Behavioural Surveys and Edge-Sensitivity Estimates of Two Populations of Free-Ranging Ringtailed Lemurs (*Lemur catta*) in Rocky Outcrop/ Savannah Mosaic Habitat at Anja Special Reserve and the Tsaranoro Valley, Southcentral Madagascar

by

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B.A., University of Victoria, 2007

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Abstract

Behaviour (activity budget, degree of terrestriality, intergroup sociality) and diet, and the impact of proximity to forest edge on both, were compared between two populations of ring-tailed lemurs (*Lemur catta*) inhabiting rocky outcrop/anthropogenic savannah-surrounded forest fragments in south-central Madagascar. Both sites—a fragment in the Tsaranoro Valley local to Andringitra National Park, and a fragment at Anja Special Reserve, adjacent to National Route 7 in the Ambalavao area—are considered sacred forests (sites of human burial) by the local people living in these regions, and are therefore subject to traditional protective prohibitions (*fady*). Both sites attract tourists, but are managed differently, and the resources available to the *L. catta* differ between sites, affecting the behaviour of the lemur populations: *L. catta* at Tsaranoro spent more time feeding, and less time resting and engaging in social behaviour compared with those at Anja, where introduced fruiting trees were available and resource abundance appeared to be relatively higher. Also, *L. catta* at Tsaranoro were less edge-avoidant, with some groups travelling over 400 meters beyond outside the forest in order to utilize resources at the tourist establishment local to the site. *L. catta* at Anja were never observed more than nine meters outside the forest. Although the fragments are of similar size and were expected to differ little, many significant behavioural dissimilarities were observed, suggesting the importance of the refinement of rapid assessment techniques for judging the habitat suitability and conservational value of small forest fragments.

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CHAPTER 1: INTRODUCTION

The nonhuman primate community of Madagascar consists entirely of lemuriform strepsirrhines (primates with sinuous nostril openings, as differentiated from simians), the ancestors of which arrived on the island 62-65 million years ago and filled the niches that are elsewhere inhabited by other types of primates (e.g. simians) and medium- and small-sized mammals (Tattersall 2006). During the 2000 years since *Homo sapiens* colonized the island, Madagascar has seen wide-scale alteration to habitat and fauna. Prior to the arrival of our species, Madagascar hosted the late Quaternary's only strepsirrhine-rich megafaunal community (Burney et al. 2004). Early generations of human arrivals introduced slash and burn agriculture starting around 2000 years ago, altering the landscape and reducing forest sizes, likely contributing to the extinction of the giant sub-fossil lemurs (Burney et al. 2004). The process of forest-clearing continues, and the fragmentation of forest threatens the island's primates, in terms of both immediate survival and genetic diversity (Ganzhorn et al. 2001, Mittermeier et al. 2008). Although Madagascar's total land mass comprises 587,045 km^2, the area capable of supporting wild lemur populations is roughly 50–60,000 km^2, or less than 10% of the island (Mittermeier et al. 2008).

Greater density and diversity of lemurs are found in the eastern and northern rainforests, with the southern and southwestern dry habitats less able to support comparable populations due to the low density of resources in these areas (Sussman 2002). The drier forests of the south, southwest, and south-central Madagascar are the habitat of *Lemur catta* (the ring-tailed lemur), and the geographically limited dry forest is becoming increasingly fragmented in these regions (Ganzhorn et al. 2001, Wells 2003); southern gallery forest is considered among the most endangered types of forest on the island (Sussman et al. 2003). Grazing and overcutting create narrow fragments running along river and stream edges, and there is evidence of river shifts (as denoted by the path of old tamarind trees left in the wake of these shifts) that carries implications for the utility of current efforts to protect these forest fragments (Blumenfeld-Jones et al. 2006, Koyama et al. 2006). The rapid loss of habitat in which *L. catta* occurs at higher densities suggests the utility of studies in other habitats. The extent of this species' range belies the disproportionate distribution of research sites; range is discussed in detail in section 1.1.4 and mapped in figure 1.1. Briefly, the northern limit of *L. catta*'s range extends to the Menabe region in western Madagascar, and the southern limit is the southernmost point of the island itself near Cap Ste. Marie (Sussman et al. 2003). Population densities are often low in the drier forest habitats, while higher densities have been observed in remaining gallery and mesic (non-dry habitat characterized by intermediate moisture) forests (Gould 2006). In the high elevation population at Andringitra Massif, in the south-central region, basic life-history traits differ from lowland conspecifics in spiny bush, gallery and dry deciduous forests (Goodman and Langrand 1996). The diet of these lemurs differs from other regions, and one Andringitra troop has been compared with *L. catta* from in the southwest, and no single food-plant species or genus is shared between these populations (Goodman et al. 2006). Although these differences are broad, research to establish baseline information about *L. catta* in non-gallery forest habitats has been slow. Rapid assessments of new sites are informative, and may generate the impetus for new and more detailed research in these areas in addition to suggesting courses of action for site management.

L. catta is noted for its adaptability—indeed, the ring-tailed lemur has been referred to as a weed species many times in the literature, a term denoting its adaptability to extreme environments, flexibility of habitat use, varied diet, and ability for populations to recover relatively quickly from natural disasters such as droughts (Gould et al. 1999, Gould 2006, Goodman et al. 2006). However, there is a focus on studying *L. catta* in continuous habitat, because much of the work investigating the species' adaptability has been conducted at two sites, both of which are larger continuous forests: Beza Mahafaly Special Reserve (referred to as hereafter BMSR), in south-western Madagascar, and Berenty Private Reserve, in the far south (history outlined in Jolly et al. 2006, and Sussman and Ratsirarson 2006, see figure 1.1 for a map of geographic distribution). This work has been oriented toward adaptation to dry habitat: the correlation between behaviour (e.g. the extreme female dominance observed in *L. catta*), and the harsh Malagasy climate predominates behavioural studies, and demographic studies are focused on the impact of seasonality and natural disasters such as droughts (e.g. Gould et al. 1999, Jolly 1984, Jolly et al. 2002, Mertl-Millhollen et al. 2003, Pride 2005, Sauther and Cuozzo 2008). These studies generally lack comparative data from sites other than one another (see Gould et al. 2003 and Jolly et al. 2002 for comparison between the BMSR and Berenty populations), because little is available. The work presented here is part of a minor (and hopefully increasing) trend towards redressing this deficiency. This is not the only trend on which my research capitalized—my study draws heavily from the theory surrounding edge effects, which is currently a popular approach in primatology to investigating the impact of anthropogenic habitat modification. This body of literature is discussed below broadly, before studies specific to lemurs are covered.

Edge may be natural or anthropogenic, and increasing amounts of anthropogenic forest fragmentation have generated ever-increasing quantities of edge. Heightened contact between nonhuman primates and humans, as well as domesticated animals, occurs in edge zones, as do alterations in the abundance of food resources and the species of parasites encountered by primates (Chapman et al. 2005). It is often noted that edge-positive responses correlate with resource use: plants are attracted to the light available on the edge, and food species may be overrepresented on the edge (Bierregaard and Dale 1996, Hefarty and Caballé 1991, Matlack 1994). Conversely, edges can increase dietary stress in wild-feeding populations by decreasing the availablility of food species that are edge-avoidant and/or by increasing the amount of time spent engaging in vigilance, thereby reducing the quality or amount of food eaten and compromising the effectiveness of the immune system (Chapman et al. 2006, Wasserman et al. 2006). It is common for individuals to vary in their willingness to utilize resources on or beyond the forest edge; in some primate species, it may be that more aggressive individuals, or even more aggressive groups, are more likely to pursue the alternate resources available on or beyond the forest edge (Sapolsky 2006).

Deforestation in many regions of *L. catta*'s range is linked to commercial and domestic charcoal production, precious hardwood poaching, and village agriculture (Sussman et al. 2003). Satellite images combined with ground surveys indicate that land cleared for charcoal before 1987 shows little woody plant re-growth 14 years later (Sussman et al. 2003). The use of forest wood for fuel is a frequent creator of edge in tropical areas—this is particularly evident in the literature on edge effects in African forest primates—because locals 'chip away' simultaneously at the trees on the outward edge of a forest and along any paths within it, creating a maze of interior-forest edge and opening the more protected areas of a forest to edge effects (Laurance 2001). The fragments that remain in some areas of Madagascar (including those at Tsaranoro and Anja) do so by the grace of local traditions prohibiting harm to sacred forests inhabited by ancestral spirits. However, such traditions continue to erode in the face of rural poverty (Harpet et al. 2008); in addition to grazing livestock in prohibited forests and extracting wood, interior edge is produced as trails are created for tourists.

Anthropogenic change has been found to increase at the edge (Watson et al. 2004). This is logical in light of the ease of harvesting fuel wood or building supplies from the edge rather than the interior—what is interesting is that surveys of species' edge responses often stop at the forest edge, a point of heightened human disturbance. Watson et al. (2004) address this in their survey of the variation between bird species in their habitat use in a littoral forest. The species were measured in terms of their distribution across forest core, edge, and the surrounding extra-forest matrix. The key element is the matrix habitat, as the study was largely focused on determining the suitability of fragmented habitat to different species, and the ability to move through matrix may influence a population's persistence in forest fragments (Laurance 1991). One of the confounding factors in predicting the effect of forest fragmentation is that matrix habitats of varying types (e.g. agricultural fields, grazing pasture, household gardens/fields, clear-cut or logged anthropogenic meadows) interact differently with different fragment habitats, and this impacts a fragment population's willingness to disperse into or otherwise utilize the matrix (Marsh 2003). This can result, on the regional level, in a mixed approached to dispersal between conspecifics, with some populations becoming genetically isolated and fragment-restricted, susceptible to population crash and local extinction.

Watson et al. (2004) found that core sites hosted significantly more species of bird than edge and matrix sites, but that edge sites hosted similar densities (of lower diversity) to the core—matrix sites were lower than either in terms of both density and diversity. These findings are in contrast to similar work, which suggests that matrix habitats are utilized by forest-specialist birds.

Lehman et al. (2006) surveyed the lemur community at Vohibola in Madagascar's southeastern rainforest, and found that edge effects are of heightened relevance for species that live in intensely fragmented areas. Lehman et al. surveyed largely folivorous species (eastern wooly lemurs [*Avahi laniger*], brown mouse lemurs [*Microcebus rufus*], red-bellied lemurs [*Eulemur rubriventer*] and eastern lesser bamboo lemurs [*Hapalemur griseus griseus*]), which lack the dietary variability of *L. catta*. The relative plasticity of species is a common thread in comparisons of edge sensitivity and the degrees to which sympatric species are impacted by fragmentation and edge (Kamilar 2003, Marsh 2003, Ménard 2003).

Tutin (1999) conducted a feeding ecology study of resident (greater spot-nosed monkeys [*Cercopithecus nictitans*] and moustached guenons [*Cercopithecus cephus*]) and visiting primates in an African forest fragment, and found that the low availability of preferred foods in the fragment combined with the comparatively high population densities of residents strongly suggest that primates living in fragments are necessarily flexible in their behaviour, even demonstrating adaptation to fragment-life. In the fragment, biomass was determined more by fallback food availability, and a pattern of flexible fission-fusion (groups dividing and coming together alternately and irregularly to pursue resources) unseen in forest-dwelling *C. cephus* was adopted by the fragment-living group. Residence in the fragment dictated ecological costs (reduced diversity and abundance of preferred foods, sporadic competition from larger visiting primates), social costs (isolation from conspecifics making immigration and polyspecific anti-predator coalitions difficult), and some benefits (relaxed direct feeding competition from larger species, the ability to fission without risk of losing the group, reduced travel costs, increased foraging-time efficiency possibly due to more detailed local resource knowledge and monitoring).

Balko and Underwood (2005) conducted a long-term study investigating the impact of forest disturbance on resource availability and utilization by black-and-white ruffed lemurs (*Varecia variegata*). Linking the abundance of food trees to local abundance, behaviour, and intraspecific spacing in *V. variegata*, it was found that the availability of fruit during key life-history events may be a limiting factor for *V. variegata* density, despite descriptions of *Varecia* as behaviourally plastic—able to adjust its social organization and density (a fission-fusion pattern) according to a variety of habitat conditions. The impact of forest disturbance on this behaviourally flexible species suggests that *L. catta*, a likewise flexible species, may be more impacted by fragmentation than would be assumed.

More analogous to *L. catta* in terms of diet, the *Eulemur* species are often considered generalist-frugivore folivores, which would suggest ecological flexibility and the ability to adapt to a variety of habitats, and therefore a lessened impact of primary forest loss for this genus (Schwitzer et al. 2007). Schwitzer et al. (2007) assessed the accuracy of this assumption with regard to blue eyed black lemurs (*Eulemur macaco flavifrons*) at a site in northwestern Madagascar. The habitat elements necessary for the species and the availability of these, as well as the size and utilization of home ranges, were compared between two sites (one primary fragment, one secondary). Density of individuals was lower and groups smaller in the secondary forest, indicating that this habitat is less rich and requires more area per animal; day ranges were between 3.8ha in the primary forest and 19.6ha in the secondary forest. These observations suggest that secondary forest was the less suitable of the two despite the authors' prior assumption that this species' flexibility would mitigate any quality disparity between primary and secondary forest.

The population density of *L. catta* at Anja Private Reserve is known to be high relative to densities from other *L. catta* sites (Gould et al. 2010), despite the small size of the fragment (less than 25 hectares) and its isolation from other forests (Bradt 2005, 2008). These small, genetically isolating forest fragments may embody ecological traps—usually, this is habitat poorly suited for reproduction and survival and unable to sustain a population, that is nonetheless preferred by a species over accessible habitats of better quality (Battin 2004). This signifies a kind of error in judgment, made by a population due to mixed signals between the cues they use to choose their habitat (e.g. short-term abundance of food resources) and the actual suitability of the habitat. The trend in this case is toward extinction, as the chosen habitats fail to sustain the population (Battin 2004). So, while low population density has been correlated with low habitat quality, as in Schwitzer et al. (2007), high population density may not necessarily correlate with increased habitat suitability. The body of literature surrounding this in population and conservation biology refers to habitats fostering high population densities as source habitats (the replacement rate for individuals is above 1:1, hence this habitat can act as locus of emigration) and habitats with low population densities as sink habitats, in which the replacement rate is below the mortality rate (Dias 1996, Pulliam and Danielson 1991). Anja meets these criteria for a source habitat, as the population has expanded steadily and continues to do so (Gould pers. comm.), but if it is entirely genetically isolated it may ultimately act as an ecological trap for its *L. catta* population. Related to this is Battin's (2004) claim that many of the models currently used in conservation research direct us away from explicitly engaging this trap dynamic, equating habitat preference with habitat quality instead. The assumption of optimality is common, and goes without demonstration in many studies; work highlighting such a shortcoming in ecological modeling is highly beneficial to conservation biology, particularly in light of the threat ecological traps might present to susceptible species.

I collected data on the edge responses of *L. catta* in two forest fragments, as well as baseline behavioural data (including activity budgets and terrestriality estimates) and broad dietary information. My intention is to contribute to a growing body of information that can be used in conservation, and to provide fresh data for comparative research contexts. Specifically, this study will be the first to measure edge responses in *L. catta*, and to gauge activity budget, population density, and general diet in largely isolated populations of *L. catta* living in rocky outcrop habitat. Furthering our understanding of *L. catta* as a highly behaviourally plasticity strepsirrhine primate is of particular interest as strepsirrhines as a group are typically considered to be more stereotypical in their behaviour than haplorrhines (e.g. monkeys, apes). Further investigation into the potential plasticity of other strepsirrhine species, particularly in Madagascar, may dictate the approach to fragmented habitat in conservation planning for these primates.

1.1 BACKGROUND: NATURAL HISTORY OF *LEMUR CATTA*

1.1.1 GENERAL DESCRIPTION

L. catta is the only member of the genus *Lemur* (Simons and Rumpler 1988, Mittermeier et al. 1994, Gould and Sauther 2007a, Mittermeier et al. 2008). This is a medium sized lemur averaging about 2.2 kg. (Sussman 1991, Gould et al. 2003) named after its characteristic ringed tail. The species is sexually monomorphic, as is true of lemurs in general (Kappeler 1990, Sauther et al. 1999); both males and females have black muzzles and eye patches, white faces, ears, and undersides, and a grey back extending to the crown of the head. Compared to the more arboreal lemurs, *L. catta* has longer limbs relative to body size (Jungers 1979).

1.1.2 SOCIAL ORGANIZATION

L. catta is a multi-male/multi-female species, with groups typically numbering between 10 and 20 individuals at the two sites where they have been most commonly studied, Berenty and

BMSR (Sauther et al. 1999). Troops are female-resident, with multiple ranked matrilines making up the core of the group and males immigrating and emigrating (Jolly 1966, Jolly 1984, Sauther et al. 1999, Sussman 1991 and 1992, Gould 2006b). The sex ratio is generally 1:1 (Sussman 1991).

The proper definition of group spatial relationships in *L. catta* is debated: depending on population density, either territorial or quasi-territorial may be accurate: behaviour differs somewhat according to habitat (Jolly et al. 1993, Sauther and Sussman 1993). More rigorous defense of home range is seen at Berenty than at BMSR, however, home range overlap occurs at both sites (Jolly et al. 1993, Sauther and Sussman 1993). If a strict definition of territoriality is applied (e.g. from Waser and Wiley [1980]: "the active defense of...home range boundaries by actual or ritual agonistic encounters, thereby maintaining essentially *exclusive* use of the home range"), *L. catta* can not be regarded as territorial. At Berenty, multiple troops sometimes time-share feeding or resting sites (Jolly 1972), and at BMSR troops expand their home ranges to overlap with one another when rare or seasonal resources are unavailable in their area (Sauther and Sussman 1993). The habitat-based variation is due to accessibility of food resources; more rigidly enforced territorial boundaries are observed in seasons of lower resource availability. Female dominance in this species may be the most extreme of any lemur (Jolly et al. 1993), and likely evolved as a mechanism for coping with marked seasonal reproduction and the erratic climate of Madagascar, as dominance confers priority of access to food resources (Jolly 1984, Wright 1999).

1.1.3 DIET AND RESOURCE USE

L. catta is generally described as opportunistically omnivorous, (Sauther et al. 1999) although mainly frugivorous/folivorous—that is, the main food category is usually either fruit or leaves depending on the season (Simmen et al. 2006). *L. catta* have been observed feeding on fruit (both ripe and unripe), leaves (young and mature), leaf stems, flowers, unripe seeds, and occasional animal prey (both vertebrate and invertebrate) (Sauther 1993, 1994, 1998, Sauther et al. 1999, Simmen et al. 2006) Also included in the diet of some troops are anthropogenic foods, including crop plants, tourist food, cooking waste/food garbage, and the feces of both humans and livestock (Jolly et al. 2002, Loudon et al. 2006, Fish et al. 2007, Gemmill and Gould 2008, LaFleur and Gould 2009). *L. catta* diet is discussed in greater detail in section 1.2.2. Food resource use is only known in detail for troops living in gallery forest habitats, (but see Gould et al., under review, for spiny forest diet).

The diet of high-altitude groups at Andringitra is distinct from that of groups in gallery or dry forest, with no species shared between Andringitra and BMSR groups (Goodman and Langrand 1996): particularly, the Andringitra population's diet does not include tamarind, which makes up over a third of the BMSR diet in some seasons and is the only food used throughout the year at that site (Goodman and Langrand 1996, Sauther 1998, Simmen et al. 2006), and is utilized intensively at Berenty during the birth and lactation season (late dry season–early wet season) and is the stable food source during the dry season (Simmen et al. 2006). The alpine plants (e.g. shrubs and lichens) that make up much of the Andringitra population's diet are absent from the BMSR diet (Goodman and Langrand 1996). The extent to which this population and the groups at lower elevations in this region differ in their diet is discussed briefly in section 4.6.

1.1.4 DISTRIBUTION AND HABITAT

L. catta is found in areas of anthropogenic savannah, as well as xerophytic, brush, scrub, gallery, spiny, and dry deciduous forests (Sussman et al. 2003, Jolly 2003, Goodman et al. 2006, Gould 2006).

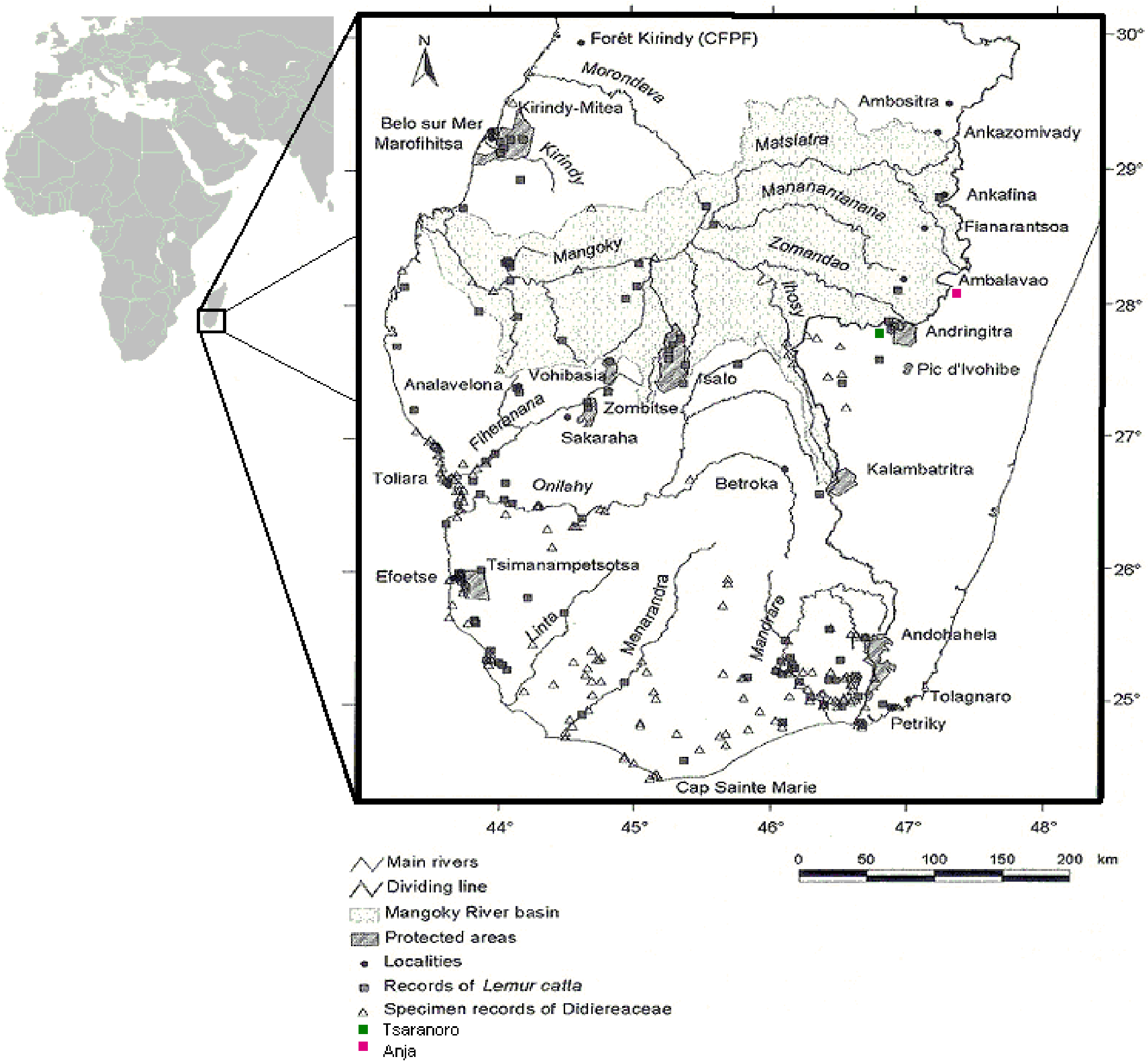

Figure 1.1: From Goodman et al. 2006. "Map showing the geographical distribution of Lemur catta and member of the plant family Didiereaceae in the southern third of Madagascar. Most site names mentioned in the test and large rivers are also shown" [map]. In: Alison Jolly, Robert W. Sussman, Naoki Koyama and Hantanirina Rasamimanana. Ringtailed Lemur Biology. Springer, New York: 2006, p.5. Edited here to be shown as an inset and to include the study sites.

The northern limit of *L. catta*'s range is Belo sur Mer or Mahababoky (on the west coast, north of the Mangoky River) and inland at Parc National de Kirindy-Mitea (both sites in the southern Menabe region) (Sussman et al. 2003, Goodman et al. 2006). This is a dry deciduous forest area, with some vegetational transition from southern spiny bush. Little fieldwork has been done in this area, although hunting of *L. catta* and other species has been reported (Goodman and Raselimanana 2003).

The Southern distribution limit is between western and eastern watersheds—a line dividing dry (western) and humid (eastern) habitats, the latter of which is devoid of *L. catta* (Sussman et al. 2003, see figure 1.1). In the south, *L. catta* is often associated with gallery forests, and in the most marginal, dry areas of the south there is evidence of seasonal or erratic habitation (Goodman et al. 2006).

1.1.5 TERRITORY USE AND EDGE SENSITIVITY

Forested territory use varies in *L. catta* depending on food availability, group size, and total population, and seasonal variation is common (Pride et al. 2006). Habitat-based variations in population density and territoriality are discussed in section 1.2.1

No work has been done to generate estimates of *L. catta*'s sensitivity to edge, and cross-site comparisons are not possible at this point, due to the lack of research on forest edge effects in this species. As *L. catta* is a 'weed species' noted for its flexibility, it may be assumed that the foraging opportunities present at a forest's edge are attractive.

1.2 ECOLOGICAL FLEXIBILITY

1.2.1 INTERSITE VARIATION

Beginning with well-studied reserves, Berenty Private Reserve in the extreme south of Madagascar is described as one of the few tracts of gallery forest remaining in the area, with lemurs along the southeastern coast otherwise existing in small sacred forests but absent in the surrounding agricultural land (Gould 2006). In gallery and second growth forests, densities range from 250 –500 individuals/km^2, with densities of 100/km^2 in scrub forest fragments (Jolly et al. 2006). Likewise, troop sizes typically range from nine individuals in scrub forest to 14-16 individuals in areas where anthropogenic foods are accessible—the largest group here numbers 26, while the smallest group, in the scrub forest, has been observed to fluctuate between four and eight individuals (Jolly et al. 2002, Koyama et al. 2002, Pride 2005). Larger populations in habitats affected by strong seasonality have been found to be more physiologically stressed, with higher intragroup resource competition than smaller groups in the same habitat (Pride 2005). Population densities in microhabitats at BMSR vary according to seasonality and relative habitat quality, although the reserve populations as a whole may represent the optimum carrying capacity for the overall habitat, 100-110 individuals including immatures, averaging 11.5/group with group sizes ranging from four to 35 (Gould et al. 2003, Sussman 1991).

The high-altitude population found in the Andringitra mountain range lives in the coldest area of Madagascar, between 900 and 2600m (tree line ending at 1950m) (Goodman and Langrand 1996, Gould 2006). High-altitude individuals demonstrate both cold-climate adaptations of coat density, and colouration differences from low-elevation groups (lighter pelage possibly due to relatively higher solar radiation exposure) (Goodman et al. 2006). Populations in the mountainous areas of Andringitra are present at very low densities (22.8 lemurs/km^2) (Goodman and Langrand 1996, Goodman et al. 2006). Home ranges of high-altitude groups are vertically oriented, with two studied groups using vertical areas from 1310-2360m and 1250-2040m respectively, and day ranges are large, with groups covering over 100ha/day (Goodman and Langrand 1996, Goodman et al. 2006). General demographic comparisons between these sites and those I surveyed are made in section 2.2.

1.2.2 ANTHROPOGENIC RESOURCE USE

Beyond the variation in diet described in section 1.1.3, there is the issue of non-naturally occurring foods introduced into the diet by humans (intentionally or otherwise). The availability of anthropogenic resources can halt the cycle of trade-off between foraging and vigilance; provisioned food resources are of higher quality than natural foods, and predation is likely mitigated by the presence of humans (Mertl-Millhollen et al. 2003). *L. catta* is gregarious in its use of human resources, earning again its ‘weed species’ designation. The pattern emerging in the literature is of ambivalence between cost and benefit: individuals may have a higher quality diet, but be subject to harm from humans and domesticated species (e.g. dogs), as well as increased parasite transmission (Cuozzo and Sauther 2004, Fish et al. 2007, Gemmill and Gould 2008, LaFleur and Gould 2009, Loudon et al. 2006, Miller et al. 2007).

1.3 RESEARCH TRENDS REGARDING *LEMUR CATTA*

Research is largely confined to gallery and deciduous forest habitats, leaving *L. catta*'s other habitats underrepresented. In light of this, other deficits are apparent: resource base variation cross-habitat is poorly researched, as is diet in the absence of tamarind (as is the case in the Andringitra mountain populations and in troops removed from a major water source/in non-gallery forest—but see Gould et al. in prep for information on *L. catta* in spiny forest nutrition and Kelley, in prep for *Opuntia* forest feeding ecology).

There is a trend towards an ethnoprimatological approach in work that touches on forest fragmentation and patterns of resource use, likely due to the importance of utilizing Malagasy cultural prohibitions in conservation, and the increasing awareness of the impact of anthropogenic resource use. Much of the information contributed to this sphere, however, is anecdotal (e.g. Loudon et al. 2006, Fish et al. 2007, Jolly et al. 2002). Despite the interest in these subjects, little comparative data are available due, again, to the concentration of research at few sites.

1.4 HYPOTHESES

My research addresses intersite variation, the relative suitability of anthropogenic savannah-surrounded forest fragments as *L. catta* habitat, and edge sensitivity between sites. Each of these topics is inherently related to the flexibility of this species throughout its range and contributes to a fuller understanding of intraspecific difference in *L. catta* ecology. Observations were made at two sites—Tsaranoro and Anja Private Reserve, discussed in chapter 2—and while some questions consider the two populations compared with data from other habitats, much of the analysis addresses difference between the two.

1.4.1a ACTIVITY BUDGETS

There are no specific hypotheses concerning the Tsaranoro and Anja activity budgets in and of themselves; however, the presentation and discussion of this data in sections 3.1.1 and 4.1.1 addresses the following questions: How do *L. catta* at these sites proportion their time? Are there differences in the amount of time the lemurs spent in various activities between sites?

1.4.1b INTERSITE VARIATION IN ACTIVITY BUDGET

Activity budget studies in primatology often find that the percentage of time spent engaging in different behaviours is dictated by various ecological conditions, including resource availability and seasonal variation; generally, the availability of resources affects variation in activity budget within a species, as groups living in lower-quality habitats must spend more time searching for and/or processing food than conspecifics in higher-quality habitats. I did not directly measure resource availability as an annual study examining seasonal differences in resource base was beyond the scope of my research—this needs to be addressed in a future study. However, resource availability can be indirectly inferred from population density, as relatively higher resource availability generally accommodates a larger population (Janson and Chapman 1999, Ramos-Fernández and Ayala-Orozco 2003, Rodriguez-Toledo et al. 2003). While the two fragments do not differ greatly in size and are both rocky outcrop forest habitat, population density is higher at Anja, which suggests that there may be differences in resource availability.

Hypothesis 1: Habitat variables (e.g. forest composition) were expected to be similar enough between sites that there would not be significant differences in activity patterns between the Tsaranoro and Anja populations, except with regard to the specific behaviours discussed in hypotheses 2-3.

Hypothesis 2: The population at Tsaranoro is expected to be less habituated to human presence, as Anja is a higher-traffic site—the Tsaranoro population is therefore expected to exhibit significantly more vigilance behaviour relative to the population at Anja.

Hypothesis 3: The Tsaranoro population is expected to vocalize significantly less frequently than the population at Anja, because the greater population density at Anja is expected to result in heightened resource and home range defense, which are contexts of increased vocalization.

1.4.2 INTERSITE VARIATION IN TERRESTRIALITY

The ratio of terrestriality to arboreality in *L. catta* living in a rocky outcrop forest-savannah habitat has not previously been reported. Likely the composition of the fragments will dictate the degree of arboreality within them, and the presence of resources beyond the forest may increase the amount of time spent terrestrially.

Hypothesis 4: Rates of terrestriality are not expected to differ significantly between sites, and both populations are expected to spend more active time terrestrial than arboreal. This is suspected because the forests are punctuated by boulders, which are absent in other habitats (e.g. gallery forest), and because the resources available in the agricultural/village land and tourism businesses local to both fragments are expected to draw the population out of the fragments to some extent, thus increasing their degree of terrestriality. Terrestriality will be higher outside the fragments than in the forests due to the decrease in trees beyond the edge.

Hypothesis 5: Both populations are expected to spend more time terrestrial than the average reported for *L. catta (*comparisons will be made with data from other sites [Berenty (Jolly 1966), BMSR (Sauther 1992 and 2002, Sussman 1972, 1974, and 1977), and Antserananomby (Sussman 1974]), but are not expected to exceed terrestriality observed in more habituated populations during periods of low predation pressure.

1.4.3 INTERSITE VARIATION IN RATE OF INTERGROUP ENCOUNTERS

Hypothesis 6: There will be little variation between the Tsaranoro and Anja populations regarding their rates of intergroup encounters because the two sites are expected to be similar in terms of habitat and population density.

Hypothesis 7: The rate of intergroup encounters at both Tsaranoro and Anja will be higher than those observed elsewhere (e.g. Berenty) due to the fragmented nature of these forests and greater population density compared to larger reserves, and the increase in competition for food resources that such fragmentation is expected to precipitate.

1.4.4 INTERSITE VARIATION IN ACTIVITY BUDGET AT GRADED DISTANCES FROM THE FRAGMENT EDGE

Hypothesis 8: Proportions of observations relative to distance from the fragments' edge (both in and beyond the fragment) will vary significantly in the cases of vigilance (significantly increasing further from the middle of the fragments), vocalization and resting (both expected to significantly decrease further from the middle of the fragments as the edge is visited by humans including tourists, and possibly by livestock, and this is expected to deter these behaviours). Other behaviours will not change in their proportion of the activity budgets as proximity to the edge differs.

Hypothesis 9: There will be no significant intersite variation in the effect of edge on different behaviours; as the fragments are of similar size and composition, as well as similar in terms of features (tourist establishments nearby, villages and rice fields surrounding the fragments, one edge bordered by large rock formations) it is expected that the sites will not significantly vary in the effect proximity to the edge has on each population's behaviour.

Hypothesis 10: Rate of intergroup encounters at graded distances from the edge will not differ in patterning between the sites; encounters are expected to occur more frequently further towards the interior of the fragments as this is where troop concentration is expected to be highest.

1.4.5 DIET COMPOSITION VARIATION BETWEEN SITES

I suspect that overall trends in resource use will be similar between the two populations, but in light of the observation that the high altitude population of *L. catta* local to Tsaranoro incorporate a higher than average proportion insects in their diet (Goodman and Langrand 1996, Goodman et al. 2006), I predict the following:

Hypothesis 11: Although the overall diet will be similar between the two groups, particularly in terms of plant use, there will be significant differences in terms of the proportion of consumption of some food classes included in their diets.

1.4.6 VARIATION IN FOOD-ITEM CLASS PROPORTIONS RELATIVE TO DISTANCE FROM EDGE

Hypothesis 12: Across distances within the fragments food class proportions will not vary, due to the expected homogeneity of vegetation edge-to-interior. However, outside the fragment proportions will diverge due to intersite variation in anthropogenic resource availability at these distances—at Tsaranoro, the garden at Camp Catta is utilized by *L. catta*, whereas *L. catta* at Anja were not observed outside the fragment during the time of my study, and anthropogenic sources of food outside the fragment are not expected to be accessible.

CHAPTER 2: RESEARCH METHODOLOGY

2.1 STUDY SITES

My study was conducted in July 2009, at sacred forest fragments in the Tsaranoro Valley (adjacent to Camp Catta, a privately owned tourist destination established in 1999 to cater to climbing and trekking-oriented adventure tourists) and at Anja Private Reserve. The sites are located in south-central Madagascar at 22°05’11 S 46°46’ 14 E (Tsaranoro) and 21°51’12 S 46°50’40 E (Anja), and are shown in figure 1.1.

Tsaranoro Valley is immediately east of the Ampiadianombilahy mountain chain in which Parc National Andringitra is found. The Tsaranoro forest fragment extends to the foot of the Tsaranoro Massif, on the side of the valley opposite the mountains bordering the National Park.

The Camp Catta grounds are heavily gardened and various cultigens were fruiting or flowering during the research period, including *Melia azadirach*, a fruiting ornamental tree native to Asia. Camp Catta and Tsaranoro fragment are not part of the National Park; the fragment has remained continuous due to its past use by local Betsileo as a burial area: this places various *fadys* or restrictions on its present use, thereby rendering it sacred. To ensure prohibitions are followed, a Malagasy guide is required for entrance into the fragment.

The Tsaranoro Valley is variable in elevation—records taken with a hand-held Garmin Oregon GPS unit were between 762m and 884m—and average temperatures in the cold season (April-September) are similar (23°C to 32°C) to other sites in the south and southwest where *L. catta* has been studied. At BMSR daytime temperatures average 34°-35° C (Sauther 1992, Sussman 1991), and at Berenty the average temperature in July is 24° C (Jury 2003). Seasonality is similar to that observed at lower altitude sites, with a cool, dry austral winter and a hot, wet austral summer.

The fragment itself is 28 hectares of continuous rocky-outcrop forest, largely temperate but with some rainforest species (e.g. bamboo) and desert scrub plants (see fig 2.1) occurring as well.

Figure 2.1 – Scrub flora at Tsaranoro (unidentified). (Photo by A. Cameron)

The topography of the fragment is intensely varied, with denser, wetter forest occurring at higher elevations within the fragment—particularly closer to the massif—and drier forest occurring in the lower areas. A system of trekking trails runs through the forest. These trails may follow older footpaths used by local villagers, but have been updated—some steeper trail areas have large stones in place as steps. At the end of the continuous fragment is an area of non-continuous forest tapering out in a gradient into a few scattered trees in savannah and former rice fields; this gradient of non-continuous forest is discussed further in section 2.4.4. The fragment is not fenced and the movement of the lemurs within and beyond the fragment into the savannah habitat is not restricted or restrained in any deliberate way. Research was conducted throughout the fragment and surrounding area, including the garden area of Camp Catta. Figure 2.2 is a satellite image of the fragment, with the continuous forest area marked and Camp Catta (to the north) labelled.

Figure 2.2 – Satellite view of Tsaranoro fragment (Photo from GoogleMaps)

The Valley is largely covered in gardens and dried rice fields in long, low terraces, with scattered small communities. While evidence of prohibited wood collection and tree felling for use as fuel wood, etc. was common in the National Park, I saw no wood collection from the sacred forest; however, Zebu are herded by the local Betsileo throughout the valley and the National Park, and were found grazing in the sacred forest on one occasion, which is nominally forbidden. Certainly, Zebu and other livestock were restricted from accessing the fragment, and dogs in particular (which congregated around Camp Catta and the other tourist accommodations at Meva Camp nearby) were kept from following groups into the fragment. However, when *L. catta* entered the Camp, dogs freely chased and harassed them, but were never observed following the lemurs back out of the camp site.

The Anja fragment is located directly off Route Nationale 7 roughly 15km south of Ambalavao. The fragment is 23 hectares and more strictly rocky-outcrop forest than the Tsaranoro fragment; cultigens like *Melia azadarach* are also much more common than in the Tsaranoro fragment. It is bordered on the east side by large rock formations, which run parallel to Route Nationale 7, approximately 350 metres from the edge of the fragment. Bordering the south side is an artificial lake in which Tilapia are farmed, and which allows the rice terraces on the north side of the fragment to remain irrigated (as opposed to the dry terraces at Tsaranoro). The lake is channelled toward the rice terraces via a small creek running through the forest at the front of the fragment. Before reaching the terraces, the creek is diverted into a small pond used by villagers and domestic animals; this pond is crossed by the foot path into the fragment and is partially bordered by a large boulder on which *L. catta* were encountered on multiple occasions. The region as a whole differs little from Tsaranoro with respect to water availability, but water availability is high in the fragment itself due to the presence of the lake.

Elevations recorded at Anja were between 925 and 1000 metres, from the foot of the slope descending from the road up to the sheer face of the rock formation. Boulders dominate the centre of the fragment, and are much taller than rock formations in the fragment at Tsaranoro. The bulk of the forest occurs in a band around these rocks, areas of which are modified with introduced plants which may have precipitated the increase in fragment size between 1999 (8 ha) and 2009 (23 ha). Stands of *M. azadarach* trees can be found in the lower part of the fragment. As at Tsaranoro, trails follow irregular routes through the fragment, passing by traditional burial areas.

The *L. catta* at Anja are, as at Tsaranoro, free to move within and beyond the fragment, which is not fenced or otherwise enclosed. Tourists with guides were frequently observed making use of the fragment at Anja; and the reserve is maintained by the Anja-Miray Association (*miray* meaning of one mind [Hallanger 1973]) as a community business. Related to this is that Camp Catta is oriented toward adventure tourism (climbers, paragliders, trekkers), and must be travelled to via several hours on rough, unpaved roads, while Anja is located directly off a paved, national highway, and caters to tourists interested in seeing easily accessible wildlife, thus Anja experienced a much higher volume of tourists than Camp Catta (approximately 10 times that site's daily average based on my notes).

2.2 SUBJECTS OF STUDY

The fragment at Tsaranoro is home to approximately 60 *Lemur catta* in an indeterminate number of groups; the smallest group encountered was two individuals and the largest 15, but smaller groups or sub-groups of up to six individuals often joined groups of similar size before splitting again. These *L. catta* have not been previously studied, but are for the most part habituated to observation; groups ranging further back toward the massif were less habituated than troops from lower elevations, where human encounters were more frequent.

The Anja fragment is home to a confirmed 99 *L. catta*, and the total population is likely over 200 individuals, as there are expected to be groups that were missed during the census. The most common group size is 16 individuals, with the smallest group encountered numbering four and the largest 21. Table 2.1 compares the Tsaranoro and Anja fragment population demographics to those from other sites. Population densities are higher than those reported for other sites.

Table 2.1 – Between site comparison of broad population demographics with data from Goodman et al. 2006, Gould et al. 1999, Gould et al. 2003, Jolly et al. 2002, Kelley in prep., Koyama et al. 2002.

Site	Habitat	Number of groups	Average population	Individuals/hectare
Tsaranoro	Rocky outcrop forest	6	≈60 individuals	2.2
Anja	Rocky outcrop forest	5-12	≈150 individuals	6.5
BMSR	Gallery and dry forest	9-11	96 individuals	1.2
Berenty Reserve	Gallery forest	8	<200 individuals	2
Berenty Reserve	Spiny forest fragment	3	20-27 individuals	1.3
Andringitra	Rocky outcrop Forest	-	-	0.23
Cap Sainte Marie	*Opuntia* forest	-	-	.017

As at Tsaranoro, the Anja lemurs are habituated to human presence, although they have not previously been studied—likewise, those found in less accessed areas of the fragment were less habituated. Overall, the *L. catta* at Anja were more habituated to human presence compared with the Tsaranoro population.

Guides at both sites reported that *L. catta* inhabit much smaller and more removed fragments of rocky-outcrop forest near to, but disconnected from, the >20ha fragments. These may serve to increase gene flow at both sites, but I could not personally confirm the presence of these remote groups at either site.

Groups sampled at both sites included those found outside the fragment (at both sites dry anthropogenic savannah with scattered trees and rock formations—and the lake, at Anja—see figures 2.3 and 2.4). Routes taken through the fragments were varied in order to encounter groups throughout each fragment, rather than focusing on the more habituated groups that ranged closer to the fragment peripheries.

Figure 2.3 – Anthropogenic savannah at Tsaranoro (left) and Anja (right). (Photos by A. Cameron)

Figure 2.4 – Tilapia farming lake forming the south border of the fragment at Anja. (Photo by A. Cameron)

Sex determination of *L. catta* is straightforward in adults, as females have visible, black vulva and males have large scrotums, visible wrist spurs, and larger canines which extend over the lower lip when the mouth is closed (Jolly 1966), but capture and in-depth classification were not possible due to the length of the study and the prohibitions against capturing lemurs in the sacred fragments. Individuals of all sex and age classes are represented in the behavioural data, with no distinction made or weighting based on sex or age.

2.3 SCHEDULING OF SAMPLING SESSIONS

Research was conducted in July, 2009, as part of an initial survey of population, habitat, edge effects, feeding ecology, behavioural endocrinology, and parasite profile of the *L. catta* in these fragments by Dr. Lisa Gould and Denise Gabriel and me. Data were collected over 10 days at each site, between 0800 and 1200 or 1300, and again starting at 1300 or 1400 until twilight (generally 1650 to 1700). These hours broadly overlap with the hours of peak activity for *L. catta* (between 0800 and 1130, and 1400 and 1800 (Gould 1996b). Scans began in the morning as soon as a group was encountered (which was punctually at the start of the day at Anja, and highly variable at Tsaranoro), and would resume again after-the lemurs' midday rest period with the same group or another, if encountered first. The irregularity in encountering subjects to sample at Tsaranoro meant that data collection was necessarily ad hoc, which was replicated at Anja to allow for a stricter comparison of the site-to-site data. This precluded scan sampling of groups at specific distances from the edge or particular parts of the fragment at specific times of the day.

2.3.1 DATA COLLECTION AND SAMPLNG TECHNIQUES

I collected behavioural data at the troop level, with information on behaviour and strata use recorded for every visible individual at five minute intervals. By the end of a sample session an accurate tally of the number of individuals in the group could be made, and the number of individuals not accounted for at each five minute interval were tallied and retroactively included in that scan as 'out of sight'(Lehner 1996). Scan sampling (described in next section) was chosen because it allowed me to obtain data that were representative across all individuals, and to collect multiple types of data rapidly. Given the time frame of the research season, it would have been impossible to collect such data had focal animal sampling been used.

I recorded coordinates at the location of the approximate centre of each group when it was first encountered, and retook coordinates at the next approximate centre of the group after every individual had left the area encompassed by the spread of the furthest group members when the previous coordinate was recorded.

I sought out new groups and avoided more than three sample sessions with the same group, in order to prevent the overrepresentation of any particular group.

2.4 DATA COLLECTION

2.4.1 DATA COLLECTORS

We had a local guide at each site—Jean Paul at Tsaranoro and Clovis at Anja Reserve (last names not known). These guides assisted me in walking the perimeter of each fragment and recording the coordinates of the edge, as well as in locating groups at the beginning of the day and new groups throughout each day.

2.4.2 BEHAVIOURAL RECORDING

Five minute group scan sampling (Martin and Bateson 1993) was used to collect behavioural data for this study. At five-minute intervals (timed by digital watch) a group scan would be recorded, noting the behaviour of each visible group member (including food type when feeding), whether the animal was terrestrial or arboreal (see 2.4.4), group size, coordinates, date and time. I did not restrict data from analysis on the basis of sample session length. In total, 3598 observations of individual behaviour were recorded at Anja and 1851 were recorded at Tsaranoro. At both sites roughly 1/3 (33.05% at Anja, 35.93% at Tsaranoro) of observations were individuals counted as ‘out of sight.’ These ‘out of sight’ observations are excluded from totals discussed in the results (chapter 3), and activity budget percentages reported are percentages of the total observations excluding the ‘out of sight’ numbers.

Scans at five minute intervals allowed enough time to record the behaviour, strata position, and food item choices of <20 group members and accurately record each one at the five-minute mark; this recording method also gave me time to walk around the lemurs through difficult terrain while at low risk of missing a scan or losing track of some group members. Coordinates were noted between scans after location changes. In conducting scans, I focused on keeping as many individuals in sight as possible rather than keeping strictly the same group members in sight—lacking specific study groups precluded rotation through focal animals within each group to ensure representational behavioural data, and focal animal selection might have increased sampling bias toward less active or skittish individuals.

Included in the counts are behaviours where terrestriality or arboreality were not noted: vocalization and locomotion can be identified while an individual is obscured from view, and were recorded only when visual contact had been established with the individual and the behaviour occurred within 10 metres of my position (in these cases terrestriality or arboreality could have been inferred, but such inferences are excluded from the counts).

Similarly, for vocalization, indeterminate number of participants are counted as one observation of vocalization—so if all or most of the group is vocalizing but I was unable to obtain a good certain count, I counted it as if it had been one individual, which under-represents vocalization to some extent: e.g., if an entire group was alarm calling, and I could see each group member vocalizing at the sample time, it was recorded individually, as (for example) 14 instances of vocalization. If, however, out of sight individuals were vocalizing as well and/or it was difficult to distinguish vocalizers among visible animals, it was counted as one instance of vocalization.

Intergroup encounters were noted as occurring (see results 3.4), but were not included in activity budget data, although scans were continued during intergroup encounters, and behaviours recorded (e.g. locomotion, agonism) are included in the activity budget data. Intergroup encounters were recorded *ad libitum* and will be discussed without statistical analysis;

this is true of specific vocalizations, which are not differentiated from one another statistically but will be discussed in the context of between-site comparison (results 3.1.3, discussion 4.1.3).

2.4.3 ETHOGRAM

Ethograms for *L. catta* have been published in relation to research conducted at Berenty and Beza Mahafaly (Jolly 1966, Taylor 1987, Gould 1996a and 1996b, Ellwanger 2007). These were the basis for the ethogram used in this study, which is somewhat simplified to accommodate the length of study and modified for relevance to this research. Table 2.4 is a list of the behaviours used in this study (summarized, with the ethogram); the ethogram is essentially the same as is used in all behavioural studies of *L. catta*, creating comparability between data sets.

Table 2.2 -- Ethogram for *Lemur catta*, developed by Jolly 1966, Taylor 1987, Gould 1996a and 1996b, modified for 5-minute interval scan sampling at Tsaranoro and Anja by A. Cameron.

Observation type	Description
Behavioural	
Feed	-An individual is chewing and has an item of food in or held to its mouth.
Rest	-An individual is relaxed and motionless; this category conflates sleeping and sitting behaviours counted separately in other studies for simplicity.
Rest in contact	-Two or more individuals are relaxed and motionless while in direct physical contact with one another. The individuals were individually counted as resting in contact. Other behaviours that occurred while an individual was resting in contact (autogrooming, vocalization) were counted separately in addition to resting in contact.
Locomotion	-The individual is active and not stationary, moving through the habitat, including through food trees during feeding.
Sun	-The individual is stationary with forearms spread to absorb solar heat.
Vigilance	-The individual is visibly alert, with a more rigid-that-usual body posture/movement. Focused gaze, vocalizations including alarm calls, and to some extent ear posture indicate of vigilance as well. This behaviour may be slightly underrepresented due to the degree of certainty I required to record an observation of vigilance.
Vocalization	-The individual is making purposeful oral sounds, generally low grunts to indicate stress. The following categories were noted as described but are subsumed into ‘vocalization’ for statistical analysis.
Territorial call*	-Specific vocalization made to inform other groups of group presence/position.

Terrestrial alarm*	-Specific scream made when a predator/threat is detected on the ground; also used at Anja as an alternate territorial call.
Aerial alarm*	-Specific scream made when a predator/threat is detected in the air.
Contact call*	-Specific vocalization made when an individual is unable to see or locate its group in the immediate area. This is a short-range call.
Lost call*	-Specific vocalization made when an individual is unable to see or locate its group. This is a long-range call.
Autogroom	-The individual is grooming itself with its tooth-comb.
Allogroom	-Two or more individuals groom each other with their tooth-combs.
Agonism	-The individual is chasing/being chased, fighting, or otherwise physically intimidating/being physically intimidated by another individual. Behaviours in this category are typically more highly defined and divided, but agonistic interactions were rare during my study.
Scent Mark**	-The individual is smearing musky discharge on a branch or other feature of the environment via wrist spur or anal gland.
Defecation**	-The individual is expelling bodily waste. Typically this occurs on a group-wide scale over 5-10 minutes.
Drink	-The individual is drinking from a source of water; torso and head are lowered and lips are meeting the liquid.
Lick**	-The individual is running its tongue over a surface (e.g. a rock face) but is not visibly ingesting a food (in cases where individuals licked insect eggs from leaves, a feeding observation was recorded.
Forage**	-The individual is visibly searching for food items, within a small area: overturning leaves or debris. Moving through a food tree is not included in foraging because no searching was involved in food trees at my sites.
Play**	-The individual is engaging in spontaneous, erratic activity while relaxed.
<u>Strata</u>	
Terrestrial	-When an individual is observed on the ground or exposed boulder†
Arboreal	-When an individual is off the ground (in a tree or vines) †

*conflated in statistical analysis with vocalization in general; results reported separately in section 3.1.3 and discussed in 4.1.3
**included in statistical analysis as part of an 'other' category
†Described in section 2.4.5

2.4.4 FOOD ITEM DEFINITIONS

Foods eaten were recorded with observations of feeding, although food resource use was not a focus of my study due to the difficulty in having samples identified by species, as the guides were familiar with primarily vernacular names of plants in the reserves. Items eaten were grouped as fruit, vegetation (leaves, vine, stems) insects, or soil. Fruit were most often *M.*

azadarach fruit and figs, although some unknown fruits were eaten as well. Vegetation includes all non-fruit plant parts (leaves, vine, stems) of all stages of maturity. Using basic plant-part categories allowed for quick recording during observation, and was used to look at broad trends in resource use between sites and at different distances from the edge.

2.4.5 DETERMINATION OF STRATA USE

Strata refers to the graded habitats vertically oriented in a forest; here either terrestrial or arboreal. Terrestrial as defined in the ethogram (table 2.4) refers to behaviours that took place on the ground; on boulders or rock formations regardless of size or height; on ground vegetation lacking support sufficient for the lemur on it to be >1 metre elevated above the ground. Arboreal refers to behaviours that took place in trees or other vegetation capable of supporting the individual >1 metre above the ground. The issue of classifying behaviours that took place on very tall boulders as either terrestrial or arboreal was dictated by my interest in rapidly assessing the effect edge has on behaviour in these fragments, particularly the relative timidity of *L. catta* at various distances from the edge. The boulders, while elevated, were highly exposed, and it has been suggested (Goodman and Langrand 1996) that *L. catta* frequenting exposed rock are not only potentially more vulnerable to aerial predation, but modify their behaviour because of this potential threat. This suggested to me that the boulders should be included in the terrestrial observations because this was the 'riskier' behaviour category, as opposed to the more cautious arboreal behaviours.

2.4.6 POSITION RELATIVE TO EDGE – GPS DATA COLLECTION

To measure the distance of sampled groups from the fragments' edges, I walked a large portion of the perimeter of each fragment and collected exact coordinates all along the edge. The edge was generally visible (see fig. 2.5) and sufficiently naturally demarcated for this walking coordinate collection. These exact coordinates were used to calibrate the positioning of perimeter guidelines on satellite views of each fragment in GoogleEarth, version 5.1.3534.0411.

Figure 2.5 – Fragment edge at Anja showing the delineation between forest (right) and anthropogenic savannah (left). (Photo by A. Cameron)

The fragment sizes (23 and 28 ha) were generated using the perimeter measuring tool along this same edge in GoogleEarth Pro 4 (Microsoft 2007). Using the established perimeter, the shortest distance between the group and the edge was determined for use as the distance-from-edge measure in statistical analysis. Measurements between the coordinates for the centre of the group during behavioural scans and the nearest edge were done in GoogleEarth ten times for each individual scan coordinate and then averaged, to mitigate the impact of the satellite images not being available at the highest resolution and measurements therefore being variable by meters.

2.5 DATA ANALYSIS

2.5.1 DATA STORAGE

While in the field, data were recorded in notebooks in the format outlined in Appendix A. When I returned to Victoria, the data were entered into Microsoft Excel (Microsoft 2007) spreadsheets to tabulate frequencies of behaviour categories, numbers of terrestrial and arboreal observations, and food item categories, as well as correlate these factors with distance from the edge. Statistical calculations were done using the Graphpad Software QuickCalcs 2x2 contingency table (http://www.graphpad.com/quickcalcs/contingency1.cfm); this calculator uses the method of summing small P-values recommended for Fisher's exact test by statisticians (Agresti 1992), which is not used by all statistical programs or calculators.

2.5.2 STATISTICAL DATA ANALYSIS

For site comparison statistics, all the data are pooled for each specific site and within-site variation is not considered in order to make general Tsaranoro–Anja comparisons. Differences between the two sites (e.g. number of terrestrial observations vs. arboreal observations) were evaluated using Pearson's Chi-square ($\chi2$) test, unless the total observed cell count was <20 or the expected cell count was <5 (e.g. observations of scent marking, aerial alarm calls, etc.), in which case Fisher's Exact test was used because it better examines significance between very small samples. The Chi-square calculates the significance (probability value) of the relationship between two dichotomous variables via a two by two cross-table. The difference between the data observed and the data expected is calculated as in the Chi-square test for independence; however, the estimate of significance that the Chi-square gives is likely less accurate when the value of one or more of the expected cell frequencies is <5, which is why Fisher's test was used.

The significance level was set at 0.05 for all tests. Pearson's Chi-Square and Fisher's test examine the relationship between two variables, and because I was looking at the difference between sets of data but not interested in the direction of the difference, all analyses were two-tailed.

2.5.3 DISTANCE AGGREGATIONS FOR COMPARISONS ACROSS THE EDGE-TO-INTERIOR GRADIENT

Behavioural data were grouped according to distance from the edge of the fragment (both inside the forest and outside in the savannah) in order to illustrate broad differences. Scan data were divided into six groups for each site: >40 metres in from the edge, 39.99-15m in from the edge, 14.99-0m in from the edge, 0-14.99m beyond the edge, 15-39.99m beyond the edge, and

>40m beyond the edge. These are shown as colour overlays on satellite images of the fragments in figures 2.6 and 2.7. Measurements to the edge were taken in any dense forest adjacent to the continuous fragment, as shown in figure 2.6 (these areas are not included in the perimeter shown in figure 2.2, which denotes only the edge of the continuous fragment).

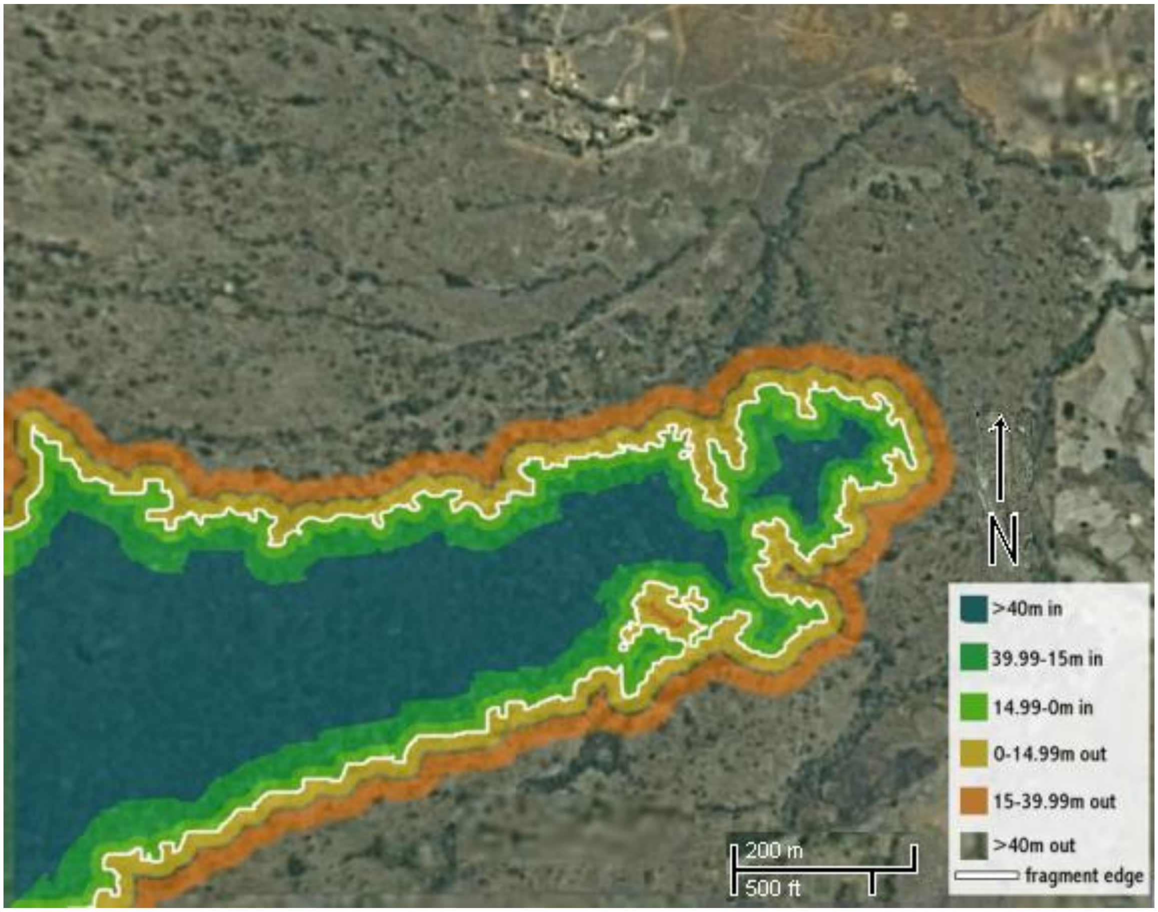

Figure 2.6 – Distance aggregates at Tsaranoro.

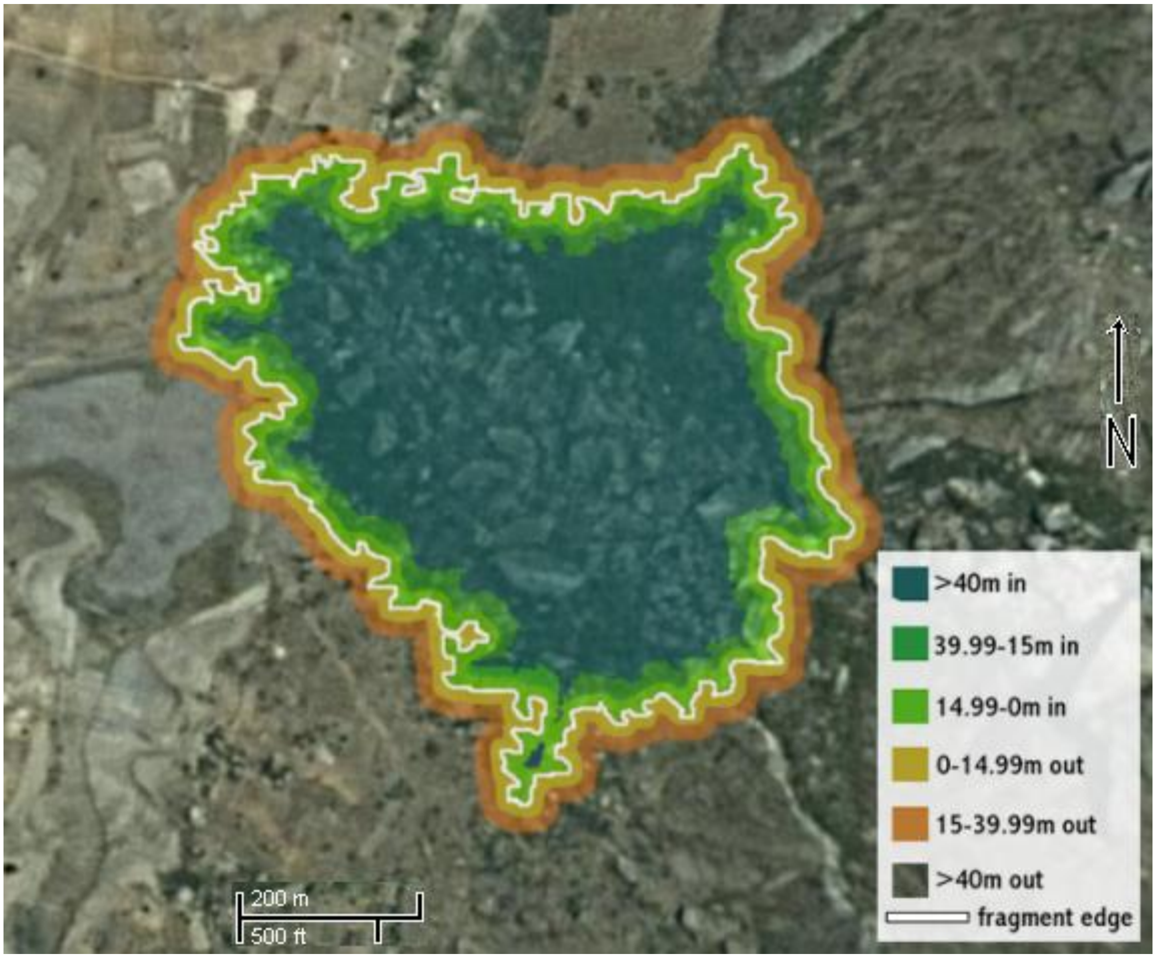

Figure 2.7 – Distance aggregates at Anja.

I have separated the behavioural observations into these aggregates because the penetration of microenvironmental alterations into forest fragments tends to decrease further into the forest (Bierregaard et al. 1992, Kapos 1989, Laurance et al. 2001). Microenvironmental changes include alterations in temperature, humidity, amounts of photosynthetically active radiation (PAR), and soil moisture, and these impact forest composition (Kapos 1989). The within-forest distances chosen for comparison here are based on the literature on these edge effects (discussed below). The distances outside the forest mirror these, because although microenvironmental changes in the matrix surrounding the forest are not expected on the scale seen within the fragment, I was interested in having more detailed information on how far each population ranged outside the fragments and whether increasing distance from the fragments impacted behaviour.

All observations made more than 40 meters inside the fragment are aggregated, based on Kapos (1989), who found that temperatures and photosynthetically active radiation, which increase closer to the edge, penetrated to this distance in a 100 ha fragment of Amazonian forest, indicating that a compositional difference in fragments may occur at this point. This is supported by Kapos et al. (1993), who found that the percentage of forest gaps from treefalls was at maximum incidence in the first 40 meters from the edge. Within the body of edge effect literature this distance represents an estimate of the maximum distance for incursion of matrix conditions (Williams-Linera 1990), suggesting this distance as a good cut-off point beyond which is considered the fragment core.

Observations made within the first 40 meters of the fragment were split into two aggregates, divided at 15 meters in from the edge. This distance was chosen as the dividing point based on a number of studies: Kapos (1989) found that the relative water contents of leaves more than 15 meters from the edge was higher than samples from the edge in eight of 12 transects. Williams-Linera (1990) measured edge effects in a Panamanian forest during the dry season, and found that changes in maximum temperature were not significant beyond 15 meters from the forest edge, and that tree mortality was 14 times higher within 15 m of the edge. Phenological surveys in temperate deciduous forests have found that edge effects on stem density, basal area, and leaf area density extend up to 15 meters from the edge of clearings (Miller and Lin 1985, Ranney et al. 1981).

It is important to note that the distances I have chosen are based on a body of research that is dominated by South American studies. The comparability of the fragments referred to in the literature to my study sites is difficult to ascertain, and different distances could have been selected based on approximate distances of compositional changes within each fragment. In lieu of phenological assessment at each site, which was beyond the scope of my study, I follow

Murcia’s (1995) suggestion that researchers increase the replicability of their surveys by choosing standard measures rather than letting the fragments’ size dictate this. However, influential factors such as forest age, matrix type, and management history should ideally be factored in, such that there would be standardized measures for a range of fragment types. A broad enough body of literature does not exist for the selection of more site-specific standardized measures than those used in this study.

CHAPTER 3: RESULTS

3.1 ACTIVITY BUDGETS

3.1.1. ACTIVITY BUDGET FIGURES

The two fragments are highly similar to one another in terms of size and forest composition. Activity budgets of the *L. catta* at Tsaranoro and Anja at the time of my study are presented in table 3.1 with corresponding figures from other sites (high and low quality gallery forest habitat at BMSR—'reserve' and 'camp' groups respectively [Gemmill 2007, see also Gemmill and Gould 2008]; Berenty's gallery forest [Rasamimanana et al. 2006]; two *Opuntia* (cactus) forest sites at Cap Sainte Marie (Bevaro Moravato and Tsankalamanga), where resource availability is thought to be low [Kelley in prep]). Specific data for the all behaviours in the 'other' category are listed in Appendix B—of note is that scent marking and play, which were rare during my study, are important behaviours in other seasons.

Table 3.1 – Activity budget figures for *L. catta* listed according to research site.

	Tsaranoro	**Anja**	**BMSR Camp**	**BMSR Reserve**	**Berenty Gallery**	**Bevaro Moravato**	**Tsankala-manga**
Feeding	23.1	17.14	11	12	33.5	9.7	6.7
Resting	27.15	34.74	40†	36†	44.5†	25.5	22.8
Locomotion	12.98	15.19	25	28	13.5	18.6	16.4
Sunning	3.37	0.42			6.5	11.8	14.1
Vigilance	5.73	3.45	0	0			
Vocalization	7	8.05					
Drinking	0	1.04					
Autogrooming	1.69	2.78	10	9		9.5	8.4
Other	0.67	1.25					
Scent marking	0.17	0.33	1	2		0.2	0
Foraging	0.34	0	1	4			
Social*	18.29	16.18	12	9		24.7	31.6
Agonism	0.17	1.78	9	6			
Resting in contact	17.45	11.66				20.2	24.9
Allogrooming	0.67	2.49			2	4.5	6.7
Play	0	0.25				0.1	0
TOTAL	99.99	99.98	100	100	100	100	100
**Active total	52.03	53.15	60	64	49	54.3	52.3
**Inactive total	47.97	46.82	40	36	51	45.7	47.7

*Used in the Berenty and Beza studies' activity budget figures: conflates allogrooming, resting in contact, agonism, and play.

**From Rasamimanana et al. 2006
†Combines resting and resting in contact.

Following Rasamimanana et al. (2006), these can be divided into active and resting behaviours: grouping resting, sunning, and resting in contact as inactive behaviours and the others as active behaviours. *L. catta* at Tsaranoro were inactive during 47.97% of scan records, and active for 52.03%. *L. catta* at Anja were inactive during 46.82% of scan records, and active for 53.15%. The discussion section will address these figures in relation to feeding time as a percentage of active time across sites; these data are presented in table 3.2, below.

Table 3.2 – Ratio of feeding to total time spent active across *L. catta* research sites.

	Tsaranoro	Anja	BMSR Camp (Gemmill 2007)	BMSR Reserve (Gemmill 2007)	Berenty Gallery (Rasamimanana et al. 2006)	Bevaro Moravato (Kelley in prep)	Tsankala-manga (Kelley in prep)
Feeding	23.1	17.14	11	12	33.5	9.7	6.7
Active total	52.03	53.15	60	64	49	54.3	52.3
Percent of active time spent feeding	44.4	32.25	18.33	18.75	68.37	17.86	12.81

3.1.2. INTERSITE VARIATION IN ACTIVITY BUDGET

At Tsaranoro, a significantly greater number of scan records than at Anja were of feeding (Pearson's Chi-Square, χ2 = 18.26, df = 1, p <0.0001), sunning (χ2 = 50.60, df = 1, p <0.0001), vigilance (χ2 = 10.34, df = 1, p <0.00013), and resting in contact (χ2 = 22.7, df = 1, p <0.0001).

At Anja, a significantly greater number of scan records than at Tsaranoro were of resting (χ2 = 20.98, df = 1, p <0.0001), agonism (χ2 = 16.8, df = 1, p <0.0001), drinking (χ2 = 12.39, df = 1, p = 0.000432), autogrooming (χ2 = 4.03, df = 1, p <0.0447), allogrooming (χ2 = 14.13, df = 1, p <0.00017).

There were no significant differences between sites in terms of observations of locomotion (χ2 = 3.13, df = 1, p = 0.07686), or vocalization (χ2 = 1.24, df = 1, p = 0.2943).

Of the eleven behaviours compared here, nine significantly differed in rate of occurrence site-to-site, and two did not. The number of behaviours in the ‘other’ category (outlined in table 2.2) did not differ significantly ($\chi 2 = 2.48$, df = 1, p 0.1153) site-to-site.

The proportion of ‘out of sight’ observations was significantly greater ($\chi 2 = 4.52$, df = 1, p 0.0335) at Tsaranoro, where 35.93% of observations were of group members known to be nearby but whose behaviour was obscured, versus Anja, where 33.05% of observations were ‘out of sight.’

Hypothesis 1 (section 1.4.1b), that there would be no significant differences beyond vigilance and vocalization rates, is not supported by these results. Hypothesis 2 (section 1.4.1b) is supported, as rates of vigilance are significantly higher at Tsaranoro. Hypothesis 3 (section 1.4.1b) is not supported; one of the few behaviours that did not significantly differ site-to-site was vocalization.

3.1.3 INTERSITE VARIATION IN VOCALIZATION

Group cohesion grunts and stress grunts were the most common and generic of the vocalizations observed at both sites, accounting for 93.81% of all vocalization observations at Anja and 91.57% at Tsaranoro (not a significant difference between site in the percentage of total observations of vocalization made up by these generic vocalizations: $\chi 2 = 0.46$, df = 1, p = 0.4977). The number of observations of other calls made during scan samples are shown in table 3.1, and discussed in section 4.1.3.

Table 3.3 – Specific Vocalizations at Tsaranoro and Anja

Vocalization type	Tsaranoro	Anja
Territorial call	0	1
Terrestrial predator alarm	0	11
Aerial predator alarm	1	0
Contact call	5	0
Lost call	1	0

All vocalizations were grouped for statistical analysis due to the low counts of other calls; however, these vocalizations occurred sufficiently frequently for the difference to be analyzed via Fisher's Exact test. Terrestrial alarm calling was observed significantly more frequent at Anja (p = 0.0203); but no significant difference was found in rate of territorial calls between sites (p = 1.0); contact calling was observed significantly more at Tsaranoro (p = 0.0039); lost calls and aerial predator alarms were also observed significantly more frequently at Tsaranoro than Anja (both p = 0.0001).

3.2 INTERSITE VARIATION IN TERRESTRIALITY/STRATA-USE

At Tsaranoro 39.96% of all observations were of *L. catta* engaging in behaviour while terrestrial, and at Anja it was 24.26% (see table 3.3). This is a highly significant difference between the sites ($\chi 2$ = 87.1, df = 1, p = <0.0001). This does not support hypothesis 5 (section 1.4.2), that both populations would exceed the average degree of terrestriality observed in this species. It should be noted that there were some observations without coordinates that are excluded here and included in the overall counts for the sites, so an average of the inside and outside percentages is not the same as the percentage given above for all observations.

Table 3.4 – Observations of terrestriality at Tsaranoro and Anja

	Tsaranoro		Anja	
	Total observations	Percent	Total observations	Percent
Observations of terrestriality	428	39.96	559	24.26
Observations of arboreality	643	60.04	1745	75.74
Total observations	1071	100	2304	100

In the above data, I do not differentiate between active and resting behaviours: to measure the difference I summed the terrestrial and arboreal observations paired with resting behaviours, and subtracted the resting number from the total number of observed behaviours (see table 3.5).

Table 3.5 – Observations of terrestriality separating resting and active behaviours

	Tsaranoro		Anja	
	Total observations	Percent	Total observations	Percent
Resting terrestrial	105	33.40	169	20.28
Resting arboreal	209	66.60	664	79.72
Total resting observations	314	100	833	100
Active terrestrial	323	42.67	390	26.51
Active arboreal	434	57.33	1081	73.49
Total active observations	757	100	1471	100

The difference between the sites when active and resting behaviours are separated is highly significant, both between resting terrestriality ($\chi2 = 87.1$, df = 1, p = <0.0001) and between active behaviours while terrestrial ($\chi2 = 59.951$, df = 1, p = <0.0001). The *L. catta* at Anja spend significantly less time terrestrial than those at Tsaranoro, both when resting and when active.

Separating observations made within the fragments from those made outside, terrestriality was observed in 31.60% of recorded behaviours inside the fragment at Tsaranoro and in 45.02% of the behaviours recorded beyond the edge. At Anja terrestriality was observed in 21.18% of behaviours recorded inside the fragment and 30.74% in behaviours recorded beyond the edge. The difference between the two sites in terms of degree of terrestriality inside the fragment is significant ($\chi2 = 21.87$, df = 1, p = <0.0001) as is the difference in degree of terrestriality outside the fragment ($\chi2 = 15.79$, df = 1, p = <0.0001). Neither group spent more active time terrestrial than arboreal, which does not support hypothesis 4 (section 1.4.2), although terrestriality increased outside both fragments as predicted.

3.3 INTERSITE VARIATION IN NUMBER OF INTERGROUP ENCOUNTERS

Intergroup encounter observations were recorded when the particular lemur group being followed came into contact with another group with which they did not fuse peaceably (discussed in section 4.1.3). These encounters were generally agonistic and involved increased vigilance, increased vocalization, and often chasing between two or more individuals. This was more the case at Anja, although no differentiation was made during observation regarding encounters of different intensities.

Ad libidum recording of the encounters observed shows that Tsaranoro *L. catta* averaged 0.5 encounters/day (over 10 days) and the Anja *L. catta* averaged 1.5 encounters/day (over eight days). Hypotheses 6 and 7 (section 1.4.3), that there would be little difference between sites and that rates would be higher than elsewhere, were not supported.

3.4 EDGE EFFECTS: VARIATION IN BEHAVIOUR RELATIVE TO DISTANCE FROM THE EDGE

In order to address the impact that proximity to the edge or ranging outside the fragments might have on the behaviour of *L. catta* at Tsaranoro and Anja, I collected location data and behaviour data simultaneously. The aggregation of data based on distance is discussed in section 2.5.3, and see figures 2.6 and 2.7 for satellite images of the fragments with colour overlays showing these distances.

3.4.1 TOTALS AND PROPORTIONS OF OBSERVATIONS AT GRADED DISTANCES FROM THE EDGE

Table 3.6 – Observation counts grouped by Distance Aggregate

	Tsaranoro		Anja	
	Total observations	Percent	Total observations	Percent
>40m in	137	11.63*	1435	61.8**
39.99-15m in	172	14.6	379	16.32
14.99-0m in	150	12.73	245	10.55
0-14.99m out	327	27.76**	263	11.33*
15-39.99m out	19	1.61**	0	0*
>40m out	373	31.66**	0	0*
ALL	1178	99.99	2322	100

* Significantly lower than at the other site (p = 0.05)
** Significantly higher than at the other site (p = 0.05)

3.4.2 INTERSITE VARIATION IN ACTIVITY BUDGETS AT GRADED DISTANCES FROM THE FRAGMENT EDGE

The Tsaranoro and Anja populations differed in their allocation of time across the staggered distances used to aggregate observations for statistical analysis of the effect of edge on behaviour. The similarity of the variation in proportions of observations visible in the data aggregates to what I observed in the field supports the conclusion that the activity budget figures accurately reflect the prioritizing of certain behaviours according to the proximity of the fragment’s edge in *L. catta* at Tsaranoro and Anja. This section focuses on feeding, resting, vigilance and vocalization. I’ve chosen to focus on these behaviours to track the effect of edge proximity, as feeding is an important behaviour and resting, vigilance and vocalization are addressed specifically in hypothesis 8. Full activity budgets and detailed statistics are listed in Appendix C. Detailed proportions for the ‘other’ category (see ethogram, section 2.4.3) of the activity budgets can be found in at the end of Appendix B. Presented here are scatter plots illustrating the distance-based fluctuations in percentage of time spent engaged in the specific behaviours on which the discussion of these results centres.

Edge effects graphed by behaviour

Figures 3.1-3.4 indicate significant differences within and between sites in the percentage of time spent feeding, resting, vigilant, and vocalizing (respectively) at different distances (p = 0.05). Significant differences from the site averages were calculated to assess the fluctuation in time allocation; the site averages are listed in table 3.1.

Feeding

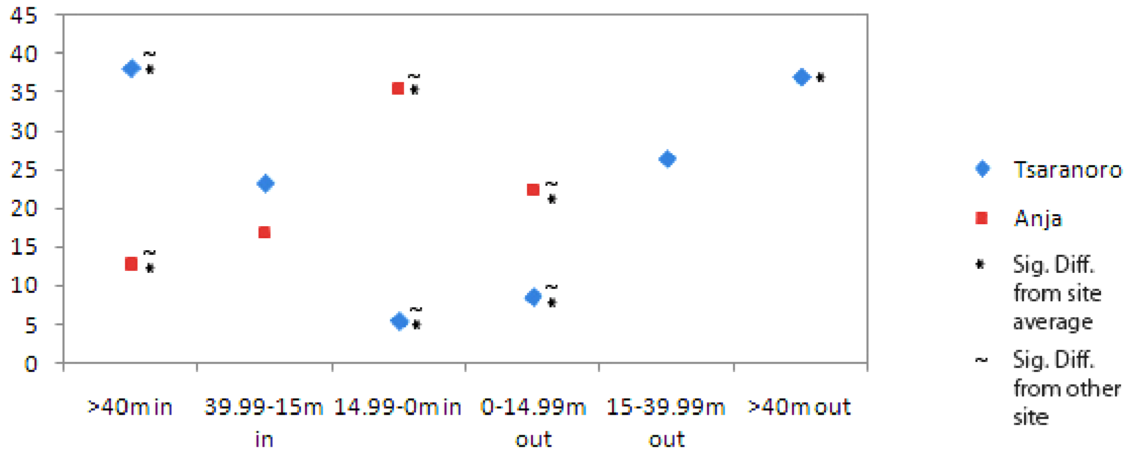

Figure 3.1 – Percentage of observations made up of feeding, by distance aggregate

Resting

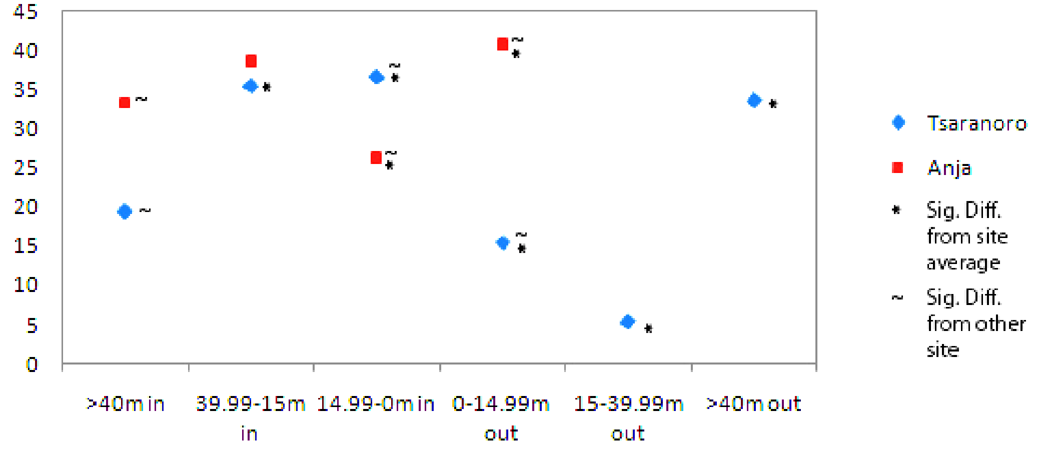

Figure 3.4 – Percentage of observations made up of resting, by distance aggregate

Vigilance

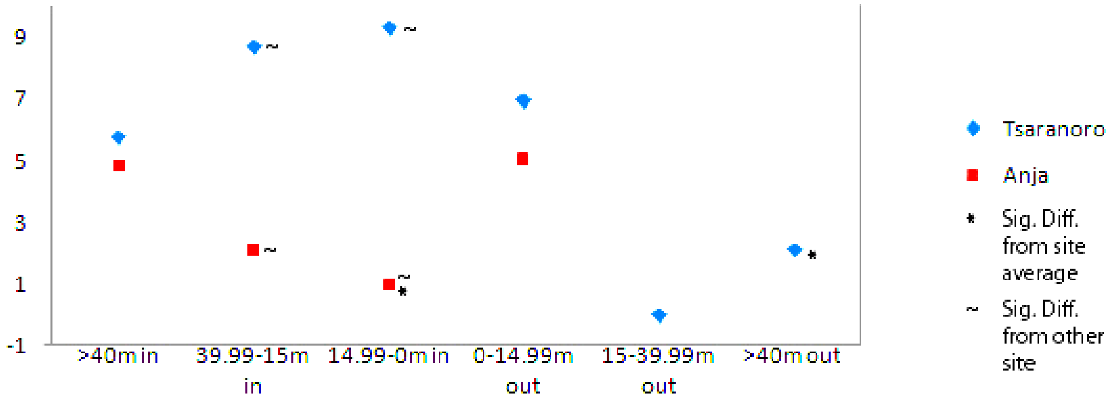

Figure 3.5 – Percentage of observations made up of vigilance, by distance aggregate

Vocalization

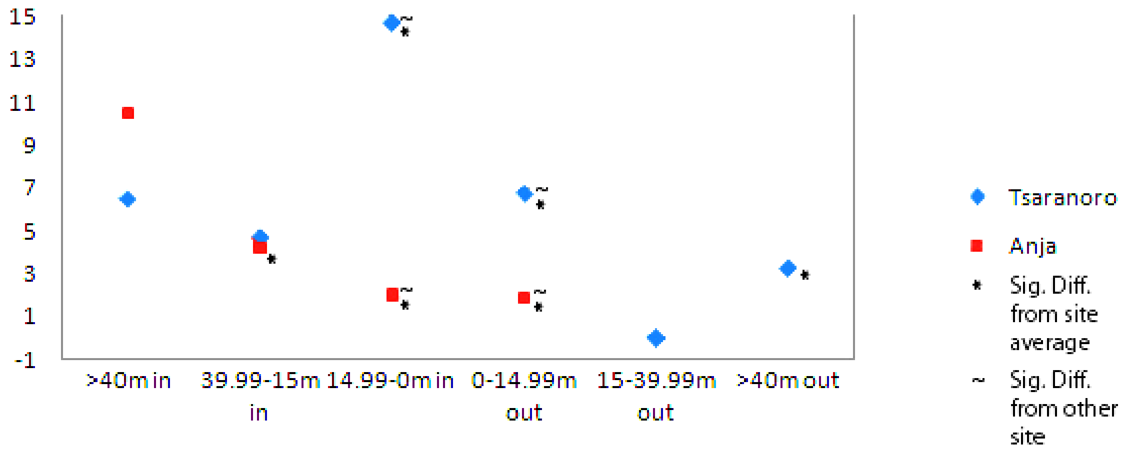

Figure 3.6 – Percentage of observations made up of vocalization, by distance aggregate

The results presented above and those listed in Appendix C do not support hypothesis 8 (section 1.4.4): proportions of observations relative to distance from fragment edge were expected to change significantly only in the cases of vigilance and vocalization, but activity budgets overall varied across the gradient. Vigilance does increase closer to the edge at both sites, but decreased outside the fragment at Tsaranoro. Vocalization decreased closer to the edge, as expected, but resting did not. Hypothesis 9 (section 1.4.4) is also unsupported, as the sites differ significantly in the patterning of the effect of edge on each behaviour.

3.4.3 RATE OF INTERGROUP ENCOUNTERS AT GRADED DISTANCES FROM THE EDGE

The data listed in table 3.14 represent the number of times at each distance that an intergroup encounter was taking place during a 5-minute scan interval. These encounters were of shorter duration and less frequent at Tsaranoro, in contrast to Anja, where skirmishes lasted for multiple scan intervals. Hypothesis 10 (section 1.4.4), that encounters would occur more frequently at the interior, is essentially supported, however the patterning does differ between sites. These observations are discussed in chapter 4 (section 4.4.3).

Table 3.7 – Observations of Intergroup Encounters Listed by site and Distance from the Edge

	Tsaranoro	Anja
>40 metres in from edge	2	11
39.99-15 metres in from edge	0	1
14.99-0 metres in from edge	0	2
0-14.99 metres out from edge	3	4

3.5 RESOURCE USE

Foods consumed during scans were recorded in general categories: fruit, vegetation (non-fruit plant parts including leaves, stems, flowers, etc.), insects, soil (included in table 3.8 as 'other'). No identification of plant species is included in these results; these are broad observations for the purposes of describing and comparing the diet categories at both sites in general terms.

3.5.1 DIET COMPOSITION VARIATION BETWEEN SITES

Table 3.8 – Cold season dietary proportions at Tsaranoro and Anja compared to gallery forest (Soma 2006) and spiny forest (Gould et al., under review)

Food item category	Tsaranoro	Anja	Berenty Gallery	Berenty Spiny
Fruit	52.14%	59.81%	31.7%	9.8%
Vegetation	31.52%	38.98%	62.5%	82.8%
Insect	16.34%	0.24%	2.6%	5.6%
Other	0%	0.97%	3.2%	1.8%
Total	100%	100%	100%	100%

The difference in proportion of diet is significant in the case of the insect category ($\chi2$ = 68.374, df = 1, p = <0.0001). The fruit and vegetation categories are on the edge of significance but are not markedly different ($\chi2$ = 3.796, df = 1, p = 0.0514 and $\chi2$ = 3.827, df = 1, p = 0.0504 respectively). The difference between sites regarding soil use is not significant (Fisher's Exact, p = 0.3037). These results support hypothesis 11 (section 1.4.5).

3.6 VARIATION IN FOOD-ITEM CLASS PROPORTIONS RELATIVE TO DISTANCE FROM EDGE

Broad differences in diet can be further compared across the gradient of distance aggregates.

Table 3.9 – Food item class proportions by distance aggregate at Tsaranoro

	>40m in	39.99-15m in	14.99-0m in	0-14.99m out	15-39.99m out	>40m out
Fruit	28.57%	22.86%	0%	11.11%	100%	77.04%
Vegetation	61.22%	51.42%	100%	18.51%	0%	16.3%
Insect	10.2%	25.71%	0%	70.37%	0%	6.66%
Soil	0%	0%	0%	0%	0%	0%

Table 3.10 – Food item class proportions by distance aggregate at Anja

	>40m in	39.99-15m in	14.99-0m in	0-14.99m out
Fruit	57.53%	65.63%	89.29%	35%
Vegetation	53.76%	34.38%	10.71%	56.67%
Insect	0%	0%	0%	1.67%
Soil	0%	0%	0%	6.67%

These results show that food class proportions varied across the edge-to-interior gradient inside the fragments, contrary to hypothesis 12 (section 1.4.6). However, proportions outside the fragment do differ, as predicted.

CHAPTER 4: DISCUSSION

4.1 ACTIVITY BUDGETS

Variations in activity budget, or time allocation, between populations of conspecifics living in disparate habitats are generally considered to be attributable to variation in the energy—most usually in the form of food—available in the environment (Marsh 1981, Menon and Poitier 1996, Hanya 2004). Foods storing relatively less energy, such as leaves, require species with a dietary focus on these foods to devote more energy to digestion than species focusing on higher energy foods, such as fruit and insects. This will be reflected in the activity budgets of these species; if compared, folivorous species are generally observed to spend more time resting than species focusing on, for instance, insectivory, which will generally spend more time foraging and locomoting (Milton 1980, Fleagle 1999). Furthermore, conspecifics between populations often differ in time devoted to resting and other non-feeding/foraging behaviours with the introduction of anthropogenic resources to some groups (Brennan et al. 1985, Altmann and Muruthi 1988).

Variation in resource availability/use occurs between the populations of *L. catta* at Berenty, Beza Mahafaly Special Reserve, and Andringitra (Goodman et al. 2006, Sauther 1994 and 1998, Simmen et al. 2003 and 2006, Soma 2006) and between microhabitats at BMSR (Yamashita 2006, Gemmill and Gould 2008). The largely frugivorous/folivorous and occasionally omnivorous *L. catta* (Sauther 1992 and 1998, Gould 2006) will alter its diet to suit the resources available, and variation in activity budget is expected to co-occur with variation in habitat and diet. As time was not sufficient for phenological data to be collected for this study, informal observations of habitat and diet observations at Tsaranoro and Anja are correlated with the statistical differences observed between the site activity budgets.

4.1.1 ACTIVITY BUDGETS AT TSARANORO AND ANJA

Activity budget data are commonly collected in primatological studies, as the proportion of time spent engaging in each behaviour relative to others illustrates the general time-energy balance of a population and serve to indicate food availability at a site (Clutton-Brock and Harvey 1977, Li and Rogers 2004).

Data were collected for this study during the cold season, when resource scarcity and female-female competition are less severe than in other seasons (e.g. during the lactation season (Sauther 1992), and all comparisons are made with data collected in the cold season. Activity budgets from the cold season at other sites are listed in table 3.1.

L. catta at Tsaranoro were feeding and resting for the majority of observation records, and were locomoting and engaging in social behaviours (agonism, allogrooming, resting in contact, play) in just under a third of the observations. This pattern of time allocation indicates a population with low overall energy-minimization requirements; *L. catta* in habitats or microhabitats with lower resource availability have a higher resting-to-feeding-time ratio relative to conspecifics in higher quality habitat during the same season (e.g. in hot season at Berenty [Ellwanger 2007] and in cold season at BMSR [Sauther et al. 2006]), and tend to reduce the proportion of time spent in affiliative social behaviours (Ellwanger 2007, Gemmill 2007, Sauther et al. 2006).

L. catta at Tsaranoro followed a similar pattern of activity to that observed at higher quality reserve sites (Rasamimanana et al. 2006). Agonism was observed rarely at this site, indicating again that feeding competition was low at Tsaranoro during the study period. Vigilance was high at Tsaranoro for *L. catta* compared to rates observed at BMSR by Gemmill (2007). The high proportion at Tsaranoro is attributed to the population being relatively unhabituated and the omnipresence of small-to-medium sized birds of prey in the valley.

The majority of observations at Anja were of resting and feeding, with affiliative social behaviour and locomotion accounting for just under a third of the observations. This pattern of time allocation indicates a population with low overall energy-minimization; the proportion of time spent resting is low but not unusual. Rather, it is the ratio of time spent engaging in active social behaviours that is indicative of high resource availability, with *L. catta* at Anja spending a higher proportion of their time engaged in allogrooming than conspecifics in the gallery forest at Berenty (Rasamimanana et al. 2006).

The percentage of time active at Anja is similar to the pattern observed in populations found in higher quality habitat (Rasamimanana et al. 2006). Agonism was observed rarely at this site, indicating that, like Tsaranoro, feeding competition was low at Anja during the study period. This low rate of agonism implies that fragment size may not impact the pattern of seasonality in agonism previously reported for *L. catta* in larger forests like BMSR (Sauther 1992).

Vigilance was high at Anja for *L. catta* compared to groups observed at BMSR by Gemmill (2007). This population was known to be habituated prior to our study because of the high amount of tourism at the site (Bradt 2005, 2008), and birds of prey are less commonly sighted at Anja. The high frequency of vigilance observed at both sites is likely due to group-level variations in boldness, the frequency of intergroup encounters/overall high population density, and the frequent presence of large, noisy tourist groups—which, despite their obvious habituation, the *L. catta* at Anja responded to with increased vigilance. Section 4.1.2 continues the discussion of activity budget by addressing the differences between the Tsaranoro and Anja data.

4.1.2 INTERSITE VARIATION IN ACTIVITY BUDGET

Variation between *L. catta* research sites is reflected in a variety of factors, including group size (Gould et al. 2003, Jolly et al. 2002 and 2006, Koyama et al. 2002, Pride 2005), population density (Gould et al. 2003), diet (Goodman and Langrand 1996, Goodman et al. 2006, Gould 2006, Pride 2005), and degree of terrestriality (Goodman et al. 2006). Group sizes and population densities of nonhuman primates tend to be lower in low quality or ‘degraded’ habitat—that is, habitat with lower resource availability and hence lower carrying capacity (Janson and Chapman 1999, Rodriguez-Toledo et al. 2003). Comparisons between activity budget data collected from troops living in higher and lower quality habitat at BMSR reflect the phenological differences and general difference in quality/suitability between the two (Gemmill

2007, Gemmill and Gould 2008). Activity budget comparisons between apparently similar sites such as Tsaranoro and Anja can indicate differences that the physical features of the sites would not suggest. Related is my first hypothesis (section 1.4.1b), which stated that the activity budgets would generally mirror one another—this was not the case, suggesting that there may be resource variation between the fragments, although phenological data is needed to assess this.

Feeding

L. catta at Tsaranoro were observed feeding significantly more than those at Anja. This is suspected to be due to the overall higher proportion of fruit and other vegetation in the diet at Anja (discussed in section 4.6), which is available in larger packets and requires less feeding time than insects, which made up very little of the diet at Anja and a sixth of the diet at Tsaranoro. Many of the differences in activity budget observed between the two populations can be attributed to the abundance of *Melia azederach* at Anja and the dominance this one resource has in this population's diet. Invasive cultigens are included in the diet of many primates, either due to preference for these foods (which are often easier to process) or because natural food sources are scarce. Crop raiding primates, for instance, immediately increase their foraging efficiency because crop plants are generally higher in energy per item, concentrated in the habitat, and easy to process (Altmann and Muruthi 1988, Brennan et al. 1985, Fa 1986, Saj et al. 1999). This is likely the case at Anja—the population here has high foraging efficiency and is able to proportion time to non-feeding/foraging activities. Related to this is the greater availability of water in this habitat, discussed below in relation to the frequency of observations of drinking site-to-site.

Drinking

The availability of water is expected to enhance the quality and utilizability of the fragments as habitat for *L. catta*; the presence of water may, in part, account for some of the overlap in activity budgets between these sites and gallery forest habitat at Berenty (Rasamimanana et al. 2006, see table 4.1). The *L. catta* at Anja were observed drinking significantly more than those at Tsaranoro, which were never observed drinking, although fresh running water can be found in both fragments. The difference between the sites could reasonably be attributed to greater availability of water at Anja, although roughly half the observations of drinking at this site were from inside the fragment, at a small open well that was not larger than water sources inside the Tsaranoro fragment. Possibly the *L. catta* at Tsaranoro were not sufficiently comfortable to drink while under observation. If, however, there exists a legitimate difference in water availability between the populations, it would serve to further explain the greater proportion of time spent feeding at Tsaranoro, as in the absence of potable water, moisture must be obtained from food sources. It has been suggested by Ellwanger (2007) that water availability may be a limiting factor in activity levels in *L. catta*, and moreover, that one-to-one, food items may be lower in energy in habitats that are lower in moisture, resulting in a greater proportion of time spent feeding in these habitats.

Goodman et al. (2006) discuss water availability in *L. catta*'s range, noting that *L. catta* are able to live in habitats without sources of water but that the availability of moisture overall is a limiting factor on *L. catta* presence in a given habitat. Both of my study fragments, but Anja in particular, are unusual in that water is available year-round; this is not the case at Berenty or BMSR. One of the likely reasons populations at Tsaranoro and, again, particularly Anja are so large relative to other sites (see table 2.1) is the availability of water.

Resting, sunning and resting in contact

L. catta is a species with a low basal metabolic rate, and as such spends a great deal of time at rest or inactive (Rasamimanana et al. 2006). Higher quality habitat appears to correlate with decreased activity, even as higher resource availability results in increased time spent feeding (Ellwanger 2007, Gemmill 2007, Rasamimanana et al. 2006, Sauther et al. 2006).

L. catta at Anja were observed resting significantly more than those at Tsaranoro, although the Tsaranoro inactive total is higher because *L. catta* at Anja have significantly lower rates of sunning and resting in contact. Less time spent inactive in other ways likely contributes to the pool of time spent resting at Anja, and troops at Tsaranoro were much less likely to settle in to a group siesta in front of observers.

Time spent resting and resting in contact at both Tsaranoro and Anja was similar to troops studied in the *Opuntia* forest habitat at Cap Sainte Marie by Kelley (in prep). However, relative to the Cap Sainte Marie *L. catta*, the Tsaranoro and Anja spend more time feeding and may therefore have access to a greater quantity of food. Troops studied at BMSR by Gemmill (2007) were active for a greater proportion of their time than either fragment population, but also spent less time feeding. The ratio of feeding time to total time active site-to-site may be informative on this point (see table 3.2). The variation between habitats suggests that the similarity between the Tsaranoro and Anja populations to the Cap Sainte Marie troops in terms of proportion of time spent resting and resting in contact is not informative of resource availability and is not a measure of habitat similarity. The proportions listed in table 3.2 likely reflect relative habitat quality, as the Cap Sainte Marie sites are sparse brush, scrub, and *Opuntia* forests where resources are widely scattered.

Locomoting

There was no significant difference between the sites regarding time spent locomoting, and *L. catta* at both sites are similar to the gallery forest at Berenty (Rasamimanana et al. 2006), as opposed to troops at Cap Sainte Marie (Kelley in prep.) or at BMSR, where troops spent over 10% more time locomoting than at Tsaranoro or Anja (Gemmill 2007). This indicates that *L. catta* in small fragments reduce time spent travelling, possibly due either to the restrictive sizes of the forests or the concentration of resources therein.

Vigilance

The Tsaranoro *L. catta* are less habituated to humans than those at Anja, and there is a corresponding difference in the number of observations of vigilance observed, with a significantly higher proportion of vigilance at Tsaranoro as predicted in hypothesis 2 (section 1.4.1b). Proportions of specific calls, discussed in section 4.1.3, indicate that predation pressure may be higher at Tsaranoro, as when predator abundance is equal between sites, increased vigilance should correspond with decreased canopy cover (Enstam and Isbell 2002), and Tsaranoro appeared to be the more densely forested of the two fragments. In addition to this, it has been observed that *L. catta* at BMSR exhibit higher rates of vigilance toward potential predators than conspecifics in other troops (Gould 1996a), which is in keeping with the population at Anja exhibiting less vigilance despite their much higher population density and rate of intergroup encounters. As well, *L. catta* in larger groups exhibit lower vigilance than conspecifics in smaller groups during the same season at BMSR, indicating that the larger group sizes at Anja likely account for lower vigilance to some extent (Gould and Sauther 2007b). This influence of group size on vigilance rates is common (Clutton-Brock and Harvey 1977, Overdorff et al. 2002, Sauther 2002).

While the lemurs at Tsaranoro were observed ranging beyond the edge and those at Anja were not, the percentage of observations made up by vigilance was lower in observations made outside the fragment, suggesting that the difference between sites in terms of ranging beyond the edge likely does not account for the difference in time spent vigilant at the time of year when my study took place.

Overall vigilance at both sites is high compared to *L. catta* studied at BMSR (Gemmill 2007, Gould 1996a), particularly given that the study took place during the cold season, when predation pressure has been suggested to be lower relative to the hot season when newborn and weanling infants may attract increased predation (Gould 1996a, Gould and Sauther 2007b). However, it is possible that, as no infants at these ages were present, group spatial cohesion was not necessitated and the groups at Tsaranoro, which were extremely small/fragmented into small units, were more vigilant than those at Anja, where larger, more cohesive groups likely facilitate a collective relaxation regarding predator-related vigilance (Hamilton 1971, Roberts 1996). Possibly, the greater human presence in the fragment at Anja also mitigates the need for predator-related vigilance (LaFleur and Gould 2009), although this may not have an impact on habituated *L. catta*, which tend to be less conscious of human presence (Gould, pers comm).

Vocalization

The *L. catta* at both sites can be considered unusually quiet compared to gallery forest sites (Gould, pers comm). The proportion of observations did not differ significantly site-to-site, contrary to hypothesis 3 (section 1.4.1b). No activity budget data including vocalization as a behavioural category could be found, however, it has been reported that troops at Berenty alarm call without pause for hours (Ellwanger 2007, Gould and Sauther 2007b, Sauther 1989), but the *L. catta* at Tsaranoro and Anja appear to be similar to the near-silent population studied at high altitudes in Andringitra by Goodman and Langrand (1996), where habitat is exposed and silence may aid in the avoidance of aerial predators. The fragments are more open than the forest habitats inhabited by gallery forest-dwelling *L. catta* at Berenty, which may increase the risk and perception of risk from predators (Enstam and Isbell 2002); further research at the Tsaranoro and Anja fragments should assess the canopy cover using the same methodology used in phenological surveys of Berenty and Beza Mahafaly (Blumenfeld-Jones et al. 2006, Sauther 1998), so that comparisons can be made on that level. Section 4.1.3 discusses my vocalization observations in further detail.

Agonism

The *L. catta* at Anja were observed engaging in agonistic interactions significantly more often than those at Tsaranoro. This is likely related to the higher population density at Anja (see table 2.1) which—despite the more abundant fruiting trees and hence higher availability of resources within the Anja fragment—resulted in higher rates of intergroup encounters at Anja (see section 4.4) and likely contributes to a higher level of stress in this population. Comparison of cold season agonism rates between the camp and reserve troops at BMSR indicates that higher quality usurpable resources (available to the camp-ranging troop) are associated with increased agonism (Gemmill 2007). Although agonism observed specifically in the context of feeding was not differentiated in the data from other agonistic interactions, this was the only type of agonism observed at Tsaranoro, whereas at Anja agonism took place in feeding contexts less commonly. I suspect that agonism that took place in the context of feeding at Anja rarely involved usurpation of food items—the major source of fruit, for example, was *Melia azedarach*, which has small fruit, in abundance.

Autogrooming

L. catta at Anja were observed autogrooming significantly more than those at Tsaranoro. This could be due to the greater population density at Anja. *L. catta*, particularly males (likely due to their low feeding priority and overall heightened social vulnerability), have been observed to over-groom when under stress (Gould pers comm). This behaviour was in evidence at Anja, as many individuals (both male and female, but more often male) had groomed the fur off the ends of their tails and had begun to lose segments due to continued over-grooming. Such over-grooming and mutilation may be attributed to over-crowding at this site, despite the abundance of high quality foods. Possibly, the steady stream of tourists contributes to such behaviour despite the lack of concern the *L. catta* demonstrate regarding their presence.

L. catta studied in the cold season by Gemmill (2007) at BMSR and by Kelley (in prep.) at Cap Sainte Marie allocated approximately 10 percent of their time to autogrooming, much more than at Tsaranoro and Anja. Relative to these groups, *L. catta* at Tsaranoro, Anja, and Berenty (where time allocated to autogrooming was similar to that observed at Anja [Rasamimanana et al. 2006]) spent a greater proportion of time feeding, and it may be that higher resource availability results in troops and populations that devote less time to activities like grooming, including allogrooming (discussed below).

Allogrooming

As with autogrooming, *L. catta* at Anja were observed allogrooming significantly more than those at Tsaranoro. Allogrooming is much more disparate between sites than autogrooming, and this could again be attributed to the crowding at Anja resulting in higher levels of calming affiliative behaviours. *L. catta* at BMSR and Cap Sainte Marie spend roughly 9 percent of their time allogrooming, despite the lower feeding-to-total-active-time ratios at these sites (see table 4.2) and presumably heightened need for energy minimization.

4.1.3 INTERSITE VARIATION IN VOCALIZATION

L. catta use representational signalling in their vocalization repertoire, with predator-specific alarm calls and other situation-specific communication calls (Jolly 1966, Sauther 1989, Sussman 1972). While the proportion of time allocated to vocalizing at each site is discussed in section 4.1.2, no distinction was made in terms of type of vocalization. Focusing on distinct, identifiable calls, the data were suggestive of intersite variation in predation and degree of habituation.

The groups at Tsaranoro spent much of the time travelling in separate, smaller groups (e.g. four individuals), which would meet periodically—likely over the course of a day, but the duration of these group fissions is unknown. These meetings between smaller groups were facilitated by loud contact calls and lost calls. Conversely, the denser and more concentrated population at Anja travelled in larger, more cohesive troops averaging 16 individuals, which would facilitate passage through various areas of the fragment by alarm calling back and forth with other troops to negotiate spacing or provide notice of impending encounters between groups. Interestingly, this was more often the terrestrial predator alarm rather than territorial alarm, as described in Gould and Sauther (2007b), Sauther (1989) and Jolly (1966). Both calls were used, and as the call and response was the same with both, and calls were always simultaneous to travel within the fragment by one or both troops calling, it seems likely that the terrestrial predator alarm has been repurposed at Anja for use as a territorial call; this is an excellent example of the behavioural flexibility necessary for negotiating the social constraints of living in small fragments.

However, the aerial alarm (described in Gould 1996a, Gould and Sauther 2007b, Jolly 1966, Sauther 1989) sampled during scans at Tsaranoro was a genuine response to predation, as this call occurred in response to a small bird of prey flying low through the forest, coming close to group members and perching within view. The Tsaranoro *L. catta* were never sampled making terrestrial predator alarm calls, although they did occur between scans while the camp troop (which was one of two definite groups observed at Tsaranoro that were equivalent in size to the average at Anja) was being chased and harassed by the dogs frequenting Camp Catta, which occurred multiple times. The camp troop alarm called in short bursts rather than a sustained call as is typically observed in *L. catta*—dogs have previously been reported harassing *L. catta* at Berenty and BMSR, and these encounters are followed by a long period of terrestrial predator alarm calling (Ellwanger 2007, Sauther 1989, 1998, and 2002, Gould and Sauther 2007b).

This pattern of anti-predator calling may be related to the presence of aerial predators in the Tsaranoro valley; smaller birds of prey often perched in trees at Camp Catta and many medium-sized and large birds of prey daily circled the fragment, camp, open fields, and cliffs surrounding the camp. The camp was relatively exposed habitat—the trees are too spread out to offer much cover and the troop spent much of their time sunning on or locomoting over roofs (fig 4.1)—but the presence of humans may have mitigated the perception of threat in camp (discussed in section 4.4.2).

Figure 4.1 – *L. catta* exposed on rooftop at Camp Catta. (Photo by A. Cameron)

The presence of humans in camp likely also mitigates some of the threat posed by the dogs; however, at Berenty, village dogs are responded to with the longest duration of alarm-calling and increased vigilance observed in the spiny forest, despite being familiar to the *L. catta* and in the presence of human observers (Ellwanger 2007). This suggests a much greater hesitancy to vocalize loudly on the part of the Tsaranoro *L. catta*. It has been noted that the high degree of terrestriality observed in *L. catta* leaves them frequently exposed to ground *and* aerial predators (Gould 1996a, Gould and Sauther 2007b, Jolly 1966, Sussman 1972, Sauther 1989, 2002) and that vigilance is much higher when *L. catta* are terrestrial. (Gould and Sauther 2007b) The high degree of terrestriality observed in the Tsaranoro population, particularly outside the forest fragment, may be related. The Tsaranoro *L. catta* were never observed using loud alarm calls due to human presence alone, and would respond instead with increased vigilance or essentially silent departure when sufficiently disturbed. This may suggest that the *L. catta* at Tsaranoro perceive humans within the forest as a threat insomuch as they create noise and may attract predators. Site to site between Anja and Tsaranoro and across microhabitats at Tsaranoro (e.g. fragment and camp), vulnerability to predation likely differs. Balancing vigilance with resource procurement and other activities site to site and microhabitat to microhabitat may result in varied or fluid anti-predator strategies (Gould and Sauther 2007b), and the differences in vocalization I observed may be indicative of this at Tsaranoro.

4.2 INTERSITE VARIATION IN TERRESTRIALITY/STRATA-USE

Terrestriality differed significantly between the Anja and Tsaranoro populations, with *L. catta* at Tsaranoro over 15% more terrestrial than at Anja. When observations of resting are removed from the total, the margin of difference between the sites increases slightly to over 16%, with the Tsaranoro population spending more active time on the ground. This is counter to my fourth hypothesis (section 1.4.2), that the populations would not differ significantly and would both spend the majority of their active time on the ground.

L. catta at Anja were never observed more than 10m beyond the edge of the fragment and spent much of their time arboreal in fruiting trees, which are more numerous at Anja than Tsaranoro. Groups at Tsaranoro were observed outside the continuous fragment frequently, either in the loose mosaic forest grading down into the dry rice fields east of the fragment, or at Camp Catta and the open savannah surrounding it through which the camp-frequenting group travelled. Higher terrestriality was observed outside the fragment at both sites, as predicted based on the sharp decrease in trees beyond the forests' edges.

Anja is in line with other sites in comparisons of previously reported levels of terrestriality, with an average of 30% reported most commonly (Jolly 1966, Sussman 1972, 1974, and 1977)—this is counter to hypothesis 5 (section 1.4.2), that both sites would be above average. Sussman (1974) observed 29.93% terrestriality in *L. catta* at Antserananomby and 36.16% terrestriality in *L. catta* at Berenty. This was averaged over the course of 18 months, and is comparative with my cold season data in a general sense, indicating that more habituated groups are prone to greater terrestriality. Sauther (1992) reported 75% terrestriality for *L. catta* at BMSR during some months, dropping to 3% in others, although percentages were not reported for individual months in this study (the average across all seasons was 32%). Cross-season terrestriality figures for Tsaranoro and Anja would indicate the impact of within-site resource availability.

Sauther (2002) found that group size and predator pressure interact and affect terrestrial foraging at BMSR, with the smaller group in her study drastically reducing time spent foraging terrestrially when predator pressure was high (from 19.59% to 5.5%) and the larger group reducing much less (from 18.65% to 16.47%). Arboreality made up more than half the observations outside both fragments, and I suspect this is related to avoidance of terrestrial human observers regardless of degree of habituation, because while there are many dogs at Camp Catta and in the surrounding villages, no terrestrial predators were observed in or anywhere around the Anja fragment (possibly because the village association recognizes that dogs mix poorly with the lemurs). It is possible that the *L. catta* at Tsaranoro are, as a population, in the habit of spending time terrestrially in order to accept tourist hand-outs of food. This was never observed at Camp Catta or elsewhere in the valley, but due to 2009 being a fallow year for Malagasy tourism (a political coup deposed the now former president, and riots in the capitol resulted in military action and civilian deaths), it is difficult to assess what is usual for the site in this respect. It is the case that the camp group habitually spent the afternoon around the bungalow area of Camp Catta and migrated up to the bar and patio at dusk (around 1600h) each evening, approximately the time at which, had there been many tourists staying in the camp, the patio would have been full of people snacking and drinking (see figures 4.2 and 4.3).

Figure 4.2 – Patio at Camp Catta (Photo by A. Cameron)

Figure 4.3 – *L. catta* crossing the patio roof, to the roof of the restaurant. (Photo by A. Cameron)

Future work at these sites, particularly phenological surveys assessing seasonal resource availability, forest density, and the relative abundance of refuges from predation in each habitat and during years with a tourist flow closer to average, may serve to better illuminate the factors influencing the variation in terrestriality between Tsaranoro and Anja.

4.3 INTERSITE VARIATION IN NUMBER OF INTERGROUP ENCOUNTERS

Sauther (2002) notes that intergroup encounters in *L. catta* often escalate to a relatively high degree of agonism, generally resulting in one group being successfully chased off. My observations did not support hypothesis 6 (section 1.4.3), that there would be no difference between sites. *L. catta* at Tsaranoro averaged 0.5 encounters/day and those at Anja averaged 1.5 encounters/day. This is also counter to my seventh hypothesis (section 1.4.3) that encounter rates would be higher than at other sites.

Population density at Anja is the highest reported for *L. catta* (see table 2.1), and the rate of agonistic intergroup encounters per day is close to that reported for gallery forest *L. catta* in the hot season at Berenty (1.80 encounters/day [Ellwanger 2007]). Pride (2005) found that the best predictors of stress hormone levels in females during the resource-low hot season were daily food intake and rates of intergroup agonism, while other possible factors (e.g. predator alarm rates) did not correlate. This suggests a direct link between reduced resource availability and increased feeding competition and rate of intergroup encounters.

The rate of intergroup encounters at Anja might be seen as high, particularly in light of the fact that *L. catta* have lower energy demands and higher resource availability during the cold season; *L. catta*'s physiological and behavioural adaptations to Madagascar's seasonal environment include fat storage and fur regrowth during the hot season (Pereira et al. 1999), and decreased intragroup feeding agonism in cold season (Sauther 1993). Also, in the cold season females are not transporting or nursing infants, and males are not engaging in the high rate of scent-marking displays and dominance contests seen in the courtship season (Jolly 1966).

Given the concentration of *L. catta* at Anja, however, the rate of intergroup encounters may be very low (more comparative data, specifically from the cold season, are necessary to determine this). I suspect that this is due to the group spacing and fission-fusioning behaviour observed at Anja. Sussman (1974) suggested that intergroup encounters may be a mechanism for maintaining group integrity. If territoriality and group integrity were similar to that observed at Berenty or BMSR, the dense population at Anja would likely experience extreme stress; relaxing both home range defence and intergroup agonism would reasonably serve to alleviate stress in a crowded population. Sauther (2002) observed groups at BMSR with overlapping home ranges and found that they engaged in both agonistic and benign encounters regularly. In Gould's (Gould and Overdorff 2002) study, daily encounters between the 3 study groups occurred, and while these were sometimes agonistic the groups often tolerated one another in the same area.

4.4 EDGE EFFECTS: VARIATION IN BEHAVIOUR RELATIVE TO DISTANCE FROM THE EDGE

Forest fragmentation impacts primate populations in two main ways: primates are randomly distributed among fragments (some host primates and some do not), and post-fragmentation, factors such as insufficient forest size may cause local extinctions (Marsh 2003). Animal species differ in their willingness to utilize non-core (edge) forest or the surrounding matrix, so estimates of a species' tolerance of these microhabitats are useful in conservation planning (Watson et al. 2004, Tutin 1999). Particularly informative in this sense are estimates of the impact of proximity to forest edge on behaviour within and beyond the forest fragment in small fragments (Lehman et al. 2006).

Primatological surveys of a species' presence within a forest relative to distance from edge are used to understand the species' requirements in a given habitat. Species are generally referred to as edge-sensitive, edge-positive or omnipresent (Lehman et al. 2005). Group-to-group edge tolerance within a site may differ as well, and it has been suggested that in addition to scoring an entire species, individual groups within a fragment can differ in their willingness to use edge. It is often implied that more aggressive groups can and do make use of the opportunities for foraging that found on the edge, particularly when anthropogenic resources are available. My field season was not long enough to establish home ranges or day ranges for particular groups within each fragment (in particular the fluid group structures at both sites made this difficult); future research at these sites can establish more individualized characterizations of the fragment groups, rather than focusing on them at the population level.

However, at the population level, the proportions of specific behaviours across the edge-to-interior gradient can be compared within and between sites. Using the coordinate data collected, distance from the edge can be calculated for a group as a whole over the course of behavioural scan sampling, and this distance measurement can be used to rank any behavioural changes that occur as a function of distance from the fragment's edge.

4.4.1 TOTALS AND PROPORTIONS OF OBSERVATIONS AT GRADED DISTANCES FROM THE EDGE

Marsh (2003) has noted that four predominant characteristics of fragment-surviving species have become evident: these species have small or variable home range size, a low or flexible degree of frugivory, overall behavioural and dietary plasticity, and the capacity to access or utilize the surrounding matrix. These are all characteristics known for *L. catta* (Gould et al. 1999, Gould 2006, Jolly et al. 1993, Jolly 2003, Sauther 1992, 1993, 2002, Soma 2006), so it was my hypothesis that *L. catta* at both sites would be omnipresent.

The *L. catta* at Anja were never observed outside the forest fragment, and the majority of observations at that site were made >40m from the edge of the fragment, inside the forest. This is in contrast to the *L. catta* at Tsaranoro, which were most often observed either >40m from the edge outside the fragment (generally at Camp Catta, but also in isolated fruit trees on the edge of the agricultural fields near the forest), or on or just outside the edge (0-14.99m).

The difference is illustrative of the divergent characters of fragment use observed between the two populations. The draw of high quality anthropogenic foods at Camp Catta in years with steady tourism might mitigate the threat posed by travelling through open savannah in the valley. Anja's population is likely less inclined to venture far outside the fragment due to the abundant resources within the fragment and the absence of cover outside the fragment. As well, the approach of the Anja Village Association may differ from that of the Camp Catta staff. At Anja every attempt was made to control tourist observation of the *L. catta*, and contact between the lemurs and humans was never observed; likely, *L. catta* at this site are discouraged by local villagers from dispersing into the surrounding agricultural and community areas. At Camp Catta, conduct around the lemurs frequenting the camp was up to tourist discretion, and the appearance of the lemurs outside the fragment may be encouraged. However, tourism was particularly low in 2009, and it is unknown whether contact with the *L. catta* is discouraged or ignored in years with greater tourism.

The Tsaranoro population is in line with observations from BMSR, where study troops frequently range outside denser forest into agricultural fields or other matrix areas (Gemmill 2007, LaFleur and Gould 2009). The Anja fragment is more isolated from other forests (and populations of *L. catta*) than the Tsaranoro fragment, and if this is in tandem with avoidance of ranging outside the fragment, Anja's population may experience inbreeding depression. Inbreeding depression and subsequent local extinctions have been observed in a number of fragment populations of primate species (Boinsky and Sirot 1997, Dietz et al. 2000, Pope 1996), and more information about this population is needed in order to assess these risks. Longitudinal research at Anja could determine the rate at which individuals immigrate into the fragments, and genetic testing should be conducted to assess the degree of gene flow.

4.4.2 INTERSITE VARIATION IN ACTIVITY BUDGETS AT GRADED DISTANCES FROM THE FRAGMENT EDGE

Feeding

The patterning of feeding time strongly indicates whether resource procurement plays a part in the presence of *L. catta* outside the fragments at these sites. How alterations in feeding time correlate with other behaviours (e.g. vigilance) provides a sketch of the costs and benefits of ranging beyond the fragments' edges.

The populations differed from one another in relation to the proportion of time spent feeding at different distances, counter to hypothesis 9 (section 1.4.4). In the absence of phenological data to determine whether food tree concentration correlates with time spent feeding in each distance aggregate, it is difficult to substantiate whether this is a function of resource distribution or predator/human avoidance. Food trees appeared both to be more common and bear more fruit at distances closer to the edge, as predicted by the greater penetration of photosynthetically active radiation at the edge (Kapos 1989). If this is the case, the significantly higher proportion of time spent feeding in the interior relative to the average for all observations at Tsaranoro indicates that this population might feed more frequently when cover (both trees and terrestrial vegetation) is more available. The patterning of feeding observations at Anja is in keeping with expected food tree locations, although this may be artificial—tied to the pattern of planting and greater presence of cultigens close to the edge.

Resting

The patterning of resting observations relative to the edge may be informative insomuch as resting leaves an individual vulnerable and the relative proportion of resting in the activity budgets of each distance aggregate may indicate microhabitat-specific variation in the perception of risk.

L. catta sampled in the cores of both fragments spent less time resting than those closer to the edge, counter to hypothesis 8 (section 1.4.4); these individuals were less habituated than those observed closer to the edge, particularly at Anja. The decreased proportion of time devoted to resting between 14.99 and 0 meters from the edge inside the fragment by *L. catta* at Anja may be due to the distribution of fruiting trees within the fragment—that is, feeding cuts in to resting time at these distances. The pattern at Tsaranoro appears to correspond neatly to the expectation of risk, such that time devoted to resting declines sharply outside the fragment and rebounds at the furthest distances due to the presence of Camp Catta.

Vigilance

Tsaranoro's higher overall vigilance can be attributed to the Anja population being more habituated to the presence of humans; the patterning of vigilance at each site is reflective of this as well. At Anja, groups in the forest core and just outside the forest exhibited the most vigilance, suggesting that the perception of risk increased outside the forest, and that there may be interior-specific troops that are less habituated—this was as predicted in hypothesis 8. At Tsaranoro, vigilance decreases steeply outside the fragment; specifically, the low proportion of vigilance at the furthest distances outside the fragment (observations made in the Camp Catta grounds) is likely reflective of the much greater habituation of the camp-ranging troop, and possibly the mitigating influence of human presence has on predation.

Enstam (2007) proposed that open microhabitats can be taken advantage of via the use of very specific (individual trees, branches) elements of the area to increase the visibility of predators. This is consistent with observations made at these distances in my study; *L. catta* in the open savannah crossed from larger landscape features (boulders, trees) quickly and stayed close to cover, with a limited group spread (see Appendix C for locomotion figures across the edge-to-interior gradient). This strategy has been observed in Chacma baboons in the Namib Desert (Cowlishaw 1997), suggesting that it may be a successful strategy for utilizing the savannah matrix at this site. *L. catta* within the camp spent the majority of their time either in trees in the small orchard secluded behind the bungalows, or on rooftops with unobstructed views of the camp and sky.

Vocalization

Alterations in the amount of vocalization partially mirror the patterning of vigilance observations at both sites. Interior-forest groups vocalized more than troops at intermediate distances at Anja, likely due to the presence of observers. Although alarm calling in response to humans was uncommon, low-volume grunts were constant. *L. catta* at Tsaranoro vocalized significantly more just inside the fragment, likely tied to the coordination of small foraging groups (which were not observed at Anja). Vocalization drops steeply outside the Tsaranoro fragment and rebounds slightly in Camp Catta; this is likely to avoid detection by predators (discussed in section 4.1.3).

4.4.3 RATE OF INTERGROUP ENCOUNTERS AT GRADED DISTANCES FROM THE EDGE

The proportioning of encounters matches closely with the proportioning of observations of all behaviours, indicating that conflicts generally occur in 'preferred' areas of the fragments, where more groups are congregating relative to other areas inside or near to the fragments. This is in support of hypothesis 10 (section 1.4.4). Future work at these sites might map, via GPS, locations of major food sources (e.g. fig trees, etc.) and use these data to track locations of conflicts relative to resource occurrence. In small fragments such as those at Tsaranoro and Anja, mapping of environmental elements and correlation with behavioural observations is achievable, and may be informative, particularly in cases such as intergroup encounter rates, which vary according to factors that are in part determined by edge proximity, but do not appear to relate directly to distance from edge.

4.5 RESOURCE USE

Diet changes according to habitat—the best illustration of this is that *L. catta* in gallery forests rely heavily on tamarind trees for portions of the year, to the extent that many researchers have referred to tamarind as a keystone resource (Gould 2006, Koyama et al. 2006, Mertl-Millhollen et al. 2003, Simmen 2006), and this resource is entirely absent from the diets of *L. catta* studied at the high elevation area of Andringitra (Goodman and Langrand 1996). The *L. catta* at high elevations on the massif include items in their diet absent elsewhere, like lichens, and focus more heavily on some food categories, like invertebrates (Goodman and Langrand 1996, Goodman et al. 2006).

The occurrence of this variation suggests disparate habitat suitability and therefore microhabitat-specific conservation potential. As I was interested in the overall quality of the habitats at Tsaranoro and Anja relative to other sites as well as what differences might exist between what appear to be highly similar forest fragments, I recorded the type of food eaten with observations of feeding. Due to the length of study, samples of every item eaten could not be collected or were not possible to identify, so this discussion is limited to food item categories rather than species. Although this is a broad view, the trends are nevertheless visible and in line with what was observed at the site.

4.5.1 DIET COMPOSITION VARIATION BETWEEN SITES

The results are in line with the variation observed in activity budget between sites. Because the fragment at Anja contains many stands of regularly fruiting trees, that population focuses more on fruit and other vegetation. The presence of fewer patches of fruit at Tsaranoro likely contributed directly to this population's significantly higher dietary proportion of insects, which was predicted in hypothesis 11 (section 1.4.5). It is the availability of fruit that dictates the consumption of insects rather than vice-versa because *L. catta* are relatively large lemurs, with adults over 2kg in weight—well beyond the 500g body weight threshold at which insects are more energetically costly to obtain than they are rewarding to eat in the absence of other foods (Conroy 1990), which suggests the lower desirability of insects as food items relative to fruit for this species. However, although fruits are larger and occur in greater concentration—generally considered less energetically taxing to obtain—the majority of insects consumed at Tsaranoro were aphids licked off of leaves, which may account in part of their high dietary proportion at this site. It should be noted that aphids are extremely seasonal and it is likely that insect consumption is far lower at other times of year—*L. catta* in the spiny forest at Berenty also incorporate a high proportion of insect foods into their diet during the cold season relative to the hot season (Gould et al. under review).

The proportion of insects included in the Tsaranoro diet during the time of this study is high relative to figures for the nearby high-altitude Andringitra population, despite the fact that in the cold season one of the five most important elements of the diet in that population is locusts (Goodman et al. 2006). However, at Berenty, *L. catta* begin to allocate increased feeding time to insects in July, peaking at 15.7% and 14.1% of feeding time in November and December respectively, when preferred resources are low (Soma 2006).

Fruit consumption rates are expected to hold true to fruit availability, and the Tsaranoro and Anja populations appear to have much great access to fruit compared to gallery and spiny forest *L. catta* sampled in the same season (see table 3.8). Concordantly, vegetation makes up a lower proportion of the diets at Tsaranoro and Anja than those in the gallery and spiny forest at Berenty (Gould et al. under review, Soma 2006).

While only the dietary proportion of soil does not differ significantly site-to-site in my study, geophagy was observed *only* at Anja. The consumption of soil occurred at the lake edge, and may be related to the proportion or type of fruit (largely *Melia azedarach*) in the diet at Anja, which makes up a bordering-on-significantly larger proportion of the diet at that site relative to Tsaranoro. *L. catta* are known to engage in geophagy at other sites, and this is thought to be related to the mitigation of dietary tannins (Gould et al. 2009).

4.6 VARIATION IN FOOD-ITEM CLASS PROPORTIONS RELATIVE TO DISTANCE FROM EDGE

Food class proportions were not expected to vary with proximity to edge inside the forests, due to the predicted homogeneity of vegetation edge-to-interior (hypothesis 12, section 1.4.6), but this was not found to be the case. These results illustrate both the proportioning of resources at the sites (throughout and beyond the fragments) and the flexibility of resource use by *L. catta* in these highly variable habitats. At Tsaranoro, groups focused on vegetation within the fragments, and pursued higher energy resources beyond the edge (insects and fruit in the savannah, focusing on fruit at Camp Catta). At Anja, food item class choices appear to be dictated by the patterning of *Melia* groves within the fragment—the 89.29% proportion of fruit just inside the fragment (14.99-0m from the edge) is consistent with my impression that the fragment has been artificially enlarged with these fruiting trees.

CHAPTER 5: CONCLUSION

This study has reiterated the flexibility of activity budgeting, strata use, and site-demography in *L. catta*, and confirms the assumption that this species is edge-tolerant in fragmented habitat. In demonstrating these characteristics, this study adds to the body of knowledge on *L. catta* that can be used to maintain this species' presence in the wild. As a flagship for Malagasy fauna and conservation, the utility of such information extends beyond the immediate concern for the species itself. Further work should be done to expand the knowledge of how this species and others extend their range by utilizing habitats of varying quality, and how fluid social structures and flexible behaviour contribute to this ability; *L. catta* was expected to be a species capable of this, but the greater range of variation in sociality, population density and ecology suggested for this species by this study may have implications for primate species considered to be less flexible. That is, although plasticity is expected in weed species, the sheer scope is not well predicted by the existing literature, and it seems likely that this might be the case in species that are currently considered to be more rigidly bound to the social systems, population densities, and ecology that have been observed and reported.

Studies of animal populations persisting in isolated fragments have indicated that many species are highly non-patterned in their responses to fragmentation, with conspecifics varying site to site; thus far, identifying patterns in primate species has been difficult (Marsh 2003). However, it has become apparent that fragment-living species tend to share four major traits, outlined in section 4.4.1. These are: small or variable home ranges, a low or flexible degree of frugivory, overall behavioural and dietary plasticity, and the capacity to access and/or utilize matrix habitat (Bicca-Marques 2003, Estrada and Coates-Estrada 1996, Laurance 1991, Lovejoy et al. 1986, Marsh 2003, Onderdonk and Chapman 2000, Silver and Marsh 2003, Tutin and White 1999). The observations of fluid group structure and low intergroup territoriality in the *L. catta* at both Tsaranoro and Anja suggest that fragment-living may push a species to exhibit greater than usual flexibility. This echoes observations made by Tutin (1999) in a cercopithecoid primate: fragment-living group *C. cephus* exhibited a pattern of flexible fissioning unseen in forest-dwelling conspecifics. These observations recommend forest fragments as study sites for work oriented toward fleshing out our understanding of a species' ecological limits and repertoire of variation, which is of great utility in conservation planning. Related to this is the importance of generating knowledge on the long-term suitability of habitats, as suitability may either correlate or be at odds with a habitat's attractiveness to a given species; Greenberg (1989) suggests that neophobia (avoidance of new foods, situations) may be selected against when plasticity is adaptive. In increasingly fragmented landscapes, plasticity is indeed adaptive, and if this results in selection against neophobia, *L. catta* may proliferate in habitats that are undesirable in terms of population health—e.g. genetically isolating fragments, and sites close to humans and livestock where increased parasite transmission occurs (Fish et al. 2007).

This was the first study to address the effect of forest fragmentation and assess edge sensitivity in populations of *L. catta*, and it was found that, while *L. catta* were omnipresent throughout the fragments and were observed in the surrounding matrix at both sites, proximity to the edge impacted rates of vigilance (significantly increasing further from the middle of the fragment at Tsaranoro, and increasing on the edge and in interior-fragment groups at Anja), and vocalization (which decreased sharply further from the middle of the fragment at Anja, although edge-ranging groups at Tsaranoro were more vocal than groups from middle distances within the fragment). These results suggest that line transect surveys of a species' occurrence in and around fragments (as in Lehman et al. 2006) provide a less fine-grained picture of the impact of edge, and may belie the degree of hesitancy exhibited in utilizing edge or matrix microhabitats.

Hesitancy to spread into matrix habitat may impact immigration and emigration from fragment populations and hence the genetic health of populations. Restricted emigration and immigration leading to inbreeding has been observed in fragment-living groups of many primate species (Boinsky and Sirot 1997, Dietz et al. 2000, Pope 1996) and the fact that *L. catta* at Anja were never observed more than 10 meters beyond the fragment's edge during my study must be further investigated in light of the prospect of diminished genetic health. This engages the suggestion that the site may be an ecological trap; the population density at Tsaranoro is much lower than that at Anja, but *L. catta* at this site were observed spreading into the savannah matrix and may be part of a metapopulation spanning the valley and nearby national park, while the resource present at Anja foster a larger and larger population with no apparent means of dispersal.

Much of the pattern that emerges from my study in terms of feeding, resting, and social behaviours is dictated by site-specific differences in forest composition, with the two fragments varying from one another in a variety of ways that were not predicted; the same distances from the edge represented different microhabitats site-to-site. However, the effect edge proximity had on intergroup encounters was similar in pattern between the sites, with more encounters occurring in the middle of the fragments and on the edge outside, likely because troop density is high in the middle of the fragments and because edge-ranging troops may be more aggressive or daring in their pursuit of resources.

The effect that edge had on diet, specifically, at both sites indicates once again the intersite variation in microhabitats at the same distances within and outside the fragments; the proportion of fruit relative to the edge at Anja indicates where fruiting trees have been planted at this site, and the abundance of insects in the diet at Tsaranoro (and largely absent at Anja) may signify that this population is seeking out alternative resources during a period of low availability of preferred foods, similar to observations made at Berenty by Soma (2006).

The findings presented here suggest that the human management of resources in and local to small forest fragments has considerable impact on *L. catta* behaviour and demography at these sites, to a greater extent than overall habitat type or fragment size. This being the case, the conservation potential of each such fragment for *L. catta* must either be determined on a site-by-site basis, or alternatively, a survey of fragments across *L. catta*'s range should be conducted and might indicate certain groupings or commonalities along lines other than size and habitat type—

management style and visitor/tourist type are vectors I suggest as important based on the results and observations presented here.

Non-invasive rapid assessment demands straightforward methodology and a broad, site-level focus. To that end, the use of a GPS unit is ideal and in the future, a non-invasive identifying marker (e.g. slow-dissolving adhesive tags) or a similar method might be adopted to provide extra dimensionality to location data, such that troop movements could be tracked and edge sensitivity could be discussed at the group rather than population level, both in long term and short term low-impact studies. Work of this kind will prove useful not only in mapping site-specific differences in ecology—thereby fleshing out the known range of flexibility for a given species such as *L. catta*—but in developing site-specific conservation plans that are tailored to the local level of the site and account for site-particulars such as variation in resource base, water availability, forest composition, et cetera. Micro-level information such as this may be easier for locals stewarding sacred forests to make use of, because it does not generalize on the basis of species (i.e. using information from Berenty and Beza Mahafaly to make inferences about the requirements of *L. catta* elsewhere) or habitat type. Specifically, the data collected from Anja indicate a population in danger of crashing, as the density of individuals may either outpace the local resource base and/or cause a decline in overall population health. It is in the best financial interests of the village to maintain this population, but current management practices are ad hoc. A survey of the type utilized in this study, which is relatively simple to perform and produces a wide breadth of data, could be standardized and used by any entity managing a fragment population, from a conservation agency to a village association; the local production of this type of information might aid in its dissemination and increase the interest taken in understanding the dynamics of a population, in addition to (and in aid of) fostering more knowledgeable, higher quality stewardship. It is my hope that this approach might have a positive impact on long-term population sustainability as fragmentation continues and ecotourism increases the attractiveness of fragment management for locals, in Madagascar and elsewhere.

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Appendix A. Data Sheet Collection Template

Date___________ Time____________
Coordinates________________________
Group Number __________

Time	Activity	Food-type	Number of Individuals	Terr/Arb	Coordinates/ Elevation	Notes

Appendix B. **LOW-COUNT OR 'OTHER' BEHAVIOURS**

Behaviour	Tsaranoro		Anja	
	Observations	Percentage of activity budget	Observations	Percentage of activity Budget
Scent marking	2	0.17	8	0.33
Defecation	2	0.17	14	0.58
Licking	0	--	2	0.08
Foraging	4	0.34	0	--
Play	0	--	6	0.25
Total 'Other'	8	0.68	30	1.24
Total Observations	1186		2409	

Observation counts of behaviours that occurred at only one site or too few times to analyze using Pearson's Chi-Square are listed in table 3.2. These behaviours are incorporated in the activity budget data (section 3.1.1) and in figures 3.1 and 3.2 as the 'other' category.

L. catta at Anja engaged in scent marking, defecation, drinking, licking, and play more often than the lemurs at Tsaranoro. Foraging occurred significantly more often at Tsaranoro (Fisher's Exact two-tailed test, p = 0.0118).

'OTHER' BEHAVIOURS ACCORDING TO DISTANCE AGGREGATE

>40 metres in from the Edge

	Tsaranoro	**Anja**
Scent marking	0	0.35
Defecating	1.46	0.98
Licking	0	0
Foraging	1.46	0
Play	0	0.21
TOTAL	100.1	100.1

39.99 to 15m in from the Edge

	Tsaranoro	**Anja**
Scent marking	0.58	0
Defecating	0	0
Licking	0	0.53
Foraging	0.58	0
Play	0	0
TOTAL	100.1	100.1

14.99 to 0m in from the Edge

	Tsaranoro	**Anja**
Scent marking	0	0
Defecating	0	0
Licking	0	0
Foraging	0	0
Play	0	1.22
TOTAL	100.1	100.1

<u>0 to 14.99m, on the Edge and Outside the Fragment</u>

	Tsaranoro	**Anja**
Scent marking	0.31	0
Defecating	0	0
Licking	0	0
Foraging	0.31	0
Play	0	0
TOTAL	100.1	100.1

<u>15 to 39.99m from the edge, outside the fragment</u>

Scent marking	0
Defecating	0
Licking	0
Foraging	0
Play	0
TOTAL	100

<u>>40m from the edge, outside the fragment</u>

Scent marking	0
Defecating	0
Licking	0
Foraging	0
Play	0
TOTAL	100

Appendix C. **EFFECT OF EDGE: FULL ACTIVIY BUDGETS AND SIGNIFICANCES FOR SECTION 3.4.2**

>40 metres in From the Edge

Observations made inside the fragments at distances greater than 40 metres from the edge are summarized below comparing the two sites.

Activity comparison at >40m, by percentage of observations at this distance

	Tsaranoro	**Anja**
Feeding	38.69	12.96
Resting	19.71	33.59
Locomotion	14.6	14.91
Sunning	9.49	0.42
Vigilance	5.84	4.32
Vocalization	7.3	11.22
Agonism	0	2.09
Drinking	0	1.46
Autogrooming	0	2.93
Allogrooming	0	3.07
Resting in contact	1.46	11.5
Other	2.92	1.54
TOTAL	100.1	100.1

These differences were significant in the cases of feeding ($\chi 2$ = 64.19, df = 1, p = <0.0001), resting ($\chi 2$ = 11.01, df = 1, p = 0.000906), sunning ($\chi 2$ = 86.179, df = 1, p = <0.0001), autogrooming (Fisher's Exact test, p = 0.0456), allogrooming (Fisher's Exact test, p = 0.0283), resting in contact (Fisher's Exact test, p = <0.0001), and foraging (Fisher's Exact test, p = 0.0075).

Behaviours that differed significantly from the site average (across all distances) at Tsaranoro were feeding ($\chi 2$ = 16.03, df = 1, p = <.0001), sunning ($\chi 2$ = 11.95, df = 1, p = 0.000546), and resting in contact ($\chi 2$ = 23.62, df = 1, p = <.0001) and at Anja were feeding ($\chi 2$ = 11.96, df = 1, p = 0.000544) and vocalization ($\chi 2$ = 16.03, df = 1, p = 0.000116).

39.99 to 15m in From the Edge

Observations made inside the fragments at distances between 39.99 and 15 metres from the edge are summarized below comparing the two sites.

Activity comparison at 39.99-15m, by percentage of observations at this distance

	Tsaranoro	**Anja**
Feeding	23.26	16.89
Resting	35.47	38.79
Locomotion	12.79	8.18
Sunning	2.91	0.26
Vigilance	8.72	1.85

Vocalization	5.23	5.01
Agonism	0	0.53
Drinking	0	0
Autogrooming	3.49	1.58
Allogrooming	2.33	1.58
Resting in contact	4.65	24.8
Other	1.16	0.53
TOTAL	100.1	100

These differences were significant in the cases of sunning (Fisher's Exact, p = 0.0127), and vigilance (χ2 = 14.58, df = 1, p = 0.000134).

Behaviours that differed significantly from the site average (across all distances) at Tsaranoro were resting (χ2 = 5.129, df = 1, p = 0.0235), allogrooming (Fisher's Exact, p = 0.0542), resting in contact (χ2 = 18.48, df = 1, p = <0.0001), and at Anja were locomotion (χ2 = 13.191, df = 1, p = 0.0003), vocalization (χ2 = 4.289, df = 1, p = 0.0384), drinking (Fisher's Exact, p= 0.0397), and resting in contact (χ2 = 48.552, df = 1, p = <0.0001).

<u>14.99 to 0m in From the Edge</u>

Observations made inside the fragments at distances between 14.99 and 0 metres from the edge are summarized below comparing the two sites.

Activity comparison at 14.99-0m, by percentage of observations at this distance

	Tsaranoro	**Anja**
Feeding	5.33	34.29
Resting	36.67	26.53
Locomotion	8.67	21.63
Sunning	6.00	0.41
Vigilance	9.33	0.82
Vocalization	14.67	2.04
Agonism	1.33	2.04
Drinking	0	0
Autogrooming	0.67	2.86
Allogrooming	0	1.63
Resting in contact	17.33	6.53
Other		
TOTAL	100	100

These differences were significant in the cases of feeding (χ2 = 43.65, df = 1, p = <0.0001), resting (χ2 = 4.52, df = 1, p = 0.033501), locomotion (χ2 = 11.24, df = 1, p = 0.000801), sunning (Fisher's Exact, p = 0.0009), vigilance (χ2 = 17.36, df = 1, p = <0.0001), vocalization (χ2 = 23.29, df = 1, p = <0.0001), and resting in contact (χ2 = 11.43, df = 1, p = 0.000723)

Behaviours that differed significantly from the site average (across all distances) at Tsaranoro were feeding (χ2 = 25.249, df = 1, p = <0.0001), resting (χ2 = 5.954, df = 1, p = 0.0147), vocalization (χ2 = 10.813, df = 1, p = 0.0010), and at Anja were feeding (χ2 = 42.934, df = 1, p = <0.0001), resting (χ2 = 6.688, df = 1, p = 0.0097), locomotion (χ2 = 6.936, df = 1, p =

0.0084), vigilance (χ2 = 4.958, df = 1, p = 0.0260), vocalization (χ2 = 11.590, df = 1, p = 0.0007), resting in contact (χ2 = 5.393, df = 1, p = 0.0202), play (Fisher's Exact, p = 0.0429).

0 to 14.99m, on the Edge and Outside the Fragment

Observations made outside the fragments at distances between 0 and 14.99 metres from the edge are summarized below comparing the two sites.

Activity comparison at 0-14.99m, by percentage of observations at this distance

	Tsaranoro	**Anja**
Feeding	8.56	22.81
Resting	15.6	41.44
Locomotion	10.09	19.77
Sunning	0.61	0.38
Vigilance	7.03	4.56
Vocalization	8.26	1.9
Agonism	0	2.28
Drinking	0	1.52
Autogrooming	2.45	3.04
Allogrooming	1.22	0.76
Resting in contact	45.57	1.52
Other		
TOTAL	100.1	99.98

These differences were significant in the cases of feeding (χ2 = 23.33, df = 1, p = <0.0001), resting (χ2 = 49.28, df = 1, p = <0.0001), locomotion (χ2 = 11.08, df = 1, p = 0.000873), vocalization (χ2 = 11.48, df = 1, p = 0.000703), agonism (Fisher's Exact, p = 0.0076), drinking (Fisher's Exact, p = 0.0390),

Behaviours that differed significantly from the site average (across all distances) at Tsaranoro were feeding (χ2 = 33.920, df = 1, p = <0.0001), resting (χ2 = 18.421, df = 1, p = <0.0001), sunning (χ2 = 7.240, df = 1, p = 0.0071), vocalization (χ2 = 21.331, df = 1, p = <0.0001), resting in contact (χ2 = 112.584, df = 1, p = <0.0001), and at Anja were feeding (χ2 = 5.232, df = 1, p = 0.0222), resting (χ2 = 4.654, df = 1, p = 0.0310), vocalization (χ2 = 13.019, df = 1, p = 0.0003), and resting in contact (χ2 = 25.605, df = 1, p = <0.0001).

15 to 39.99m From the Edge, Outside the Fragment

Observations made outside the Tsaranoro fragment at distances between 15 and 39.99 metres from the edge are summarized below.

Activity at 15-39.99m, by percentage of observations at this distance

Feeding	26.32
Resting	5.26
Locomotion	26.32
Sunning	36.84
Vigilance	0
Vocalization	0
Agonism	0
Drinking	0

Autogrooming	5.26
Allogrooming	0
Resting in contact	0
Other	0
TOTAL	100

No *L. catta* were observed at this distance from the fragment edge at Anja, and no intersite comparison can be made statistically.

Behaviours that differed significantly from the site average (across all distances) were resting ($\chi 2 = 4.566$, df = 1, p = 0.0326) and sunning ($\chi 2 = 55.888$, df = 1, p = <0.0001).

>40m From the Edge, Outside the Fragment

Observations made outside the Tsaranoro fragment >40 metres from the edge are summarized below.

Activity at >40m, by percentage of observations at this distance

Feeding	37
Resting	33.78
Locomotion	15.82
Sunning	1.07
Vigilance	2.14
Vocalization	3.22
Agonism	0
Drinking	0
Autogrooming	1.07
Allogrooming	0
Resting in contact	5.9
Other	0
TOTAL	100

Behaviours that differed significantly from the site average (across all distances) were feeding ($\chi 2 = 28.175$, df = 1, p = <0.0001), resting ($\chi 2 = 6.091$, df = 1, p = 0.0136) and sunning ($\chi 2 = 5.474$, df = 1, p = 0.0193), vigilance ($\chi 2 = 7.881$, df = 1, p = 0.0050), and vocalization ($\chi 2 = 7.090$, df = 1, p = 0.0078).