lydekkarianus* use introduced cacti, mainly *Opuntia elata*, as sleeping sites (Nekaris, 2000), while other primate species such as *Papio anubis* are becoming especially reliant on *Opuntia stricta* for sustenance during periods of drought (Strum, pers comm); the extent to which the CSM *L. catta* are reliant on cactus hedges appears to be unique.
- It is likely that the extended ranging distance of two males in October was to seek social/mating opportunity, and that this is the reason why *L. catta* have in the past been observed within the CSM Reserve during this month**.** Moreover, the dispersion of *Opuntia,* most notably *O. stricta,* appears to have facilitated this migration, especially through the otherwise largely inhospitable coastal landscape.
- Similarly, while there has long been documentation that *L. catta* eat *Opuntia* (e.g., Shaw, 1879; Elliot, 1913), the CSM *L. catta* appear to rely upon the cactus fruits as their principal food during certain months. In fact, the primary consumption of

Opuntia by both troops over many months of the year, especially during the austral winter months, is comparable to the gallery forest lemurs' reliance on *Tamarindus* fruit (see Sauther, 1992). The question of whether *L. catta* occurs in the CSM region only because of the large population of *O. stricta* that have been established there will be addressed in the summary chapter, chapter seven.

- The Tsankalamanga troop fed most heavily on the species that is an important resource to the local Antandroy population, the fruits of the cultivated, hedge-forming *Opuntia monacantha*. However, the Bevaro Moravato troop fed most heavily on the invasive and very widespread *O. stricta*, which is believed by the Antandroy to kill livestock, degrade the landscape, and poison the local fauna. In fact, the chief of Bevaro Moravato was extremely fearful the first time he observed a ring-tail lemur feeding on a fruit of this variety, and he tried to stop it from continuing. Finally, although the *raketambazaha* troop was not a focal troop, it is likely that this troop fed heavily on the cultivated *O. ficus-indica* var. *inermis,* which grows only in fields and is surrounded by hedges of spiny variants of cultivated *O. monacantha*. The question of whether there are significant nutritional differences between *O. monacantha* and *O. stricta* will be discussed in chapter five. However, the choice between the two *Opuntia* species may also affect intraspecific social behavior. Social organization and feeding competition are the primary topics of the next chapter.

CHAPTER 4

Flexibility and Context of Social Organization

My goal in this chapter is to shed light on the question of whether previously observed social behaviors of *Lemur catta* are largely fixed in the makeup of the species, largely affected by environmental richness and seasonality, or whether assumed species-typical behaviors are in fact affected by social factors such as intense intratroop familiarity and a near absence of intertroop contact. To accomplish this goal, I will (1) compare the social organization of Cap Sainte-Marie *L. catta* to the behaviors described as typical through gallery forest and semi-captive studies, (2) test for relationships between patterns in agonism and feeding context, (3) test for changes in dyadic bond strength within CSM troops through social cohesion patterns, and (4) examine adult to immature relationships in the contexts of alloparenting, male care and infanticide.

Background

In its social organization, *L. catta* is unique among the living Primates in three important respects. First, *L. catta* is female dominant and resides in multimale-multifemale groups much like several species of *Eulemur* (Ossi and Kamilar, 2006). The species has several characteristics that are reminiscent of terrestrial anthropoid primates (Kappeler, 1990; see Chapter Two). Second, in contrast to the cross-sex pair-bonded tendencies of other Lemuridae, *L. catta* troop members most typically bond with their own sex (Jolly, 1998). Third, although females are the philopatric sex (Sussman, 1992; Erhart and Overdorff, 2008), close affiliative relationships among female troop members often don’t extend beyond a dyad; and dominance hierarchies of both sexes are neither necessarily linear nor inherited (Taylor and Sussman, 1985; Nakamichi and Koyama, 1997; Jolly, 1998; but see Takahata et al., 2005; Gemmill and Gould, 2008). Some of these characteristics, such as female dominance, appear to be a fixed social behavior in *L. catta (*Jolly, 1966; Kappeler, 1990; see Sauther, 1992; Pereira and Kappeler, 1997). Other characteristics however, appear to be more plastic. This chapter is about the flexibility of social organization in *L. catta*.

One known flexible behavioral characteristic in *L. catta* is the extent to which males and females form partnerships, which is easily identifiable in this species in that dyads are either markedly affliative with one another or markedly adversarial (Pereira and Kappeler, 1997; Jolly, 1998)[1]. For example, researchers studying *L. catta* at Berenty have found that there is variation in whether only one male or multiple males will associate closely with female troop members (Nakamichi and Koyama, 1997). In this example, both the social structure and the environment of the two Berenty troops are nearly identical. In fact, other studies on male-female partnerships have failed to find clear proximate mechanisms that explain variation of this characteristic (see Gould, 1996). Yet male-female partnership is often associated with the characteristic of male parental care (see Palombit, 1999), a characteristic that is believed to be largely absent within *L. catta* as a species and is in contrast to the behavior of the often sympatric *Propithecus verreauxi* (Jolly, 1966; Gould, 1994). In fact, *L. catta* males have been characterized as being only “occasionally affiliative” in that they have been observed playing and grooming infants from time to time (Whitten, 1987; Gould, 1994). However, males are the least likely to alloparent while females without infants are the most likely to alloparent (Gould, 1994).

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[1] These partnerships differ from baboon “friendships” in that they do not necessarily function as a means of protection from other group members (Jolly, 1998; also see Smuts, 1989). In addition, unlike “friendships”, these partnerships are often composed of a mother and an adult female daughter.

Another characteristic that has been described to typify *L. catta* is the higher rate of intraspecific agonistic behavior this species has towards conspecifics in the wild relative to other lemuroid species (Erhart and Overdorff, 2008). This appears to hold true even when accounting for absolute percentages of social behavior, although the amount of agonism observed is rarely over 1.0% of all social activity (see Sussman et al., 2005, Table 1; Sussman and Garber, 2007, Table 39.1). Female *L. catta* are responsible for a majority of this agonism as females not only direct agonistic behavior towards males significantly more often than the reverse (Sauther and Sussman, 1993, Table 2), but females also tend to repeatedly target other female troop members (Pereira and Kappeler, 1997; Jolly, 1998). In fact, female to male agonism represents only a minority of intratroop agonistic interactions, and male to female directed agonism is extremely rare (Kappeler, 1990).

Feeding is a primary context in which directional agonistic behavior among female *L. catta* occurs (Sauther and Sussman, 1993; also see Kappeler, 1990; but see Sussman and Richard, 1974). Known as contest competition in the primate literature, feeding aggression between females is expected to peak when food resources, mainly fruit and flower species, are clumped in space, highly nutritious, and generally scarce in the environment (Wrangham, 1980; Isbell, 1991; Pruetz, 2009). Recent studies also account for the temporal availability of a resource, the ephemeral presence of flowers for example (see Pruetz, 2009). While Wrangham's (1980) model is based on the premise that primates live in groups to defend food resources from other groups, van Schaik (1983) hypothesizes that there are no advantages to group feeding and the primary function of groups to is minimize predation pressure (see also Isbell, 1991; Sauther, 1992). Specific to *L. catta*, results have been mixed. Sauther (1992) found that lactating and pregnant females used a scramble competition strategy to minimize intragroup competition, i.e., these females (1) fed on (young) leaves, (2) fed alone relative to other troop members or (3) fed next to a lower ranking individual. In contrast, Gemmill and Gould (2008) did not find a correlation between resource availability and agonism, but they did find that female to female aggression correlated with food size. In other words, when females fed on food items that in general took longer to consume, they were more vulnerable to having these food items aggressively taken from them by other female troop members. Last, although Sbeglia et al. (2010) did note that the highest mean rates of agonism took place in the context of provisioned food for one group of semi-free ranging *L. catta*, they found no statistical relationship between changes in rates of agonism within focal groups and food presence.

Another predictor of agonistic frequencies among *L. catta* dyads is phases of the mating cycle. Repeated female to female targeted aggression appears to peak during the premating (the three months prior to mating) and birthing seasons (Pereira and Kappeler, 1997), while male to male agonism is highest during the mating season (Gould, 1997; also see Taylor and Sussman, 1985). Conversely, as noted above, Sauther (1992) found that feeding competition in general is low during the lactation period because new mothers change their feeding behavior during that time.

A final form of dyadic agonism that has been observed among *L. catta* is adult to infant directed agonsim (e.g., Pereira and Weiss, 1991; Hood, 1994; Hood and Jolly, 1995; Jolly, 1998). Since adult to infant agonism sometimes leads to death of the infant, this behavior has been described by some as infanticide (Pereira and Weiss, 1991; Hood, 1994; van Schaik and Kappeler, 1997; Palombit, 1999). However, the observed infant killings by adult *L. catta* do not follow the definition of infanticide as defined as "the systematic hunting down and killing of a suckling infant, almost always by an adult male" (Jolly, 2007: 244; see Sussman, 1992; see also Hood, 1994 for a dissenting view). Moreover, the hypothesized advantage of infanticidal behavior, to have a mother return to the mating condition sooner so as to breed with the killer (Hood, 1994; Jolly, 2007; see also Hrdy, 1977), can only be speculated as applicable in a species that is a strict seasonal breeder (see Pereira and Weiss, 1991). Jolly (1998; also see Hood and Jolly, 1995) describes adult to infant killings as "behaviorally imposed mortality (from Dittus, 1979)," as Jolly has observed that most socially caused infant deaths are the result of two common behaviors of the species: (1) the tendency for troop members to approach vocalizing infants, and (2) adult female to female agonism. In other words, most observations of adult to infant agonism have been observed primarily as by-products during periods of intertroop conflict among adult troop members and secondarily through intratroop female to female targeted aggression (Hood, 1994; Hood and Jolly, 1995; Jolly, 1998).

Methods

To compare the social organization of CSM *L. catta* to the behaviors deemed typical through gallery and semi-captive studies, I have conducted activity budget analyses and have calculated rates of affiliative and agonistic behaviors. I have also sorted agonistic behaviors by category (i.e., active vs. passive, low intensity vs. high intensity) (Sbeglia et al., 2010), to test for associations between types of agonism and sex or age class of recipients. These tests were conducted using chi-square tests. To mitigate the problem of autocorrelation, I have conducted these tests on only a percentage of randomly selected data (Rasmussen, 2010). These data were resampled 1,000 times.

For feeding behaviors, I first compared monthly top quartile food consumption with feeding cohesion patterns. Definitions of feeding cohesion are per Sauther (1992, 2002). A troop member was categorized as group feeding if it fed within 3 m of at least one other individual. Conversely, a troop member was categorized as a solitary feeder if it was observed feeding 8m or further away from any other troop member[2]. Second, I conducted Spearman rank-order correlations to test for associations between feeding agonism and feeding, and between feeding agonism and overall levels of daily agonism.

To obtain social dyad information, I calculated half-weight association indices (Lehner, 1996). Social bonds with infants were only analyzed from January through July, after the infants were first observed moving largely independently from their mothers. Social bonds with the immigrant males in the Bevaro Moravato troop were only analyzed from the months of May through July, after the males were integrated troop members[3]. Similar types of analyses were conducted with the Tsanakalamanga troop to account for any biases caused by death and migration (see chapter five). I also calculated half-weight association indices to demarcate changes in dyadic pairings during the birth season. I used the same relative bond strength scales for the seasonal comparisons as I did for the yearly comparisons, which is described in detail later in the chapter. Last, I used 15 minute scan sampling data to obtain information on the kinds of interactions other troop

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[2] Since an individual may be categorized as group feeding even if it was only feeding near one other troop member, I acknowledge that the following results may give an appearance of more feeding cohesion than was actually the case. Therefore, group feeding in this section is not synonymous with feeding cohesion. Moreover, this methodology does not account for the possibility that an individual was selective in whom it chose to feed next to in various feeding contexts.

[3] I have defined integration as the first time an immigrant male is observed social grooming with another troop member.

members had when within 1m of mothers during this period (i.e., social grooming, huddling, or incidental [e.g., selfgroom, feed, sun, rest, move]).

Results

Activity budgets

The CSM troops spent the same percentage of time moving and traveling per year (21.1% vs. 21.4%). However, the activity budgets of the two troops differed somewhat in the percent of time the troop members spent resting, sunning and feeding. While the Bevaro Moravato troop spent more of its time feeding (13% vs. 9.2%) and sunning (5.4% vs. 3.9%), the Tsankalamanga troop spent more of its time resting/sleeping (35.8% vs. 30.3%) (**Fig. 4.1**).

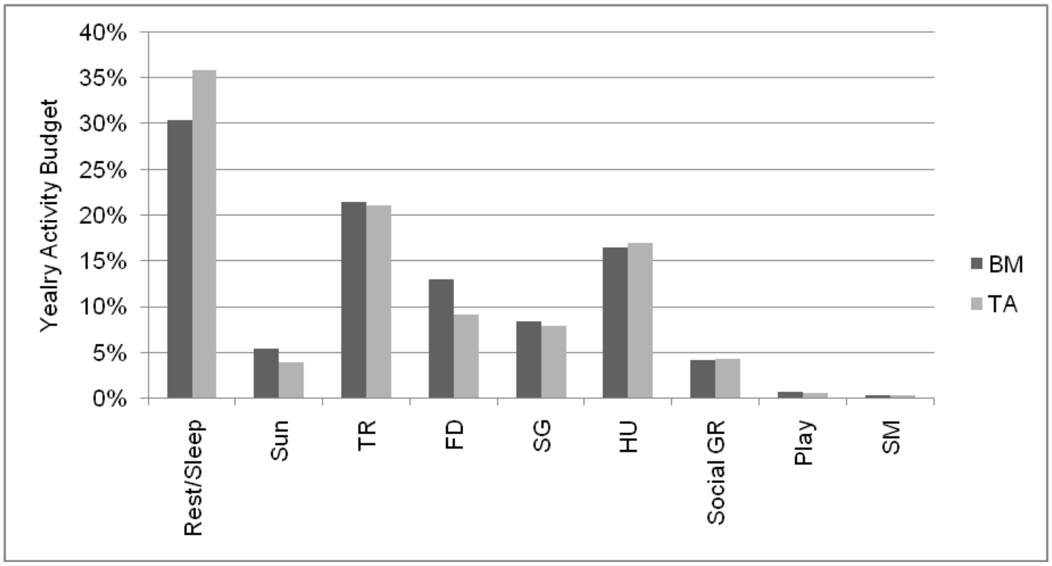

Fig. 4.1. Activity budgets of the two CSM troops. Rest/sleep includes all solitary resting and sleeping behavior, Sun is solitary sunning, TR includes all movement behaviors, FD is feeding, SG is self grooming, HU includes passive huddling, self grooming in huddles, and sunning in huddles, Social GR includes both directional and mutual grooming, Play is play, and SM is scent marking.

The study troops were also similar in the percentage of time they spent in affiliative active social behaviors, i.e., mutual and directional grooming (4.1% vs. 4.3%) and play (0.6% vs. 0.7%). In total, active social behaviors comprised 4.8% of the total activity budget for the Bevaro Moravato troop and 4.9% of the total activity budget for the Tsankalamanga troop. Finally, passive social behaviors, i.e., huddling and scent marking, comprised (16.5% vs. 17.0%) and (0.3% vs. 0.3%) respectively of the total activity budgets of the two troops.

Play behavior was almost exclusively an activity for immatures (juveniles and infants) (**Fig. 4.2**). In both troops, all possible dyads of immatures played with one another. With very few exceptions, when adults did engage in play, it was the resident adult males who played with the young troop members (B1, R9, WS, B7) (**Fig. 4.3**).

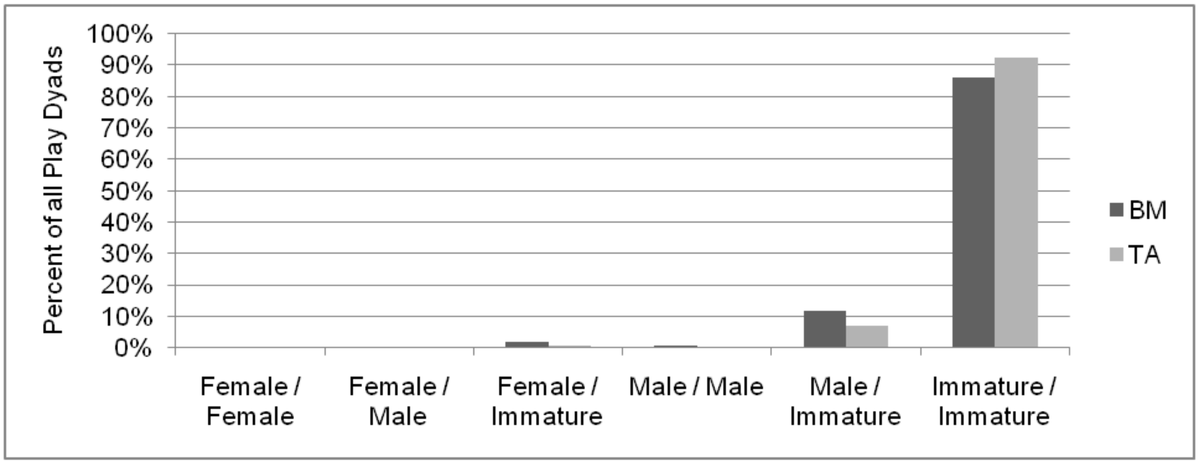

Fig. 4.2. Play behavior percentages of both CSM troops analyzed by sex/age class. BM = Bevaro Moravato troop, TA = Tsankalamanaga troop.

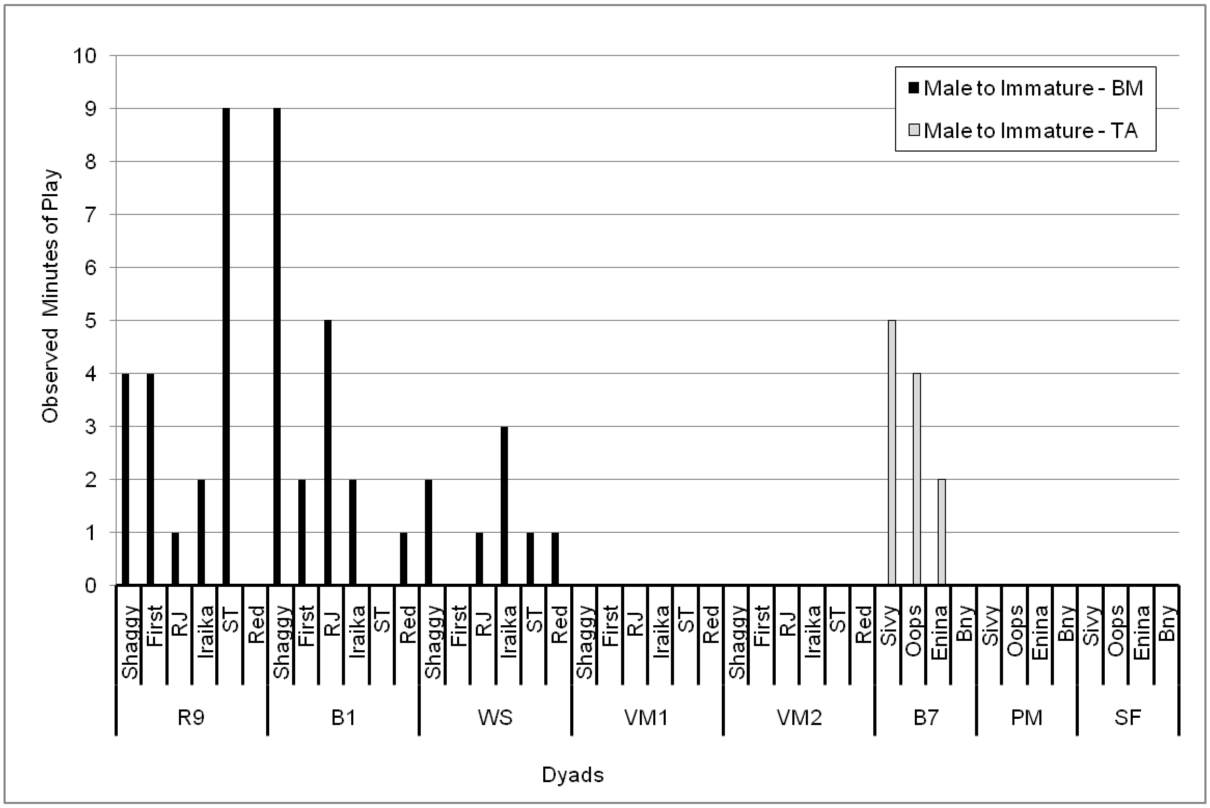

Fig. 4.3. Play dyads in the Bevaro Moravato and Tsankalamanga troops. BM = Bevaro Moravato, TA = Tsankalamanga. Vertical lines demarcate male to immature play dyads.

Immatures also most commonly engaged in social grooming. Immature/female social grooming was the highest category in both troops (**Fig. 4.4**). Male/immature grooming was the second highest category in the Bevaro Moravato troop, while male/female and immature/immature grooming occurred the most frequently in the Tsankalamanga troop. In both troops, male/male grooming and female/female grooming occurred the least frequently.

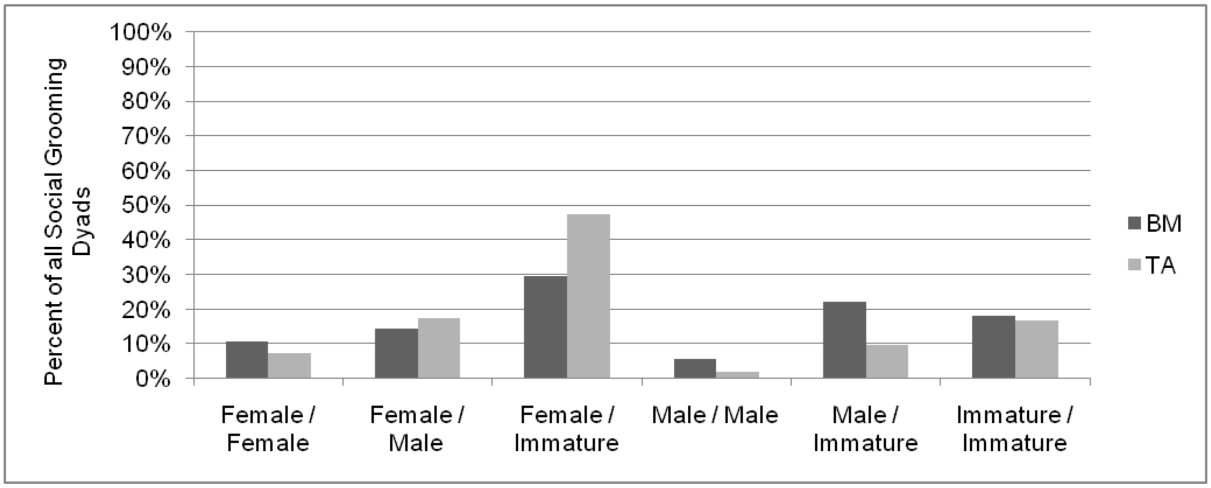

Fig. 4.4. Social grooming percentages of both CSM troops analyzed by sex/age class. BM = Bevaro Moravato troop, TA = Tsankalamanaga troop.

Male/immature social grooming dyads loosely paralleled male/immature playing dyads, although there were a few exceptions. The most notable exception was the grooming dyad SF and Enina in the Tsankalamanga troop (**Fig. 4.5**).

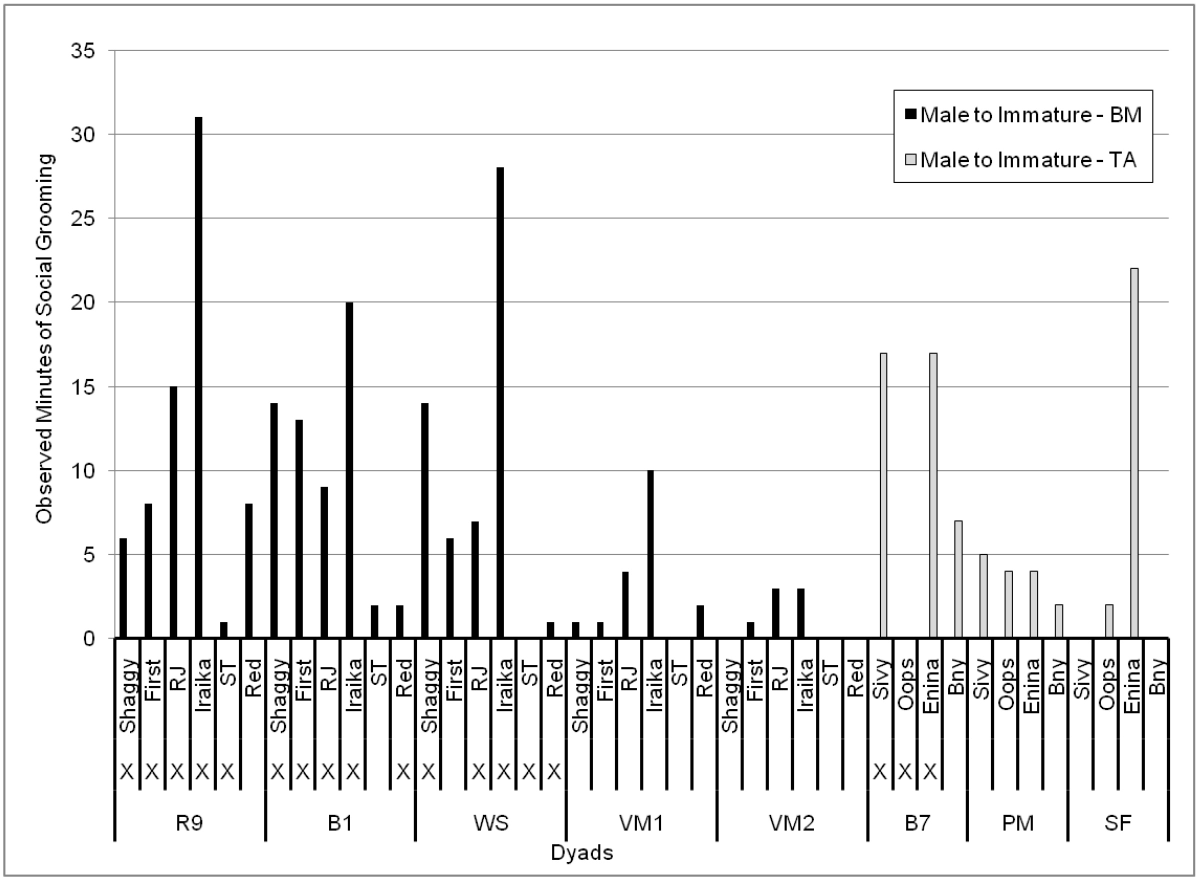

Fig. 4.5. Adult male to immature social grooming dyads in the Bevaro Moravato and Tsankalamanga troops. BM = Bevaro Moravato, TA = Tsankalamanga. Vertical axis is number of observed minutes of social grooming throughout the year. X indicates observed play dyads (see **Fig. 4.2**).

Agonistic measurements

In the Bevaro Moravato troop, I observed 428 counts of agonistic behaviors during 33,998 minutes of behavioral observation (1.26%). A little over half of this agonism was in the form of displacements (52.3%), a form of low-intensity agonism (Sbeglia et al., 2010; **Fig. 4.6**). Chatter Squeals, vocalizations that did not result in any escalated physical behaviors, composed 20.8% (n = 89) of all observed agonism[4]. Non-biting physical contact, which included cuffs, slaps, pushes, lunges, tail-pulling, pounces, hits, grabs and ear boxing, was the third most frequent agonistic behavior at 14.0% (n =

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[4] Sbeglia et al. 2010 categorize both displacements and chattersqueals as forms of low-intensity agonism. All other forms of agonism described in this paper are categorized by Sbeglia et al. as high intensity.

60). Bites/nips were the most potentially damaging form of agonism observed among the CSM troops; and comprised 2.6% (n = 11) of all agonistic activity in the Bevaro Moravato troop. However, no bites or any other form of agonism resulted in visible lacerations. In sum, most agonism in the Bevaro Moravato troop was nonphysical (i.e., chatter squeals, displacements, tail wagging and chases) (83.4%).

In the Tsankalamanga troop, I observed a total of 147 counts of agonistic behaviors during 19,238 minutes of behavioral observation, a little over half of what I observed within the Bevaro Moravato troop (0.76%). Similar to the Bevaro Moravato troop, most of these behaviors were displacements (49.0%, n = 72). However, non-biting physical agonism occurred the second most often (23.13%, n = 34) while bites/nips were only observed twice. As with the Bevaro Moravato troop, neither of these bites caused visible wounding.

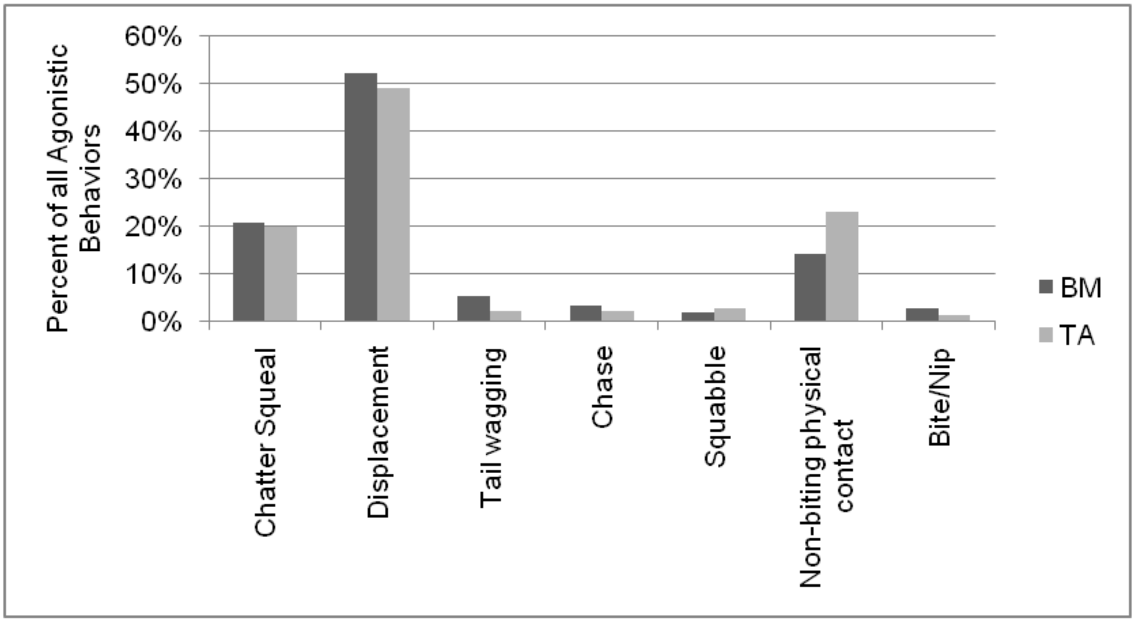

Fig. 4.6. Breakdown of agonistic behaviors. BM = Bevaro Moravato, TA = Tsankalamanga.

Broad categories of social behaviors were also analyzed by rates per hour. When measured in this way, the Bevaro Moravato troop engaged in all categories of social behaviors more frequently than the Tsankalamanga troop except in passive social behaviors (**Table 4.1**). The greatest difference between the two troops was in low intensity agonsim. The Bevaro Moravato troop engaged in this kind of behavior 42% more often did the Tsankalamanga troop.

Table 4.1. Affiliative and agonistic social behaviors analyzed by average rates per hour. Passive affiliative behaviors are huddling and scent marking. Active affiliative behaviors are play and social grooming. Low intensity agonism is comprised of chattersqueals and displacements. High intensity agonism includes bite/nips, chases, non-biting physical contact, squabbles, and tailwagging (as per Sbeglia et al., 2010). BM is the Bevaro Moravato troop. TA is the Tsankalamanga troop.

	Passive Affiliative Behavior	**Active Affiliative Behavior**	**Low Intensity Agonism**	**High Intensity Agonism**
BM	10.04	5.40	0.55	0.20
TA	11.26	4.27	0.32	0.14

There were 279 identified cases of adult to adult directed agonism in the Bevaro Moravato troop. These cases were not necessarily independent events. If an adult displaced two other adults in a single displacement, this single event was counted twice so as to account for the sex of both individuals. In general, adult to adult directed agonism in the Bevaro Moravato troop was lowest in September, at the start of the birth season (**Fig. 4.7**). However, this form of agonism declined precipitously the following month. Female to male directed agonism, occurred in April, at the end of the premating season/start of the mating season. Male to male directed agonism peaked slighter thereafter. No male to male agonism was observed four of the 12 months, and none of these months were concurrent. Female to female directed agonism was lowest in September, the month when the first infant was born. The month with the highest female to female directed agonism was January.

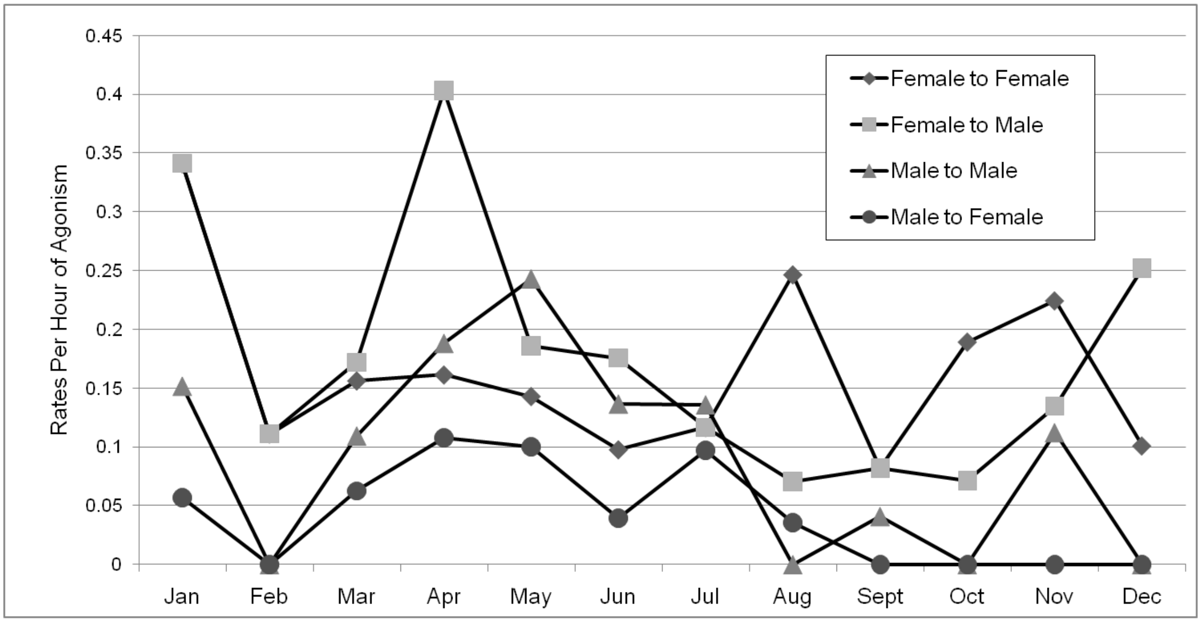

Fig. 4.7. Rates per hour of adult to adult directed agonism in the Bevaro Moravato troop relative to total behavioral data recorded each month.

In the Tsankalamanga troop, all adult directed agonism was low (a total of 49 cases); no month exceeded 0.24 bouts of agonism per hour (**Fig. 4.7**). By far the most frequent form of adult directed agonism was female to male (n = 32). As with the Bevaro Moravato troop, this form of agonism peaked during the end of the premating season. Similarly, male to male agonism (n = 11) peaked during the mating season. Female to female directed agonism was only observed in three months of the study, and the peak of this agonism, which occurred in May, was only .06% of all monthly activity. Last, no adult agonism was observed for two of the months, and these months were nonconsecutive.

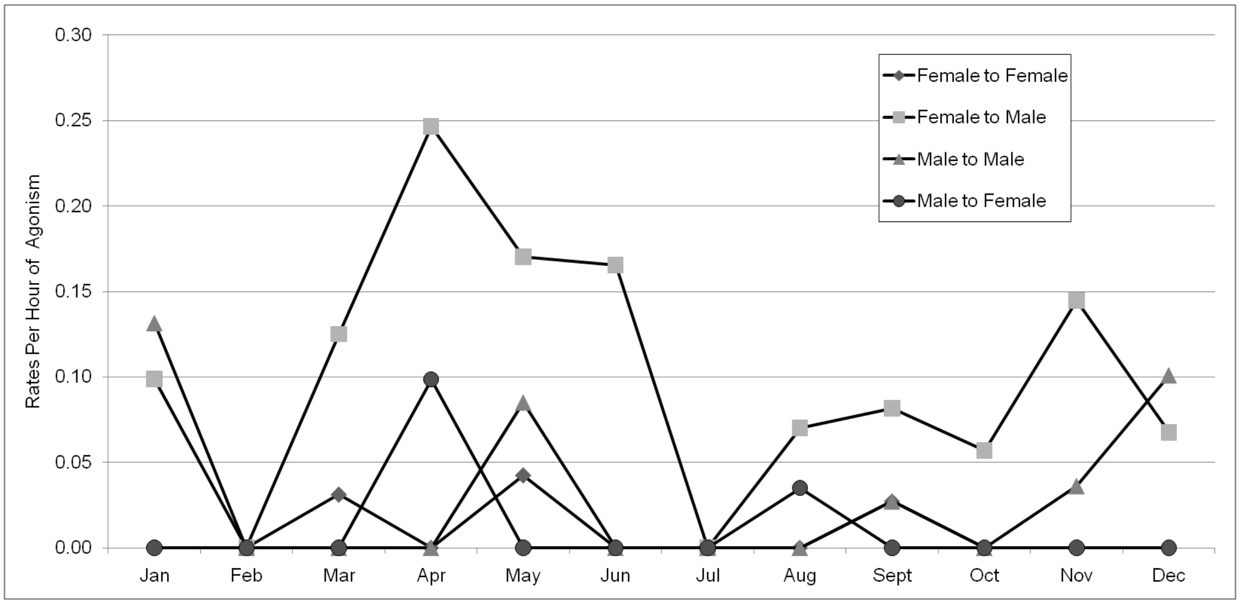

Fig. 4.8. Rates per hour of adult to adult directed agonism in the Tsankalamanga troop relative to total behavioral data recorded each month.

In both troops, females were responsible for a majority of the agonism (**Table 4.2, Table 4.3**). This was especially the case in the Tsankalamanga troop. Also, although nonphysical agonism was the dominant type of agonism received by both age classes (**Fig. 4.9; Fig. 4.10**), adults were the primary recipients of displacements and immatures received the highest proportion of physical contact aggression. In fact, chi-square tests showed there was a significant association between the types of agonism directed by females and the age class of the individuals (BM: $X^2 = 24.330$, d.f. 1, $p < .001$, $n = 273$; TA: $X^2 = 5.096$, d.f. 1, $p < .05$, $n = 88$). However, the significant results with the Tsankalamanga troop may have been a Type I error due to autocorellation (Rasmussen, 2010). For while the results of this test remained robust with the Bevaro Moravato troop when 40%[5] of the cases were randomly selected and the test was simulated 1000 times ($X^2 = 13.545$, d.f. 1, $p < .001$, $n = 120$), this was not the case with the Tsankalamanga

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[5] 40% was the minimum amount that could be selected in order for there to be an expected count of 5 or more for all cells of the chi-square test.

troop when 55% of the cases were randomly selected and then bootstrapped 1000 times ($X^2 = 2.535$, d.f. 1, $p = .111$, $n = 48$).

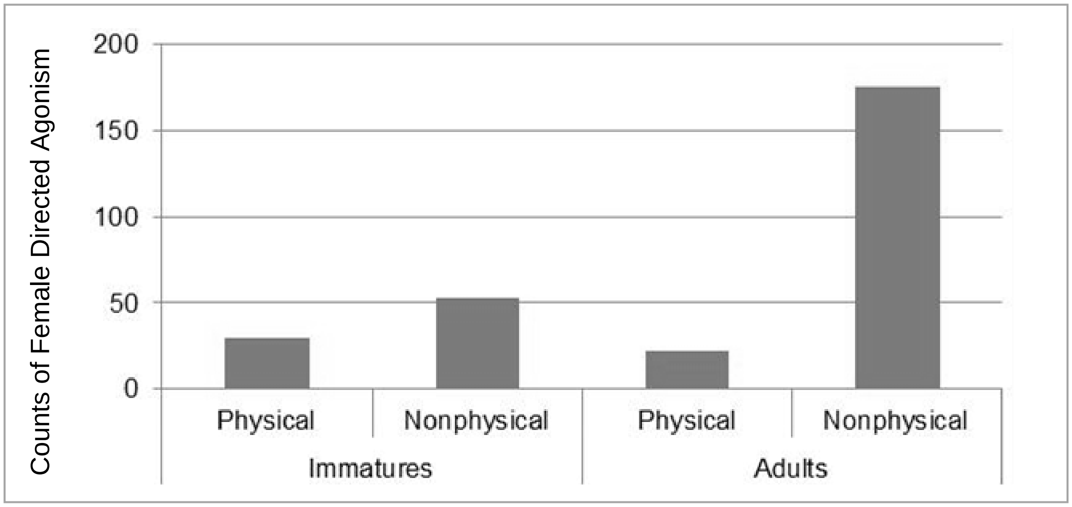


Fig. 4.9. Counts of female directed agonism sorted by age class and type of aggression in the Bevaro Moravato troop throughout the year. Physical aggression refers to all contact aggression (cuffs, hits, pushes, nips). Nonphysical aggression refers to all other types of agonism (e.g., displacements, chatter squeals, chases).

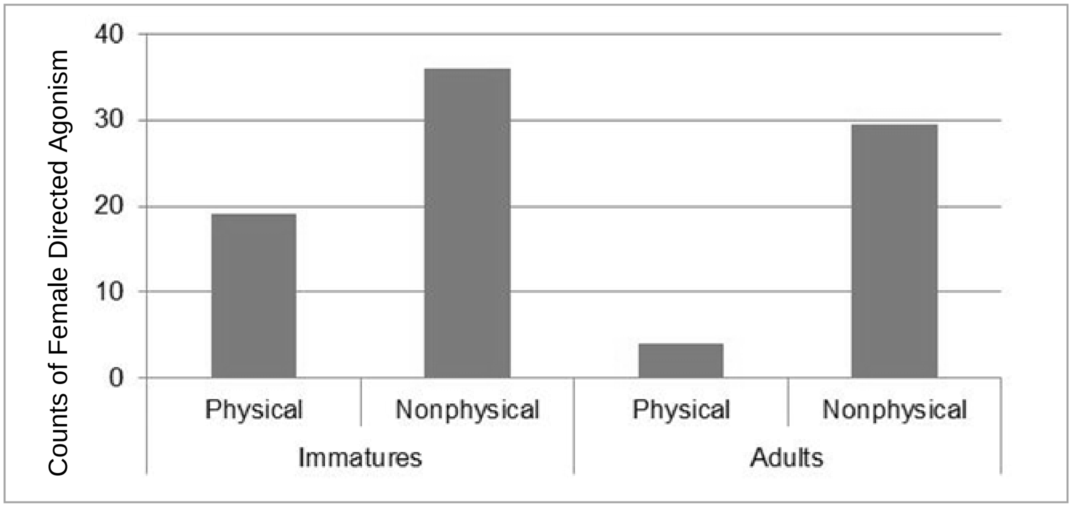


Fig. 4.10. Counts of female directed agonism sorted by age class and type of aggression in the Tsankalamanga troop throughout the year. Physical aggression refers to all contact aggression (cuffs, hits, pushes, nips). Nonphysical aggression refers to all other types of agonism (e.g., displacements, chatter squeals, chases).

Table 4.2. Breakdown of identifiable directional cases of agonism by sex/age class within the Bevaro Moravato troop from August 2007 through July 2008. Low intensity and high intensity agonism are per Sbeglia et al., 2010. n = 439.

Bevaro Moravato Troop	**Low Intensity**	**High Intensity**
female -> male	16.6%	6.4%
female -> female	18.2%	2.7%
female -> immature	11.6%	6.6%
male -> male	10.5%	3.2%
male -> female	4.6%	1.4%
male -> immature	2.5%	1.6%
immature -> male	3.4%	2.3%
immature -> female	1.4%	0.7%
immature -> immature	2.7%	3.6%
	71.5%	**28.5%**

Table 4.3. Breakdown of identifiable directional cases of agonism by sex/age class within the Tsankalamanga troop from August 2007 through July 2008. Low intensity and high intensity agonism are per Sbeglia et al., 2010. n = 134.

Tsankalamanga Troop	**Low Intensity**	**High Intensity**
female -> male	19.4%	4.5%
female -> female	1.5%	0.7%
female -> immature	26.1%	13.4%
male -> male	6.7%	1.5%
male -> female	2.2%	0.0%
male -> immature	3.0%	0.0%
immature -> male	1.5%	3.0%
immature -> female	1.5%	0.0%
immature -> immature	6.7%	8.2%
	68.7%	**31.3%**

Feeding Behaviors

Top quartile foods

In both CSM troops, fruit was a top-quartile food item every month of the year (**Table 4.4**). The largest fruits consumed by the troops were that of *Opuntia monacantha* and *O. stricta*. In the Bevaro Moravato troop, *O. monacantha* was the top-quartile food in June, and *O. stricta* was the/a top-quartile food throughout the austral winter months of July through October. In the Tsankalamanga troop, *O. monacantha* and *O. stricta* were the/a top-quartile food for all months except June and the austral summer months of December, January and February.

Table 4.4. List of the focal troops' monthly top quartile foods. With the exception of the *Grewia* sp., which were a combination of fruits and leaves, all consumed top-quartile food items were fruit**.**

Month	**Bevaro Morvato**	**Tsankalamanga**
January	*Strychnos decussata*	*Grewia punctata* *Grewia cyclea*
February	*Phyllanthus amanu*	*Terminalia fatrae*
March	*Phyllanthus amanu*	*Opuntia monacantha*
April	*Terminalia fatrae*	*Phyllanthus amanu*
May	*Commiphora* sp. (voampike)	*Opuntia monacantha* *Canthium* sp. (la jandsy)
June	*Opuntia monacantha*	*Metaporana* sp. (kililo)
July	*Opuntia stricta*	*Opuntia monacantha*
August	*Opuntia stricta* *Leptadenia* sp.	*Opuntia monacantha*
September	*Opuntia stricta*	*Opuntia monacantha*
October	*Opuntia stricta* *Phyllanthus amanu*	*Opuntia stricta*
November	*Strychnos decussata*	*Opuntia stricta* *Azima tetrachanta*
December	*Strychnos decussata*	*Boscia* sp. (sasavy)

Group feeding

Members of the Bevaro Moravato troop were observed feeding within 3m of at least one other individual 83.26% of the time (n = 388**),** were observed feeding between 3 - 8 m 9.2% of the time (n = 43), and were observed feeding alone 7.51% of the time (n = 35). When broken down by month, Bevaro Moravato troop members fed within 3 m of other individuals over 90% of the time 6 of the 12 months and fed within 3 m of other individuals over 80% of the time 8 of the 12 months (**Fig. 4.11**). Group feeding was lowest during the austral winter months and dropped to less than 50% of the time throughout the months of August and September. Finally, the pattern of feeding cohesion did not differ if only females, the more agonistic sex, were included in the analyses (**Fig. 4.12**).

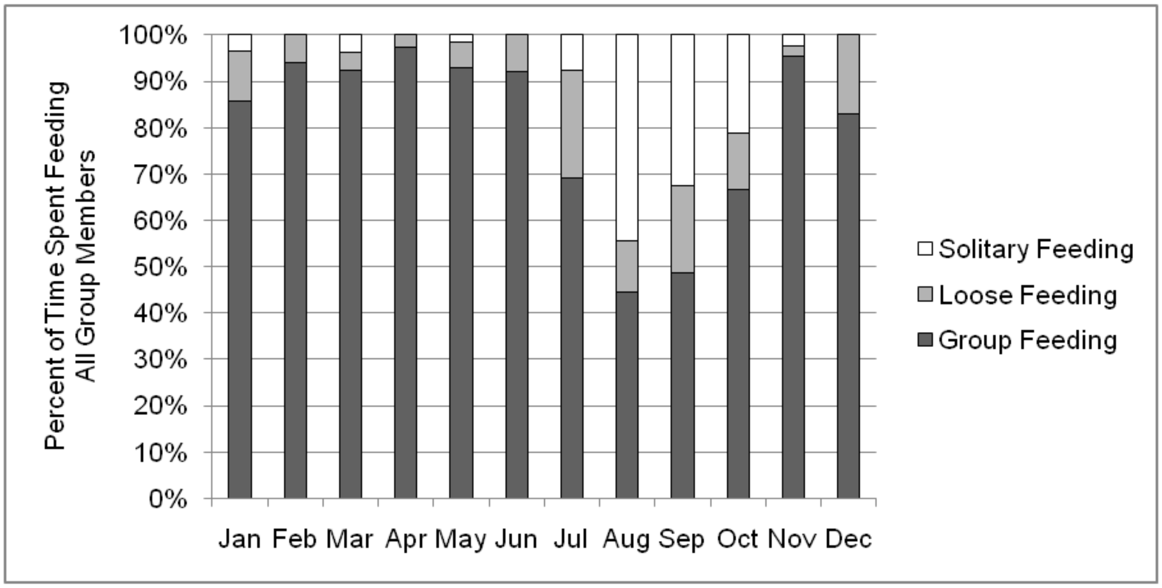


Fig. 4.11. Feeding proximity of Bevaro Moravato troop members recorded by month. Group feeding is defined as feeding within 3m or less of any other troop member (Sauther, 2002). Loose feeding is defined as feeding 4 -7m of any other troop member. Solitary feeding is feeding 8m + away from other troop members (Sauther, 2002).

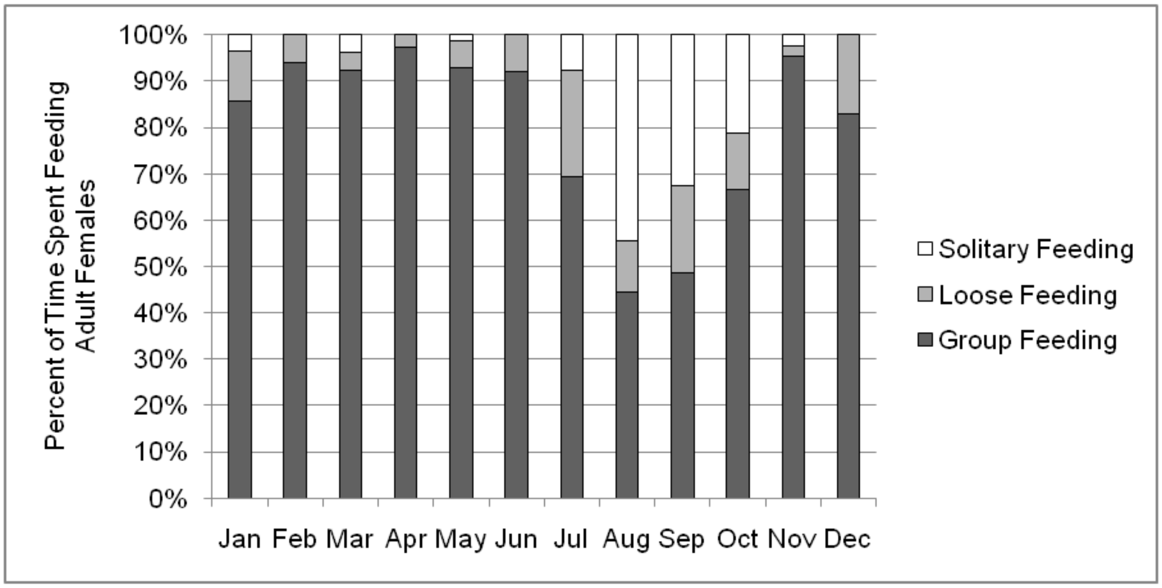


Fig. 4.12. Feeding proximity of the Bevaro Moravato females recorded by month. Group feeding is defined as feeding within 3m or less of any other troop member (Sauther, 2002). Loose feeding is defined as feeding 4m -7m of any other troop member. Solitary feeding is feeding 8 m + away from other troop members (Sauther, 2002).

In comparison, members of the Tsankalamanga troop were observed feeding within 3 m of at least one other individual 82.4% of the time (n = 145), were observed feeding 3-8 m from another individual 4.0% of the time (n = 7), and were observed feeding alone 13.60% of the time (n = 24) (**Fig. 4.13**). When analyzed by month, all feeding was group feeding in the months of January and July, and in no month was group feeding observed less than 50% of the time. Yet in contrast to the Bevaro Moravato troop, group feeding patterns were slightly different for males and females (**Fig. 4.14**). Specifically, while the two females were extremely cohesive co-feeders the majority of the year, there was no co-feeding in September, the month when G10 gave birth. However, cohesive feeding between the two females began again in October, the month when NC gives birth.

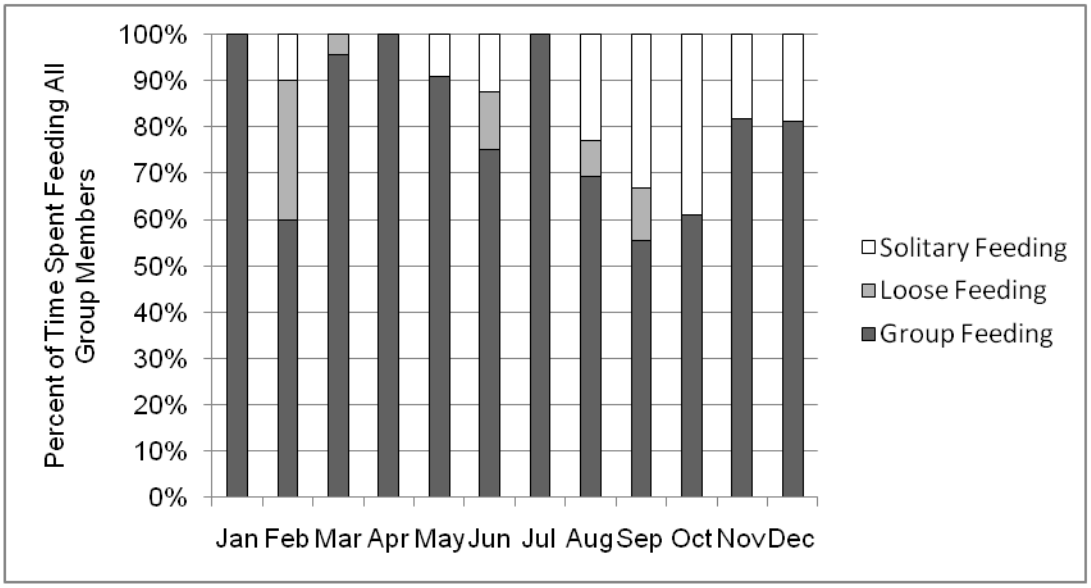


Fig. 4.13. Feeding proximity of Tsankalamanga troop members recorded by month. Solitary feeding is defined as feeding within 3m or less of any other troop member (Sauther, 2002). Loose feeding is defined as feeding 4m to 7m of any other troop member. Solitary feeding is defined as feeding 8m + away from other troop members (Sauther, 2002).

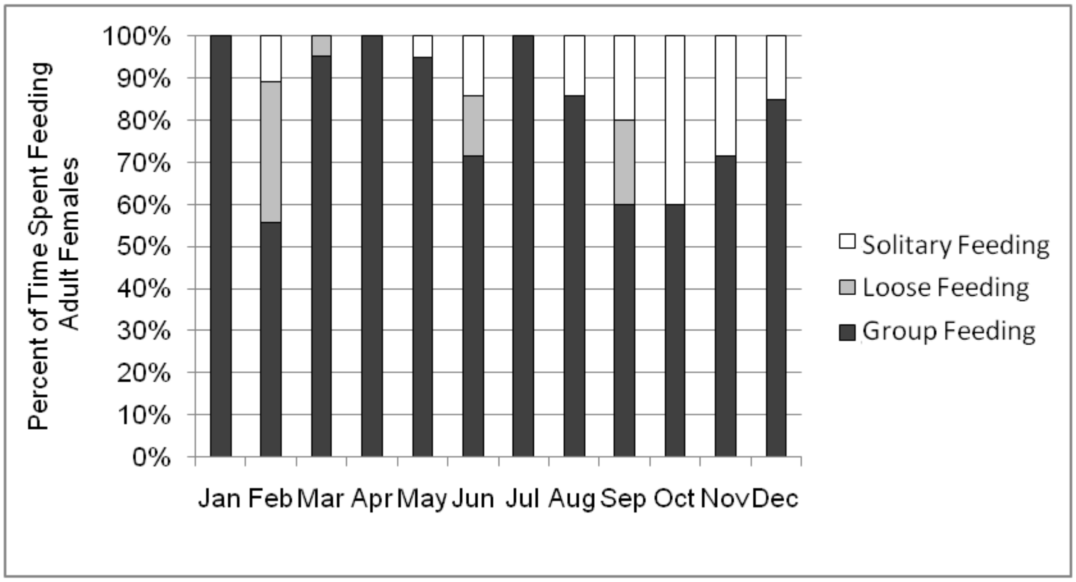
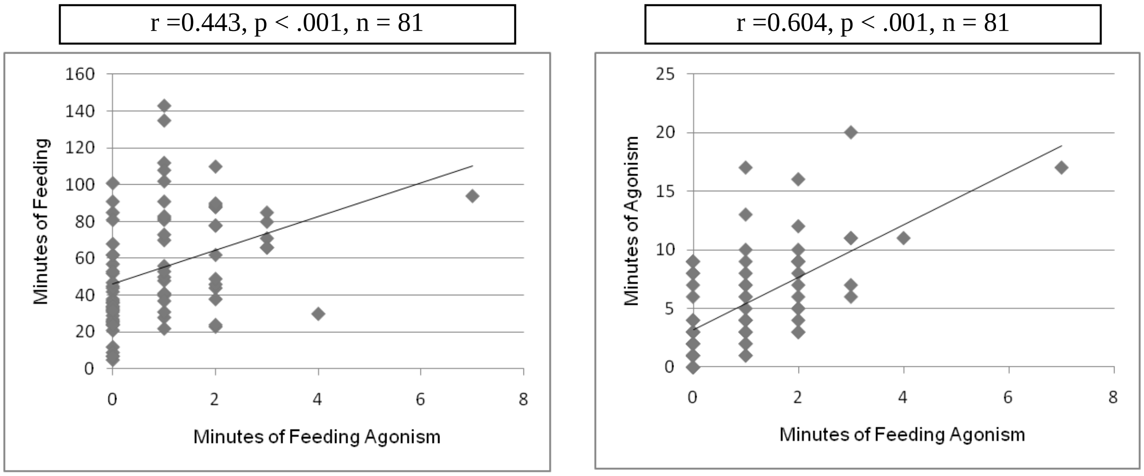


Fig. 4.14. Feeding proximity of the two adult Tsankalamanga females recorded by month. Solitary feeding is defined as feeding within 3m or less of any troop members (Sauther, 2002). Loose feeding is defined as feeding 4m to 7m from the troop. Solitary feeding is defined as feeding 8m + away from other troop members (Sauther, 2002).

Feeding agonism

Feeding agonism was low relative to both total feeding time and general agonism (**Fig. 4.15-Fig. 4.16**). In the Bevaro Moravato troop, peaks of feeding agonism did not coincide with peaks of female to female agonism but coincided with the mating season, when male to male agonism peaked (**Fig. 4.7**). There was no feeding agonism in October. With this troop, daily feeding agonism was associated with both daily time spent feeding and with daily overall agonism levels (**Fig. 4.15**).



r =0.443, p < .001, n = 81

r =0.604, p < .001, n = 81

Fig. 4.15. Relationships between feeding and feeding agonism in the Bevaro Moravato troop by day.

In the Tsankalamanga troop, feeding agonism peaked during the month of March at 0.24% of total minutes of behavioral data. In no other month did feeding agonism exceed 0.12% of all observed daily behaviors. There was no feeding agonism from the months of April through June, when feeding agonism was high in the Bevaro Moravato troop. In addition, there was no significant association between daily occurrences of feeding agonism and daily time spent feeding with this troop.

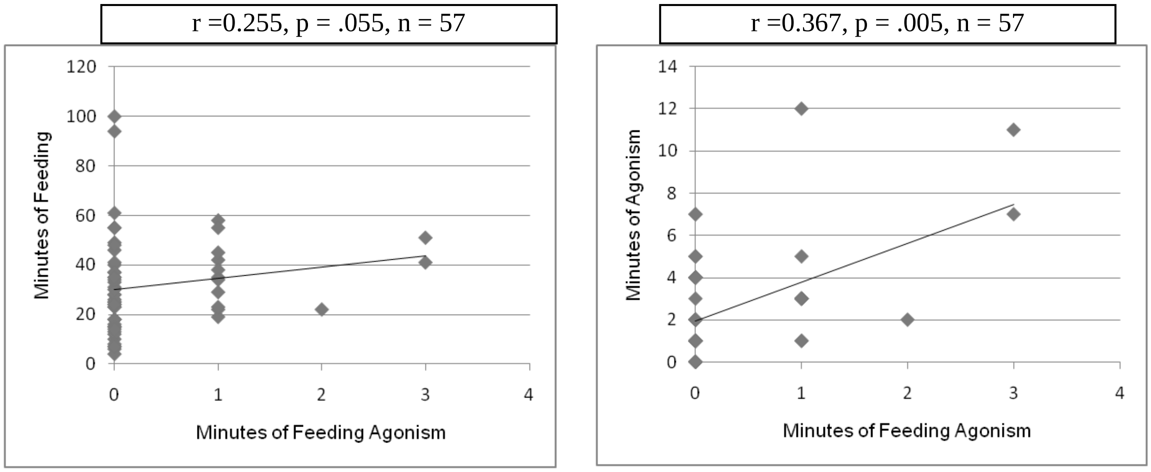


Fig. 4.16. Relationships between feeding and feeding agonism in the Tsankalamanga troop by day.

Social Dyads

Bond strength description and rationale

Bond strengths range from 0 to 1, where 1 equals complete association within 1 m throughout the year and 0 equals no association within 1 m throughout the year. Absolute strong bonded dyads are all dyads with an association above 0.66, which means that they were within 1 m of each other at least two-thirds of all observations. Relative strong bonded dyads are lower than .66 but are among the strongest dyadic bonds in relation to all possible troop combinations. The cutoff point I used for the relative strong bonded dyads was chosen after I viewed the patterns of dyadic pairs on a graph as illustrated in **Fig. 4.17**. In the Bevaro Moravato troop, there was a break in the data to differentiate relative strong bonded dyads with moderate bonded dyads (**Fig. 4.17**). However, since there was no obvious break between moderate bonded dyads and weak bonded dyads, I categorized the lowest one-third of the dyads as weak bonds. For the Tsankalamanga troop, both cut off points were decided by breaks in the data that approximated thirds (**Fig. 4.18**). The names and bond strengths of the dyads that border cutoff points are acknowledged in the text of the figures.

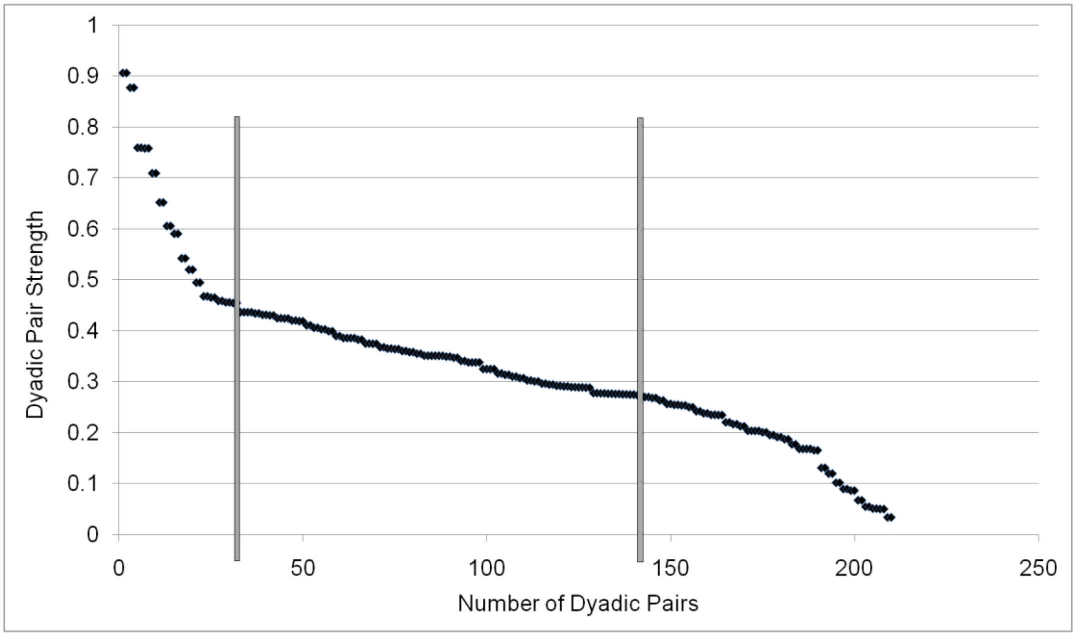


Fig. 4.17. Fallout of dyadic pairs in the Bevaro Moravato troop. Vertical scale is 1-0, where 1 = within 1 m 100% of possible time. Horizontal scale is number of dyadic pairs. Lines demarcate relative bond cutoff points.

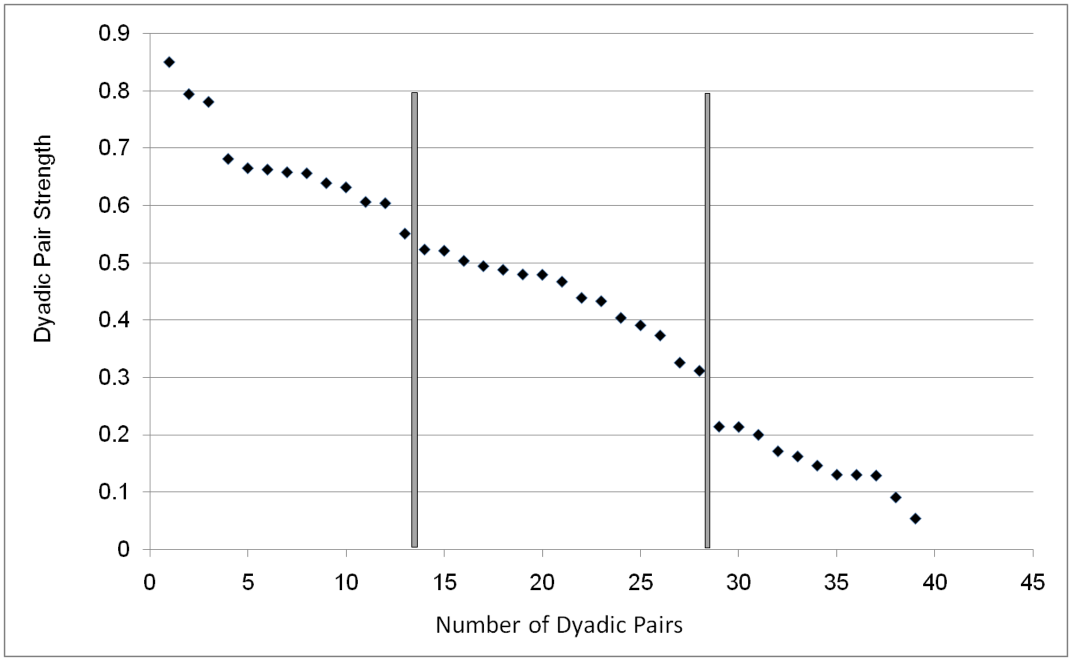


Fig. 4.18. Fallout of dyadic pairs in the Tsankalamanga troop. Scale is 1-0, where 1 = within 1 m 100% of possible time Horizontal scale is number of dyadic pairs. Lines demarcate relative bond cutoff points.

Results

The strongest dyadic bonds for the Bevaro Moravato troop when measured on a yearly scale ranged from 0.91 (Red and Iraika) to 0.46 (RJ and Shaggy). Moderate bonds ranged from 0.45 (G14 and VM2) to 0.28 (G14 and Mena). Weak bonds ranged from 0.27 (B1 and RJ) to 0.03 (VM1 and R9). With one exception, strong bonds were comprised entirely of infants/juveniles to infants/juveniles and females to infants/juveniles (**Fig. 4.19**). Moreover, all females had a strong bond with only one infant or juvenile except for Mena, who had a strong bond with two, Iraika and Red. In fact, these three comprised the strongest yearly bonds of all troop members (Red and Iraika = 0.91, Mena and Red = 0.87, Mena and Iraika = 0.76). Red was Mena’s youngest daughter, and Iraika was likely born to Mena the year before. The next strongest bond was the known mother/daughter duo, G14 and First (0.76). The last suspected mother/juvenile duo, R1 and the juvenile male RJ, had a bond strength of 0.65, which was below that of the two infants, Red and First (0.71), and the infant/juvenile bond First and RJ (0.65). The female juvenile Shaggy was the only young individual who did not have any form of strong bond with a female. Instead, her strongest bond was with an adult male, B1, and this bond strength was relatively strong throughout the year (0.59). All of the juveniles and infants had a relative strong bond with a minimum of two other immature troop members.

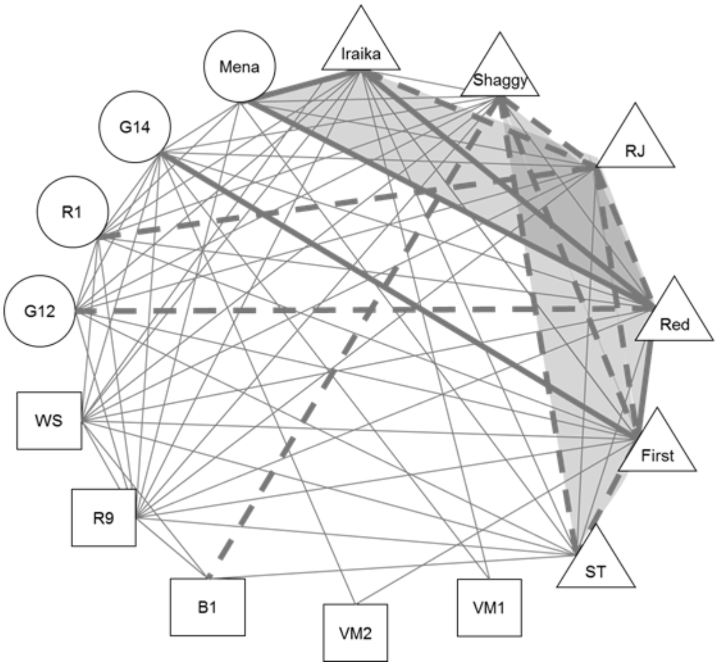


Fig. 4.19. Social dyads of the Bevaro Moravato troop throughout the year. Data were analyzed using a half-weight association index (Lehner, 1996). □ = adult males; ○ = adult females; Δ = juveniles, infants, and the subadult, ST. Bond strengths are based on a scale of 0 to 1, where 1 = complete association within 1m throughout the year and 0 = no association within 1m throughout the year. Absolute strong bonds range from 0.91 (Red and Iraika) to0 .71 (Red and First) and are demarcated with a bold line. Relative strong bonds are demarcated with a dashed line and range from 0.65 (R1 and RJ) to 0.46 (RJ and Shaggy). Moderate bonds range from 0.45 (G14 and VM2) to 0.28 (RJ and B1) and are demarcated with a thin line. Weak bonds range from 0.27 (R1 and B1) to 0.03 (R9 and VM1) and are not shown. Shaded areas depict strong bond areas.

Half-weight association indices indicate a change in dyadic pairings during the birth season. Notably, G14 and R9 formed a relative strong bond soon after she gave birth to an infant in early September (approx. Sept. 3rd), and this bond continued throughout the birth season (.46-.60; **Fig. 4.20, Fig. 4.21**). R9 also developed similar strong bonds during that time with the subadult male, ST (0.47) and the female juvenile, Shaggy (0.46). In addition, R1’s bond with RJ, her probable son, strengthened from a relative strong bond to an absolute strong bond. R1 gave birth to an infant on September 9, but her infant disappeared two weeks later. Last, the strongest relative bond during this time was between the adult male B1 and the female juvenile Shaggy (0.59).

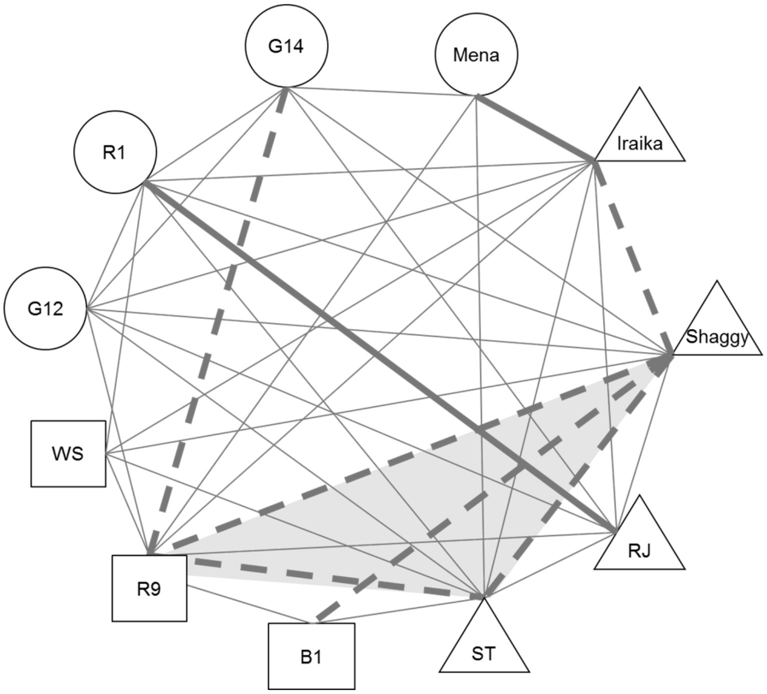


Fig. 4.20. Social dyads of the Bevaro Moravato troop from September 3 (date of infant birth) through December. Data were analyzed using a half-weight association index (Lehner, 1996). □ = adult males; ○ = adult females; Δ = juveniles, infants, and the subadult, ST. Bond strengths are based on a scale of 0 to 1, where 1 = complete association within 1m throughout the year and 0 = no association within 1m throughout the year. Absolute strong bonds range from 0.85 (R1 and RJ) to 0.83 (Iraika and Mena) and are demarcated with a bold line. Relative strong bonds are demarcated with a dashed line and range from 0.59 (B1 and Shaggy) to 0.46 (R9 and Shaggy). Moderate bonds range from 0.45 (G14 and Shaggy) to 0.28 (R9 and Mena) and are demarcated with a thin line. Weak bonds range from 0.27 (WS and B1) to 0.10 (B1 and Mena) and are not shown. Shaded area depicts strong bond areas.

Starting in October, the Bevaro Moravato troop became exceptionally cohesive (**Fig. 4.21**). This is the month when 1) Mena gave birth to twins and the month when 2) the vahiny (immigrant) males first made an appearance at Bevaro Moravato. From October through December, every troop member had at least one strong dyadic relationship. Mena had the strongest possible bond (1.0) with her probable daughter Iraika during this time, soon after she gave birth. However, Mena only maintained a strong bond with Iraika. From October through December, G14 developed relative strong bonds with R1 (0.64), Shaggy (0.56), and RJ (0.48) as well as maintained her strong bond with R9 (0.60). Last, of all troop members, B1 and Shaggy had the strongest relative bond throughout the entire birth and infant dependency season. However, Shaggy also developed absolute strong bonds with the female juvenile Iraika and the subadult male ST from the months of October through December. Shaggy was the only troop member to have absolute strong dyadic bonds with more than one other troop member, and she was only one of five troop members to be part of any absolute strong dyadic pair.

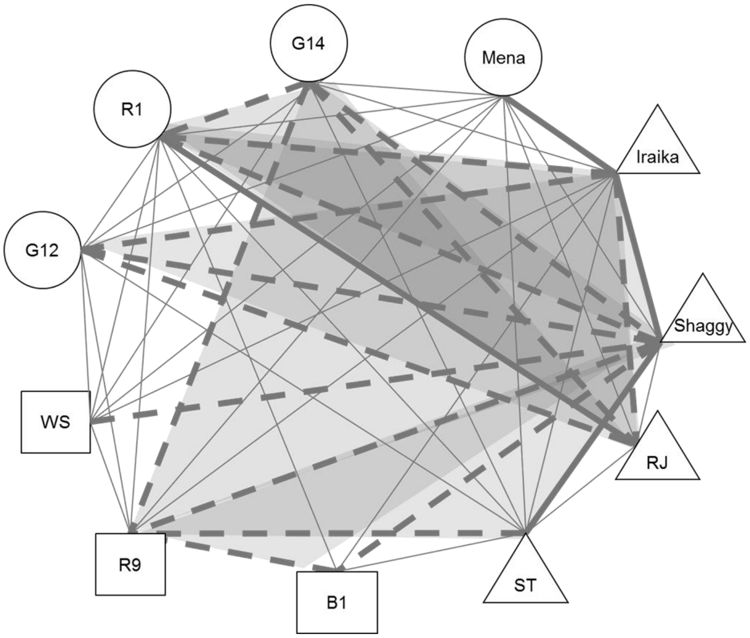


Fig. 4.21. Social dyads of the Bevaro Moravato troop from October 21 (first sighting of Mena's infants) through December. Data were analyzed using a half-weight association index (Lehner, 1996). □ = adult males; ○ = adult females; Δ = juveniles, infants, and the subadult, ST. Bond strengths are based on a scale of 0 to 1, where 1 = complete association within 1m throughout the year and 0 = no association within 1m throughout the year. Absolute strong bonds range from 1 (Mena and Iraika) to 0.72 (ST and Shaggy) and are demarcated with a bold line. Relative strong bonds are demarcated with a dashed line and range from 0.65 (B1 and Shaggy) to 0.45 (ST and Mena). Moderate bonds range from 0.44 (ST and Iraika) to 0.28 (RJ and Mena) and are demarcated with a thin line. Weak bonds range from 0.27 (WS and ST) to 0.1 (B1 and Mena) and are not shown. Shaded areas depict strong bond areas.

When analyzed by sex and age class, adult males spent the least amount of time in close proximity to either new mother in the Bevaro Moravato troop (**Table 4.5, Table 4.6**). However, adult males spent more time social grooming with G14 than did either adult females or immatures (**Table 4.5**). Immatures huddled the most frequently with both new mothers, but adult females spent nearly as much time huddling with G14 as did the juveniles and infants. Last, adult males were the least likely of the sex and age classes to be seen engaging in nonsocial activities while within close proximity to either of the females. Thus, when males were in close proximity to new mothers, they were more likely to be there to engage socially with the mother and infants than were other females or immatures.

Table 4.5. Activities of other troop members who were within 1m of G14 throughout the period she had a dependant offspring (September 9 through December), analyzed by sex and age class. Groom includes mutual grooming and all directional grooming regardless of whether G14 was the groomer or the groomee. Incidental includes all nonsocial activities other troop member engaged in when within 1m or less of G14 and her infant (e.g., self groom, rest, sleep, feeding, movement, travel). Play is all play behavior that involved G14 and one other individual.

Activity	**Sex/Age Class of Troop Member Within 1m of G14**					
	Female		**Male**		**Immatures**	
Groom	2	4.00%	5	12.50%	1	1.89%
Huddle	17	34.00%	12	30.00%	19	35.85%
Incidental	31	62.00%	23	57.50%	33	62.26%
Play	0	0%	0	0%	1	1.88%
Total # of Activities	50	100%	40	100%	53	100%

Table 4.6. Activities of other troop members who were within 1m of Mena throughout the period she had (a) dependant offspring (October 21 through December), analyzed by sex and age class. Groom includes mutual grooming and all directional grooming regardless of whether Mena was the groomer or the groomee. Incidental includes all nonsocial activities other troop member engaged in when within 1m or less of Mena and her infant(s) (e.g., self groom, rest, sleep, feeding, movement, travel). Play is all play behavior that involved Mena and one other individual.

Activity	**Sex/Age Class of Troop Member Within 1m of Mena**					
	Female		**Male**		**Immatures**	
Groom	0	0%	0	0%	2	5.26%
Huddle	6	31.85%	8	57.14%	18	47.37%
Incidental	13	68.42%	6	42.86%	18	47.37%
Play	0	0%	0	0%	0	0%
Total # of Activities	19	100%	14	100%	38	100%

In comparison to the Bevaro Moravato troop, there were more absolute strong bonds at .66 or higher in the Tsankalamanga troop. The two strongest bonds in the Tsankalamanga troop were the mother/infant bonds between G10 and Oops (0.85) and NC and Bny (0.79) (**Fig. 4.22**). Only G8, a young adult female who died early in the study, and B7, the resident adult male, had no strong bonds with other troop members[6]. Relative bond strengths were also higher within this troop as the lowest relative strong bond was between the two adult females at 0.55. Moderate bond strengths ranged from 0.52 (Bny and Enina) to 0.31 (Oops and the immigrant adult male, SF). Weak bonds ranged from 0.21 (the transient male PM and the juvenile male, Sivy) to 0.05 (G8 and B7). Both adult females had strong bonds with three and five troop members respectively.

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[6] It is important to note, however, that G8 and B7 appeared to be in frequent close contact to an adult male in this troop, but he died during the pilot study phase. The importance of having strong dyadic pairs from a health standpoint will be discussed in the next chapter.

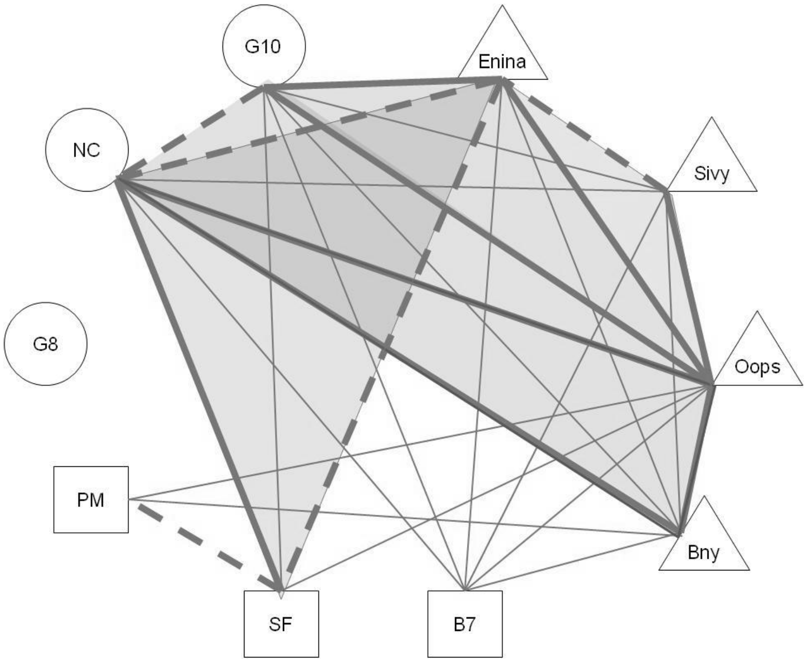

Fig. 4.22. Social dyads of the Tsankalamanga troop throughout the year. Data were analyzed using a half-weight association index (Lehner, 1996). □ = adult males; ○ = adult females; Δ = juveniles, infants, and the subadult, ST. Bond strengths are based on a scale of 0 to 1, where 1 = complete association within 1m throughout the year and 0 = no association within 1m throughout the year. Absolute strong bonds range from 0.85 (G10 and Oops) to 0.66 (Bny and Oops), and are demarcated with a bold line. Relative strong bonds are demarcated with a dashed line and range from 0.64 (Enina and Sivy) to 0.55 (G10 and NC). Moderate bonds range from 0.52 (Bny and Enina) to 0.31 (Oops and SF) and are demarcated with a thin line. Weak bonds range from 0.21 (PM and Sivy) to 0.05 (G8 and B7) and are not shown. Shaded areas depict strong bond areas.

Also in contrast to the Bevaro Moravato troop, bond strengths in the Tsankalamanga troop remained largely unchanged during the birthing season. Soon after she gave birth, G10 developed a strong bond with the male juvenile Sivy (0.72), and this bond continued throughout the months she had a dependant infant (0.77) (**Fig. 4.23-4.24**). In addition, a strong bond also developed between the juveniles Enina and Sivy (.82). Finally, although the bond between the adult female NC and the male juvenile Sivy strengthened soon after the birth of G10's infant (0.58), this bond reduced to the yearly bond strength (0.47-0.49) after NC gave birth to her own infant in late October (**Fig. 4.24**).

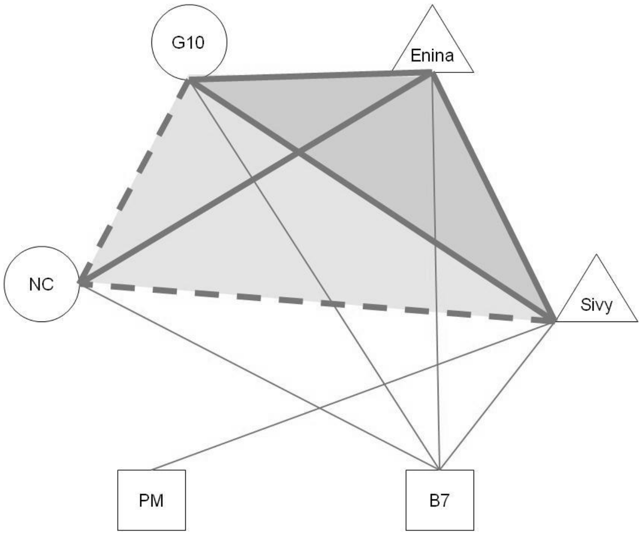

Fig. 4.23. Social dyads of the Tsankalamanga troop from September 8 (first sighting of G10's infant) through December. Data were analyzed using a half-weight association index (Lehner, 1996). □ = adult males; ○ = adult females; Δ = juveniles, infants, and the subadult, ST. Bond strengths are based on a scale of 0 to 1, where 1 = complete association within 1m throughout the year and 0 = no association within 1m throughout the year. Absolute strong bonds range from 0.91 (G10 and Enina) to 0.71 (NC and Enina) and are demarcated with a bold line. Relative strong bonds are demarcated with a dashed line and range from 0.60 (G10 and NC) to 0.58 (Sivy and NC). Moderate bonds range from 0.52 (B7 and G10) to 0.35 (NC and G10) and are demarcated with a thin line. Weak bonds range from 0.25 (NC and PM) to 0.13 (B7 and PM) and are not shown. Shaded areas depict strong bond areas.

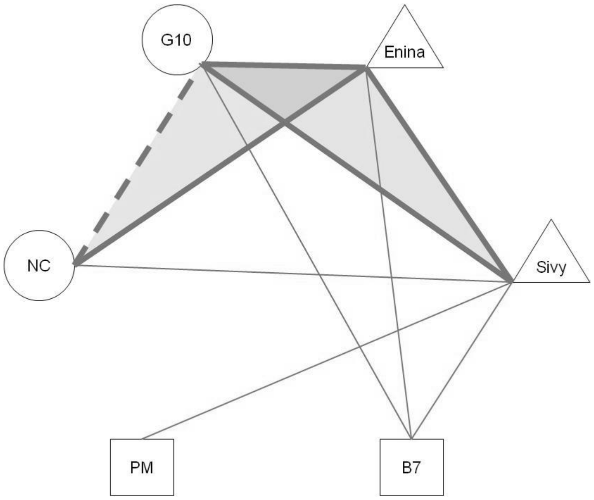

Fig. 4.24. Social dyads of the Tsankalamanga troop from October 24 (birth of NC's infant) through December. Social dyads were analyzed using a half-weight association index (Lehner, 1996). □ = adult males; ○ = adult females; Δ = juveniles, infants, and the subadult, ST. Bond strengths are based on a scale of 0 to 1, where 1 = complete association within 1m throughout the year and 0 = no association within 1m throughout the year. Absolute strong bonds range from 0.81 (G10 and Enina) to 0.69 (Sivy and Enina) and are demarcated with a bold line. The relative strong bond, which ranks at 0.57, is demarcated with a dashed line (G10 and NC). Moderate bonds range from 0.49 (B7 and G10) to 0.31 (Sivy and PM) and are demarcated with a thin line. Weak bonds range from 0.30 (B7 and NC) to 0.12 (B7 and PM) and are not shown. Shaded areas depict strong bond areas.

When analyzed by sex and age class, G10 spent less time in close proximity to the lone male of the troop, B7, than she did with either the other adult female or the two juveniles (**Table 4.7)**. In fact, B7 and G10 spent almost no time engaged in social behaviors with one another during this time. In contrast, NC spent about as much time with B7, both in proximity and social measurements, as she did with all other troop members (**Table 4.8**).

Table 4.7. Activities of other troop members who were within 1m of G10 throughout the period she had a dependant offspring (September 8 through December), analyzed by sex and age class. Groom includes mutual grooming and all directional grooming regardless of whether G10 was the groomer or the groomee. Incidental includes all nonsocial activities other troop member engaged in when within 1m or less of G10 and her infant (e.g., self groom, rest, sleep, feeding, movement, travel). Play is all play behavior that involved G10 and one other individual.

Activity	**Sex/Age Class of Troop Member Within 1m of G10**					
	Female		**Male**		**Juvenile**	
Groom	5	11.90%	2	7.41%	9	15.79%
Huddle	10	23.81%	1	3.70%	13	22.81%
Incidental	26	61.90%	24	88.89%	31	54.39%
Play	1	2.38%	0	0.00%	4	7.02%
Total # of Activities	42	100%	27	100%	57	100%

Table 4.8. Activities of other troop members who were within 1m of NC throughout the period she had a dependant offspring (October 24 through December), analyzed by sex and age class. Groom includes mutual grooming and all directional grooming regardless of whether NC was the groomer or the groomee. Incidental includes all nonsocial activities other troop member engaged in when within 1m or less of NC and her infant (e.g., self groom, rest, sleep, feeding, movement, travel). Play is all play behavior that involved NC and one other individual.

Activity	**Sex/Age Class of Troop Member Within 1m of NC**					
	Female		**Male**		**Juvenile**	
Groom	2	9.52%	1	4.55%	0	0.00%
Huddle	2	9.52%	4	18.18%	10	22.22%
Incidental	17	80.95%	17	77.27%	31	68.89%
Play	0	0.00%	0	0.00%	4	8.89%
Total # of Activities	21	100%	22	100%	45	100%

Discussion

In chapter three, I noted a clear difference in ranging behaviors between the two CSM troops. Yet in this chapter, activity budget analyses indicate that both troops moved/traveled the same amount of time throughout the year (**Fig. 4.1**). As noted in chapter three, there was an inverse correlation between day range and social behavior in the Tsankalamanga troop. Based on this analysis alone, it appeared that social behavior is an expendable activity to be minimized during times of travel. These data however, suggest that time spent in social behavior is remarkably similar between the two troops, both at the general level and in the detailed breakdowns. In fact, the only difference between the two troops was that while the Tsankalamanga troop tended to rest and sleep more often, the Bevaro Moravato troop tended to feed more often. Moreover, this difference in sleeping/resting between the two troops is likely even larger than that which is suggested in the figure, as data collection on the Tsankalamanga troop often didn't begin until after the lemurs were awake and sunning (see chapter two), and in the context of energetics, sunning should also be included as another form of resting. Therefore, it appears that feeding and resting, not social behavior, is affected by environmental conditions. This finding is consistent with observations of *Eulemur* groups and other species that adopt an "energy conservation strategy", in which primate groups that reside in drier, less productive environments compensate by resting more often than their conspecifics (see Menon and Poirier, 1996; Ossi and Kamilar, 2006).

Another notable finding was the high percentage of time both troops spent in (active) affiliative social behavior compared to gallery forest and semi-captive troops. The only reported observation of more frequent active social activity was by Jolly, who reported one instance of exceptionally high active social activity at 7.1% (Sussman and

Garber, 2007; see also Sussman et al., 2005, Table 1). In addition, despite the high percentage of time the CSM troops spent in active affiliative behavior, the CSM *L. catta* spent no more time engaged in agonistic activity, 1.06% (BM) and .67% (TA) respectively, then do gallery forest *L. catta* (0.5% to 1.4% [Sussman and Garber, 2007]). These results could be due to data collection differences. For example, as pointed out by Sussman and Garber (2007), 1) there has been some inconsistency in the criteria used for defining social behavior across studies[7], 2) some of the studies only include a subset of the troop in the analysis, and 3) many of the studies were conducted for only part of a season. To check for these biases, I analyzed the data twice. First, as per Gould (1994), a male-only activity budget analysis on active social behavior for the CSM troops is 4.4% (BM) and 3.0% (TA). Thus, while the activity budget for one troop remained largely the same, the social activity budget for the troop with no permanent male residents dropped by almost 2%. Second, as per Jolly (unpublished data in Sussman and Garber, 2007), I reanalyzed activity budget data for only the birth season (Sept.-Nov.). In this case, the social activity budget of the Bevaro Moravato troop dropped to 3.4%, while the social activity budget for the Tsankalamanga troop remained much the same at 4.3%. Thus, while the other reported percentages could be lower than what would be expected if data were collected on the entire troop for a year, it’s unlikely that the CSM *L. catta* engaged in less social behavior than gallery forest and semi-free ranging troops. This is in contrast to what I predicted would be the case for a troop in which residence appears to be constant and resources appear to be scarce (also see Lee, 1986; Li and Rogers, 2004). Based on these analyses, two primary conclusions can be drawn: 1) time spent in social

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[7] This first point is relatively minor. For the most part, active social behavior is consistently defined as social grooming and play.

behavior for CSM *L. catta* is not affected by group size, group composition or group isolation; and 2) when resources in the environment are scarce, less time is spent feeding, more time is spent resting, but time spent in social behavior is not affected (also see Menon and Poirier, 1996; Sussman et al., 2005).

Specific to agonism, CSM females behaved much like their gallery forest conspecifics in that they were the primary instigators of aggression (**Table 4.2, Table 4.3**). However, the female targeted aggression that characterizes this species was not the dominant form of agonism expressed within either CSM troop (see Kappeler, 1990; Pereira and Kappeler, 1997; Jolly, 1998). In fact, female to female high intensity agonism (see Sbeglia et al., 2010) occurred infrequently and most of this kind of agonism was female to male directed and female to immature directed.

CSM *L. catta* fed within 3 m of at least one other troop member 83.3% (BM) and 82.4% (TA) of the time. When measured on a monthly scale, group feeding was almost always highest when the top-quartile foods were native species and lowest when the top-quartile foods were *Opuntia*. In the Tsankalamanga troop particularly, group feeding was 100% for two of the months that the top-quartile food was a native species and July was the only exception to this trend (**Table 4.4; Fig. 4.13**). The fruit of *O. monacantha* and *O. stricta* were largely available year round, and these fruits were approximately four to ten times larger than any other food item consumed by the CSM *L. catta*. If the animals dispersed when feeding on these fruits to prevent agonism, then these findings are consistent with Gemmil and Gould (2008). Alternately, the tendency to disperse when feeding on the cactus fruits could also have to do with the distribution of *Opuntia* in the environment. This assertion is supported by June feeding cohesion data in the Bevaro

Moravato troop, as feeding cohesion that month was high even though the troop fed primarily on *O. monacantha*, the variety of cactus fruit that grew from their sleeping hedges, in lieu of the widely dispersed *O. stricta* (**Table 4.4; Fig. 4.11., Fig. 4.12**). Moreover, since the troop was most cohesive the months of October through December (**Fig. 4.21**), the high percentage of group feeding in November likely reflects an increase of group cohesion in general rather than dietary strategies. Finally, the fact that adult female troop members followed the same feeding cohesion patterns as all other troop members does not support the theory that feeding dispersal is an alternative strategy (scramble competition) to female (contest) feeding competition.

While feeding cohesion roughly followed patterns of native vs. cactus fruit consumption, agonism in the context of feeding had more to do with troop agonism levels in general than with feeding *per se*, although feeding agonism in the Bevaro Moravato troop was significantly associated with feeding time. However, adult directional agonism patterns observed in gallery forests and semi-captive conditions differed at CSM. For example, the spike in female to male directed agonism during the early part of the mating season is consistent with what would be expected from the dominant sex when the more subordinate sex is trying a “trial and error” mating approach with a strict seasonal breeder (**Fig. 4.7, Fig. 4.8**). In addition, the spike in male to male agonism is consistent with typical *L. catta* mating season behavior. Alternatively, although a spike in female to female targeted aggression in the Bevaro Moravato troop did occur in January, which could arguably be considered part of the premating season, this peak dropped precipitously in February and there was no female to female agonism in the Tsankalamanga troop in January despite the nearly identical birth seasons. More significantly, female to female targeted aggression, and agonism in general, was very low in September in the Bevaro Moravato troop, the first month of the birth season. Conversely, September was one of only three months in the Tsankalamanga troop where there was any female to female agonism. Last, while there was no female to female agonism in the Tsankalamanga troop during the lactation season, a relatively high amount of this kind of agonism occurred during this time in the Bevaro Moravato troop. Moreover, females in both troops spent most of this season feeding in close proximity to other females, which is in contrast to that which occurs in gallery forest environments (see Sauther, 1992). It is of note that the presence of *Opuntia* cannot explain this divergence in behavior between the two different environments, as the lemurs spent much of this season (Sept./Oct.-Jan./Febr.) feeding on native fruit species (**Table 4.4**).

As for forms of agonism, there were no observations of infanticidal behavior by either adult male or female troop members. However, this does not mean that the troop perceived no threat from outside members. For example, it is of interest that group cohesion tightened considerably in the Bevaro Moravato troop, but not the Tsankalamanga troop, starting the month of October. October marked the first sighting of the two immigrant males. Moreover, although there were no observations of male to immature agonism in the Tsankalamanga troop, the male infant Bny disappeared soon after the arrival of the immigrant male SF, the reemergence of PM, and the disappearance of the then resident male B7 mid-May. May is notable in that it is part of the mating season and was a month of relatively high female to male and male to male agonism (**Fig. 4.8**). Bny's skeleton was later found at the base of the troop's main sleeping hedge with a hole in his skull. It is possible that this hole was made by the canine of a ring-tailed lemur. It is also possible that the hole was pierced by the claws or talons of a cat or hawk, and that Bny was able to escape immediate death only to then die in the sleeping hedge. Last, it is of note that the juvenile male Sivy died from obvious illness a week prior, which could mean that Bny died from illness and the hole developed post mortem. In sum, while it is unlikely that Bny's death was the result of infanticide, behaviorally imposed mortality cannot be ruled out as a cause of death for this infant (see Jolly, 1998).

While there were no observations of infanticidal agonism, there was a disproportion in the kind of agonism adult females directed towards other adult and juvenile troop members (**Table 4.2-Table 4.3**). Although somewhat subtle, females in both troops were significantly more likely to displace and chase adult troop members, while they would instead slap, cuff, and nip at the troops' juveniles (**Fig. 4.9, Fig. 4.10**). This type of female to infant (e.g., mother/offspring) behavior has been observed before in other primate studies (Bernstein and Ehardt, 1986), and kinship has been found to be a predictor of high intensity agonism among semi-free ranging *L. catta t*roops (Sbeglia et al., 2010). In this study, high intensity agonism was not necessarily mother to infant directed, but was instead female to immature directed. Based on the data, I believe that CSM *L. catta* expressed two major forms of agonism. The first kind was mainly expressed in the form of displacements (also known as supplanting) and was likely an expression of dominance and antagonism (Lehner, 1996). I propose that the second kind of agonism, however, which has been labeled in Sbeglia et al.'s (2010) study as "high intensity agonism", was in this study more likely to be a form of discipline or socialization. In addition, I believe that all female troop members participated in this behavior towards the troops' immatures regardless of their direct relationship to the immature. By socialization, I don’t necessarily mean that the behavior in question would be something critical to the survival of the offspring; feeding from a toxic plant for example. Moreover, there may not have been a direct intent to alter the behavior of the immature, although that may have been the consequence. For example, juveniles playing near resting adults would be cuffed after several incidents of bumping into resting adults. One of the females would finally hit the nearest juvenile and give a chatter squeal. As a result, the play behavior would either stop or move away from the irritated adults.

An alternative explanation could be that juveniles were recipients of high intensity agonism because of their proximity to all other troop members (see Bernstein 2004), and in fact, active social behavior analyses (**Fig. 4.2, Fig. 4.4**) as well as half-weight association indices indicate that CSM troops are juvenile bonded (**Fig. 4.19, Fig. 4.22**). Moreover, it is possible that juveniles were the primary recipients of physical agonism because adult troop members were not afraid of the repercussion of getting physical with a smaller troop member. However, there are two reasons why I feel that at least part of what is occurring is socialization. First, juveniles weren’t the most frequent recipients of agonism in general, just high intensity agonism. Therefore, proximity alone could not be the reason as a successful displacement requires just as close proximity to an individual as does a hit or a cuff. Second, in the Bevaro Moravato troop, there was some, albeit low, high intensity male to immature directed agonism. Yet there was no male to immature high intensity agonism in the Tsankalamanga troop. The Bevaro Moravato troop differs from the other troop in that three adult males and one subadult male were residents of the troop throughout the study. In contrast, not a single male remained within the Tsankalamanga troop throughout the same study period. Therefore, it could be argued that high intensity agonism directed from Bevaro Moravato males to troop immatures was more accepted by the female members because these males were integrated parts of the communal whole.

Last, multiple behaviors observed among the CSM *L. catta* challenge the characterization of male *L. catta* as indifferent, or only occasionally affiliated to, immatures (see Jolly, 1966, p. 161; Gould, 1992; also see Whitten, 1987). First, the strong, consistent social bond between the adult male, B1, and the female juvenile, Shaggy, mirrors the troops' mother/offspring bonds in intensity and consistency (**Fig. 4.19-Fig. 4.21**). In fact, Shaggy's strong bond with B1 not only remained constant throughout the study period, but she also developed strong bonds with the two other resident adult males in September, at the start of the birth season, when male *L. catta* at gallery forest sites tend to intensify bonds with immatures (Gould, 1994). Since Shaggy was born before the start of the study, it is not clear whether her mother died or simply ignored her. What is clear, however, is that even if B1's strong bond with Shaggy developed after she was weaned, his bond with her mirrors that of the bonds the other two juveniles and the two infants had with their likely mothers.

Second, as noted earlier, males played with infants and juveniles more than did females, and male to immature social grooming was the second most frequent form of social grooming in the Bevaro Moravato troop. In addition, although males were always the least likely to be in close proximity to new mothers (**Table 4.5, Table 4.6, Table 4.7, Table 4.8**), males who were in close proximity to G14 during the birth season were more likely to groom her and her infant than were females and juveniles (**Table 4.5)**. Moreover, a strong bond between G14 and the male R9 developed immediately after the birth of her infant, (**Fig. 4.20**), and this pattern continued throughout the birth and infant dependency season (**Fig. 4.21**).

Third, the lack of strong bond development between Mena and male troop members does not likely reflect male indifference but rather female prevention. Mena was by far the most aggressive female in the troop and was responsible for 26.6% of all directional agonism. Conversely, Mena received less agonism than any other troop member (2.5%) except for that of her male infant, Red. In fact, Mena maintained the strongest possible bond with her (likely) daughter, Iraika, throughout the birth and infant dependency season; they were within 1 m of each other 100% of the time, and Mena was not strongly associated with any other troop members. Also, Iraika was the only troop member to regularly allocarry an infant, as she was observed carrying her (probable) younger sister on 16 different occasions. The next most frequent allocarrier was G12, and she was observed carrying infants on only three occasions.

In the Tsankalamanga troop, bonds between males and infant/juveniles were less apparent. Soon after the mating season, the female juvenile, Enina, developed a close proximity bond with an adult male, SF, despite the fact that she was also closely bonded with the two adult females (**Fig. 4.22**). Sivy, the male juvenile, had no tight bonds with any adult troop members when measured on a yearly scale. Data from the early birth season, however, indicate that he was closely bonded with both adult females during that time (**Fig. 4.23**). Moreover, males were not only least likely to be in close proximity to new mothers, they were also most likely to be conducting other (nonsocial) activities when they were within the new mothers' proximity (**Table 4.7, Table 4.8**). Conversely, males played and social groomed with immatures more often than females played with immatures (**Fig. 4.2**), and more often than females groomed other females (**Fig. 4.4**). Last, there were no observations of allocarrying in this troop by either sex, and there were no observations of allonursing in either troop.

Thus, what both troops have in common is a general lack of female bonding relative to gallery forest and semi-captive troops, both during the infant dependency season and throughout the year in general (see Jolly, 1966; Taylor, 1986; see Gould, 1992). In the Tsankalamanga troop, there was also a lack of male membership, which may have prevented the full potential expression of male to immature care. In the Bevaro Moravato troop, however, the males' interactions with the troop's immatures was much like affiliative parenting, the second highest form of parental care in primate species (Whitten, 1987; see Gould, 1992). Since the Bevaro Moravato troop is largely isolated, it is possible that kinship is the explanation for why the unique relationships between males and immatures occurred in this troop (see Sbeglia et al., 2010) and some might even argue that paternity certainty may be the cause for the higher than expected parental behaviors (see Buchan et al., 2003). Unfortunately, genetic material was not taken from troop individuals, so there is no way of knowing. Yet this does not explain the absence of such behavior among male ring-tail lemurs in other troops. What I believe best explains the close male/immature relationships in the Bevaro Moravato troop is the general lack of female bonding combined with the lack of emigration of male troop members. For when females did have a close bond with even a juvenile female (Mena and Iraika), alloparental care outside of this partnership was nearly absent. Conversely, when there was no interest in an immature (i.e., Shaggy), a male filled that role (B1). In sum, the only evident pattern from the data is that immatures were central to the troop for both female and male troop members, and that when not prevented by other troop members, mainly mothers, males were eager to interact affiliatively with the young. In fact, findings from this study call into question the parental catergories “occasional affiliation”, “tolerance,” etc.(Whitten, 1987), as these categories insinuate that male behavior is independent of female influence.

Chapter Summary

- CSM troops spent nearly identical amounts of time engaged in all measured active and passive social behaviors (i.e., play, social grooming, huddling and scent marking). In comparison with gallery forest *L. catta*, CSM troops spent more time throughout the year in active affiliative behaviors and about the same amount of time engaged in agonistic intratroop behaviors. These findings minimize the importance of ecological models that hypothesize that the primary function of groups is to form alliances with kin against other groups.
- Troop members fed more cohesively the months when native fruit species were the top quartile food species and they fed less cohesively the months when *Opuntia* fruits were the top quartile species. Since the cactus fruits are 4 to 10 times larger than native fruit species, it is possible that the lemurs dispersed while eating these fruits to minimize feeding agonism (a form of scramble completion). However, there was a high percentage of feeding cohesion in the Bevaro Moravato troop the only month when *Opuntia monacantha* was its top-quartile food. Unlike *O. stricta*, *O. monacantha* is a clumped resource that is found primarily in hedges that have been planted around crops. Therefore, the dispersed feeding during months of *Opuntia* consumption may be better explained by the dispersed and widespread nature of *O.*

stricta vegetation.

- In contrast to what is understood as typical *L. catta* social organization, female troop members were neither necessarily female bonded nor was female targeted aggression the dominant agonism form. However, there were also very few adult preferred partnerships of any kind. Instead, all analyses indicate that juveniles and infants were central to troop dynamics.
- Although agonism was associated with feeding agonism and group feeding with the Bevaro Moravato troop, feeding agonism at CSM was more closely associated with overall patterns in agonism levels than with feeding time, i.e., during the mating season. There was no evident pattern between female to female directed agonism, and, in contrast to that which has been reported in other studies, female to female agonism in the Bevaro Moravato troop was lowest in the early birth season. Moreover, there was very little similarity in seasonal agonism patterns between the two CSM troops.
- In the Bevaro Moravato troop especially, there was a significant difference in type of agonism and age class of recipient. This difference in type may reflect a difference in intent; i.e., agonism *per se* vs. socialization, and may at least partly explain why female to female agonism trends didn't follow any predicted patterns. The topic of socialization in mammalian groups in general and in primate groups specifically is a gaping hole in a field of research in which alloparenting, pair bonding and infanticide are dominant themes.
- Resident males at CSM interacted affiliatively with troop immatures throughout the year. I believe that the reason for the intensification of paternal-like behaviors at CSM

is at least partly due to a breakdown in female bonding as there seemed to be only one example in each troop of a multigenerational matriline, i.e., a grandmother presence. In addition, with the Bevaro Moravato troop specifically, there were no instances of male dispersal. Therefore, I suggest that *L. catta* males in general have predispositions to care for intratroop immatures, but expression of this behavior is typically prevented by socially dominant female matrilines comprised of multigenerational adults, and is further weakened by regular male dispersal. In fact, studies at gallery forests have found trends that suggest this may be the case (see Gould, 1992).

- Finally, females at CSM may be less bonded because lemurs at this site don’t live long enough to establish generational matrilines. The health and nutrition of this population is the topic of the next chapter.

CHAPTER 5

Health, Nutrition and the Environment

Prior to starting the behavioral observations of this study, two young females from the Tsankalamanga troop were found dead. Randall Junge, the wildlife veterinarian who conducted the health assessments for this study, performed a necropsy on one of the females and found no evidence of trauma or organ damage. By the end of the study, the troop was half its original size. While it seems evident that the mass mortality of this troop was abnormal, a primary question of this study is whether the low density population that characterizes the Cap Sainte-Marie region is associated with inadequate nutrition or an absence of water. Specifically, since the widespread presence of *Opuntia stricta* especially is a relatively recent change in the ecology of *L. catta*, there is the question of whether this introduced plant is associated with any negative health consequences in this population. The objectives of this chapter are to: 1) assess the overall health and nutrition of the Cap Sainte-Marie (CSM) troops through comparisons with closely monitored gallery forest and North American (semi) captive populations, 2) to compare the diet of the CSM focal troops with gallery forest conspecifics, and to 3) attempt to answer why the Tsankalamanga troop suffered such high mortality.

Background

In the last ten years, health assessment data have been taken on a number of wild lemur populations (n = 17) from which baseline values of health and nutritional status can be based (see Junge et al., 2011). Data from these assessments have been particularly informative for testing hypotheses on how lemur health is affected by anthropogenic disturbance (Irwin et al., 2010; Junge et al., 2011). In studies on gallery forest *L. catta* populations, low-quality scrub habitat and contact with anthropogenic environments were found to have detrimental effects on the health and nutrition of *L. catta* troops (c.f. Crawford et al., 2006; Sauther et al., 2006). At CSM, the troops not only live in low-quality (scrub) habitat, but they also share their habitat with the local Antandroy human population. There are four anthropogenic aspects of the CSM troop's environment that may be especially costly for these lemurs.

First, since the only sleeping sites for CSM *L. catta* are the cactus hedges that typically surround crop fields, there is suspicion among the local villagers that ring-tailed lemurs are crop raiders. Although I was told by the farmers that this behavior was only a small problem, primate species that are perceived as crop raiders are typically treated with hostility and are susceptible to human caused life-threatening injuries or death (e.g., Strum, 1994; Siex and Struhsaker, 1999; Hill, 2000; Saj et al., 2001; Fuentes, 2002; Wheatley et al., 2002; Tweheyo et al., 2005; Wieczkowski, 2005; Sprague and Iwasaki, 2006).

Second, as has been described in the previous two chapters, both species were major components of the troops' diets. *Opuntia* is introduced in Madagascar, and there has been no research on how its presence affects the region's native bird and mammalian populations (Ferguson, 2002; Middleton, 2002; Middleton, 2003). However, the local Antandroy believe that *O. stricta* is toxic when consumed. In fact, the local chief at Bevaro Moravato was visibly upset the first time he watched a ring-tailed lemur consume one of these fruits. Non-native species elsewhere have proven to be detrimental *to L. catta*. At Berenty for example, the consumption of the introduced *Leucaena leucocephala* by *L. catta* has been primarily linked to alopecia and secondarily linked to increased infant mortality and lethargy (Crawford et al., 2006).

Third, although the lemurs appear to be well adapted living among cacti, the lemurs' use of cacti for shelter resulted in injuries that wouldn't have occurred if this vegetation hadn't been present in their environment. During my pilot study, I observed a lemur with a serious eye injury that appears to have resulted from a cactus thorn puncture wound. When I returned for the long-term study, one of the adult males was missing an eye. Moreover, during this study, one female may have died as a direct result of a villager trying to flush out the troop from *Opuntia monacantha* by beating the vegetation with a stick.

Fourth, dental abscesses, higher rates of agonism, and elevated levels of stress have been found among lemur groups that feed on human food scraps, refuse, and livestock fodder (Sauther et al., 2006). At CSM, all three of these kinds of foods could be found within the focal troops' home ranges. However, as specified in **Table 3.3**, none of these foods were primary components of the CSM troops' diets.

Methods

Results in this chapter have been divided into sections. The first section is a descriptive analysis of the births and deaths that occurred in both troops throughout the study. These results are then compared with demographic data that have been acquired at the gallery forest reserves, Berenty and Beza Mahafaly.

In the second section, health assessment data are compared between the two

CSM troops and among data sets of captive and wild populations. Raw comparative data are from Tsimanampetsotsa National Park (TSNP)[1]. To eliminate seasonality as a factor, comparisons between CSM lemurs and TSNP lemurs are only based on values from late July. In addition, health assessment values from CSM lemurs are compared with published mean values from Beza Mahafaly and captive individuals (Miller et al., 2007).

In the third section, diet lists of the two focal troops at CSM are compared with the diets of other wild populations. In addition, I compare the estimated nutrition intake of CSM *L. catta* with the current diet recommendations for provisioned *L. catta*. The estimated nutritional values of the CSM troops are based on the analysis of 41 plant samples, which represent the top 75% of each CSM troop's monthly diets (see chapter two for detailed methodology).

In the fourth and final section of results, I present water content values of the plants consumed by CSM *Lemur catta* throughout the study. In this section, I also compare the water content of the native plants to the water content of *Opuntia*.

Qualitative Results

Birth records

The birth season for both troops at CSM were within the typical birth season range of gallery forest troops; early September through early to mid-October (Jolly et al., 2002). Moreover, much like the scrub forest populations at Berenty, the birth rates at CSM were very high; all but one young adult female gave birth. In contrast, gallery forest and tourist troops at Berenty tend to have lower birth rates.

The birth of twins is very rare in all environments. In general, twinning

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[1] Raw data will also soon be available from Beza Mahafaly.

occurs only within gallery forest troops, and the record at Berenty was three sets of twins and one set of triplets out of 204 births (Jolly et al., 2002). At Beza Mahafaly, there were no observed multiple births over a six year observation period (Gould et al., 2003). It is therefore notable that Mena, the dominant female from the Bevaro Moravato troop, had twins. It is even rarer for both twins to survive. In fact, statistics based on data from 1963 to 2002 at Berenty record only two known cases in which both twins survived past the age of three months (Jolly et al., 2002). One of Mena's twins was found dead at less than two weeks of age. This infant was found intact on the ground in an exposed field that the lemurs used as a travel route. Since this infant was found while following the lemurs during their daily travel early in the morning, I believe that the infant had dropped off the day before. Despite its exposure to the elements, there was no predatory or scavenger damage to the infant's body.

Last, infant survival rates for both CSM troops were similar to infant survival in Berenty's scrub forest populations and to Beza Mahafaly in general during non-drought years ($\geq$50%) (Sussman, 1991; Gould et al., 1999; Jolly et al., 2002; Gould et al., 2003). While two of four infants died in the Bevaro Moravato troop, one of two infants died in the Tsankalamanga troop. Moreover, only one female in each troop appeared to have two viable offspring two years in a row. In both cases, it was the oldest female troop member (Mena and G10). In contrast, infants of the oldest females at Beza Mahafaly have the highest mortality rates (Sussman, 1991; Gould et al., 2003). This may be an indication that the oldest females at CSM are younger than the oldest females at Beza Mahafaly, and in fact both of the CSM females were estimated to be only 9 to 12 years of age (**Table 2.2, Chapter Two**).

Juvenile and adult mortality

Throughout the 15 month study, there was only one non-infant death in the Bevaro Moravato troop. This animal was an adult female estimated to be of prime age (**Table 2.2**). Her remains, which only consisted of intact skin and bones, were found August 16th on the entrance floor of one of the troop's sleeping hedges. She was last observed alive July 27th. This female and other troop members frequently slept in a bough of the cactus hedge several meters above where her body was found.

In contrast, there were five non-infant deaths in the Tsankalamanga troop: one old male, one young male, two young females, and one subadult male. All but the subadult male died in the months of June through August 2007. The subadult male died late April 2008, just three weeks before the infant Bny disappeared.

The old male (R3) most likely died of a respiratory illness; his breathing could be heard meters away about a week before he was found dead in the sleeping hedge late July. This male was estimated to be the oldest of all assessed individuals (**Table 2.2**). One of the young adult females, G8, was found dead in the same sleeping hedge two weeks later, after strong storms hit the area. Early *ad libitum* data indicate that G8 and R3 spent a great deal of time huddling with one another prior to his death. In fact, she was often observed alone after his death, and she had separated herself from the other troop members a few days prior to when she was found dead (c.f. Chapter Four).

The third death that was indisputably illness or sickness related was the subadult male. Prior to his disappearance, he slept on the open ground while his troop members traveled and fed. He eventually rejoined them in the sleeping hedge that evening, but he was never seen again. I suspect he died in the sleeping hedge, but this one was impenetrable to human entrance.

The causes of the last two deaths are more obscure. The young female, R3, died the first week of June 2007 and was the first female to die in the study. Since she died in the same impenetrable hedge and before the troop was habituated, I do not know whether her death was illness related. However, she was never seen again after one of the guides banged at the hedge with a stick in a misguided attempt to herd the troop to a more visually suitable location. The last death was that of the young male B5. He was the second individual to be found dead, in late June 2007. His body was found collapsed over an isolated *Opuntia monacantha* shoot (approximately 3m in height) in an otherwise open environment. Prior to his death, he acted as a sentinel group member when he was threatened. Based on the position of his body, it is not clear whether he died from exposure or whether he was the victim of a stone throwing.

In both comparative and absolute terms, the death rate of the Tsankalamanga troop was exceptionally high. Since I did not follow the neighboring troop(s), I do not know whether this mass mortality characterized the Tsankalamanga area. Based solely on the numbers of the Tsanakalamanga troop, the estimated mortality rate for noninfant females at Tsankalamanga was 0.4 and the noninfant mortality rate for males was 0.5 (not counting B7 and PM, who are assumed to have migrated rather than have died). In addition, since the total non-infant population size for the isolated Bevaro Moravato troop was only 14 with a noninfant female population size of 7, the death of only one female in the Bevaro Moravato troop translates into a noninfant female mortality rate of 0.14, (or 0.07 at the troop level). In comparison, mortality rates at Beza Mahafaly and Berenty, when calculated by sex, average at .07 to .08 for both males and females per year (Sussman, 1991).

Physical examinations

In May 2007 and again in late July 2008, all resident adult members of the Bevaro Moravato troop and all but one female adult resident from the Tsankalamanga troop (who eluded capture) were anesthetized and given the health assessments (see chapter two for a detailed description). At the time of the captures, all individuals were assessed as healthy by physical exams (e.g., weight, temperature, pulse, respiration, dental wear).

In 2007, two individuals (G14 and B5) were completely free of any external afflictions. One older female individual (Mena) had a torn right ear and a notched left ear. Five individuals had broken tails (Mena, G2, B7, G12, R9, R6). Six individuals carried mites (*Liponyssella madagascariensis*[2]). These mites were found in their ears (Mena), on their faces (G10), on their tails (G2, WS, B7), on their chest (R1), and on their scrotums (WS, ST). Four individuals had lice, *Trichophilopterus babakotophilus*[3]. In all cases, lice were found on their tails (G10, B1, B7, G8). A few individuals had superficial thorn pricks, which most likely occurred during the captures. Only one individual (B1) had a major thorn penetration. This thorn was found in his tail.

In 2008, three of the four adult females who received physicals were possibly pregnant (R1, Mena, G10). One female (G10) had new scar tissue on her leg. Last, one male who wasn't noted as having lice before (R9) had lice found on this tail.

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[2] Mites were identified by Hans Klompen, Ohio State University.

[3] Lice were identified by Noah Whiteman, University of Missouri.

Quantitative Results

Health assessments

CSM troop and capture comparisons

The fat-soluble vitamins that were analyzed in this study to be compared with other wild *L. catta* populations were: 25- hydroxyvitamin D (25-OHD), retinol, γ-tocopherol, and α-tocopherol. There were significant differences between the two CSM troops in circulating vitamin levels[4] of 25-OHD (Z = -2.72, p = .004) and in γ-tocopherol (Z = -2.484, p = .012) (**Table 5.1**). There were also significant between-capture[5] differences in retinol (Z = -2.336, p = .018, n = 7).

Table 5.1. Vitamin values of the Bevaro Moravato troop and the Tsankalamanga troop obtained during the May health assessments. *denotes a statistically significant difference between assessments at the .05 level. ** denotes a statistically significant difference between assessments at the .01 level.

	Bevaro Moravato		**Tsankalamanga**	
Parameter	**Mean ±SD**	**n**	**Mean ±SD**	**n**
25 -OHD µmol/L **	45.5 ±17.5	8	100.5 ± 18.8	4
Retinol (µg/dL)	19.6 ± 2.3	8	18.8 ± 5.6	3
γ-Tocopherol (µg/dL) *	13.0 ± 3.6	8	2.7 ± 4.6	3
α- Tocopherol (µg/dL)	279.5 ± 70.8	8	300.3 ± 20.2	3

In addition to vitamin levels, between capture differences were found in physical (weight and vital signs), CBC (complete blood count), chemistry, and mineral data. In the physical data, there were significant between capture differences in the weight of the animals (Z = -2.207, n = 7, p = .027).The range of values in body weight for the first capture were 1.6kg to 2kg (**Table 5.2;** see also **Table 2.2** for a complete list of May 2007 weights), and the range of values in body weight for the second capture were 1.9kg to 2.25 kg (**Table 5.2**). Of those who gained weight,

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[4] Since only two members from the Tsankalamanga troop were included in the second round of health assessment data, all between group comparisons are based solely on first capture data.

[5] Only one individual in the Tsankalamanga troop was assessed twice (G10). Therefore, between capture differences mainly reflect differences for members of the Bevaro Moravato troop.

three were possibly pregnant during the second assessments, and one had been assessed in 2007 as a young adult (R9; see **Table 2.2**).

Table 5.2. Weights of individuals in May 2007 and July 2008. See **Table 2.2** for relative age assessments.

Individual	**Weight (kg) May 2007**	**Weight (kg) July 2008**
B1 ♂	1.65	1.95
G10 ♀	1.60	2.10
R9 ♂	2.00	2.15
G14 ♀	2.10	2.15
R1 ♀	1.80	2.05
WS ♂	1.90	1.90
Mena ♀	1.90	2.25

In the CBC data, significant between capture differences were found in packed cell volume (PCV) percentages (Z = -2.201, n = 7, p = .028).

Table 5.3. Complete blood cell data comparisons between the May 2007 health assessments and the July 2008 health assessments of CSM *L. catta*. *denotes a statistically significant difference between assessments at the .05 level.

	May 2007		**July 2008**	
Parameter	**Mean ±SD**	**n**	**Mean ±SD**	**n**
White blood cells/µL	10,857.1 ± 3,343.0	7	10,781.6 ± 3959.7	7
Packed Cell Volume (%) *	55.9 ± 5.8	7	45.7 ± 5.3	7

Serum chemistry profiles included aspartate transaminase (AST), alanine aminotransferase (ALT), total bilirubin (T Bili), alkaline phosphatase (Alk Phos), gamma-glutamyl transpeptidase (GGT), total protein (TP), albumin, globulin, blood urea nitrogen (BUN), creatinine, P (phosphorus), calcium (Ca), glucose, sodium (Na), potassium (K), chloride (Cl), and creatinine phosphokinase (CPK). Significant between capture differences were found in BUN (Z = -1.120, n = 7, p = .034), creatinine (Z = -2.375, n = 7, p = .018) and Ca (Z = -2.207, n = 7, p = .027) (**Table 5.4**).

Table 5.4. Serum chemistry value comparisons between May 2007 health assessments and July health assessments of CSM *L. catta*. AST = aspartate transaminase, ALT = alanine aminotransferase , ALP = alkaline phosphatase, GGT = gamma-glutamyl transpeptidase , BUN = blood urea nitrogen, Ca = calcium, Na = sodium, K = potassium, Cl = chloride, CPK = creatine phosphokinase. *****denotes a statistically significant difference between assessments at the .05 level.

	May 2007		**July 2008**	
Parameter	**Mean ±SD**	**n**	**Mean ±SD**	**n**
AST (IU/L)	28.0 ±11.9	7	39.7 ±15.7	7
ALT (IU/L)	38.1 ± 11.3	7	34.0 ± 8.3	7
Total bilirubin (mg/dL)	0.6 ± 0.1	7	1.0 ± 0.5	7
ALP (IU/L)	82.6 ± 25.0	7	65.9 ± 12.9	7
GGT (IU/L)	21.6 ± 25.1	7	9.8 ± 4.3	7
Total protein (g/dL)	8.6 ± 0.9	7	8.5± 1.0	7
Albumin (g/dL)	4.8 ± 0.5	7	4.8 ± 0.3	7
Globulin (g/dL)	3.8 ± 0.5	7	3.6 ± 0.8	7
BUN (mg/dL)*****	11.7 ± 5.1	7	7.3 ± 3.2	7
Creatinine (mg/dL)*****	1.2 ± 0.3	7	0.8 ± 0.2	7
Ca (mg/dL)*****	9.2 ± 0.5	7	8.7 ± 0.3	7
Glucose (mg/dL)	173.6 ± 72.0	7	169.6 ± 83.5	7
Na (mEq/L)	144.3 ± 5.2	7	140.0 ± 5.6	7
K (mEq/L)	4.5 ± 0.6	7	4.3 ± 0.6	7
Cl (mEq/L)	112.9 ± 5.5	7	110.1 ± 3.5	7
CPK (IU/L)	969.7 ± 430.1	7	1,006.3 ± 510.2	7

Last, dietary element profiles that were also compared with captive and other wild populations included: cobalt (Co), copper (Cu), selenium (Se), zinc (Zn), iron (Fe), total iron binding capacity (TIBC), ferritin and transferrin saturation (Trans Sat). Only two individuals from the second health assessments were tested for Fe, TIBC, ferritin, and Trans Sat levels (**Table 5.5**). Significant between capture differences were found in levels of Co (Z = -2.028, n = 7, p = .043), Cu (Z = -2.197, n = 7, p = .028) and Se (Z = -2.197, n = 7, p = .028).

Table 5.5. Dietary elements and iron metabolism indices from data collected on CSM *L. catta* during May 2007 and July 2008 health assessments. Co = cobalt, Cu = copper, Se = Selenium, Zn = zinc, Fe = iron, TIBC = total iron binding capacity, Trans Sat = transferrin saturation. *denotes a statistically significant difference between assessments at the .05 level. ^{1}denotes actual values.

	May 2007		**July 2008**	
Parameter	**Mean ±SD**	**n**	**Mean ±SD**	**n**
Co (µg/ml)*	0.5 ± 0.1	7	0.4 ± 0.1	7
Cu (µg/ml)*	1.7 ± 0.3	7	1.3 ± 0.2	7
Se (µg/ml) *	196.6 ± 19.1	7	230.3 ± 28.3	7
Zn (µg/ml)	1.6 ± 0.8	7	1.3 ± 0.4	7
Fe (µg/ml)	126.0 ± 87.0	4	146; 255^1	2
TIBC (µg/dL)	401.3 ± 45.6	4	344; 386^1	2
Ferritin (µg/dL)	105.8 ± 53.56	4	24; 157^1	2
Trans Sat (g/dL)	31.4 ± 22.1	4	37.7; 74.1	2

CSM compared with other sites

There were no significant between site differences in the sex distribution (U = 98.0, $n_1 = 25 + n_2 = 8$, p = .951) and weight (U = 68.0, $n_1 = 25 + n_2 = 8$, p = .190) of CSM and Tsimanampetsotsa (TSNP) *L. catta.*

However, significant between site differences (CSM: TSNP) were found in both white blood cell counts (WBC) (U = 18.0, $n_1 = 25 + n_2 = 8$, $p < .001$) and in packed blood cell counts (PVC) (U = 35.5, $n_1 = 25 + n_2 = 8$, p = .005) (**Table 5.6**).

Table 5.6. Complete blood cell data comparisons between *L. catta* from CSM and *L. catta* from Tsimanampetsotsa (TSNP), Beza Mahafaly, and captive populations. Raw data from TSNP are from Junge (unpublished data) and most values from TSNP were formally analyzed and presented in Dutton et al. 2003 and Miller et al. 2007. Values from Beza Mahafaly and zoo populations are from Miller et al. 2007, Table 2. Results from May are listed as a second value when there were significant between-capture differences. *8denotes a statistically significant difference between CSM and TSNP at the .01 level.

	CSM		**TSNP**		**Beza Mahafaly**		**Captive**	
Parameter	**Mean ±SD**	**n**	**Mean ±SD**	**n**	**Mean ±SD**	**n**	**Mean ±SD**	**n**
White blood cells/mcl**	11.02 ± 3.7	8	4.92 ± 1.9	25	6.9 ± 2.2	59	8.64 ± 3.8	1,226
Packed Cell Volume (%)**	44.4 ± 6.2 55.9 ± 5.8	8 15	37.8 ± 4.7	25	43.5 ± 4.5	59	50.5 ± 6.2	1,249

Significant between site differences in serum chemistry profiles were found in values of T Bili (U = 0.0, $n_1 = 20 + n_2 = 8$, $p < .001$), GGT (U = 16, $n_1 = 20 + n_2 = 6$, $p = .006$), TP (U = 3, $n_1 = 20 + n_2 = 8$, $p < .001$), albumin (U = 23, $n_1 = 20 + n_2 = 6$, $p = .003$), globulin (U = 2.5, $n_1 = 20 + n_2 = 8$, $p < .001$), BUN (U = 19.0, $n_1 = 20 + n_2 = 6$, $p = .001$), Ca (U = 35.0, $n_1 = 20 + n_2 = 8$, $p = .021$), Cl (U = 25.5, $n_1 = 20 + n_2 = 8$, $p = .004$), and CPK (U = 3.0, $n_1 = 20 + n_2 = 8$, $p < .001$) (**Table 5.7**).

Table 5.7. Serum chemistry value comparisons between CSM *L. catta* and *L. catta* fromTsimanampetsotsa (TSNP) , Beza Mahafaly (Beza), and captivity. Raw data are from Junge and most values have been previously analyzed and presented in Dutton et al. 2003 and Miller et al. 2007. Values from Beza Mahafaly and captivity are from Miller et al. 2007, Table 3. Results from May are listed as a second value when there were significant between-capture differences. *denotes a statistically significant difference between CSM and TSNP at the .05 level. **denotes a statistically significant difference between CSM and TSNP at the .01 level. AST = aspartate transaminase, ALT = alanine aminotransferase , ALP = alkaline phosphatase, GGT = gamma-glutamyl transpeptidase , BUN = blood urea nitrogen, Ca = calcium, Na = sodium, K = potassium, Cl = chloride, CPK = reatine phosphokinase.

	CSM		**TSNP**		**Beza Mahafaly**		**Captive**	
Parameter	**Mean ±SD**	**n**	**Mean ±SD**	**n**	**Mean ±SD**	**n**	**Mean ±SD**	**n**
AST (IU/L)	39.6 ±14.3	8	70.7 ± 62.3	20	64.6 ± 45.1	27	48 ± 37	816
ALT (IU/L)	36.1 ± 7.6	8	44.8 ±14.8	20	53.6 ±11.2	27	94 ± 59	763
Total bilirubin (mg/dL)**	0.9 ± 0.5	8	0.25± 0.1	20	0.4 ± 0.1	27	0.6 ± 0.4	838
ALP (IU/L)	65.8 ± 14.0	8	60.5 ±17.1	20	114.1 ± 42.2	27	222 ± 109	864
GGT (IU/L)**	10.0 ± 4.3	6	16.3 ± 4.1	20	13.4 ± 3.7	27	28 ± 18	483
Total protein (g/dL)**	8.2± 1.2	8	5.6 ± 0.7	20	5.8 ± 0.7	27	7.3 ± 0.8	755
Albumin (g/dL)**	4.8 ± 0.4	8	4.3 ± 0.4	20	4.3 ± 0.4	27	5.7 ± 0.9	673
Globulin (g/dL)**	3.4 ± 1.1	8	1.3 ± 0.4	20	1.5 ± 0.4	27	1.6 ± 0.9	660
BUN (mg/dL)*	6.4 ± 3.7 11.0 ± 5.1*	8 14	13.3 ± 4.5	20	7.3 ± 6.0	27	22 ± 8	903
Creatinine (mg/dL)	0.8 ± 0.2 1.2 ± 0.3*	8 14	0.9 ± 0.3	20	0.8 ± 0.2	27	1 ± 0.3	891
Ca (mg/dL)*	8.7 ± 0.3 9.2 ± .49*	8 14	8.0± 1.1	20	8.1± 0.5	26	9.7 ± 0.9	851
Glucose (mg/dL)	146.1± 54.2	8	136.2 ± 36.9	20	188.6 ± 80.1	27	142 ± .2	901
Na (mEq/L)	141.9± 3.5	8	137.4 ± 12.7	20	145.0 ± 6.7	26	148 ± 5	747
K (mEq/L)	4. 3 ± .6	8	4.0 ± 1	20	3.3 ± .6	26	4.4 ± .6	754
Cl (mEq/L)**	111.3 ± 1.6	8	99.7 ± 12	20	103.4 ± 4	27	108 ± 6	740
CPK (IU/L)**	910.9 ± 409.7	8	5,237.9 ± 5,452.4	20	4,508.8 ± 2,959.9	27	1,363 ± 1,248	259

Statistics were not conducted on comparative values of Fe, TIBC, ferritin, and transferrin saturation (**Table 5.8**). Of the shared dietary elements that were tested between CSM and TSNP, statistical differences were found in mineral levels of Cu and Zn (Cu: $U = 2.0$, $n_1 = 18 + n_2 = 8$, $p < .001$) (Zn: $U = 7.0$, $n_1 = 18 + n_2 = 8$, $p < .001$).

Table 5.8. Dietary elements and iron metabolism indices between CSM *L. catta* and populations from Tsimanampetsotsa (TSNP), Beza Mahafaly, and captivity. Raw data are from Junge (unpublished data). However, many of these values have been previously analyzed and published in Dutton et al. 2003 and Miller et al. 2007. Values from Beza Mahafaly and captivity are from Miller et al. 2007, Table 4. Results from May are listed as a second value when there were significant between-capture differences. **denotes a statistically significant difference between CSM and TSNP at the .01 level. ^{1}denotes values from the May health assessments, which are present here to aid in comparisons between the sites since sample sizes in July are so small. All three statistically tested samples of iron metabolism measurements from the May health assessments were significantly higher than the July TSNP values. FE: CSM > TSNP ($p = .024$), TIBC: CSM > TSNP ($p < .001$), ferritin: CSM > TSNP ($p = .004$). Co = cobalt, Cu = copper, Zn = zinc, Fe = iron, TIBC = total iron binding capacity, Trans Sat = transferrin saturation.

	CSM		**TSNP**		**Beza**		**Captive**	
Parameter	**Mean ±SD**	**n**	**Mean ±SD**	**n**	**Mean ±SD**	**n**	**Mean ±SD**	**n**
Co (µg/ml)	0.4 ±.1	7						
	0.5 ± 0.2	13						
Cu (µg/ml)**	1.3 ± 0.2	7	0.8 ± 0.2	18	1.6 ± 0.0	26		
	1.6 ± 0.3	13						
Se (µg/ml)	196.6 ± 19.1	7						
	230.3 ± 28.3	7						
Zn (µg/ml)**	1.3 ± 0.4	8	0.7 ± 0.2	18	3.1 ± 0.4	27		
Fe (µg/ml)	200.5 ± 77.1	2	71.4 ± 31.9	18	155.1 ± 42.2	27	261 ± 1.0	60
	114.4 ± 59.3^1	9						
TIBC (µg/dL)	365.5 ± 30.4	2	240.7 ± 37.4	18	308.5 ± 43.9	27		
	378.2 ± 60.1^1	9						
Ferritin (µg/dL)	91 ± 94.1	2	46.3 ± 31.8	18	169 ± 1.6	27		
	114 ± 59.3^1	9						
Trans Sat (g/dL)	55.9 ± 25.7	2	30.6 ± 14.8	18				
	31.4 ± 22.1^1	4						

Last, significant differences between CSM *L. catta* and TSNP *L. catta* were found in circulating vitamin levels of 25-OHD, γ -tocopherol, and α-tocopherol (25-OHD: $U = 9.0$, $n_1 = 20 + n_2 = 8$, $p < .001$) (γ-tocopherol: $U = 12.5$, $n_1 = 16 + n_2 = 8$, $p = .001$) (α-tocopherol: $U = 24.5$, $n_1 = 20 + n_2 = 8$, $p = .003$) (**Table 5.9**).

Table 5.9. Vitamin values between CSM *L. catta* and *L. catta* populations from Tsimanampetsotsa (TSNP), Beza Mahafaly, and captivity. Raw data from TSNP are from Junge (unpublished). However, much of these values have been previously analyzed and presented in Dutton et al. 2003 and Miller et al. 2007. Mean values from Beza Mahafaly and captivity are from Miller et al. 2007, Table 4. Both values have been listed when there are also significant between troop differences at CSM. BM = Bevaro Moravato, TA = Tsankalamanga (May assessments only). **denotes a statistically significant difference between CSM and TSNP at the .01 level. 25-OHD = 25-hydroxyvitamin D.

	CSM		**TSNP**		**Beza**	
Parameter	**Mean ±SD**	**n**	**Mean ±SD**	**n**	**Mean ±SD**	**n**
Vitamin D (μmol/L)**	67.4 ± 25.0	7	28.1 ± 12.3	20	34.1 ± 14.8	27
	45.5 ±17.5(BM)	8				
	100.5 ±18.8(TA)	4				
Retinol (μg/dL)	21.7 ± 4.7	7	19.0 ± 5.2	18	21.6 ±3.7	26
γ -Tocopherol (μg/dL)**	7.6 ± 2.4	8	15.6 ± 5.8	16	18.1 ± 5.4	26
	13.0 ± 3.6(BM)	8				
	2.7 ± 4.6 (TA)	3				
α -Tocopherol (μg/dL)**	364.5 ± 220.3	8	195.4 ± 59.8	20	184.8 ± 55.9	26

Diet

By plant part and species

Intra-site comparisons

When food types were analyzed by month, there were some differences in the diets of the two troops. For every month, the primary food type consumed by the Tsankalamanga troop was fruit (**Table 5.10**; see also **Table 3.3**). While fruit also composed a majority of the diet for the Bevaro Moravato troop nine months of the year, leaves were the primary component of the Bevaro Moravato troop's diet from the months of August through October. In addition, with the exception of the month of April, members of the Bevaro Moravato troop consumed more flowers, especially throughout the months of January, March, July, August and September (**Table 5.10**; see also **Table 3.3**). Conversely, the yearly summary of the two troops' diets by food type were markedly similar (**Table 5.11**).

Table 5.10. Monthly percentages of food type. FR = fruit and seeds, LV = leaves, FL = flowers, IN =insect, OT = other.

Month	Type	Bevaro Moravato % Consumed	Tsankalamanga % Consumed
January	FR	44.1%	59.8%
	FL	23.3%	3.2%
	LV	30.9%	36.8%
	IN	.7%	0%
	OT	.7%	0%
February	FR	85.6%	65.7%
	FL	6.4%	6.3%
	LV	6.8%	21.6%
	IN	1.5%	6.3%
	OT	0%	0%
March	FR	58.7%	58.8%
	FL	5.0%	1.5%
	LV	33.1%	38.3%
	IN	3.1%	1.5%
	OT	0%	0%
April	FR	80.3%	52.4%
	FL	11.3%	17.7%
	LV	7.7%	29.9%
	IN	.5%	0%
	OT	0%	0%
May	FR	87.2%	75.9%
	FL	0%	0%
	LV	12.9%	22.3%
	IN	.2%	1.9%
	OT	0%	0%
June	FR	62.5%	53.2%
	FL	0%	0%
	LV	36.6%	46.8%
	IN	.8%	0%
	OT	0%	0%
July	FR	59.3%	62.6%
	FL	5.9%	1.4%
	LV	34.7%	34.8%
	IN	0%	0%
	OT	0%	1.4%
August	FR	25.8%	86.2%
	FL	19.0%	2.7%
	LV	55.2%	11.1%
	IN	0%	0%

Month	Type	Bevaro Moravato % Consumed	Tsankalamanga % Consumed
	OT	0%	0%
September	FR	35.3%	59.8%
	FL	20.3%	12.8%
	LV	44.0%	27.4%
	IN	.4%	0%
	OT	0%	0%
October	FR	44.2%	67.0%
	FL	9.8%	9.0%
	LV	46.2%	23.2%
	IN	0%	0%
	OT	0%	.5%
November	FR	66.8%	62.7%
	FL	6.3%	10.2%
	LV	26.0%	27.0%
	IN	.5%	0%
	OT	.3%	0%
December	FR	84.7%	80.2%
	FL	.9%	0%
	LV	14.5%	29.8%
	IN	.3%	0%
	OT	0%	0%

Table 5.11. Yearly percentages of the focal troops' diets at CSM by food type

	Bevaro Moravato	Tsankalamanga
Fruit and seeds	64.7%	65.9%
Leaves	25.5%	25.2%
Flowers	8.4%	6.8%
Insect	1.3%	2.0%
Other	0.0%	0.1%

Neither focal troop from CSM was observed entering human latrine sites (open ground waste centers) nor were they observed feeding on any fecal material save for that of *Geochelone radiata*, the radiated tortoise. Similarly, although the zebus were typically fed within the fields that were circumscribed by the lemurs' sleeping hedges, the lemurs were never observed feeding on the fodder, which was typically burnt *Opuntia monacantha* pads. However, the lemurs did feed on discarded skins of *O. monacantha* fruit. While the Bevaro Moravato troop was observed feeding on these scraps on seven different days, the Tsankalamanga troop was observed feeding on *O. monacantha* scraps three different days. This was the only human food scrap that the lemurs consumed.

Many plant species were only consumed in the sacred forest habitats (**Table 5.12)**. However, the leaves of both *Alluaudia procera* and *Cedrelopsis grevei* were the only species consumed for more than 10 minutes of the total yearly observations of feeding behavior. Moreover, there was no overlap in the species consumed between the two focal groups even though species such as *A. procera* were present in sacred forests at both sites.

Table 5.12. The list of plant species consumed exclusively in sacred forest habitats by CSM *L. catta*. n = the number of observed minutes each plant was consumed throughout the year.

Bevaro Moravato	**n**	**Tsankalamanga**	**n**
Alluaudia procera	56	*Cedrelopsis grevei*	23
Euphorbia sp. “tsambara”	9	*Terminalia mantaly*	8
Euphorbiaceae “razilazana”	8	*Albizzia* sp. “tsikifarefare”	3
Cedrelopsis grevei	6	*Terminalia ulexioides*	3
“Rothmannia” sp. “sofikomba”	3		
Citrullus lanatus	2		
Cynanchum perrieri	2		
Phyllanthus sp. *“*solhotse”	1		
Xerosicyos danguyi	1		

Both troops spent most of their feeding time on (plant) species that were also consumed by the other troop. While BM spent 70.9%, of its feeding time consuming mutual species, the Tsankalamanga troop spent 82.8% of its feeding time consuming mutual species (**Table 5.13**; **Table 5.14**). However, the Bevaro Moravato troop fed most often on the fruit of a small tree, *Strychnos decussata*, which was not consumed by the Tsankalamanga troop (**Table 5.10**). In contrast, the Tsankalamanga troop concentrated almost one fourth of its feeding time on the fruits of *Opuntia monacantha* (**Table 5.14**).

Table 5.13. Food species of the Bevaro Moravato troop from August 2007 through July 2008 organized into two lists 1) foods included in the diet of the Tsankalamanga troop, and 2) foods consumed only by the Bevaro Moravato troop. Foods are listed in receding order of observed consumption. BM = Bevaro Moravato, TA = Tsankalamanga.

BM Shared Species w/TA	% of Diet	BM Unique Species	% of Diet
Phyllanthus amanu	8.96%	*Strychnos decussata*	11.85%
Opuntia stricta	7.78%	*Commiphora* sp.	4.66%
Metaporana sp.	7.76%	*Azima tetracantha*	3.66%
Terminalia fatrae	6.60%	*Flueggea virosa*	1.32%
Opuntia monacantha	6.57%	*Alluaudia procera*	1.25%
Terminalia ulexioides	4.00%	*Tabernaemontana modesta*	0.91%
Zygophyllum madecassum	3.68%	Acanthaceae ‘indet. plant”	0.75%
Mimosa sp.	3.66%	*Euphorbia hirta*	0.64%
Rinorea sp.	3.59%	*Terminalia* sp.	0.55%
Leptadenia sp.	3.27%	*Pouzolzia mandrarensis*	0.30%
Paederia sp.	2.57%	*Strychnos madagascariensis*	0.30%
Aloe vahombe	2.00%	*Vepris* sp.	0.27%
Buxus madagascariensis	1.86%	*Kalanchoe integrifolia*	0.23%
Grewia cyclea	1.46%	*Euphorbia* sp.	0.20%
Commiphora simplicifolia	0.96%	*Poupartia* sp.	0.20%
Grewia punctata	0.75%	"fatikekolahy"	0.20%
Zygophyllum depauperatum	0.75%	Euphorbiaceae “indet. plant”	0.18%
Fabaceae “indet. plant”	0.68%	*Opuntia ficus-indica* var. *inermis*	0.18%
Poupartia junior	0.68%	unidentified insect nest	0.18%
Gymnosporia linearis	0.61%	*Phyllanthus amanu*	0.16%
Flacourtia ramontchi	0.52%	*Psiadia restita*	0.14%
Aloe divaricta	0.30%	*Rhigozum madagascariensis*	0.14%
Adenia sp.	0.27%	*Diospyros* sp.	0.11%
termites	0.27%	"kolovy"	0.09%
Croton sp.	0.25%	*Abutilon asiaticum*	0.09%
Maerua filiformis	0.20%	*Cucums* sp.	0.09%
Diospyros sp.	0.18%	Formicidae “indet. plant”	0.09%
cicadas	0.16%	*Psiadia altissima*	0.09%
Cedrelopsis grevei	0.14%	“*Rothmannia”* sp.	0.07%
Ficus marmonata	0.14%	*Achyrocalyx decaryi*	0.05%
Grewia sp.	0.07%	*Citrullus lanatus*	0.05%
Terminalia mantaly	0.07%	*Ipomoea batatas*	0.05%

BM Shared Species w/TA	% of Diet	BM Unique Species	% of Diet
Cynanchum perrieri	0.05%	spiders	0.02%
Marsdenia sp.	0.05%	*Xerosicyos danguyi*	0.02%
Alluaudia dumosa	0.02%		
Phyllanthus sp.	0.02%		

Table 5.14. Food species of the Tsankalamanga troop from August 2007 through July 2008 organized into two lists 1) foods included in the diet of the Bevaro Moravato troop, and 2) foods consumed only by the Tsankalamanga troop. Foods are listed in receding order of observed yearly consumption. BM = Bevaro Moravato, TA = Tsankalamanga.

TA Shared Species w/BM	% of Diet	TA Unique Species	% of Diet
Opuntia monacantha	23.76%	*Azima tetracantha*	5.25%
Metaporana sp.	8.79%	*Boscia* sp.	3.08%
Opuntia stricta	8.05%	*Psiadia restita*	2.23%
Terminalia fatrae	5.54%	*Canthium* sp.	1.83%
Zygophyllum madecassum	4.68%	*Operculicarya decaryi*	1.60%
Grewia cyclea	2.86%	"matiake"	1.31%
Adenia sp.	2.51%	*Opuntia ficus-indica* var. *inermis*	0.51%
Flacourtia ramontchi	2.51%	*Tarenna* sp.	0.34%
Grewia punctata	2.28%	*Bulkophylum* sp.	0.23%
Paederia sp.	2.11%	*Albizzia* sp.	0.17%
Aloe vahombe	1.88%	*Cissus quadrangularis*	0.17%
Mimosa sp.	1.88%	*Manihot esculenta*	0.17%
Phyllanthus amanu	1.88%	*Stereospermum variabile*	0.11%
Cedrelopsis grevei	1.31%	dirt	0.06%
Leptadenia sp.	1.31%	*Geochelone radiata* feces	0.06%
Grewia sp.	1.20%	*Kalanchoe beharensis*	0.06%
Poupartia junior	1.14%	*Xerosicyos danguyi*	0.06%
Maerua filiformis	1.09%		
Diospyros sp.	0.97%		
Croton sp.	0.74%		
Ficus marmonata	0.74%		
Aloe divaricta	0.69%		
Zygophyllum depauperatum	0.63%		
Marsdenia sp.	0.51%		
Phyllanthus sp.	0.51%		
Rinorea sp.	0.51%		
Terminalia mantaly	0.46%		
Alluaudia dumosa	0.40%		

TA Shared Species w/BM	% of Diet	TA Unique Species	% of Diet
termites	0.40%		
Buxus madagascariensis	0.29%		
Cynanchum perrieri	0.29%		
cicadas	0.23%		
Commiphora simplicifolia	0.17%		
Gymnosporia linearis	0.17%		
Terminalia ulexioides	0.17%		
Fabaceae “indet. plant”	0.06%		

Inter-site comparisons

The diet composition of the CSM troops is very similar to that which was first observed by Jolly (1966) during her pioneer study at Berenty. To review, the CSM troops consumed fruit approximately 65% of the time, leaves 25% of the time, and flowers 8% of the time (**Table 5.11**). In comparison, Jolly observed *L. catta* at Berenty consume fruit 70% of the time, leaves 25% of the time, and flowers 5% of the time (Sussman in press).

CSM *L. catta* consumed the leaves, flowers, or fruits of a total of 71 different plant species during the 2007-2008 field season. In comparison, Sauther (1992) observed two troops of *L. catta* at Beza Mahafaly feed on a total of 62 different plant species during a yearlong study, and over 100 different plant species are known to be consumed by troops at Berenty (Simmen et al., 2006). Sussman (1972) observed *L. catta* at Antserananomby consume a total of 20 plant species from the months of July to September. Similarly, the CSM troops were observed consuming a combined total of 25 different plant species during these months (BM = 21; TA = 13; see also **Table 3.3**).

The plant species consumed by CSM *L. catta* that are also consumed by

Berenty *L. catta* include: *Alluaudia dumosa, A. procera, Aloe vahombe, Azima tetracantha, Cedrelopsis grevei, Flacourtia ramontchi, Maerua filiformis,* and *Operculicarya decaryi.* When the plants that could be categorized only at the genus level are added, the shared genera include *Commiphora, Croton, Euphorbia, Ficus, Grewia, Phyllanthus,* and *Metaporana*. Of these shared taxa, *Alluaudia procera* (BM only), *Aloe vahombe, Azima tetracantha, Cedrelopsis grevei, Maerua filiformis, Operculicarya decaryi* (TA only), and *Metaporana* each composed over 1% of the CSM troops' diets (**Table 5.13; Table 5.14;** see also **Table 3.3**).

The plant species consumed by CSM *L. catta* that are also consumed by Beza Mahafaly *L. catta* include: *Azima tetracantha, Cedrelopsis grevei, Cynanchum perrieri, Flacourtia ramontchi, Grewia cyclea,* and *Maerua filiformis*. When plants are categorized at the genus level, the shared list also includes *Euphorbia, Flueggea,* and *Metaporana*. Of these shared taxa, *Azima tetracantha, Cedrelopsis grevei, Grewia cyclea, Maerua filiformis,* and *Metaporana* each composed over 1% of the CSM troops' diets (**Table 5.13**; **Table 5.14**).

Last, the plant species consumed by CSM *L. catta* that were also consumed by *L. catta* at Antserananomby during the austral winter months include *Flacourtia ramontchi, Terminalia mantaly, Adenia, Grewia,* and *Paedria*. However, *Paedria* is the only kind of plant that was also consumed by the CSM troops during the austral winter months, and *Flacourtia ramontchi* (TA only) was the only other shared taxon consumed at all during the July to September timeframe (see **Table 3.3**).

Nutrient analyses

Based on the primary dietary recommendations for primates (Committee on Animal Nutrition, 2003), the estimated yearly percentages of crude protein (CP) were relatively low in the diets of both CSM troops (**Table, 5.15**). However, these values compare with the estimated CP consumption of provisioned troops on St. Catherines Island[6] (**Table 5.15**; Dierenfeld and McCann, 1999), and the standard deviation of the values include numbers that are within the recommended range (**Table 5.15**). Phosphorus (P) was also low in the CSM troops' overall diets but comparable with the estimated P intake of the St. Catherines' population. In contrast, macromineral concentrations of calcium (Ca) and sodium (Na) were high both in relation to primary recommendations and in comparison with the provisioned troops at St. Catherines. Iron (Fe) and manganese (Mn) were very high in the plants most frequently consumed by the CSM troops.

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[6] While nutrient analyses from St. Catherines Island is based on the collection of 100% of the plant taxa consumed by *L. catta* observed for three two-day observation periods four months a year (a month per season) (Dierenfeld and McCann, 2003), nutrient analyses from CSM is based on the top 75% of the species observed to be consumed by *L. catta* for roughly four days a week, 10 hours a day throughout the year. In addition, while three to five samples of each plant taxa were analyzed from St. Catherines, only one to two samples of each plant taxa were analyzed from CSM. Thus, results between the two sites should be interpreted with these different methodologies in mind.

Table 5.15. Nutrient composition of plants consumed by *L. catta* at three different sites: St. Catherines Island in Georgia, USA, which is a population of free-ranging lemurs that are partially provisioned, and the two CSM focal troops. Values are presented as weighted means and standard deviations on a dry basis. Primary dietary recommendations and the values obtained from St. Catherines Island are from Dierenfeld and McCann (1999) and the Committee on Animal Nutrition (2003). NDF = neutral detergent fiber, Ca = calcium, Mg = magnesium, Na = sodium, P = phosphorus, Cu = copper, Fe = iron, Mn = manganese, Zn = zinc, WSC = water soluble carbohydrates. * (10) is the recommended value for Zn from the NRC, 1978. While the recommended values from many of the nutrients have been refined since 1978, the recommended concentration of zinc appears to have changed the most markedly. One likely reason for the pronounced recommended increase is to prevent Zn deficiency, especially in pregnant females, as iron can affect the absorption of Zn (NRC, 2003). However, it is likely that primates can have diets with zinc concentrations that are much lower than 100 mg/kg as nonpregnant rhesus monkeys were found to have normal plasma levels when fed an air-dried diet of 12 mg/kg (NRC, 2003).

	St. Catherines n= 61	**Bevaro Moravato (CSM) n = 28**	**Tsankalamanga (CSM) n = 28**	**Primate dietary recommendations**
CP (%)	11.52 ± 6.74	11.50 ± 6.36	12.72 ± 8.68	15-22
NDF (%)	38.38 ± 16.73	35.95 ± 14.50	29.38 ± 15.23	10 to 30
Ca (%)	0.63 ± 0.19	1.17 ± 1.07	1.59 ± 1.17	0.8
Mg (%)	0.35 ± 0.29	0.28 ± 0.14	0.39 ± 0.36	0.08
Na (%)	0.08 ± 0.04	0.29 ± 0.61	0.49 ± 1.61	0.20
P (%)	0.25 ± 0.04	0.16 ± 0.06	0.19 ± 0.30	0.6
Cu (mg/kg)	13.59 ± 6.00	7.29 ± 15.45	13.50 ± 57.44	20
Fe (mg/kg)	65.03 ± 20.19	431.57 ± 666.41	453.29 ± 660.26	100
Mn (mg/kg)	48.60 ± 18.63	110.93 ± 208.91	106.46 ± 159.18	20
Zn (mg/kg)	35.42 ± 4.03	15.32 ± 6.81	17.82 ± 6.40	100 (10)*
WSC		25.76 ± 16.78	31.78 ± 25.10	

For all nutrient values, large standard deviations were due entirely to higher than average outliers and extreme values. Moreover, there were outliers for every nutrient except for CP and WSC.

Neutral detergent fiber (NDF) concentrations were high in *Operculicarya decaryi* and *Terminalia fatrae* (**Table 5.16**). These plants were only consumed by the Tsankalamanga troop, and these plants were primarily consumed during the austral summer months. When estimated intakes of NDF% were analyzed on a yearly scale, however; the Tsankalamanga troop appears to have ingested less of this nutrient (**Table 5.15**).

Table 5.16. Plant species with neutral detergent fiber (NDF) concentrations that were outliers relative to all CSM plant species analyzed. Percent consumed refers to the percentage of observed monthly consumption of the species relative to all feeding behavior.

Troop	Month	Species	% Consumed	Mineral	Concentration
TA	January	*Terminalia fatrae*	10.2	NDF	66.6%
TA	February	*Terminalia fatrae*	28.0	NDF	66.6%
TA	March	*Terminalia fatrae*	14.7	NDF	66.6%
TA	November	*Operculicarya decaryi*	8.8	NDF	70.2%

With the exception of *Psiadia restita*, all of the plants analyzed from CSM were low in phosphorus. *Aloe vahombe* has a P concentration that is a high outlier when compared with the rest of the CSM's diet but is still low by absolute standards (**Table 5.15; Table 5.17**). *A. vahombe* is also high in Zn, by both relative and absolute standards (**Table 5.15; Table 5.18**).

Table 5.17. Plant species with phosophorus (P) concentrations that were outliers and extreme values relative to all CSM plant species analyzed. Percent consumed refers to the percentage of observed monthly consumption of the species relative to all feeding behavior.

Troop	Month	Species	% Consumed	Concentration
TA	January	*Psiadia restita*	10.8	2.8%
BM	August	*Aloe vahombe*	9.5	0.36%
TA	September	*Aloe vahombe*	12.8	0.36%
BM	September	*Aloe vahombe*	20.3	0.36%
BM	October	*Aloe vahombe*	9.8	.36%
TA	October	*Aloe vahombe*	9	0.36%

Table 5.18. Plant species with zinc (Zn) concentrations that were outliers and extreme values relative to all plant species analyzed from CSM. Percent consumed refers to the percentage of observed monthly consumption of the species relative to all feeding behavior.

Troop	Month	Species	% Consumed	Mg/kg
TA	January	*Grewia cyclea*	12.7	40
BM	August	*Aloe vahombe*	9.5	37
BM	September	*Aloe vahombe*	20.3	37
TA	September	*Aloe vahombe*	12.8	37
TA	October	*Aloe vahombe*	9	37

Plants with very high Ca concentrations were consumed by both troops, notably through consumption of the leaves of the native and abundant *Zygophyllum madecassum* shrubs (**Table 5.19**). Leaves from this plant were also very high in Na (**Table 5.20**) and Mg (**Table 5.21**). However, while concentrations of Na and Mg were high in both samples of *Z. madecassum* that were analyzed, Ca values of *Z. madecassum* dropped to 3.69% in the September/October sample.

Table 5.19. Plant species with calcium (Ca) concentrations that were outliers and extreme values relative to all plant species analyzed from CSM. Percent consumed refers to the percentage of observed monthly consumption of the species relative to all feeding behavior.

Troop	**Month**	**Species**	**% Consumed**	**Concentration**
BM	January	*Zygophyllum madecassum*	12.2	4.99%
TA	February	*Zygophyllum madecassum*	6.3	4.99%
TA	March	*Zygophyllum madecassum*	5.4	4.99%
TA	April	*Flacourtia ramountry*	6.5	4.44%
TA	April	*Zygophyllum madecassum*	7.3	4.99%
BM	September	*Flueggea virosa*	5.7	6.49%
BM	November	*Mimosa* sp.	10.2	4.44%

Table 5.20. Plant species with sodium (Na) concentrations that were outliers and extreme values relative to all plant species analyzed from CSM. Percent consumed refers to the percentage of observed monthly consumption of the species relative to all feeding behavior.

Troop	**Month**	**Species**	**% Consumed**	**Concentration**
BM	January	*Zygophyllum madecassum*	12.2	6.732%
TA	January	*Adenia* sp.	10.2	0.718%
TA	January	*Psiadia restita*	10.8	0.626%
TA	February	*Adenia* sp.	14.4	0.718%
TA	February	*Zygophyllum madecassum*	6.3	6.732%
TA	March	*Zygophyllum madecassum*	5.4	6.732%
TA	April	*Zygophyllum madecassum*	7.3	6.732%
TA	April	*Adenia* sp.	6.5	0.718%
TA	May	*Cantium* sp.	14.8	1.737%
BM	August	*Leptadenia* sp.	17.7	0.497%
BM	September	*Flueggea virosa*	5.7	1.801%
TA	September	*Zygophyllum madecassum*	15.4	8.382%
BM	October	*Leptadenia* sp.	5.7	0.497%
TA	October	*Zygophyllum madecassum*	9	8.382%
BM	November	*Leptadenia* sp.	5.2	0.497%

Table 5.21. Plant species with magnesium (Mg) concentrations that were outliers and extreme values relative to all plant species analyzed from CSM. Percent consumed refers to the percentage of observed monthly consumption of the species relative to all feeding behavior.

Troop	Month	Species	% Consumed	Mineral	Concentration
BM	January	*Zygophyllum madecassum*	12.2	Mg	1.69%
TA	February	*Zygophyllum madecassum*	6.3	Mg	1.69%
TA	March	*Zygophyllum madecassum*	5.4	Mg	1.69%
BM	April	*Zygophyllum madecassum*	7.3	Mg	1.69%
TA	May	*Cantium* sp.	14.8	Mg	0.87%
TA	September	*Zygophyllum madecassum*	15.4	Mg	1.96%
TA	October	*Psiadia restita*	10.8	Mg	1.37%
TA	October	*Zygophyllum madecassum*	9	Mg	1.96%
BM	November	*Alluaudia procera*	5	Mg	0.9%

Fe was high among the plants analyzed from CSM (**Table 5.15**). Two samples from the species *Zygophyllum depauperatum* and *Opuntia stricta* had Fe concentrations that were extremely high at 1,420 mg/kg and 2,590 mg/kg respectively (**Table 5.22**). However, another sample of *Opuntia stricta,* collected in January, had an iron content of only 147 mg/kg.

Table 5.22. Plant species with iron (Fe) concentrations that were extreme values relative to all CSM plants analyzed. Percent consumed refers to the percentage of observed monthly consumption of the species relative to all feeding behavior.

Troop	Month	Species	% Consumed	Mg/kg
BM	June	*Zygophyllum depauperatum*	6.6	1420
BM	July	*Opuntia stricta*	34.6	2590
TA	October	*Opuntia stricta*	34	2590
TA	November	*Opuntia stricta*	18.1	2590

Both samples of *Opuntia stricta* also had extremely high Mn content, 441 mg/kg and 1,300 mg/kg (**Table 5.23**). *Alluaudia procera*[7], a tree that was primarily found only around tombs in the CSM region, also had extremely high levels of Mn, 629 mg/kg. Commonly eaten native and abundant plants were also found to have high Mn levels; notably the leaves of the *Adenia sp*. (moky) vine at 222 mg/kg, and the fruits of *Phyllanthus amanu* bush at 217 mg/kg.

Table 5.23. Plant species with manganese (Mn) concentrations that were outliers and extreme values relative to all plant species analyzed from CSM. Percent consumed refers to the percentage of observed monthly consumption of the species relative to all feeding behavior.

Troop	**Month**	**Species**	**% Consumed**	**Mg/kg**
BM	January	*Opuntia stricta*	7.4	1300
TA	January	*Adenia* sp.	10.2	222
TA	February	*Opuntia stricta*	8.3	1300
TA	February	*Adenia* sp.	9	222
TA	April	*Adenia* sp.	6.5	222
BM	July	*Opuntia stricta*	34.6	441
BM	August	*Opuntia stricta*	28.2	441
BM	September	*Phyllanthus amanu*	4.4	217
BM	October	*Alluaudia procera*	13.6	629
BM	October	*Opuntia stricta*	23.4	441
BM	October	*Phyllanthus amanu*	14	217
TA	October	*Opuntia stricta*	23.4	441
BM	November	*Alluaudia procera*	13.6	629
BM	November	*Opuntia stricta*	5	1300
BM	December	*Phyllanthus amanu*	11.4	217

Last, the yearly weighted average of estimated Cu in the plants species consumed by CSM lemurs was within range of dietary recommendations (**Table**

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[7] *Alluaudia procera* is a tree that is native to Madagascar and endemic to the country's subarid deciduous and southwestern thornbush region (Rauh, 1995; Schatz, 2001). However, it is disputed whether the sparse presence *of A. procera* outside of sacred forests in the CSM region is due to the fact that this species is commonly cut and used by the local Antandroy for housing and cooking (Mbola, pers comm; see also Rauh, 1995; Ratsirarson and Silander, 2003), or because it is not naturally present in this region but is planted as ornaments around tombs.

5.15). However, the focal troops each consumed the leaves of an abundant and endemic vine species with extremely high, perhaps even toxic (NRC, 2005), levels of this mineral. While the Bevaro Moravato troop consumed relatively large amounts of *Leptadenia* sp. (nonosora) with a copper content of 199 mg/kg, the Tsankalamanga troop consumed relatively large amounts of *Adenia* sp. (moky) with a copper content of 370 mg/kg (**Table 5.24**).

Table 5.24. Plant species with copper (Cu) concentrations that were outliers and extreme values relative to all plant species analyzed from CSM. Percent consumed refers to the percentage of observed monthly consumption of the species relative to all feeding behavior.

Troop	Month	Species	% Consumed	Mg/kg
TA	January	*Adenia* sp.	10.2	370
TA	February	*Adenia* sp.	9	370
TA	April	*Adenia* sp.	6.5	370
BM	May	*Cantium* sp.	14.8	18
BM	August	*Leptadenia* sp.	17.7	119
BM	October	*Leptadenia* sp.	5.7	119
BM	November	*Leptadenia* sp.	5.2	119

Water content

The average weighted water content of the plant species consumed by the Tsankalmanga troop was higher than the average weighted water content of the plant species consumed by the Bevaro Moravato troop (TA: 70.95 ± 15.88%; BM: 59.59 ± 20.95%)[8]. There were two outlier species in water content, and both of these species had low water content relative to all of the other plant species consumed at CSM (**Table 5.25**). Both of these samples were from commonly eaten native and abundant plants, both samples were consumed by the Bevaro Moravato troop, and both of these samples were consumed in the month of August (see also **Table 3.3; Table 5.25**).

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[8] see chapter two for methodology

Table 5.25. Samples of plant species with water contents that were outliers relative to all plants consumed at CSM.

Troop	Month	Species	% Consumed	Amount
BM	August	*Mimosa* sp.	12.9	10.64
BM	August	*Grewia punctata*	9.5	10.98

When aggregated by (sub)species on a yearly scale, 10 of the 71 plant species consumed by the CSM troops had mean and/or median water contents of over 80% (**Table 5.26**). The plants with the highest mean (and median) water content were the flowers and leaves of the endangered *Aloe vahombe* species (two varieties differentiated locally as “Vahotrandana” and “Vahobey”), the leaves of the common and abundant *Zygophyllum madecassum* bush, and *Opuntia monacantha*. All of these plants are estimated to contain 88-91% water. Included in the 10 species of plants with 80% or more water content are the cultivated cactus *O. ficus-indica* var. *inermis*, *O. stricta*, and the invasive liana species *Cissus quadrangularis*. The remaining two species with over 80% water content not mentioned above, *Kalanchoe integrifolia* and *Adenia* sp. (moky), are native and abundant to the region.

Table 5.26. Water content in plants consumed by CSM *L. catta*.

Plant	Mean	Standard deviation	Median	n
Aloe vahombe "vahotrandana"	90.7%	9.0%	91.4%	9
Aloe vahombe "vahobey"	88.8%	2.5%	88.3%	4
Zygophyllum madecassum	88.2%	3.0%	88.7%	36
Opuntia monacantha	85.7%	3.0%	88.0%	52
Alluaudia procera	84.5%	4.7%	82.8%	6
Opuntia ficus-indica var. *inermis*	83.7%	0.9%	83.7%	4
Kalanchoe integrifolia	82.9%	5.9%	85.9%	9
Opuntia stricta	82.6%	3.8%	82.1%	55
Cissus quadrangularis	81.9%	12.2%	78.8%	2
Adenia sp.	79.6%	6.2%	81.8%	11
Terminalia ulexioides	78.0%	1.2%	78.8%	4
Xeroolaena sp.	77.0%	13.9%	74.2%	2
Aloe divaricta	76.6%	7.8%	78.1%	11

Plant	**Mean**	**Standard deviation**	**Median**	**n**
Albizzia sp.	75.8%	2.6%	76.8%	6
Cucumis sp.	75.7%	2.0%	76.0%	6
Rinorea sp.	74.1%	4.8%	72.4%	9
Commiphora simplicifolia	73.9%	10.6%	78.4%	10
Bulkophylum sp.	73.4%	4.9%	78.0%	8
Fabaceae	73.3%	8.0%	74.6%	11
Zygophyllum depauperatum	71.3%	9.3%	70.1%	8
Achyrocalyx decaryi	71.1%	11.7%	72.1%	13
Cantium sp.	70.7%	4.1%	70.8%	4
Paedria sp.	70.3%	4.5%	70.9%	17
Phyllanthus amanu	69.6%	10.9%	71.3%	10
Pouzolzia mandrarensia	68.3%	1.5%	69.6%	4
Liane metaporana	68.0%	3.7%	69.2%	10
"sojasoja"	66.4%	4.1%	68.8%	2
Phyllartron sp.	65.6%	6.0%	66.1%	3
Azima tetrachanta	65.4%	6.0%	66.7%	8
"fatikekolahy"	64.9%	8.5%	65.4%	6
Flueggea virosa	64.1%	7.9%	66.0%	14
Cynanuim perrieri	64.1%	17.5%	72.5%	4
Cedrelopsis grevei	63.8%	8.0%	60.7%	7
"sassavy"	62.8%	0.3%	62.6%	2
Rhigozum madagascariensis	62.1%	14.3%	68.8%	7
Commiphora sp.	62.0%	2.4%	63.2%	2
Spomea batatas	60.3%			1
Grewia punctata	60.1%	20.3%	56.4%	13
Flacourtia ramountry	59.7%	3.5%	59.4%	8
Operculicarya decaryi	59.7%	1.9%	58.4%	2
Croton sp.	59.1%	0.3%	59.0%	3
Maerua filiformis	58.8%	4.1%	61.1%	2
Leptadenia sp.	58.0%	9.6%	64.8%	8
Psiadia restita	57.9%	18.1%	63.3%	9
Leptadenia sp.	57.6%	14.5%	64.5%	24
Poupartia junior	56.3%			1
Grewia sp.	54.9%	3.0%	54.0%	7
Vepris sp.	54.5%	1.7%	55.5%	2
"horantrana"	54.2%	0.6%	53.9%	2
Metaporana sp.	52.8%	14.4%	54.5%	30
Diospyros sp.	52.5%			1
"matiske"	50.9%	1.7%	50.8%	3
Terminalia fatrae	48.6%	15.6%	50.5%	7

Plant	**Mean**	**Standard deviation**	**Median**	**n**
Buxus madagascariensis	48.3%	2.7%	46.8%	2
Mimosa sp.	48.2%	19.8%	48.8%	13
Ficus marmonata	43.8%	22.5%	43.2%	4
Stereospermum variabile	43.3%	7.6%	43.2%	4
Euphorbiaceae “indet. plant”	43.1%	18.0%	25.0%	5
Manihot utilissima	40.7%			1
Terminalia mantaly	40.4%			1
Poupartia sp.	39.8%	6.8%	39.6%	4
Euphorbia hirta	38.7%	15.8%	50.2%	6
Terminalia sp.	38.1%	16.7%	35.4%	5
Grewia cyclea	38.1%	18.5%	35.2%	19
Diospyros sp.	35.3%	3.2%	33.4%	2
Tabernaemontana modesta	35.2%	9.4%	31.4%	5
Euphorbia sp.	33.8%	5.1%	30.8%	2
Cantium sp.	33.4%	20.4%	27.4%	6
Strychnos madagascariensis	30.8%			1
Ahutilon asiatiaim	23.1%	1.9%	23.1%	4
Terminalia sp.	21.0%	0.9%	21.5%	2
Stereospermum sp.	20.2%	5.8%	23.5%	2
Tarerna sp.	18.1%	10.1%	18.1%	6

Of the introduced species with high water content, *O. monacantha* and *O. stricta* were the only introduced species that was a major component of the troops’ monthly diets (**Table 5.13-Table 5.14**). If these species were removed from the Bevaro Moravato troop’s environment, this troop’s diet would still consist of plants with high water content throughout the year, although they would likely consume considerably less water in the months of July and August (**Fig. 5.1-Fig. 5.2**). However, the change in water consumption without *Opuntia* in the environment would be more dramatic for the Tsankalamanga troop, especially during the austral winter months (**Fig. 5.3-Fig. 5.4**). In fact, finding an equivalent source of sustenance during these months would be necessary for this troop.

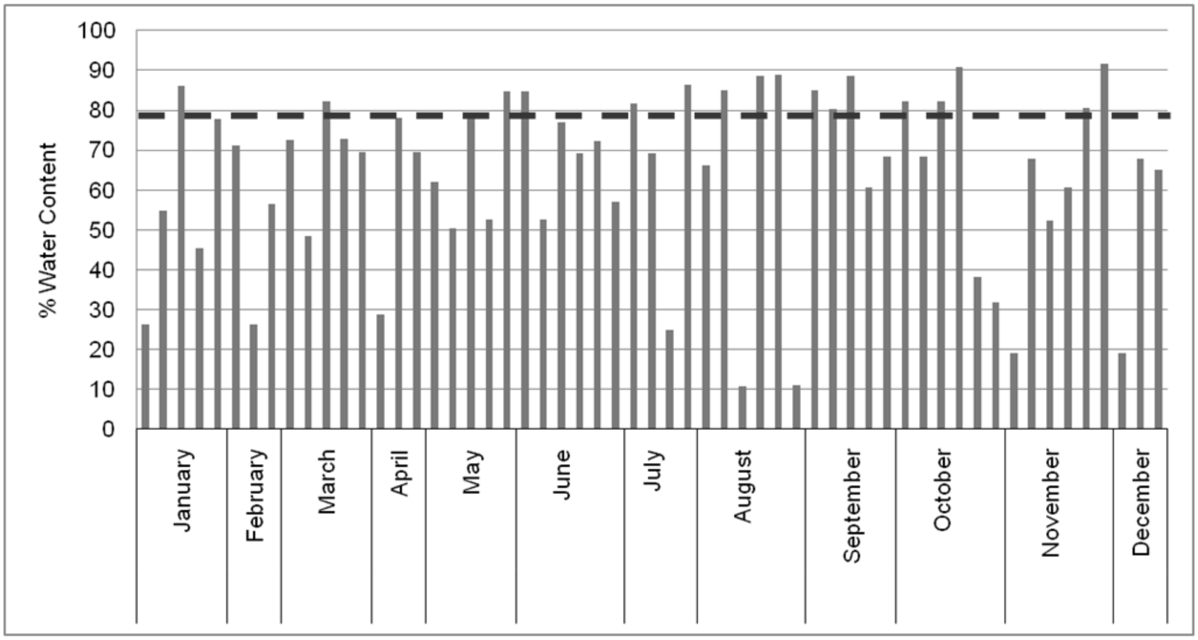

Fig. 5.1. Percent water content of the monthly top 75% species consumed by the Bevaro Moravato troop. Grey vertical lines demarcate different plant species. Horizontal dashed line is placed at 80% water content to demarcate the lowest measured water content of *Opuntia,* specifically *O. stricta*.

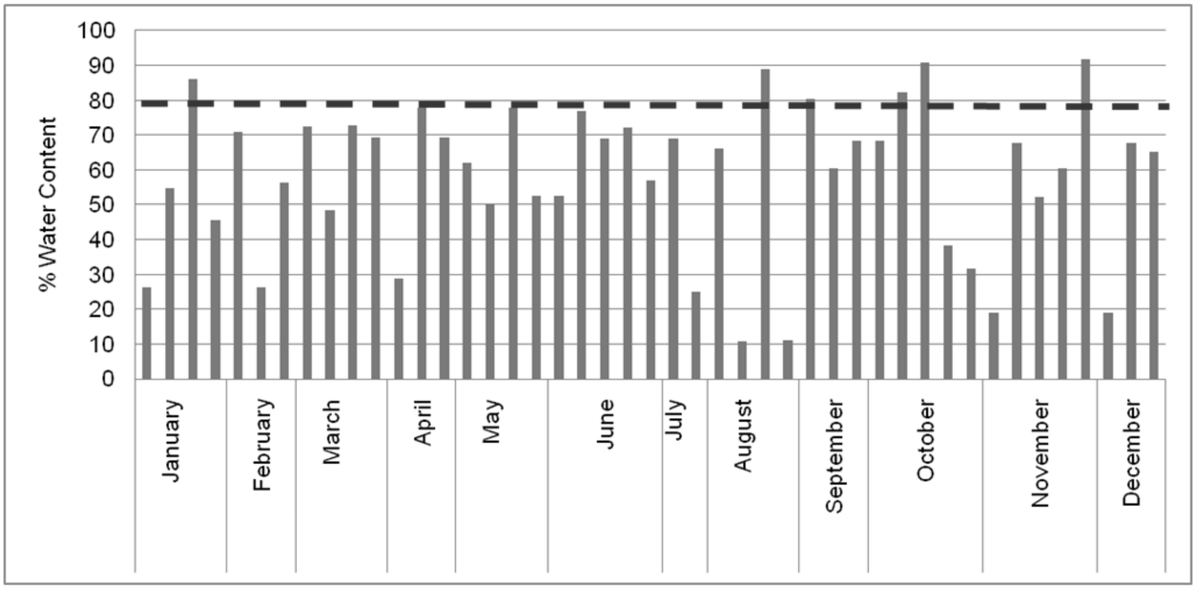

Fig. 5.2. Percent water content of the monthly top 75% species consumed by the Bevaro Moravato troop with *Opuntia* removed. Grey vertical lines demarcate different plant species. Horizontal dashed line is placed at 80% water content to demarcate the lowest measured water content of *Opuntia,* specifically *O. stricta*.

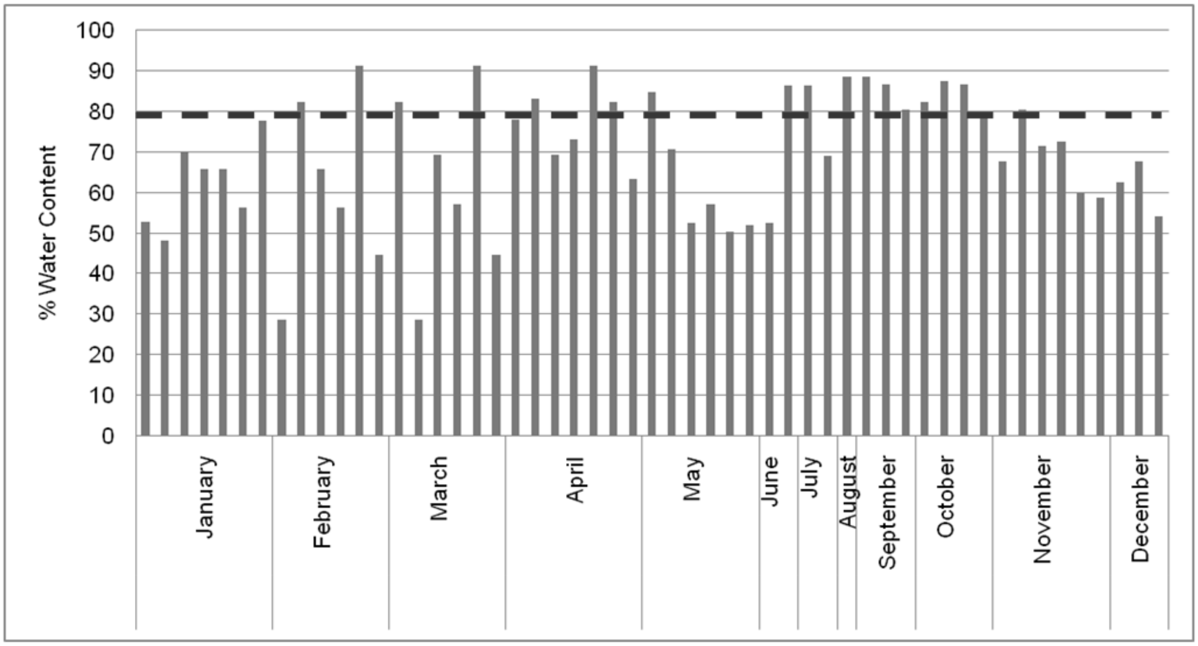

Fig. 5.3. Percent water content of the monthly top 75% species consumed by the Tsankalamanga troop. Grey vertical lines demarcate different plant species. Horizontal dashed line is placed at 80% water content to demarcate the lowest measured water content of *Opuntia,* specifically *O. stricta*.

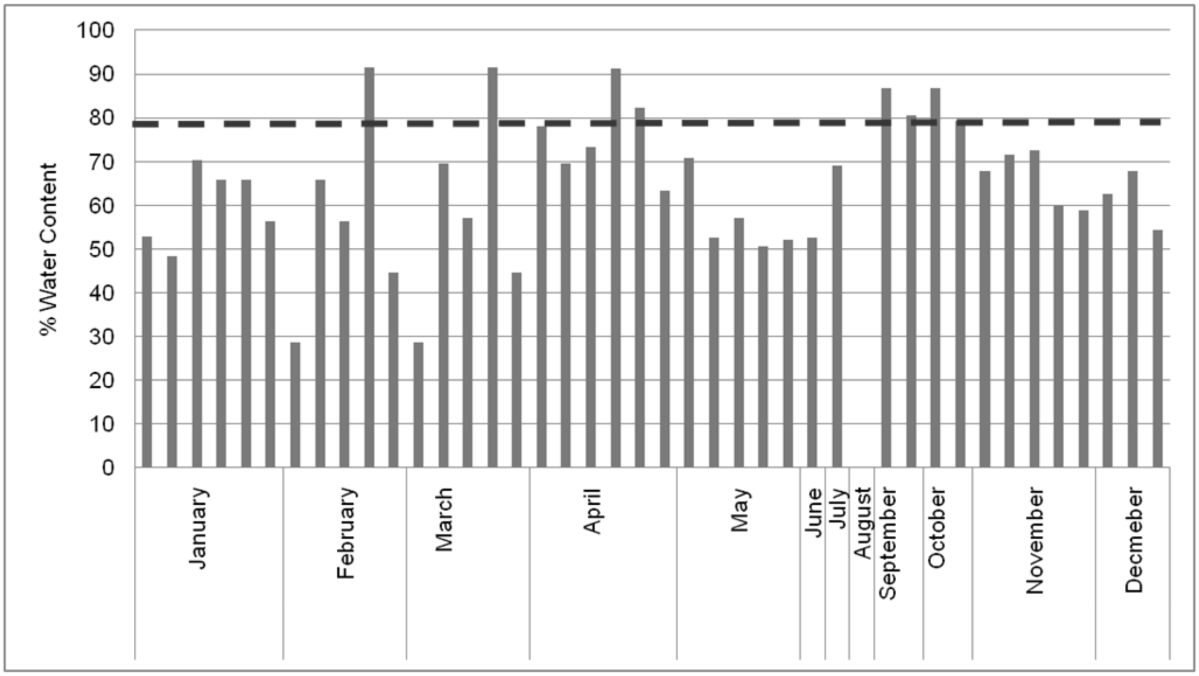

Fig. 5.4. Percent water content of the monthly top 75% species consumed by the Tsankalamanga troop with *Opuntia* removed. Grey vertical lines demarcate different plant species. Horizontal dashed line is placed at 80% water content to demarcate the lowest measured water content of *Opuntia,* specifically *O. stricta*.

Last, to assess water content differences in the plants consumed during the months of the health assessments, weighted water content data from the months of May and July were compared with one another (**Fig. 5.5**). The median water content of plants consumed by CSM lemurs was around 60% in the month of May and a little over 80% in the month of July (**Fig. 5.5**). However, the range in water content of the plants consumed was roughly equal.

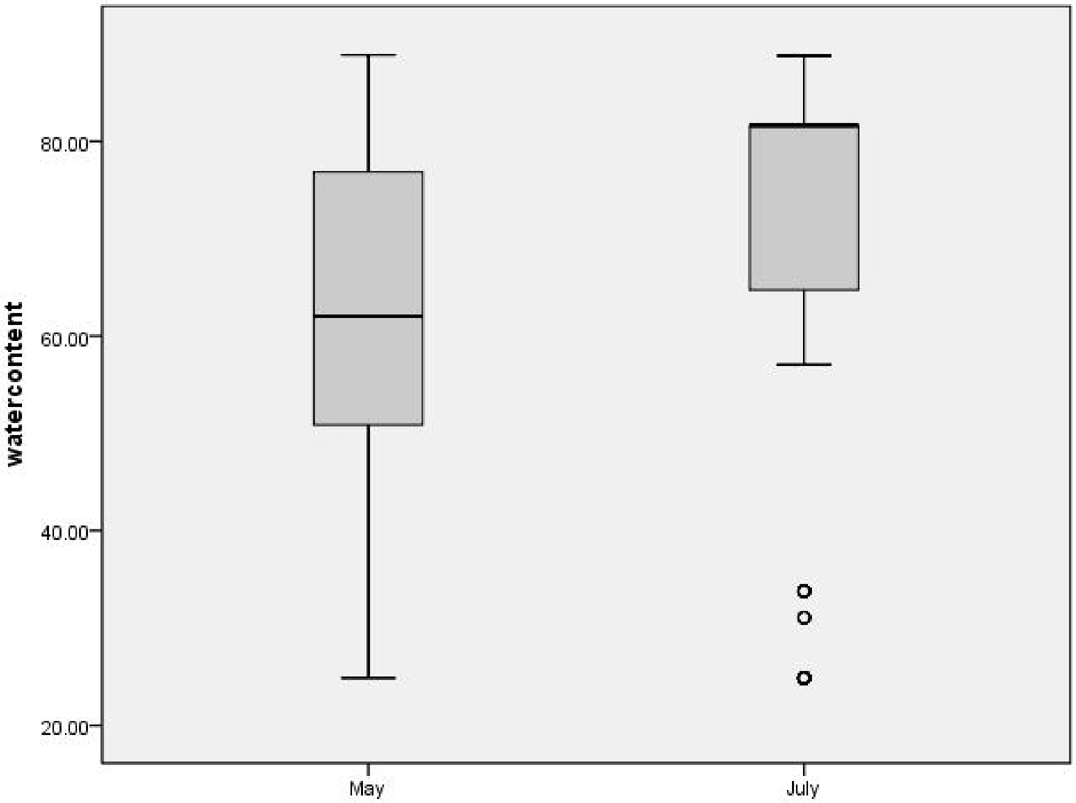

Fig. 5.5. Boxplot of plants consumed by the CSM troops during the months of the health assessments, May and July. Vertical axis is the mean percentage of water content in the plants consumed that month. Data have been weighted to mirror observed consumption.

Discussion

It is evident through the health assessment analyses that CSM *L. catta* are in good physical condition. Moreover, the analyses reveal few clues as to why the Tsankalamanga troop suffered such a high mortality in comparison with the Bevaro

Moravato troop as there were very few statistical differences in health data between the troops and only a small number of statistical differences between the two capture dates. In contrast, there were multiple statistical differences in health data between CSM *L. catta* and comparative populations. The clinical relevance of these differences is discussed below.

Clinically relevant health assessment markers

Elevated WBC counts in this population may indicate low grade chronic infections from thorn pricks and penetrations (Junge, pers comm). This would also explain the results of the protein analyses. While total protein is the sum of albumin and globulin, albumin is affected by liver function and nutrition, and globulin is affected by immune system stimulation (Junge, pers comm). Relative to other *L. catta* populations, CSM lemurs have an elevated total protein (TP) level, with statistically higher globulin levels but comparable albumin levels. More antibodies would be consistent with the hypothesis that these lemurs are constantly fighting infection (Junge, pers comm). It is important to emphasize, however; that the elevated WBC does not suggest that the lemurs were sickly (Junge, pers comm.). Only one major thorn penetration was found in our physical assessments (in the tail of B1) and only one lemur had a WBC that exceeded a normal value, which is estimated to be 9.4 ± 4.0 (ISIS, assessed in 2010), with a reading of 22.7. This lemur was B7, the only resident male in the Tsankalamanga troop whom is presumed to have survived the entire field study. Also notable were the similar serum albumin levels in the CSM lemurs, especially during the August assessments, and the relatively stable levels between the May and July assessments. Low serum albumin is often associated with a form of kwashiorkor and is expressed via a change in coat condition to brown/orange backs and tails (Berg et al. 2009). CSM lemurs were notably more orange pigmented than their Berenty conspecifics during the dry season, and especially during the months of September and October (Jolly, pers comm). Thus, the comparable serum albumin levels among the troops in July suggest that either the CSM lemurs were not physiologically affected despite the change in pelage or that July was too early in the dry season to detect this effect. In fact, most CSM individuals still had relatively grey and black coats during this time.

Several results of the health assessments, especially the May health assessments, indicate that CSM *L. catta* tend to be less hydrated than other wild populations. In addition to elevated TP, they also had higher packed cell volume (PCV%), which indicates lower levels of hydration. PCV% among the CSM lemurs was particularly high during the May health assessments but comparable to the mean PCV% of Beza Mahafaly and captive lemurs during the July assessments (**Table 5.6**). Two other indicators of low hydration, BUN and creatinine, were also significantly higher during the May health assessments, even though BUN levels were still low relative to TSNP and captive ring-tailed lemurs (**Table 5.7**). One additional indicator of low hydration is high Cl (Junge pers comm). CSM Cl values were high in both seasons relative to reference values (ISIS, unpublished reference).

Although the CSM lemurs were less hydrated than other populations, all values were above species reference threshold for dehydration (ISIS unpublished reference; Junge, pers comm). Moreover, it appears that the less hydrated state of the CSM population, especially in May, were not due to lack of available water. As indicated in chapter two, there was rain at CSM in May but little to no rain in July. Therefore, the CSM lemurs should have had more access to standing water collected in rocks during May, and dew should have been consistently present in the mornings of both months of the health assessments. However, drinking by a focal animal was only observed once out of 53,236 observations. CSM *L. catta* were not in the habit of licking dew in the morning, and it is evident that CSM *L. catta* obtain most of their water from plant material. Differences in hydration between the months of May and July more likely result from the CSM lemurs' tendency to heavily consume *Opuntia* in July (**Table 5.13-Table 5.14; Fig. 5.1 – Fig. 5.4**). Although *Opuntia* and other foods with high water content were also available in May, these were not as frequently consumed (**Fig. 5.5**). Thus, although other factors such as mating activity in the month of May and more environmental exposure at CSM in general could contribute to lower hydration levels, the CSM *L. catta* did little behaviorally to exploit opportunities to obtain water.

Dietary markers for normal mammalian metabolism, Cu and Zn (Miller et al., 2007), were higher at CSM but were within range of values obtained at Beza Mahafaly (**Table 5.8**). Moreover, CSM *L. catta* had (statistically) higher serum Fe and TIBC values than the lemurs at Beza Mahafaly and TSNP, and lower mean ferritin values than the Beza Mahafaly sample (**Table 5.8**). The trend of high Fe and TIBC but relatively low ferritin is similar to the *L. catta* that live in degraded habitat at Beza Mahafaly (Miller et al., 2007). While serum Fe measures free iron in the blood, TIBC measures how many binding sites to iron are open, and ferritin is a transport molecule that increases with iron availability (Junge, pers comm). The high serum Fe may seem contradictory to the high TIBC and low ferritin markers. However, serum Fe is a labile marker that is unreliable as an indicator of iron metabolism (Williams and Junge 2008), and the elevated levels of TIBC were not pathologically high (Miller et al., 2007; Junge, pers comm). Thus, although CSM *L. catta* have a diet that is clearly high in Fe (**Table 5.15**), the pattern of high TIBC and low ferritin is indicative of diets that are lower in iron (Junge, pers comm).

The seeming contradiction in iron intake between the health assessments and the nutrition analyses may be related to a diet high in Mn, which can theoretically interfere with Fe absorption but rarely lowers iron levels (Acu-Cell Nutrition, 2011). Both troops had diets that were high in trace mineral Mn (**Table 5.15**), and plants with exceptionally high Mn content were consumed (with the Bevaro Moravato troop especially) throughout the year (**Table 5.23**). In addition, *Mimosa* is a plant that is known to bind Fe, and may be important in preventing iron overload in primates (Spelman et al., 1989; Dierenfeld, pers comm). For both CSM troops, the flowers and leaves of *Mimosa* sp. (Tarampeko) were a notable component of their diets (**Table 5.13**-**Table 5.14**; see also **Table 3.3**). However, while *Mimosa* sp. was consumed by the Bevaro Moravato troop most months of the year, the Tsankalamanga troop did not feed from this plant from the months of June through October **(Table 3.3**).

Another significant difference between the CSM population and other populations was in Vitamin D (25-OHD) levels, which is affected by both diet and the environment (Miller et al., 2007; Junge, pers com). 25-OHD was especially high among members of the Tsankalamanga troop and fluctuated little between health assessments, which ranged among individuals from 81-199 in May, to 89, 108 in August (**Table 5.1**; **Table 5.9**). 25-OHD levels in the Bevaro Moravato troop were much lower in May (15-76) than in August (41-91) and were significantly lower in general than Vitamin D levels in the Tsankalamanga troop (**Table 5.1**; **Table 5.9**). However, 25-OHD levels among the CSM population in general were significantly higher than that of the TSNP lemurs and the mean 25-OHD level of the Beza Mahafaly population (**Table 5.9**). Vitamin D metabolism requires exposure to UV radiation in the skin (Dutton et al., 2003; Miller et al., 2007). Therefore, Vitamin D could be an indirect index of environmental exposure in the Tsankalamanga troop. In fact, 25-OHD levels were highest among males from the Tsankalamanga troop (B7 [May: 119 µmol/L], R3 [May: 114 µmol/L], and SF [July: 108 µmol/L]), followed by a male in the Bevaro Moravato troop (WS [July: 91 µmol/L] and females in the Tsankalamanga troop (G10 [July: 91 µmol/L], G8 [May: 89 µmol/L]). These results coincide with association indices (**Fig. 4.19-Fig. 4.24**) in which least bonded individuals (or new immigrant males[9]) also tend to have the highest 25-OHD levels. In addition, Miller et al. (2007, Table 5) also found differences in Vitamin D levels between males and females, with the least bonded sex having higher levels (Miller et al., Table 5). The relationship between environmental exposure and health will be further explored in the next chapter, chapter six.

Last, differences in Vitamin E, specifically γ-tocopherol and α-tocopherol, reflect dietary differences. γ-Tocopherol levels taken in May were low among the Tsankalamanga troop in relation to the values of all other measured free ranging troops (**Table, 5.4**; ISIS database). In contrast, α-tocopherol levels were high among

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[9] Health data were only collected on one immigrant male, SF.

the CSM troops and varied widely among the individuals. While leaves are a major source of α-tocopherol, seeds and nuts are a primary source of γ-tocopherol (Jiang et al., 2001; Sheppard and Pennington, 1993). These differences effect dietary differences between the troops: while the Bevaro Moravato troop spent most of its time consuming two different native *Terminalia* species throughout the month of April, the Tsankalamanga troop consumed less fruit in general but more leaves (**Table 5.10**; see also **Table 3.3**). However, the Tsankalmanga troop also consumed relatively large amounts of *Opuntia monacantha* fruit and seeds (see Kunyanga and Imungi, 2009). Physiologically, differences in γ-tocopherol levels likely had little effect on the individuals; γ-tocopherol has less Vitamin E activity (Sheppard and Pennington, 1993; but see also Jiang et al., 2001). Moreover, γ-tocopherol levels of the two assessed members of the Tsankalamanga troop were within the range of the Bevaro Moravato troop (6-7 µg/dL) by the July health assessments.

Overall, CSM lemurs appear to be neither dehydrated nor malnourished. Plant analyses support this finding, although the plants that were analyzed appear to have been low in phosphorous relative to recommended levels (**Table 5.15**). Yet even with P, the flowers of *Aloe vahombe* appear to have been an important seasonal source of this essential mineral (as well an important source of Zn and water), and this season coincided with the birth season (**Table 5.17**). Thus, there were no indicators that CSM *L. catta* suffer from any significant on-going dietary component depletions (NCR, 2003).

Possible nutritional consequences of *Opuntia* consumption

One of the more surprising aspects of this study was the focal troops' disinterest in consuming cultivated plants and other anthropogenic sources. Although the sleeping sites of both troops were always located in *Opuntia monacantha* hedges that encompassed fields or gardens, November was the only month when any crop raiding behavior was observed by either troop. Cassava, *Manihot utilissima*, composed 1.3% of the Tsankalamanga troop's diet that month. Similarly, the leaves of ravimbangeda, *Ipomea batatas*, composed 0.5% of the Bevaro Moravato troop's diet in November. In contrast to observations at Beza Mahafaly (Sauther et al., 2006), CSM *L. catta* were never observed feeding on cooked foods, cattle forage or human/domestic animal excrement.[10] The only non-native food species that the CSM *L. catta* consumed with any regularity were the fruits of *Opuntia*.

Mineral content of *Opuntia monacantha* is comparable to the native plant species consumed by the CSM *L. catta*. The fruits of this plant appear to have supported the Tsankalamanga troop through especially the late austral winter months, not only as a source of nutrients, but as a source of water (**Figs. 5.3-5.4**; see also **Table 3.3**). Although this troop clearly suffered, it is the abundant availability of this species that has likely allowed *L. catta* in the Tsankalamanga to persist. Similarly, the high water content and resilience of *O. stricta* to drought conditions is believed to be the primary reason why the Kenyan population of *Papio anubis* did not suffer the mass mortalities that recently devastated much of the wildlife in that country (Strum, pers comm). The water content of *O. monacantha* averaged even

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[10] I did observe a few *ad libitum* observations of feedings on radiated tortoise (*Geochelone radiata*) excrement, however.

higher than *O. stricta*, and the importance of the former species to the survival of the Antandroy during times of drought has been discussed in chapter one.

Opuntia stricta levels of Fe and Mn measured very high in some samples. High Fe was also measured in the lemurs through the health assessments while other, less labile markers of iron intake (e.g., TIBC and ferritin) indicated low iron diets. The contradiction between Fe and the other markers may reflect a diet in which foods with high iron content are only occasionally consumed. At this site, *O. stricta* may be the carrier of this concentrated iron source. In fact, the effect of Fe intake from *O. stricta* is indirectly supported through individual cases. For example, the oldest (and dominant) female in the Bevaro Moravato troop, Mena, had a Fe level of 255 µg/dL in the July 2007 health assessment when *O. stricta* was heavily consumed but had a Fe level of only 8 µg/dL during the May 2007 health assessment, when *O. stricta* was not consumed. The mean ISIS value of Fe is 226 ± 109 (unpublished data), which is close the July Fe level. Yet the high Fe level was likely not from the fruit *per se* but rather from another source that adhered to the skin of the fruit. A second sample of *O. stricta,* collected in January, was found to have a much lower iron content value than that which was collected in July (147 mg/kg vs. 2,590 mg/kg; **Table 5.22**). Moreover, the pulp of *O. stricta* from a *Papio anubis* site in Kenya was found to have a Fe value of only 8 mg/kg (Kunyanga and Imungi, 2009). It is therefore possible that the sample collected in July was contaminated by soil, as the red laterite soil (basement rocks) that characterizes much of Madagascar was present, in conjunction with the unconsolidated sands and tertiary limestones, in the ranges of the CSM lemurs' habitat (see Du Puy and Moat, 2003). Regardless, the excessively high value from the July sample at CSM does not necessarily misrepresent the value of *O. stricta* as a source for obtaining Fe for these ring-tailed lemurs; for even if the skins weren't the source of Fe, the physical structure of the skins made them an ideal medium for soil adhesion, and Fe levels in the animals rose significantly when this plant was consumed.

Analyses of the pulp alone in *Opuntia stricta* (and of also *O. monacantha*) indicate that the fruits of this plant are high in vitamin, mineral, betalain pigment, and antioxidant content in general (Kunyanga and Imungi, 2001; Gentile et al., 2004; Piga, 2004). Yet while it is evident that *O. stricta* isn't devoid of minerals, it may be toxic. Iron and manganese recommendations for primates are 100 mg/kg and 20 mg/kg respectively (Committee on Animal Nutrition, 2003), and the CSM lemurs are estimated to consume excessive levels of these minerals on a yearly basis (**Table 5.15**). While little is known about the maximum tolerance level of dietary minerals for lemurs, a Fe of 2590 mg/kg, which was found in a sample of *O. stricta* (**Table 5.22**), exceeds the tolerance level for all domestic animal species (cattle, sheep, swine, poultry, horse, rabbit) except swine (NRC, 2005). Yet as described above, it is possible that high Mn status mitigates possible acute Fe overloads (Dierenfeld, pers comm), and Mn levels have little to no effect on the development, reproduction and general health of other primate species, mainly *Macaca mulatta* (NRC, 2003). Last, it is important to reemphasize here that it was the Bevaro Moravato troop that consumed the most *O. stricta*, the troop in which only one adult died throughout the field season.

Based on the preliminary research conducted in this study and the comparative research that is currently being conducted by Strum and colleagues (in prep.), it seems that the *Opuntia* species have had little detrimental effect on the health of *L. catta* in this region (or the baboons in Kenya) and in fact has benefited this population in both nutrition and shelter. However, there are at least two major aspects of the plants' biology that need to be further examined. First, the *Papio anubis* who feed from *O. stricta* peel the skin and remove the burrs before consuming the fruit (Strum, pers comm.). With the exception of G10 from the Tsanakalmanga troop, who on several occasions was observed rolling the fruits on the ground before consuming them, the lemurs ate the fruit either directly off the plant or from the ground with no preparation. Therefore, it is possible that the burrs, and even the seeds, caused internal health problems that were not detected through the health assessments. In fact, the Antandroy believe that their livestock die after consuming the fruits of *O. stricta* (but Strum has not found conclusive evidence of this in Kenya). Second, while the effect of this plant on native vegetation has not been rigorously evaluated (see chapter one), the invasive nature of *O. stricta* has made the removal of this species from the CSM Special Reserve an on-going problem for the local forestry officials. While *O. stricta* appears to most aggressively invade areas that have already been cleared both in the CSM village areas and in Kenya's Eastern Laikipia Plateau (Strum, pers comm), systematic research on the effects of *Opuntia* on the CSM region's native vegetation needs careful investigation. Specifically, a very important question that needs to be researched is whether *O. stricta* is outcompeting native vegetation that is only found in the region's sacred forests.

The dietary importance of sacred forests

It would seem likely that plant species are in the sacred forests that are not present elsewhere in the CSM lemurs'environment. However, as described in detail in chapter three, the use of these forests by the CSM *L. catta* diverged markedly between the two troops. While sacred forests were included in much of the Bevaro Moravato troop's core area, there were months in which the Tsankalamanga troop rarely or never traveled to one. Moreover, the Bevaro Moravato troop often fed from choice food items within these forests, while this behavior was not observed with the Tsankalamanga troop (see chapter three). In this chapter, I report that while there were several plant species that were exclusively consumed in the sacred forest habitats (**Table 5.12**), *Alluaudia procera*[6] was the only plant that could be considered a major food, and this plant was only consumed by the Bevaro Moravato troop (**Table 5.13**). Thus, despite the Bevaro Moravato troop's frequent ranging to these sites throughout the year, sacred forests do not exclusively contain important food sources for the CSM *L. catta*. The importance of sacred forests as shelter for CSM *L. catta* will be further examined in chapter six.

Chapter Summary

- Daily contact with *Opuntia* spines may have made the CSM *L. catta* population susceptible to chronic low grade infections. Evidence for this was found through high WBC and TP with statistically higher globulin levels but comparable albumin levels.
- In comparison to other free ranging troops, several health assessment indicators (e.g., high total protein, PCV%, BUN, creatinine) indicate that CSM *L. catta*

were less hydrated in comparison to other free ranging troops. However, the lemurs were not dehydrated, just less hydrated, than their conspecifics. To some extent, this less hydrated status was behaviorally driven.

- Serum albumin levels among the CSM lemurs were normal in both health assessments despite the change in coat condition to brown/orange backs and tails during the birth season through the austral winter months. In addition, CP was relatively low in the diets of CSM *L. catta*, although these levels were not low enough to indicate deficiency. Thus, while this change in pelage could be a factor of sun bleaching, these lemurs (especially lactating females) could also suffer from short seasonal bouts of kwashiorkor, a form of malnutrition caused by lack of protein.
- The diets of the CSM *L. catta* were largely comprised of native species that are abundant in the region. Moreover, CSM *L. catta* consumed several native species that are also consumed by gallery forest populations at Berenty and Beza Mahafaly. In sum, the diets of CSM *L. catta* were comparable to gallery forest sites in species diversity, and the general food type composition of the troops' diets was similar to that which was first observed at Berenty in the late 1960s**.**
- Several native plants, such as *Aloe vahombe*, *Mimosa* sp. (Tarampeko), and *Zygophyllum madecassum* were especially important as sources of nutrition for CSM *L. catta*. Of these species, the endangered species *A. vahombe* is also consumed by *L. catta* at the gallery forest site, Berenty. The blooms of *A. vahombe* are consumed by *L. catta* during months that coincide with the birth season and may be an important seasonal source of P, Zn and water for *L. catta*

throughout south/southeast Madagascar.

- With the major exception of *Opuntia monacantha*, plants grown for human consumption (mainly crops) were rarely consumed by CSM *L. catta* and for most months were completely ignored.
- Mineral, WSC and NDF content of *O. monacantha* was neither exceptionally high nor exceptionally low in relation to the native plant species consumed by CSM *L. catta*. In contrast, samples of *O. stricta* were exceptionally high in Fe and Mn. While the high Mn concentrations likely had little effect on the lemurs' health and may have even controlled for iron overload, the high Fe concentrations, whether from the soil from the actual skins, may have boosted individual Fe levels to normal status during the months this species was consumed.
- Many native plant species at CSM had extremely high water content, over 80%. However, *O. monacantha* was a crucial source of water (and sustenance) for the Tsankalamanga troop during the late austral winter months.
- Although the Bevaro Moravato troop often fed within the sacred forest habitats (chapter three), few if any key food resources for this population exist exclusively in these habitats.
- Dietary analyses indicate that the Tsankalamanga troop had a monotypic diet in the late austral winter months. However, the seasonal deaths of this troop started at the onset of the austral winter. Thus, it appears that the only nutritional factor related to high seasonal mortality in the Tsankalamanga troop may have been the consistently high Vitamin D, which may serve as a proxy for exposure. Although

Vitamin D correlates with UV exposure, I believe that it was not the heat and sun exposure that directly contributed to the troop’s onset of illness and death but rather the correlated exposure to the cooler temperatures, winds and rain. This theory will be examined in the next chapter, thermoregulation**.**

CHAPTER 6

Thermoregulatory Behaviors and the Environment

There are two objectives to this chapter. The first is to determine whether CSM *Lemur catta* used behavioral thermoregulation to adjust to cold and/or hot temperature extremes. The second is to examine intertroop differences between the two CSM troops in thermoregulatory behaviors that may help explain why the Tsankalamanga troop suffered seasonally during the austral winter months while the Bevaro Moravato troop seemed largely unaffected.

Background

A primate's response to thermal conditions is dependent on both its physiology and its behavior. For example, although baboons appear to lack mechanisms for effective brain cooling (Brain and Mitchell, 1999; reviewed in Hill et al., 2004), Stelzner and Hausfater (1986) found that the greatest thermal stress for Amboseli baboons (*Papio cynocephalus*) is heat loss during periods of cooler temperatures. To minimize heat loss, this species will rest primarily in hunched positions with their backs to the wind (Stelzner and Huasfater, 1986). Similar behavior has been observed among Guinea baboons (*Papio papio*) (Anderson and McGrew, 1984); see also Stelzner and Hauasfater, 1986). Hunched and curled positions tend to minimize convection through concealment of the ventral region of the body while maximizing dorsal surface area (e.g., Stelzner and Hausfater, 1986; Morland, 1993; Bicca-Marques and Calegaro-Margues, 1998). Conversely, the behavior of chacma baboons (*Papio ursinus*) in the Namib Desert is characterized by the baboons' need to keep body temperatures from becoming too heated (Brain and Mitchell, 1999). To alleviate thermal overload, chacma baboons not only orient day range travel to reach shaded cliff areas mid-day, but they also rest and groom more often on these days

(Hill, 2006). Hamadryas baboons in Ethiopia, which live in environments similar in climate to that at CSM (chapter two, see also Kummer, 1995) orient day ranges around water holes and midday rest. Yet these baboons also huddle in small groups in the early morning hours, presumably to minimize heat loss (pp. 80-81). This species, as well as chacma baboons that live in mountain ranges, sleep on cliffs rather than trees to maximize the use of the heat that absorbed in the rock during the day (Anderson, 1982).

In comparison to baboons (e.g., *Papio cynocephalus*), *L. catta* and the sometimes sympatric *Eulemur* ssp.[1] have poorly developed sweat glands (Montagna, 1962; Hiley, 1976). However, *L. catta* and *Eulemur* also have low water flux rates (a metabolic adaptation for conserving water), and low field metabolic rates (FMR) that are comparable to desert animals (Simmen et al., 2010; see also Donati et al., 2011). Furthermore, *L. catta* is recognized for its specialized sunning behavior, which is a posture that maximizes solar radiation to the sparsely haired and darkly pigmented ventral surface of the animal. Sunning behavior is also characteristic of the only other diurnal lemur species that occurs in a majority of *L. catta* habitat, *Propithecus verreauxi,* and of the desert dwelling mongoose species *Suricata suricatta.* Thus, this species appears to be well adapted for the hot and dry conditions that characterize the CSM region. Although lemurs in general also lack *arrectores pilorum* muscles to erect their fur for insulation against cold temperatures (Montagna, 1962; Jablonski et al., 2009), they do have hollow body hairs that trap and warm air within the actual follicles (Montagna, 1962; Jablonski et al., 2009). This specialized physical characteristic is shared by *Ursus maritimus*, the polar bear (Jablonski et al., 2009).

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[1] *Lemur catta and Eulemur rufus* are sympatric in the deciduous forests of western Madagascar (e.g., Antserananomby), at the northern boundary of natural habitat for *L. catta*. In addition, *E. rufus* and *E. collaris* have both been introduced at Berenty.

At Cap Sainte-Marie (CSM), differences between the two focal troops in ranging behavior, activity budget, and health status may be associated with microclimatic differences between the two sites. As indicated in chapter two, monthly temperatures at the Tsankalamanga site were on average 10ºF higher than those recorded at Bevaro Moravato, while monthly low temperatures between the two sites were similar **(Fig. 2.3**). Moreover, as indicated in chapter three, the habitat of Bevaro Moravato contained twice as much sacred forest as did the Tsankalamanga site while *Opuntia monacantha* hedges, the only other major source of shelter for the lemurs, comprised a quarter of the Tsankalamanga troop's habitat (**Fig. 3.4**). Thus slight differences in habitat composition may account for the lemurs' exposure to temperature extremes, wind and rain, which may have placed the Tsankalamanga troop at greater risk of hardship and infection.

Methods

In this chapter, I first compare sunning and huddling data to minimum daily temperature and maximum wind speed data. While the function of sunning in this species is well documented, huddling with group members while in the curled position can further augment heat retention and is used among many social primates when temperatures are low (e.g. Stelzner and Hausfater, 1986; Takahashi, 1997; Bicca-Marques and Calegaro-Margues, 1998, reviewed in Anderson, 2000). Temperature and wind data were typically measured within five meters of the animals and approximately at the animals' height. Since ambient temperatures at CSM never fell below 55F (see chapter two), wind chill is negligible at this site (Bluestein and Zecher, 1999).

Second, to identify whether substrate use by CSM *L. catta* was based on ambient temperature, substrate data were divided into four major categories (i.e., hedges, tree/shrubs, ground and tombs), and were separated by temperature bands. Data for this analysis were taken at hourly intervals. In addition, to test for the effects of seasonality and to directly compare results of this study with recent studies on *E. collaris* (mainly Donati et al., 2011), substrate data were also analyzed by season as defined by Donati et al. (2007)[2].

In the third set of analyses, I compare general activities to ambient temperature. Sprawling with stretched out limbs (also known as the prone position), which maximizes the exposure of a primates' ventral surface to dissipate heat, is a common postural response to high temperature extremes among CSM *L. catta* and other primate species (e.g. Stelzner and Hausfater, 1986; Bicca-Marques and Calegaro-Margues, 1998; but see Donati et al., 2011). Although I did not discriminate sprawling verses other postures (e.g., curling, sitting) for these analyses (Donati et al., 2011), I test in these analyses whether high ambient temperature has an effect on the amount of time CSM *L. catta* spend in inactivity throughout the day. Resting/daytime sleeping to ambient temperature comparisons are also analyzed by season. Other activities that I compare in relation to ambient temperature are day range (also known as daily path length) and feeding. Day range data are based on hourly GPS readings.

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[2] Even though this study was conducted at the relatively nearby SE Madagascar site of Sainte Luce Conservation Area, seasonality as has been defined at Sainte Luce is not directly applicable to CSM. For example, while Donati et al. defined a wet season as a season in which rainfall exceeded 100mm of rain a month, there were only two nonconsecutive months at CSM, February and May, in which this occurred. Ironically, May is included in the season described as hot-dry. In addition, the cool season was defined as including months in which average temperatures were 21C (70F) or lower. I recorded no days at CSM in which there were 70F average temperatures or less. Thus, although there were noticeable differences in the CSM ecology on a seasonal basis, seasonality as observed elsewhere at even relatively nearby sites in Madagascar does not exist at this site.

Results

Minimum ambient temperature correlations

Despite the discrepancy in morning data collection times between the two sites[3], there are very similar and significant negative associations between minutes of sunning per day and minimum daily temperatures for both troops (BM: r = -.825, n = 79, p < .001, two-tailed, **Fig. 6.1**; TA: r = -.832, n = 56, p < .001, two-tailed, **Fig. 6.2**)[4]. In addition, sunning behavior ceased when minimum daily temperatures neared 80F.

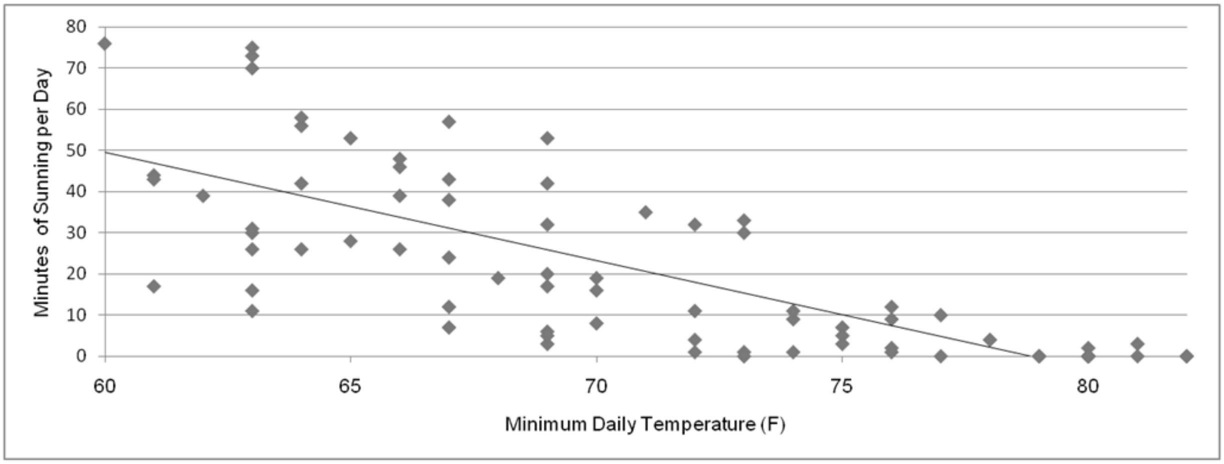

Fig. 6.1 Scatterplot of recorded minimum daily temperature to minutes per day that the Bevaro Moravato troop spent in sunning activity. Minimum daily temperature data typically reflect the temperature at the site before sunrise. r = -.825, p < .001, two-tailed.

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[3] Morning temperature and behavioral data from the Tsankalamanga troop were not collected at daybreak, the time when minimum temperatures peak (Ostner, 2002), principally because this troop's home range was over two hours away from camp and because the two troop members that wore radio collars (which greatly assisted in detection of the troop's location) died early in the study (see chapter five). Thus, morning climatic data for the Tsankalamanga troop is limited in number of days, and data recording for the days that are included in the analyses did not begin until 7:30 a.m.-8:30 a.m (see chapter two).

[4] Humidity levels were not measured throughout the study and thus correlations with temperature had to be limited to ambient temperature, rather than perceived temperature (Hill et al., 2004; Donati et al., 2011).

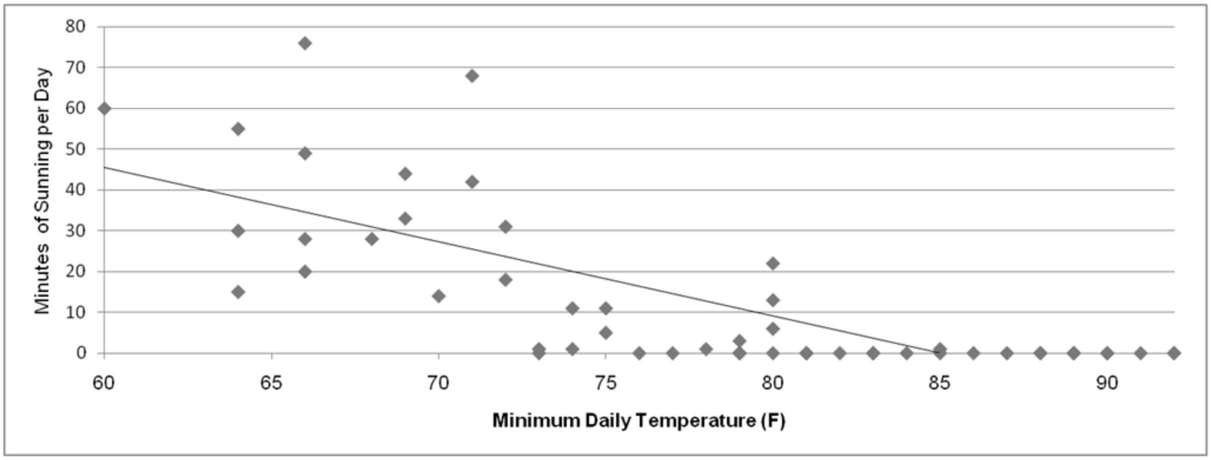


Fig. 6.2 Scatterplot of minimum daily temperature to minutes per day that the Tsankalamanga troop spent in sunning activity. Minimum daily temperature data typically reflect the temperature at the site between 7:30-8:30 in the morning. r = -.832, p < .001, two-tailed.

However, there was no association between minimum daily temperature and minutes spent huddling per day among members of the Bevaro Moravato troop (r = - .155, n = 79, p = .172, two-tailed **Fig. 6.3**), while there was a weak but significant negative association between minimum daily temperature and minutes of huddling per day among members of the Tsankalamanga troop (r = - .364, n = 56, p = .006, two-tailed, **Fig. 6.4**).

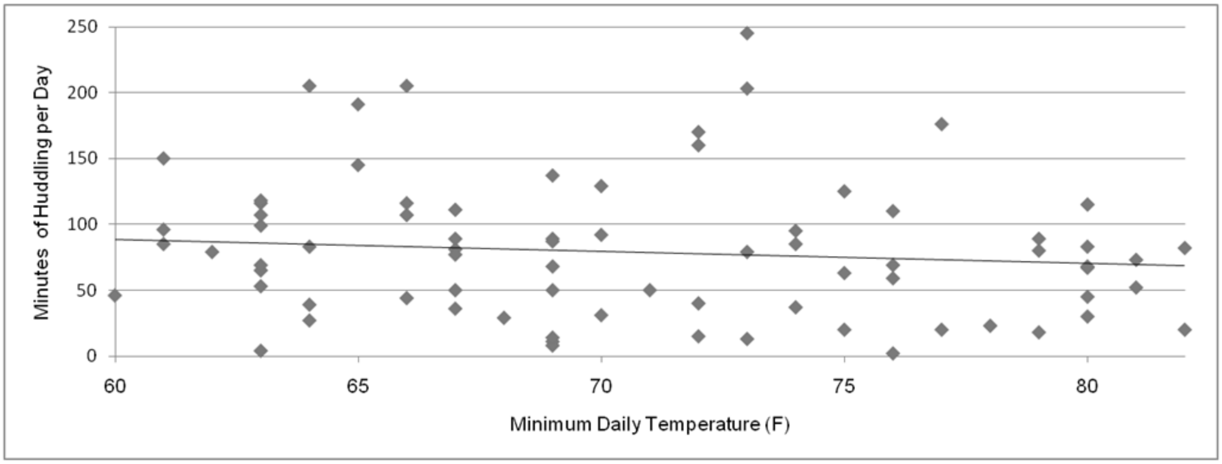


Fig. 6.3 Scatterplot of recorded minimum daily temperature to minutes per day that the Bevaro Moravato troop spent huddling. Minimum daily temperature data typically reflect the temperature at the site before sunrise. r = -.155, p = .172.

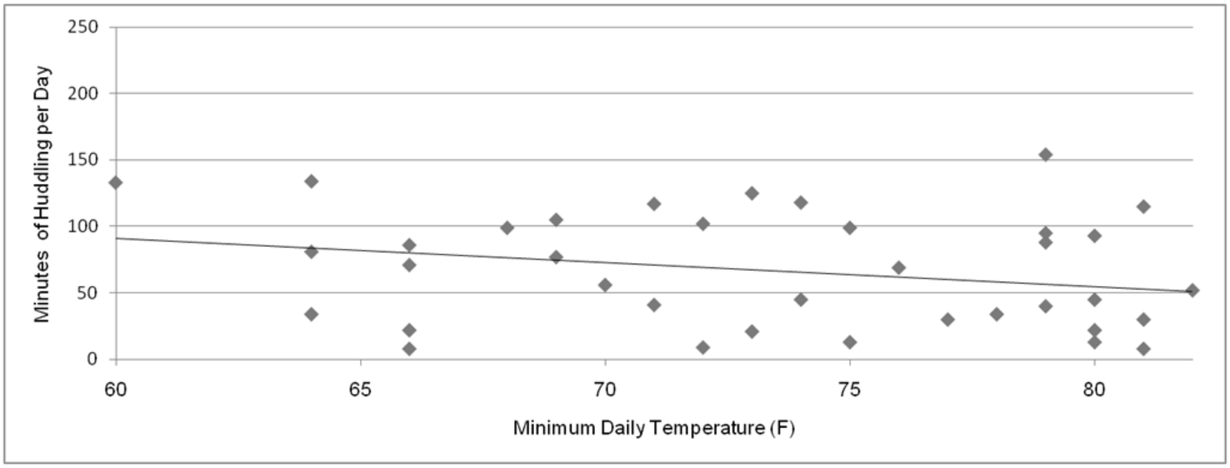


Fig. 6.4. Scatterplot of recorded minimum daily temperature to minutes per day that members of the Tsankalamanga troop spent huddling. Minimum daily temperature data typically reflect the temperature at the site between 7:30-8:30 am. r = - .364, p = .006, two-tailed.

Wind data correlations

Wind data were not collected from May through July because two different wind gauges broke during this study. Based on the data available, peak wind exposure for the troops appeared to have occurred during the transitional season following the austral winter months (**Fig. 6.5-Fig. 6.6**). Both troops were never recorded in environments that exceeded 16mph winds, and the lemurs would often inhabit environments in which no wind speed could be detected regardless of the season. In comparison, wind data collected from 1979-1998 at the nearest airport reported wind speed ranges from 9.9 mph in May through July to 16.2 mph in October (Vincelette et al., 2008).

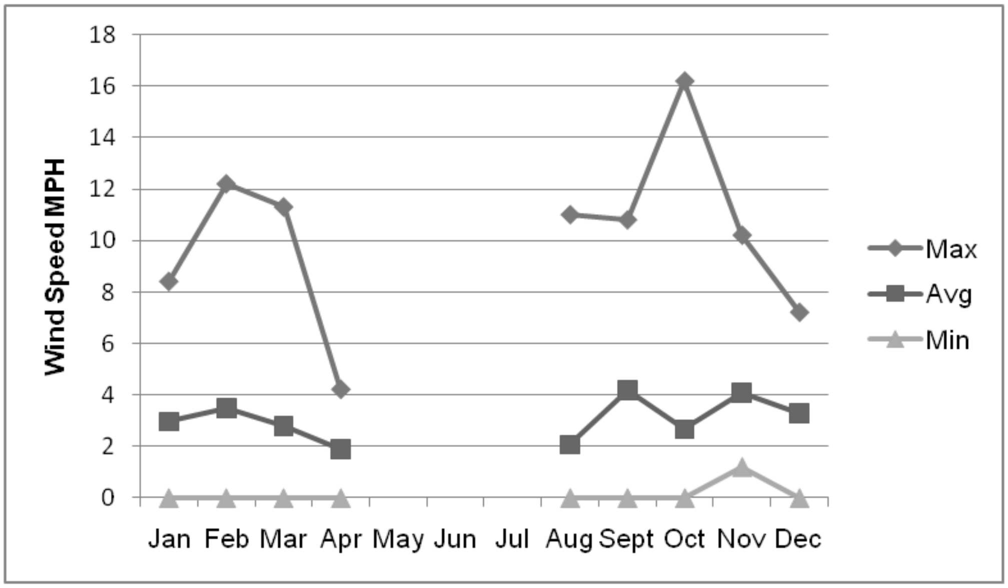


Fig. 6.5. Wind data taken during the all-day follows of the Bevaro Moravato troop from August 2007 through April 2008. Wind data were taken at hourly intervals.

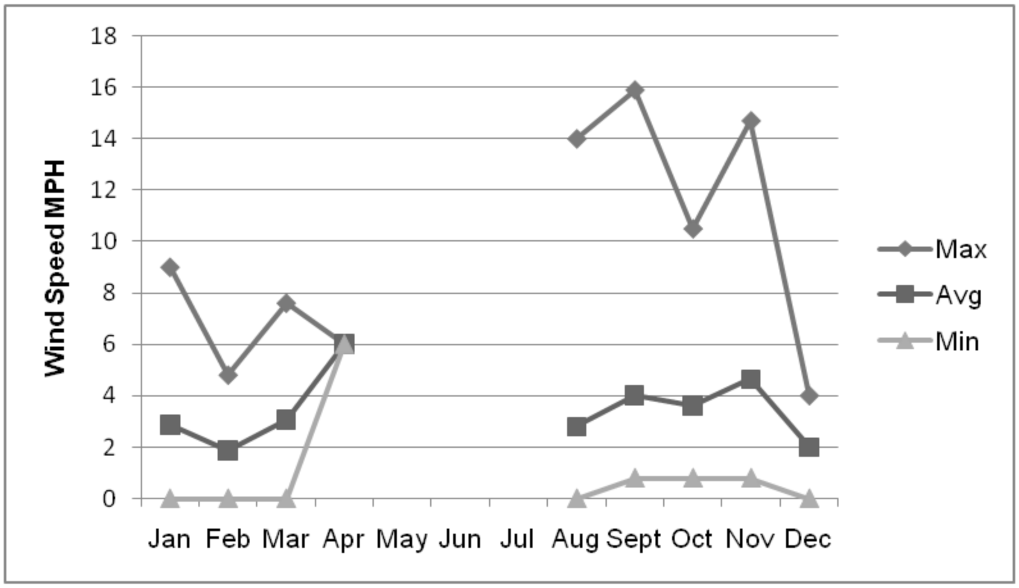


Fig. 6.6. Wind data taken during the all-day follows of the Tsankalamanga troop from August 2007 to April 2008. Wind data were taken at hourly intervals.

When maximum daily wind data were compared with huddling data, there were weak but significant and positive associations between the behavior and this climatic variable for both troops (BM: r = .352, n = 52, p = .011, two-tailed, **Fig. 6.7**; TA: r = .396, n = 41, p = .010, two-tailed, **Fig. 6.8**).

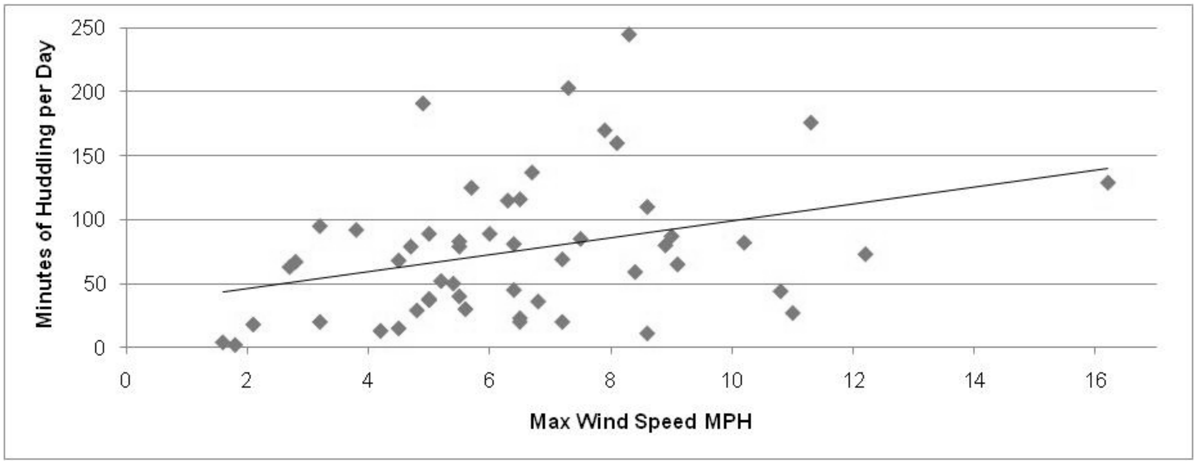


Fig. 6.7. Scatterplot of time spent huddling throughout the day to daily maximum wind speed among members of the Bevaro Moravato troop. r = .352, p = .011, two-tailed.

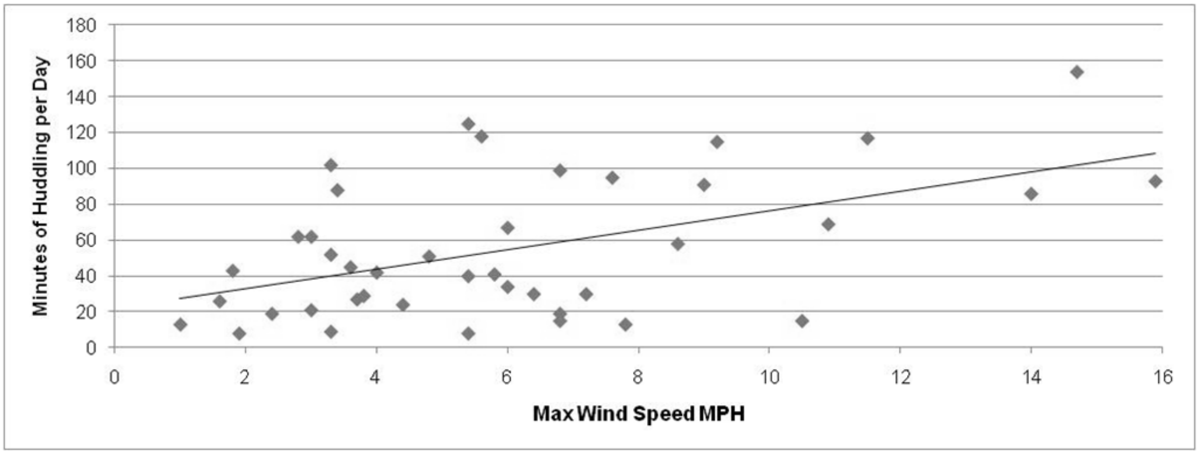


Fig. 6.8. Scatterplot of time spent huddling throughout the day to daily maximum wind speed among members of the Tsankalamanga troop. r = .396, p = .010, two-tailed.

Temperature effects on substrate use

When substrate use was divided by temperature bands on a yearly scale, hedges were most frequented in cooler temperatures, while the lemurs tended to use the ground more as temperatures rose (**Fig. 6.9-Fig. 6.10**). However, while the Bevaro Moravato troop tended to move to ground substrate when the temperatures reached 80ºF+, the Tsanakalamanga troop didn’t maximize ground use until temperatures were 90ºF+. Also, although less data in general were collected at the Tsankalamanga site, more 100º+F data points were recorded from that location.

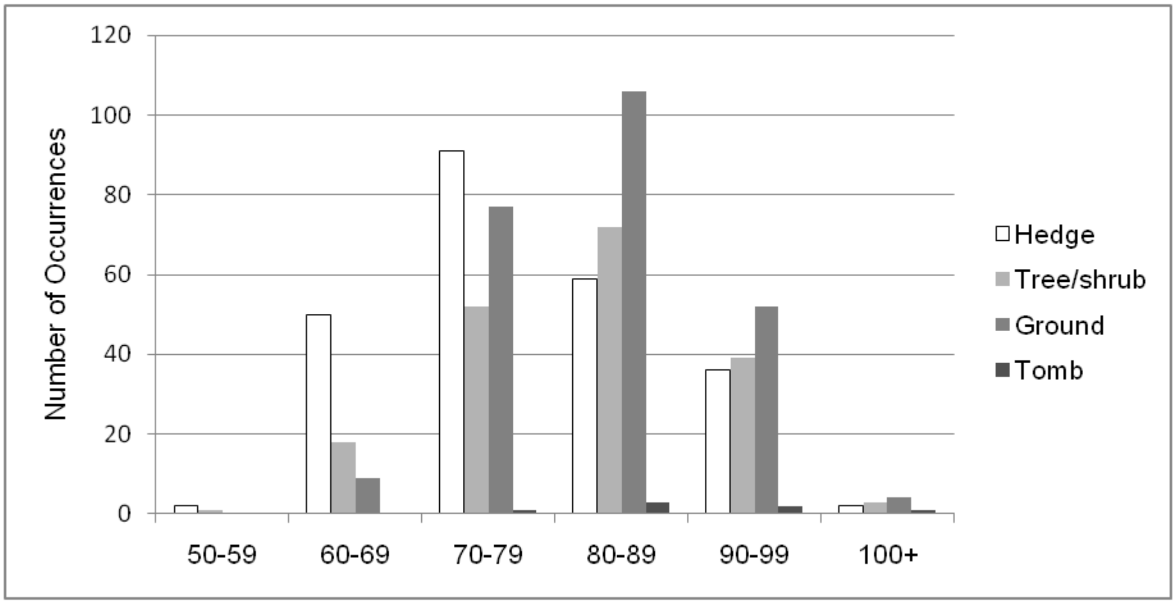


Fig. 6.9. Minutes of time that the Bevaro Moravato troop spent in the four main categories of substrate by temperature band from August 2007 through July 2008. Data are based on hourly recordings.

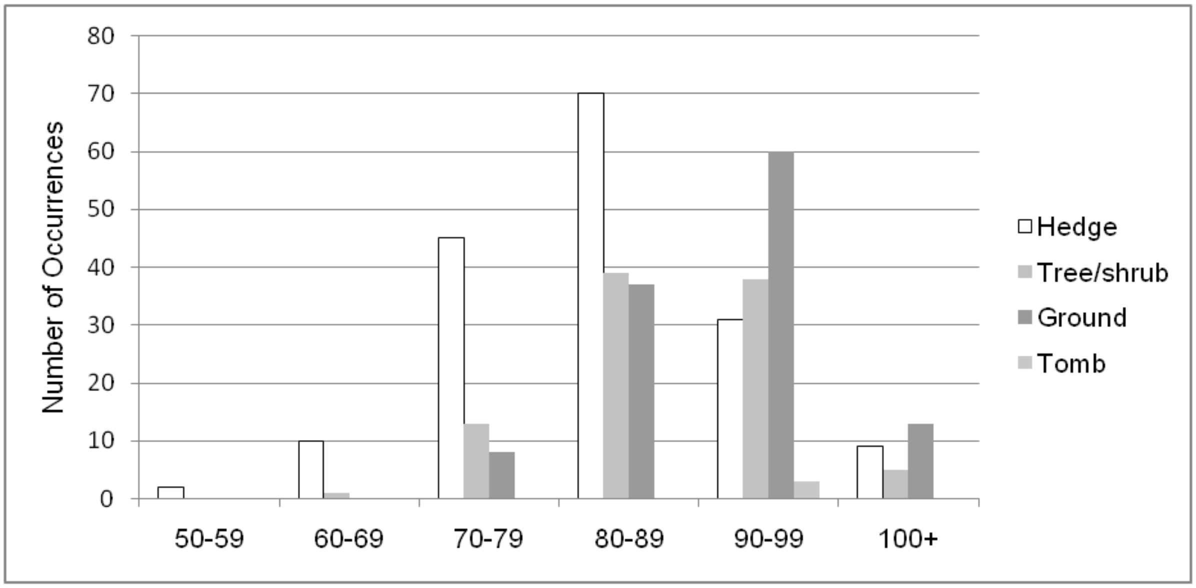
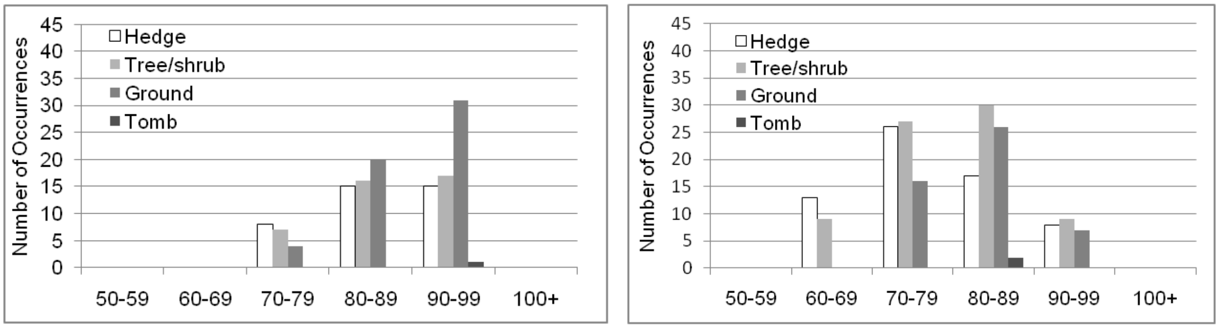


Fig. 6.10. Minutes of time that the Tsankalamanga troop spent in the four main categories of substrate by temperature band from August 2007 through July 2008. Data are based on hourly recordings.

When analyzed on a trimonthly (seasonal) scale, substrate use patterns diverged markedly from the yearly patterns. Trees and shrubs were the primary substrate used among members of the Bevaro Moravato troop once temperatures reached 70ºF during the months of March through May (**Fig. 6.11**). In addition, hedge use became one of the primary substrates for this troop once temperatures exceeded 90F°+ from the months of June through November.

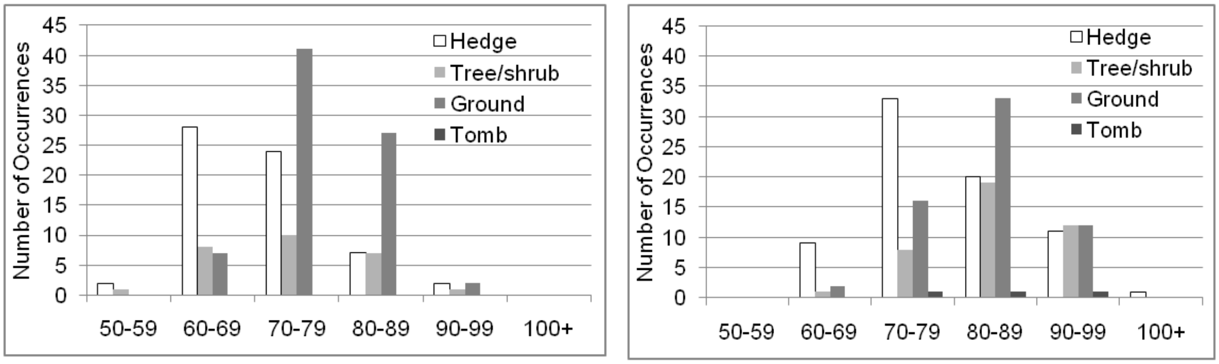
With the Tsankalamanga troop, seasonal substrate use by temperature band diverged markedly from the troop's perceived yearly pattern. For example, there appeared to be no pattern in substrate use from the months of December through March once temperatures reached 80°F. In addition, trees/shrubs were preferred to ground use in the 90ºF+ temperatures from April through May, while hedges were the preferred substrate regardless of the temperature from the months of June through August. Last, substrate use by temperature band from the months of September through November for this troop mirrored that of the Bevaro Moravato troop's yearly trend (**Fig. 6. 12**).

In sum, only one consistent pattern could be detected for both troops through both types of analyses; CSM *L. catta* resided almost exclusively in the *Opuntia monacantha* hedges when temperatures were under 70ºF. In fact, hedges were preferred to all other substrates for sunning behavior, and preference of hedge use for sunning remained robust even when all other substrates were grouped as one in chi-square tests (BM: X^2 [1, n = 1,849] = 91.35, p < .001; TA: X^2 [1, n = 757] = 9054, p = .002). With the Tsankalamanga troop, hedges were also used as the primary substrate for huddling: (X^2 [1, n = 3,318] = 116.60, p < .001). Conversely, although general substrate use appeared to have little to no association with temperature once conditions exceeded 70°F, there was a significant positive association between time spent resting and sleeping on the ground (outside of enclosed *O. monacantha* hedges) and daily maximum temperature for both troops (BM: r = .442, n = 80, p < .001; TA: r = .546, n = 56, p < .001).



December – February

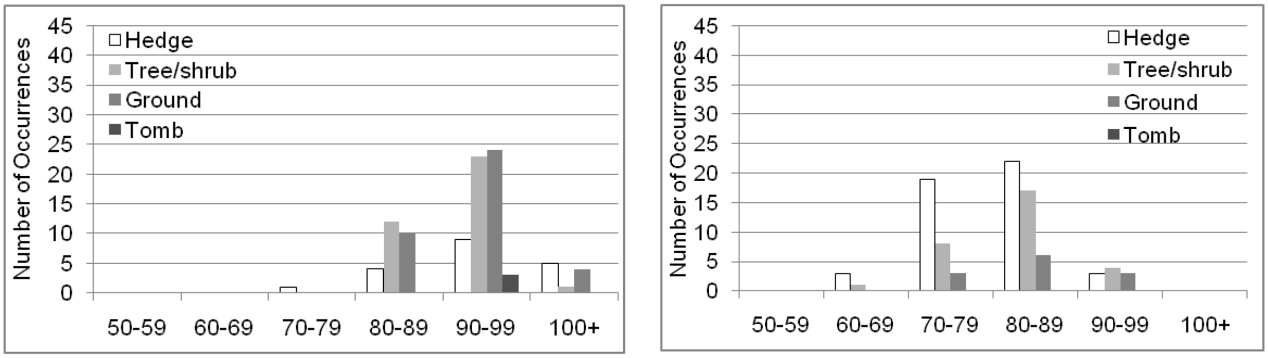
March – May



June – August

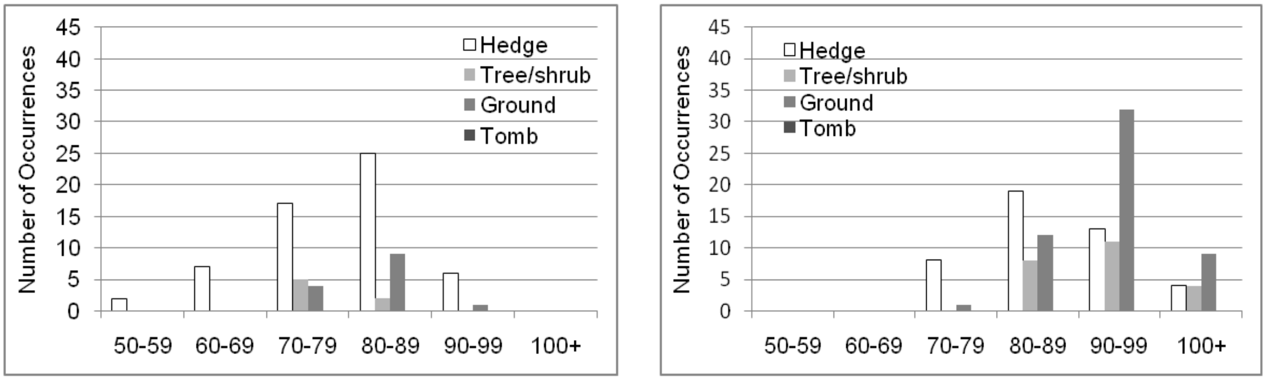
September – November

Fig. 6.11. Minutes of time that the Bevaro Moravato troop spent in the four main categories of substrate by temperature band from August 2007 through July 2008. Data have been broken into seasons as defined by Donati et al., 2007 (see footnote 2). Data are based on hourly recordings.



December – February

March – May



June – August

September – November

Fig. 6.12. Minutes of time that the Tsankalamanga troop spent in the four main categories of substrate by temperature band from August 2007 through July 2008. Data have been broken into seasons as defined by Donati et al., 2007 (see footnote 2). Data are based on hourly recordings.

Temperature effects on daily activity

When daytime resting/sleeping behavior was divided by season, the highest percentages of solitary inactivity occurred during the austral summer months of the year, December through February (**Fig. 6.13**). Notably, the Tsankalamanga troop spent almost 50% of its daytime activity in solitary resting/sleeping behavior during this time. In addition, there was a significant seasonal difference with this troop between these austral summer months and the other seasons, while no seasonal trend was evident with the Bevaro Moravato troop (**Fig. 6.13**).

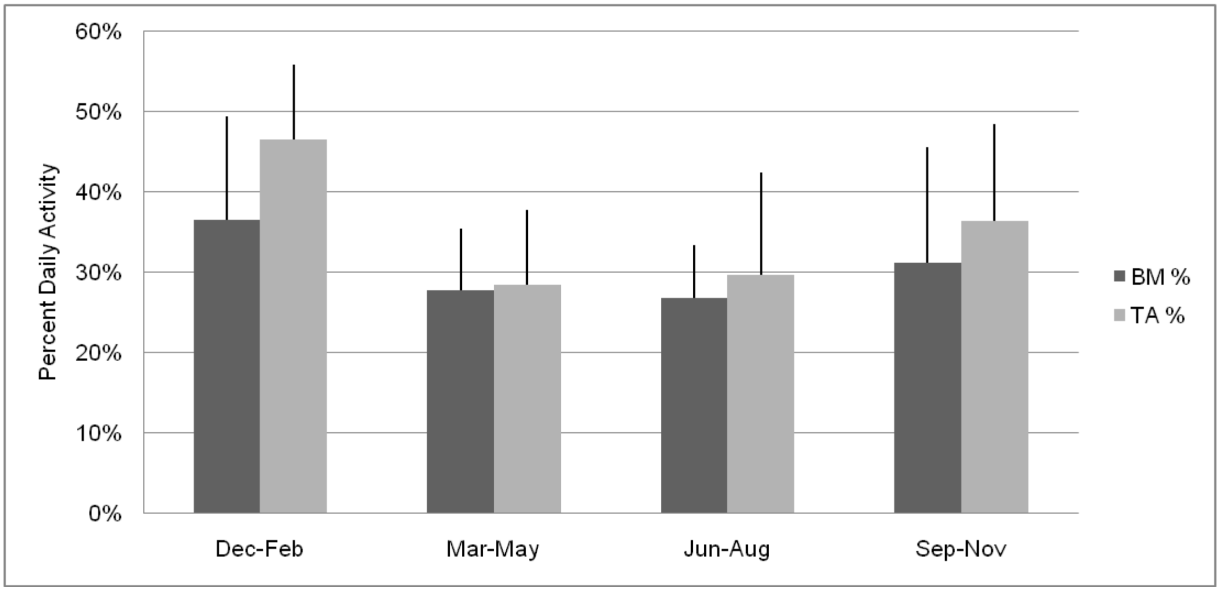


Fig. 6.13. Percentage of time the CSM troops spent in solitary resting and sleeping behavior by season. BM = Bevaro Moravato, TA = Tsankalamanga. Months have been divided by season as defined by Donati et al., (2007, 2011). In this study, December through February was the hottest months, followed by September through November. June-August was the coolest months. Error bars signify daily SD.

On a daily scale, average temperature was positively and significantly associated with the amount of time that both troops spent resting and sleeping alone throughout the day[5] (BM: r = .602, n = 80, p < .001, **Fig. 6.14**; TA: r = .558, n = 56, p < .001, **Fig. 6.15**).

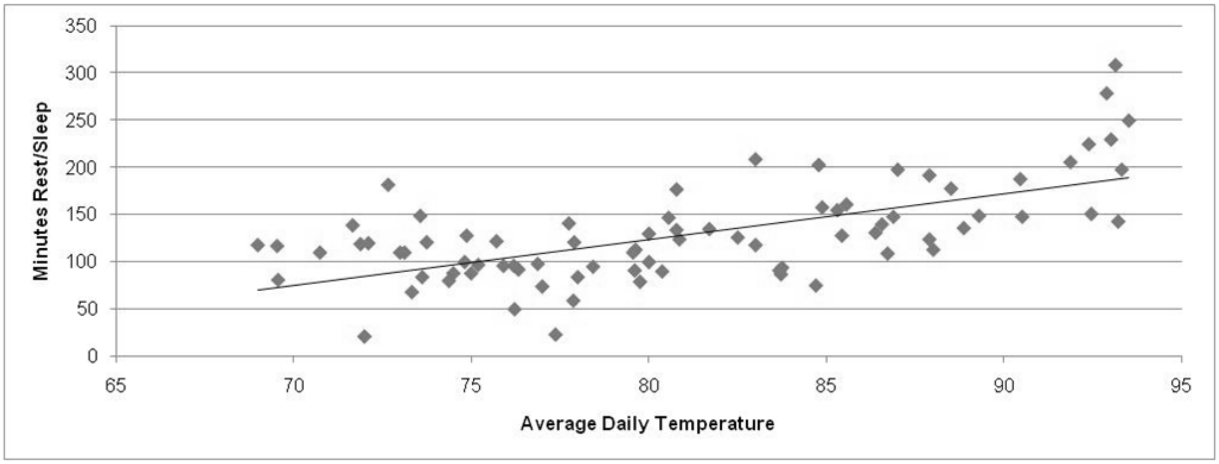


Fig. 6.14. Scatterplot of minutes the Bevaro Moravato troop spent resting/sleeping throughout the day (with huddling removed) to average daily temperature. Temperature is measured in F. r = .602, p < .001.

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[5] Since daybreak temperatures were not recorded at Tsanakalamanga, average temperatures are likely slightly inflated.

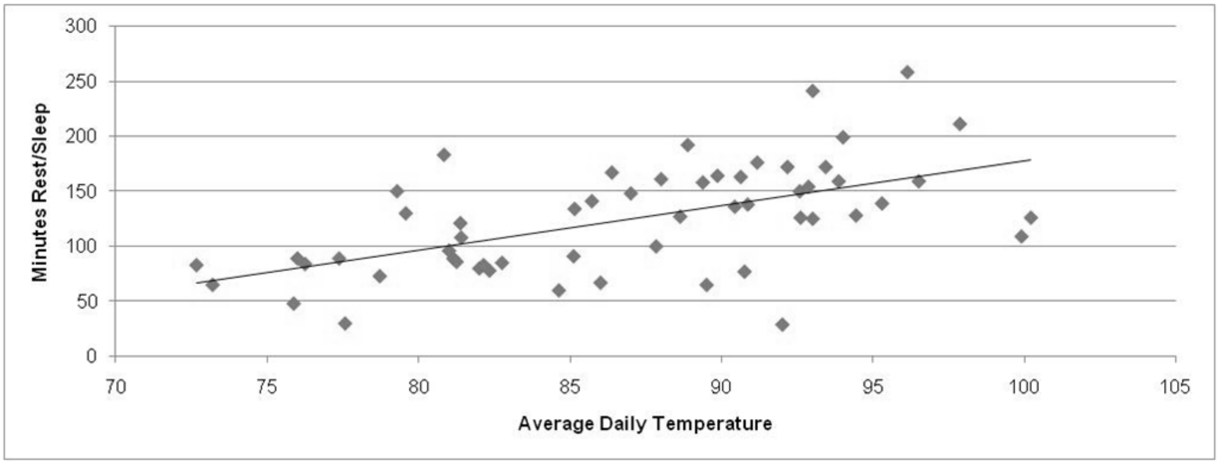

Fig. 6.15. Scatterplot of minutes the Tsankalamanga troop spent resting/sleeping throughout the day (with huddling removed) to average daily temperature. Temperature is measured in F. r = .558, p < .001.

Huddling in the Bevaro Moravato troop was highest during the transitional season, which was a period of relative warmth but also the season when wind speeds tended to peak (**Fig. 6.5; Fig. 6.16**). In comparison, huddling behavior in the Tsankalamanga troop was highest throughout the coolest months of the year (**Fig. 6.16**). However, huddling behavior varied greatly throughout all seasons with both troops, and differences among the seasons were not significant (**Fig. 6.16**).

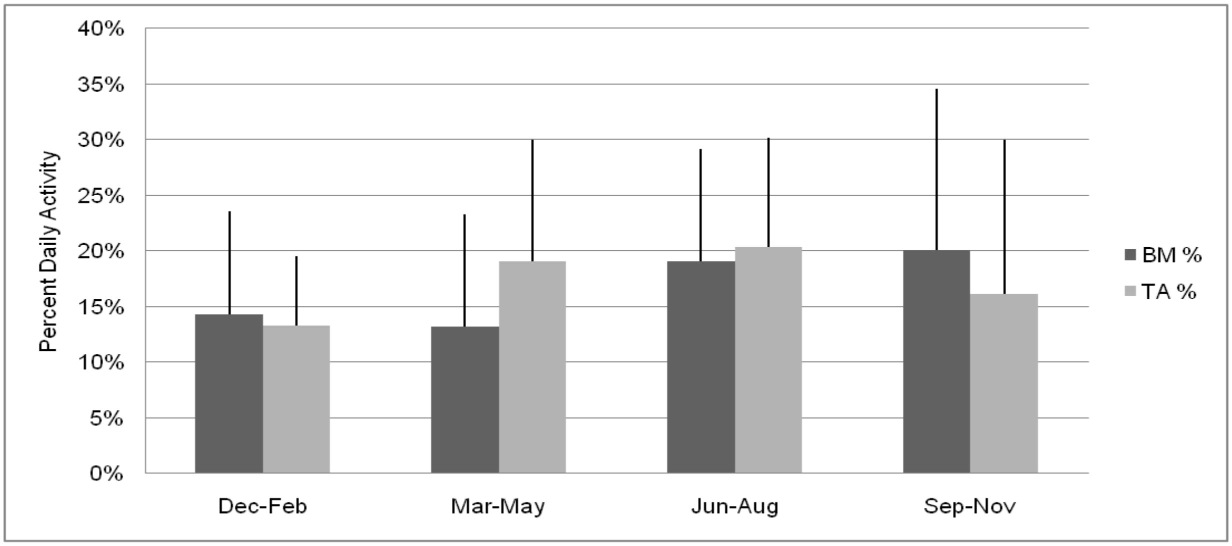

Fig. 6.16. Percentage of time both CSM troops spent in huddling behavior by season. BM = Bevaro Moravato, TA = Tsankalamanga. Months have been divided according to Donati et al., (2007; 2011). In this study, December through February was the hottest months, followed by September through November. June-August was the coolest months. Error bars signify daily SD.

Last, when feeding and ranging behaviors were correlated with ambient temperature, the behaviors of the two troops differed markedly from one another. With the Bevaro Moravato troop, there was no correlation between day range length and daily average temperature (r = -.01, n = 79, p = .931; **Fig. 6.17**). However, there was a weak and positive association between time spent feeding throughout the day and temperature (r = .236, n = 80, p = .035; **Fig. 6.18**). In contrast, the ranging behavior of the Tsankalamanga troop was significantly and positively associated with daily average temperature, with travel distance peaking when average temperatures were in the low 90ºF range. (r = .490, n = 56, p < .001; **Fig. 6.19**). Yet there was no association between temperature and time spent feeding (r = -.021, n = 56, p = .880, **Fig.6.20**).

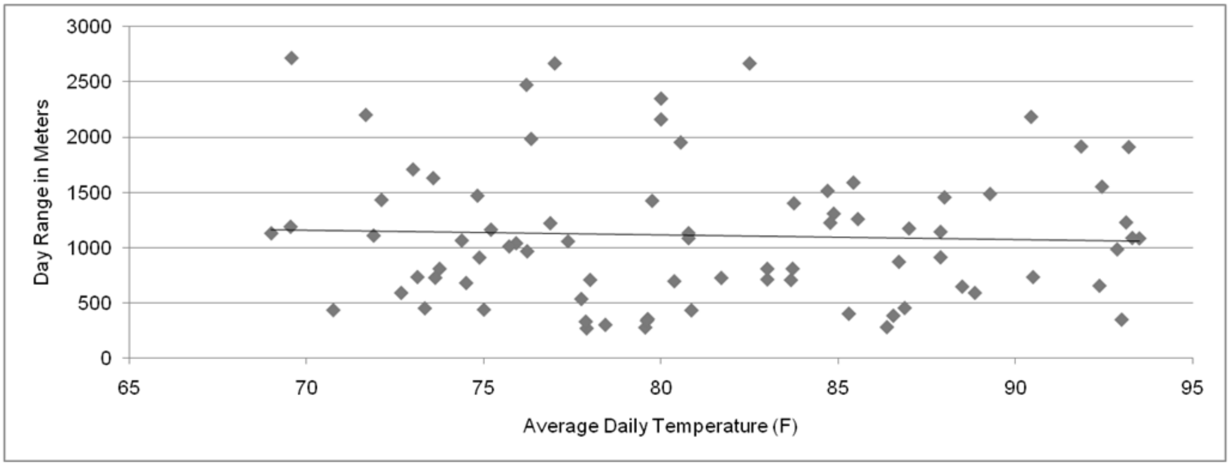

Fig. 6.17. Scatterplot of day range to average daily temperature in the Bevaro Moravato troop. r = -.01, p = .931.

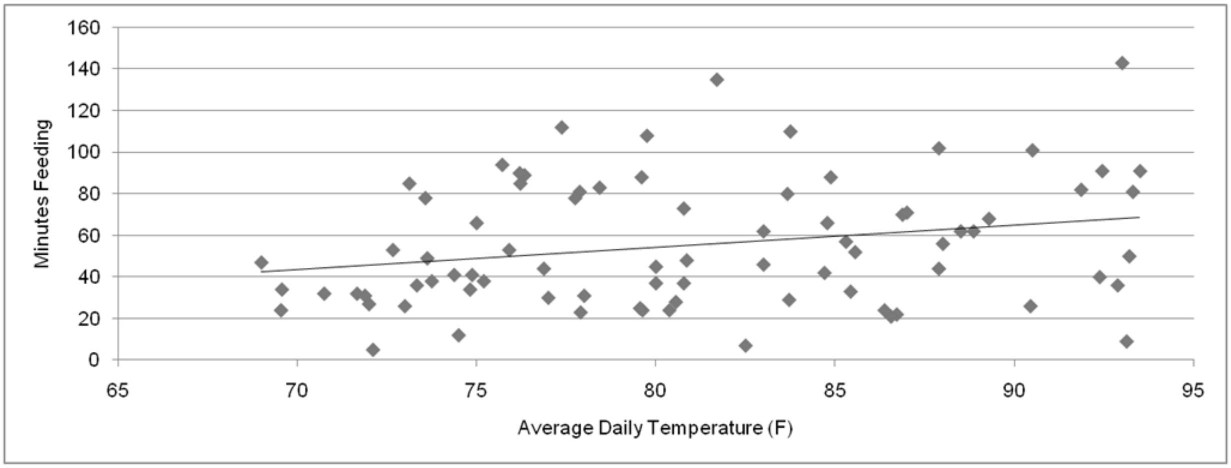

Fig. 6.18. Scatterplot of minutes spent feeding throughout the day to average daily temperature in the Bevaro Moravato troop. r = .236, p = .035.

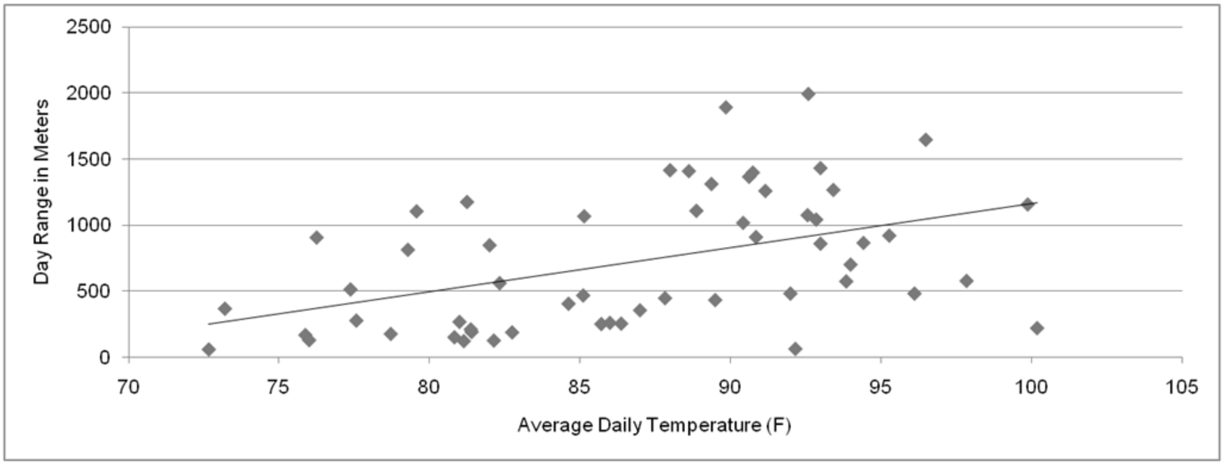

Fig. 6.19. Scatterplot of day range to average daily temperature in the Tsankalamanga troop. r = .490, p < .001.

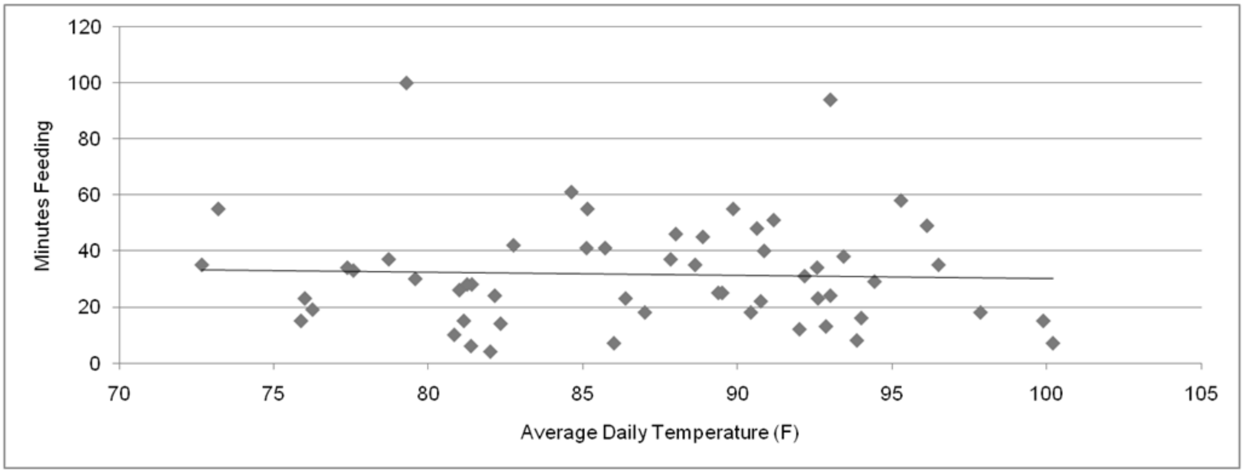

Fig. 6.20. Scatterplot of minutes spent feeding throughout the day to average daily temperature in the Tsankalamanga troop. Temperature is measured in F. r = -.021, p = .880.

Discussion

There were marked postural consistencies in the way the two CSM *L. catta* troops responded to climatic changes in their environment (**Fig. 6.1-Fig. 6.2; Fig. 6.7-Fig. 6.8; Fig. 6.14-Fig.6.15**). The best example of this is with sunning behavior, in which strong associations between sunning behavior and ambient temperature indicate that CSM *L. catta* clearly used this posture to increase body temperature. Moreover, the two troops had a specific substrate (hedges) in which they preferred to conduct this activity, and they had a temperature point of around 80ºF at which all sunning behavior ceased (**Fig. 6.1-Fig. 6.2)**. Conversely, the role of huddling for CSM *L. catta* appears to be more complex. The weak but significant correlations between wind data and huddling behavior at CSM indicate that huddling had some importance as a thermoregulatory behavior when conditions made sunning unfeasible. However, while other studies on group living lemur species, including a study on *L. catta* in North America, have found trends between time spent huddling and seasonal variation (see Moreland, 1993; Pereira et al., 1999; Donati et al., 2011), there was little to no consistent association among CSM lemurs in huddling time to ambient temperature or seasonality (**Fig. 6.3-Fig. 6.4; Fig. 6.16**). In contrast to CSM, sunlight is sometimes only attainable for lemurs elsewhere in the emergent canopy layers (e.g. Ostner, 2002; Donati et al., 2011). Thus, difference in environment likely at least partly explains why similar trends between ambient temperature and huddling behavior were not evident in this study.

Huddling and sociality

Despite the weak association between huddling and climate, huddling behavior was common among CSM *L. catta* (see chapter four). With the Bevaro Moravato troop especially, huddling was most prevalent during the birth season months of September through November (**Fig. 6.14**). Although these months also coincide with the windiest months of the year (**Fig. 6.6**), it is of note that the troop was not only most cohesive during the birthing season, but when other troop members were in close contact with new mothers, these individuals tended to exhibit affiliative contact through huddling rather than social grooming (**Table 4.4; Table 4.5**). In contrast, other species that have evolved specialized sunning behaviors, mainly *Varecia variegata*, are almost never observed huddling with one another (Pereira et al., 1988; Morland, 1993), even though wild populations tend to reside in primary rainforest habitats (Morland, 1993). Differences in body size may partly explain this near absence of behavior in the latter species (Pereira et al., 1988). However, *Varecia* groups tend to be much smaller than *L. catta* troops, have low levels of interindividual affiliation between group members, and display fission-fusion sociality (Pereira et al., 1988; Moreland, 1993). It therefore seems that since both species have adopted sunning behaviors as a primary means to regulate body temperature, and since the eastern rainforest environment is more shaded, but possibly less windy, than the environmental conditions at CSM, the near absence of huddling in the former species and the frequent expression of this behavior in the latter species indicates that a primary function of huddling behavior in *L. catta* is social maintenance.

Thus, I propose that the function of huddling as a social behavior for *L. catta* especially has yet to be adequately researched for the following reasons: 1) this species has adopted sunning behavior as the primary means of thermoregulation, 2) this species tends to live in social groups that are larger than any other extant prosimian species, and 3) the passive nature of huddling may be more reflective of an affiliative behavior than social grooming because it is indicative of sustained trust and acceptance. In fact, immigrant males in this study did not seem to be fully integrated troop members until they were observed huddling with troop residents (see chapter four).

Intertroop differences

Huddling in the Tsankalamanga troop was weakly associated with cool and windy conditions (**Fig. 6.4; Fig. 6.8**), and this troop spent most of its time in the hedges irrespective of the temperature for the six cooler months of the year (**Fig. 6.12**). Conversely, the Tsankalamanga troop also rested and slept alone almost half of the day during the warmest months of the year (**Fig. 6.12**), and more 100ºF+ data points were recorded at Tsankalamanga despite the fact that less total data were collected from this troop (**Fig. 6.9 – Fig. 6.10**). Thus, it is evident that in comparison with the Bevaro Moravato troop, the Tsankalamanga troop reacted more to the hot and cold extremes of its environment, and it is likely that this troop was more vulnerable to environmental exposure.

The troops also differ in how they change their ranging and feeding behavior in response to average daily temperatures. While there was a weak positive correlation between feeding behavior and average daily temperature with the Bevaro Moravato troop (**Fig. 6.18**), average daily temperature had no effect on the Tsankalamanga troop's feeding behavior (**Fig. 6.20**). Yet notably, the Tsankalamanga troop rarely spent more than a total of an hour a day feeding regardless of the average daily temperature (**Fig. 6.20**) while the Bevaro Moravato troop would feed over twice that amount of time once average daily temperatures surpassed 75°F (**Fig. 6.18**). In contrast, there was no correlation between ranging behavior and average daily temperature with the Bevaro Moravato troop (**Fig. 6.17**), but day ranges for the Tsankalamanga troop were significantly longer on warmer days (**Fig. 6.19**), and feeding behavior increased on days when the troop ranged further (**Fig. 3.8b**). In consequence, while feeding time in general was low for the Tsankalamanga troop when compared with the Bevaro Moravato troop, feeding behavior was especially reduced on days that the troop did not range far.

As described in chapter three, reduced ranging activity in the Tsanakalamanga troop occurred for months at a time, mainly throughout the austral winter months (**Fig. 3.5b; Fig. 3.7b**). In addition, although seasons as defined at neighboring sites did not exist at CSM, the seasonal deaths of the Tsankalamanga troop coincided with what were the coolest months of the year. Moreover, huddling and activity data indicate that this troop was vulnerable to climatic conditions while the Bevaro Moravato troop for the most part was not. However, climatic conditions at this site during the austral winter months were hardly extreme: ambient temperature rarely fell below 60ºF, there were no exceptional rain storms during the months when the deaths occurred, and wind conditions have historically been lowest during this season. It therefore seems implausible that members of the Tsankalamanga troop died seasonally from exposure *per se*. One alternative explanation is that members of the Tsankalamanga troop were not in good enough physical condition at the onset of the austral winter to survive, thus making an already weak population more vulnerable to seasonal shortages (discussed in Simmen et al., 2010). However, health assessments conducted both prior to and in the middle of the austral winter did not find any indication of a chronically unhealthy population (chapter five). Another alternative explanation is that this population was made susceptible to pathogens during this time because of their largely sedentary behavior and monotypic diet. It is also possible that *Opuntia* is a vector for these pathogens; an unidentified fungus has been observed on the fruits of *O. stricta* (Strum, pers comm). Unfortunately, since no necropsies were conducted on the individuals and no fungal or soil samples were collected for lab analyses, little more than conjectures on why these lemurs died can be made at this time. Finally, it is possible that these multiple deaths were the result of bad luck, or demographic stochasticity. I can only conclude that while the multiple deaths in the Tsankalamanga troop tended to coincide with the austral winter months, these deaths were not directly caused by either environmental exposure or starvation.

Regrettably, the remote location and unsustainable mortality rate of the Tsankalamanga troop make it likely that this troop will be dissolved before this question can be further investigated. Yet there is much to be gained through continued research in the Bevaro Moravato region. The value of the Bevaro Moravato troop as a flagship for primate ecology research, invasive biology research, and conservation education initiatives at CSM will be discussed in the next and final chapter, the summary chapter.

Chapter Summary

- As expected, there were strong correlations between sunning and daily minimum temperatures with both troops. In addition, there was no sunning activity on days when initial morning temperatures were 80ºF or higher.
- On warmer days, both troops spent significantly more time resting and sleeping (with huddling removed). However, while this behavior appeared to peak during the austral summer months with the Tsankalamanga troop (December through February), no such trend was evident with the Bevaro Moravato troop.

- With the Bevaro Moravato troop, huddling behavior was only associated with daily maximum wind speed. However, huddling behavior in the Tsankalamanga troop was associated with both maximum wind speed and minimum ambient temperature.
- Both troops resided in hedges almost exclusively when temperatures were below 70°F. This was also the primary substrate both troops used for sunning behavior, and the primary substrate the Tsankalamanga troop used for huddling behavior.
- In addition, both CSM troops tended to rest and sleep on the ground when ambient temperatures were high.
- As indicated through wind data especially, it is probable that *L. catta* huddle to minimize heat loss. However, the role of huddling as an affliliative behavior may be especially central to *L. catta* sociality for the following reasons: 1) *L. catta* is one of only a few primates to have evolved a specialized sunning posture; 2) huddling behavior is rarely observed in other Lemuridae species that have evolved specialized sunning postures; and 3) data from the largely temperate site of Bevaro Moravato indicate that the peak period of huddling behavior with this troop coincided with the birth season, when the troop was also the most cohesive, rather than with cold and windy weather.
- Last, analyses conducted for this chapter substantiate the impression obtained through the previous chapters that the Tsankalamanga troop was more susceptible to environmental fluctuations than was the Bevaro Moravato troop. However, moderate temperatures, a near absence of heavy rains, and low wind speeds during the austral winter months contradict my initial impression (and that of the guides) that members of the Tsankalamanga troop died of exposure *per se*.

CHAPTER 7

Dissertation Summary

Over four decades of research have been conducted on *Lemur catta* in the wild. Yet I have documented behaviors from the Cap Sainte-Marie (CSM) population that have never before been observed in other *L. catta* groups. In addition, by observing this species in an unstudied environment, I have found alternative meanings for other behaviors that have been previously described in the literature. In this final chapter, I first discuss the behaviors that can most impact our current understanding of *L. catta* behavioral ecology. I then summarize the results of the questions and hypotheses that were raised in chapter one. In the third component of this chapter, I discuss the basic premise of this dissertation: why lemurs in this region are less successful than their gallery forest conspecifics. Finally, I conclude this dissertation with directions for future research both ex-situ and in the field, generally, and I provide a brief update on present life in this poorly understood region.

Behaviors of Particular Interest

The most extraordinary findings of this project was the regularity with which these lemurs utilized the planted *Opuntia monacantha* hedges for sleeping, sunning, feeding, social grooming, and even for play. In fact, it would be easy to mistakenly believe that these animals were naturally occurring cactus dwellers.

Also notable was the observed ranging behavior of the two immigrant males who became integrated members of the Bevaro Moravato troop. With the major exception of travel, the CSM *L. catta* population was largely arboreal and in fact spent less time on the ground than has been recorded among gallery forest *L. catta* (see Sauther, 1992). However, the distance of the two males' travel, most if not all of which had to have been conducted on the ground through brush and scrub habitat, is highly atypical of the species. In fact, similar behavior has only been documented within a fragmented population of *Gorilla gorilla diehl* (Bergl and Vigilant, 2007), a primate species that is almost exclusively terrestrial.

In addition, analyses of the social behavior of these groups indicate that agonism among troop members was not necessarily synonymous with aggression and/or fear. In chapter four, I reported that peaks of agonism varied between the two focal troops and only loosely followed agonism trends observed among gallery forest *L. catta* during the premating, mating, birthing and lactating seasons (see Gould, 1997; Pereira and Kappeler, 1997, Sauther, 1992). These differences in agonistic patterns also did not seem to be related to the consumption of *Opuntia.* In fact, the only pattern of agonism noted in this study was in the disproportion of physical agonism directed by adults to juveniles. I believe that this pattern was more akin to socialization than to overt aggression for three reasons: 1) juveniles weren't the biggest recipients of overall agonism, just physical agonism; 2) physical agonism directed towards immatures was mainly from females and resident males, and 3) troops were juvenile centered. This last point, spatial proximity, is especially salient in understanding the context of aggression in social relationships (Bernstein, 2004). Both displacements and physical contact require close proximity. However, while displacements work because the aggressor involuntarily minimizes the space between his or herself and the aggressed, physical contact requires that the two individuals are already in close proximity to one another. Therefore, the disproportionate amount of physical aggression towards juveniles in the Bevaro Moravato troop especially, none of which was severe, indicates to me that the function of this aggression was not to break or damage the social bond but instead to shape behavior (see also Bernstein, 2004).

Similarly, males in the Bevaro Moravato troop especially interacted affiliatively with troop immatures perceptibly more often than has been recorded elsewhere. While all resident males appeared to share this characteristic, one male to juvenile bond (a motherless female) matched the intensity of the troop's mother/infant bonds. Although it is possible that this male was the father, male to immature bonds as described in this study are not believed to characterize the species (Whitten, 1987; Gould, 1994). However, infant sharing by females and the formation of large nursery groups of immatures do characterize the species (Sussman, 1977). Based on this study and previous findings elsewhere, I believe that *L. catta* males, in general, may have predispositions for paternal behavior, but that expression of this behavior is typically subdued because *L. catta* society in gallery forests is typified by female dominant dyads and regular male migration (see also Sussman, 1977).

Last, as described in chapter six, I found that with the Bevaro Moravato troop specifically, huddling behavior served primarily as an affiliative social behavior and only secondarily as a thermoregulatory behavior. In fact, huddling within the troop occurred most frequently during the birth season and was the primary means of contact by which other troop members interacted with new mothers. As with parental care, huddling for affiliative purposes may be characteristic of this species; it may just not be as apparent at sites where huddling also occurs to minimize exposure or to compensate for heavier shade.

Hypotheses

Q1: behaviors of CSM *L. catta*

The two hypotheses on behavioral differences between CSM troops and gallery forest troops were primarily addressed in chapters three and four. In chapter three, I noted that the large home ranges of the CSM population seem to support the theory that primate species in resource-stressed environments have large home ranges relative to their conspecifics. However, detailed analyses on the home range behavior of the Tsankalamanga troop indicated that home ranges were minimized when resources were exceptionally scarce. A primary reason for this pattern was evident in the Tsankalamanga troop in particular and may be due to differences in distribution patterns between *Opuntia monacantha*, *O. stricta,* and the gallery forest troops' primary food; the fruit of the tree species *Tamarindus indica* (see Koyama et al., 2006). In addition, reduced home range size is also associated with troop density in an area (Koyama et al., 2006). Thus, troop avoidance also partly may explain the intrasite difference in home range behavior between the Bevaro Moravato troop and the smaller Tsankalamanga troop.

In chapter four, using descriptive statistic comparisons and half-weight association indices I illustrated that *L. catta* at CSM spent more time engaged in active and passive affiliative social behaviors but a comparable amount of time engaged in agonistic social behaviors than do gallery forest *L. catta*. This finding that largely isolated troops would spend more time in intratroop affiliative behaviors than densely populated gallery forest populations counters the prediction of the socioecological model (see Sussman et al., 2011), in which the primary function of group affiliation is to defend resources from other groups (Wrangham, 1980). Also in contrast to gallery forest troops, female to female affiliative bonds were not central components of CSM troop social behavior. In fact, there were very few adult pair bonds of any sex combination at CSM. Conversely, female targeted aggression also didn’t characterize troop dynamics, and in fact I didn’t observe any aggression leading to wounds among any troop members. Instead, it was the troops’ immatures that were central to CSM *L. catta* social networks. In fact, the strongest bonds were comprised among juveniles and infants, among immatures and adult females, and in one case, between an adult male and a juvenile. Thus, the CSM troops have distinctive youth focused social frameworks. It is within this framework that the frequency and type of social behavior I observed during this study were best understood.

Q2*: health status of CSM *L. catta

The second set of hypotheses addressed the question of whether CSM *L. catta* suffered from chronic health problems or nutritional deficiencies. I first hypothesized that CSM *L. catta* would have more restricted diets than gallery forest *L. catta*. In my second hypothesis, I predicted that CSM *L. catta* would have signs of nutritional distress: e.g., deficiencies in essential minerals and vitamins, dehydration, and low body weights. Moreover, since small troop size is associated with resource scarcity at gallery forest sites (see Pride et al., 2006); I predicted that nutritional deprivation would be especially evident among members of the Tsankalamanga troop. Both of these hypotheses were addressed in chapter five.

Contrary to my first prediction, I found that the diets of CSM *L. catta* were comparable to gallery forest sites in species diversity and composition when measured on a yearly scale. In fact, CSM *L. catta* consumed several of the same species as do gallery forest *L. catta*, mainly: *Aloe vahombe, Azima tetracantha, Cedrelopsis grevei, Cynanchum perrieri, Flacourtia ramontchi, Grewia cyclea* and *Maerua filiformis*. Conversely, I also found that the Tsankalamanga troop had a limited diet from July through September in which the planted hedges of *Opuntia monacantha* provided their primary food. Yet although troop size of neighboring troops in the Tsankalamanga area may have been relatively small (see chapter two), what I did not account for with the latter hypothesis was that the Tsankalamanga troop had only recently been a troop of 11 individuals (vs. the original size of 12 with the Bevaro Moravato troop). In this context, the prediction that troop size is associated with resource scarcity has limited value.

In addition, despite the Tsankalamanga troop's largely monotypic diet of *Opuntia monacantha* during the austral winter months, there were no clear indications that either troop suffered from some nutrient deprivation. For example, although the pelages of lemurs in both troops turned rust/orange during the dry season through the months of September and October, the diets of both troops were not deficient enough in crude protein levels to (strongly) indicate that the lemurs suffered from kwashiorkor, a form of malnutrition caused by lack of protein (Dierenfeld, pers comm.; Berg et al., 2009). In addition, the body weights of CSM *L. catta* were within the range of body weights for gallery forest *L. catta*, and significant differences in body weights between health assessments were likely due to pregnancy and maturation. Moreover, elevated total packed cell volume percentages, protein, creatinine and chloride levels signify that CSM *L. catta* were less hydrated in comparison to other free ranging troops (ISIS reference; Junge, pers comm). However, there were no indications that these lemurs were clinically dehydrated (Junge, pers comm.), and in fact it is likely that they were able to obtain sufficient water from the plants they consumed year round. Last, there were indications that the CSM *L. catta* population suffered from chronic low grade infections, and a possible cause of death for several of the lemurs in the Tsankalamanga troop may have been from an unidentified virus or pathogen. Yet, despite the unsustainable death rate in the Tsankalamanga troop, there were no indicators in the health and nutrition analyses to suggest that CSM *L. catta* were unhealthy. In fact, this population did not suffer from some of the chronic ailments that plague captive and gallery forest *L. catta* (e.g., Spelman, 1989; Crawford et al., 2006; Sauther et al., 2006).

Q3: **the importance of *Opuntia***

The role of *Opuntia* in the region was a secondary theme of this dissertation, and I constructed three hypotheses related to the importance of this introduced genus in the region. In the first hypothesis, I predicted that the planted *Opuntia monacantha* hedges would be the central place of refuge for the CSM *L. catta*. This hypothesis was principally addressed in chapters three and six. Without exception, *O. monacantha* hedges were the only sleeping sites for both troops throughout this study. In addition, I found that both troops spent over one-third of their daily activity time in the *O. monacantha* hedges throughout the year. However, monthly activity time in the hedges varied widely between the two troops and did not follow a seasonal trend. Conversely, in chapter six I reported that hedges were the only place of refuge when temperatures dropped below 70ºF and that they were the primary substrate both troops used for sunning behavior. Finally, the Tsankalamanga troop used hedges as the primary substrate for huddling behavior, which appears to have been for thermorgulatory purposes as well as for social expression (Kelley et al., in prep).

In the second hypothesis, I predicted that *Opuntia* would be the primary fruit consumed by the CSM population during the austral winter months. Analyses conducted in chapters three and five confirmed this hypothesis. However, I did not foresee that the two CSM troops would have very different feeding behaviors in relation to the two primary cactus species in the area, *O. monacantha* and *O. stricta*. Specifically, although *Opuntia* was the primary fruit consumed by the Bevaro Moravato troop from the austral winter months of June through October, the troop fed heavily on the planted *O. monacantha* in June but then concentrated its feeding efforts on the widespread *O. stricta* the other four months. In contrast, the Tsankalamanga troop concentrated its feeding activity on *O. monacantha* during this same period and, in fact, fed heavily from this species from the months of February through October. Only in November did this troop feed heavily on the fruits of *O. stricta*, probably because the fruits of *O. monacantha* were out of season that month, thereby making one or the other species of *Opuntia* an important food for this troop 10 of the 12 months of the year.

In the third hypothesis, I predicted that *O. monacantha* and *O. stricta* would be nutritionally different from the endemic foods consumed in the region. This hypothesis was addressed in chapter five. In this chapter, I reported that CSM *L. catta* consume adequate if not slightly higher than recommended levels of calcium and magnesium, yet neither *O. monacantha* nor *O. stricta* appear to be the primary source of these nutrients. In fact, mineral, neutral detergent fiber (NDF), and water soluble carbohydrate (WSC) content of *O. monacantha* was neither exceptionally high nor exceptionally low in relation to the native plant species consumed by these lemurs. In contrast, samples of *O. stricta* tested exceptionally high in iron (Fe) and manganese (Mn) and may have been a primary source of iron for lemurs in this region. Last, the fruits of both *Opuntia* species had water content levels that averaged over 80%, which is high but not necessarily higher than several other heavily consumed native species in the region. In addition, *Opuntia* fruit was most heavily consumed during the season when temperatures were the relatively coolest. However, because other foods with higher water content were not available during the austral winter months, the fruits of *Opuntia* were likely critical sources of water for the lemurs during these months.

Q4: **how the behavioral ecology of CSM *L. catta* can affect local perception**

Finally, inadequate access to basic resources wasn't the only potential threat for this population of *L. catta*. For the Bevaro Moravato troop especially, the troop's habitat was completely integrated within a region that was frequented by the daily village life of the local people. Thus, because these lemurs were so vulnerable to possible human predation, the last question I asked in this dissertation, through a two part hypothesis, is how the behavioral ecology of these lemurs could affect local perception of them. In the first part of the hypothesis, I predicted that CSM *L. catta* would spend significantly more time within the *O. monacantha* hedges than at the sacred forest sites. Secondly, I predicted that since most of these hedges encircle crops, these lemurs could be perceived as crop raiders and were thereby vulnerable to human malfeasance when within the hedges. Conversely, since I believed that sacred forests were sites of reverence, I predicted that the lemurs would be largely protected when they were in the sacred forest habitats. Components of the hypothesis were addressed in chapters three, five and six.

In chapter three, I reported that the two troops had very different behaviors in relation to their use of sacred forest habitat. Mainly, the Bevaro Moravato troop's home range consisted of almost three times as much sacred forest habitat as it did *O. monacantha* hedge, and sacred forests were a regular component of the troop's monthly core area. In addition, sacred forests were primary feeding sites despite the fact that all of the troop's primary food plants were also available outside of sacred forest habitat. Conversely, although the Tsankalamanga troop's home range was comprised of nearly equal amounts of *O. monacantha* hedge and sacred forest habitat, sacred forests were not always included in the troop's monthly core range or even monthly home range. Similarly, there were months when no feeding bouts were observed within sacred forest habitat for this troop, and in fact this troop rarely left the confines of an *O. monacantha* hedge.

In chapter five, I reported that, with the major exception of *O. monacantha*, feeding from field crops only occurred in November. Similarly, these foods only comprised 1.3% and 0.5% of the Bevaro Moravato and Tsankalamanga troops' total diets that month. Thus, it is clear that these lemurs rarely raided field crops. Moreover, it is of note that one of the Tsankalamanga troop's primary sleeping hedges surrounded an abandoned field that had been invaded by *O. stricta*. However, the hedge was still frequented by villagers for the *O. monacantha* fruit. At the end of the study, it still was not clear whether the lemurs' consumption of the *O. monacantha* fruit was thought of as crop-raiding behavior by the local people.

As for the lemurs' protection in sacred forest habitat, this prediction was best answered through a single experience. Without exception, plants in sacred forests were revered, and it was taboo to pick leaves from the plants or to even walk too close to plants that bordered graves. Moreover, in stark contrast to the noise of village life that characterized the hedges, sacred forests were often quiet, uninhabited by humans, and peaceful. Therefore, it came as a great surprise when the only time I observed a blatant attack on the lemurs occurred in a sacred forest. Since I interrupted the attack, I do not know whether the two young men intended to kill or just chase the lemurs. However, based on this incident, it seems clear that strict taboos that still apply to the forests do not necessarily translate to protection of the fauna that reside within them.

Why So Few *L. catta* at CSM?

The basis of this dissertation is the assumption that *L. catta* at CSM are less prosperous than the gallery forest populations at Berenty and Beza Mahafaly (see also Jolly et al., 2002; Sussman et al., 2006; Axel and Maurer, 2011). However, in the Bevaro Moravato troop specifically, individuals were not malnourished, the troop used several hedges that provided excellent shelter, and few if any nonhuman predators or even competitors for resources lived in their habitat. In addition, only one adult died throughout the entire 15 months of observation, and the size of this troop was comparable to *L. catta* troops that live in the gallery forest reserves (see Sussman, 1991; Koyama et al., 2002; Gould et al., 2003; Axel and Maurer, 2011). Yet, even though there is every indication that this troop thrived in its habitat, it still was the only troop that lived within the Bevaro Moravato area. In fact, I estimate that the population density of the entire CSM region is only .017/ha, which is much lower than the densities of *L. catta* that live in the spiny forest habitats of Berenty and Beza Mahafaly, 1.3/ha and 1.2/ha respectively (Gould et al., 2010). Although low *L. catta* density is exactly what one would predict in areas with low forest canopy density (Sussman et al., 2006), there may be other factors that have contributed to the exceptionally low population density at CSM. One such other factor may be that the lemurs in the region were hunted sometime prior to the start of the study. Yet since there is no substantive evidence that this has occurred, there is little reason to belabor this point. Two other possible factors merit in-depth discussion.

Scenario 1: lemurs need (sacred) forest

The first possible explanation is that the sacred forests are a limiting factor. For although *L. catta* is the most environmentally flexible of the extant Malagasy primates, this species will go to great extremes to live within gallery forest environments. For example, Axel and Maurer (2011) have found that many *L. catta* groups will live near patches of gallery forest that are less than 1 ha even when the region is characterized by dry, deciduous forest. In addition, *L. catta* is absent in the driest (spiny) forests when alternative forest types are nearby (Axel and Maurer, 2011). Similarly, Gould et al. (2010) have found that when *L. catta* populations inhabit small, isolated mixed habitat forests that average 25 ha, home range size of the troops will become very small to support densities of 2.2/ha to even 6.5/ha.

At CSM, the sacred forests, which are not preferred habitats for *L. catta* elsewhere, are only 5 to 13 ha in size. It is therefore possible that sacred forests at CSM can no longer support a viable population of *L. catta*. Thus, the lemurs have learned to adapt by expanding their home ranges across large areas to incorporate as much forest habitat as is needed to survive. Finally, this change in behavior has perhaps become possible only because the dense patches of naturalized *O. stricta* can be used as corridors when traveling among the fragments.

In this first scenario, the lemurs could have inhabited the region well before the arrival of any introduced *Opuntia*. However, a related question that has been posed regarding the population *of L. catta* at CSM is whether this environment could have even supported a lemur population prior to the arrival of *Opuntia*.

Scenario 2: CSM lemurs need *Opuntia*

As has been discussed earlier, the distance traveled by the two males who later became integrated members of the Bevaro Moravato troop is reminiscent of a form of migratory (i.e., atypical dispersal) behavior. It may therefore seem plausible that the population at CSM was founded by troops of *L. catta* that traveled similar distances in search of viable habitat after the introduction of *Opuntia*. However, with other primate species such as gorillas and macaques, extended travel bouts of this distance have typically only been documented with individuals or with pairs, not with entire primate groups (Tattersall and Sussman, 1985; Bergl and Vigilant, 2007; pers obs). Similarly, Pontzer and Wrangham (2006) found that juvenile chimpanzees cannot physically range as far as adults. In consequence, mothers with juveniles have significantly smaller day ranges than other group members. Therefore, the observation of the males' migration does not necessarily indicate that entire troops were able to have traveled similar distances.

Scenario 3: a proposed reconstruction

Although both CSM troops consumed large quantities of *Opuntia*, they also consumed a variety of high nutrient native vegetation throughout the year, e.g., *Aloe vahombe* (P, Zn, H_20), *Terminalia fatrae* (NDF), and *Zygophyllum madecassum* (Mg, Ca, Na, H_20). In addition, highly seasonal endemic sources of nutrition, such as *Aloe vahombe*, coincide with *L. catta* birth and lactation; and the CSM *L. catta* have a diet that seems well integrated with the hypothesized stable isotope biogeochemistry of the spiny forests of south/southwest Madagascar in the recent past (Crowley et al., 2011). Therefore, the dependency CSM *L. catta* have on *Opuntia* today seems to be indicative of habitat loss rather than of unsuitable habitat in the past. Last, it is of note that CSM *L. catta* move with agility and ease within the *Opuntia*; this signifies to me that this species was well-adapted to move within and among spiny vegetation before the arrival of the introduced cacti.

A more problematic issue is to determine what the CSM troops used as sleeping trees prior to the introduction of *Opuntia monacantha*. When it comes to sleeping behavior, *L. catta* is a species of habit, and ongoing research indicates that troops use the same sleeping trees year after year (Mertl-Millhollen, 2000). Therefore, it does not seem likely that an entire population would have abandoned former sleeping sites for *O. monacantha* unless these sleeping sites have since disappeared. For both gallery forest and mixed habitat forest *L. catta*, their primary sleeping trees are *Tamarindus indica* (Meredith and O'Mara, pers comm). In fact, much like the *O. monacantha* hedges at CSM, *T. indica* trees are not only the primary sites of shelter for gallery forest *L. catta*, but the fruits of *T. indica* are also the most important food source for these lemurs (Jolly, 1966; Sussman, 1972; Sauther, 1992).

At CSM, there was one *T. indica* tree within the study's vicinity. Contrary to what would seem plausible, it was found within the Tsankalamanga troop's home range, was very large and lush, and was revered as sacred by the local villagers. However, there was not a single *T. indica* in any of the sacred forests. Moreover, in stark contrast to gallery forest populations, the Tsankalamanga troop never fed from the tree and, in fact, the troop was only observed in the tree two times. Since *T. indica* is generally an integral component of *L. catta* ecology, it is of great interest to me that this troop essentially ignored this tree.

Although I believe it is probable that extant members of both focal troops have never been dependant on *Tamarindus indica* for food or shelter, I also believe it is possible that there were once more *T. indica* in the area (Defoe, 1729). Yet although large swaths of dry forest can be cleared with little effort (see Jolly et al., 2006; Kelley et al., 2007), there is no *T. indica* presence in the sacred forests and no nearby rivers from which gallery forests can be based. Therefore, if gallery forests with *T. indica* ever existed in the region, it is likely that most of these trees either disappeared prior to the arrival of humans (Burney, 1993; Muldoon, 2010) or soon thereafter.

In conclusion, I propose[1] that *L. catta* did inhabit the CSM region prior to the arrival of *Opuntia* and human settlements[2]. With the arrival of humans, some portion of their native habitat undoubtedly disappeared, but these lemurs were able to find a new niche in the *O. monacantha* hedges when the vegetation was introduced to the region around 200 years ago. Like the Antandroy people, *L. catta* likely suffered when *O. monacantha* was largely eradicated in the region (Raven, pers comm). Yet with the reintroduction of *O. monacantha* and the introduction of *O. stricta,* new troops were able to migrate to the area, possibly from relatively nearby vanishing forests, and establish a presence at CSM. These troops learned to adapt to this environment by expanding home range size through the dense *O. stricta* thickets to maximize access to resources.

To conclude, large home range and low density appears to be indicative of *L. catta* in this region. However, it is obvious by the example of the vanishing Tsankalamanga troop that *L. catta* in low density populations are especially vulnerable to

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[1] The conclusions drawn on the historical reconstruction of *L. catta* presence at CSM were through numerous correspondences with Dr. Laurie Godfrey, University of Massachusetts; Dr. Peter Raven, Missouri Botanical Garden; and Dr. Robert Sussman, Washington University, St. Louis.

[2] Subfossil findings of *L. catta* dated by Godfrey to approximately 8000 BP in southeast Madagascar corroborate this conclusion (see also Crowley, 2010).

extirpation when multiple members of a troop die, regardless of the cause, in a single year. Moreover, I am not aware of a source population from which other *L. catta* could disperse from to replenish the CSM population.

Future Research

Comparative research

Findings from this study have provided a baseline of information from which future comparative research should be pursued. A specific example is the finding that the home range area of CSM *L. catta* is over ten times larger than that which has been found elsewhere. This finding has significant implications not only for obtaining a more accurate assessment of *L. catta* presence (Sussman, pers comm.), but also for understanding the effects lemurs can have on their environment. For example, Crowley et al. (2011) have recently cited small home range size as a reason why extant primate species in south/southwest Madagascar may not be effective seed dispersers for this habitat. Findings from this study indicate that small home range size for *L. catta* is a result of the lemurs' preference for (gallery forest) environment, rather than a reflection of physiological limitations. A pursuit of research on the role of *L. catta* as seed dispersers based on this new finding is beneficial not only for reconstructing the past, but also for understanding the possible role of *L. catta* in the spread of *Opuntia*.

In addition, the Bevaro Moravato troop engaged in high rates of social behavior, was highly cohesive, and primarily expressed low intensity agonism that was more associated with socialization than with feeding competition. These behaviors were observed in an environment that was 1) isolated from other *L. catta* troops, and 2) in an environment largely free of predators. Since current socioecological theories are premised on the principles that (female) intratroop relationships are governed by intertroop food defense (Wrangham, 1980), predation (van Schaik, 1983), or a combination of these factors, a detailed study on the sociality and feeding behaviors of this troop merits further investigation (see Sussman et al., 2011). Specifically, although consumption of *Opuntia* may obscure indications of contest competition at this site (see Sauther, 1992 regarding *Tamarindus indica*), a future comparative study on the feeding behaviors of the Bevaro Moravato troop with Berenty troops could be pursued through focused research on how females behave when feeding from shared native resources, e.g., the flowers of *Aloe vahombe*, which are 1) highly clumped, 2) abundant locally but scarce generally, 3) highly seasonal, 4) and are important sources of nutrition for females during the early lactation season (see also Pruetz, 2009).

Another example of research that should be pursued is the finding that *O. stricta* may be a source of high iron content. Ex-situ analysis on the concentration of condensed to hydrolysable tannins in the plant samples of the CSM troops' diet is currently being supervised by Professor Juha-Pekka Salminen at the University of Turku. Results from these analyses will then be compared with similar research on gallery forest *L. catta*. This is important for understanding how tannins bind iron to inhibit iron overload (hemosiderosis) (Spelman et al., 1989; Gould, submitted). While the most important food for gallery forest populations, the fruit of *Tamarindus indica* (Gould, 2006), is noted for its high tannin content, it is unknown whether there is comparable high tannin sources at CSM. The question of how CSM *L. catta* absorb iron, or rather convert Fe^{3+} to Fe^{2+} (Spelman et al., 1989), is of particular interest in light of the fact that the troops' source of high iron is from a recently introduced species.

Last, continued research on the relationship between physiology and behavior for thermoregulation in *L. catta* is being pursued through a collaborative project that includes behavioral analysis from CSM and anatomical analysis on skin samples (Kelley, Jablonski, Chaplin and Sussman). In addition, research on the function of huddling in Malagasy primates with specialized sunning behaviors should be pursued with species that are both allopatric (*Varecia*) and sympatric (*Propithecus verreauxi*) with *L. catta*. Last, to fully understand the mechanisms of behavioral thermoregulation and its evolutionary processes, similar comparative research should be pursued on both other primate species and distantly related mammalian species that share characteristics with *L. catta*. For example, it is of interest that CSM *L. catta* exhibit some similar behaviors (e.g., spend more time resting on the ground) during high temperature extremes to forest dwelling chimpanzees (Kosheleff and Anderson, 2009; Sanz, pers comm). Alternatively, little is known about the behavioral thermoregulation of the meerkat (*Suricata suricatta*), a species that, like *L. catta*, has specialized sunning behaviors, lives in (relatively) large social groups (which is atypical for most other mongoose species), and inhabits (semi) desert environments (MacDonald, 1995).

Unique to CSM

Since this study was conducted on village land, this project only succeeded because I worked within the value system of the Antandroy villagers. Village greetings always had to precede all day follows; guides had to be chosen by the village chief, and rules of taboo had to be strictly followed. For example, it was strictly taboo to collect plant samples from sacred plants. Hence, I learned that it was best to have the guides collect the plant samples. Similarly, the first health assessment phase of this project was regarded with suspicion and, in fact, the project almost ended prematurely because the villagers suspected that the early deaths of the Tsankalamanga troop were caused by the collars, and because they thought the "abandoned" hedge had been too damaged from the darting. Based on this experience, I chose to minimize invasive procedures throughout the remainder of this project. In fact, the only reason I chose to conduct the second round of health assessments was because the collars needed to be removed.

Conversely, I found that the villagers were extremely interested in the lemurs' diets and loved to be challenged on the identification of local plants. In addition, I found that interest in the lemurs increased across the village population as the project progressed, and a foundation of trust developed among the local forestry department, the villagers of the region, and the very small group of westerners who were involved in this project. Finally, unlike so much of Madagascar, there is no threat of habitat destruction in this region. The forests that remain are protected by sentiments much stronger than government labels, and the lemurs have learned to adapt to the habitat that remains.

Based on these observations, I am optimistic that this site has unique value as a site of an on-going collaborative anthropological and ecological project. Specific goals of this project should be: to 1) obtain density estimates of *L. catta* in the broader geographic area; 2) pursue research on the significance of sacred forests and *Opuntia* as components of *L. catta* ecology, 3) continue behavioral ecology research through all-day follows with the Bevaro Moravato troop, 4) create a catalog of the plants consumed by the lemurs, 5) pursue research on the effects of *O. stricta* to the region's ecology, 6) share research findings, especially in regards to the effects of *O. stricta* on both local wildlife and livestock, with local villagers, and 7) assess whether the human/lemur interactions I have observed in the Bevaro Moravato region are consistent throughout the region. Although ambitious in design, I believe that the foundation has been set for such a project to be implemented. Comparative research on the effects of *O. stricta* on the behavioral ecology of olive baboons (*Papio anubis*) is currently being investigated in regions where this cactus has recently occupied Kenya (Strum, in prep). Through collaborative grants, Strum and I believe that a project with an emphasis on invasion biology in general and *Opuntia* specifically is important because of the cacti's apparent profound effect on the ecology of these primates and the people surrounding them. Finally, it is of note that the idea for a community based project that is centered on the Bevaro Moravato troop is not only of interest to me. A Malagasy ecologist who worked for the southern division of ANGAP, the national forestry department, approached me with the idea for a continuing collaborative project.

Concluding Remarks

As I complete this dissertation, southern Madagascar has had another year of extreme hardship. In 2010, this region had to endure two droughts, two cyclones, a locust infestation, and the continued neglect of an unstable national government (IRIN, 2011). In the immediate CSM region, ANGAP officials abandoned plans to have the Bevaro Moravato troop monitored after the southern office went through staff reorganization and financial cuts. Yet despite the personal hardship and lack of financial incentive, one of the guides, the chief's young son Mialasoa, continues to monitor the lemurs. Thus, although the future of this ring-tailed lemur population is tenuous, the Bevaro Moravato troop at least continues to be regarded as a valued component of the village habitat. It is this idea, the idea that these lemurs are valuable not only as research subjects but as remarkably resilient and complex beings in their own right, that will most powerfully protect them. If this idea can be internalized among the Antandroy youth, then the lemurs will have yet another generation of protection. As best stated by the pioneers of ring-tailed lemur field research, “The future of ring-tailed lemurs is not a story of their biology. It is a story of how people value their habitat and their survival” (Jolly et al., 2006).

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