Ecological flexibility in a disturbed landscape: An assessment of the behavioural and health ecology of ring-tailed lemurs (*Lemur catta*) in relation to forest fragmentation

by

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B.Sc., Queen's University, 2007

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SUPERVISORY COMMITTEE

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ABSTRACT

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Habitat fragmentation potentiates biodiversity loss worldwide. Species preservation requires an integrated understanding of wildlife-habitat relationships; however, responses to habitat fragmentation may vary considerably as a function of the species ecological flexibility and the unique attributes of each fragment habitat. In this dissertation, I explore the behavioural and health ecology of an ecologically flexible primate, the ringtailed lemur (*Lemur catta*), occupying forest fragments in south-central Madagascar that differ in isolation, degree of anthropogenic pressure, and *L. catta* food resource structure. Anja Special Reserve is a 34 ha rocky-outcrop forest fragment that is highly isolated from other forests containing *L. catta*. *L. catta* in this reserve have access to abundant food and water resources year-round due to the introduction of non-native fruit trees and the construction of an artificial lake adjacent the reserve, which support a population density of *L. catta* (6.6 lemurs/ha) that is higher than at any other site in which the species has been studied. In comparison, the Tsaranoro Valley forest is a 53 ha rocky-outcrop forest fragment that is surrounded by a matrix of grassy savannah and a few anthropogenic crops. While land clearing is pronounced in the valley, a few fragments remain within range for *L. catta* dispersal. *L. catta* in this fragment have limited access to introduced or anthropogenic resources and the population density (1.13 lemurs/ha) is one-sixth that at Anja. During the late dry season of 2010 and mid- to late-wet season of 2011, I collected continuous time focal animal data to examine behavioural patterns related to habitat use (ranging, matrix use, terrestriality), activity budgets, and feeding ecology of *L. catta* in each fragment. In addition, I examined two health parameters, stress and endoparasitism, through the collection of fecal samples from focal individuals. I compared these variables between and within populations to examine the potential impacts of habitat fragmentation on an ecologically adaptable primate. *L. catta* at Anja depended on smaller home range areas and a focused diet consisting largely of introduced food resources, and correspondingly exhibited lower energy expenditure, while spending more time engaging in rest and social acitivities when compared with the Tsaranoro lemurs. In comparison, *L. catta* at Tsaranoro occupied large home ranges, traveled greater distances to forage in the matrix habitat surrounding the fragment, and exhibited a more broad-based dietary strategy that contained few introduced or anthropogenic resources. From a health perspective, *L. catta* at Anja exhibited higher stress levels throughout the study period, while *L. catta* at Tsaranoro exhibited a greater prevalence of endoparasites, which may be reflective of differences in the social pressures and ranging patterns of *L. catta* between the two fragments, respectively. These results illustrate differences in the quality of the habitats and the potential fitness consequences that the *L. catta* populations must cope with, with important implications regarding the long-term suitability of these fragments for sustaining these populations. Such information is integral when assessing the viability of wildlife populations in degraded landscapes and should be a primary consideration for wildlife managers in biodiversity conservation.

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To Andy
For always believing in me
This is for us

1 INTRODUCTION

1.1 Habitat loss and global biodiversity

Habitat loss and fragmentation are among the most critical drivers of global biodiversity loss (Wilson, 1992; Smith et al., 2009). Species extinction rates have increased by 100-1000 times those indicated by the fossil record, before human population expansion encroached on nearly all of the earth's biomes (Pimm et al., 1995), and up to 50% of higher taxonomic groups remain at high risk of extinction (Millenium Ecosystem Assessment; MEA, 2005). Species loss can be directly related to the rate at which habitats are degraded or altered (Pimm and Askin, 1995), primarily due to commercial, agricultural, and infrastructural development (Wilcove et al., 1998; Smith et al., 2009). For terrestrial species, the loss of global forest cover is particularly threatening. Forests make up half of the world's terrestrial biomes and comprise 91 of the Global 200 priority ecoregions for conservation, recognized for their species richness, endemic species, unusual higher taxa, unusual ecological or evolutionary phenomena, and global habitat rarity (Olson and Dinerstein, 2002). Of these forest ecoregions, 86% have a conservation status of Vulnerable, Endangered, or Critically Endangered. According to the FAO's Global Resource Assessment 2010 (FAO, 2010), the net rate of global forest loss (total deforestation minus gains due to afforestation or natural expansion) over the last two decades is estimated at 4.9 million ha/yr. This is equal to 0.16% of the world's total forest area annually. The largest losses in forest cover have been observed in the tropics, with an annual rate of change of 0.4-0.9%, and includes areas cleared for anthropogenic land conversions and forests that are ecologically degraded due to fragmentation, logging, and fires (Mayaux et al., 2005).

Natural ecosystems are critical not only as habitat to unique species and drivers of future evolution, they also provide essential services (e.g., erosion prevention, climate regulation, water retention, maintaining soil fertility) that support and sustain human populations (Daily et al., 1997; DeFries et al., 2004). Due to the current rate of land conversion worldwide – anthropogenic activities utilize 21.8% of global land area (Hoekstra et al., 2005) – and the inherent value of ecosystem services (estimated at $33 trillion US annually) (Costanza et al., 1998), priorities for conservation have shifted in scale from the protection of individual, critically endangered species and regions, to the protection of entire biomes and preservation of global biodiversity (Hoekstra et al., 2005). However, conserving ecosystems and sustaining ecosystem function requires an integrated understanding of the interactions between organisms and their environment, including biogeographical patterns, community structures, population and metapopulation dynamics, resource distributions, and individual behaviour and health (Deem et al., 2001). In ecosystems where considerable habitat loss and fragmentation have occurred, assessments of suitable patch sizes, degree of connectivity, and habitat quality become critical in evaluating the potential of habitat remnants for sustaining regional biodiversity.

1.2 Species responses to habitat loss and fragmentation

As environmental zones become degraded or converted in form, significant alterations emerge in the spatial features of the affected landscape. Habitats become fragmented to varying degrees, being both reduced in size and isolated from other suitable habitat (Fahrig, 2003). Residual patches are surrounded by an alternative landscape variety (e.g., savannah, agriculture, urban), creating an artificial boundary, or ‘edge’, between habitat and non-habitat as perceived by a particular individual or species (Lidicker, 1999). Such structural changes impact both the amount and suitability of habitat remaining for resident species and, under many circumstances, present considerable ecological challenges to which individuals must adapt if they are to persist under the disturbed conditions.

In recent decades, habitat loss and habitat fragmentation have become primary focuses of research for ecologists (Soule, 1986; Forman, 1996), with unique questions pertaining to the scale of ecological effects associated with each (Andren, 1994; Fahrig and Merriam, 1994; Noss and Csuti, 1997; Bender et al., 1998). *Habitat loss* is characterized by changes in landscape composition and is accompanied by a proportional loss of individuals occupying the affected area (Wiegand et al., 2005). If the remaining population numbers and community structure are insufficient to retain species fecundity then local extinctions are imminent (Lovejoy et al., 1986; Marsh, 2003; Fahrig, 2003). Thus, when examining the effects of habitat loss on a region or species, ecologists ask questions on a landscape scale, including topics related to metapopulation dynamics, connectivity between fragments, and gene flow (Estrada and Coates-Estrada, 1996; Pope, 1996; Cosson et al., 1999; Gravitol et al., 2001). *Habitat fragmentation* is characterized by additional effects that result from the altered habitat configuration (Wiegand et al., 2005), including changes to group sizes and population densities of patch residents (Milton, 1982; Estrada and Coates-Estrada, 1988, 1996; Terborgh et al., 1997; Tutin, 1999; Tutin and White, 1999), and the availability and distribution of resources necessary to sustain viable populations and species richness (Johns and Skorupa, 1987; Tutin, 1999). Thus, when investigating fragmentation effects on local species, ecologists focus questions on the population scale, investigating topics related to wildlife-habitat relationships, species interactions, and population health. Several theoretical and empirical studies have illustrated the influence that these combined effects have on species abundance and distribution within a degraded landscape, and the importance of these studies on species preservation (e.g., Ims et al., 1993; Andren, 1994; Fahrig and Merriam, 1994; Fahrig, 2003; Bender et al., 1998; Fuhlendorf et al., 2002; Wiegand et al., 2005).

Predicting the effects of habitat loss and fragmentation requires a conceptual understanding of species-specific biological and ecological characteristics as they pertain to habitat use (Wiegand et al., 2005). At a spatial scale, patch size and connectivity dictate the carrying capacity of habitats for various species and the capacity for dispersal and gene flow between populations (Fahrig, 2003). For example, in experimentally constructed habitat fragments, Haddad (1999) and Haddad and Baum (1999) found that habitat corridors between patches increased the population density of three open-habitat butterfly species (*Juononia coenia*, *Phoebis sennae*, and *Eutoieta claudia*), but had no effect on the density of the generalist species, *Papilio troilus*. Considerable variation exists in the spatial patterns of habitat loss from a landscape (Fahrig, 2003), and species response patterns to a reduction in habitat will depend on species-specific factors such as home range size, dispersal ability, use of dispersal habitat, dietary flexibility, and mode of locomotion (e.g., Estrada and Coates-Estrada, 1996; Haddad, 1999; Haddad and Baum, 1999; Tutin, 1999; Crooks, 2002). In an analysis of fragmentation effects on free-ranging carnivores in southern California, Crooks (2002) found considerable differences in species sensitivities to fragmentation based largely on body mass and home range size. Occurrence of badgers (*Taxidea taxus*), long-tailed weasels (*Mustela frenata*), spotted skunks (*Spilogale gracilis*), mountain lions (*Felis concolor*), bobcats (*F. rufus*), and coyotes (*Canis latrans*) showed a negative relationship with habitat patch size and isolation, whereas striped skunks (*Mephitis mephitis*) and raccoons (*Procyon lotor*) appeared to be unaffected by fragmentation effects. Gray foxes (*Urocyon cinereoargenteus*), feral domestic cats (*Felis catus*), and opossums (*Didelphis viriniana*) were sensitive to fragment area but responded positively to fragment isolation (Crooks, 2002). Predicting species responses to habitat fragmentation is not always straightforward. For example, Onderdonk and Chapman (2000) were unable to identify any predictor variables for primate population abundance in forest fragments in Kibale National Park, Uganda, based on species characteristics. However, species most likely to be sensitive to disturbance are those with small geographic ranges that may become isolated to a few patchily distributed habitat fragments within a region (Gaston, 1991).

From a patch suitability perspective, the relative impact of changing ecological conditions within a disturbed habitat is also species-specific. Species vary significantly in their ability to adapt to alterations in their surroundings, and a species' degree of ecological flexibility may indicate its future success within a fragmented landscape. For some species, particularly those that are highly specialized to a narrow range of environmental conditions, disruption of habitat structure may have negative effects on various aspects of their biology or ecology, including impacts on population size (Bender et al., 1998; Bentley et al., 2000), distribution (Arroyo-Rodriguez et al., 2008; Devictor et al., 2008), diet (Loucks et al., 2003; Cristobal-Azkarate and Arroyo-Rodriguez, 2007), social organization (Manor and Saltz, 2003), and physiology (Chapman et al., 2006; Martinez-Mota et al., 2007). On the other hand, species with a more generalized life history strategy that are able to thrive in a wide range of environmental conditions, by adjusting their diet to include alternative plant types (Bentley et al., 2000; Juan et al., 2000; Gorresen and Willig, 2004; Asensio et al., 2006) or exotic food resources (Rodriguez-Luna et al., 2003; Prange et al., 2004), decreasing their ranging area (Neves and Rylands, 1991; Estrada and Coates-Estrada, 1996; Prange et al., 2004), and altering their activity budget to minimize energy expenditure (Juan et al., 2000; Silver and Marsh, 2003), have an increased likelihood for survival in altered habitats. In fact, since generalist species fare so well in a broad range of habitat types and environmental conditions, they tend to replace ecological specialists in highly fragmented landscapes (Marvier et al., 2004).

However, for specialist and generalist species alike, marked intraspecific variation (i.e., variation among populations of the same species) may exist with respect to fragmentation responses based on spatial and temporal attributes unique to each fragment (e.g., size, shape, isolation, tree density/diversity, species interactions) (Laurance and Bierregaard, 1997; Crooks and Soule, 1999; Terborgh et al., 2001; Laurance et al., 2002; Gillespie and Chapman, 2008). With the removal or conversion of habitat within a landscape, a combination of abiotic and biotic effects penetrate remnant patches and contribute to the restructuring of vegetative composition and function and the abundance, distribution, and interactions of resident species (Harper et al., 2005). Habitat quality is defined as “the ability of the environment to provide conditions appropriate for individual and population persistence" (Hall et al., 1997). This may include features such as resource abundance/distribution, protection from predators, and shelter from adverse climatic conditions, and can have considerable influence on the viability of a given species within a fragment. Since habitat selection can confer a fitness advantage for populations by providing the conditions conducive to reproductive success and survival, the ability to distinguish between low- and high-quality habitats is an important evolutionary adaptation for mobile organisms (Clark and Shutler, 1999).

Species distribution models have found that proportion of good quality habitat within an accessible landscape area is the strongest predictor of species population size and distribution (e.g., Pulliam, 1988; Andren, 1994, 1996; Diffendorfer, 1998; Wiegand et al., 2005). The *source-sink model* (Holt, 1985; Pulliam, 1988) describes how habitat patches of varying quality contribute to population dynamics in a heterogeneous landscape. In source habitats, fitness is greater than one (i.e., natality is higher than mortality) and thus a density-dependent net emigration of individuals is expected. In sink habitats, fitness is less than one (i.e., mortality is higher than natality) and thus a net immigration of individuals is expected. Occupation of sink habitats may result from spill over from a source habitat (i.e., when the carrying capacity of the source habitat is exceeded) or as a result of some constraint on dispersal, e.g., passive dispersal of seeds by wind or water, dominance-dependent despotic distribution in which subordinates are excluded from high quality habitat, or temporal barriers (lack of corridors, unsuitable matrix habitat) preventing occupation of more suitable habitat (Dias, 1996; Diffendorfer, 1998; Boughton, 1999). Species that engage in a more active dispersal and have the ability to select for habitat quality tend instead towards a balanced dispersal

(Diffendorfer, 1998). The *balanced dispersal model* predicts that species occupy habitat patches of varying quality based on each habitat's carrying capacity, such that fitness is always greater than or equal to one (McPeek and Holt, 1992; Lemel et al., 1997; Diffendorfer, 1998). Thus, no sink habitats exist; rather each habitat sustains population numbers according to its unique ecological conditions (Diffendorfer, 1998). However, the picture becomes less clear in anthropogenic landscapes where edges and matrix habitats may provide maladaptive cues with respect to habitat quality. In such landscapes, individuals may select for poor quality habitats above habitats of higher quality due to factors such as access to novel resources (e.g., crops, human food waste, introduced resources), perceived predator protection, or a lack of competition over space and resources (Remes, 2000). The potential for such habitats to sustain population numbers over time will depend on the longevity of these factors and the species' ability to adapt to other, potentially threatening, ecological conditions.

Evaluating habitat quality and a fragment's capacity to sustain local populations may prove difficult considering the marked variation both between and within species regarding sensitivity to habitat loss and fragmentation and the numerous ways in which a habitat may be altered. In addition, it may be difficult to extrapolate whether a population is in a state of equilibrium following significant ecological change without a clear understanding of the population dynamics pre- and post-fragmentation (Kareiva and Wennergren, 1995). However, assessments of the demographics, behaviour, and ecology of populations can provide important insight regarding species viability within a fragmented landscape. Comparisons of space-use (home range size, ranging patterns, use of the matrix), activity budgets, resource structure, and health have each been used by ecologists to determine intraspecific variation in sensitivity to fragmentation and to project the future capacity of fragmented habitats to sustain population numbers over time.

1.3 Assessing behavioural and health ecology in relation to habitat fragmentation

Space-use

Since an animal's success within a region depends on its ability to secure the resources required for survival, ecologists can infer integral information about fragment suitability based on studies of wildlife-habitat relationships. 'Habitat' is an organism-specific term referring to "the resources and conditions present in an area that produce occupancy – including survival and reproduction – by a given organism" (Hall et al., 1997). Presumably, unless constrained in some fashion (see discussion of source-sink habitats above), an animal will not select a habitat for occupancy unless it provides the necessary conditions for basic survival. As such, the ways in which wildlife populations act on and within a habitat provides useful information with respect to a species capacity to adapt to changes in its environment. For example, Ims et al. (1993) showed variable space-use response patterns in voles (*Microtus oeconomus*) and capercaillie grouse (*Tetrao urogallus*) subject to differing degrees of fragmentation, which depended on the scale of fragmentation relative to home range requirements and the social behaviour of the species. When habitat fragmentation occurred on a scale smaller than home range requirements, intrinsically non-aggressive/territorial individuals congregated within a fragment with a high degree of overlap (fusion response), whereas aggressive/territorial individuals showed little home range overlap and settled in patches in which competition was low (fission response). However, when habitat fragmentation occurred on a large scale, such that the home range of individuals was larger than the fragment itself, individuals expanded their territories to include multiple fragments within dispersal distance (Ims et al., 1993). This study demonstrates the considerable intraspecific variation that can be present in space-use in response to fragmentation, which the author notes may have important implications for species viability in a region. Individuals that show a fusion response (i.e., those that exhibit spatial congregation with conspecifics) may experience increased resource competition, intensified social interactions, and/or increased parasite transmission (Ims et al., 1993). Individuals living in groups that fission (i.e., those that exhibit spatial separation from conspecifics) may experience a loss of genetic variability and/or increased pressure from interspecific competitors. Individuals that expand their territories may experience energetic costs associated with locomotion and/or exposure to predators when moving through non-habitat ('matrix') areas (Ims et al., 1993). Several other studies have found similar patterns of intraspecific variation in space-use parameters in response to fragmentation, including differences in home range size (e.g., Andreassen et al., 1998; Pires and Fernandez, 1999; Li and Rogers, 2005; Hinam and Clair, 2008), ranging distance (e.g., Schtickzelle et al., 2006), matrix use (e.g., Ricketts, 2001; Selonen and Hanski, 2003; Anderson et al., 2007), and activity budgets (e.g., Mahan and Yahner, 1999; Pozo-Montuy and Serio-Silva, 2007; Wong and Sicotte, 2007). Identifying ecological attributes of habitat fragments at the spatial level (e.g., fragment size, degree of isolation, distance to conspecifics, food resource distribution) that impact space-use parameters of resident species is fundamental for assessing population viability within a disturbed landscape.

Resource structure and feeding ecology

Since the process of fragmentation can have considerable effects on the structure and composition of vegetation within a habitat (Myers, 1983; Luken 1988; Harrington et al., 1989; Huenneke and Vitousek, 1990; Medley, 1993; Woods, 1993; Laurance et al., 1998; Brown and Gurevitch, 2004; Theoharides and Dukes, 2007), and since diet is a fundamental component of a species' ecology (e.g., Krapu, 1974; Coelho et al., 1976; Young and Isbell, 1991; Barton et al., 1996; Chapman and Chapman, 1999; Cristobal-Azkarate and Arroyo-Rodriguez, 2007), assessing the dietary habits of species reveals important information regarding intraspecific responses to habitat fragmentation. Population size is strongly correlated with the abundance and nutritional quality of food resources in the environment (Hobbs and Hanley, 1990); thus, the structure of food resources is a limiting factor on species abundance when confined to a finite fragment. Moreover, home range size is generally negatively correlated with food abundance (Taitt, 1981; Broughton and Dickman, 1991; Tufto et al., 1996; Powell et al., 1997; McLoughlin et al., 2000; Simon, 1975; Hixon, 1980) and food availability (Wauters and Dhondt, 1992; Joshi et al., 1995); thus, the amount of habitat space required by an organism will depend on the proportion and distribution of accessible food items in a region.

Fragmentation may alter the availability of native food resources within a habitat (Medley, 1993; Laurance et al., 1998), while simultaneously introducing novel items for procurement (e.g., invasive or exotic species, cultivated species, human food waste) (Myers, 1983; Luken 1988; Harrington et al., 1989; Huenneke and Vitousek, 1990; Woods, 1993; Brown and Gurevitch, 2004; Theoharides and Dukes, 2007), thereby reshaping the foraging strategies of an individual or population within its environment. In addition, habitat fragments may vary in availability of important fallback foods (high abundance items utilized when preferred foods are unavailable) (Umapathy and Kumar, 2003; Hanya, 2004; Yamakoshi, 2004; Laden and Wrangham, 2005; Marshall and Wrangham, 2007) that may be critical for population survival in times of food scarcity (Kawecki, 1995; Robinson and Wilson, 1998). For example, Tutin (1999) found that primate species abundance varied in a fragmented forest as a function of dietary flexibility and the ability to incorporate important fallback foods into the diet. Moustached guenons (*Cercopithecus cephus*) were the only species to reside in the study fragment and exhibited considerable flexibility in feeding habits when compared with continuous forest groups. In addition, greater spot-nosed monkeys (*Cercopithecus nictitans*)*,* grey-cheeked mangabeys (*Cercocebus albigena*)*,* and black colobus monkeys (*Colobus satanas*) were observed visiting the forest fragment regularly. All species exhibited a decrease in general fruit consumption, due to a reduction in the diversity and abundance of fruit in the fragment, and instead spent large portions of time feeding on fallback foods (insects, leaves, flowers, seeds) and alternative plant parts (leaf petioles, bark, pith). In contrast, chimpanzees (*Pan troglodytes*) showed little dietary diversity and, although frequently observed in the fragment, only visited during times of seasonally high fruit abundance. For many fragment-dwelling populations, dietary flexibility is one of the primary factors dictating population viability (e.g., Carey and Peeler, 1995; Cowlishaw and Dunbar, 2000; Zanette et al., 2000; Silver and Marsh, 2003; Nakagawa et al., 2007; Riley, 2007; Irwin, 2008). Species that are able to alter the composition of their diet based on the abundance of resources immediately available, include alternative resources (native or introduced) in the diet, and/or exploit resources from surrounding non-habitat (‘matrix’) are more likely to be successful in fragment habitats (e.g., Barbour and Litvaitis, 1993; Bentley et al., 2000; Silver and Marsh, 2003; Chaves et al., 2012). Assessing intraspecific variation in dietary strategies provides information on resource availability and distribution, the relative abundance of fallback foods, and nutritional quality, and may be indicative of the fitness potential of fragment-dwelling populations.

Stress

Due to its close correlation with fitness and mortality (e.g., Pride, 2005a), in recent decades ecologists and conservationists have used stress as an indicator of the overall health and well being of wildlife populations (Romero, 2004). The stress response is a complex suite of hormonal, physiological, and behavioural changes that enables an individual to cope with unpredictable or potentially harmful stimuli in the environment (e.g., Selye, 1946; Sapolsky, 2003; Romero and Butler, 2007). Although adaptive in the short-term, prolonged activation of the stress response interferes with physiological processes throughout the body, impeding cardiac and brain function, growth, sexual maturation, reproductive success, and immune response (Monjan, 1981; Kiecolt-Glaser et al., 1984; Golub and Gershwin, 1985; Sapolsky, 1996, 2003, 2005; Yang and Glaser, 2002). Habitat loss and fragmentation is associated with a variety of ecological stressors that may be experienced by wildlife populations – e.g., dietary stress due to loss of food resources, predation and exposure to exotic species, intensified inter- and intraspecific competition due to crowding, pressure to relocate, enhanced social demands – all of which are important factors in determining population abundance and fitness.

Glucocorticoids (GCs) are a class of steroid hormones that are released into the bloodstream in response to a stressor (Nelson, 2000; Sapolsky et al., 2000). Typically deemed the ‘stress hormone’, GCs are an accurate and reliable tool for quantifying the stress response in wildlife populations. Due to the ability to measure them non-invasively (urine and fecal excreta contain GC concentrations that are reflective of plasma levels) (Stavisky, 1994; Whitten et al., 1998; Wasser et al., 2000), GCs have been used increasingly to monitor the physiological impact of habitat loss and fragmentation on various wildlife species (e.g., fish: Turner et al., 2003; birds: Wasser et al, 1997; Fowler, 1999; Suorsa et al., 2003; Lucas et al., 2006; Walker et al., 2006; elk: Millspaugh et al., 2001; wolves: Creel et al., 2002; African elephants: Foley, 2001; bears: Busch and Hayward, 2009; spotted hyenas: van Meter et al., 2009). This includes a recent surge of studies focusing on stress in free-ranging primates occupying disturbed habitats (e.g., *Colobus* spp.: Chapman et al., 2006; *Alouatta* spp.: Cristobal-Azkarate et al., 2007; Martinez-Mota et al., 2007; Behie et al., 2010; *Ateles geoffroyi*: Rangel-Negrin et al., 2009; *Lophocebus albigena*: Jaimez et al., 2012; *Eulemur rubriventer*: Tecot, 2013). At baseline levels GCs play a regulatory role in energy processes, influencing feeding behaviour and mediating the availability of glucose and fats in the body (reviewed by Landys et al., 2006). Only during times when there is a sufficient energy imbalance (i.e., energy demand exceeds energy supply – ‘type I allostatic overload’; McEwen and Wingfield, 2003) do baseline GC levels tend to increase, inducing changes in body condition and behaviour that help an individual cope with noxious stimuli (e.g., food deprivation, predator presence, extreme climatic events such as storms or droughts) (Sapolsky et al., 2000; Wingfield et al., 1998; Busch and Hayward, 2009). This ‘fight-or-flight' response is characterized by an increase in heart rate, dilation of the pupils, increased blood flow to the muscles, constricted blood flow to the gastrointestinal tract, mobilization of the body's energy stores, piloerection, and increased respiration rate (Axelrod and Reisine, 1984; Wingfield, 2005), and is maintained to promote survival until the perturbation passes. In contrast, when increases in energetic demand result from long term or permanent changes in the environment but in the absence of energy constraints (e.g., significant social conflicts or dysfunctions due to crowding – 'type II allostatic overload'), an emergency fight-or-flight response is not triggered and the stress response can only be regulated by learning or adaptation to the environment (McEwen and Wingfield, 2003; Wingfield, 2005). Chronic release of GCs in anthropogenically-altered habitats can be an indication of an individual's inability to habituate to the disturbance (e.g., Creel et al., 2002; Martinez-Mota et al., 2007; Tarlow and Blumstein, 2007; van Meter et al., 2009) and, therefore, GCs provide a useful tool for monitoring species sensitivity to habitat fragmentation.

Parasitism

Wobeser (1981) defined *disease* as "any impairment that interferes with or modifies the performance of normal functions, including responses to environmental factors such as nutrition, toxins, and climate; infectious agents; inherent or congenital defects, or combinations of these factors." Impairments that limit an individual's fitness or inhibit it from realizing its ecological role in an ecosystem may hold critical implications for its ability to persist under its current environmental conditions, and should be of primary concern to habitat management and conservation (Deem et al., 2001). Disease transmission may be facilitated in disturbed habitats as a result of changes in host demography (increased isolation, increased host density, inbreeding) (Lyles and Dobson, 1993; Lafferty, 1997; Smith et al., 2009; Clough, 2010), exposure to novel carriers (humans, domesticated animals, vermin) (Lafferty and Gerber, 2002; Pedersen et al., 2007; Goldberg et al., 2008), and alterations in the ecological conditions of the environment that may compromise host body condition (poor nutrition, stress) and/or increase parasite reproductive success (Dobson and Hudson, 1992; Hudson et al., 1992; Lafferty and Kuris, 2005; Gillespie and Chapman, 2006). Thus, wildlife populations that are highly specialized, isolated from conspecifics, or occupying habitats of poor quality may be particularly vulnerable to extinction if infection rates are elevated (Cleaveland et al., 2002; Daszak et al., 2000; Hochachka and Dhont, 2000; Smith et al., 2009).

Wildlife parasitology has been generating considerable attention as it applies to population health in disturbed habitats. Parasites are a pivotal part of any ecosystem, comprising a significant proportion of biodiversity and contributing to the abundance and adaptation of host populations (e.g., Swinton et al., 1998; Begon et al., 1999; Hudson et al., 1998; Nunn et al., 2003). In order to understand the ecological processes governing a particular species or habitat it is essential to appreciate the structure and dynamics of the co-habiting parasite community. Free-living animals may harbour a diverse array of parasite species (e.g., some host populations of red grouse, *Lagopus lagopus scotica*, contain more than 40 different parasites) (Dobson et al., 1992), and coping with multiparasite infections presents a considerable challenge for hosts, often with significant fitness consequences. Yet many parasites go unnoticed in wildlife populations, only having negative consequences for those individuals with poor immune function or experiencing particularly high transmission rates.

The situation changes, however, when the ecological balance of a habitat is disrupted (Ancranez et al., 2003). Pathogenicity in a host species is often correlated with parasite abundance and richness; therefore, habitat alteration that promotes the transmission of parasites within and between host species can significantly increase the pathogenicity of an otherwise commensal host-parasite association (Holmes, 1996). Parasites that usually play a regulatory role in large ecosystems can have detrimental impacts on wildlife populations subject to heavily restricted habitat areas, where stress may be high and immunocompetence may be compromised. Shrinking habitat fragments increase wildlife population densities, bringing inhabitants into close and more frequent contact, thus perpetuating disease spread (Dobson and May, 1986; Scott, 1988), and producing an avenue of transmission to novel parasite fauna through increased exposure to exotic or introduced animal species (e.g., wildlife-livestock contact in fragments surrounded by pastures and agricultural crops). Moreover, human activities regularly alter landscapes in ways that impact disease transmission by creating novel habitats for the colonization and propagation of parasite species (Lafferty and Kuris, 1999). For example, Southgate (1997) found that deforestation and the construction of dams in the Senegal River Basin lead to algal blooms in close-proximity ponds and streams due to a reduction in acid run-off from leaf litter, creating desirable habitat for snails that serve as an intermediate host for trematodes of the genus *Schistosoma*. Parasitic infections are capable of causing large-scale population declines for wildlife, both locally and globally (e.g., Daszak et al., 2000), and as the occurrence and spread of disease can be a sensitive indicator for the changing health ecology of a species (Dutton et al., 2003), data on parasite communities within a habitat are a valuable tool for evaluating population responses to environmental change (Stuart and Strier, 1995).

While it may be difficult to project species viability in fragmented habitats without significant longitudinal data on population dynamics, ecologists and wildlife managers can gain some insight into the stability of populations through efforts to understand wildlife-habitat relationships. Evaluations of space-use and activity budgets, diet and resource structure, stress, and disease ecology provide information with respect to habitat quality and the capacity of a fragment to sustain a population over time. Moreover, extending evaluations to include multi-site comparisons of populations of the same species can highlight intraspecific variation in responses to fragmentation that may have important consequences for population fitness, reproductive success, and longevity in a region. This information is integral with respect to the conservation of valuable ecosystems to house regional biodiversity in degraded landscapes.

1.4 Madagascar: a microcosm of fragmentation effects

Madagascar, a large island (587,041 km^2) in the Indian Ocean, has an extraordinary evolutionary history and relatively recent human occupation that affords a unique opportunity for evaluating the impacts of habitat fragmentation on wildlife. It separated from the African continent somewhere between 160 and 180 million years ago and has remained isolated, approximately 400 km off the southeastern coast of Africa, for approximately 88 million years (Storey, 1995; Storey et al., 1997; Tattersall, 2006). This geographic isolation perpetuated the evolution of exceptional flora and fauna, giving rise to one of the world's richest biodiversities.

Madagascar’s prehistoric environment was conducive to supporting a notable subset of megafauna, including pygmy hippopotamuses, elephant birds, tortoises, and lemurs significantly larger than extant species, enabling them to survive and flourish well into the late Quaternary period (Burney et al., 2004). However, due to ecological transformations caused almost exclusively by environmental modifications following the arrival of humans in the late Holocene (i.e., a more widespread fire ecology and replacement of woody vegetation by grasslands and agricultural fields) (Burney, 1997), each of these megafaunal species soon became extinct (Burney et al., 2004). Today, Madagascar is recognized as a country of ‘megadiversity’, as it is home to >12 000 species of plants (85% of which are endemic) (Schatz, 2000; Goodman and Benstead, 2005) and >800 species of land vertebrates (of which 52-60% of birds and 92-100% of amphibians, reptiles, and mammals are endemic) (Goodman and Benstead, 2003). Yet this incredible biodiversity is increasingly threatened by human population growth, resource extraction, and loss of habitat. Madagascar’s forest cover has steadily decreased since human occupation ~2300 years ago, and as much as 90% of the original expanse of forest has been lost (Green and Sussman, 1990; DuPuy and Moat, 1998). Forest fragmentation due to anthropogenic activity continues to steadily increase throughout the country (Green and Sussman, 1990; Goodman and Rakotondravony, 2000; Hannah et al, 2008), and represents one of the leading concerns for species conservation (Ganzhorn et al., 2001).

Madagascar is world-renowned for its lemur inhabitants, an endemic group of strepsirrhine primates, which in recent decades have attracted much attention for their unique characteristics and tourist appeal. The entire infraorder Lemuriformes is thought to have evolved from one or a few common ancestor(s) that arrived on the island between

50 and 60 million years ago (Yoder, 1996; Kappeler, 2000; Poux et al., 2005; Mittermeier et al., 2006; Tattersall, 2006) by making oceanic crossings from adjacent continents via a transient land bridge or series of smaller, isolated and possibly floating land connections (Krause et al, 1997; Tattersall, 2006). Millions of years of geographic isolation promoted the adaptive radiation of lemurs, which, due to a variety of rare adaptations, were able to thrive in Madagascar's variable and often unpredictable environments (i.e., high intra- and inter-annual rainfall variability, frequent cyclones, drought) (Wright, 1999; Richard and Dewar, 2007). The once heavily forested landscape, devoid of most land mammals found on the continents, probably enabled lemur species to occupy nearly the entire island of Madagascar – from the wet rain forests of the east to the dry deciduous and spiny forests of the west and south, and even at high altitudes in the central plateau (Goodman and Rasolonandrasana, 2001; Ganzhorn et al., 2006). However, conflict with humans over space and resources introduced new selective pressures to which numerous lemur species were unable to adapt, leading to the mass extinction of three families of giant lemurs towards the end of the first millennium and numerous local extirpations in the remaining families throughout the second millennium (Burney et al., 2004; Godfrey and Irwin, 2007). At present, nearly half (~41%) of the extant species is considered threatened or endangered, and a large majority of the remaining species lack sufficient evaluation of population status (IUCN Red List, 2008; Mittermeier et al., 2012).

While the extent of Madagascar's original forest cover is not definitively known (Kull, 2000), it is clear that current rates of deforestation, primarily as a result of unsustainable agricultural practices, urban development, and logging for fuelwood and charcoal production (Green and Sussman, 1990; Harper et al., 2007), are seriously threatening the future of biodiversity across the island. The vast span of habitats once available for lemurs has been reduced to pockets of fragmented forest and small, protected reserves. In the 1950s, humid, dry, and spiny forests covered 160 000 km^2 (27%) of the total land area; by 2000, only 99 015 km^2 (15%) of forest remained (i.e., a loss of nearly 40% in 50 years) (Harper et al., 2007). Deforestation rates have ranged from 0.3% (1950s to 1970s) to 1.7% (1970s to 1990s) per year, with the greatest reductions occurring in the humid and dry forests (43% and 41%, respectively) of the east, west and north (Harper et al., 2007). The loss of 'core forest' (intact forest >1km from a non-forest edge) has left nearly half of all forest habitats confined to patches of <500 km^2, a quarter of which are less than 10 km^2 (Harper et al., 2007). In recent years, forest destruction has been exacerbated by the current state of political instability (United Nations OHCHR, 2012), with illegal logging for precious hardwood (e.g., rosewood and ebony) critically threatening the habitat patches where lemurs remain (http://whc.unesco.org/en/news/500). Currently, this biological anomaly is greatly threatened and the country is considered to be one of the highest conservation priorities on the planet (Ganzhorn et al., 2001; Brooks et al., 2006; Kremen et al., 2008). At this rate of habitat loss, it is imperative that conservation strategies be implemented to preserve viable populations of Madagascar's incredibly diverse wildlife.

1.5 A fragmentation story: *Lemur catta* in Madagascar's central highlands

This dissertation explores intraspecific variations in habitat use, activity patterns, diet, and health ecology of ring-tailed lemurs (*Lemur catta*) inhabiting forest fragments of Madagascar's central highlands as a consideration of habitat suitability in a degraded landscape. *L. catta* is a flagship species for Madagascar's unique biodiversity and the threat that habitat disturbance holds for the future of the island's endemic species. It occurs in many forest habitats throughout south, southwest, and south-central Madagascar, including gallery, dry deciduous, and scrub forests, spiny desert, and the high altitude ericoid bush and rocky outcrop vegetation of the west and the central plateau (Jolly, 1966; Sussman, 1977; Sauther et al, 1999; Goodman et al., 2006; Gould, 2006; Gould et al., 2011; Kelley, 2011; LaFleur, 2012; Cameron and Gould, 2013). *L. catta* has been studied extensively since the first observations of the species were made by Petter (1958, 1962a,b) and Jolly (1966). However, until very recently (see Gould et al., 2011; Kelley, 2011; Lafleur, 2012; Cameron and Gould, 2013), much of what is known of *L. catta* has come from parcels of gallery forest habitats in two protected research sites – Beza Mahafaly Special Reserve (600 ha) in Madagascar's southwest and Berenty Reserve (250 ha) in the south (reviewed by Gould, 2006). Outside of these protected reserves, *L. catta* habitats are being heavily disturbed by fires, logging, and land clearing for livestock grazing, agriculture, and infrastructural development, and populations of *L. catta* are now heavily restricted to isolated forest fragments (Sussman et al., 2003; Goodman et al., 2006; Bodin et al., 2006; Gould and Gabriel, in prep.). Despite being a highly adaptable primate, likely an evolutionary response to considerable habitat variability throughout its range, this relatively recent large-scale habitat disturbance has been shown to impact *L. catta* abundance (e.g., population density is much lower in disturbed forests and habitats of poor quality) (Sussman et al., 2003; Kelley, 2011; Lafleur, 2012). However, little is known about the specific effects of habitat fragmentation on *L. catta* behavioural and health ecology and the implications that it may hold for the species' longevity throughout southern Madagascar.

Study species – *L. catta* is a monomorphic, female-dominant species, which exhibits clear and relatively stable intra-group dominance hierarchies and marked breeding seasonality (Jolly, 1984; Sauther, 1998; Sauther et al., 1999; Wright, 1999; Gould et al., 2003; Gould et al., 2011). The species is highly gregarious and lives in multi-male, multi-female social groups containing approximately 10 to 25 individuals (although group sizes vary greatly in different habitats), in which females remain in their natal group and males disperse at sexual maturity (Jolly, 1966; 1998; Gould, 1996; Sauther et al., 1999). Female-targeted aggression is frequently high between unrelated individuals, with high-ranking females exerting their dominance for access to resources and during intergroup encounters (Vick and Pereira, 1989; Pereira and Kappeler, 1997; Sauther et al., 1999; Jolly et al., 2002; Koyama et al., 2002; Gould et al., 2003; Takahata et al., 2005).

L. catta exhibits a frugivorous/folivorous diet, while also showing signs of 'opportunistic omnivory' (Sauther, 1998; Sauther et al., 1999; Simmen et al., 2006). The species consumes a wide spectrum of food types throughout the year (based on seasonal availability), including stems, fruits, leaves, flowers, insects and soil (Sauther et al., 1999; Jolly, 2003; Simmen et al., 2006; Gould et al., 2011; Kelley, 2011; LaFleur, 2012). The generalist nature of its feeding ecology is beneficial in harsh, resource-scarce, and highly unpredictable environments (Gould et al., 1999; Sauther et al., 1999). Southern Madagascar is characterized by distinct wet and dry seasons, with highly variable resource availability. High quality resources are abundantly available in the wet season (October-April) when 99% of the annual rainfall occurs (Sauther et al., 1999), whereas only lower quality resources can be found in small quantities during the dry season (May to August). Food scarcity in the dry season may be a significant natural stressor for *L.*

catta, particularly when group sizes are large and competition is high (Pride, 2005b). Reproduction is seasonally tuned based on the availability of specific food resources. Females gestate throughout the dry season when resources are scarce, give birth during an initial peak of food production (early to late Septemeber), and lactate as the wet season begins and resources, primarily young leaves, become more abundant (Sauther, 1998; Sauther et al., 1999). The birth and lactation season is associated with particularly high energetic demands, due to rapidly growing infants and the metabolic cost of producing protein-rich milk, and may, therefore, represent a time of heightened physiological and social stress for females (Cavigelli, 1999). In gallery forests, infant mortality is high for this species, averaging between 30 and 51%, and reaching up to 80% in drought years (Gould, et al., 1999, 2003). The mating season is restricted to approximately 3 weeks (between late April and late May), during which each female is receptive for a period of only 6 to 24 hours, and males are required to compete for access to mates during this highly constrained breeding season (Sauther et al., 1999).

Marked behavioural and physiological flexibility have rendered *L. catta* an 'edge' or 'weed' species (Gould et al., 1999, 2003; Sauther et al., 1999). The species is able to cope with extreme seasonality, exploit a broad range of food resources, and can occupy more habitat types than any diurnal lemur species (Gould et al., 1999, 2003; Sauther et al., 1999; Goodman et al., 2006). While original studies of *L. catta* classified it as strictly diurnal, recent evidence suggests that it should be reclassified as cathermeral due to significant nocturnal activity (LaFleur, 2012; Parga, 2012; Donati et al., 2013). Home range size of *L. catta* varies from 4 to 110 ha (Jolly et al., 1993, 2002; Gould et al., 2003; LaFleur, 2012) and it represents the only definitively semi-terrestrial species of the extant lemurs (Sauther et al., 1999). It spends 30% of its time, on average, engaging in terrestrial locomotion and activities (Jolly, 1966; Sussman 1972, 1977), and may exhibit up to 75% terrestriality depending on habitat and season. Populations in disturbed habitats will readily exploit anthropogenic resources (e.g., crop raiding; comsumption of human trash; Figure 1.1) and have been observed within close proximity to both humans and livestock (Loudon et al., 2006; Gemmill and Gould, 2008). However, *L. catta* remains heavily reliant on a few fallback foods when other resources are unavailable (e.g., Sauther and Cuozzo, 2009; LaFleur and Gould, 2009; Gould et al., 2011; Kelley, 2011; LaFleur, 2012), and population crashes have been documented during periods of extreme food scarcity (e.g., drought) (Gould et al., 1999; Jolly et al., 2002).

Figure 1.1 *Lemur catta* exploiting herbaceous ground vegetation from village gardens adjacent Anja Special Reserve in Madagascar's south-central highlands

Study sites – The majority of studies on *L. catta* behavioural ecology have focused on gallery forest habitat (reviewed by Sauther et al., 1999; Koyama et al., 2002; Gould et al., 2003; Gould, 2006), with a few focusing on species variation in spiny bush and spiny forest habitat in the southern portion of *L. catta*'s range (Berenty Reserve: Gould et al., 2011; Cap Sainte Marie: Kelley, 2011; Tsimanampetsotsa National Park: LaFleur, 2012). However, few studies have examined *L. catta* populations in more northern parts of its geographic range (but see Goodman and Langrand, 1996; Cameron and Gould, 2013; Gabriel, 2013). Madagascar's central highlands region is one of the most devastated landscapes on the island (Gade, 1996). Human occupancy in the central highlands dates to the 7th century (Gade, 1996), and subsequent land clearing for cattle grazing and agricultural cultivation achieved primarily by slash-and-burn methods ('tavy') promoted an increase in grasslands at the expense of forest cover by the 16th century (Gade, 1996; Goodman and Benstead, 2003). Pastoral farming became well developed with the introduction of European crops, including manioc, sweet potato, peanut, and maize, to the traditional rice, yams and taro (Gade, 1996). With a growing human population and an increase in anthropogenic landscape modification, reduction in forest cover became drastic in the 20th century and most of the remaining forest habitat is now limited to small fragments, patchily dispersed throughout the region (Gade, 1996; Goodman and Benstead, 2003).

Having once been covered in forests up to 2600 m in elevation, the region is now dominated by homogenous secondary grasslands of impoverished, non-native flora (Gade, 1996). Only patches and strips of semi-deciduous forest and rupicolous vegetation, comprising a mixture of southern dry adapted vegetation (e.g., *Aloe, Euphorbia*, *Pachypodium, Kalanchoe*) and temperate high plateau species (e.g., *Podocarpus madagascariensis*, *Weinmannia* spp., *Pandanus* spp., *Symphonia* spp.), remain (Goodman and Benstead, 2003). A large mountain range (500-2600 m elevation) bisects the region north to south, creating a pronounced climatic divide from the humid, oceanic east to the more arid west, and a marked shift in altitudinal zones ranging from tropical lowlands to subalpine highlands. This region exhibits a highly seasonal climate, transitioning between a distinct hot, humid season (November-March) and a cold, dry season (April-October), with an annual rainfall of 1179 mm (Dewar and Richard, 2007). Low temperatures can vary from 14°C in the lowlands to -10°C at high altitudes.

The locality was once extremely rich in vertebrates, containing one of the richest avian diversities in the entire eastern escarpment and the most diverse mammalian fauna in all of Madagascar, including the highest representation of lemur species (Goodman and Benstead, 2003). Many of these species remain only in protected plots of forest and in the large Andringitra National Park. Species diversity in the region varies according to elevation, with marked variations in species richness at vegetative transitional zones, e.g., frugivores decrease with increasing elevation, while omnivores are more persistent throughout (Goodman et al., 2001). Remarkably, *L. catta* can be found throughout this geographic region, including at elevations above 2050 m (Goodman et al., 2006; pers. obs.), and possesses behavioural adaptations that enable it to move easily among rocky outcrop terrain (Figure 1.2). Given the unique habitat and relatively recent degradation of forest in the highlands when compared with other ecoregions on the island, this region offers a rare locale for examining *L. catta'*s ecological responses to habitat fragmentation.

Figure 1.2 *Lemur catta* locomoting across a granite rock face at Anja Special Reserve in Madagascar's south-central highlands

I selected two study sites in the central-highlands region (Figure 1.3) that are of similar size and biodiversity, yet they differ in isolation, *L. catta* resource structure, and level of disturbance. In addition, the population densities of *L. catta* in these fragments differ considerably.

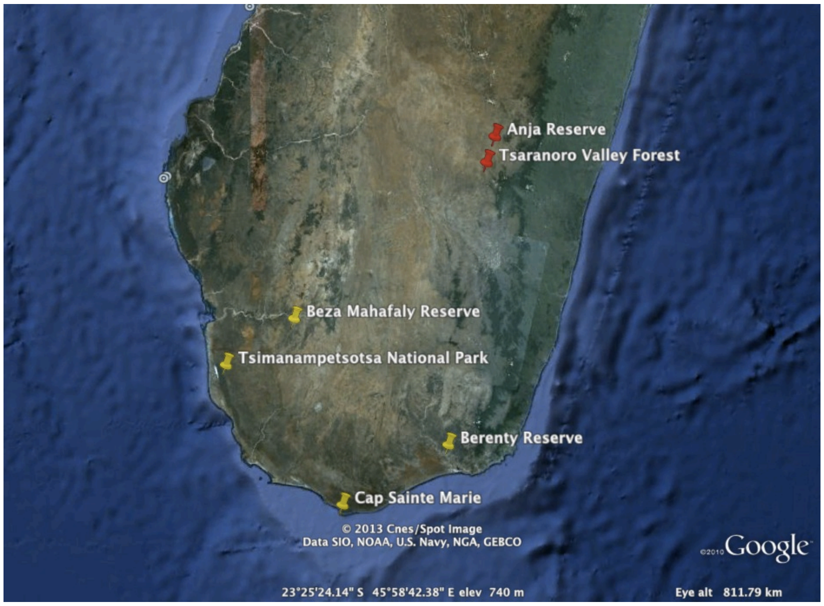

Figure 1.3 Map of the location of the two study sites, Anja Reserve and Tsaranoro Valley Forest (in red), in relation to other sites (in yellow) in which *L. catta* has been studied in southern Madagascar.

Anja Special Reserve is a 34 ha fragment (Figure 1.4), located 12 km S of the town of Ambalavao, approximately 350 m from the heavily traveled Route Nationale 7 highway (21° 51' S latitude and 046° 50' E longitude). It was designated a protected area in 1999 governed by a local cooperative, Association Anja Miray, and now functions as one of the most popular ecotourism sites in Madagascar for viewing *L. catta* and other native flora and fauna (http://anjacommunityreserve.netai.net/anja.htm). Vegetation is a mixture of endemic (e.g., *Aloe, Kalanchoe, Adina microcephala, Erythroxylum platycladum*) and introduced (e.g., *Melia azedarach*, *Psidium cattleianum, Grewia,* *Passiflora incarnata*) species (Gould and Gabriel, in prep). Prior to its protected status, many of the native tree species (e.g., *Ficus* and *Adansonia* spp.) were removed by selective logging from within the forest (Razafimandimby, pers. comm.). The exterior portion of the forest was cleared for rice and maize cultivation and introduced tree species, *Melia azedarach* and *Psidium cattleianum* (guava), were planted for shade, timber, and fruit production. Aided by *L. catta* as an excellent seed disperser (Simmen et al., 2006), these trees have become rapidly established throughout the reserve. The immediate matrix surrounding the fragment (>10 m from the forest edge) consists of grasslands, rice fields, and a small river to the north, and rocky savannah, village gardens (these have been removed since the time of study; Clarke, pers. comm.), and a small anthropogenically-constructed lake to the south. A 1500 m rock face borders the eastern edge of the forest and vegetation reaches to a maximum elevation of 1066 m (Google Earth, 2012). Large granite boulders divide the fragment north to south; however, the *L. catta* groups move freely from one side of the fragment to the other, climbing up and over the large rock faces. Anja is isolated from all other forest containing *L. catta* by at least 8 km and the landscape lacks forest tracks that may serve as corridors for *L. catta* dispersal. Thus, the population appears to be highly contained within the fragment, with little to no immigration/emigration of individuals. Approximately 225 *L. catta* occupy the fragment at a density of 6.6 lemurs/ha (Cameron and Gould, 2013) – a higher population density than has ever been previously reported for *L. catta* in other habitat types (e.g., Beza Mahafaly gallery and dry forest: Sussman, 1991; Gould et al., 2003; Berenty gallery, scrub and spiny forest: Jolly et al., 2002; Pride, 2005a,b,c; Gould et al., 2011;

Cap Sainte Marie spiny bush: Kelley, 2011; Tsimanampetsotsa spiny forest: LaFleur, 2012).

Figure 1.4 Photograph of Anja Reserve and surrounding landscape (northern exposure) as seen from atop the large rock boulders that bisect the fragment (altitude: 975 m)

The Tsaranoro Valley Sacred forest is a remote, 53 ha fragment (Figure 1.5) located in the valley of the Andringitra mountain range (2600 m elevation) and the Karambony mountain massif (1650 m elevation), 55 km SW of Ambalavao (22° 05' S latitude and 046° 46' E longitude). Grasslands dominate the landscape, forests having been cleared for rice cultivation and cattle grazing. However, a few forest fragments remain in relatively close proximity to the Tsaranoro fragment, within *L. catta* dispersal distance (2-10 km) (maximum dispersal distance of *L. catta* is unknown; however, at Beza Mahafaly, one *L. catta* male was reported 20km from the reserve; Gould pers. comm.). Furthermore, the large Andringitra National Park (31 160 ha) is located only 12 km from the Tsaranoro Valley, and it is possible that these forest remnants provide habitat patches to enable *L. catta* movement between primary and fragmented forests in the region. The Tsaranoro forest is designated sacred land due to the presence of ancestral tombs of the local Betsileo people, and resource extraction is controlled by the valley king (Andrianomena, pers. comm.). Vegetation consists of a mix of xerophytic and rocky-outcrop ("rupicolous") vegetation (e.g., *Aloe, Kalanchoe, Ficus*, *Dombeya*, *Turraea sericea, Harungana madagascariensis*). However, selective logging has removed many of the large, native trees from within the forest (e.g., *Ficus* and *Adansonia* spp.), and, unlike at Anja, the forest has not been re-established by introduced species. *M. azedarach, P. cattleianum,* and *Mangifera indica* are present, yet uncommon, in the matrix surrounding the fragment. The matrix is comprised primarily of grassy savannah and a few rice fields, and a village and three tourist camps are located within 1km of the forest edge. Approximately 60 *L. catta* occupy the fragment at a density of 1.13 lemurs/ha – one sixth that which is found at Anja (Cameron and Gould, 2013).

Figure 1.5 Photograph of the Tsaranoro Valley Forest and surrounding landscape (south-eastern exposure) as seen from atop Chameleon rock (altitude: 1200 m)

This is the first project to examine ecological responses of *L. catta* to forest fragmentation. In addition, until very recently (Cameron and Gould, 2013; Gabriel, 2013), no study had examined *L. catta* behaviour and ecology in this geographic region and habitat type. My aim is to investigate intraspecific variation, between and within the study sites, with respect to how *L. catta* utilize and are affected by the environment in which they reside. In order to highlight the various ways in which fragmentation affects habitat suitability for *L. catta*, I have organized this manuscript as a series of four focused studies addressing specific aspects of *L. catta* behavioural and health ecology. In Chapter 2, I examine the spatial components of *L. catta*'s behaviour in forest fragments. Specifically, I address differences in habitat use (home range size, ranging patterns, matrix use, terrestriality), activity budgets, and energy expenditure between and within sites and discuss these differences as they relate to habitat quality. In Chapter 3, I investigate differences in the feeding ecology of *L. catta*. Given the distinct resource structure of the two fragment habitats, resulting from the respective fragmentation histories and ongoing anthropogenic activities (i.e., agriculture, tourism, resource extraction), I discuss how different dietary strategies may help to sustain viable populations of *L. catta* at each site. In Chapter 4, I consider the ecological correlates of stress in *L. catta*, focusing on two variables, food resource abundance and population density, as potential stressors in the study fragments. By examining fecal glucocorticoid levels (fGCs) and behavioural variables (feeding effort, territory marking, and territory defence) between and within sites and across reproductive periods, I explore likely sources of stress for the *L. catta* populations associated with their current habitat conditions. Finally, in Chapter 5, I investigate the endoparasite communities present in the study populations. Specifically, I compare parasite prevalence and cases of multiple infections as a function of environmental exposure, host population density, and season to establish baseline health parameters and to identify the ecological factors associated with fragmentation that may facilitate disease spread.

Throughout these chapters, I address the general prediction that despite the fact that *L. catta* is an ecologically adaptable species and that the native vegetative structure of the two study fragments is similar, the unique alterations to habitat structure and quality that came about with large-scale habitat loss within each region will affect the demographics, behaviour, and health ecology of *L. catta* inhabitants. The marked variation in population density between the study populations points to intersite differences in resource structure and availability, interactions among conspecifics, and potential for disease transmission (Cowlishaw and Dunbar, 2000) that may have important consequences on *L. catta* population fitness and therefore its ability to persist in the forest fragments. Little is currently known about the consequences of forest fragmentation to *L. catta*, perhaps due to the frequently cited ecological flexibility of the species (Gould et al., 1999, 2003; Sauther et al., 1999) and thus ability to persist in degraded habitats. However, given this dearth of information on the ecological effects of fragmentation on *L. catta* and the increasing forest loss throughout the species geographical range (Sussman et al., 2003; Goodman et al., 2006; Bodin et al., 2006; Gould and Gabriel, in prep.), it is important to understand the potential impacts of fragmentation on the behavioural and health ecology of the species in order to assess its longevity in response to current and future environmental pressures. In addition, it may provide a framework for incorporating emerging global viewpoints with respect to anthropogenic disturbance and ecosystem health into the current perspectives on changing Malagasy environments, as well as contribute to the growing literature surrounding the impacts of habitat loss and fragmentation on wildlife populations worldwide.

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2 *LEMUR CATTA* IN FRAGMENTED FORESTS: ACTIVITY BUDGETS, ENERGY EXPENDITURE, AND HABITAT USE

The following chapter is adapted from “Gabriel, D.N. 2013. Habitat use and activity patterns as an indication of fragment quality in a strepsirrhine primate. International Journal of Primatology 34: 388-406”.

2.1 Abstract

Considerable variation exists within populations of the same species in responses to habitat fragmentation. Habitat use by resident populations is related to the abundance and stability of resources in time and space; thus, space-use is of primary importance for evaluating habitat quality. In this chapter, I examine between- and within-site differences in the ranging behaviour, matrix use, and activity budgets of ring-tailed lemurs (*Lemur catta*) inhabiting two distinct forest fragments – Anja Special Reserve and Tsaranoro Valley Sacred Forest – in Madagascar’s central highlands. My intention is to test the prediction that intraspecific variation in habitat use and activity patterns is indicative of fragment quality. At Anja, *L. catta* have access to abundant year-round anthropogenic resources (introduced fruit trees, village gardens, water), while the population at Tsaranoro is reliant on seasonally variable and patchily distributed resources throughout the forest and matrix. *L. catta* at Anja occupied smaller home ranges, had shorter daily path lengths (DPLs), and spent less time foraging and more time resting, locomoting, and engaging in social and territorial behaviour. In contrast, groups at Tsaranoro occupied larger home ranges, had longer DPLs, relied heavily on the matrix, and spent a greater proportion of their activity budget engaging in foraging behaviour. These differences illustrate how intersite variation in habitat quality may influence the behavioural and ecological strategies of resident species and is an important consideration for

conservation managers when assessing the capacity of forest fragments to sustain populations over time.

2.2 Introduction

Tropical forests are enduring the highest rates of land conversion and habitat loss compared with any other biome worldwide (Meyers, 1993; Mayaux et al., 2005; FAO, 2011). Thus, once large expanses of continuous tropical forest habitat are being increasingly restricted to small, isolated forest fragments. Given considerable variation with respect to the spatial, temporal and ecological effects associated with fragmentation (Fahrig, 2003; Wiegand et al., 2005), it can be difficult to predict how large-scale habitat disturbance will impact resident species. As 90% of primate species are found in tropical forests (Mittermeier and Cheney, 1987; Marsh, 2003), identifying the ecological characteristics of fragmented habitats that impact on the health and fitness of primate populations within a region is critical for successful species preservation.

While it is widely accepted that habitat loss (i.e., change in amount of habitat) holds negative implications for biodiversity (e.g., Belisle et al., 2001; Gurd et al., 2001; Stuart et al., 2004), the effects of habitat fragmentation (i.e., change in habitat distribution and/or isolation) on wildlife can be both positive (e.g., McGarigal and McComb, 1995; Collinge and Forman, 1998; Belisle et al., 2001) and negative (e.g., Rosenberg et al., 1999; Kurki et al., 2000; Fahrig, 2002; reviewed in Fahrig, 2003). In studies of primate species, clear predictor variables for how a given species will fare in fragmented landscapes have remained elusive (Onderdonk and Chapman, 2000). Some primates are generally absent from fragments altogether (*Chiropotes sananas*: Rylands and Keuroghlian, 1988; *Ateles paniscus:* Estrada and Coates-Estrada, 1996; *Cercopithecus* *mitis* and *Lophocebus albigena*: Onderdonk and Chapman, 2000). Others are present in fragments, yet exhibit alterations in demography or ecology, such as reductions in population and group size (*Alouatta palliata*: Estrada and Coates-Estrada, 1996; McCann et al., 2003; *Colobus guereza*: Onderdonk and Chapman, 2000), increases in foraging effort and flexibility (*Macaca silenus*: Menon and Poirier, 1996; *Eulemur collaris*: Donati et al., 2011), changes in day and nighttime acitivty patterns (*Eulemur macaco flavifrons*: Schwitzer et al., 2007), and declines in social activity (*A. palliata*: Clarke et al., 2002). Some primates appear to remain neutral or may even respond favourably to fragmentation effects (*C. cephus*: Tutin, 1999; *Microcebus rufus* and *Propithecus diadema edwardsi*: Lehmann et al., 2006).

Several studies suggest that interspecific variation in fragmentation sensitivity can be attributed to differences in the functional characteristics of species (e.g., body size, dispersal capacity, ecological specialization) (Henle et al., 2004; Ewers and Didham, 2006; Devictor et al., 2008). Yet considerable variation in responses to fragmentation also exists among populations of the same species (McLoughlin et al., 2000). In addition to altering the configuration of a habitat within a landscape, the process of fragmentation alters habitat properties (Ficher and Lindenmayer, 2007; Laurance, 2008; Bennett and Saunders, 2010), including vegetative composition (van den Berg et al., 2001), habitat heterogeneity (Law and Dickman, 1998; Kadmon and Allouche, 2007), and species distributions/interactions (e.g., interspecific competition, predation pressure, crowding) (Waser, 1987; Buskirk et al., 1999; Kremsater and Bunnell, 1999; Irwin et al., 2009). Thus, much of this intraspecific variation may extend from differences in the unique ecological conditions of individual fragments or fragment landscapes (Fleishman et al., 2002).

Habitat quality refers to the suitability of a habitat to provide the conditions necessary for survival (e.g., food and water resources, shelter, protection from predators, access to conspecifics) (Hall et al., 1997). In fragmented landscapes, habitat patches may vary in quality based on the regional abundance and predictability of resources in time and space (McLoughlin et al., 2000), both within the remaining forest and in the surrounding non-habitat ('matrix'). Since an animal's fitness is dependent on its capacity to access its resource requirements from the environment, space-use is one of the most important considerations for evaluating habitat quality (Ims et al., 1993) and a fragment's capacity to support a population of a given species over time (Ims et al., 1993; Franklin et al., 2000). Home range size (e.g., Andreassen et al., 1998; Li and Rogers, 2005; Hinam and Clair, 2008), ranging distance (e.g., Schtickzelle et al., 2006), matrix use (e.g., Ricketts, 2001; Selonen and Hanski, 2003; Anderson et al., 2007), and patterns of activity (e.g., Mahan and Yahner, 1999; Pozo-Montuy and Serio-Silva, 2007; Wong and Sicotte, 2007) are all subject to intraspecific variation in fragmented habitats related to habitat quality.

Madagascar is among the highest global priorities for biodiversity conservation, largely as a result of rapid rates of land conversion and habitat loss (Ganzhorn et al., 2001; Brooks et al., 2006). Due to their endemism, incredible diversity, and highly threatened status (Mittermeier et al., 2012), the strepsirrhine primates of the infraorder Lemuriformes represent a critical flagship taxon for conservation in Madagascar (Durbin, 1999). Among these, the ring-tailed lemur (*Lemur catta*) is the most ecologically flexible of the diurnal lemurs (recent evidence suggests that the species should be reclassified as cathemeral; see LaFleur, 2012; Parga, 2012; Donati et al., 2013), capable of inhabiting diverse forest types throughout south, southwestern, and south-central Madagascar (Jolly, 1966; Sussman, 1977; Sauther et al, 1999; Goodman et al., 2006; Gould, 2006; Kelley, 2011; LaFleur, 2012). *L. catta* is a semi-terrestrial, frugivore/folivore and readily exploits anthropogenically-modified landscapes (Sauther et al., 2006; Gemmill and Gould, 2008; LaFleur and Gould, 2009). Yet despite marked ecological flexibility (Sauther et al., 1999; Gould et al., 1999, 2003; Gould, 2006), *L. catta* remains highly sensitive to habitat disturbance, with populations occurring at much lower densities in degraded forests and habitats of poor quality (e.g., spiny bush habitats of the far south) (Sussman et al., 2003; Kelley, 2011; Lafleur, 2012).

Like many other primates (Cowlishaw and Dunbar, 2000; Marsh, 2003), *L. catta* is now restricted to forest fragments throughout much of its range (Sussman et al., 2003; Goodman et al., 2006; Bodin et al., 2006; Gould and Gabriel, in prep.). However, to date, no study has examined the ecological responses of *L. catta* to fragmentation, and with a few exceptions (Glessner and Britt, 2005; Irwin, 2008; Lahann, 2008), research pertaining to fragmentation effects on biodiversity in Madagascar has been limited to assessments of edge effects and species abundance/distributions (Ganzhorn, 1995; Vallan et al., 2004; Watson et al., 2004; Lehmann et al., 2006; Quemere et al., 2010; Randrianambinina et al., 2010). In this chapter, I examine habitat use and activity patterns in populations of *L. catta* occupying two forest fragments in Madagascar's central highlands. The two study sites vary markedly in isolation and resource structure, and thus offer an excellent opportunity to examine the ecological responses of *L. catta* to fragments of different quality. Based on the differences in demographics and behaviour observed in fragment-dwelling primate species compared with those living in continuous forest (e.g., Clarke et al., 2002; Li and Rogers, 2005; Wong and Sicotte, 2006; Estrada and Coates-Estrada, 1996; McCann et al., 2003; Onderdonk and Chapman, 2000; Menon and Poirier, 1996), and the vast differences in population densities found in *L. catta* occupying various habitat types (Sussman et al., 2003; Kelley, 2011; Lafleur, 2012; Cameron and Gould, 2013), I test the prediction that intraspecific variation in habitat use and activity patterns in *L. catta* is indicative of fragment quality. Specifically, I assess population differences in ranging behaviour, matrix use, activity budgets, and energy expenditure and discuss how these variables relate to the distinct resource structure of the habitat fragments.

2.3 Methods

Study sites – Anja Special Reserve is a 34 ha, mixed-vegetation, rocky-outcrop fragment located 12 km S of the town of Ambalavao (21° 51’ S latitude and 046° 50’ E longitude), and has been protected for community-driven ecotourism since 1999 (Razafimandimby, pers. comm.; http://anjacommunityreserve.netai.net/anja.htm). The fragment is completely isolated from all other forest patches by the Route Nationale 7 highway to the west and a 1500m-high mountain range to the east (Google Earth, 2012). The nearest forest patch containing *L. catta* is at least 8 km away (Gould, pers. comm.), and dispersal is likely heavily impeded by the largely anthropogenic landscape. The forest is comprised of xerophytic and deciduous vegetation, including a mixture of endemic (e.g., *Aloe, Kalanchoe, Adina microcephala, Erythroxylum platycladum*) and introduced (e.g., *Melia azedarach*, *Psidium cattleianum, Grewia, Passiflora incarnata*) species (Gould and

Gabriel, in prep.). The northern edge of the fragment is mosaic habitat that consists of grasslands, rice paddies, and a small river, while the southern edge is adjacent to rocky savannah, village gardens and an artificial lake used for cattle watering and pisciculture. In recent decades, introduced fruit trees, *M. azedarach and P. cattleianum*, have become widely established throughout the forest (Razafimandimby, pers. comm.). These trees now constitute greater than 25% of the total forest canopy (Gabriel, unpublished data), and provide abundant year-round food resources for the residing *L. catta* (Gould and Gabriel, in prep; Chapter 3).

The Tsaranoro Valley sacred forest is a remote, 53 ha fragment situated directly east of the Andringitra mountain range and 55 km SW of Ambalavao (22° 05’ S latitude and 046° 46’ E longitude). The Karambony mountain massif (1650 m in elevation) borders the western edge of the forest and the matrix consists of open rocky savannah, a river lined by fruit trees, and a few crops and rice fields. Similar to Anja, the forest vegetation is a mixture xerophytic and deciduous species (e.g., *Aloe, Kalanchoe, Dombeya*, *Turraea sericea, Adina microcephala, Buddleja madagascariensis, Diospyros*). Several native fruit trees (e.g., *Ficus* and *Adansonia* spp.) have been selectively removed from within the fragment (Andrianomena, pers. comm.); however, unlike Anja, the forest has not been heavily re-established by introduced alternatives. *M. azedarach* and *P. cattleianum* are present, yet uncommon, in the matrix, as are other larger fruit-bearing trees such as *Mangifera indica, Harungana madagascariensis* and *Ficus* spp. A small village and three camps for adventure tourism are located within one kilometer of the forest fragment. Large-scale land clearing, primarily using slash-and-burn methods (‘tavy’) for cattle grazing and agriculture, has occurred throughout the valley (Andrianomena, pers. comm.); however, a few fragments remain within a 2-10 km radius of the study site that may offer additional habitats for *L. catta* dispersal (maximum dispersal distance of *L. catta* is unknown; however, *L. catta* at Beza have been reported to disperse up to 20km; Gould, pers. comm.).

Neither Anja nor Tsaranoro contain other diurnal or cathemeral lemur species, and throughout the study duration predators of *L. catta* were rarely observed, with only infrequent sightings of raptors (*Polyboroides radiates* and *Buteo brachypterus*), boas, and domestic dogs. Anja guides also report seeing 'Ampaha', a wild cat, in the region (http://anjacommunityreserve.netai.net/anja.htm), which is a potential predator of *L. catta*.

Study subjects – At the time of study, the population of *L. catta* at Anja consisted of approximately 225 individuals, at a density of 6.6 lemurs/ha (Cameron and Gould, 2013). There were 13 groups of lemurs with an average of 16 animals/group, including immatures (Gould and Gabriel, in prep). The population of *L. catta* at Tsaranoro contained approximately 60 *L. catta* at a density of 1.13 animals/ha (Cameron and Gould, 2013). Six groups occupied the fragment with an average group size of 12 animals, including immatures (Gould and Gabriel, in prep.). Two groups of *L. catta* were observed at each site, with a total of 16-17 animals/group. Group composition across the study period is presented in Table 2.1.

Table 2.1 Group composition, male dispersal/immigration and number of focal animals in each study group

Group	Composition	# of dispersing/immigrant males	# of focal animals
Anja			
AL	5F, 8M, 3J, 3I	0/0	13
AB	6F, 6M, 4J, 5I	0/1	12
Tsaranoro			
TR	6F, 7M, 3J, 5I	3/1	13(11)*
TM	5F, 6M, 5J, 2I	0/1	11(12)*

Parentheses denote the number of focal animals following the male dispersal period. One male from TR emigrated to TM between study months and was included in the focal sessions of TM for the remainder of the study period.

Groups were selected based on the area of the fragment that they occupied, such that the various habitat structures within each site were well represented within group ranging patterns. At Anja, the territory of Lake Group (AL) encompassed the lower southwestern portion of the reserve, providing access to a large area of *M. azadarach* and *P. cattleianum*, as well as seasonally available crop vegetables (since the time of study these crops have been removed; Clarke, pers. comm.), herbaceous ground vegetation, and water from the human-constructed lake bordering the reserve. Boulder Group (AB) primarily occupied the upper northwestern portion of the reserve and their territory provided only limited access to *M. azadarach* and *P. cattleianum*, and they were never observed foraging in the crops or drinking from the lake. At Tsaranoro, both Rangers Group (TR) and Meva Group (TM) regularly foraged on fruits, leaves, and flowers from small trees and bushes in the open savannah surrounding the fragment, particularly in the dry season when forest resources were limited. However, their nightly sleeping trees were within the fragment interior.

The study period spanned the late dry season (beginning of September to late November) of 2010 and mid- to late- wet season (beginning of March to end of May) of 2011. Consecutive four-day follows were carried out by DG and field assistants, R. Simmons and I. Schneider-Crease, for each group at each site in rotating three-week periods. For example, weeks one through three were dedicated to following AL and AB groups at Anja over rotating four-day periods, and weeks four through six were spent following TR and TM groups at Tsaranoro in similar fashion, throughout the duration of the study. An equal number of follow days was spent with each group and in each of the two study periods (16 days/group/period). Observations were made between the hours of 0700 and 1700, which included the groups' active daytime hours and a one to three hour midday rest period (these were the hours for which local Anja guides were available, and the hours were maintained at Tsaranoro for consistency of comparison). A total of 685 h of focal animal data were collected throughout the duration of the study period: 208 h from Lake Group (AL) and 158 h from Boulder Group (AB) at Anja, and 160 h from Rangers Group (TR) and 159 h from Meva Group (TM) at Tsaranoro.

Home range and habitat utilization – Seasonal home range sizes and daily path lengths (DPL) of each group were determined via GPS coordinates taken daily throughout the study period, with early September to late November of 2010 representing the dry season and early March to late May of 2011 representing the wet season (Goodman et al., 2006). I defined seasonal home range as the area used by a group during each three-month period. This included areas that were visited for a particular food resource that may have overlapped with other groups' home ranges. At Anja, many groups have overlapping home ranges due to the high population density, and each group defends certain core areas of its range for access to preferred resources. This is particularly evident in groups occupying the lower southwestern portion of the fragment. In contrast, at Tsaranoro there is little home range overlap among groups and intergroup encounters are comparatively infrequent (Chapter 4). Coordinates were recorded upon locating the focal group each morning and subsequently each time the group moved to a new location (feeding or sleeping tree) throughout the day. In order to control for missing data points due to focal groups being out of view, coordinates were only considered for days consisting of >6hrs of continuous follow, during which time the location of the groups was in clear view or could be found within a 20 minute time span. When there was considerable distance between the focal group and myself (>20 m), I approached the location to record an accurate coordinate once the group had moved on or at the end of the study day. This reduced bias arising from differences in visibility within and between sites and across seasons. A total of 995 location points were recorded throughout the study period: 221 for AL and 197 for AB at Anja, and 317 for TR and 260 for TM at Tsaranoro.

GPS coordinates were entered into ArcView GIS software and Google Earth Pro (Google, 2012) to calculate home range size and DPL. The daily path length (DPL) of each group was calculated as the total distance focal groups moved in a single day. Several methods can be employed in order to calculate the home range size of animals (Worton, 1987; Powell, 2000), and the method selected can yield very different results (e.g., in primate species: Boyle et al., 2009; Grueter et al., 2009). The traditional minimum convex polygon (MCP) method, although widely utilized, can often overestimate home range size due to the inclusion of never or seldom visited areas within a habitat (Ostro et al., 1999; Powell, 2000; Burgman and Fox, 2003). To minimize the effect of peripheral data points, I used an 'adjusted' MCP (*as per* Mills and Gorman, 1987; Li and Rogers, 2005; Grueter et al., 2009) when determining the home range size of *L. catta* groups. For each group, I created irregular polygons from each DPL in Google Earth Pro (Google, 2012) by plotting connector points to correspond with the time-sequenced GPS coordinates taken throughout the follows. Thus, in contrast to connecting the outermost points of the location data, the resulting polygons incorporated only the area used by the group in their day range. I then summed all of the day range polygons together from each season and traced the outer-most edge to determine the seasonal home range. A comparison of home range size using this 'adjusted' MCP and the traditional MCP technique is displayed in Table 2.2.

Table 2.2 Comparison of seasonal home range size (ha) of *L. catta* study groups using the traditional minimum convex polygon method (MCP) and an adjusted MCP method (a-MCP)

Group	**Home Range Size (ha)**			
	Dry Season		**Wet Season**	
Anja	MCP	a-MCP	MCP	a-MCP
AL	5.8	*3.9*	2.6	*1.4*
AB	11.6	*6.3*	12.3	*4.9*
Tsaranoro				
TR	24.0	*18.1*	10.1	*6.6*
TM	28.4	*16.6*	12.7	*10.7*

Italicized values from the adjusted MCP analysis are used when reporting results

I used fixed kernel density estimations (KDE) to examine the intensity of habitat utilization throughout *L. catta*'s home range (Silverman, 1986). KDEs are a nonparametic statistical method for examining the probability for which an individual or group will be observed in a particular area of their home range, thereby providing information with respect to habitat use and preference (Seaman and Powell, 1996). I used fixed KDEs, with the smoothing parameter (h_{ref}) (as defined by Worton, 1995), to examine the utilization distributions of each group throughout their range. The core area of habitat used by each group was defined by the 30% kernel density contour (based on visual inspection of the contours that represented the highest probability of utilization by each group). In addition, the maximum distance that each group traveled beyond the forest perimeter was determined for each full-day follow. I determined terrestriality by noting the location of individuals continuously throughout focal sessions and calculating the proportion of time that each animal spent terrestrially (all individuals positioned on the ground or elevated on a rock surface were classified as terrestrial).

Activity budgets and energy expenditure – To determine activity budgets and the total energy expenditure of group members, ten-minute continuous-time focal animal samples (Altmann, 1974) were collected, noting all behaviours and interactions with conspecifics and the start time of each behaviour. Focal individuals consisted of all adult males and females in each group. Distinguishing sex in *L. catta* is possible due to conspicuous external sex organs, including large male testes size and elongated female clitoris (Jolly, 1966; Drea and Weil, 2008), and the presence of antebrachial scent glands in males located near a keratinized spur (Jolly, 1966; Evans and Guy, 1968). Further identification of individuals was achieved using notable, characteristic markings, such as variations in eye-ring shape, tail shape and size, body coloring, and distinct injuries or abnormalities (e.g., scars, deformed limb growth, cataracts, loss of an eye). All characteristics were identifiable from at least 25 m with binoculars and could be recognized by myself and field assistants. Juveniles and infants were excluded from focal observation, as reliable identification of individuals could not be made. During sampling, focal animals were selected by rotating between sexes and through all individuals in a group when possible. A total of 685 h of focal animal data were collected throughout the duration of the study period: 208 h from AL and 158 h from AB at Anja, and 160 h from TR and 159 h from TM at Tsaranoro.

Behaviours that were used to analyze activity budgets were grouped into the following categories: forage (feed, drink), rest (rest, sun), social (autogroom, allogroom, play), locomote, and territorial (scent mark, stink fight). Time budgets of focal individuals were determined for each behavioural category as the proportion of time spent engaging in each activity (i.e., number of hours per activity divided by the total number of observation hours).

Energy expenditure was calculated using formulae established by Coelho (1974) to estimate the energy budgets of primates on the basis of body weight and the time spent engaging in various activities. Indexes of energy expenditure, "k" values, for each activity were adapted from Leonard and Robertson (1997) to adjust for the activity budget of *L. catta* (*as per* Rasamimanana et al., 2006; Table 2.3). Activities included in determining energy expenditure were feed, rest, locomote, groom, sun, play, and sleep. Since total observation hours varied daily based on the amount of time group members were kept in constant view, time values were adjusted to estimate daily rates (based on a 10-hour observation day) and rates per hour (*as per* Leonard and Robertson, 1997).

Table 2.3 Index of energy expenditure, ‘k’ values, for various *L. catta* activities

Activity (i)	Index of energy expenditure (k)
Forage	1.38
Rest	1.25
Groom	2.35
Sun	1.25
Play	2.35
Sleep	1.00

Values taken from Leonard and Robertson (1997) and Rasamimanana et al., (2006)

Total energy expenditure was calculated for each focal individual as follows:

Total Energy Expenditure $(TEE) = \sum_i^n C_i$

$C_i = k_i BMT_i$ = energy expended (kCal) while engaging in activity “i” by an individual.

k_i = index of energy expenditure for activity “i”, with the exception of locomotion (see below).

T_i = time (hrs) spent in activity “i” by an individual in a 10-hour observation day.

$BM = 45.5W^{0.75}$ = basal metabolism predicted from Kleiber’s formula (1961), where BM = $70W^{0.75}$, and reduced by 65% (*as per* Rasamimanana et al., 2006) due to the lower resting metabolism of lemur species when compared to other primates (Daniels, 1984; Richard and Nicoll, 1987; Drack et al., 1999).

W = body weight (kg) based on average weights for free-ranging *L. catta* of 2.2kg (Sussman, 1991; Koyama et al., 2007).

Energy expended in quadrupedal locomotion was calculated using the following formula (adapted by Leonard and Robertson, 1997):

$C_{locomote} = (0.041W^{0.6})\ DC + (0.029W^{0.75})T_{locomote}$

W = body weight (g), as above

$T_{locomote}$ = time (hrs) spent locomoting by an individual in a 10-hour observation day.

DC = distance covered (km) by an individual in a 10-hour observation day, calculated using a handheld global positioning system (GPS) device.

Statistical Analysis – When determining between-site differences in terrestriality, activity budgets and energy expenditure (N=49 individuals), nested ANOVAs were used to control for group effects. When a significant group effect was found, one-way ANOVAs followed by TukeyHSD post-hoc tests were used to examine group differences (N=24 and 25 individuals) for each variable. To determine seasonal differences in DPL between sites (N=44 and 67 days), Mann-Whitney U tests were used since data did not satisfy the assumptions of parametric statistical tests. Unpaired t-tests were used to determine differences in energy expenditure according to sex (N=49 individuals), and paired t-test were used to determine differences in DPL and energy expenditure according to season (N=44 and 67 days). For all statistical tests, significance threshold was $P < 0.05$. Standard error is the reported measure of variability.

2.4 Results

Home range and DPL – Home range and DPL varied by site and season. Mean seasonal home range size at Anja was smaller than that at Tsaranoro (dry season: 5.1 ± 1.2 vs. 17.4 ± 0.8 ha; wet season: 3.2 ± 1.8 vs. 8.7 ± 2.1 ha). All focal groups had larger ranges in the dry season compared with the wet season (mean = 49.25%, range = 33-64%; Table 2.2). Differences in DPL between sites were significant for both the dry (Mann-Whitney U test; U=46, $P<0.0001$) and wet (U=144, $P<0.0001$) seasons, with *L. catta* at Anja exhibiting shorter DPLs than those at Tsaranoro (Figure 2.1). DPL did not vary within sites by group (Mann-Whitney U test; Anja: 474.0 ± 33.7 vs. 407.4 ± 30.4 m, *P*=0.12; Tsaranoro: 866.3 ± 69.3 vs. 839.9 ± 68.4 m, *P*=0.79) or by season (paired t-test; Anja: 451.5 ± 34.4 vs. 432.7 ± 28.1 m, *P*=0.69; Tsaranoro: 891.9 ± 66.0 vs. 903.9 ± 63.0 m, *P*=0.90).

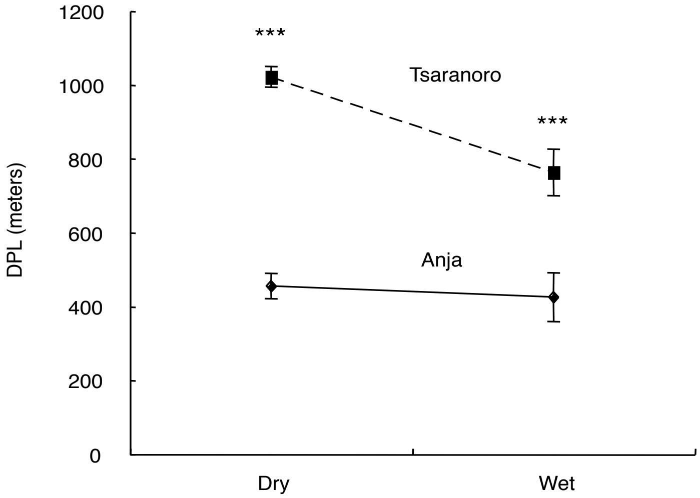

Figure 2.1 Between-site comparison of daily path length (DPL) in meters (mean ± SE) of *L. catta* in the dry season of 2010 (N=55 days) and wet season of 2011 (N=56 days). Asterisks denote statistically significant differences between sites (Mann-Whitney U Test; *P*<0.0001)

Matrix use and utilization distributions – Utilization distributions of habitat in the dry season for each group are displayed in Figure 2.2. At Anja, *L. catta* were rarely observed beyond the forest perimeter. AL had a core area of activity (30% kernel contour) that was 43% and 81% smaller than that of AB in the dry and wet seasons, respectively (dry season: 0.8 ha vs. 1.4 ha; wet season: 0.6 ha vs. 3.2 ha).

At Tsaranoro, groups TR and TM frequently utilized the matrix; however the utilization distribution varied by group and by season. For TR, the core area of activity (30% kernel contour) of 3.45 ha in the dry season and 1.83 ha in the wet season was centered entirely within the forest interior, and matrix area was included in kernel contours of >30% (3.45 ha) and 70% (5.98 ha) in the dry and wet seasons, respectively.

In contrast, for TM, the core area of activity was centered entirely within the matrix in both seasons (30% kernel contour: dry season = 7.18 ha; wet season = 3.80 ha). TM rarely foraged within the forest interior, but returned to the forest at dusk each day to sleep. Both groups also traveled greater distances beyond the forest perimeter in the dry season (TR - mean = 181.85 ± 46.4 m; TM - mean = 542.03 ± 44.4 m) when compared to the wet season (TR - mean = 23.85 ± 11.2 m; TM - mean = 366.32 ± 16.8 m).

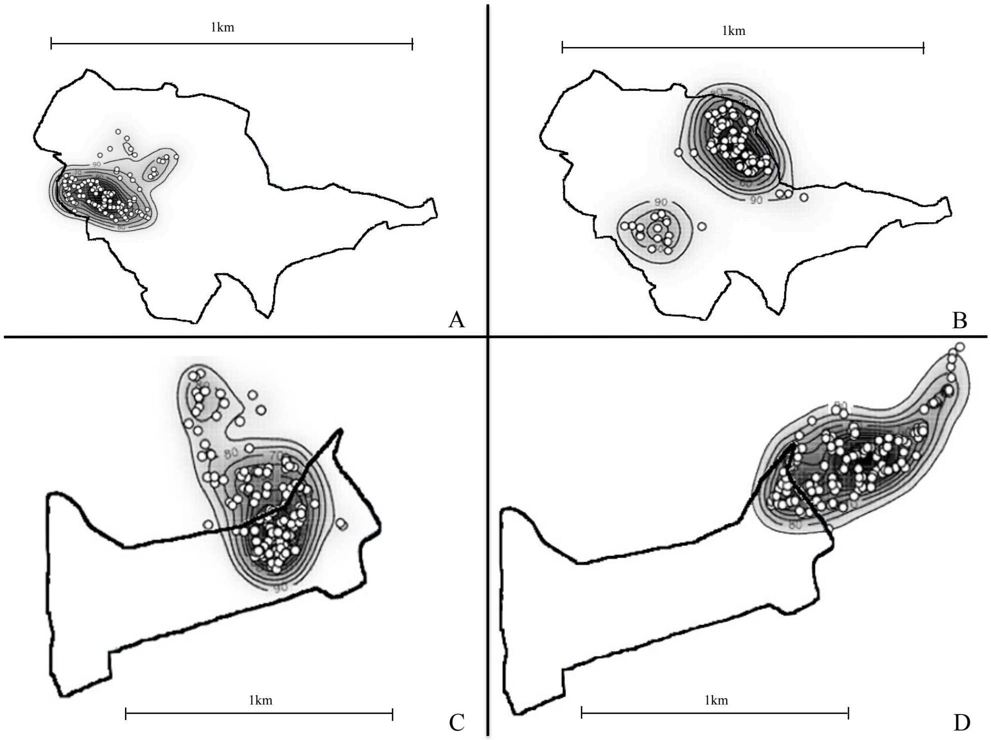

Figure 2.2 Utilization distributions of *L. catta* at Anja Reserve (panel A=AL group; panel B=AB group) and Tsaranoro Valley Forest (panel C=TR group; panel D=TM group) during the dry season (September to November) of 2010. Black outlines represent the forest perimeter of each fragment. Contours represent 10 to 90% kernel utilization distribution estimates in 10% increments. Open circles represent location data (GPS coordinates; N=995) for study groups

Terrestriality – I found no between-site difference in the proportion of time that *L. catta* was terrestrial (0.29 vs. 0.25, nested ANOVA: *P*=0.31). However, there were differences in terrestriality according to group (one-way ANOVA; F=31.52, df=3, *P*<0.0001), with

AL spending more time terrestrial when compared to AB (*P*<0.0001) at Anja, and TM spending more time terrestrial when compared to TR (*P*=0.03) at Tsaranoro (Figure 2.3).

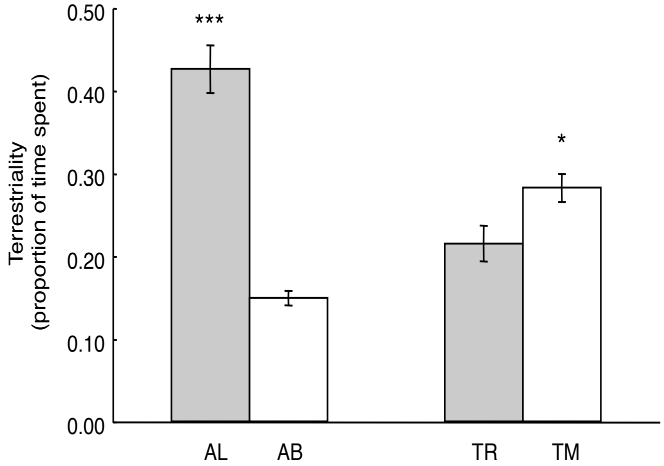

Figure 2.3 Comparison of the proportion of time spent terrestrially (mean ± SE) by group for *L. catta* at Anja (AL and AB; N=25 animals) and Tsaranoro (TR and TM; N=24 animals). Asterisks denote statistically significant differences within-sites (One-way ANOVA; '***' *P*<0.0001; '*' *P*=0.03)

Activity budgets – Time budgets varied by site for all behavioural categories: [nested ANOVA; (forage: F=122.61, df=1, *P*<0.0001); (rest: F=26.64, df = 1, *P*<0.0001); (social: F=47.76, df=1, *P*<0.0001); (locomote: F=23.55, df=1, *P*<0.0001); (territorial: F=29.08, df=1, *P*<0.0001)]. *L. catta* at Anja spent a greater proportion of time resting, socializing, locomoting, and engaging in territorial behaviour, while *L. catta* at Tsaranoro spent more time foraging (Figure 2.4). However, there were also significant group effects on foraging (nested ANOVA; F=6.00, df=3, *P*=0.005), social (nested ANOVA; F=10.68, df=3, *P*=0.0002), and locomoting behaviours (nested ANOVA; F=7.98, df=3, *P*=0.001). At Anja, there were group differences in time budgets for foraging (one-way ANOVA; F= 44.87, df=3, *P*=0.009), socializing (one-way ANOVA; F= 23.04, df=3, *P*=0.003) and locomoting (one-way ANOVA; F=13.17, df=3, *P*=0.001) behaviours; AL spent more time socializing and locomoting, while AB spent more time foraging (Figure 2.5). At

Tsaranoro there were group differences in time spent socializing (one-way ANOVA; F=23.04, df=3, *P*=0.04), with *L. catta* in TM engaging in more social behaviour than those in TR (Figure 2.5).

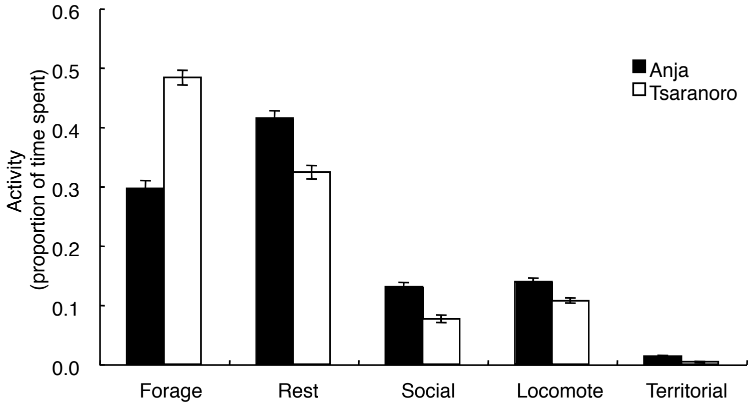

Figure 2.4 Between-site comparison of the proportion of time spent engaging in different activities (mean ± SE) by *L. catta* at each of the study sites (N=49 animals). Statistical significance was achieved for all behavioural categories (nested ANOVA; $P<0.0001$).

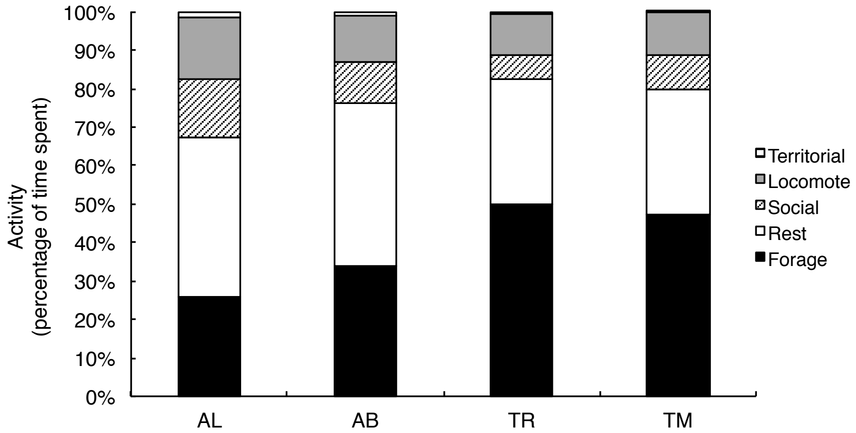

Figure 2.5 Comparison of the activity budget (mean percentage of time spent in each activity) by group for *L. catta* at Anja (AL and AB; N=25 animals) and Tsaranoro (TR and TM; N=24 animals)

Energy expenditure – Total energy expenditure varied by site (nested ANOVA; F=80.71, df = 1, *P*=0.001); *L. catta* at Anja had lower mean energy expenditure when compared with those at Tsaranoro (95.1 ± 2.2 vs. 111.5 ± 2.2kCal). There was also a significant group effect on energy expenditure (one-way ANOVA; F=39.62, df=3, *P*<0.0001); AL expended more energy on average than AB at Anja (*P*<0.0001), and TR had higher mean energy expenditure than TM (*P*=0.02; Figure 2.6). Energy expenditure did not vary by sex (105.6 ± 2.6 vs. 101.0 ± 2.9 kCal; *P*=0.17) or season (104.5 ± 2.0 vs. 101.5 ± 2.1 kCal; *P*=0.19).

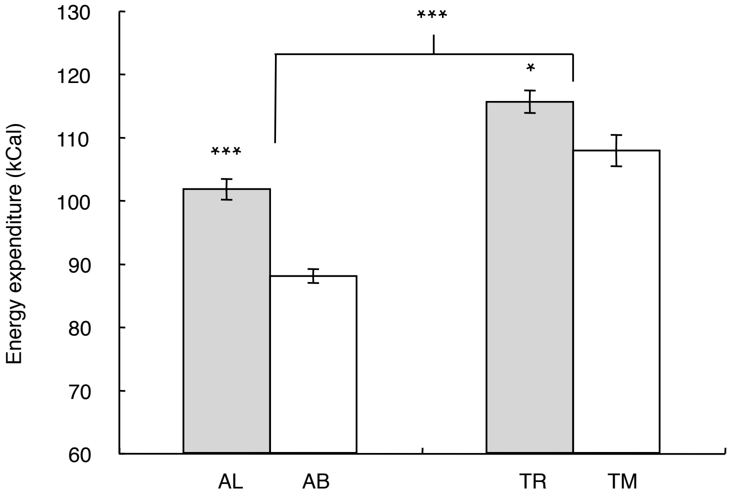

Figure 2.6 Comparison of energy expenditure (kCal) (mean ± SE) by group for *L. catta* at Anja (AL and AB; N=25 animals) and Tsaranoro (TR and TM; N=24 animals). Asterisks denote statistically significant differences between and within sites (nested and one-way ANOVA; '***' *P*<0.0001; '*' *P*=0.03)

2.5 Discussion

The results show that *L. catta* at Tsaranoro depend on much larger habitat areas when compared with the Anja population, as illustrated by their larger home range size, extended DPLs, and regular use of the matrix. Factors such as interspecific competition (Waser, 1987; Buskirk et al., 1999) and predation pressure (Irwin et al., 2009) are unlikely causes of this result. First, *L. catta* is the only diurnal lemur species in each of the fragments (recent evidence suggests that this species should be reclassified as cathemeral; see LaFleur, 2012; Parga, 2012; Donati et al., 2013). Second, at Anja, the absence of nearby continuous forest means that predators of *L. catta* are scarce in the area (see Methods), with the exception of hybrid feral cats (*Felis silvestris*) and wild cats ('Ampaha'). It is likely that predation pressure is actually greater at Tsaranoro due to the closer proximity of continuous forest (Andringitra National Park is only 12km from the Tsaranoro Valley), which houses populations of *L. catta's* natural predators, including raptors and fossa (*Cryptoprocta ferox*) (Goodman et al., 1997; Goodman and Rasolonandrasana, 2001). Nor can crowding explain the increased home ranges and DPLs of the Tsaranoro lemurs, since the population density at Anja is six times greater than that at Tsaranoro. Competition-induced territoriality, brought on by high population density, may partially account for the smaller home ranges of the Anja lemurs, a relationship that has similarly been described in root voles (*Microtus oeconomus*) inhabiting fragmented habitats (Andreassen et al., 1998). This is further demonstrated by the fact that *L. catta* at Anja spent more time marking and defending its territory when compared to Tsaranoro groups, suggesting that the Anja lemurs are experiencing higher rates of intergroup competition over resources.

It is likely that the differences in ranging patterns between the two populations can be attributed to variability in the distribution and quality of food resources. The range of the Anja groups is restricted almost entirely to within the forest bounds, with the exception of lemurs exploiting food and water resources from the village gardens, rice paddies, and man-made lake in the immediate matrix. The high concentration of introduced trees, *M. azedarach* and *P. cattleianum*, at Anja provides abundant and consistent access to food resources for *L. catta* throughout the annual cycle (Gould and Gabriel, in prep; Chapter 3), which require relatively little effort to procure. This reduced foraging effort leaves more time available for social activity (grooming and play behaviour), consistent with that found in other primate species residing in habitats with abundant food resources (Clarke et al., 2002; Li and Rogers, 2005; Wong and Sicotte, 2007). In contrast, I found that *L. catta* at Tsaranoro spent a greater proportion of time foraging compared with the Anja population, and regularly traveled and foraged in the matrix. The selective logging of native fruit trees within the forest appears to have affected the groups' ranging behaviour, as the Tsaranoro lemurs foraged on patchily distributed trees and shrubs scattered in the matrix. Throughout its habitat, *L. catta* tend to occupy larger home ranges when occupying resource limited habitats (O'Connor, 1987; Sussman, 1991; Kelley, 2011; LaFleur, 2012) compared with those in habitats of higher resource quality (Jolly, 1966; Sussman, 1991; Budnitz and Dainis, 1975). Similarly, a negative correlation between territory size and habitat quality has been demonstrated in other primate (*Colobus vellerosus*: Wong and Sicotte, 2007; *Macaca fuscata*: Maruhashi et al., 1998), as well as non-primate species (*Capreolus capreolus*: Tufto et al., 1996; *Ursus arctos*: McLoughlin et al., 2000; *Sceloporus jarrovi*: Simon, 1975; *Paradoxurus hermaphroditus*: Joshi et al., 1995). In addition, long daily travel distance has been linked to a patchy and unpredictable distribution of food resources within a habitat (Altmann and Muruthi, 1988; Barton et al., 1992; Yamagiwa and Mwanza, 1994; Gillespie and Chapman, 2001).

Ranging and activity patterns also varied within the study sites, which may point to heterogeneity in habitat quality within the fragments (Kadmon, 1993; Didham et al., 1998; Tews et al., 2004; Kadmon and Allouche, 2007). At Anja, AL occupied a smaller home range and exhibited a more concentrated core activity than that of AB, particularly in the wet season. The range of AL consisted of a disproportionately high concentration of *M. azedarach* and *P. cattleianum* compared with other areas of the forest. It also borders the fragment edge and the group frequently exploited resources from the village gardens and man-made lake adjacent the reserve. I found that *L. catta* in AL also spent more time terrestrially than AB, regularly traveling on the ground and feeding on fallen fruits, likely due to the fact that they are highly habituated to tourist exposure. In contrast, AB occupied a region of the fragment that had limited access to introduced and anthropogenic resources, and *L. catta* primarily fed arboreally (see also Chapter 3). The fact that AL correspondingly spent less time foraging and more time engaging in social behaviours when compared with AB, suggests that these novel resources were potentially of high nutritional quality (Clarke et al., 2002; Li and Rogers, 2005; Wong and Sicotte, 2007). This is further supported by the fact that AB occasionally crossed the reserve to access *M. azedarach* and *P. cattleianum* outside of their territory. Additionally, despite utilizing a smaller area of the fragment, AL traveled more and had higher energy expenditure than AB, which may result from a higher caloric intake (Stephens and Krebs, 1986; Marshall and Wrangham, 2007). Nutritional analyses would greatly enhance comparisons with respect to within-site variation in resource quality.

At Tsaranoro, both TR and TM were frequently observed outside of the fragment; however, the utilization distribution of the two groups varied greatly with respect to matrix use. TM concentrated nearly all of its activity in the rocky savannah surrounding the forest, traveling terrestrially and feeding on small shrubs and patchily distributed fruit trees (Gabriel, unpublished data), while TR spent large portions of time within the canopy of the forest interior. For primates, flexibility for traveling and foraging in the matrix, often in highly diverse vegetation, is one characteristic that promotes species viability in fragmented landscapes (e.g., Naughton-Treves, 1998; Cowlishaw and Dunbar, 2000; Anderson et al., 2007; Pozo-Montuy and Serio-Silva, 2007; Kelley, 2012). *L. catta* at Tsaranoro may be exhibiting a type of dietary niche separation in order to optimize foraging efficiency in a heterogeneous landscape, while minimizing intergroup competition. This flexibility for matrix use may sustain population numbers of *L. catta* by providing an additional foraging habitat, thus greatly increasing the usable area of the fragment (Anderson et al., 2007).

Finally, the fact that at Anja overall energy expenditure for *L. catta* was lower than at Tsaranoro may point to the potential fitness benefits associated with occupying a high quality fragment (Bernstein et al., 1991; Pulliam, 2000). In habitats of higher quality, less energy is required for resource procurement and more energy can be allocated to survival and reproduction (Lee and Hauser, 1998; Godfrey, 2003; Johnson, 2007). Territory quality has been similarly linked to fitness in vervet monkeys (*Cercopithecus aethiops*) in disturbed landscapes (Lee and Hauser, 1998). Since favourable habitats are more likely to sustain population numbers over time (Godfrey, 2003), selection of high quality habitat can have important consequences for species viability in fragmented landscapes. *L. catta*'s ecological flexibility and capacity for using anthropogenic landscapes enables it to persist in a wide range of disturbed habitats (Sauther et al., 2006; Gemmill and Gould, 2008; LaFleur and Gould, 2009; Kelley, 2011). However, given the intensification of habitat loss and fragmentation throughout Madagascar (Harper et al., 2007; Ganzhorn et al., 2008), and the lack of longitudinal studies on the response of *L. catta* to habitat disturbance, the long-term viability of *L. catta* populations in forest fragments remains uncertain. In many areas, including the Tsaranoro forest, selective logging continues within fragments, creating extended survival pressures for resident populations (i.e., for resource procurement, shelter, predator protection). I suggest that monitoring intraspecific variation in habitat use and activity patterns can provide important information regarding the sensitivity of *L. catta* populations to fragmentation and is therefore a useful consideration for the regional conservation of this species.

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3 *LEMUR CATTA* IN FRAGMENTED FORESTS: FEEDING ECOLOGY

3.1 Abstract

Fragmentation affects the vegetative composition of habitats, thus altering the resources available for fragment-dwelling primate populations. Studies suggest that primates that display dietary flexibility and are able to rely on critical fallback foods in resource-scarce conditions will be more likely to persist in forest fragments. However, comparisons of dietary shifts in populations inhabiting fragments differing in resource structure (i.e., loss of native food species, presence of anthropogenic and introduced resources) remain rare. In this chapter, I examine the feeding ecology of two populations of ring-tailed lemurs (*Lemur catta*) occupying mixed vegetation, rocky outcrop forest fragments in Madagascar's south-central highlands, to investigate dietary shifts related to forest fragmentation in an ecologically flexible species. The *L. catta* populations varied in dietary diversity, seasonal diversity of food species and types consumed, and reliance on fallback foods in place of preferred food resources. The results reveal considerable intraspecific variation in diet associated with differences in the resource structure of the two fragments, which may be indicative of discrepancies in the nutritional quality of food items present in these habitats. I discuss this variation with respect to the capacity of fragments to support viable populations of *L. catta* over time and the importance of monitoring dietary shifts for species conservation.

3.2 Introduction

The process of habitat fragmentation may affect the presence, abundance, distribution and/or phenology of food resources as a result of: 1) abiotic effects related to fragmentation (e.g., exposure to sun, wind, water; altered micronutrients) that alter the composition and distribution of plant species at habitat edges (Laurance et al., 1998), particularly with respect to fruit-bearing species; 2) anthropogenic resource extraction, which may remove native tree species from the forest interior and surrounding matrix (Medley, 1993); and 3) the introduction and establishment of exotic or invasive plant species (Myers, 1983; Luken 1988; Harrington et al., 1989; Huenneke and Vitousek, 1990; Woods, 1993; Brown and Gurevitch, 2004; Theoharides and Dukes, 2007). Such changes to vegetative composition have corresponding impacts on primate diets (Irwin, 2008). Since alterations in diet can impact many facets of a species' ecology, including ranging behaviour (Cristobal-Azkarate and Arroyo-Rodriguez, 2007), demography (Coelho et al., 1976; Chapman and Chapman, 1999), sociality (Barton et al., 1996), reproduction (Sauther, 1998), and health (Chapman et al., 2005; Milton, 1996; Irwin, 2008), understanding the nature of dietary shifts in fragment-dwelling populations is of primary concern for species conservation (Irwin, 2008; Chapman et al., 2000; Fairgrieve and Muhumuza, 2003).

One of the critical variables impacting a primate species' success in fragmented habitats is its degree of dietary flexibility (Colishaw and Dunbar, 2000). Primates that are able to feed from many different plant species (Onderdonk and Chapman, 2000; Crockett, 1998; Pinto et al., 2003; Rivera and Calme, 2006; Silver and Marsh, 2003), incorporate various plant types into the diet (Asensio et al., 2007; Juan et al., 2000; Rodriguez-Luna et al., 2003), and consume novel or introduced food types (Bicca-Marques and Calegaro-Marques, 1994; Onderdonk and Chapman, 2000; Mbora and Meikle, 2004), are likely to show increased viability and longevity in disturbed habitats. For example, black howler monkeys (*Alouatta pigra*) in continuous forest may devote up to half of their feeding time to a single *Ficus* species, whereas fragment-dwelling populations consume a greater number of plant species, dedicating less time to each (Rivera and Calme, 2006). When compared to continuous forest populations, lion-tailed macaques (*Macaca silenus*) in fragments consume more flowers and introduced species and less fruit and insects (Umapathy and Kumar, 2000). Fragment-dwelling moustached guenons (*Cercopithecus cephus*) consume a lower proportion of fruits, seeds, and flowers from various plant species, and a higher proportion of insects and leaves (Tutin, 1999), and black-and-white colobus (*Colobus guereza*) populations in forest fragments shift their diet to include vegetative species rarely consumed in continuous forest, although the plant parts consumed (leaves, fruit, and lichens) were similar in each (Onderdonk and Chapman, 2000).

In addition, populations in disturbed habitats are often limited by the relative abundance of fallback foods (McKey, 1978; Irwin, 2008). Fallback foods are items of high abundance but relatively low nutritional quality, and are utilized when preferred foods become scarce or unavailable (Hanya, 2004; Laden and Wrangham, 2005; Yamakoshi, 2004; Marshall and Wrangham, 2007). Fallback foods can be further divided into two distinct classifications: staple and filler fallback foods (Marshall and Wrangham, 2007). Staple fallback foods are consumed year-round, are uniformly distributed, and seasonally may constitute nearly 100% of the diet in the absence of preferred foods. In contrast, filler fallback foods are utilized seasonally, are patchily distributed, and are never consumed exclusively (Marshall and Wrangham, 2007). Fallback foods have great relevance in primate population dynamics, particularly in fragmented habitats, since they can dictate survival during times of food scarcity (Kawecki, 1995; Robinson and Wilson, 1998) and are, therefore, considered paramount in shaping the physiology, socioecology, and behaviour of a wide variety of primate species (e.g., Bauchop, 1971; Chivers and Hladik, 1984; Tutin et al., 1991; Steenbeek and van Schaik, 2001; Lambert et al., 2004; Marshall and Wrangham, 2007).

Ring-tailed lemurs (*Lemur catta*) are a flagship species for assessing the impacts of habitat loss and fragmentation on the lemurs of Madagascar, since they are international symbols for the island's unique biodiversity. *L. catta* is an ecologically flexible species, occupying a wide range of habitat types throughout south, south-central, and southwestern Madagascar (Tattersall, 1982; Sussman, 1974; Jolly, 2003; Goodman et al., 2006), including gallery, dry deciduous, and spiny forests, spiny bush, and high-altitude ericoid bush and rocky outcrop ('rupiculous') vegetation (Sauther et al., 1999; Goodman et al., 2006; Gould, 2006; Kelley, 2011; LaFleur, 2012). However, the large continuous forest that once expanded much of this species' geographical range is rapidly disappearing due to anthropogenic forces (e.g., logging, agricultural development, land clearing for cattle grazing) and populations of *L. catta* are now largely restricted to isolated forest fragments, with marked changes in demography and behaviour reported in highly disturbed habitats (Sussman et al., 2003; Sauther et al., 2006; Gemmill and Gould, 2008; Gabriel, 2013; Chapter 2).

L. catta is an opportunistic frugivore/folivore, which feeds on a wide variety of plant species and food types, including ripe and unripe fruits, young and mature leaves, leaf stems, flowers, flower stems, insects, and soil (Sauther et al., 1999; Jolly, 1966; Sussman, 1972, 1974; Budnitz and Dainis, 1975; Rasamimanana and Rafidinarivo, 1993; Sauther, 1993, 1998; Yamashita, 2002; Simmen et al., 2003, 2006; Soma, 2006; Gould et al., 2011). In gallery forest, *L. catta* denotes 30 to 60% of its feeding budget to fruit, 30 to 51% to leaves/herbs, 5 to 12% to flowers, and less than 5% on insects (Sauther et al., 1999; Soma, 2006); however, *L. catta* feeding behaviour may vary substantially based on habitat type, season and reproductive state (Budnitz, 1978; Sussman, 1991; Sauther, 1994, 1998; Sauther et al., 1999; Simmens et al., 2006; Gould et al., 2011; Kelley, 2011; LaFleur, 2012). Yet despite exhibiting considerable dietary flexibility, *L. catta* is heavily reliant on the availability of key seasonal resources throughout the annual cycle, and reproduction is timed to coincide with peaks of important food types (Sauther, 1998). For example, in gallery forest, *L. catta* are highly dependent on *Tamarindus indica* due to its asynchronous production of young leaves, flowers, and fruits throughout the annual cycle (Jolly, 1966; Rasamimanana and Rafidinarivo, 1993; Sauther, 1998; Mertl-Millhollen et al., 2003; Simmen et al., 2006). Similarly, in the dry spiny forest at Cap. Sainte Marie in Madagascar's far south, *L. catta* relies heavily on the fruits of the invasive *Opuntia* tree (Kelley, 2011). Indirect evidence points to the critical nature of such resources in *L. catta* fitness and survival – a severe drought in 1991 and 1992 that substantially reduced the availability of primary food resources at Beza Mahafaly Reserve in southern Madagascar resulted in drastic female and infant mortality in the drought and post-drought years

(Gould et al., 1999, 2003). Thus, the loss of any key species from within a habitat could critically impact *L. catta* population survival (Sauther, 1998; Gould et al., 2011).

It is suggested that Madagascar's highly seasonal and erratic climate (high intra- and inter-annual rainfall variability; frequent cyclones; drought) (Dewar and Richard, 2007) has led to the evolution of life history strategies among lemurs geared toward conserving energy, especially during times of high reproductive demands and low seasonal food availability ('The Energy Conservation Hypothesis') (Wright, 1999). Adaptive traits exhibited by *L. catta* include those that minimize energy expenditure (e.g., sperm competition, seasonal breeding, low quality milk production) and those that maximize energy intake (e.g., territoriality, female dominance, weaning synchrony) (Wright, 1999). These strategies facilitate the maximal intake of nutritional resources as they become seasonally available, particularly for lactating females and weaning infants, such that *L. catta* can cope with the energetic stress brought on by Madagascar's harsh ecology (Jolly, 1966; 1984; Richard, 1987; Young et al., 1990; Wright, 1999; Dewar and Richard, 2007). Habitat disturbance can significantly alter the native vegetative composition of a habitat, introducing novel ecological pressures and resource conditions, and the strategies employed to cope with such changes are likely to vary considerably between populations of *L. catta* based on the unique energetic constraints with which each population is faced.

While several studies have examined the feeding ecology of primate species occupying forest fragments in comparison to larger, continuous forest tracts (e.g., Rivera and Calme, 2006; Fairgrieve and Muhumuza, 2003; Umapathy and Kumar, 2000; Tutin, 1999; Onderdonk and Chapman, 2000; Irwin, 2008), to date, few have investigated intraspecific dietary shifts given unique changes to vegetative composition in different forest fragments. In addition, while the diet of *L. catta* is well documented in gallery and dry deciduous forest habitats (Sauther, 1994, 1998; Simmen et al., 2006; Gould, 2006), research has only begun to shed light on *L. catta*'s dietary flexibility in other habitat types (Gould et al., 2011; Kelley et al., 2012, LaFleur, 2012). In this chapter, I examine the feeding ecology of two populations of *L. catta* inhabiting rocky outcrop forest fragments of Madagascar's south-central highlands. Both fragments contain a mixture of endemic and introduced species consisting of xerophytic and deciduous vegetation. However, they differ considerably in vegetative structure due to unique fragmentation histories (i.e., degree of selective logging, type of matrix habitat, presence of anthropogenic and introduced resources) and the population densities of *L. catta* at the two sites differ markedly. Anja Special Reserve features a matrix of anthropogenic resources (i.e., village gardens and a small man-made lake), and, following the selective logging of many of the large, native fruit trees, the interior of the forest has been heavily re-established by introduced alternatives (e.g., *Melia azedarach* and *Psidium cattleianum*). This fragment supports a population density of *L. catta* (6.6 lemurs/ha) that is higher than at any other site in which the species has been studied (e.g., Beza Mahafaly gallery and dry forest: Sussman, 1991; Gould et al., 2003; Berenty gallery, scrub and spiny forest: Jolly et al., 2002; Pride, 2005a,b,c; Gould et al., 2011; Cap Sainte Marie spiny bush: Kelley, 2011; Tsimanampetsotsa spiny forest: LaFleur, 2012). In comparison, the landscape surrounding the Tsaranoro Valley sacred forests is dominated by grassy savannah, and, as with Anja, many of the native tree species have been removed within and around the fragment due to decades of selective logging. However, this fragment features only a patchy distribution of introduced and anthropogenic resources that are largely scattered throughout the matrix, and the population density of *L. catta* is only one sixth that at Anja (1.13 lemurs/ha) (Cameron and Gould, 2013)

As population density may be substantially influenced by food resource abundance (Chapman and Chapman, 1999) and dietary quality (Milton, 1984, 1993; Terborgh, 1986; Chapman and Fedigan, 1990; Oates et al., 1990; Cristobal-Azkarate and Arroyo-Rodriguez, 2007), I tested the following predictions:

1) Since selection of dietary items is largely dependent on the quality of food sources (Wrangham et al., 1998; Markkola et al., 2003), I predict that the difference in population density between the two fragments is reflective of variation in the plant species and food types that are available to *L. catta*. Therefore, it is expected that the type of food species consumed will vary between fragments, with the Anja lemurs consuming a greater proportion of introduced and anthropogenic resources in place of native species when compared with the Tsaranoro population.
2) Given that the climate in southern Madagascar fluctuates between a distinct hot, wet period (November to April) and a cool, dry period (May to October) (Jolly, 1966; Jolly et al., 2006), I predict that the diet of *L. catta* at the two study sites will vary across reproductive periods according to the seasonal availability of food items. In addition, since *L. catta* reproduction is heavily dictated by the phenology of key food resources (Sauther, 1998), the relative proportions of food items consumed (i.e., fruit, leaves, flowers) should differ for reproductive females when compared with males and non-reproductive females, with reproductive

females consuming higher proportions of energy and protein-rich foods (e.g., young leaves) (Sauther, 1994; Sauther et al., 1999; Gould et al., 2011).

3) Since fragmentation results in shifts in the vegetative composition of forests and the potential loss of preferred food species (Medley, 1983; Laurance et al., 1998), I predict that the diets of *L. catta* in the study fragments will include critical fallback foods that are available in times of relative food scarcity (McKey, 1978; Kawecki, 1995; Robinson and Wilson, 1998; Irwin, 2008).

3.3 Methods

Study sites – Anja Special Reserve and the Tsaranoro Valley sacred forest are located in the Fianarantsoa province of Madagascar's central plateau. This region is separated from the eastern rainforests by the Ankaratra massif mountain chain, which runs south from Antananarivo and reaches a maximum elevation of 2642 m above sea level. Vegetation is comprised of southern dry-adapted plants (e.g., *Aloe, Euphorbia*, *Pachypodium, Kalanchoe*) mixed with temperate species of the high plateau (e.g., *Podocarpus madagascariensis*, *Weinmannia* spp., *Pandanus* spp., *Symphonia* spp.). Anja is a 34 ha granite outcrop forest fragment surrounded by an anthropogenic matrix of village gardens and grassy savannah. It is located <400 m from the heavily traveled Route Nationale 7 highway, 12 km S of the town of Ambalavao (21° 51' S latitude and 046° 50' E longitude). Following decades of extensive land clearing and selective logging in the area surrounding the reserve, Anja was established as a community run ecotourism venture in 1999 (Razafimandimby, pers. comm.; http://anjacommunityreserve.netai.net/anja.htm). Prior to gaining its protected status, many of the large, native trees (e.g., *Adansonia* and *Ficus* spp.) were removed from the forest perimeter for maize production, and introduced tree species, *Melia azedarach* and *Psidium cattleianum*, were planted for shade and fruit cultivation (Razafimandimby, pers. comm.). *M. azedarach* is native to Asia and Australia and became naturalized in Madagascar in the 20th century for use as fuelwood and timber and as an ornamental shade tree (Razafimandimby, pers. comm.). *M. azedarach* grows rapidly (up to 4m in 30 months), can reach 40 m in height (Dharani et al., 2010), and thrives in disturbed areas lacking primary forest canopy (Godfrey, 1988). It produces an abundance of small fruit clusters (each fruit is approximately 1.5 cm in diameter) that are long-maturing and remain intact after leaf fall (Dharani et al., 2010). The fruits are toxic in large amounts (Huang et al., 1995; Hare, 1998; Phua et al., 2008); however, for birds and mammals that can tolerate their consumption (Corlett, 2005), they provide a good source of carbohydrates (Italo et al., 2009). *P. cattleianum*, native to South America, is a highly invasive species in tropical forests, frequently outcompeting natural vegetation and capable of establishing in both disturbed areas and intact forests (Huenneke and Vitousek, 1990). It produces large, juicy fruits in the austral summer months (December to April in southern Madagascar), which are consumed by a wide range of bird and mammalian species (Huenneke and Vitousek, 1990) and may also be eaten by humans. *M. azedarach* and *P. cattleianum* have become heavily established within and surrounding the Anja fragment and now constitute an estimated 75% of the forest canopy in certain areas of the reserve (Gabriel, unpublished data).

The Tsaranoro Valley sacred forest lies at the base of the 1650m Karambony mountain massif, 55 km SW of Ambalavao and 20km east of Andringitra National Park (22° 05’ S latitude and 046° 46’ E longitude). Land clearing is pronounced in the valley, largely due to nearly a century of slash and burn agriculture, rice cultivation, and cattle grazing. One of only a few forest fragments that remains in the area, Tsaranoro is protected as sacred land due to the cultural traditions of the local peoples (the forest houses ancentral Betsileo tombs), and all resource extraction from within the fragment bounds is regulated and approved by the valley king (Andrianomena, pers. comm.). The matrix surrounding the fragment consists primarily of open, grassy savannah, as well as a few rice paddies and agricultural crops used by people from the small village nearby. Three camps, established for adventure tourism, are also located in close proximity (within 1 km) to the forest. As with Anja, selective logging has removed many of the native trees within and surrounding the fragment (e.g., *Adansonia* and *Ficus* spp.; Andrianomena pers. comm.), and while a few patches of introduced fruit trees (e.g., *Mangifera indica*, *M. azedarach*, *P. cattleianum*) can be found throughout the matrix, these species have not become widespread in the landscape. Endemic species found within the forest that are used as lemur food items include *Turraea serica, Adina microcephala, Diospyros* and *Dombeya* spp.

Data collection – The Anja fragment contains approximately 225 *L. catta* in 13 groups (Cameron and Gould, 2013). The population of *L. catta* at Tsaranoro consists of approximately 60 *L. catta* in 6 groups. Two groups of *L. catta* were studied at each of the two sites during the late dry season (early September to late November) of 2010 and mid- to late- wet season (early March to late May) of 2011. Each group was composed of 16-17 individuals including adults, juveniles, and infants. Group composition is displayed in Table 3.1. During the hours of 0700 to 1700 daily, myself and field assistants, R. Simmons and I. Schneider-Crease, followed each group in consecutive four-day blocks, rotating between sites every three weeks, for a total of 16 days/group/study period.

Feeding data were collected using continuous-time focal animal sampling of ten- minutes duration (Altmann, 1974), with all adult males and females included in focal observation (11-13 indiviudals/study group). Identification of focal individuals was achieved using characteristic markings (e.g., eye-ring shape, tail shape/size, body colouring) and/or physical injuries and abnormalities (e.g., deformed limb growth, loss of an eye, large scarring), and individuals could be recognized from at least 25 m using binoculars.

Table 3.1 Group composition, male dispersal/immigration and number of focal animals in each study group

Group	**Composition**	**# of dispersing/immigrant males**	**# of focal animals**
Anja			
AL	5F, 8M, 3J, 3I	0/0	13
AB	6F, 6M, 4J, 5I	0/1	12
Tsaranoro			
TR	6F, 7M, 3J, 5I	3/1	13(11)*
TM	5F, 6M, 5J, 2I	0/1	11(12)*

Parentheses denote the number of focal animals following the male dispersal period. One male from TR emigrated to TM between study months and was included in the focal sessions of TM for the remainder of the study period.

I defined a ‘feeding bout’ as the duration from when a focal animal began ingesting food items to when the animal terminated feeding and engaged in another behaviour (e.g., rest, locomote, groom, aggression). A new bout was recorded if ingestion of food items resumed. Rotating between sexes and all individuals in the group, focal sessions included noting the duration of all feeding bouts, the food type (leaves, fruit, flowers, buds, stems, insects, soil) and species consumed, and the location of the feeding bout (i.e., arboreal vs. terrestrial). With the help of trained, local Malagasy guides, attempts were made to identify the scientific names of all plant species consumed. When scientific species could not be determined, Malagasy vernacular names were used. In addition, the duration of all bouts of resting behaviour were recorded. A total of 685 h of focal animal data were collected throughout the duration of the study, 182 h of which were dedicated to feeding – 35.5 h from Lake group (AL) and 40 h from Boulder group (AB) at Anja, and 60.5 h from Rangers group (TR) and 46 h from Meva group (TM) at Tsaranoro.

***Statistical analysis* –** The number of plant species consumed by *L. catta* was tallied for each site over the study duration and across reproductive periods, with the dry season being comprised of the early lactation (03-Sep-10 to 15-Oct-10) and late lactation (17-Oct-10 to 24-Nov-10) periods and the wet season being comprised of the pre-mating (10-Mar-11 to 04-Apr-11), mating (05-Apr-11 to 02-May-11), and post-mating periods (04-May-11 to 27-May-11). In addition, the proportion of time in all feeding bouts spent foraging on each food type (leaves, fruit, flowers, buds, stems, insects, soil) was determined for each focal animal and averaged by site and by sex throughout the study, as well as across reproductive periods. Finally, the percentage of total feeding time spent arboreally and terrestrially was calculated for each individual and averaged across study groups.

Between-site differences (N=49 individuals) in the number of plant species consumed, the location of feeding bouts, and the proportion of time in feeding bouts spent engaging in geophagy were determined using nested ANOVAs to control for group effects. When a significant group effect was found, one-way ANOVAs followed by TukeyHSD post-hoc tests were used to determine differences in the variables according to group. To determine if there was a seasonal effect on the number of plant species consumed at each site (N=24 and 25 individuals), a within-subject repeated measures ANOVA was used, followed by paired t-tests to examine differences in each pair of reproductive periods separately. The number of species consumed per season was log transformed for statistical tests to meet the assumptions of normality. T-tests were used to determine differences in food types consumed between sites (N=49 individuals). Lastly, matched pairs Mann-Whitney U tests were used to examine differences in seasonal food types consumed within each site according to sex (N=11-14 individuals), as well as to determine seasonal differences in the amount of time spent resting and feeding at each site according to sex (N=11-14 individuals). For all statistical tests, the threshold of significance was set at $P<0.05$. Standard error is the given measure of variability.

3.4 Results

Total number of plant species consumed – Overall, *L. catta* at Tsaranoro consumed a greater number of plant species when compared with those at Anja (32 vs. 24 species). A list of all plant species and plant parts consumed is presented in Tables 3.2 (Anja) and 3.3 (Tsaranoro).

Table 3.2 List of the plants consumed by *L. catta* at Anja Special Reserve in the late dry season (September to November) of 2010 and mid-late wet season (March to May) of 2011

Scientific Name (Family)	**Vernacular (or common) Name**	**Plant Part**
*Adina microcephala** (Rubiaceae)	Soaravy, Sohihy	l
Albizia spp. (Fabaceae)	Sambalahy	l
Barringtonia racemosa (Lecythidaceae)	Manandrondro, Manondro, Menandrano	fr
Capparis spp. (Capparaceae)	Roy	fr
Capsicum spp. (Solanaceae)	Sakay	l
Carissa spinarum (Apocynaceae)	Fantsimbala	fr
Cerastium africanum (Caryophyllaceae)	Tsivandrenikely	

*Erythroxylum platycladum** (Erythroxylaceae)	Menahihy	fr
Ficus spp. (Moraceae)	Abado, Carica, Hopy, Nononka	b, fr, l
*Gaertnera arenaria** (Rubiaceae)	Tanatananala	b
Grewia spp. (Malvaceae)	Sely	fr
*Harungana madagascariensis** (Hypericaceae)	Tambihitse	fr
Justicia gendarussa (Acanthaceae)	Dinga dinga	l
Liana	Kisira	fl, l
Melia azedarach (Meliaceae)	Melia	fr, l
Passiflora incarnata (Passifloraceae)	Passiflora	fr, l
Psidium cattleianum (Myrtaceae)	Guava	fr
*Saldinia littoralis** (Rubiaceae)	Voamasandreniolo	
Solanum lycopersicum (Solanaceae)	Tomato	fr
*Turraea sericea** (Meliaceae)	Lafara	fr
Unknown	Hidy	b, fr, l
Unknown	Kasoa Mena	fr
Unknown	Komoay	
Unknown	Mamatsikariva	fr
Unknown	Ombianty	l
Unknown	Tsara	l
Unknown	Vahatonara	

l = leaves; fl = flowers; fr = fruit; b = buds; s = stems; '*' = endemic or native to Madagascar
In cases where guides could only provide vernacular names of plants, scientific identification was achieved through reference to Randriatafika and Rabenantoandro (2008), the Missouri Botanical Garden catalogue of Madagascar flora (www.mobot.org/MOBOT/Madagasc) and the Catalogue of the Vascular Plants of Madagascar (http://www.tropicos.org)
Malagasy vernacular names are listed in isolation when scientific identification of species could not be made

Table 3.3 List of the plants consumed by *L. catta* at the Tsaranoro Valley forest in the late dry season (September to November) of 2010 and mid-late wet season (March to May) of 2011

Scientific Name (Family)	**Vernacular (or common) Name**	**Plant Part**
*Adina microcephala** (Rubiaceae)	Soaravy, Sohihy	l
Albizia spp. (Fabaceae)	Sambalahy	fl, fr
*Anisophyllea fallax** (Anisophylleaceae)	Hazomasy	fr
Aphloia theiformis (Apholiaceae)	Voafotsy	fr, l
Bremeria spp.* (Rubiaceae)	Fatora	b, fl, fr
*Buddleja madagascariensis** (Loganiaceae)	Sevafotsy	fl, fr
Diospyros spp.* (Ebenaceae)	Torovoka, Hazontaha, Hazomainty	fr

Dombeya spp.* (Malvaceae)	Selinala	s
_Erythroxylum platycladum_* (Erythroxylaceae)	Menahihy	fl, l
Ficus spp. (Moraceae)	Abado, Carica, Hopy, Nononka	b, fr
Grewia spp. (Malvaceae)	Sely	fr
_Harungana madagascariensis_* (Hypericaceae)	Tambihitse	fl, fr
Ilex spp. (Aquifoliaceae)	Hazondramo	fl
Kalanchoe spp. (Crassulaceae)	Kalanchoe	l
Liana	Kisira	fr, l
Mangifera indica (Anacardiaceae)	Mango	fr
Melia azedarach (Meliaceae)	Melia	b, fr, l
Mystroxylon aethiopicum (Celastraceae)	Vovona	fr
_Poupartia minor_* (Anacardiaceae)	Sakoa	fr
Psidium cattleianum (Myrtaceae)	Guava	fr
_Tricalysia cryptocalyx_* (Rubiaceae)	Hazonkira	fr
_Turraea sericea_* (Meliaceae)	Lafara, Mampisarak	b, fl, fr, l
Vepris elliottii (Rutaceae)	Ampoly	fl, fr
Unknown	Anakatsimba	fr
Unknown	Fandafika	fr
Unknown	Fanera	fl, fr
Unknown	Fopoho	fr
Unknown	Hazodrea	fr
Unknown	Hidy	fl, fr, l
Unknown	Mena Tendro	fr
Unknown	Ombilaza	fl, fr

l = leaves; fl = flowers; fr = fruit; b = buds; s = stems; '*' = endemic or native to Madagascar
In cases where guides could only provide vernacular names of plants, scientific identification was achieved through reference to Randriatafika and Rabenantoandro (2008), the Missouri Botanical Garden catalogue of Madagascar flora (www.mobot.org/MOBOT/Madagasc) and the Catalogue of the Vascular Plants of Madagascar (http://www.tropicos.org)
Malagasy vernacular names are listed in isolation when scientific identification of species could not be made

I found a significant between-site difference in the mean number of plant species consumed by each individual over the study duration (nested ANOVA; F=96.55, df=1, *P*<0.0001; Figure 3.1A) and per reproductive period (nested ANOVA; F=115.61, df=1, *P*<0.0001; Figure 3.1B).

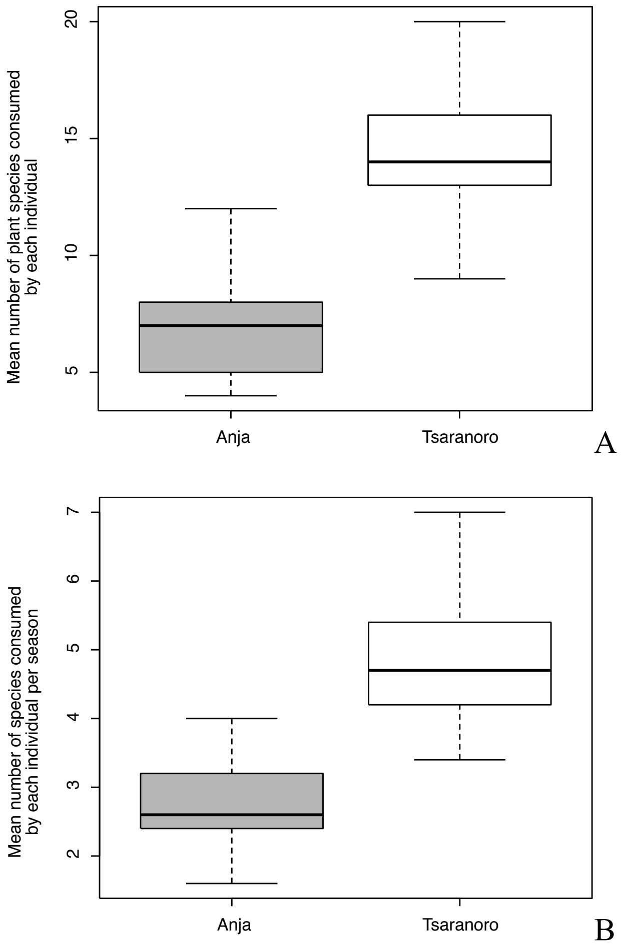


Figure 3.1 Comparison of the mean number of plant species consumed per individual by *L. catta* at Anja and Tsaranoro (N=49) over the study period (A) and per season (B). Y-error bars represent the range of data; boxes represent the upper (75%) and lower (25%) quartiles; bolded horizontal line represents the sample median.

There was also a seasonal effect on the mean number of plant species consumed per individual at each site (one-way ANOVA; F=5, df=4, *P*=0.001; Tsaranoro: F=10, df=4, *P*<0.0001; Table 3.4). *L. catta* at Anja consumed the highest number of plant species in the late lactation period when compared with all other reproductive periods, and also consumed a greater number of plant species in early lactation when compared to the mating period (Figure 3.2). At Tsaranoro, *L. catta* consumed the greatest number of plant species in the late lactation period and the lowest number of plant species in the mating period (Figure 3.2).

Table 3.4 Statistical comparison (Student's paired t-tests) of the mean number of plant species consumed per individual by *L. catta* at Anja and Tsaranoro across reproductive periods.

X	Late Lactation		Pre-Mating		Mating		Post-Mating	
	t	***P***	***t***	***P***	***t***	***P***	***t***	***P***
Anja								
Early Lact.	-3.7	**0.008**	2.3	0.11	3.1	**0.03**	4.6	0.82
Late Lact.		---	7.7	**0.000**	6.0	**0.000**	0.6	**0.001**
Pre-Mating				---	0.8	0.82	-1.7	0.27
Mating						---	-2.6	0.09
Post-Mating								---
Tsaranoro								
Early Lact.	-5.1	**0.000**	3.6	**0.005**	8.9	**0.000**	3.0	**0.01**
Late Lact.		---	7.3	**0.000**	14.3	**0.000**	6.5	**0.000**
Pre-Mating				---	7.1	**0.000**	-1.0	0.33
Mating						---	-8.5	**0.000**
Post-Mating								---

Bolded values represent statistical significance ($P<0.05$)

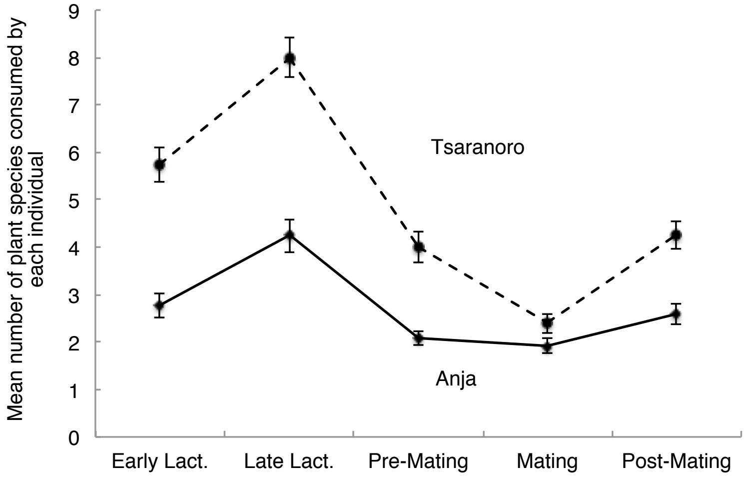


Figure 3.2 Seasonal comparison of the number of plant species (mean ± SE) consumed per individual by *L. catta* at Anja (N=25) and Tsaranoro (N=24) across reproductive periods.

At Anja, 65.84% of all feeding bouts were comprised of the top three most frequently consumed plant species: *Melia azedarach* – 41.29%, *Ficus* spp. – 12.69%, *Psidium cattleianum* – 11.86%. Each of the other plant species consumed contributed to less than 3% of the total feeding budget. Examining reproductive periods separately, *M. azedarach* was the most frequently consumed plant species in all seasons, making up between 30.32 and 51.86% of feeding bouts, with the exception of the mating season during which an equal proportion of the feeding budget was dedicated to both *M. azedarach* and *P. cattleianum* (31.51%; Table 3.5). Consumption of *P. cattleianum* was highly seasonal, comprising the highest percentage of the feeding budget during the pre-mating (28.7%) and mating (31.5%) periods (Table 3.5). Feeding time for *P. cattleianum* also varied by group: AL dedicated up to 53% of its feeding budget to *P. cattleianum* seasonally, while AB spent a maximum of 12.5% of its feeding time consuming fruits of this species. Consumption of *Ficus* spp. was also highly seasonal, comprising the greatest percentage of the feeding budget during the early lactation period (22.4%; Table 3.5), and varied by group: AL and AB spent a seasonal maximum of 10.1% and 47.4% of the feeding budget on *Ficus* spp. fruits, respectively.

At Tsaranoro, the top five most frequently consumed plant species constituted only 46.47% of total feeding bouts: *M. azedarach* – 15.78%, *Ficus* spp. – 9.58%, *Harungana madagascariensis* – 7.30%, *Tricalysia cryptocalyx* – 7.22%, *Grewia* spp. – 6.59%. At this site, dietary composition of *L. catta* groups was broad-based and highly seasonal; each species comprised less than 30% of the diet in a given season (Table 3.5). Feeding times for *M. azedarach* and *Ficus* spp. also varied by group: TM consumed *M.*

azedarach more frequently than TR (27.3 vs. 6.6%), and TR consumed *Ficus* spp. more frequently than TM (12.4 vs. 6.0%).

Table 3.5 List of the plant species most frequently consumed by *L. catta* at Anja and Tsaranoro according to reproductive period

	Early Lactation		Late Lactation		Pre-Mating		Mating		Post-Mating	
	Species	%	Species	%	Species	%	Species	%	Species	%
Anja	*M. azedarach* *Ficus* spp	**47** **22**	*M. azedarach* *Ficus* spp Mamatsikariva	**48** **20** **8**	*M. azedarach* *P. cattleianum* *Ficus* spp	**30** **29** **13**	*M. azedarach* *P. cattleianum*	**32** **32**	*M. azedarach* *P. cattleianum*	**52** **12**
Tsara	*M. azedarach* *H. madagasc.* *V. elliotti* *Ficus* spp. *T. cryptocalyx*	**22** **13** **12** **9** **9**	*M. azedarach* *T. cryptocalyx* *H. madagasc.* *Diospyros* spp. *Ficus* spp. *V. elliotti* *M. indica* *E. platycladum*	**15** **14** **12** **8** **7** **6** **6** **5**	*M. aethiopicum* *Ficus* spp. *P. cattleianum* *M. azedarach* *Grewia* spp. Liana Fandafika	**11** **10** **10** **9** **9** **7** **6**	*Grewia* spp. *P. cattleianum* Fandafika *M. azedarach*	**27** **14** **10** **7**	*Grewia* spp. *Ficus* spp. *M. azedarach* Fanera Liana *P. cattleianum*	**19** **17** **17** **12** **7** **6**

Values are rounded to the nearest percent. Full scientific names are listed in Table 3.1. Malagasy vernacular names (non-italicized) are given where scientific identity is unknown. Food items listed account for items that made up >5% of the feeding budget in each season

Proportion of food types consumed – At Anja, fruit and leaves comprised 87% of the overall feeding time of *L. catta* and less than 2% of feeding time was spent on flowers, stems, buds, and insects combined (Figure 3.3A). At Tsaranoro, fruit, leaves, and flowers comprised 91% of the overall feeding time of *L. catta* and less than 5% of feeding time was spent on soil, stems, buds, and insects combined (Figure 3.3B). *L. catta* at Anja spent a significantly greater percentage of their overall feeding time consuming leaves when compared to the Tsaranoro population (t-test; t=5.1, *P*<0.0001), whereas *L. catta* at Tsaranoro spent a greater percentage of time consuming fruit (t-test; t=-2.2, *P*=0.03) and flowers (t=-6.0, *P*<0.0001).

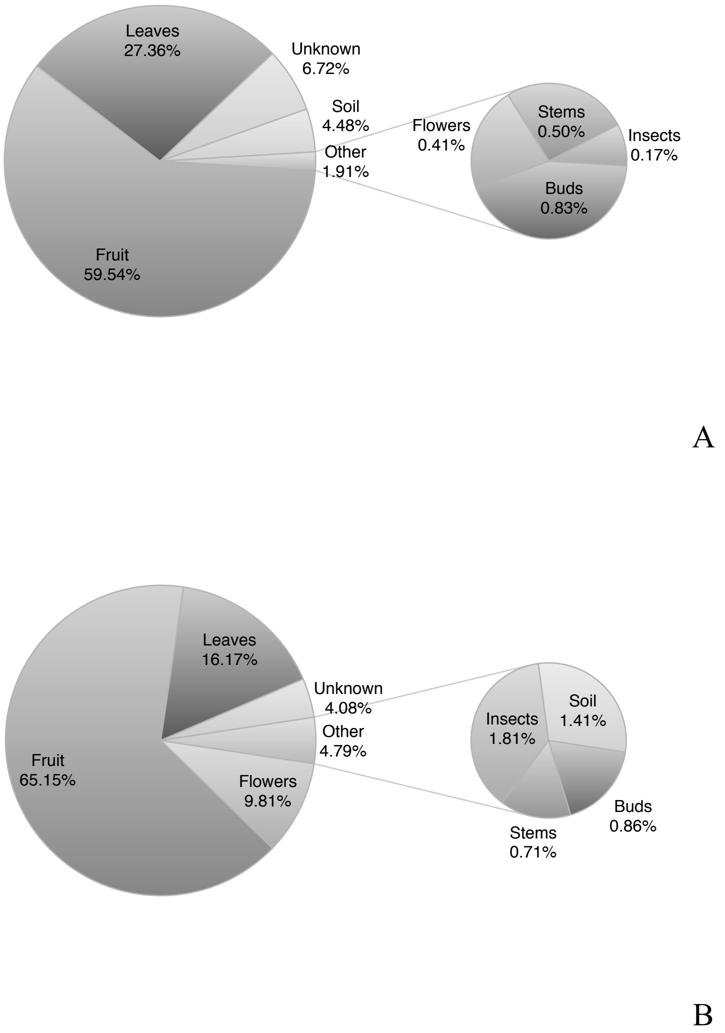
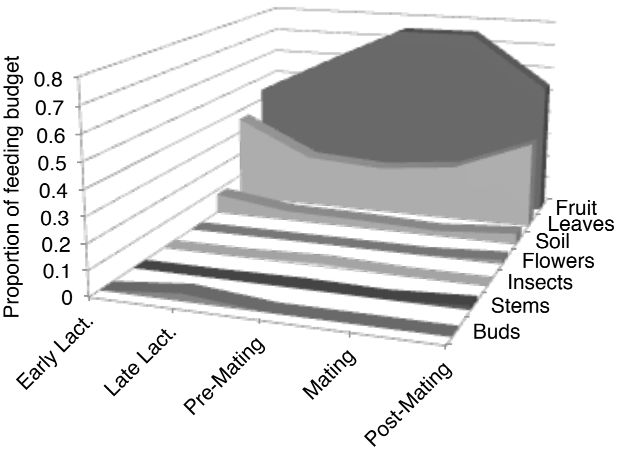
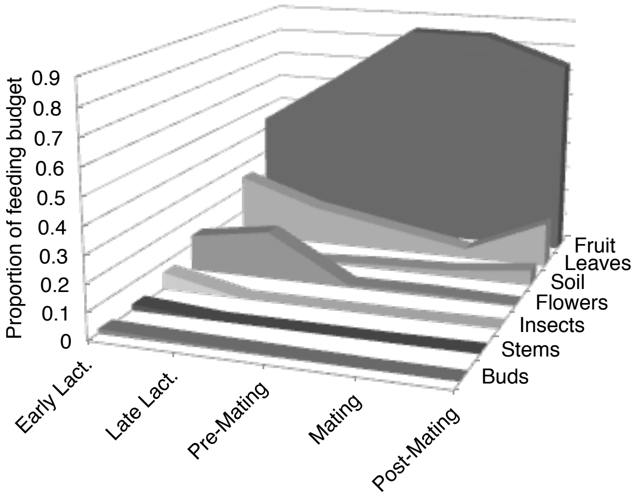


Figure 3.3 Comparison of the proportions of food types consumed by *L. catta* at Anja (A) and Tsaranoro (B) over the duration of the study.

At both sites, the percentage of time spent feeding on fruits varied across seasons (repeated measures ANOVA; F=2.34, df=4, *P*=0.05; Tsaranoro: F=8.5, df=4, *P*<0.0001; Figure 3.4A,B). *L. catta* spent a greater proportion of time feeding on fruits during the pre-mating and mating periods when compared with the other reproductive periods (Table 3.6). Overall, there was no seasonal effect on the proportion of time spent feeding on leaves (repeated measures ANOVA; Anja: F=1.5, df=4, *P*=0.20; Tsaranoro: F=1.88, df=4, *P*=0.12); however, the highest rates of leaf consumption corresponded with the lowest rates of fruit consumption by *L. catta* (Figure 3.4A,B).



A



B

Figure 3.4 Proportion of feeding time spent consuming various food types by *L. catta* at Anja (A) and Tsaranoro (B) across reproductive periods.

Table 3.6 Statistical comparison (Student's paired t-tests) of the percentage of time spent feeding on fruit by *L. catta* at Anja and Tsaranoro across reproductive periods.

X	Late Lactation		Pre-Mating		Mating		Post-Mating	
	t	***P***	***t***	***P***	***t***	***P***	***t***	***P***
Anja								
Early Lact.	-1.4	0.75	-4.0	**0.005**	-3.4	**0.02**	-0.9	1.0
Late Lact.		---	-2.8	0.06	-2.2	0.19	0.9	1.0
Pre-Mating				---	0.9	1.0	-1.7	**0.003**
Mating						---	4.2	**0.01**
Post-Mating								---
Tsaranoro								
Early Lact.	-4.4	**0.001**	-8.4	**0.000**	-8.0	**0.000**	-5.0	**0.000**
Late Lact.		---	-6.9	**0.000**	-4.9	**0.000**	-1.4	0.37
Pre-Mating				---	0.1	0.91	2.7	**0.05**
Mating						---	2.3	0.1
Post-Mating								---

Bolded values represent statistical significance

There were no sex differences in food types consumed across seasons, with the exception of females consuming a greater proportion of leaves than males at Tsaranoro in the post-mating period (mean = 0.22 ± 0.06 vs. 0.14 ± 0.03; Mann-Whitney U test; U=50, p=0.05). There were also no differences in food types consumed between lactating and non-lactating females at either site.

Resting and Foraging Behaviour – At Anja, there was no difference in the proportion of time spent feeding between the dry and the wet seasons (Mann Whitney U test with matched pairs; females: U=11, *P*=0.06; males: U=46, *P*=0.71); however, both sexes spent a greater proportion of the activity budget resting during the dry season (Mann Whitney

U test with matched pairs; females: U=6.2, *P*=0.007; males: U=88, *P*=0.02; Figure 3.5A). At Tsaranoro, females and males spent a greater proportion of time feeding during the dry season (Mann Whitney U test with matched pairs; females: U=64, *P*=0.003; males: U=77; *P*=0.001) and a greater proportion of time resting during the wet season (Mann Whitney U test with matched pairs; females: U=31, *P*=0.005; males: U=40, *P*=0.003; Figure 3.5B).

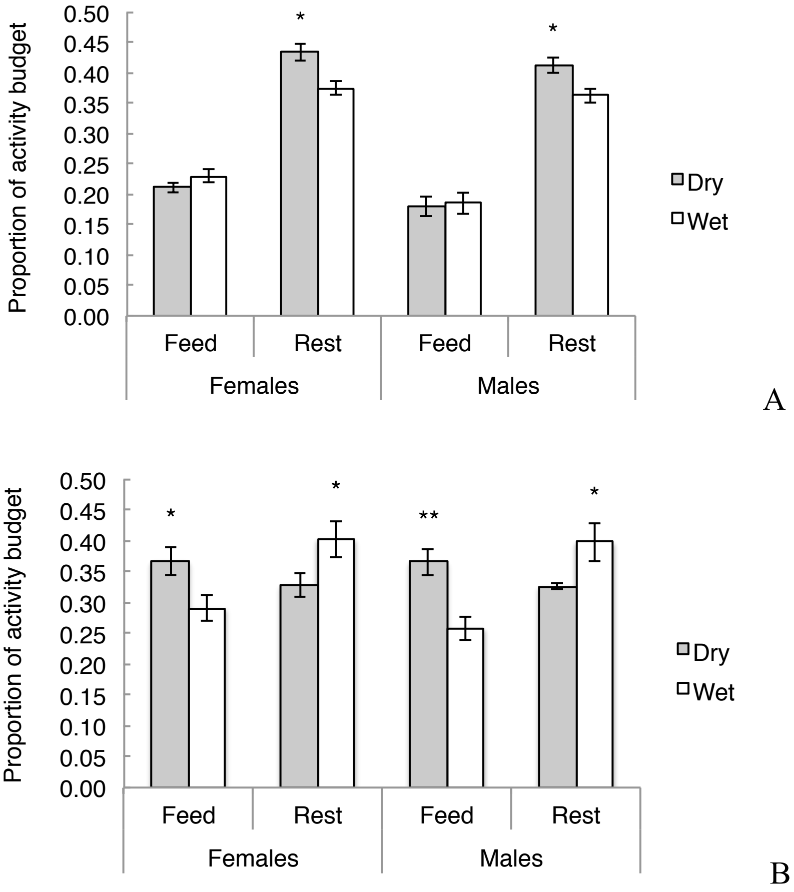


Figure 3.5 Comparison of the proportion of the activity budget (mean ± SE) spent feeding and resting by *L. catta* at Anja (A) and Tsaranoro (B) in the dry season of 2010 and wet season of 2011. Asterisks denote statistically significant differences (Mann Whitney U test with matched pairs; '**' *P*<0.001; '*' *P*<0.05)

Location of feeding bouts – The location of feeding bouts (i.e., arboreal vs. terrestrial) varied significantly both between (nested ANOVA; F=19.84, df=1, p<0.0001) and within sites (one-way ANOVA; F=29.91, df=3, p<0.0001). AL spent a greater proportion of time during feeding bouts feeding terrestrially when compared with all other groups (AL: 35%; AB: 11%; TR: 10%; TM: 20%; *P*<0.0001); however, AB did not differ in the proportion of time spent feeding terrestrially when compared with the Tsaranoro groups (AB vs. TR: *P*=0.97; AB vs. TM: *P*=0.06). The Tsaranoro groups also differed from each other (*P*=0.01), with TM spending more time feeding terrestrially compared with TR (Figure 3.6).

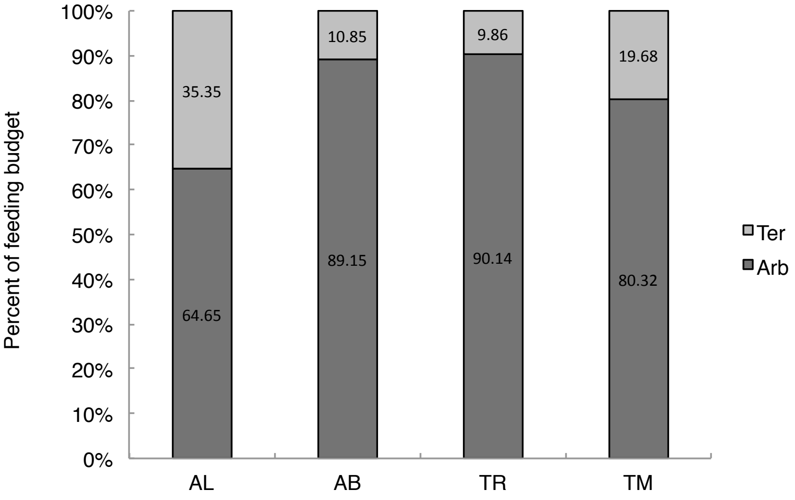


Figure 3.6 Proportion of overall feeding time spent feeding arboreally versus terrestrially for *L. catta* groups at Anja (AL and AB) and Tsaranoro (TR and TM) over the duration of the study period.

Geophagy – I found that the proportion of time in all feeding records spent engaging in geophagy varied by site (nested ANOVA; F=23.89, df=1, p<0.0001); however, there was also a significant group effect (nested ANOVA; F=22.63, df=3, p<0.0001). AL spent a greater proportion of the feeding budget engaging in geophagy when compared to all other groups (AL: 7%; AB: 1%; TR: 1%; TM: 2%; one-way ANOVA; *P*<0.0001); no other group differences were observed (AB vs. TR: *P*=0.97; AB vs. TM: *P*=0.96; TR vs. TM: *P*=0.79) (Figure 3.7).

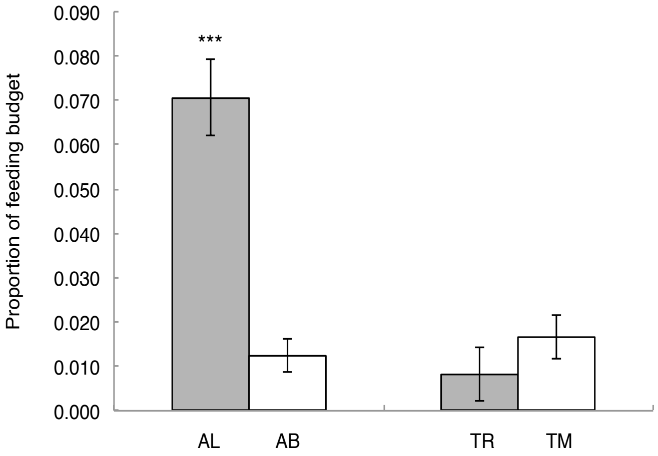


Figure 3.7 Between- and within-site comparison of the time spent engaging in geophagy (mean±SE) by *L. catta* groups at Anja (AL and AB) and Tsaranoro (TR and TM) over the duration of the study period. Asterisks denote statistically significant differences (one-way ANOVA; '***' *P*<0.0001).

3.5 Discussion

The diversity of food species consumed between the two study fragments supports the notion that *L. catta* exhibits a high degree of dietary flexibility compared with other diurnal lemurs (Sauther et al., 1999; Gould et al., 1999, 2003; Gould, 2006), which enables it to inhabit a wide range of habitat types and to persist in highly degraded areas (Goodman et al., 2006; Gemmill and Gould, 2008; LaFleur and Gould, 2009). However, the species diversity included in feeding bouts at both study sites is considerably less than what has been reported in other habitat types in which *L. catta* reside. For example, in gallery forest at Beza Mahafaly Reserve, *L. catta* consume an average of 61 food species annually (Sauther, 1998; Simmen et al., 2006), and similar diversity has been observed in spiny bush (Cap Sainte Marie: Kelley, 2011) and spiny forest (Tsimanampetsotsa National Park: LaFleur, 2012) habitats in the far south. At Berenty Reserve, the dietary diversity of *L. catta* contains an annual mean of 109 species, which is reflective of the large composition of introduced plant species and access to some anthropogenic food and water resources at this site (Simmen et al., 2006). In contrast, I found that *L. catta* at Anja and Tsaranoro consumed a total of 24 and 32 plant species, respectively. This may be partially accounted for by the limited duration of the study; prior studies have reported on cumulative annual species diversity. However, a study of *L. catta* feeding ecology at the same sites in the early dry season (July and August) of 2010 indicates a similar diversity, with a high degree of overlap in each population's diet (Gould and Gabriel, in prep.). Thus, it is also probable that the lower dietary diversity of plant species observed here is at least in part due to the fragmentation history of the forests, though this could also be tied to a lower regional diversity of food species when compared with more southern *L. catta* habitats. Both sites have been subject to decades of selective logging of large, native trees by local villagers (e.g., *Adansonia* and *Ficus*; Andrianomena and Razafimandimby, pers. comm.), and at Tsaranoro this logging continues, although it is now heavily regulated. In addition, the process of fragmentation can have significant impacts on vegetative composition due to associated edge effects, leading to tree mortality, a loss of forest biomass, and increased treefall gaps, wood and leaf litter, and climbing vines (Laurance et al., 2006). Together these effects would be expected to considerably alter the vegetative structure of the forests, and the lower dietary diversity of *L. catta* in the Anja and Tsaranoro fragments may reflect a loss of key food species from *L.catta*'s dietary profile when compared to more intact forests. A similar reduction in dietary diversity has been reported for diademed sifaka (*Propithecus diadema*) inhabiting forest fragments when compared to those in continuous forest habitats (Irwin, 2008).

The differences in the number of plant species consumed between sites also points to variations in the vegetative composition found between the two fragments. *L. catta* at

Anja relied on a lower number of plant species, both overall and on a seasonal basis, when compared to the Tsaranoro population. At Anja, the loss of native fruit trees has been largely replaced by introduced alternatives, primarily *M. azedarach* and *P. cattleianum*, upon which the *L. catta* population heavily relies. *M. azedarach* was the most frequently consumed species in nearly all of the reproductive periods studied, representing over 40% of the total population feeding budget, and is an important year-round food source for *L. catta* in this fragment (Cameron and Gould, 2013). *P. cattleianum* appears to be an important seasonal resource, constituting up to 30% of the seasonal feeding budget of *L. catta*. These species are widely established within the Anja fragment, and *L. catta* travel relatively short distances to access these sources (Gabriel, 2013; Chapter 2). In comparison, at Tsaranoro *L. catta* groups relied on a wide range of endemic and introduced species and dedicated no more than 27% of their seasonal feeding budget consuming a single species. Introduced resources, such as *M. azedarach, P. cattleianum,* and *Mangifera indica*, are comparatively rare at Tsaranoro and are patchily distributed in the matrix surrounding the forest fragment. In addition, many of the native fruit trees have been removed from within the interior of the forest and while groups spent some time feeding on endemic species inside the forest (e.g., *T. serica, Diospyros, Dombeya* spp.; Gabriel, unpublished data), *L. catta* at Tsaranoro travel large distances to procure alternative resources scattered throughout the matrix (Gabriel, 2013; Chapter 2). Thus, it seems that the Tsaranoro groups employ a more broad-based dietary strategy as a means of coping with less concentrated resources that require more energy to obtain, similar to that which has been reported for fragment-dwelling howler monkeys (*A. pigra*) (Rivera and Calme, 2006).

As predicted, the diet of *L. catta* at the two study sites showed strong seasonal variation in both plant species consumed and composition of plant parts. However, this was much less pronounced for *L. catta* at Anja; *M. azedarach* was always consumed at the highest frequency and contributed a minimum of 30% of feeding time throughout the study period. *L. catta* exploits resources as they become seasonally available in order to fulfill its nutritional requirements and maximize energy intake year round (Sauther 1994, 1998; Yamashita, 2002). Both populations spent more time feeding on fruit during the pre-mating and mating periods, in accordance with reports for *L. catta* in other habitat types (Sauther, 1998; Gould, 2006; LaFleur, 2012). These reproductive periods coincide with the height of the wet season in southern Madagascar, when fruits are available in large quantities and provide a rich source of energy for lactating females and newly weaned infants, as well as offering valuable energy stores for mating and the upcoming resource-scarce dry season (Ullrey et al, 2003; Sauther, 1998; Sauther et al., 1999). Correspondingly, both populations spent slightly more time feeding on leaves during the post-mating and early lactation periods, which coincide with the early and late dry season, respectively, when fruits are typically of lower abundance. Leaves are an energy efficient, protein-rich food source (Waterman et al., 1988), and are particularly important for gestating and lactating female primates (e.g., *Indri indri*: Pollock, 1977; *L. catta*: Sauther, 1994, 1998; *Varecia variegata rubra* and *Eulemur fulvus albifrons*: Vasey, 2002; *Cercopithecus sabaeus*: Harrison, 1983; *Cebus* spp.: Fragaszy, 1986; Robinson, 1986; Rose, 1994; *Saimiri oerstedi*: Boinski, 1988; *Pongo pygmaeus*: Fox et al., 2004). LaFleur and Gould (2009) found that following a cyclone in 2003 that devastated fruit production by *T. indica, L. catta* groups exhibited marked food switching, consuming large proportions of leaves from forest (e.g., *Maerua filiformes*, *Secamone* sp.) and introduced non-forest species (e.g., *Ipomoea batatas*, *Argemone mexicana*), indicating that leaves may also constitute a significant portion of the diet of *L. catta* during fruiting failures due to fragmentation or natural disasters.

However, the fact that *L. catta* at each site differed in the time spent feeding on fruit, leaves, and flowers may point to differences in the relative abundance and nutritional quality of the food resources in each fragment. The consistent availability of fruit, primarily from *M. azedarach*, *P. cattleianum*, and *Ficus* spp., at Anja across seasons may enable *L. catta* to fill its energy requirements more steadily throughout its annual reproductive cycle, thus providing flexibility for feeding on nutrient-rich leaves when seasonally available, which require relatively little effort to procure. In comparison, *L. catta* at Tsaranoro may be less nutritionally selective due to greater seasonal changes in the availability of food resources, and therefore must acquire nutrients in large amounts when adequate resources can be found, as is typical of *L. catta* in other habitats (Sauther, 1994, 1998; Soma, 2006; Gould et al., 2011; LaFleur, 2012). *L. catta* at Anja may also be consuming a higher quantity of fruit by mass per unit time, due to both the high concentration of fruits from *M. azedarach* and the large size of fruits from *P. cattelianum* and *Ficus* spp., thus requiring less time to meet its caloric fill. These arguments assume that *L. catta* at Anja maintain a higher quality diet when compared with the Tsaranoro lemurs. Alternatively, it may be that due to a crowding effect, and therefore greater competition over spatially limited food resources, the Anja lemurs are actually obliged to consume a lower quality diet, consisting of greater quantities of leaves, than the less densely populated Tsaranoro *L. catta*. Ellwanger and Gould (2011) found differences in dietary selectivity among *L. catta* occupying gallery and spiny forest habitat at Berenty Reserve in southern Madagascar. *L. catta* in spiny forest was observed to spend significantly more time consuming fruit, primarily from the species *Gyrocarpus americanus* and *Tarenna* spp., whereas the gallery forest group spent more time consuming the leaves of *Leucaena lercoephalla*, *Pithecellobium dulce*, and *Azadirachta indicus*. The authors attributed these differences at least partially to the level of competition induced by spatial patterns of feeding. Contest competition is more likely to occur over food items that are highly clumped, such as fruits, thus more space is required between individuals consuming these items in order to avoid intense inter-individual agonism (Wragham 1980, van Schaik, 1989; Ellwanger and Gould, 2011). As such, *L. catta* at Anja may also be consuming more leaves as a dietary strategy to deal with inter- and intra-group competition brought on by crowding due to a high population density (6.6 lemurs/ha; Cameron and Gould, 2013). In addition, it is likely that differences exist in the nutritional content of plant parts of the various species consumed by each population, which would also affect the dietary selectivity of *L. catta*. Information on feeding intake rates at both sites, as well as nutritional analyses of ingested plant parts would lend greatly to the results found here.

At both sites, the lack of a seasonal difference between males and females in the types of food consumed, as well as between lactating and non-lactating females, is surprising given the influence of reproduction on feeding behaviour in *L. catta* (Sauther, 1994; Sauther et al., 1999; Gould et al., 2011), i.e., reproductive females require a higher concentration of energy and protein-rich foods compared with adult males (Sauther, 1994,1998; Rasamimanana and Rafidinarivo, 1993). LaFleur and Gould (2009) suggest that sex differences in seasonal feeding behaviour of *L. catta* may only be evident in resource-stable environments. It is possible that given the relatively recent fragmentation history at Anja and Tsaranoro and the lack of seasonal variety in resource selection relative to other habitats in which *L. catta* have been studied (see above), sex-specific foraging strategies have not been adopted in these populations. In addition, *L. catta* at Anja and Tsaranoro may be employing different behavioural strategies to offset the energetic costs of reproduction (Berkovitch, 1997; Dufour and Sauther, 2002; Gould et al., 2011). The 'Energy Conservation Hypothesis' posits that lemur species have evolved unique life history strategies to cope with the energetic stress that results from Madagascar's strong seasonality and harsh ecology (i.e., variable intra- and inter-annual rainfall; frequent cyclones; droughts) (Jolly, 1966; 1984; Richard, 1987; Young et al., 1990; Wright 1993; 1999; Dewar and Richard, 2007). These include traits that are geared toward minimizing energy expenditure ('energy conserving strategy'; e.g., sperm competition; seasonal breeding; low quality milk production) or maximizing energy intake from scarce resources ('energy frugality strategy'; e.g., territoriality, female dominance, fibrous diet, weaning synchrony) (Wright, 1999). *L. catta* occupying different habitat types may adopt different energy conservation strategies given the unique ecological conditions with which they are faced. For example, Ellwanger and Gould (2011) found that *L. catta* occupying spiny forest at Berenty Reserve, where quality resources are patchily distributed and highly contested (Sauther, 1993), minimized time spent engaging in active, energetically-costly behaviours, and spent more time resting during the resource-scarce dry season when compared with gallery forest groups. LaFleur (2012) notes that *L. catta* females occupying spiny forest at

Tsimanampetsotsa National Park in southwestern Madagascar employ an energy maximizing strategy by increasing foraging effort during the reproductively costly dry season, while males adopt an energy minimizing strategy by feeding less, resting more, and scent marking to display territorial boundaries.

The feeding ecology of *L. catta* at Anja and Tsaranoro indicates a similar divergence in behavioural strategies for energy conservation between habitats. At Anja, I found that *L. catta* spent equal amounts of time feeding in both the dry and wet seasons; however, groups rested more in the dry season. The high abundance of food resources available year-round at Anja may enable *L. catta* to 'energy minimize' by resting more during the energetically-costly lactation period (Sauther, 1994, 1998; Rasamimanana and Rafidinarivo, 1993; Loudon et al., 2008), similar to that which has been described for *L. catta* occupying other habitat types (Sauther, 1994; Loudon et al., 2008; Ellwanger and Gould, 2011; Kelley; 2011). This is further demonstrated by the lower overall energy expenditure observed in the Anja lemurs compared with those at Tsaranoro (Gabriel, 2013; Chapter 2). While resources at this site are not in short supply, a strategy for minimizing energy expenditure may be beneficial for *L. catta* at Anja in order to cope with the intense social stressors associated with high-density group living (i.e., inter-group feeding and mating competition due to overlapping home ranges) and competition over highly monopolized resources (Chapter 4). In contrast, *L. catta* at Tsaranoro appear to employ an energy maximizing strategy by spending less time resting and more time foraging during the resource-scarce dry season. The Tsaranoro groups also spent a greater proportion of time feeding overall, expended more energy, occupied larger home ranges, and traveled greater distances to feed on patchily distributed resources when compared with those at Anja (Gabriel, 2013; Chapter 2). Thus, it appears that the resource conditions present at Anja and Tsaranoro – due to unique fragmentation histories, introduction of non-native plant species, and continuing anthropogenic pressures – have facilitated the adaptation of different behavioural strategies to maximize energy conservation given distinct ecological and environmental challenges.

Differences in foraging strategies are also evident within sites, likely due to considerable heterogeneity in resource structure and quality within forest fragments (Kadmon, 1993; Didham et al., 1998; Tews et al., 2004; Kadmon and Allouche, 2007). At Anja, AL group occupies a region of the fragment that features anthropogenic resources (i.e., village gardens and a man-made lake border the reserve), which *L. catta* in this group frequently exploit. In addition, this area is frequented by tourist groups that visit the reserve to view *L. catta* and the lemurs in AL group are highly habituated and rarely travel arboreally or retreat to the forest canopy for protection. As a result, *L. catta* in this group may forage terrestrially more often both to access novel anthropogenic resources and because they encounter terrestrial food sources (i.e., fallen fruits of *M. azedarach*, *P. cattleianum*, and *Ficus* spp.) at a higher rate than would be expected under more natural conditions. Anthropogenic and introduced resources are also highly monopolized and heavily defended by groups that occupy the territory (Chapter 4). Feeding terrestrially may increase foraging efficiency, and reduce metabolic costs of locomotion (O'Neill, 2012), and therefore conserve energy for use in intergroup competition over access to valuable foraging patches. *L. catta* in AL group also spent more time engaging in geophagy, which may provide mineral supplements to the diet and adsorb the highly toxic substances found in the fruits of *M. azedarach* (Krishnamani and

Mahaney, 1999), thereby increasing terrestrial foraging time. In comparison, AB group occupies a more interior portion of the fragment, has little access to anthropogenic and introduced resources (with the exception of a patch of *M. azedarach* trees from which they regularly fed), is not highly habituated, and engages in much lower rates of intergroup encounters due to a lower regional density of *L. catta* and reduced home range overlap in this area of the fragment (Gabriel, unpublished data). At Tsaranoro, TM traveled greater distances in the matrix when compared to TR and often exploited resources from smaller shrubs and ground vegetation, whereas TR focused more time foraging in the forest canopy in addition to foraging amongst the matrix vegetation (Gabriel, 2013; Chapter 2). As with AL at Anja, higher rates of terrestrial feeding may be a strategy to conserve energy, in this case due to the locomotor costs of long foraging distances (Taylor et al., 1982; Leonard and Robertson, 1997; Bishop, 1999).

Since fragmentation is associated with the removal of native vegetation from within a habitat, a key factor to population viability in fragmented habitats is the abundance and availability of fallback foods (McKey, 1978; Kawecki, 1995; Robinson and Wilson, 1998; Irwin, 2008). Fallback foods can predict survival in heavily disturbed areas since they either (i) provide a continual abundance of different plant parts throughout the annual cycle (staple fallback food), or (ii) produce food items in large amounts during critical periods of food scarcity (filler fallback food) (Hanya, 2004; Knott, 2005; Laden and Wrangham, 2005; Lambert et al., 2004; Ungar, 2004; Yamakoshi, 2004; Marshall and Wrangham, 2007). At Anja, the removal of large native fruit trees within and surrounding the reserve has promoted the establishment of *M. azedarach* and *P. cattleianum*, which serve as staple and filler fallback foods, respectively, as indicated by the results. Similar to gallery forest *T. indica* for *L. catta* (Sauther, 1998; Simmen et al., 2006) and *Bakerella clavata* for sifaka (Irwin, 2008), *M. azedarach* has a continual phenology and asynchronously produces leaves and slowly maturing fruits (Dharani et al., 2010), which are available year-round and provide a rich source of carbohydrates (Italo et al., 2009) for *L. catta* during the typically resource-scarce dry season. *P. cattleianum* is a highly seasonal resource and produces large quantities of fleshy fruits that are consumed by *L. catta* throughout the wet season, comparable to the gallery forest species *Salvadora augustifolia* (Sauther, 1998). However, *P. cattleianum* is asymmetrically distributed throughout the reserve and consumption rates vary considerably between groups. At the time of study, AL group occupied a home range with a high concentration of *P. cattleianum*, and accordingly spent nearly half of its seasonal feeding budget consuming the large fruits of this species. On the other hand, AB had limited access to *P. cattleianum*, and while they occasionally migrated within the reserve to exploit this resource, they were frequently chased away by other groups that occupied the territory (Gabriel, unpublished data). Unlike at Anja, *L. catta* at Tsaranoro have little access to these valuable fallback foods and do not appear to focus on any specific food species in times of resource scarcity.

Ecological models, such as the source-sink model (Pulliam, 1988) and the balanced dispersal model (McPeek and Holt, 1992; Lemel et al., 1997; Diffendorfer, 1998), predict species spatial distributions in heterogeneous habitats, with important implications regarding population fitness potential. In these models, habitats of low resource quality may be unsustainable for population viability since they will have an average fitness of less than one (source-sink model) or will have a low carrying capacity (balanced dispersal model). The fact that the population density of *L. catta* at Tsaranoro is one-sixth that at Anja suggests that, in addition to having lower resource availability (Chapman and Chapman, 1999), *L. catta* in this fragment may be consuming a diet of lower nutritional quality compared with the Anja lemurs (Milton, 1984, 1993; Chapman and Fedigan, 1984; Oates et al., 1990; Cristobal-Azakarate and Arroyo-Rodriguez, 2007). However, LaFleur (2012) suggests that the presence of introduced species, such as *T. indica* in gallery forest and *M. azedarach* and *P. cattleianum* at Anja*,* and invasive species, such as *Opuntia* spp. in the spiny bush of Cap Sainte-Marie (Kelley, 2011), may overshadow what we would expect to be the dietary profile of *L. catta*. It is unlikely that the resource conditions at Tsaranoro deviate significantly from those seen in other habitats throughout *L. catta*'s range, and are probably of higher quality when compared with the arid spiny bush and spiny forest habitats of the far south (e.g., Berenty scrub and spiny forest: Gould et al., 2011; Cap Sainte Marie spiny bush: Kelley, 2011; Tsimanampetsotsa spiny forest: LaFleur, 2012). This is demonstrated by the high birth rates of the Tsaranoro females (in the groups studied, 73% of the adult females carried infants; Gabriel, unpublished data), and the fact that infant mortality at Tsaranoro (43% at 10 months of age; Gabriel, unpublished data) is within range of that which has been reported for *L. catta* in other habitats (Sussman, 1991; Gould et al., 1999, 2003; Jolly and Pride, 1999). Given the highly variable and unpredictable environment in which *L. catta* evolved (Sauther, 1998; Sauther et al., 1999; Gould et al., 1999, 2003; Dewar and Richard, 2007), it is probable that *L. catta* possesses the life history strategies to cope with the resource conditions present in the Tsaranoro landscape. Therefore, without further change to the resource structure, and in the absence of stochastic events, Tsaranoro is likely to sustain the current population numbers of *L. catta*.

On the other hand, the artificial resource structure at Anja appears to supply an over-abundance of energy that is readily available given *L. catta*'s dietary flexibility (Sauther et al., 1999; Jolly, 1966; Sussman, 1972, 1974; Budnitz and Dainis, 1975; Rasamimanana and Rafidinarivo, 1993; Sauther, 1993, 1998; Yamashita, 2002; Simmen et al., 2003, 2006; Gould et al., 2011). This fragment is thus capable of supporting a population that may be well above a natural carrying capacity – Anja boasts a higher population density than has ever been previously reported for *L. catta* in other habitat types (e.g., Beza Mahafaly gallery and dry forest: Gould et al., 2003; Sussman, 1991; Berenty gallery, scrub and spiny forest: Jolly et al., 2002; Pride, 2005a,b,c; Gould et al., 2011; Cap Sainte Marie spiny bush: Kelley, 2011; Tsimanampetsotsa spiny forest: LaFleur, 2012). While it is unknown whether the resources at Anja are of actual better quality when compared with those at Tsaranoro, or rather that they are simply of greater abundance and consistency of availability, the nutritional status of individuals at Anja is likely high. This is reflected by the high reproductive success (twinning is common at Anja, yet rarely reported in the wild) and low infant mortality (mortality rate was 12.5% at 10 months of age; Gabriel, unpublished data) observed in the Anja population when compared with other *L. catta* habitats. However, the crowded conditions at Anja and lack of dispersal capacity for *L. catta* may present other ecological challenges (e.g., heightened intergroup competition over resources, space, and breeding opportunities; inbreeding depression; elevated disease transmission rates) that may threaten the sustainability of this population. Phenological and nutritional analyses are essential for evaluating the dietary quality of the lemur food resources within and surrounding the two fragments and would greatly enhance our understanding of the foraging strategies of these lemur populations. Furthermore, continued monitoring of population demography and feeding ecology at each of these sites will be extremely valuable for assessing *L. catta*'s ability to cope with forest fragmentation over time.

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4 *LEMUR CATTA* IN FRAGMENTED FORESTS: THE STRESS RESPONSE

4.1 Abstract

Ecological and social challenges arising from habitat fragmentation can be a significant source of stress for inhabitant populations. If prolonged, such stresses can pose a threat to the longevity of a species within a fragmented landscape. In this study, I investigate the ecological correlates of stress in free-ranging ring-tailed lemurs (*Lemur catta*) inhabiting two forest fragments in south-central Madagascar, which vary markedly in anthropogenic pressure, resource structure, and population density of *L. catta*. At Anja Special Reserve (34 ha), food plants and water resources introduced within and surrounding the forest support the highest density of lemurs/ha compared with other sites at which *L. catta* has been studied. By comparison, *L. catta* in the Tsaranoro Valley sacred forest (53 ha) have limited access to introduced resources and the population density is one-sixth that at Anja. Throughout the late dry season of 2010 and mid- to late-wet season of 2011, I studied behaviour, habitat utilization, and fecal glucocorticoid (fGC) levels of adult *L. catta* in both fragments. Throughout the study period, levels of fGC were significantly higher in *L. catta* at Anja when compared with those at Tsaranoro. At both sites, fGC levels were lowest during the pre-mating period, but seasonal differences in fGC did not vary by sex or reproductive state. Behaviourally, *L. catta* at Tsaranoro exhibited a greater feeding effort than those at Anja, while the Anja lemurs displayed higher rates of territorial marking and defense behaviours. I discuss the results in the context of resource acquisition, reproductive pressures, and intergroup competition

and suggest that social challenges associated with high-density group living may contribute to stress in *L. catta* inhabiting densely populated forest fragments.

4.2 Introduction

Habitat disturbance can act as an environmental stressor in animal populations due to factors such as a loss of resources, a loss of home range area, and/or crowding (e.g., Wasser et al., 1997; Foley et al., 2001; Millspaugh et al., 2001; Creel et al., 2002; Rangel-Negrin et al., 2009). These perturbations can lead to elevated activation of the body's hypothalamic pituitary axis (HPA) and the release of stress hormones (glucocorticoids; GCs) that act upon body systems to aid an individual in coping with an acute stress (Selye, 1946; Asterita, 1985; Moberg, 1985; Nelson, 2000; Sapolsky et al., 2000; Sapolsky, 2003; Romero, 2004). The immediate effects (minutes to hours) of GC secretion include mobilization of stored energy (glucose, lipids), activation of the cardiovascular system, and regulation of the immune system (Sapolsky et al., 2000), thereby promoting the suppression of reproductive and defense behaviours and stimulation of foraging, escape, and resting behaviours (Wingfield and Ramenofsky, 1999; Wingfield and Kitaysky, 2002; McEwen and Wingfield, 2003). As such, the primary role of GCs is to activate systems in the body that promote survival in the presence of a stressor until the stressor is removed and homeostasis can be restored (Sapolsky et al., 2000). Although adaptive in the short-term, prolonged GC release (days to months) can negatively impact the body, leading to long-term inhibition of the reproductive system, immunosuppression, muscular dystrophy, disruption of neuronal cell function, and suppression of growth (Sapolsky et al., 2000; Wingfield and Romero, 2001; Abbott et al., 2003), consequently having clear deleterious effects on individual survival and fitness (Sapolsky, 1996, 2003, 2005; Wingfield and Ramenofsky, 1999).

GCs can be readily extracted from fecal excreta and have been shown to accurately reflect plasma levels (e.g., Cavigelli, 1999; Stavisky, 1994; Wallner et al., 1999; Wasser et al., 2000; Whitten et al., 1998; Starling et al., 2010), thus providing a reliable, non-invasive tool for quantifying the stress response in wild populations. As such, fecal GCs (fGCs) are now being used extensively to evaluate stress in a wide range of mammalian taxa (e.g., rodents: Harper and Austad, 2001; ungulates: Dehnhard et al., 2001; Millspaugh et al., 2001; Mostl and Palme, 2002; Turner et al., 2002; African elephants: Foley et al., 2001; African wild dogs: Monfort, et al., 1998; spotted hyena: Goymann et al., 1999; Dloniak et al., 2004; sea lions: Hunt, et al. 2004; primates: e.g., Cavigelli, 1999; Muller and Wrangham, 2004; Gould et al., 2005; Fichtel et al., 2007; Setchell et al., 2008; Brockman et al., 2009; Starling et al., 2010). Since chronic stress can be an indicator of a population's long-term viability in a region, and because animal populations in some fragmented habitats exhibit chronically higher stress hormone levels compared with those residing in intact forest (Chapman et al., 2006; Johnstone et al., 2012; Martinez-Mota et al., 2007; Rangel-Negrin et al., 2009), measuring GC levels in wildlife populations can provide important insight with respect to habitat quality, energy expenditure, and health status in the face of habitat change (Romero, 2004).

Intraspecific variation in GC levels in fragment-dwelling populations may be associated to the nature and extent of habitat change. As forests become more fragmented, habitat patches become smaller, more isolated, and dominated by “edges” (Cordeiro et al. 2001; Irwin, 2008; Lehmann et al., 2006; Lidicker, 1999; Tutin, 1999). In addition to changing the spatial configuration of a landscape, the process of fragmentation can impose a variety of abiotic (e.g., exposure to sun, wind, temperature, humidity) and biotic (e.g., resource distributions, interactions among and between species) effects within a habitat, the impacts of which can significantly alter the abundance and distribution of plant and animal residents (Lidicker, 1999; Fahrig, 2003). Elevated stress levels in wildlife populations have commonly been linked to poor nutritional intake resulting from alterations in food resource distribution and availability (e.g., Saltz and White, 1991; Foley et al., 2001; Pride, 2005a; Chapman et al., 2006; Wasser, et al., 2004; Jenni-Eiermann et al., 2008; Kitaysky et al., 1999), since GCs play an important role in regulating internal energy stores (Busch and Hayward, 2009). For example, Wasser and colleagues (2004) showed that grizzly bears (*Ursus arctos*) and black bears (*U. americanus*) inhabiting heavily fragmented and resource-scarce areas of Jasper National Park, Canada, had higher fGC levels when compared to those found in more resource-rich, although highly human-disturbed, regions. Similarly, Chapman et al. (2006) found that fGC levels were higher in fragment-dwelling red colobus monkeys (*Piliocolobus tephrosceles*) compared with those occupying continuous forest, and that the variance in cortisol across populations could be predicted by food availability.

On the other hand, fragmentation may also introduce opportunities for the procurement of non-traditional food resources (e.g., via crop and village raiding, access to introduced food species, adaptation to alternative fallback foods) that are often of higher nutritional quality than native foods, thereby leading to improved foraging efficiency and higher energetic yields for individuals (Saj et al., 1999; Tutin, 1999; LaFleur and Gould, 2009). Such quality resources can become highly monopolized, particularly under disturbed or crowded conditions (Sauther et al., 2006), a likely effect of reductions in size and abundance of suitable habitat. Heightened social pressures from increased competition over space and resources may also be related to elevated stress levels. Foley (2001) found a positive correlation between group size, intraspecific competition, and fGCs in wild populations of African elephants (Foley, 2001), and Pride (2005b) observed a similar relationship in ring-tailed lemurs inhabiting scrub forest. Thus, identifying the variables associated with habitat fragmentation that may activate a stress response in fragment-dwelling populations requires evaluation both of the ecological conditions present in a habitat (e.g., resource structure and quality) and the social and competitive interactions among resident species.

Ring-tailed lemurs (*Lemur catta*) offer a unique opportunity for examining stress related to fragment living. *L. catta* is a gregarious primate species, highly adapted to an erratic and severe climate, with strong seasonal variation in food availability (Sauther, 1998; Sauther et al., 1999; Gould et al., 1999, 2003). They are strict seasonal breeders and females gestate and lactate at the end of the dry season when lemur food resources are less abundant (Jolly, 1984; Sauther, 1998; Wright, 1999; Gould et al., 2011) to time infant weaning with the annual peak in food availability (Sauther, 1998). *L. catta* is also highly ecologically flexible (Sauther et al., 1999; Gould et al., 1999, 2003; Gould, 2006), being both semi-terrestrial and feeding generalists, and will readily disperse across non-forested areas (Goodman et al., 2006) and exploit anthropogenically-modified landscapes (Sauther et al., 2006; Gemmill and Gould, 2008; LaFleur and Gould, 2009; Cameron and Gould, 2013). Nonetheless, the natural habitat of *L. catta* is rapidly disappearing throughout its range and populations are now largely restricted to isolated forest fragments (Sussman et al., 2003; Goodman et al., 2006; Bodin et al., 2006; Gould and Gabriel, in prep.).

To date, no studies have examined the hormonal impact of habitat disturbance on *L. catta*; however, notable demographic and behavioural variations have been observed in populations occupying degraded habitats, including decreased sociality, human food exploitation, increased intra- and intergroup agonism, and altered body condition (Pride, 2005a; Sauther et al., 2006; Gemmill and Gould, 2008). In this chapter, I examine variations in fGC levels in *L. catta* populations occupying two rocky-outcrop forest fragments surrounded by anthropogenically-produced savannah and small-scale agriculture in south-central Madagascar. The two fragments differ markedly in lemur food resource structure and the *L. catta* populations exhibit highly diverse ranging patterns (Chapter 2), feeding ecology (Chapter 3), and population densities (Cameron and Gould, 2013; Gould and Gabriel, in prep.). Anja Special Reserve contains the highest density of lemurs/ha (6.6 animals/ha; Cameron and Gould, 2013) when compared with any other site or habitat in which they have been studied (e.g., Beza Mahafaly gallery and dry forest: Sussman, 1991; Gould et al., 2003; Berenty gallery, scrub and spiny forest: Gould et al., 2011; Jolly et al., 2002; Pride, 2005a,b,c; Cap Sainte Marie spiny bush: Kelley, 2011; Tsimanampetsotsa spiny forest: LaFleur, 2012). Food resources at Anja are plentiful due to the introduction of the non-native fruit trees, *Melia azedarach* and *Psidium cattleianum* (guava), to the reserve. The leaves and year-round fruit of *M. azedarach* make up the primary food resources for the *L. catta* inhabiting the fragment (Cameron and Gould, 2013; Chapter 3) and the fruits of *P. cattleianum* are a preferred seasonal resource during the mating and early gestation periods (Chapter 3). In contrast, the population density of *L. catta* in the larger Tsaranoro Valley sacred forest is one-sixth that at Anja (1.13 animals/ha) (Cameron and Gould, 2013). The diet of *L. catta* in this fragment is not dominated by a single tree species and groups regularly travel outside of the fragment to meet dietary needs (Gabriel, 2013; Chapter 2). Many of the native fruit trees were selectively logged in the past (Andrianomena, pers. comm.) and unlike Anja, the habitat has not been heavily re-established by tree species that serve as alternative food resources for the lemurs.

Until very recently (Cameron and Gould, 2013; Gabriel, 2013), *L. catta* populations in this habitat or region of Madagascar had not been studied, and the two research sites offer excellent examples of anthropogenic deforestation resulting in small, highly fragmented habitats. Given the between-site variation in habitat structure and the marked differences in population density, I tested the following predictions:

1) If, in the absence of introduced alternatives, fragmentation significantly alters the availability and distribution of lemur food resources and increases the effort of their procurement (i.e., ecological stress) (e.g., Saltz and White, 1991; Foley et al., 2001; Pride, 2005a; Chapman et al., 2006; Wasser, et al., 2004; Jenni-Eiermann et al., 2008; Kitaysky et al., 1999), then *L. catta* at Tsaranoro should exhibit elevated fGC levels.
2) If high-density living and highly monopolized resources result in increased intraspecific competition and territory defense (i.e., social stress) (e.g., Alexander and Roth, 1971; Judge and de Waal, 1993; Pride, 2005a,b; Honess and Marin, 2006), then *L. catta* at Anja should exhibit higher fGC levels.

3) Mean fGC levels in both populations should be highest during the lactation period, as this period coincides with the peak of the dry season in southern Madagascar and increased reproductive pressures for females dealing with the physiological demands of lactation and infant carrying (Jolly, 1984; Sauther, 1998; Cavigelli, 1999).

4.3 Methods

Study Sites – Two populations of ring-tailed lemurs residing in forest fragments in Madagascar's south-central highlands were studied in the late dry season (early September to late November) of 2010 and mid- to late- wet season (early March to late May) of 2011. Anja Special Reserve is an isolated fragment 34 ha in size, located along the Route Nationale 7 highway. The nearest fragment containing *L. catta* is at least 8 km away, separated by a landscape of granite hills, open savannah, grasslands, small villages and terraced rice paddies. The region has undergone over five decades of land conversion, primarily as a result of logging and forest clearing for cattle grazing and cultivation (Razafimandimby, pers. comm.). The Anja fragment is a rocky outcrop fragment, which features a mixture of xerophytic and deciduous vegetation (e.g., *Aloe, Kalanchoe, Ficus*, *Albizia, Turraea sericea*) (Gabriel and Gould, in prep.). The matrix consists of rocky savannah, rice paddies and village gardens, a small river, and an artificial lake used for cattle watering and pisciculture. With the removal of larger trees within and surrounding the reserve (e.g., *Adansonia* and *Ficus* spp.) prior to its protected status (Razafimandimby, pers. comm.), and aided by *L. catta* as excellent seed dispersers (Ganzhorn et al., 1999; Simmen et al., 2006), *M. azedarach and P. cattleianum* trees have become rapidly established throughout the forest.

The Tsaranoro Valley sacred forest is a remote fragment of 53 ha, east of the large Andringitra National Park (31,160 ha). It is bordered to the west by the Karambony mountain massif and the surrounding matrix is made up of open grassy fields and rice paddies. Similar to Anja, the fragment is comprised of rocky outcrop vegetation consisting of a mixture of xerophytic and deciduous species (e.g., *Aloe, Kalanchoe, Ficus*, *Dombeya, Diospyros, Turraea sericea*) (Gabriel and Gould, in prep.). Many of the native fruit trees (e.g., *Adansonia* and *Ficus* spp.) were selectively logged in the past (Andrianomena, pers. comm.) and, unlike at Anja, the habitat has not been heavily re-established by tree species that serve as alternative food resources for *L. catta*.

Behavioural data – Two groups of *L. catta* were studied at each site, with each group composed of 16-17 individuals, including adults, juveniles, and infants. Group composition is displayed in Table 4.1. Myself and field assistants, R. Simmons and I. Schneider-Crease, followed groups between the hours of 0700 and 1700 in rotating four-day periods, alternating between sites every three weeks for a total of 16-days/group/study period. Ten-minute continuous-time focal animal samples (Altmann, 1974) were used to determine individual activity budgets (feed, rest, groom, locomote, social), defense behaviours (scent mark, stink fight), and aggressive and affiliative interactions with conspecifics. Behaviours were categorized based on ethograms previously described for *L. catta* (Jolly, 1966; Taylor, 1986; Gould, 1989). All adult males and females were included in focal sessions, and could be identified from at least 25 m with binoculars by notable, characteristic markings (e.g., eye-ring shape, tail shape and size, body colouring, and distinct injuries or abnormalities). Juveniles and infants were excluded from focal observation, as they could not be reliably identified. Focal animals were selected at random, rotating between sexes and through all individuals in a group when possible. A total of 685 h of focal animal data were collected throughout the duration of the study period: 208 h from Lake Group (AL) and 158 h from Boulder Group (AB) at Anja, and 160 h from Rangers Group (TR) and 159 h from Meva Group (TM) at Tsaranoro.

Table 4.1 Group composition, male dispersal/immigration and number of focal animals in each study group

Group	Composition	# of dispersing/immigrant males	# of focal animals
Anja			
AL	5F, 8M, 3J, 3I	0/0	13
AB	6F, 6M, 4J, 5I	0/1	12
Tsaranoro			
TR	6F, 7M, 3J, 5I	3/1	13(11)*
TM	5F, 6M, 5J, 2I	0/1	11(12)*

Parentheses denote the number of focal animals following the male dispersal period. One male from TR emigrated to TM between study months and was included in the focal sessions of TM for the remainder of the study period.

The daily path length (DPL) of each group was calculated as the total distance focal groups moved in a single day via GPS coordinates taken daily throughout the study period. Coordinates were recorded upon locating the focal group each morning and subsequently each time the group moved to a new location (feeding or sleeping tree) throughout the day. In order to control for missing data points due to focal groups being out of view, coordinates were only considered for days consisting of >6hrs of continuous follow, during which time the location of the groups was in clear view or could be found within a 20 minute time span. A total of 995 location points were recorded throughout the study period: 221 for AL and 197 for AB at Anja, and 317 for TR and 260 for TM at

Tsaranoro.

Feeding effort was calculated as the mean proportion of the activity budget spent feeding multiplied by the mean DPL for each group (to account for the greater distances traveled while foraging by *L. catta* at Tsaranoro compared with those at Anja). Inter-group agonistic encounter (IGE) rate, defined as directed agonistic interactions (e.g., stink fight, lunge, chase) with members of another group, was determined as a frequency/day of observation for each group, independent of directional outcome. Territorial marking was characterized as the time (rate/hour) spent engaging in scent-marking behaviour, i.e., marking trees and other substrates with the antebrachial glands (males) or ano-genital glands (both sexes).

Fecal Sample Collection and Analysis – Fecal samples were collected non-invasively from known individuals within 10 min of defecation for fGC analysis. A total of 291 fecal samples were collected over the study period: 78 for AL and 72 for AB at Anja, and 72 for TR and 69 for TM at Tsaranoro. Multiple samples were collected for each focal individual throughout the duration of the study: 3 to 4 samples per animal in the lactation period (mean = 3.9) and 1 sample per animal in each of the pre- and post-mating periods. Samples were not collected during the short mating period (early April at Anja and mid April at Tsaranoro), as the elevated magnitude and duration of agonistic interactions between individuals at this time made identification of focal animals unreliable. Collection was restricted to the hours of 1300-1700 to control for diurnal fluctuations in fGC levels (Sousa and Ziegler, 1998; although some studies suggest that a diurnal effect on steroid levels may be attenuated when measured in feces: Cavigelli, 1999; Goymann et al., 1999). Within four hours of collection, samples were thoroughly dried in a

Coleman camp stove at 55-70°C (combined solar and tea candle heat) for 20 to 40 min, depending on ambient temperature (*as per* Brockman and Whitten, 1996 and Whitten et al., 1998). Once dried, the material was ground with mortar and pestle to a fine powder, packaged twice in aluminum foil, and sealed in a zip-lock bag. This method of fecal sample preservation yields stable, interpretable steroid profiles for at least three years (Whitten et al., 1998).

Due to differences between species and sexes in GC metabolism and secretion (Mostl and Palme, 2002; Millspaugh and Washburn, 2004; Touma and Palme, 2005), physiological or biological validation of fGC extraction techniques is essential to ensure that fGC levels reflect changes in adrenocortical activity in a given species (Touma and Palme, 2005). Physiological validation involves stimulating the adrenal cortex via the administration of adrenocorticotropic hormone (ACTH) (Palme, 2005; Martinez-Mota et al., 2008), whereas biological validation involves stimulating the adrenal cortex using a known stressful event (e.g., capture or transfer) (Terio et al., 1999; Mostl and Palme, 2002; Touma et al., 2005). In each case, fecal samples are collected pre- and post-stimulation and analyzed for changes in GC metabolite levels that represent the expected adrenocortical activity. Previous studies have demonstrated physiological validation of fGC metabolites with serum levels in other lemur species (*Propithecus verreauxi*: Fichtel et al., 2007) and biological validation in *L. catta* (Cavigelli, 1999; Starling et al., 2010; to date, no physiological validations have been conducted in *L. catta*). As such, fGC metabolites are considered an accurate and reliable index of physiological stress in *L. catta* (Cavigelli, 1999; Gould et al., 2005; Pride, 2005a,b,c; Starling et al., 2010).

GCs were extracted from fecal samples and measured via radio immunoassay (RIA) by Dr. Susan Cook at the Western College of Veterinary Medicine, University of Saskatchewan in accordance with procedures described elsewhere for *L. catta* (e.g., Cavigelli, 1999; Gould et al., 2005; Pride, 2005a,b,c; Starling et al., 2010). Dried fecal samples were weighed (0.1 +/- 0.02 g) and placed into a 13x100 mm polypropylene tube. Five ml AnalaR Methanol (MeOH) was added to each tube, the tube capped and the feces and MeOH were mixed frequently by inversion and shaking, over a 6 hour duration. Tubes were refrigerated overnight, mixed again the following morning, and then centrifuged for 30 min at 1500g. One ml of supernatant was aliquotted into 12x75 polypropylene tubes and air dried. Aliquots were reconstituted with 75 µl of absolute Ethanol (to dissolve the bile acids) followed by 925 µl phosphate buffered saline (PBS) (to dilute the steroid). These tubes were capped, vortexed and the supernatant taken directly to the assay.

As cortisol is frequently reported as the dominant GC metabolite found in primates, fGC metabolites were first tested using a solidphase cortisol radioimmunoassay (Coat-A-Count Cortisol RIA, Siemens), which revealed the expected standard curve and control values; however, test samples fell well below the standard curve [i.e., only trace amounts (<5 ng/ml) could be detected]. Samples were then reconstituted to increase the concentration by a factor of four and values remained below the range of the standards (standards ranged between 10 and 500 ng/ml). Starling et al. (2010) demonstrated that fecal corticosterone concentrations accurately reflected serum levels in *L. catta* on days 0, 1, and 2 following collection, and that serum corticosterone levels were postively correlated with serum cortisol levels. Thus, corticosterone, and not cortisol, was the fGC metabolite reported to examine seasonal, social, and reproductive correlates of stress in their study population of *L. catta* (Starling et al., 2010). In addition, other prior studies reporting "cortisol" as the fGC metabolite measured as a stress index in *L. catta* have used non-specific cortisol antibodies that detect multiple fecal steroid metabolites (Cavigelli, 1999; Pride, 2005a,b,c).

Following these lines of evidence, the fGC metabolites were retested using a double antibody radioimmunoassay for corticosterone [Corticosterone RIA (for rats and mice), MP Biomedicals, Orangeburg, NY] with the following cross-reactivities: 0.34 desoxycorticosterone; 0.10 testosterone; 0.05 cortisol; 0.03 aldosterone; 0.02 progesterone, 0.01 androstenedione, 0.01 5α-dihydrotestosterone; <0.01 cholesterol, dehydroepiandrosterone, dehydroepiandrosterone-sulfate, 11-desoxycortisol, dexamethasone, 20α-dihydroprogesterone, estrone, estradiol-17α, estradiol-17β, estradiol, pregnenolone, 17α-hydropregnenolone, 17α-hydroxyprogesterone. The corticosterone standards ranged from 25 to 1000 ng/ml. In this case, sample fGC levels fell well within range of the standard curve (dry season: 31.8 to 822.3 ng/ml; wet season: 25.5 to 484.4 ng/ml). The minimum detectable limit of the assay, as provided by the manufacturer, is 7.7 ng/ml or 1.9 ng/g feces. When extracted lemur feces were diluted in PBS, the resulting curves were parallel to the standard curve of the assay. Intra-assay coefficients of variation were 8.1% and 1.4% for sera (provided in the RIA kit) with concentrations of 131.9 and 724.6 ng/ml, respectively. Inter-assay coefficients of variation were 12.5% and 14.1% with concentrations of 97.1 and 760.7 ng/ml, respectively. Final results are expressed as nanograms of corticosterone per gram of dry feces.

Statistical Analysis – Mean fGC levels were calculated for each focal individual according to reproductive period: lactation – weeks 1-12 (September-November 2010); pre-mating – weeks 13-18 (mid-March – mid-April, 2011); post-mating – weeks 19-24 (late April – late May, 2011). Examination of fGC data revealed that the distribution of fGC concentrations was normal (graphic inspection) and homoscedastic (Monte Carlo simulations). When determining overall differences in fGC levels, feeding effort, and rates of territorial marking between the two sites, a model I nested ANOVA was used to control for group effects. A two-way ANOVA was used to determine between-site differences in fGC levels and behavioural variables according to reproductive period (N=49 animals). When differences were found, post-hoc tests of individual means were conducted using TukeyHSD tests. A one-way ANOVA with repeated measures was used to determine seasonal differences in fGC levels and behavioural variables within each site. Student's t-tests were used to determine sex differences in fGC levels (N=24 and 25 animals). A two-way ANOVA without repetition was used to determine sex and group differences in behavioural variables within each site (N=24 and 25 animals). Mann-Whitney U tests were used to determine differences in fGC levels between lactating and non-lactating females, since the data did not satisfy the assumptions of parametric statistical tests (N=11 animals). For all statistical tests, the threshold of significance was set at $P < 0.05$. Standard error is the given measure of variability.

4.4 Results

Between- and within-site differences in fGC levels **–** Overall, I found a significant between-site difference in mean fGC levels (nested ANOVA; $F=88.08$, $df=1$, $P<0.0001$); *L. catta* at Anja exhibited higher levels of fGC across the study period compared with those at Tsaranoro (Figure 4.1). There were no within-site differences in fGC levels at either site (one-way ANOVA; Anja: *P*=0.44; Tsaranoro: *P*=0.28).

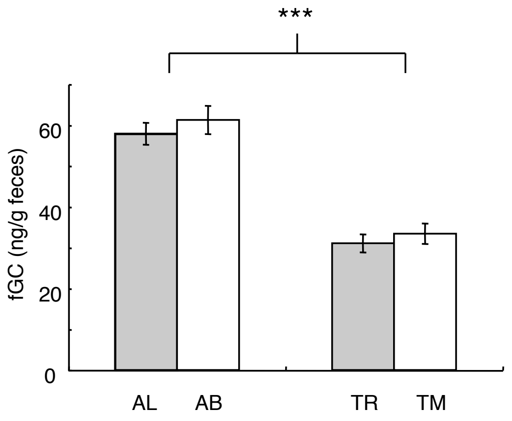

Figure 4.1 Comparison of fGC levels (mean ±SE) by group for *L. catta* populations at Anja Reserve (AL group and AB group) and Tsaranoro forest (TR group and TM group). Asterisks indicate significant differences in fGC levels within (N=24-25) and between (N=49) populations (nested ANOVA; '***' $P < 0.0001$).

I also found a significant between-site difference in fGC levels according to reproductive period (two-way ANOVA; F=6.59, df=2, *P*=0.002); *L. catta* at Anja exhibited higher mean fGC levels compared to *L. catta* at Tsaranoro in the lactation and the post-mating periods (Figure 4.2). There was no between-site difference in fGC levels in the pre-mating period (*P*=0.08).

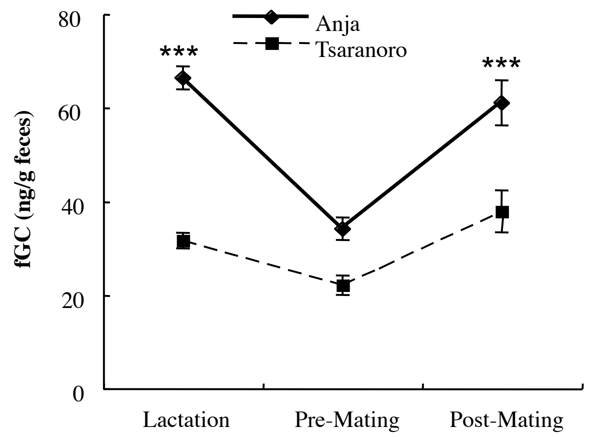

Figure 4.2 Comparison of fGC levels (mean ±SE) across reproductive periods for *L. catta* populations at Anja Reserve and Tsaranoro forest. Asterisks indicate significant differences in fGC levels between populations (N=49; two-way ANOVA; '***' $P < 0.0001$).

There was a seasonal effect on fGC levels at each site (repeated measures ANOVA; Anja: F=27.9, df=2, P<0.0001; Tsaranoro: F=8.37, df=2, P=0.0005); fGC levels were lowest during the pre-mating period when compared with the other reproductive periods (Figure 4.2). There were no within-site group differences in fGC levels across reproductive seasons, with the exception of AB exhibiting higher fGC levels compared to AL in the post-mating period (repeated measures ANOVA; F=5.8, df=6, P<0.001; Table 4.2).

Table 4.2 Mean fGC levels (±SE) across reproductive periods for each study group

	fGC (ng/g feces) ± SE		
	Lactation	Pre-Mating	Post-Mating
Anja			
AL	70.87± 3.25	28.81± 2.96	47.89± 7.01
AB	64.32± 4.71	39.36± 3.24	74.03± 3.89
Tsaranoro			
TR	31.83± 2.45	31.92± 8.51	27.51± 3.68
TM	33.27± 2.77	20.33± 2.98	46.73± 7.05

fGC levels between sexes and between lactation vs. non-lactating females – I found no overall differences in mean fGC levels between males and females at either site (Anja: 52.08 ± 2.75 vs. 55.53 ± 3.07 ng/g feces; Student's t-test; t=0.8, df=22, *P*=0.41; Tsaranoro: 28.55 ± 2.27 vs. 32.67 ± 2.73 ng/g feces; Student's t-test; t=1.4, df=20, *P*=0.17), nor were there any sex differences in mean fGC levels according to reproductive period (two-way ANOVA; F=0.56, df=2, *P*=0.58). However, when analyzing the groups separately, males in TR group exhibited higher mean fGC levels when compared with females (48.04 ± 2.14 vs. 41.43 ± 1.44 ng/g feces; Mann-Whitney U Test; U=32, *P*=0.03). I also found no differences in mean fGC levels between lactating and non-lactating females (Anja: 56.95 ± 2.91 vs. 51.80 ± 9.17 ng/g feces; Mann-Whitney U Test; U=15, *P*=0.63; Tsaranoro: 34.21 ± 6.07 vs. 31.62 ± 1.44 ng/g feces; Mann-Whitney U Test; U=14, *P*=0.93) throughout the study period.

Between- and within-site differences in behavioural measures – There was a significant between site difference in feeding effort (nested ANOVA; F=533.3, df=1, *P*<0.0001) and rates of territorial marking behaviour (nested ANOVA; F=33.6, df=1, *P*<0.0001). Overall, *L. catta* at Tsaranoro exhibited a greater feeding effort (Figure 4.3A), while *L. catta* at Anja engaged in more territorial marking behaviour (Figure 4.3B). There were no within site differences in feeding effort (two-way ANOVA; Anja: *P*=0.99; Tsaranoro: *P*=0.69) or rates of territorial marking (two-way ANOVA; Anja: *P*=0.85; Tsaranoro: *P*=0.99), nor did these behaviours vary according to sex (Student's t-test; feeding effort: *P*=0.40; territorial marking: 0.08).

Throughout the study duration, *L. catta* at Anja had higher IGE rates when compared with the Tsaranoro groups (0.8 ± 0.09 vs. 0.3 ± 0.06 encounters/day). There were also within site differences in the frequency of IGEs, with AL engaging in more IGEs compared with AB at Anja (1.04 vs. 0.48 encounters/day) and TR engaging in more IGEs compared with TM at Tsaranoro (0.33 vs. 0.27 encounters/day; Figure 4.3C).

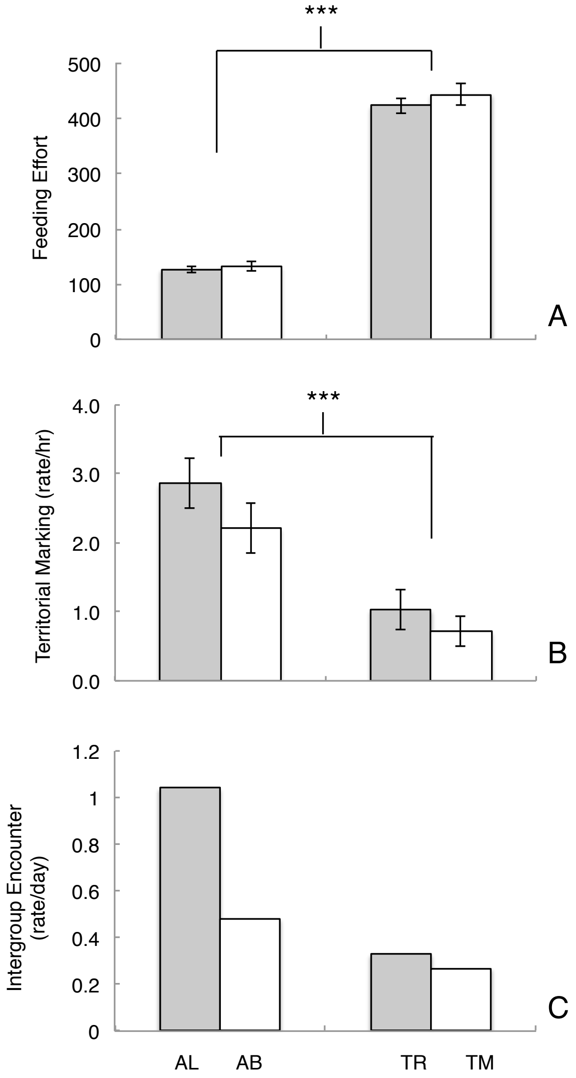

Figure 4.3 Comparison of (mean±SE) feeding effort (A), rate of territorial marking behaviour (B) and inter-group agonistic encounter rate (C) between *L. catta* groups at Anja Reserve (AL group and AB group) and Tsaranoro forest (TR group and TM group). Asterisks indicate significant differences for behavioural variables between populations (N=49; nested ANOVA; '***' $P < 0.0001$).

Feeding effort varied seasonally at Tsaranoro (repeated measures ANOVA; F=18, df=2, $P<0.0001$); *L. catta* displayed the lowest feeding effort during the pre-mating period (Figure 4.4A). The frequency of territorial marking behaviour varied across seasons at both sites (repeated measures ANOVA; Anja: F=5.42, df=2, *P*=0.006; Tsaranoro: F=4.01, df=2, *P*=0.02). *L. catta* at Anja displayed the highest rates of marking behaviour during the lactation period, whereas *L. catta* at Tsaranoro displayed the highest rates of marking behaviour during the pre-mating period (Figure 4.4B). IGE rates also varied seasonally at each site. At Anja, IGE rates were lowest during the pre-mating period, whereas at Tsaranoro IGE rates were highest at this time (Figure 4.4C).

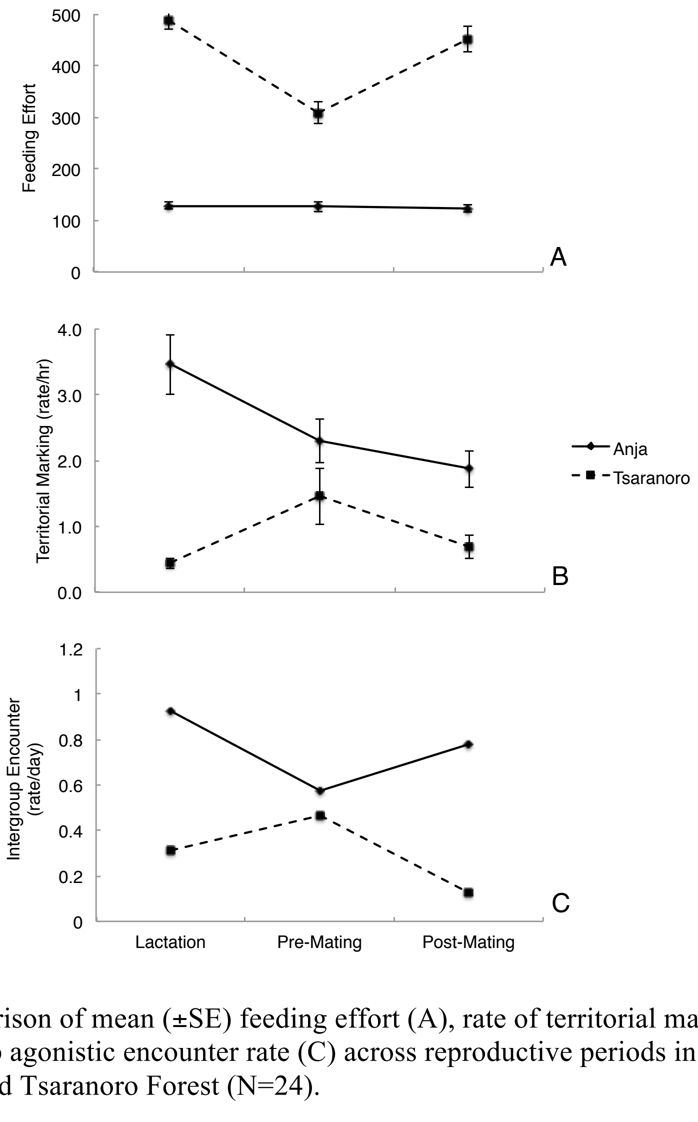

Figure 4.4 Comparison of mean (±SE) feeding effort (A), rate of territorial marking behaviour (B) and inter-group agonistic encounter rate (C) across reproductive periods in *L. catta* at Anja Reserve (N=25) and Tsaranoro Forest (N=24).

4.5 Discussion

Resource acquisition is a common stressor in fragmented habitats (Chapman et al., 2006; Dunn et al., 2009; Foley et al., 2001; Pride, 2005a; Martinez-Mota et al., 2007; Saltz and White, 1991). Prior studies of stress in *L. catta* have indicated a link between food availability and fGC levels (Cavigelli, 1999; Pride 2005a), particularly in harsher habitats where resources are more difficult to procure (Cavigelli, 1999). However, the prediction that altered resource distribution and increased feeding effort are associated with elevated fGC levels was not well supported by the results. *L. catta* at Anja have abundant and consistent access to food and water resources year-round due to the establishment and rapid growth of the introduced fruit trees, *M. azedarach* and *P. cattleianum,* throughout the reserve (Razafimandimby, pers. comm.; Cameron, 2010), and the construction of a small lake for cattle watering and pisciculture on the fragment's southern edge. Conversely, food resources for *L. catta* at Tsaranoro are patchily distributed and far more scattered throughout the landscape compared with those at Anja, such that *L. catta* groups must travel large distances outside of the forest to forage (Gabriel, 2013; Chapter 2). This was reflected by the greater feeding effort exhibited by the Tsaranoro lemurs across the study duration. In addition, unlike at Anja, introduced resources have not been heavily established within or surrounding the Tsaranoro forest and do not constitute a primary food source for *L. catta* at this site (Chapter 3). However, despite exhibiting a greater feeding effort to procure patchy resources, *L. catta* at Tsaranoro exhibited lower mean levels of fGC throughout the study period when compared with those in the Anja fragment.

Moreover, fGC levels only partially reflected seasonal variations in food availability. The distribution and abundance of resources is strongly seasonal throughout *L. catta's* range (Jolly, 1984; Rasamimanana and Rafidinarivo, 1993; Sauther, 1998). At both sites, fGC levels were lowest during the pre-mating period, which coincides with the height of the wet season in Madagascar, providing ample energy resources from fruit and young leaves (Jolly, 1984; Sauther, 1998). In contrast, fGC levels were elevated during the post-mating and lactation periods, which correspond with the beginning and end of the dry season, respectively, a time of limited food resources for *L. catta* in other regions (Jolly, 1984; Sauther, 1998). Behaviourally, feeding effort by *L. catta* at Tsaranoro, but not at Anja, reflected these seasonal changes in food availability, consistent with a greater fluctuation in seasonal resource abundance at Tsaranoro. However, seasonal changes in fGC levels were of a much lower magnitude for *L. catta* at Tsaranoro when compared with those at Anja. Lower fGC levels and magnitude of fGC fluctuation in the Tsaranoro lemurs may suggest that food scarcity did not extend beyond the predictable seasonal fluctuations of this geographic range and habitat type and thus was not a significant stressor in this population (Wingfield and Ramenofsky, 1999). *L. catta* possess life history strategies to cope with a highly seasonal and often erratic climate (Jolly, 1984; Sauther et al., 1999; Wright, 1999) and environmental changes that occur as part of a predictable annual cycle are not likely to be experienced as stressful, since animals can physiologically prepare for such events (Wingfield and Ramenofsky, 1999).

Alternatively, seasonal variations in fGC levels may be related to energetic demands associated with reproduction in *L. catta*. For many mammalian species, gestation and lactation are the most energetically costly periods for females, whereas mating is associated with peak energy demands for males (Jolly, 1984; Gittleman and Thompson, 1988; Michener and Locklear, 1990; Wade and Schneider, 1992). I found lower levels of fGC during the pre-mating period in both populations, when females are briefly exempt from the physiological costs of pregnancy and lactation and males are not yet facing the competitive challenges of mating (Gould and Ziegler, 2005; Jolly, 1966; Sauther, 1991). Hormone studies in *L. catta* from gallery forest at the Beza Mahafaly Reserve in southern Madagascar have revealed differences between sexes with respect to the role of reproductive state on stress levels. Cavigelli (1999) found that fGC levels were elevated for breeding females during the late gestation and late lactation periods; however, Gould et al. (2005) found no change in fGC levels throughout the mating and post-mating periods in adult males at the same site. In comparison, I found no sex differences in fGC levels across reproductive periods and both sexes exhibited the same patterns of fGC fluctuation throughout the study period, suggesting that stress levels were not reflective of sex-specific reproductive pressures. Furthermore, contrary to expectations, lactating females did not exhibit higher fGC levels compared with non-lactating females at either site. This finding is counter to Cavigelli's examination of females during the same reproductive period at Beza Mahafaly (Cavigelli, 1999). As above, Gould et al. (2005) suggests that for male *L. catta*, the energetic demands associated with mating occur as part of a predictable life history stage and thus this period is not necessarily stressful. Cavigelli (1999) makes a similar case for a lack of correlation between fGC levels and predation threat, food accessibility, or feeding agonism in the late dry season when female *L. catta* are facing the energetic costs of lactating. However, analyses should be extended to include gestating females and mating males at Anja and Tsaranoro, since reproductive pressures are likely to vary between sites and habitats (depending on resource availability, population size/density, opportunities for dispersal), and because these reproductive periods have been linked to elevated GC levels in other primate species (females: Vogt et al., 1981; Ziegler et al., 1995; males: Barrett et al., 2002; Fichtel et al., 2007; Ostner et al., 2008).

Finally, the results strongly support the prediction that fGC levels in *L. catta* are linked to social demands associated with high-density group living and intraspecific competition over resources (e.g., Alexander and Roth, 1971; Judge and de Waal, 1993; Pride, 2005a,b; Honess and Marin, 2006). At Anja, access to abundant anthropogenic food items (from village gardens and introduced tree species) and water resources has facilitated the support of a large and densely packed population with highly overlapping home ranges (Chapter 2) and high reproductive success [twinning is common among females and in the groups studied infant mortality was low (12.5% at 10 months of age); Gabriel, unpublished data]. However, with a lack of suitable forest patches and conspecific populations within dispersing distance (the closest fragment containing *L. catta* at least 8 km from Anja), the lemurs at Anja must cope with an elevated intensity of social interactions, including heightened competition for space and resources. This may be particularly pronounced in groups inhabiting the lower portion of the reserve, which compete for access to high quality introduced and anthropogenic resources, when compared with groups at higher elevations, which experience less home range overlap and have little exposure to these novel food items. *L. catta* groups at Anja engaged in higher rates of territorial marking and defense behaviour compared to Tsaranoro groups, and seasonal variability in IGE rates at Anja resembled seasonal fluctuations in fGC levels. Pride (2005a) reported that female *L. catta* at Berenty Reserve that engaged in the highest rates of intergroup conflict had the highest fGC levels, and animals living in the largest-sized groups also exhibited higher stress levels compared with those in medium-sized groups (Pride, 2005b). A similar relationship between stress and group size has been observed in African elephants (*Loxodonta Africana*) in Tarangire National Park, Tanzania (Foley et al., 2001), and several captive studies have indicated a link between social crowding and stress in other primate species (de Waal et al., 2000; Judge and de Waal, 1993; Sassenrath, 1970).

It is probable that the crowded condition of the Anja lemurs is atypical of their natural habitat, as the population density is higher (6.6 animals/ha) than at any other site in which they have been studied (Gould et al., 2003, 2011; Jolly et al., 2002; Kelley, 2011; LaFleur, 2012; Cameron and Gould, 2013). It is well supported that organisms possess a physiological flexibility to respond to their social environment in a way that maximizes reproductive success (reviewed by Bercovitch and Ziegler, 2002). However, for group-living animals, when social pressures become intense or unpredictable, as would be expected under unnaturally crowded conditions, individuals may encounter significant social stressors to which they are unable to adjust (McEwen and Wingfield, 2003; Wingfield, 2005). Allostasis, the process of maintaining stability throughout change (Sterling and Eyer, 1988; McEwen and Wingfield, 2003; Schulkin, 2003), may be disrupted when energetic discrepancies are present in the environment ('allostatic overload'). In addition to the physiological stress that is experienced when energy is constrained in the environment ('type I allostatic overload'), Wingfield (2005) suggests that psychosocial stress emerges when significant social challenges or dysfunctions are present in the absence of energy constraints (‘type II allostatic overload’). Both types of stressors are accompanied by secretion of GCs from the body’s HPA axis; however, when psychosocial stress is present in a population, GC secretion is likely to become chronic and cannot be regulated through an emergency fight-or-flight response (McEwen and Wingfield, 2003). The social conditions associated with the high-density group living at Anja may account for the elevated fGC levels observed in this study, indicating that the heightened intensity of intergroup interactions may be an important challenge for individuals of both sexes across seasons and reproductive periods. Of cautionary note, however, lacking a baseline profile for fGC levels in the study populations, it is not clear whether the ‘high’ levels of fGC observed at Anja reflect a chronically stressed condition or the fact that the surplus of high quality resources provide increased energy to invest in competitive interactions. With the exception of frequent intergroup encounters surrounding territory defense, the lemurs at Anja did not appear to be visibly more stressed when compared with the Tsaranoro population (e.g., coat condition was good across seasons, females exhibited a high reproductive output, individuals appeared large and healthy). Further information on population fitness, reproductive output, and other health parameters (e.g., disease processes) are required to adequately assess the population’s stress response in the face of these social constraints.

As the stress profile can be an indicator of population health and viability, the findings of this study support the importance of fGC levels as a physiological monitor for determining a species’ ability to adapt to habitat disturbance. Wingfield (2005) notes the importance of identifying the type of allostatic overload accountable for high circulating GC levels, particularly in populations at risk of declining, before making decisions regarding appropriate conservation and management of species. In addition to the pathological effects that a prolonged elevation in GC levels can have on various body systems (see Introduction), long-term deviations from allostasis can alter an individual's GC profile, such that baseline and stress-induced levels are altered (Harlow et al., 1992; Millspaugh et al., 2001) or the duration of the stress response is elongated (Busch and Hayward, 2009). Moreover, a chronically stressed condition can be inheritable for offspring that are exposed to significant stressors prenatally (Sheriff et al., 2009, 2010). These acclimation and sensitization effects alter the stress response to future stimuli and may damage an individual's ability to cope with an acute threat. Furthermore, the fitness consequences of inbreeding depression can be exaggerated under stressful conditions (Armbruster and Reed, 2005), such that stress may potentiate the genetic effects of habitat isolation. At the extreme, chronically high GC concentrations can have negative impacts on fitness and may ultimately lead to mortality (Suorsa et al., 2003; Kitaysky et al., 2007; but see Boonstra, 2012); a relationship that has been described for *L. catta* in other habitat types (Pride, 2005c). Monitoring the stress response can be a valuable tool for revealing social and ecological conditions that contribute to the sensitivity of a population to fragment living, and may be indicative of a habitat's suitability for supporting a resident population over time. This is of particular importance when isolation limits dispersal capacity, with important long-term conservation implications for a species' success within a region.

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5 *LEMUR CATTA* IN FRAGMENTED FORESTS: PARASITES

5.1 Abstract

Environmental disturbances can facilitate disease transmission in wildlife due to changes in host demography (increased isolation, increased host density, inbreeding), exposure to novel carriers (humans, domesticated animals, vermin), and alterations in the ecological conditions of the environment that may compromise host body condition (poor nutrition, stress) and/or increase parasite reproductive success. In this chapter, I report on the endoparasitic profiles of ring-tailed lemurs (*Lemur catta*) inhabiting two forest fragments – Anja Reserve and the Tsaranoro Valley sacred forest – in Madagascar's south-central highlands to assess baseline health parameters, parasite community richness, and ecological factors that may facilitate disease spread. Throughout the late dry season (September to November) of 2010 and mid- to late-wet season (March to May) of 2011, I collected 291 fecal samples non-invasively from 49 adult *L. catta* belonging to four groups to examine the component endoparasitic community in each population. Both populations harboured generalist parasites capable of infecting humans, livestock, and wildlife. *L. catta* at Anja harboured a parasite species richness consisting of three protozoa (*Endolimax nana*, *Isospora belli*, and *Balantidium coli*) and two unidentified helminths (phylum Nematoda). The species richness of parasites at Tsaranoro included two protozoa (*I. belli* and *B. coli*) and four helminths (a strongyloid, a strongyle, and two unidentified nematodes). *L. catta* at Tsaranoro exhibited a higher prevalence of helminth parasites throughout the study duration when compared to the Anja population. There was also a within site difference in the prevalence of protozoan parasites and the cases of

multiple infection during the wet season at Tsaranoro. These between and within-site variations in endoparasite infections may be reflective of differences in ranging patterns, and thus exposure to contaminated matter, and between-site differences in dietary quality. In addition, there was a strong seasonal effect on parasite prevalence and cases of multiple infections for *L. catta* at both sites, suggesting that the parasite communities infecting these populations may be sensitive to climatic variation. Due to the high exposure of *L. catta* to humans and livestock, the isolation of the forest fragments from other continuous habitat, and the negative impacts that habitat disturbance can have on host condition, I suggest that continued monitoring of host-parasite dynamics in these populations may be important for long-term population management.

5.2 Introduction

Of the numerous factors that potentiate global species extinctions as a result of environmental change (e.g., habitat loss, climate change, invasive species, loss of resources, overexploitation) (Pimm et al., 1995; Wilcove et al., 1998), infectious disease is rarely in the spotlight (Smith et al., 2006, 2009). This largely reflects the fact that pathogens tend to act locally on wildlife populations and rarely in isolation of other driving factors (Smith et al., 2006), making the relative impacts on biodiversity seem negligible. However, since disease processes are likely to have the largest impacts on populations already at risk of local extinction (Cleaveland et al., 2002; Daszak et al., 2000; Hochachka and Dhont, 2000; Smith et al., 2009), and can therefore be a significant threat to endangered species (Wilcove et al., 1998; Daszak et al., 2000; Harvell et al., 2002; Smith et al., 2009), understanding how environmental disturbance affects parasite communities is an important consideration in wildlife conservation.

Pathogen transmission associated with habitat loss and alteration is likely to increase as a function of decreasing habitat size and quality (Scott, 1988; Pimm and Askins, 1995; Gillespie and Chapman, 2008; Smith et al., 2009). Habitat fragmentation commonly restricts the movement and dispersal of species within a geographic region, thereby increasing contact between the same set of individuals and facilitating the spread of infection (Scott, 1988; Flather et al., 1994; Gillespie and Chapman, 2008; Smith et al., 2009). In this way, habitat fragmentation can have significant impacts on host-parasite dynamics, since parasite abundance and distribution can vary as a function of environmental conditions, changes in host demography, and interactions within and between species (Lafferty, 1997; Smith et al., 2009; Clough, 2010). For example, parasitism may increase in disturbed habitats if host resistance is compromised (e.g., due to exposure to novel infections, increased intensity of exposure to parasites, reductions in immune function from illness or stress) or if the density of intermediate or definitive hosts increases (e.g., due to a loss of space and/or crowding effects) (Lafferty, 1997; Lafferty and Holt, 2003; McCallum and Dobson, 2002). Populations that are isolated by fragmentation are at higher risk of population crashes due to decreases in genetic variability, which can increase susceptibility to infection (Lyles and Dobson, 1993; Smith et al., 2009). Furthermore, while pathogens that rely on a single host tend to be density-dependent, many multi-host pathogens are frequency-dependent and are thus capable of being transmitted even when host population density is low, thereby increasing the potential of local extirpations (Thrall et al., 1993; Begon et al., 1999; O'Keefe and Antonovics, 2002; Boots and Sasaki, 2003; Smith et al., 2009). For example, Begon and colleagues (1999) showed that the cowpox virus, a multi-host, directly transmitted pathogen that infects bank voles (*Clethrionomys glareolus*) and wood mice (*Apodemus sylvaticus*), is transmitted between infected and susceptible individuals as a function of their social interactions (frequency-dependent) as opposed to the number of individuals in the population (density-dependent). Similar reports of frequency-dependent transmission have been made for rabbit haemorrhagic disease (White et al., 2001), and a variety of sexually transmitted and vector-borne diseases (Getz and Pickering, 1983; Thrall et al., 1993; Antonovics et al., 1995; Lockhart et al., 1996)

Habitat disturbance often brings wildlife populations within closer proximity to humans, livestock and other domesticated animals, as well as vermin that thrive in human-populated areas, thus increasing the potential for cross-species parasite transmission (Lafferty and Gerber, 2002; Loudon et al., 2006; Pedersen et al., 2007; Goldberg et al., 2008; Loudon, 2009). Greater than 80% of pathogens that are found in domesticated animals are capable of infecting wildlife (Cleaveland et al., 2002), particularly in closely related species (Davies and Pedersen, 2008). The transmission of 75% of all threatening pathogens has been reported to result from close contact between cross-species hosts, and not from environmental exposure or vector-mediated transmission (Pedersen et al., 2007). Generalist pathogens that are capable of infecting multiple hosts have strong negative impacts on host fitness, often leading to wildlife population declines, and may, therefore, pose the greatest threat for local species extinction (Pedersen and Fenton, 2007; Pederson et al., 2007; Smith et al., 2009).

In addition, as environmental change is anticipated to continue to influence climatic shifts, i.e., towards warmer global temperatures, increased rainfall, and climatic variability [Intergovernmental Panel on Climate Change (IPCC), 2007], so too is parasitism expected to become more prevalent in wildlife populations (Costello et al., 2009; Harvell et al., 2002; Barrett et al., 2013). Warmer temperatures promote faster reproduction and ease of transmissibility of several parasite species, and since many parasites require wet conditions to complete their life cycle (Guernier et al., 2004; Nunn and Altizer, 2006), higher annual precipitation can lead to increases in parasite virulity (Froeschke et al., 2010). Shifts in climatic patterns may also alter the abundance and distribution of pathogens and their vectors (Daszak et al., 2000). For example, the expanded range of mosquito vectors associated with warming global temperatures is expected to increase transmission of mosquito-borne infections such as dengue fever and malaria (Epstein, 2000). As such, in many cases a wetter, warmer climate is likely to be positively correlated with parasite species richness (Allen et al., 2002; Hoberg et al., 2008; Larsen and Reopstorff, 1999; Guernier et al., 2004).

In primate species, pathogenicity may be difficult to detect within a population, since parasitic infections are common in nature and often produce asymptomatic and sub-lethal effects that may go unnoticed for extended durations (Murray et al., 1998; Goldberg et al., 2008). The situation changes, however, when the ecological balance of a habitat is disrupted (Ancrenaz et al., 2003). While parasite prevalence may be reduced in forest fragments due to the creation of edges – a hostile environment for parasites as a result of increased wind, sun, and aridity exposure (Fetcher et al., 1985; Murcia, 1995) – the associated changes in host density, ranging patterns, sociality, and feeding ecology may facilitate the spread of infection (Nunn et al., 2003; Nunn and Altizer, 2006; Gillespie and Chapman, 2008). Furthermore, parasite infections may compound the impacts of fragmentation for primate populations by reducing host condition and affecting nutrition, travel and predator escape, energy expenditure, and inter- and intraspecific competition (Dobson and Hudson, 1992; Hudson et al., 1992; Gillespie and Chapman, 2006). Increased prevalence of parasite infections has been observed in several primate taxa inhabiting disturbed landscapes (e.g., *Piliocolobus tephrosceles*: Gillespie et al., 2005a,b; Gillespie and Chapman, 2006; Chapman et al., 2006; *Papio hamadryas*: Ghandour et al., 1995; *Cercopithecus ascanius*: Goldberg et al., 2008; *Alouatta palliata mexicana*: Cristobal-Azkarate et al., 2010; *Lemur catta*: Loudon et al., 2006).

The survival of Madagascar's rich lemur diversity, representing more than 20% of extant primate species worldwide (Wilme et al., 2006; Mittermeier et al., 2008), is being increasingly threatened by anthropogenic influences, including urban expansion, slash-and-burn agriculture for livestock grazing, and deforestation for a growing logging industry (Myers et al., 2000; Ganzhorn et al., 2001; Harper et al., 2007; Elmqvist et al., 2007; Allnutt et al., 2008). Nearly half of the island's forest cover was lost in the latter half of the twentieth century (Green and Sussman, 1990; Harper et al., 2007), leaving a large proportion of lemur species restricted to isolated forest patches (Ganzhorn et al., 2000, 2001, 2003; Scott et al., 2006; Dunham et al., 2008; Olivieri et al., 2008; Craul et al., 2009). In addition to the direct impact that habitat change has on the health and survival of these endemic primates, changing climate patterns threaten to increase the abundance and distribution of pathogenic parasites capable of infecting lemur hosts (Barrett et al., 2013). A recent report from Barrett and colleagues (2013) describes the geographically widespread effects of climate change on parasite distributions, projecting that helminths and ectoparasites will be present in up to 80% of the remaining forested areas in Madagascar by 2080. As such, an understanding of how these pathogens may impact lemur populations, and how they may interact with fragmentation effects, may be critical for lemur conservation.

There is a considerable dearth of information on the endoparasitic profile of lemurs relative to other primate species (Nunn et al., 2003; Irwin and Raharison, 2009; Barrett et al., 2013; but see Junge and Louis, 2002, 2005a,b, 2007; Junge and Sauther, 2006; Loudon et al., 2006; Junge et al., 2008; Villers et al., 2008; Loudon, 2009; Clough, 2010). Twenty-seven helminth and 12 protozoan species have been described from lemur hosts thus far, which is likely a large under-representation of the parasitic assemblage actually present in lemur communities (Clough, 2010; Rasambainarivo and Junge, 2010). More extensive parasitological analyses conducted in other primate taxa have revealed greater parasite diversity in a much smaller species pool (Irwin and Raharison, 2009). Biomedical analyses of wild black lemurs (*Eulemur macaco macaco*), ring-tailed lemurs (*Lemur catta*), Verreaux's sifaka (*P. verreauxi*), ruffed lemurs (*Varecia variegata and V. rubra*), Decken's sifaka (*P. v. deckeni*), and red-fronted brown lemurs (*E. f. rufus*), have revealed a natural incidence of parasitism consistent with a commensal relationship with enteric bacterial flora (Dutton et al., 2003; Junge and Louis, 2005a,b, 2007; Irwin and Raharison, 2009). To date, the occurrence of pathogenic microorganisms has been rare in undisturbed populations; however, as several pathogens capable of infecting lemurs have been documented in Malagasy human populations and livestock (Rakoto-Andrianarivelo et al., 2002; Loudon et al., 2006; Loudon, 2009), detection of these pathogens may reflect a population's vulnerability to anthropogenic disturbance.

To complement investigations of wildlife responses to habitat fragmentation and the viability of forest fragments to sustain population numbers of a particular species, wildlife ecologist and conservation managers are urged to assess population health, including baseline health parameters, presence-absence data for parasite communities, and ecological factors that may facilitate disease spread (Barrett et al., 2013). As such, the aim of this chapter is to provide an overview of the parasite communities present in two populations of ring-tailed lemurs (*L. catta*) occupying forest fragments in Madagascar's south-central highlands. The fragments – Anja Special Reserve (34 ha) and the Tsaranoro Valley sacred forest (53 ha) – differ markedly in isolation, exposure to humans, livestock, and anthropogenic landscapes (i.e., agriculture, rural communities, communal water resources), and in *L. catta* resource structure. In addition, the population density of *L. catta* in the two fragments is highly diverse. I examine the component communities of protozoan and helminth parasites in *L. catta* and conduct between- and within-site comparisons of parasite prevalence to test the following predictions:

1) Since cross-species transmission of pathogens is associated with the degree of ecological overlap between species (Dobson and May, 1986; Scott, 1988; Goldberg et al., 2008; Smith et al., 2009), and since the study fragments vary markedly in extent of anthropogenic exposure (see Methods), I predict that the parasite species richness and the prevalence of infection in *L. catta* will differ between sites. Specifically, access to anthropogenic food and water sources at Anja is expected to be associated with an increase in the prevalence of pathogenic protozoa among *L. catta* via waterborne transmission (Karanis et al., 2007).
2) Since host density correlates positively with parasite prevalence and diversity (Anderson and May, 1992; Morand and Poulin, 1998; Packer et al., 1999), it is expected that *L. catta* at Anja, which occur at a population density that is six

times greater than at Tsaranoro, will exhibit higher parasite prevalence and richness when compared with those at Tsaranoro.

3) Given the marked seasonality characteristic of southern Madagascar, which fluctuates between a distinct hot, wet period (November to April) and a cold, dry period (May to September) (Jolly, 1966; Jolly et al., 2006), and the corresponding seasonal shift in parasite communities documented in other lemur species (*Microcebus murinus*: Raharivololona and Ganzhorn, 2010; *Propithecus edwardsi*: Wright et al., 2009; *Eulemur flavifrons*: Schwitzer et al., 2010), I predict that parasite prevalence, species richness, and cases of multiple infections will vary within *L. catta* populations according to season, with greater prevalence and richness in the wet season.

5.3 Methods

Study sites and animals – The two study sites are located in Madagascar's south-central highlands, a region currently dominated by secondary grasslands with small patches of fragmented forest. Relative to other biogeographic regions in Madagascar, this area has undergone recent landscape alteration, with extensive forest clearing throughout the 20th century primarily for livestock grazing and agriculture (Goodman and Benstead, 2003). Anja Special Reserve is a 34 ha rocky outcrop forest fragment that features mixed xerophytic and deciduous vegetation comprised of both endemic (e.g., *Adina microcephala, Erythroxylum platycladum, Turraea sericea*) and introduced (e.g., *Melia azedarach*, *Psidium cattleianum, Passiflora, Grewia*) species (Gould and Gabriel, in prep). It is located 12 km S of the town of Ambalavao, along the Route Nationale 7 highway (21° 51' S latitude and 046° 50' E longitude), and has been protected since 1999 for community-run ecotourism (Razafimandimby, pers. comm.; http://anjacommunityreserve.netai.net/anja.htm). It is in close proximity (~1 km) to a small village and, at the time of study, the fragment was bounded by anthropogenic landscape, including rice paddies, village gardens (these have since been removed; Clarke, pers. comm.), and a small man-made lake used for cattle watering and pisciculture. *L. catta* groups were regularly observed drinking from the lake concurrently with cattle, and local villagers used the water source for washing clothes, collecting water for the gardens, and extracting fish for food. *L. catta* also fed from the village gardens immediately adjacent the reserve. Over the duration of the study, an average of 38 tourists (range 2-194; determined via daily counts recorded throughout the study) visited the site each day in order to view *L. catta*, as well as ancestral tombs located within the forest (Gabriel, unpublished data).

The Tsaranoro Valley sacred forest is a 53 ha rocky outcrop forest fragment, similar to Anja in vegetative composition, including a combination of endemic (e.g., *Adina microcephala, Dombeya*, *Diospyros, Turraea sericea*) and introduced (e.g., *Aphloia theiformis, Grewia, Vepris elliottii*) species (Gould and Gabriel, in prep.). It is located 55 km SW of Ambalavao and 20 km east of the 31,160 ha Andringitra National Park (22° 05’ S latitude and 046° 46’ E longitude). Land clearing is extensive in the area, with nearly all of the once continuous forest now converted to open grasslands and a few crops and rice fields (Andrianomena, pers. comm.). With the exception of a few other fragments remaining within range for *L. catta* dispersal (~2-10 km radius of Tsaranoro), the study fragment is highly isolated from other primary forest by the Karambony mountain massif (1650 m elevation) to the west and the large Andringitra mountain massif (2658 m elevation) to the east. A village and three camps established for adventure tourism are located within 1 km of the forest, and *L. catta* groups were observed crossing the nearby agricultural crops and rice paddies; however, they were never seen exploiting resources from these sources. Tourist visitors to the reserve number far fewer than at Anja, with an average of 3 tourists per day (range 0-14; determined via daily counts throughout the course of the study) (Gabriel, unpublished data). Many of the large native fruit trees have been removed by selective logging from within the forest interior (e.g., *Ficus* and *Adansonia* spp.), and while extraction of timber is controlled due to cultural traditions of the local people (the forest is sacred due to presence of ancestral tombs), logging and other resource extraction by the villagers still occurred at the time of study. *L. catta* in this fragment was observed to travel long distances beyond the forest to forage in the matrix (Gabriel, 2013; Chapter 2).

The study spanned the late dry season (September to November) of 2010 and mid- to late-wet season (March to May) of 2011. Two groups of *L. catta* were studied at each site, with at total of 16 to 17 individuals/group, including immatures – Lake group (AL) and Boulder group (AB) at Anja, and Rangers group (TR) and Meva group (TM) at Tsaranoro. Group composition is presented in Table 5.1. The groups were selected based on the area of the fragment that they occupied, determined during an introductory observation period, in order to ensure that the heterogeneous habitat characteristics of each site were well represented (i.e., edge and interior of the forest and variable resource structure). Focal animals consisted of all adult males and adult females in each group, which were identified based on unique physical characteristics or abnormalities (e.g., eye-ring shape, tail shape/size, body colouring, deformed limb growth, loss of an eye, large scarring) that could be recognized by at least 25 m using binoculars. Myself and two field assistants, R. Simmons and I. Schneider-Crease, followed each focal group between the hours of 0700 and 1700 daily, rotating between groups every four days and between sites every three weeks, for a total of 16 days/group/study period.

Table 5.1 Group composition, male dispersal/immigration and number of focal animals in each study group

Group	Composition	# of dispersing/immigrant males	# of focal animals
Anja			
AL	5F, 8M, 3J, 3I	0/0	13
AB	6F, 6M, 4J, 5I	0/1	12
Tsaranoro			
TR	6F, 7M, 3J, 5I	3/1	13(11)*
TM	5F, 6M, 5J, 2I	0/1	11(12)*

Parentheses denote the number of focal animals following the male dispersal period. One male from TR emigrated to TM between study months and was included in the focal sessions of TM for the remainder of the study period.

Fecal sample collection and analysis - Fecal samples were collected opportunistically and non-invasively from known individuals for parasite analysis. Samples were collected within 10 min of defecation to minimize environmental contamination by free-living parasite species (Gillespie et al., 2008). Approximately 2 g of fecal material was extracted from the interior of the sample and divided into two equal portions. Each portion was placed in a 2 mL microcentrifuge tube: one containing 1 mL of 12% polyvinyl alcohol (PVA) and the second containing 10% formalin for later identification of protozoan and helminth parasites, respectively. Each tube was secured with a screw cap, sealed with parafilm, and labeled with the sample number, individual identification, date, and time of collection. Multiple samples were collected from each focal animal in each season: three to four samples from each animal in the dry season and two samples for each animal in the wet season. A total of 291 fecal samples were collected over the study period: 78 for AL group and 72 for AB group at Anja, and 72 for TR group and 69 for TM group at Tsaranoro.

A subset of 98 fecal samples was selected for endoparasite identification: 49 samples from the dry season and 49 samples from the wet season, such that each focal individual was represented for both seasons. Identification of endoparasites was conducted by the Chapman Lab at McGill University. Protozoan parasites were identified using a trichrome stain procedure (Wheatley, 1951; Sloss et al., 1994). This permanent staining technique enables reliable detection and identification of protozoan cysts and trophozoites. In this procedure, a small amount of fecal material that has been stored in PVA is placed on a slide and allowed to fix for 1 hour. The sample is then placed into a mixture of 70% alcohol and iodine and then stained and fixed using a trichrome solution. After 2-8 minutes, the sample is rinsed three times with increasing alcohol concentrations from 90% to 100%, followed by a clearing agent (Xylene), and allowed to dry thoroughly. Protozoa were examined using a Leica DM2500 microscope.

Helminth parasites were recovered using an ethyl-acetate fecal sedimentation technique (Ash and Orihel, 1991; Greiner and McIntosh, 2009). This protocol enables detection of larger helminth eggs and larva that do not float readily. In this procedure, one gram of feces is weighed out from each sample, diluted in approximately 2mL of water, and filtered through cheesecloth. Samples are then transferred to 15mL centrifuge tubes and centrifuged for 2.5 mins at 2500 rpm. The supernatant is discarded and the concentrated pellet is reconstituted in 7 mL of water plus 3 mL of ethyl acetate and centrifuged for 3 mins at 3000 rpm. The supernatant is discarded and the pellet reconstituted in approximately 1 mL of 10% neutral buffered formalin. Slides are prepared by placing an aliquot of pellet homogenously suspended in formalin in the center of a glass slide and covering with a cover slip. Helminths were examined at 20x magnification using a Leica DM2500 microscope. When possible, helminths were identified by the lab technician to the family level. Further identification to the genus level is an estimation based on previous endoparasite reports for free-ranging *L. catta* (Loudon, 2009) and captive lemur species (St. Louis Zoo Guide to Lemur Parasites, 2005).

Parasite infections were described based on prevalence, species richness, and incidence of multiple infections. Prevalence indicates the proportion of individuals in a population sample that are infected by a particular endoparasite species. Species richness was characterized as the number of unique endoparasite species recovered from all individuals within the sample population. Multiple infections were recorded when a single individual was infected by more than one unique endoparasite species.

Statistical analysis – Endoparasite prevalence, richness, and incidence of multiple infections were grouped by site and by group and analyzed across seasons. Chi-square tests of independence were used to determine differences in parasite prevalence (i.e., the proportion of infected inidividuals in each population) and multiple infections according to site and season (N=24 and 25 individuals). Within-site differences in parasite prevalence and multiple infections were determined using Fischer's exact tests, since the number of focal animals in each group was too small to perform chi-square analyses reliably (N=11 to 13 individuals). Statistical significance was set at $P<0.05$.

5.4 Results

Between site differences in parasites – *L. catta* at Anja harboured parasite species that included three protozoa and two helminths – *Endolimax nana* (phylum: Archamoebae), *Isospora belli* (phylum: Apicomplexa; subclass: Coccidea), *Balantidium coli* (phylum: Ciliophora), and two unidentified nematodes (phylum: Nematoda). *L. catta* at Tsaranoro exhibited a parasite species richness that included two protozoa and four helminths – *I. belli*, *B. coli*, a strongyloid (likely of the genus *Lemuricola*; subfamily: Enterobiinae), a strongyle (likely of the genus *Lemurostrongyles*; family: Strongylidae), and two unidentified nematodes (phylum: Nematoda).

There was some variation in parasite prevalence between study sites. *L. catta* at Tsaranoro exhibited a significantly higher prevalence of helminth parasites in both the dry (Chi-square test of independence: X^2=4.54, df=1, P=0.03) and wet (X^2=24.2, df=1, P<0.0001; Figure 5.1) seasons when compared to the Anja population. Similarly, *L. catta* at Tsaranoro had somewhat higher protozoan parasite prevalence than those at Anja during the dry season, whereas *L. catta* at Anja exhibited a higher prevalence of protozoan parasites during the wet season; however, these results were not significant (Chi-square test of independence; dry season: X^2=2.64, df=1, P=0.1; wet season: X^2=1.33, df=1, P=0.25; Figure 5.2). There were no between site differences in cases of multiple infections in *L. catta* in either season (Chi-square test of independence; dry season: X^2=0.17, df=1, P=0.68; wet season: X^2=2.05, df=1, P=0.15).

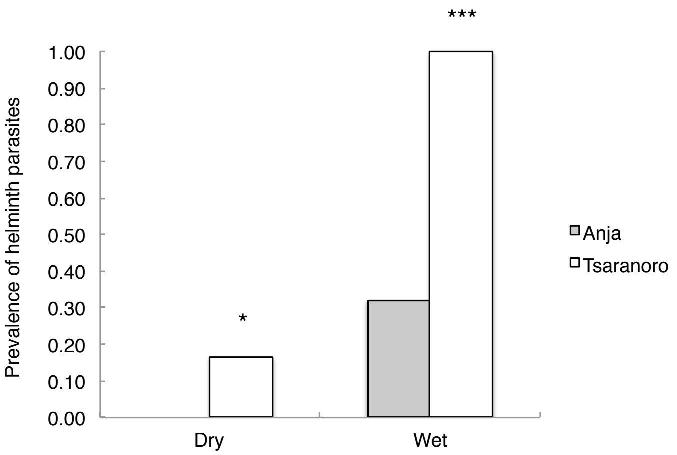

Figure 5.1 Comparison of the prevalence of helminth infections between *L. catta* at Anja and Tsaranoro during the dry season (September to November) of 2010 and wet season (March to May) of 2011. Asterisks denote statistically significant differences (Chi-square test of independence; '***' *P*<0.0001; '*' *P*<0.05)

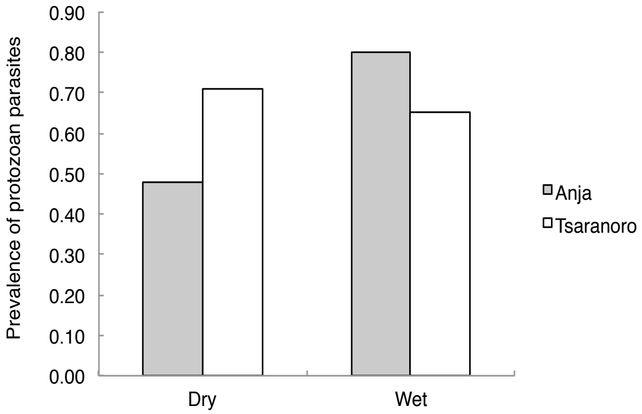

Figure 5.2 Comparison of the prevalence of protozoan parasite infections between *L. catta* at Anja and Tsaranoro during the dry season (September to November) of 2010 and wet season (March to May) of 2011.

Within-site differences – At Anja, there was no difference between groups of *L. catta* in the prevalence of protozoan (Fischer's exact test; dry season: *P*=0.24; wet season: *P*=1.0) or helminth parasites (*P*=1.0), nor in cases of multiple infections (*P*=1.0). At Tsaranoro, prevalence of parasites did not differ between groups in the dry season (Fischer's exact test; protozoa: *P*=1.0; helminths: *P*=0.3), nor did cases of multiple infections (*P*=0.3).

However, in the wet season *L. catta* in TM group exhibited a higher prevalence of protozoan parasites (Fischer's exact test: *P*=0.001) and a greater incidence of multiple infections (*P*=0.04) when compared with those in TR group (Figure 5.3).

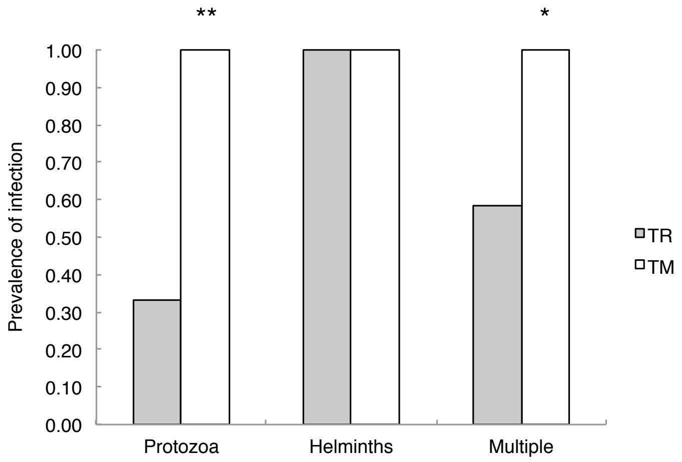

Figure 5.3 Comparison of the prevalence of protozoan and helminth infections and cases of multiple infections between *L. catta* groups at Tsaranoro during the wet season (March to May) of 2011. Asterisks denote statistically significant differences (Fischer's exact test; '**' $P<0.001$; '*' $P<0.05$)

Density dependence – I found no indication that parasite prevalence in the study populations was based on the density of hosts. Anja contains the highest density of *L. catta* (6.6 animals/ha) compared with all other sites in which they have been studied, whereas the population density of *L. catta* at Tsaranoro is one-sixth that at Anja (1.13 animals/ha; Cameron and Gould, 2013; Gould and Gabriel, in prep). However, prevalence of parasite infection was lower for *L. catta* at Anja when compared with *L. catta* at Tsaranoro, with the exception of slightly higher protozoa prevalence in Anja groups during the wet season.

Seasonal differences in parasite prevalence – I found a seasonal effect on parasite prevalence for *L. catta* at Anja. A significantly higher proportion of *L. catta* was infected by protozoan (Chi-square test of independence; X^2=5.56, df=1, *P*=0.02) and helminth

(X^2=9.52, df=1, P=0.002) parasites during the wet season when compared with the dry season (Figure 5.4). There was no difference in the prevalence of multiple infections between seasons (X^2=1.22, df=1, P=0.27).

At Tsaranoro, there was no seasonal difference in prevalence of protozoan parasites (Chi-square test of independence; X^2=0.17, df=1, P=0.68). However, *L. catta* exhibited a higher prevalence of helminth parasites (X^2=33.36, df=1, P<0.0001) and cases of multiple infections (X^2=4.04, df=1, P=0.04) in the wet season when compared with the dry season (Figure 5.5).

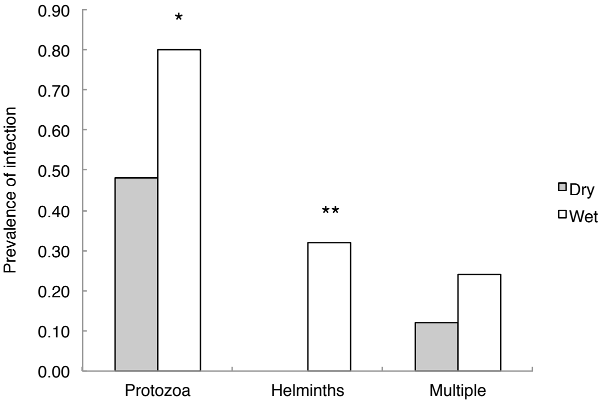

Figure 5.4 Comparison of the prevalence of protozoan and helminth infections and cases of multiple infections in *L. catta* at Anja between the dry season (September to November) of 2010 and wet season (March to May) of 2011. Asterisks denote statistically significant differences (Chi-square test of independence; '**' P<0.001; '*' P<0.05)

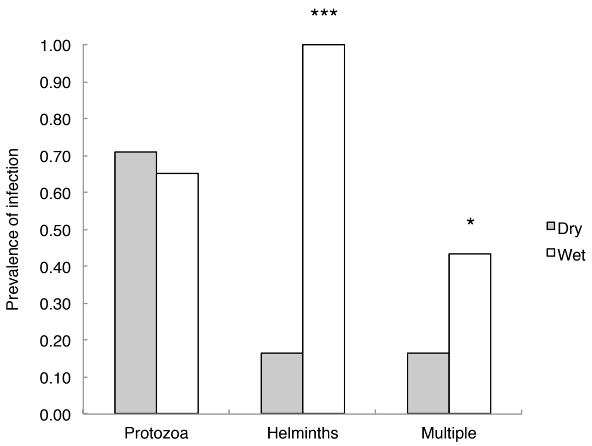

Figure 5.5 Comparison of the prevalence of protozoan and helminth infections and cases of multiple infections in *L. catta* at Tsaranoro between the dry season (September to November) of 2010 and wet season (March to May) of 2011. Asterisks denote statistically significant differences (Chi-square test of independence; '***' $P<0.0001$; '*' $P<0.05$)

5.5 Discussion

Both populations of *L. catta* harboured a parasite species richness consisting of generalist protozoa and helminths that are capable of infecting multiple hosts, including humans, livestock, and wildlife. Protozoans are unicellular eukaryotes, sizing 10-50 μm, which may exhibit symbiotic or parasitic relationships with multicellular organisms (Poulin and Morand, 2004). Parasitic protozoans often display a dormant cyst stage capable of surviving harsh environments and are commonly transmitted into their host in this form (Smyth, 1976). *E. nana* is an amoebozoa from the phylum Archamoebae that infects the intestinal tract of various animals and humans (Roberts and Janovy, 2009). It is transmitted via direct ingestion of mature cysts in contaminated food, water, and fecal material, and while largely non-pathogenic, it may cause intermittent or chronic diarrhoea (Stauffer and Levine, 1974; Silberman et al., 1999; Graczyk et al., 2005). *E. nana* is commonly mistaken for similar species, particularly of the genus *Entamoeba*, which may be responsible for several pathologies including amoebic dysentery, dehydration, tissue damage, and liver abscess (Kucik et al., 2004; Roberts and Janovy, 2009). *I. belli* is a protistan parasite in the phylum Apicomplexa, subclass Coccidia. Coccidians are spore-forming, intracellular parasites that live and reproduce within the cells of the intestinal tract of vertebrate and invertebrate hosts (Duszynski et al., 1999). Infection, known as coccidiosis, is transmitted via direct ingestion of contaminated food, water, or feces. *I. belli* can be highly pathogenic, leading to compromised immune function, dehydration, malnutrition, anemia, and sometimes death (Roberts and Janjovy, 2009). *B. coli* is a ciliated protozoan in the phylum Ciliophora. *Balantidium* spp. is transmitted via direct ingestion of contaminated food or water sources and occupies the cecum and colon of the host (Roberts and Janovy, 2009). *B. coli* infections tend to be asymptomatic in common hosts, such as pigs, rats, and other mammals, and are not readily transmissible from one species to another. However, when cross-species transmission does occur or when the host becomes immunocompromised, *B. coli* can be a serious pathogen causing ulcers, dysentery, urogenital infections, and perforation of the colon, and may result in death (Nakauchi, 1999; Roberts and Janovy, 2000).

Nematodes (roundworms of the orders Rhabditida, Strongylida, Ascarida, Spirurida, and Trichinellida) are characterized by their large species diversity (over 80 000 species have been identified, 15 000 of which are parasitic) and are the most widely identified parasites of primates (Chapman et al., 2005). Strongyles are parasitic pinworms of the subfamily Enterobiinae that infect the intestines and colon of their hosts. Infections are transmitted via direct ingestion of fecal material (Roberts and Janovy, 2009) and are generally non-pathogenic (but see Murata et al., 2002). Pinworms found in primate species belong to three genera: *Lemuricola* (found in strepsirrhine primates), *Trypanoxyuris* (found in platyrrhine primates), and *Enterobius* (found in catarrhine primates and humans) (Loudon, 2009). *Lemuricola* spp. is a class of pinworms that has been documented in all lemur families and represents the most abundant endoparasite in many studies of lemur health (Wright et al., 2009). Symptoms of *Lemuricola* spp. may include perianal itching, dehydration, weight loss, and aggressive behaviour (Barrett et al. 2013). Strongyloides are a class of nematode worms of the family Strongylidae that are common in monkeys and apes (Glen and Brooks, 1985) yet have remained rare in parasitic studies of lemurs (Chabaud et al., 1965; Junge and Sauther, 2006; Loudon, 2009), possibly due to an underrepresentation of cases in wild lemur populations. Strongylid worms exhibit a direct life cycle with alternating free-living and parasitic stages. Parasitic larvae enter the host by penetrating the skin and migrate to the lungs where they mature, enter the pharynx, and are swallowed, ultimately reaching the small intestine (Roberts and Janovy, 2009). Here the larva mature into female worms and reproduce by parthenogenesis, with the potential for autoinfection and multiplication within the host (Grove, 1996; Anderson and Anderson, 2000). Live larvae can often be seen in the fecal decrement of the host, and this was seen on several occasions in fecal samples collected from the Tsaranoro population of *L. catta*. Symptoms of infection may include dermatitis at the point of entry in the skin, coughing, tissue damage, sepsis, ulcers, and, in extreme cases, obstruction of the intestinal tract and loss of peristalsis (Roberts and Janovy, 2009). Loudon (2009) reported cases of strongylid infection of the genus *Lemurostrongylus* in both *L. catta* and *Propithecus verreauxi* at Beza Mahafaly Reserve in southern Madagascar.

The differences in endoparasite species richness found between the two study sites is likely reflective of variations in the rate of exposure to each unique parasite stemming from distinct ecological conditions in the fragments. The fact that *L. catta* at Tsaranoro harboured a higher prevalence of helminth parasites in both the dry and the wet seasons when compared with the Anja population may result from the extended territories and ranging distances exhibited by the Tsaranoro groups (Gabriel, 2013; Chapter 2). Strongyle and strongyloid nematodes are monoxenous parasites, referring to a direct mode of transmission to the definitive host (Anderson and Anderson, 2000). They include a free-living generation that can persist in the external environment and produce infective larvae that require oral ingestion or direct contact with the skin of the host (Nigon and Roman, 1952; Roberts and Janovy, 2009). Nematodes species are ubiquitous across ecological niches and free-living forms feed on a wide range of materials, including plant tissues and microorganisms present in vegetative matter and soil (Smyth, 1976). As such, hosts that encounter a high degree of habitat diversity, correlating positively with increasing range size (Dritschilo et al., 1975; Price and Clancy, 1983; Gregory, 1990), are more likely to come across a greater number of nematode parasites (Nunn et al., 2003). Thus, long daily travel distances, particularly in the form of terrestrial locomotion, would be expected to increase exposure to these parasitic species through direct contact with the environment and other individuals (Nunn et al., 2003; Vitone et al., 2004; Nunn and Dokey, 2006).

Many enteric pathogenic protozoa are transmitted via direct contact with contaminated food and water sources through the fecal-oral route (Nunn et al., 2003; Karanis et al., 2007). *L. catta* at Anja have greater access to anthropogenic food and water resources, due to the close proximity of village gardens and a man-made lake adjacent the reserve, and this would be expected to result in greater exposure to pathogenic protozoa, such as *I. belli* and *B. coli*. A higher prevalence of protozoan infection has been reported for savannah baboons (*Papio anubis*; Eley et al., 1989; Hahn et al., 2003; Weyher, 2009) and ring-tailed lemurs in disturbed gallery forest (Loudon, 2009) that frequently exploit anthropogenic food and water resources (crops, garbage piles, well water). However, contrary to expectations, prevalence of protozoa infection was only slightly higher at Anja during the wet season, and *L. catta* at Tsaranoro actually harboured a higher prevalence of protozoa during the dry season. Again, this may result from higher rates of exposure to different environmental substrates in the Tsaranoro lemurs due to longer travel distances. *L. catta* at Tsaranoro frequently traveled terrestrially throughout the matrix outside the forest fragment, and while, unlike at Anja, groups were never observed exploiting anthropogenic resources, they regularly crossed rice paddies and other agricultural crops in order to access patchily distributed fruit trees. This was particularly evident in the ranging patterns of TM group, which may explain the higher prevalence of protozoa and cases of multiple infections observed in this group during the wet season.

Differences in the nutritional status of each population may also contribute to variations in parasite infections (Chapman et al., 2005), as a low quality diet can hinder immune function and increase susceptibility of infection to some helminth parasites (Weyner, 2009). *L. catta* at Tsaranoro spend more time feeding and have a more broad-based diet when compared to the Anja population, which may reflect differences in the nutritional quality of plant resources between the two fragments; however nutritional analyses are required to confirm this prediction (Chapter 3). In addition, *L. catta* at Anja spend large portions of its feeding budget consuming fruits and leaves from the introduced tree *Melia azedarach* (Chapter 3), which have known antiparasitic properties (Nakanishi et al., 2011; Munir et al., 2012), and it is possible that this may have helped to reduce the overall parasitic burden experienced by the Anja population.

Parasite prevalence in hosts occupying disturbed habitats has frequently been linked to host population size and density, since greater contact between hosts increases infection rates of directly transmitted parasites (Anderson and May, 1992; Morand and Poulin, 1998; Poulin, 1998; Packer et al., 1999; Nunn et al., 2003). Packer et al. (1999) reported higher disease outbreaks in African lions (*Panthera leo*) corresponding with years of high population density, and in a study of 101 anthropoid primates harbouring 231 parasite taxa (helminths, protozoa, viruses, bacteria, fungi), Nunn et al. (2003) found that population density was among the highest predictors of parasite prevalence and species diversity. However, contrary to expectations, I found no evidence that parasite prevalence is host-density dependent in the *L. catta* populations, particularly with respect to helminth parasites. The population density of *L. catta* at Anja is six times greater than at Tsaranoro (6.6 animals/ha vs. 1.13 animals/ha; Cameron and Gould, 2013; Gould and Gabriel, in prep.), yet the prevalence of nematode parasites across seasons and protozoan parasites in the dry season was higher in the Tsaranoro population. Similarly, Gillespie and Chapman (2008) found no relationship between host population density and parasite prevalence in colobines inhabiting forest fragments at Kibale National Park, Uganda. Host susceptibility is a key factor in density-dependent parasite transmission, such that the density of susceptible hosts may, in fact, be significantly lower than overall population density (Packer et al., 1999; Nunn et al., 2003). Since *L. catta* at Anja have consistent, year-round access to introduced fruit trees (*M. azedarach* and *P. cattleianum*) and anthropogenic resources (e.g., village gardens, rice paddies, lake water; Chapter 3), and since *M. azedarach* contains antiparasitic properties (Nakanishi et al., 2011; Munir et al., 2012), host susceptibility may be comparably low in this population despite its high population density. Weyher (2009) suggested that a high quality diet from crop raiding and consumption of human food scraps likely accounted for a reduced susceptibility to infection by certain helminths in a population of savannah baboons (*P. anubis*). Loudon (2009) found that *L. catta* that ranged near the research camp at Beza Mahafaly and frequently consumed food scraps from human garbage and well water exhibited a lower prevalence of helminth infections when compared to groups that occupied the forest interior. However, in each of these taxa, protozoan infection was higher among individuals that exploited these novel resources (Weyher, 2009; Loudon, 2009). A comparison among a larger subset of *L. catta* populations inhabiting forest fragments with differing degrees of isolation, resource availability, and human disturbance would provide a greater understanding of host-parasite dynamics related to population density in this species.

Given that Madagascar is projected to increase in temperature by 1.1-2.6° C and in rainfall by 2050, with the exception of the south and southeastern coasts which will become more arid (Hannah et al., 2008; Tadross et al., 2008; Barrett et al., 2013), information on the seasonal nature of lemur-parasite dynamics is critical for determining future disease risk. The fact that parasite prevalence and cases of multiple infections in the study populations showed a general increase in the wet season when compared to the dry season is expected given that many parasite species exhibit greater rates of reproduction and higher virulence under warmer, wetter conditions (Guernier et al., 2004; Nunn and Altizer, 2006; Froeschke et al., 2010). Similar findings have been reported for other lemur species: Raharivololona and Ganzhorn (2010) found a higher endoparasite richness and prevalence in grey mouse lemurs (*Microcebus murinus*) during the warm, wet season in southern Madagascar, and Schwitzer et al. (2010) found higher rates of endoparasite infection during the rainy season in blue-eyed black lemurs (*Eulemur flavifrons*) inhabiting forest fragments in northwest Madagascar. Higher prevalence during the rainy season has also been reported for a strongyle nematode infecting chimpanzees (*Pan troglodytes*; Huffman et al., 1997), as well as for *Trichuris* spp. in colobine monkeys (*Colobus* spp.) in wetter habitats (Chapman et al., 2010). Parasite prevalence observed during the wet season in the study populations may forecast the infections rates that may be expected more generally with the projected climatic change across Madagascar, with higher temperatures and increased rainfall facilitating infection in *L. catta* populations, especially in the more northern portions of its geographic range (Hannah et al., 2008; Tadross et al., 2008; Barrett et al., 2013).

The impact of parasite infections in *L. catta* at Anja and Tsaranoro remains unknown, as long term monitoring of host-parasite dynamics are required to determine commensal and pathogenic states of infection. This is particularly important under the current environmental conditions since anthropogenic habitat disturbance can have significant impacts on the disease ecology of *L. catta.* Loudon and colleagues (2006) found that *L. catta* that frequented the tourist/research camp area of Beza Mahafaly Reserve in southwestern Madagascar exhibited behavioural variations that may increase the rates of parasite transmission when compared with gallery forest groups. Camp groups were more terrestrial, exploited resources from human trash pits, and engaged in coprophagy (fecal ingestion) of human, dog, and zebu cattle feces (see also Fish et al., 2007; Gemmill and Gould, 2008), all of which are behaviours associated with increased risk of infection. Gillespie and Chapman (2008) found high prevalence of parasites in fragment-dwelling colobines (*Colobus* spp.) that were likely of human or domestic animal origin, and were absent in colobus monkeys in unfragmented forest where contact between species is low (Gillespie et al., 2005a,b). Goldberg et al., (2008) found that red-tailed guenons (*Cercopithecus ascanius*) that enter crops and exploit anthropogenic resources share a higher genetic similarity in gut bacteria with humans and livestock compared with groups from undisturbed forest. Thus, habitat disturbance may produce an avenue of transmission to novel parasite fauna through increased contact with humans and domesticated animals. This is of particular concern for populations exhibiting high extinction risk since free-ranging hosts may lack evolved strategies for coping with parasites that they have not encountered previously (Holmes, 1996). Such a case was demonstrated when a wild population of black-footed ferrets (*Mustela nigripes*) in Wyoming became extirpated following exposure to canine distemper (Thorne and Williams, 1988).

In addition to increasing contact rates among species, habitat disturbance can influence disease emergence indirectly by compromising host condition. For example, inbreeding increases the expression of potentially harmful mutations, due to a reduction in genetic heterozygosity (Charlesworth and Charlesworth, 1999), which may impede pathogen recognition when they occur in immune-related allele regions (Potts and

Wakeland, 1993). Populations in fragmented habitats often become heavily isolated from conspecifics due to large dispersal distances or constraints within the surrounding non-habitat. Consequently, inbreeding can be a negative outcome of habitat fragmentation and may correspondingly influence disease emergence within a population (Potts and Wakeland, 1993; Spielman et al., 2004; Smith et al., 2009). Habitat disturbance is also associated with an increase in environmental stressors in wildlife populations (e.g., Wasser et al., 1997; Foley et al., 2001; Millspaugh et al., 2001; Creel et al., 2002; Rangel-Negrin et al., 2009), and since stress can present significant consequences with respect to immune function (Monjan, 1981; Kiecolt-Glaser et al., 1984; Golub and Gershwin, 1985; Rigby and Moret, 2000; Yang and Glaser, 2002; Sapolsky, 2005) and susceptibility to infections (Scott, 1988; Holmes, 1996; Lafferty and Kuris, 2005), greater incidence of parasite infection can be expected in disturbed habitat conditions. In addition, high parasite loads can compound host susceptibility to other diseases by lowering immune function, thus further facilitating a negative synergy between host body condition and rate of infection (Beldomenico and Begon, 2010).

These factors are important for the study populations given the extent of habitat disturbance and anthropogenic exposure in the region, and may be of particular concern for *L. catta* at Anja when compared with Tsaranoro. The population density of *L. catta* at Anja is higher than at any other site in which the species has been studied (Cameron and Gould, 2013; Gould and Gabriel, in prep.) and contact among individuals within and between groups is high, potentially facilitating disease transmission (Anderson and May, 1992; Morand and Poulin, 1998; Poulin, 1998; Packer et al., 1999; Nunn et al., 2003). *L. catta* at Anja is also in frequent contact with humans and livestock and exploits many common resources that are at high risk of contamination by multi-host parasites such as *I. belli, B. coli*, and *Lemuricola* spp., as well as other pathogenic species that were not detected in this study but have been found amongst other wild lemur populations (e.g., *Toxoplasma gondii*, *Ascaris petiti*, *Trichurus* spp., unidentified cestodes; reviewed by Junge and Sauther, 2007). Moreover, the Anja population of *L. catta* is heavily isolated from all other conspecific populations – the nearest fragment containing *L. catta* is at least 8 km away and is separated by villages, crops, rocky savannah, and a national highway. Thus inbreeding in this population is likely, although not confirmed, and could impact immunity of *L. catta* to novel diseases or outbreaks of high intensity (Potts and Wakeland, 1993; Spielman et al., 2004; Smith et al., 2009). Genetic analyses to determine male dispersal rates and inbreeding at Anja are currently being examined (Clarke, in prep.). Finally, the study groups at Anja exhibit high fecal glucocorticoid levels when compared with those at Tsaranoro, which may be indicative of a chronic stress response due to the current ecological conditions of the habitat (Gabriel et al., in prep; Chapter 4). Chronically high stress levels may compromise immune function in *L. catta* and increase its susceptibility to disease (Monjan, 1981; Kiecolt-Glaser et al., 1984; Golub and Gershwin, 1985; Scott, 1988; Holmes, 1996; Rigby and Moret, 2000; Yang and Glaser, 2002; Lafferty and Kuris, 2005; Sapolsky, 2005). Finally, although I found a similar species richness in protozoa and helminth parasites at each site, a previous study on *L. catta* population demographics and health during the early dry season of 2010 at the same sites found a higher diversity of protozoan parasites (five species vs. one) in *L. catta* at Anja (Gould and Gabriel, in prep.). Thus, while the *L. catta* groups at Anja exhibited relatively low parasite prevalence and similar species richness when compared with *L. catta* at Tsaranoro, I suggest that continued monitoring of the disease ecology of this population (i.e., over the next decade) may be critical for population sustainability.

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6 CONCLUSIONS

6.1 Summary

As the global population of humans continues to rise, it is inevitable that ever-expanding commercial, agricultural, and infrastructural development impinges upon wildlife habitats (Pimm and Askin, 1995; Wilcove et al., 1998; Smith et al., 2009). With virtually every environmental niche impacted upon by human encroachment in some form or another, habitat loss and fragmentation represent the most critical threats to the future of global biodiversity (Wilson, 1992; Smith et al., 2009). Landscapes altered by anthropogenic activities are characterized by an array of ecological effects that potentially impact the abundance and distribution of wildlife and, under many circumstances, present significant challenges to which individuals must adapt if they are to persist under the disturbed conditions. A habitat's suitability for supporting a population of a given species is dependent upon species-specific biological and ecological characteristics that enable it to persist in a habitat area, such as home range size, dispersal ability, use of dispersal habitat, dietary flexibility, and mode of locomotion (e.g., Estrada and Coates-Estrada, 1996; Haddad, 1999; Haddad and Baum, 1999; Tutin, 1999; Crooks, 2002). However, as no two habitats are altered in precisely the same way, considerable intraspecific variation in responses to habitat fragmentation can be expected. As such, assessing species sensitivity to habitat disturbance requires an integrated understanding of wildlife-habitat relationships on a regional scale. Cross-site comparisons of space-use (i.e., home range size, ranging patterns, use of the matrix), activity budgets, resource structure, and health from populations of the same species occupying various habitat patches can provide important insight regarding fragment quality and the capacity of habitat fragments to sustain populations over time.

Lemur catta is an ecologically adaptable species, capable of (i) occupying a range of habitats throughout its geographic range in southern Madagascar (Jolly, 1966; Sussman, 1977; Sauther et al, 1999; Goodman et al., 2006; Gould, 2006; Kelley, 2011; LaFleur, 2012; Cameron and Gould, 2013; Gabriel, 2013), (ii) coping with extreme seasonality and a variable and unpredictable availability of resources throughout its annual cycle (Sauther, 1998; Sauther et al., 1999; Wright, 1999; LaFleur and Gould, 2009), and (iii) opportunistically exploiting resources, native or introduced/anthropogenic (e.g., crops, invasive plant species, human food waste), using both arboreal and terrestrial locomotion (Sauther, 1998; Gould et al., 1999; Sauther et al., 1999; Simmen et al., 2006). As such, this species has been able to persist in regions inaccessible to other lemur species (e.g., altitudes >2000 m in the central plateau; Goodman and Langrand, 1997; Goodman and Rasolonandrasana, 2001; Ganzhorn et al., 2006) and in harsh habitat types throughout its geographic range (e.g., Goodman and Langrand, 1996; Gould et al., 2011; Kelley, 2011; LaFleur, 2012). However, no prior study has compared the behaviour and ecology of *L. catta* inhabiting small, isolated forest patches, a condition under which much of the species is now found (Sussman et al., 2003; Goodman et al., 2006; Bodin et al., 2006; Cameron and Gould, 2013; Gabriel, 2013), and the long-term viability of fragment-dwelling populations remains uncertain.

As predicted, the results of this dissertation demonstrate considerable intraspecific variation, between and within habitats, with respect to responses of *L. catta* to habitat fragmentation. At the time of study, the populations of *L. catta* at both Anja Reserve and

Tsaranoro Valley sacred forest appear stable. Each population has established diverse strategies with respect to habitat use, activity budgets, and foraging (Chapters 2 and 3) to optimize fitness under unique ecological conditions. At Anja, *L. catta* appear to employ an energy minimizing strategy, as has been suggested for this species at other sites where it has been investigated (Sauther, 1994, 1998; Rasamimanana and Rafidinarivo, 1993; Wright, 1999; Loudon et al., 2008). The Anja groups depended on small home range areas, highly concentrated utilization distributions, and a few key food resources, and correspondingly exhibited lower energy expenditure and foraging effort when compared with the Tsaranoro groups. In this fragment, introduced (*Melia azedarach* and *Psidium cattleianum*) and anthropogenic resources (village gardens, water from a man-made lake) provide access to abundant food items year-round, which require little effort to procure. The reduced foraging effort leaves more time available for resting and socializing (grooming and play behaviour), and may afford energy reserves that can be directed toward intergroup competitive interactions given the dense and isolated population distribution. In addition, abundant resources facilitate high birth rates (twinning is common among females at Anja) and reproductive success (infant mortality is low), thus contributing to high population fitness. At Tsaranoro, the removal of many large native fruit trees from the fragment interior (Andrianomena, pers. comm.), lack of abundant fallback foods/introduced alternatives, and the patchy distribution of food items throughout the landscape necessitates that *L. catta* occupy large home ranges and travel long distances to forage in the matrix surrounding the forest fragment. As such, I suggest that *L. catta* at Tsaranoro exhibit an energy maximizing strategy (Sauther, 1994, 1998; Rasamimanana and Rafidinarivo, 1993; Wright, 1999; Loudon et al., 2008), as indicated by greater proportions of the activity budget dedicated to feeding at the expense of time spent resting, a greater dietary breadth, and increased energy expenditure when compared with the Anja groups.

Yet despite expressing unique behavioural strategies that enable *L. catta* to occupy both fragment habitats, each habitat presents ecological challenges that may impact the long-term viability of the study populations. At Anja, the artificial resource structure appears to support a population of *L. catta* that is far above a natural carrying capacity for the size of the fragment and extreme isolation from other suitable habitat prevents dispersal. In response to an exceptionally high population density (6.6 lemurs/ha; Cameron and Gould, 2013; Gould and Gabriel, in prep.) – likely the combined result of a crowding effect associated with habitat fragmentation (Debinski and Holt, 2000), an increased productivity of food resources (Greene et al., 2002; Asbjornsen et al., 2004), and a near absence of predators or interspecific competition (Chapter 2) – *L. catta* groups at Anja are faced with an intensification of social interactions that may extend beyond their adaptive life history strategies. The study groups at Anja exhibited greater territorial marking and intergroup competition over highly monopolized resources when compared with *L. catta* at Tsaranoro, which may have contributed to the elevated levels of fecal glucocorticoids (fGCs) observed in the Anja lemurs throughout the study period (Chapter 4). Prolonged release of high concentrations of GCs in the absence of energetic constraints is indicative of a chronic stress response (McEwan and Wingfield, 2003; Wingfield, 2005), and may signify a population's inability to adapt to the ecological and social conditions of a fragmented habitat. Chronic stress can have a variety of negative consequences on individual health, including long-term inhibition of the reproductive system, immunosuppression, muscular dystrophy, disruption of neuronal cell function, and suppression of growth (Sapolsky et al., 2000; Wingfield and Romero, 2001; Abbott et al., 2003), thus impacting fitness and survivorability. In addition, the inability to disperse to habitats containing conspecifics potentiates inbreeding depression for fitness traits (i.e., reduced fecundity, high infant mortality, increased rate of disease), which may be particularly pronounced under stressful environmental conditions (Armbruster and Reed, 2005), thus presenting a significant challenge to the future success of this population.

At Tsaranoro, traveling and foraging in the matrix may increase predation pressure, particularly for juveniles and weaning infants. Infant mortality was much higher at Tsaranoro than at Anja (43% vs. 12.5%, respectively), although it is on par with rates observed in *L. catta* populations occupying other habitat types (Sussman, 1991; Gould et al., 1999; Jolly and Pride, 1999; Gould et al., 2003). Extended travel distances may also increase exposure to endoparasites through contact with contaminated material in the environment (Chapter 5), thereby increasing disease risk within the population. In addition, while *L. catta* possesses life history strategies that enable it to survive in the face of Madagascar's harsh environmental and ecological challenges (i.e., extreme seasonality, unpredictable resource availability, erratic climatic events) (Jolly, 1984; Sauther et al., 1999; Wright, 1999), due to low population numbers and limited dispersal capacity (only a few fragments containing conspecifics are within dispersal distance) the Tsaranoro population remains sensitive to local extirpation if presented with a considerable ecological threat (e.g., if forest loss continues, a stochastic disease outbreak occurs, or the area is impacted by an extreme environmental event).

6.2 Future directions

I propose that long-term monitoring of the *L. catta* populations at Anja and Tsaranoro, as well as those in other isolated forest fragments in Madagascar's central highlands, will be critical for species preservation in this geographic region. The central highlands has been devastated by deforestation, and large-scale land clearing in the 20th century perpetuated the near complete eradication of the once extensive forest cover that expanded the landscape (Gade, 1996; Goodman and Benstead, 2003). Currently, sites in this region are protected simply due to the presence of *L. catta* populations for ecotourism value and/or as a result of cultural values (such as to preserve sacred forest containing ancestral tombs), with no evaluation regarding the ecological conditions conducive to *L. catta* population viability. Instead, species management strategies should focus on examining spatial distributions and habitat use parameters, resource structure (including novel and introduced potential food items), and population health within fragmented landscapes. Analyses should be further extended to examine (i) phenological and nutritional data of *L. catta* food resources, (ii) a more complete activity budget including nocturnal activity and the location of preferred sleeping trees (i.e., is the matrix ever used at night?), and (iii) foraging strategies and health variables across the entire annual cycle. It is essential that suitable habitats be protected from further degradation, as well as corridors of land that can facilitate *L. catta* dispersal to habitats containing conspecifics. In addition, further comparisons of *L. catta* behavioural ecology are required from populations occupying a wide range of habitats throughout its geographic range in order to fully appreciate the ecological flexibility of this species. Such work has only recently begun in spiny forest and spiny bush habitats in southern Madagascar

(Berenty Reserve: Gould et al., 2011; Cap Sainte Marie: Kelley, 2011; Tsimanampetsotsa National Park: LaFleur, 2012). Without these efforts, we run the risk of misinterpreting ‘flexibility’ as ‘stability’ in *L. catta* and thus perpetuating the continued loss of habitats that can sustain population numbers.

The information presented in this manuscript can lend support to a growing knowledge of lemur ecology in habitat fragments, which is essential for the implementation and management of conservation schemes. Due to their biological endemism, and thus invaluable role in ecotourism, lemurs represent a vital indicator species for the health of Malagasy ecosystems. Conservation efforts are facing increasing obstacles related to the political instability experienced since February, 2009. Illegal logging of precious hardwood is on the rise, triggering ecological disruptions such as fire, species invasions, and habitat destruction, and threatening the future existence of some of Madagascar’s most critically endangered species (http://www.illegal-logging.info/approach.php?a_id=73). This activity is drawing international attention, including recent CITES protection of all of Madagascar’s ebony and rosewood (http://news.mongabay.com/2013/0311-hance-cites-trees.html#). As such, the conservation status of these primates may be a crucial meter for the preservation of biodiversity in Madagascar. Furthermore, due to Madagascar’s extreme isolation, relatively recent human occupancy, and rapidly altered landscape, the island represents a microcosm for globally changing landscapes. Therefore, information on species sensitivity to forest fragmentation in Madagascar may also contribute to a broader framework for monitoring the consequences of habitat disturbance on biodiversity worldwide.

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