UNIVERSITY OF CALGARY

Forest Fragmentation and Edge Effects on Eight Sympatric Lemur Species in Southeast Madagascar

by

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ABSTRACT

Extensive slash-and-burn agriculture in southeastern Madagascar has led to the fragmentation of forests in this region, creating a constricted available habitat area and increasing the proportion of forest edge. I investigated the response to forest fragmentation and edge effects in eight lemur species through comparisons of species density and diversity between fragments, as well as and correlation analyses including population distribution patterns, ecological variables, and distance from forest edge. I also include a more detailed focus on the behavioural response of *Eulemur cinereiceps*. Results were highly varied, with no species showing strong aversion to edge but with higher overall densities in larger, more connected fragments. *Eulemur cinereiceps* spent significantly more time near the forest edge while resting, but edge did not affect feeding patterns or food availability. These results suggest that conservation management should focus on maintaining large, complex fragments and improving connectivity through forest corridors.

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work, dedication, and invaluable knowledge of the forest. And to Garitia, may you rest in peace, your unfailing smile even in the most unreasonable hours of the night was always both astounding and heartening. I would also like to thank Jonah, Getia and Cosinus for assistance in my field setup, and Annemarie Rued for her collaboration in data collection. I am also indebted to the Association Nationale pour la Gestion des Aires Protégés (ANGAP), Missouri Botanical Gardens (MBG) and Durrell for their collaboration and permission to work in Madagascar.

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CHAPTER 1: INTRODUCTION

1.1 Introduction

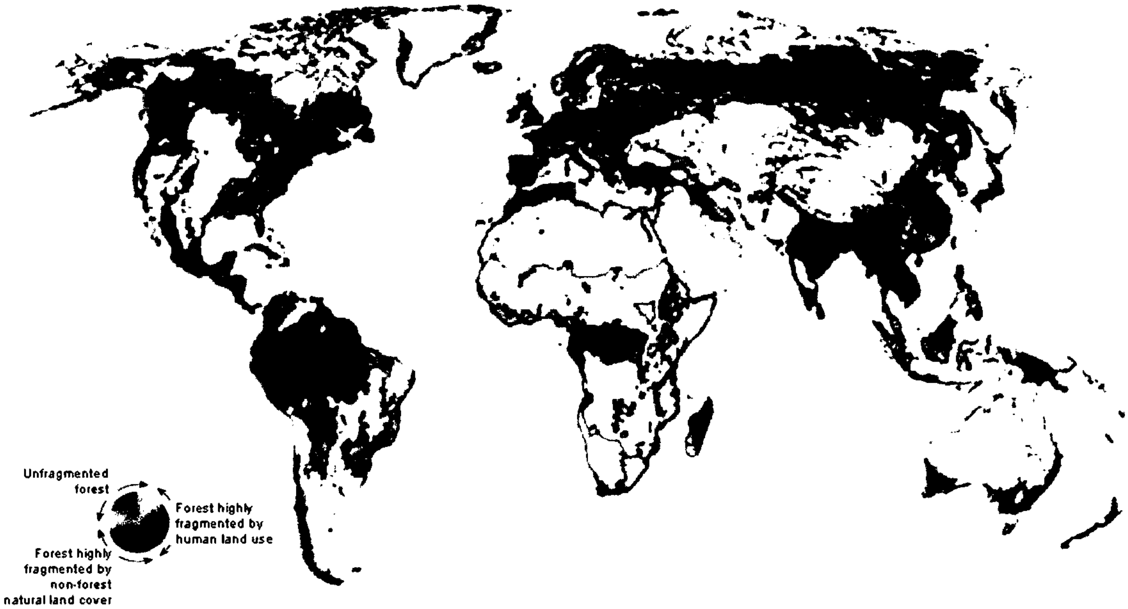
Madagascar is the fourth largest island in the world, and is home to a wide diversity of flora and fauna. Its long history of isolation has resulted in high levels of biodiversity and endemism, and adaptive radiations of many organisms have exploited the varied ecological niches of the island (Goodman 2003). Evidence of these radiations can be seen today in butterfly (Lees et al 1999, Linares et al 2009), beetle (Orsini et al 2007, Wirta et al 2008), frog (Andreone et al 2002, Wollenberg et al 2008), chameleon (Raxworthy & Nussbaum 1995, Glaw et al 1999), bird (Langrad 1990, Cibois et al 2001, Hawkins & Goodman 2003), insectivore (Douady et al 2002, Poux et al 2005), rodent (Jansa et al 1999, Poux et al 2005), carnivore (Poux et al 2005), and primate (Ganzhorn 1989, Kappeler & Heymann 1996, Poux et al 2005, Olivieri et al 2007) populations. In addition, more than 90 percent of approximately 12,000 vascular plant species found in Madagascar are endemic to the island (Schatz 2001). This exceptional species richness and endemism, coupled with the loss of over 80 percent of the island's native vegetation cover (Du Puy & Moat 1998), qualifies Madagascar as one of the top three biodiversity hotspots in the world (Myers et al 2000). Madagascar continues to suffer from rapid declines in many species due largely to clear-cutting, fire, selective logging and hunting (Smith et al 1997, Ganzhorn et al 2001, Balko & Underwood 2005, Bollen & Donati 2005). Although the unique taxa of Madagascar have made this island the focus of much needed conservation efforts, many ecosystems continue to become fragmented, and those species that rely on them face extinction.

1.2 Forest Fragmentation

1.2.1 The Effects of Forest Fragmentation

Forest fragmentation is generally defined as the reduction of continuous native forest into a number of smaller fragments that vary in size, shape, and degree of isolation (Murcia 1995). This also results in the fragmentation of habitat for forest-dwelling species; habitat encompasses the subset of physical environmental factors that any species requires for survival and reproduction (Franklin et al 2002). While fragmentation can occur naturally, the primary cause of this change is anthropogenic (Figure 1.1). Clear-cutting and slash-and-burn agriculture are the most common causes of fragmentation worldwide, and result in a new "matrix" environment surrounding the remaining forest patches (Chapman & Peres 2001). Other forms of disturbance, such as selective logging and defaunation driven by overhunting, also often co-occur in a fragmented landscape (Tabarelli & Lopes 2008). The ways in which fragmentation affects native forest wildlife is varied, and depends both on species tolerance to environmental change and their ability to utilize the encroaching matrix land. A matrix may include relatively traversable features, such as roads or rivers, or consist of larger, more inhospitable features such as clear-cut grasslands or swamps, which could isolate subpopulations unable to cross them. For example, a reluctance to travel through open spaces between forest fragments by arboreal species could confine populations to small, disjointed habitat patches, effectively eliminating gene flow between them. This will ultimately lead to a loss of genetic diversity at the population and species level that may limit the species' ability to respond to environmental changes through selection, alter the speed with which mutations are spread, and decrease diversity at loci controlling disease resistance (Young & Boyle 2000). Many arboreal forest species also act as pollinators and seed dispersers in tropical environments, so population isolation may also lead to a breakdown in plant-pollinator relationships, causing a reduction in floral genetic diversity as self-pollination and inbreeding increases (Bollen et al 2004, Law & Lean 1999).

Figure 1.1. World map distinguishing forest fragmentation into natural (blue) and human-induced (red) components. White areas were not included in the study. (Secretariat of the Convention on Biological Diversity 2006, re-projected from Wade et al 2003).



1.2.2 Island Biogeography Theory and the SLOSS Debate

Although several models exist to explain the relationships between forest fragment size and spatial configuration and species richness, population size, and population viability, it is an ongoing goal of conservationists to improve predictions regarding the consequences of fragmentation and habitat changes. MacArthur and Wilson's (1967) theory of island biogeography, which links immigration, emigration, and extinction of species to size and isolation of a habitat island, has been generally accepted in ecology for many years. One of its main tenets is that the larger the habitat island, and the closer it is to continuous habitat, the more species it should be able to support (MacArthur & Wilson 1967), thus arguing that the most effective reserves should be singular and large. Diamond (1975) later elaborated on MacArthur and Wilson's theory, maintaining that a single large reserve would both decrease the risk of extinction as well as be more likely to encompass the different minimum habitat areas required of different species for a reasonable chance of survival. However, in 1976 biologists Simberloff and Abele argued that MacArthur and Wilson's theory had not been sufficiently validated, and that while a single large reserve may be appropriate for the conservation of some species, others may be more suited to several small reserves (Simberloff & Abele 1976). Over time the debate, termed the SLOSS (single large or several small) debate, has lost momentum in the scientific literature, with most authors conceding that it is a complex issue that is largely dependent on the needs of the species to be conserved (Lahti & Ranta 1985, Hokkanen et al 2009). This complexity is further seen in the research, which has found some species to exist at higher densities in large fragments (beetles: Bierregaard et al 1992; birds: Bierregaard et al 1992, Foppen et al 2000; rodents: Foster & Gaines 1991, Ramanamanjato & Ganzhorn 2001; primates: Bierregaard et al 1992, Craul et al 2009), some in small fragments (rodents: Foster & Gaines 1991; marsupials: Laurance 1990), and some with no relationship between density and fragment size (rodents: Dooley & Bowers 1996; marsupials: Laurance 1990; primates: Bernstein et al 1976, Onderdonk & Chapman 2000, Ramanamanjato & Ganzhorn 2001). Current research on species-area relationships should therefore focus on the ecological requirements of the species in question, and attempt to account for the wide range of environmental changes that commonly occur as a result of forest fragmentation, such as habitat loss, creation of forest edge, post-isolation proliferation of invasive species and atypical climatic conditions, and changes in biological relationships (Tabarelli & Lopes 2008).

1.2.3 Metapopulation Theory and Source-Sink Dynamics

In some cases, a species is able to cross the matrix between seemingly isolated forest fragments. The populations within those fragments are therefore linked to one another by dispersal, creating a network referred to as a metapopulation (Levins 1969). The main tenet of metapopulation theory is that the presence of a given species in an area is dependent on the balance between rates of local extinction and local population establishment from other populations in the landscape (Hanski 1994). In this system, the fragmented landscape becomes a mosaic of 'source' and 'sink' habitats, in which demographically unviable local subpopulations of a species ('sinks') are maintained only by an influx of immigrants from a viable "source" population (Pulliam 1998). Populations of most species occupy habitats that vary in quality (Watkinson & Sutherland 1995), and those habitat patches that are lowest in quality are more likely to contain sink rather than source populations (Namba et al 1999). However, the classification of habitat as high or low quality depends on the specific requirements of the species in question. In a fragmented landscape, understanding the dynamics between possible source and sink habitat fragments is important, as the species in a sink will ultimately become extinct if the source population is removed. This understanding requires knowledge of population demography at the subpopulation level, what habitat conditions are responsible for variation in subpopulation demography, and the movement of individuals among source and sink fragments (Donovan et al 1995).

Overall, the physical and biological effects of forest fragmentation are poorly understood (Foggo et al 2001). It is intuitive to predict that faunal population sizes will be reduced or eliminated with decreasing fragment size, but not all species respond equally to climatic and vegetation changes in a fragmented landscape (see sources above). Understanding landscape-level population dynamics is therefore dependent on an understanding of local-level environmental conditions, on a scale that is relevant to the individuals within a species.

1.3 Edge Effects

1.3.1 Characteristics of the Forest Edge

As forest fragmentation progresses, patches of forest become smaller with a greater ratio of perimeter to total fragment area. One of the most immediate consequences is that a greater proportion of the forest is exposed to the environmental influence of conditions in the matrix. These external conditions penetrate into the forest at its boundaries, creating an edge zone (hereby referred to as "forest edge") of altered forest environment that may or may not be hospitable to native forest species (Malcolm 1994). Forest edge can be classified either as an inherent edge, which is a natural feature of the landscape related to topography, soil type, presence of open water, or geomorphic factors, or an induced edge, which is caused by natural and human disturbances such as fire, flooding, erosion, timber harvest, planting, or grazing (Thomas et al 1979). This process of environmental modification in forest edges is known as edge effects (Laurance 1991, Skole & Tucker 1994), and is highly variable in strength and penetration depth depending on both forest and matrix characteristics. According to Murcia (1995), there are three categories of edge effects found in all forest environments: abiotic, direct biotic, and indirect biotic. Abiotic effects include light intensity, temperature, humidity, wind, and soil moisture. Direct biotic effects are often the result of abiotic effects, and include changes in vegetation structure and diversity, faunal abundance and diversity, and food availability. Lastly, indirect biotic effects are defined as changes in species interactions as a consequence of direct biotic edge effects, and include competition, predation, and parasitism.

Edges are often the most altered areas of fragmented forests, and edge effects can penetrate from several to several hundred meters into the interior (Li et al 2007, Broadbent et al 2008, Olupot 2009). These effects have been found to influence forest structure (Laurance & Bierregaard 1997, Didham & Lawton 1999, Mesquita et al 1999), diminish seedling recruitment (Sork 1983, Bruna 2002), and create an influx of invasive plant species (Peters 2001). In addition, native wildlife species have been shown to exhibit a preference or aversion to forest edges, a characteristic determined by measuring population densities along a gradient from forest edge to interior. Differing levels of edge tolerance are potentially linked to variation in food quality and quantity (Anderson & Boutin 2002, Bruna 2002, Lehman et al 2006a), rates of predation (Andren & Angelstam 1988, Winter et al 2000, Anderson & Boutin 2002, Schlaepfer 2003), prevalence of anthropogenic disturbance (de Santo et al 2002, Balko & Underwood 2005), and abiotic conditions (Sisk et al 1997, Foggo et al 2001, Schlaepfer 2003) as a function of distance to forest edge.

1.3.2 Edge Effects and Fragment Characteristics

The proportion of forest edge to forest interior is a direct result of the shape and size of the fragment. For example, a small fragment will have a greater proportion of forest edge relative to fragment size than a large block of forest, and in some cases a fragment can become so small that there is virtually no interior forest left (Figure 1.2). Forest fragment shape also determines the ratio of edge to interior forest, as a round and compact forest patch will have less relative edge than an elongated or convoluted forest patch (Figure 1.3). As discussed in the previous section, an increase in the proportion of forest edge may have a negative effect on the sustainability of interior forest ecosystems, which may ultimately lead to a loss of biodiversity if native forest species become locally extinct. However, a complex edge will also increase the chances that dispersing individuals in the matrix will encounter the fragment due to a high edge-to-interior ratio, and in many cases will also decrease the distance between fragments (Ewers & Didham 2006).

Figure 1.2. An illustration of how edge effects can reduce interior forest. Shown are various forest fragment sizes and the percentage of interior forest available, given a 240 m wide section of edge influence (from Franklin 1992).

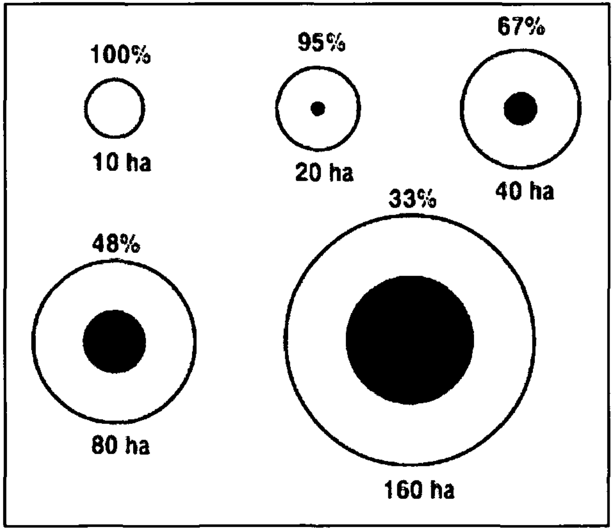
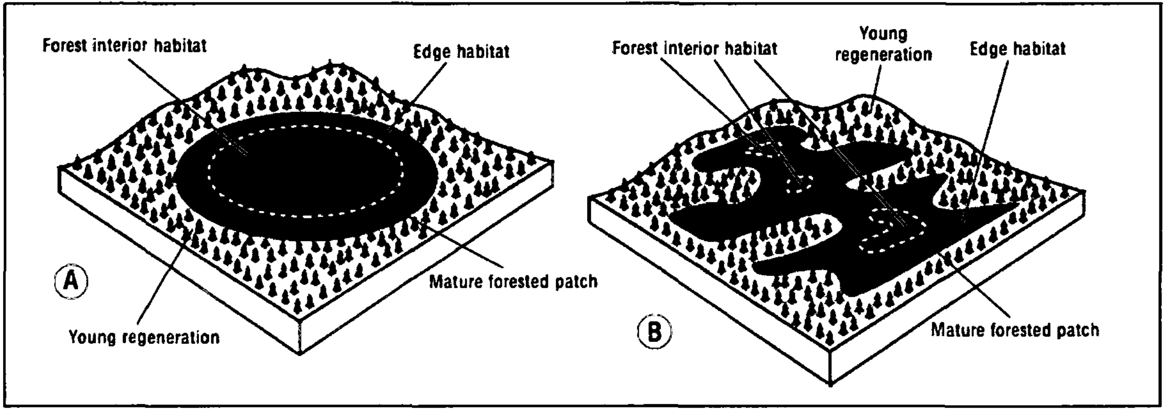


Figure 1.3. An illustration of how patch shape affects the amount of forest edge and forest interior. (A) A round fragment tends to have a greater amount of interior forest and less edge. (B) An irregularly shaped fragment has more edge and less interior forest (from B.C. Ministry of Forests and B.C. Ministry of Environment, Lands and Parks 1996).



1.4 Study Sites and Species

1.4.1 Agnalazaha and Manombo

The sites of Agnalazaha (S 23° 11.175' E 47° 43.095') and Manombo (S 23° 01.697' E 47° 43.838') are located in the province of Fianarantsoa on the southeastern coast of Madagascar (Figure 1.4). This area is characterized by high rainfall with annual and seasonal fluctuations, heaviest during the cyclone season between January and March (Johnson 2002, Ratsimbazafy 2002). Both Agnalazaha and Manombo are known to be high in biodiversity, being home to a variety of lemurs, rodents, carnivores, raptors and invertebrates (Ratsimbazafy 2002, HE Andriamaharoa pers. comm.). However, these sites are broken into distinct forest fragments of varying size, shape and degree of isolation, and are bordered by an induced edge surrounded by anthropogenic grassland matrix. In addition to anthropogenic disturbance, Agnalazaha and Manombo have also been affected by a natural stochastic event in the form of Cyclone Gretelle, which struck the region in

1997 and resulted in the uprooting of more than 50% of Manombo's woody vegetation (Ratsimbazafy 2002), with similarly substantial impacts at Agnalazaha (HE Andriamaharoa unpub. data).

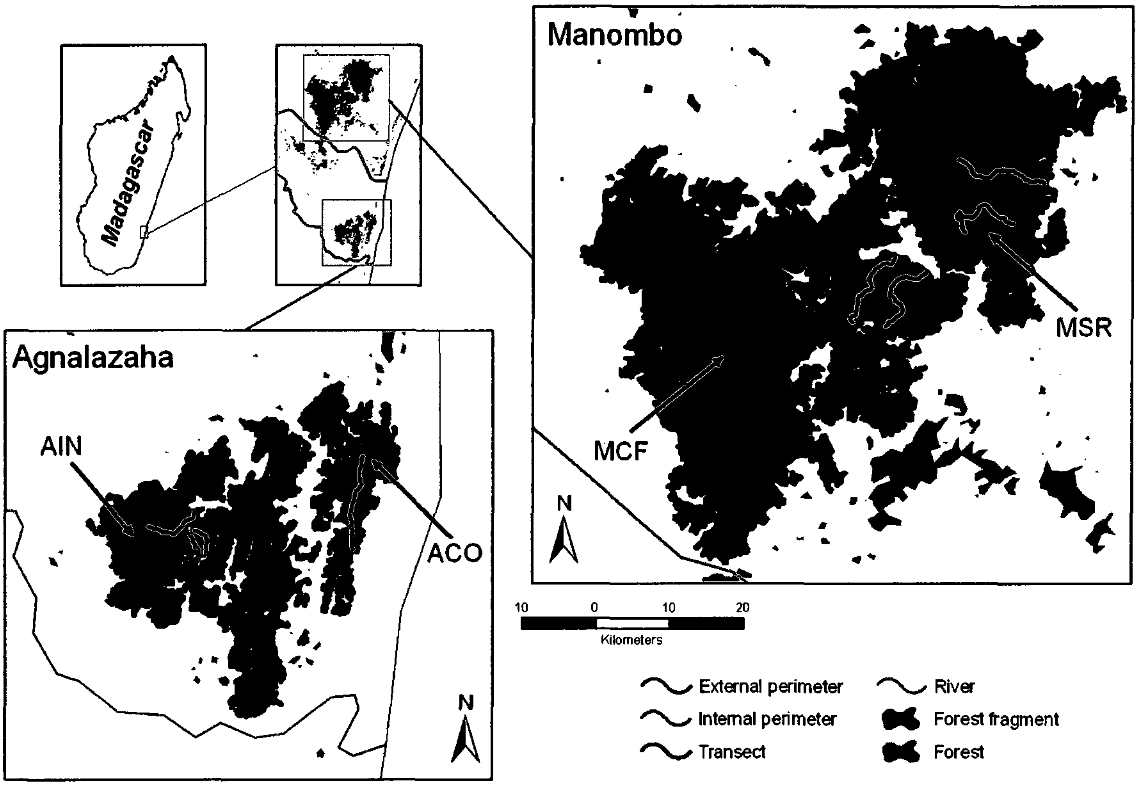
Agnalazaha

Agnalazaha consists of two distinct fragments of littoral forest, characterized by a low canopy (< 10 m), low altitude (0-20 m asl) and sandy white soils (Dumetz 1999) interspersed with swamp areas. This site is under the management of Missouri Botanical Garden (MBG) in partnership with local communities, and is highly degraded and discontinuous, being perforated by the surrounding matrix and a large network of trails. The most prominent threat to this ecosystem is the practice of slash-and-burn agriculture, or *tavy*, which is frequently accompanied by bushfires. These fires are often not controlled, resulting in even further forest loss (Bollen & Donati 2006). Other known threats in the region include clear-cutting, mining, selective logging, and hunting of native forest species (Johnson & Overdorff 1999, Balko & Underwood 2005, Lehman et al 2006a). Littoral forest has been identified as one of the most threatened ecosystems in Madagascar, once occurring in a 1-5 km wide band along the eastern coast, but is now highly fragmented and represents less than 10 percent of its original area (Consiglio et al 2006). Occupying an area of approximately 1240 ha, Agnalazaha is one of the largest and best-preserved littoral forest fragments remaining (Birkinshaw et al 2009). While there has been very little past research at this site, behavioural ecological studies of *E. cinereiceps* at Agnalazaha have been ongoing from December of 2005 to the present, led by Andriamaharoa (pers. comm.) with the aim to assess the risk of extinction for this species.

Manombo

The site of Manombo consists of an approximately 15,730 ha mosaic of lowland rainforest, littoral forest, and anthropogenic grassland matrix (Ratsimbazafy 2002). Less than half of the Manombo area remains forested, and that which is left is highly fragmented as a result of *tavy* agriculture, selective logging for precious woods, and cutting for secondary products, such as honey (FB Ralainasolo pers. comm., Johnson & Overdorff 1999, Ratsimbazafy 2002). Manombo consists of four large fragments, two of which are analyzed in this study: Parcel I of the Special Reserve, managed by Madagascar National Parks, and the Classified Forest, managed by the Ministry of Environment, Forests and Tourism (MEFT) and administered locally by the Interregional Direction of Environment, Forests and Tourism (DREFT). Both of these fragments are comprised of lowland rainforest, ranging in elevation from 0-137 m asl and characterized by a relatively high canopy (~20 m), a sparse herbaceous stratum, and vegetation consisting of 90% endemic Malagasy species prior to Gretelle (Ratsimbazafy 2002). Immediately following the cyclone, however, invasive plant species significantly altered vegetation structure and plant species diversity at Manombo (Ratsimbazafy 2002). In Manombo's Special Reserve and Classified Forest, ongoing research by Durrell Wildlife Conservation Trust focuses on *V. variegata editorum* and *E. cinereiceps* as two flagship species for conservation. Manombo Project Coordinator Ralainasolo is leading these studies, with a focus on collecting long-term behavioural and ecological data.

Figure 1.4. Site maps of Agnalazaha and Manombo outlining the four forest fragments in this study: AIN (Agnalazaha inland fragment), ACO (Agnalazaha coastal fragment), MSR (Manombo Special Reserve) and MCF (Manombo Classified Forest).



1.4.2 Lemur Species

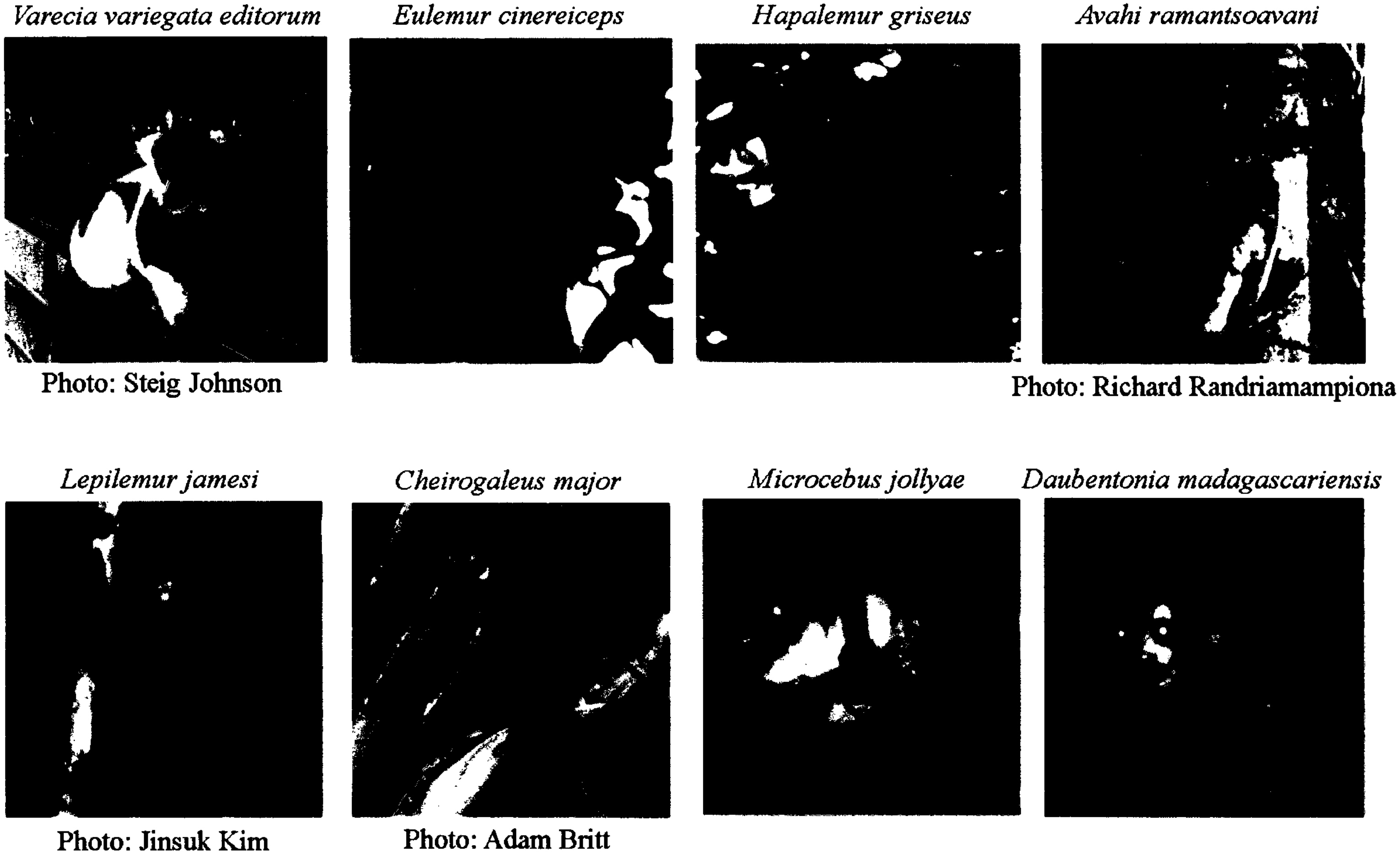
Between the sites of Agnalazaha and Manombo, there are eight known lemur species representing eight different genera. These include the southern black-and-white ruffed lemur (*Varecia variegata editorum*, at Manombo only), the gray-headed lemur (*Eulemur cinereiceps*), the eastern lesser bamboo lemur (*Hapalemur griseus*), Ramantsoavana's southern woolly lemur (*Avahi ramantsoavani*), James' sportive lemur (*Lepilemur jamesi*, at Manombo only), the greater dwarf lemur (*Cheirogaleus major*), Jolly's mouse lemur (*Microcebus jollyae*), and the aye-aye (*Daubentonia madagascariensis*) (taxonomy based on Mittermeier et al 2008) (Figure 1.5). These species represent varying levels of endangerment as reported by the International Union for Conservation of Nature (IUCN) (2009) (Table 1.1). Although not all of the species are considered at risk of extinction, all for which sufficient data are available are known to be decreasing in numbers.

Table 1.1. IUCN Red List status for the lemur species of Agnalazaha and Manombo.

Species	**Status**	**Population Trend**
Varecia variegata editorum	Critically Endangered[1]	Decreasing
Eulemur cinereiceps	Endangered[2]	Decreasing
Hapalemur griseus	Vulnerable[3]	Decreasing
Avahi ramantsoavani	(data deficient)	(unknown)
Lepilemur jamesi	(data deficient)	(unknown)
Cheirogaleus major	Least Concern [5]	(unknown)
Microcebus jollyae	(data deficient)	(unknown)
Daubentonia madagascariensis	Near Threatened[4]	Decreasing

[1] Critically Endangered: Facing an extremely high risk of extinction in the wild
[2] Endangered: Facing a very high risk of extinction in the wild
[3] Vulnerable: Facing a high risk of extinction in the wild
[4] Near Threatened: Close to qualifying for or is likely to qualify for a threatened category in the near future
[5] Least Concern: Widespread and abundant taxa are included in this category

Figure 1.5. Study Species at Agnalazaha and Manombo.



Varecia variegata editorum

Eulemur cinereiceps

Hapalemur griseus

Avahi ramantsoavani

Photo: Steig Johnson

Photo: Richard Randriamampiona

Lepilemur jamesi

Cheirogaleus major

Microcebus jollyae

Daubentonia madagascariensis

Photo: Jinsuk Kim

Photo: Adam Britt

Varecia variegata editorum

Varecia variegata editorum is one of three subspecies of *V. variegata* (ruffed lemur) that occupies the mid-altitude rainforests of eastern Madagascar. This diurnal large-bodied species weighs an average of 3.65 kg (Dew & Wright 1998), and is considered the most frugivorous extant lemur, spending 74-90% of its overall feeding time on a wide diversity of fruits (Ratsimbazafy 2002, Vasey 2002, Vasey 2005). The majority of fruits fed on by *V. variegata* are swallowed whole, with seeds passing through intact and showing high sprouting success (Dew & Wright 1998). As a genus, *Varecia* is known to maintain large home ranges of primary forest and have a long daily path length (Dew & Wright 1998, Vasey 2005), making this species capable of dispersing seeds over long distances.

The subspecies *V. v. editorum* is currently reported only in Mantadia National Park, Ranomafana National Park, and Manombo Special Reserve (Andrainarivo et al 2008). It has been classified by the IUCN Red List as critically endangered with declining numbers (Table 1.1), having undergone a decline of 80% over a period of 27 years (IUCN 2009). This species is primarily threatened by *tavy* agriculture, logging, and mining, and is also one of the most widely hunted lemur species due to its large body size (Ratsimbazafy 2002). Population densities in Manombo have been recorded ranging from 0.4 to 2.5/km^2, the lowest of all recorded *V. variegata* densities (Vasey 2003). In a pre- and post-cyclone analysis of *V. v. editorum* behavioural ecology, Ratsimbazafy (2002) found that this population resorted to a wider variety of food resources and spent more time resting as a way of coping with low fruit availability, and is slowly recovering in numbers.

Eulemur cinereiceps

The genus *Eulemur* includes eleven different species and is the most widespread lemur genus in Madagascar (Johnson 2006, IUCN 2009). *Eulemur cinereiceps* (previously known as *Eulemur albocollaris*; see Johnson et al 2008), or the gray-headed lemur, is a cathemeral medium-sized lemur, weighing between 1.7 and 2.7 kg (Johnson 2002). Their diet consists primarily of fruit, ranging from 60% to more than 90% of their total intake (Overdorff & Johnson 2003, Ralainasolo et al 2008). Being among the largest-bodied frugivores at Agnalazaha and Manombo, *E. cinereiceps* is likely crucial to ecosystem maintenance at these sites (Overdorff & Johnson 2003, Bollen et al 2004). This species is found in only two protected areas (Andringitra National Park and Manombo Special Reserve) between the Andringitra Massif and the Mananara River in southeastern Madagascar, and has a total range of only 700 km^2 (see Chapter 3 Figure 3.1), the most restricted of any species in its genus (Irwin et al 2005). *Eulemur cinereiceps* is classified as endangered with decreasing numbers (IUCN 2009) (Table 1.1), a trend exacerbated by ongoing habitat destruction and hunting pressure (Johnson 2002). These threats are visible and ongoing to varying degrees at both Agnalazaha and Manombo. From June to August of 1995, Johnson and Overdorff (1999) conducted a survey at of *E. cinereiceps* that included the Manombo Special Reserve, estimating mean density as 0.086 individuals/ha. Low densities of *E. cinereiceps* at this and other sites were speculated to be the result of extensive fragmentation, as well as hunting and logging activities in the forest. More current estimates of density are also quite low, though recent comparisons between densities of *E. cinereiceps* in Manombo before and after cyclone Gretelle show that 2007 population levels have rebounded to pre-cyclone levels (13.5 ± 3.2 individuals/km^2 in 1997 vs. 13.6 ± 6.4 individuals/km^2 in 2007), although vegetation measures still showed substantial decline (Johnson et al, in press). This suggests that *E. cinereiceps* are relatively resilient to habitat disturbance and are able to respond capably to unpredictable environmental conditions. Due to their endangered status, limited range, frugivorous nature and presence in all forest fragments at Agnalazaha and Manombo, *E. cinereiceps* was chosen as a representative species for determining the effects of fragmentation and disturbance in the forest, and for proposing new ideas for the protection of this and other lemur species. The behavioural ecology and response to forest fragmentation and edge effects of *E. cinereiceps* are examined in Chapter 3.

Hapalemur griseus

The genus *Hapalemur* encompasses the gentle and lesser bamboo lemurs, and includes 5 species. This diurnal genus is small-bodied (0.75-1.1 kg, Tattersall 1982) yet highly folivorous, and known for a diet consisting primarily of bamboo, supplemented with mature leaves and some fruit during the wet season months (Overdorff et al 1997). *Hapalemur griseus*, commonly known as the eastern lesser bamboo lemur, has been recorded to subsist on a diet of 50-80% bamboo, but is considered the generalist of the bamboo lemur species due to its relatively flexible diet (Mutschler 1999, Grassi 2006). This species has been known to capably subsist on diets devoid of bamboo in forests that are highly degraded (Grassi 2006), making it somewhat resilient to habitat disturbance. This may explain how *H. griseus* exists both at Manombo and Agnalazaha, although no bamboo has been recorded in previous botanical surveys at these sites (Ratsimbazafy 2002, pers. obs.). In addition to a more generalist diet, *H. griseus* has the widest range in its genus, being found between Lake Aloatra to Ranomafana in the east, and at the Tsingy de Bemaraha, Tsiombikibo, Baie de Baly, Tsingy de Namoroka and Bongolava regions in the northwest (Rabarivola et al 2007). However, *H. griseus* has undergone a reduction of more than 30% in the past 27 years, and is classified as vulnerable with decreasing numbers (IUCN 2009).

Avahi ramantsoavani

The genus *Avahi*, commonly known as the woolly lemurs, includes eight different species, all of which are nocturnal and folivorous with a body size of less than 1 kg (Mittermeier et al 2008). At Ranomafana National Park, a site about 200 km north from the study site, male *Avahi* were recorded to have diet of 100% young and mature leaves (Harcourt 1991). While they are known to supplement their diet with small amounts of flowers and fruits (Mittermeier et al 2006), *Avahi*'s diet is mainly of low quality, providing a possible explanation for its low levels of activity even during waking hours. *Avahi* can be found sleeping in large, hollow trees during the day, and are subject to predation pressures by diurnal hawks and eagles that take them from their sleep holes (Wright 1999). The study species *A. ramantsoavani* has been recently upgraded to species level from *A. meridionalis ramantsoavani* in light of new molecular evidence (Andriantompohavana et al 2007). As this species has only been recently described, further data are needed to describe its distribution, ecology, population status and threats. *Avahi ramantsoavani* is currently only known to exist at Agnalazaha and Manombo. Although under pressure from forest degradation at these sites, this species is believed to be less vulnerable to hunting pressures particularly in Agnalazaha, as they tend to range in swampy areas where it is difficult to hunt (HE Andriamaharoa pers. comm.).

Lepilemur jamesi

Lepilemur jamesi, commonly known as James' Sportive Lemur, is one of 24 sportive lemurs in the genus *Lepilemur*, and represents one of 11 new *Lepilemur* species described in 2006 (Louis et al 2006b, Hoffmann 2008). *Lepilemur* as a genus is characterized by a nocturnal activity pattern and a primarily folivorous diet, a surprising fact considering they generally weigh less than 1 kg (Mittermeier et al 2006, 2008). On average, *Lepilemur* will spend between 70% to almost 100% of their feeding time on leaves (Thalmann 2001). During the day, *Lepilemur* sleeps in dense vegetation or holes in hollow trees high above the ground (Rasoloharijaona 2008), implying sensitivity to any habitat disturbance that results in a sparser forest canopy or targets large trees (i.e. selective logging). This genus is also predated on by raptors and fossa, factors that may affect their distribution and forest use (Fichtel 2007). *Lepilemur jamesi* is a newly described species (see Louis 2006b), so data regarding its distribution, ecology, population status and threats are sparse. It is currently known to occur from south of the Manampatrana River to north of the Mananara River (Mittermeier et al 2008), and is found at Manombo but is absent at Agnalazaha. In addition to threats from habitat disturbance, this species is hunted in Manombo from their sleep holes during the day, and it is believed that they disappeared from Agnalazaha for this reason (HE Andriamaharoa pers. comm.).

Cheirogaleus major

Cheirogaleus major, or Geoffroy's dwarf lemur, is one of seven nocturnal *Cheirogaleus* species with a body weight between 150 to 600 g, depending on season (Mittermeier et al 2008). This species is widespread in eastern Madagascar, ranging from Andohahela in the south to the Sambava region in the north (Lahann 2007, IUCN 2009). They are also found at Bemeraha and Bongolava in the west (Thalmann 2000). *Cheirogaleus* is known to enter long-term or daily torpor in response to low ambient temperatures between May and October in the southeast region (Sainte Luce: Bollen et al 2004), though some studies suggest that this species experiences hibernation, a more sustained state of torpor governed by seasonal cues, to maximize energy conservation (Geiser & Ruf 1995). This may result in an underestimation of density during this study period. During their period of inactivity, *Cheirogaleus* species live off of reserves of fat stored in their large tails (Fietz & Ganzhorn 1999). The diet of *C. major* is comprised mainly of fruit (69-86%), supplemented with flowers, arthropods and gum (Wright & Martin 1995, Lahann 2007). Population densities of *C. major* are largely unknown, and recent examination of the taxonomy of *Cheirogaleus* suggests revision is needed (Mittermeier et al 2008). Presently, the species appears to be widespread and abundant, and is currently classified as being of least concern with unknown trends in population (IUCN 2009) (Table 1.1).

Microcebus jollyae

Microcebus jollyae, commonly known as Jolly's mouse lemur, is one of sixteen species in the genus *Microcebus*, famous for their small size among primates. This genus is widespread throughout Madagascar, existing wherever suitable habitat remains, and are often the most abundant mammals in the area where they occur (Mittermeier et al 2006). *Microcebus* relies on a diet predominantly of small fruits, flowers, invertebrates, and small vertebrates, supplemented with gums and larvae secretions (Joly & Zimmermann 2007, Lahann 2007). The species *Microcebus jollyae* weighs approximately 60 g and inhabits eastern forests from southeast of Ranomafana National Park to Manombo Special Reserve (Mittermeier et al 2008). Recent work on *Microcebus* taxonomy suggests that there are two *Microcebus* species present at the southernmost range of *M. jollyae* (Louis et al 2006a), so further data may be required before assigning a firm species designation. Like *C. major*, *M. jollyae* is known to enter long-term or daily torpor (Schmid 1994) between May and October in other littoral forest sites of southeastern Madagascar (Sainte Luce, 185 km south of study sites: Bollen et al 2004; Mandena, 210 km south of study sites: Lahann 2007), so densities may be underestimated during this study period.

Daubentonia madagascariensis

Daubentonia madagascariensis, commonly known as the aye-aye, is the only species of its genus. This unique nocturnal species weighs an average of 3 kg (Mittermeier et al 2008) and occupies a woodpecker- or squirrel-like foraging niche, feeding predominantly on nuts and wood-boring insects (Sterling 1994, Erickson 1995, Lhota et al 2008). Classified as near threatened with decreasing numbers (IUCN 2009), *D. madagascariensis* is found in eastern forests from Ampanefana to Andohahela National Park, and in western forests from Montagne d'Ambre to the Tsingy de Bemaraha National Park, and on the island of Nosy Mangabe (IUCN 2009). Although *D. madagascariensis* is adaptable to a variety of forest types and has a widespread range, populations are dwindling due to a decline in habitat area and quality (IUCN 2009). In addition, this species has a reputation in Madagascar as a harbinger of bad luck and so is often killed on sight by locals (Simons & Meyers 2001). *Daubentonia madagascariensis* is a notoriously difficult species to study in its natural habitat due to its extremely elusive nature, and reports of presence are often based only on signs of feeding (i.e. holes gnawed in trees and hard-shelled fruits) (Mittermeier et al 2006).

1.5 Research Goals and Questions

The goal of this study is to examine how fragmentation changes forest habitat, specifically at the forest edge, and what affect these changes have on the distribution of eight sympatric lemur species at Agnalazaha and Manombo. The analyses of lemur response to fragmentation aims to link landscape-level patterns with local-level ecological processes by comparing a large-scale population and vegetation survey with a focused behavioural study of a representative species that will examine response to fragmentation and edge effects. Chapters 2 and 3 will therefore address the question of how forest fragmentation affects lemur populations on these two scales, and Chapter 4 will attempt to bridge landscape and local research in a discussion of the conservation implications for Agnalazaha and Manombo and the metapopulations of lemur species there. The following will be addressed in Chapters 2 and 3:

1.5.1 Chapter 2

Chapter 2 commences with a description of the spatial characteristics of forest fragments at Agnalazaha and Manombo, and follows with an analysis of abiotic characteristics, vegetation structure, anthropogenic disturbance, and lemur population density in each fragment in an effort to determine which characteristics are subject to edge effects and which affect lemur distribution. These analyses aim to determine the consequences, if any, of forest fragmentation for each species, and how this may inform conservation management decisions. This chapter addresses the following questions:

1. How does lemur diversity and density vary between forest fragments of varying size, shape, isolation, forest type, and disturbance levels?
2. How do densities of lemur species at Agnalazaha and Manombo differ from forest edge to interior?
3. What characteristics (abiotic, biotic) correlate with edge-to-interior densities of each lemur species at Agnalazaha and Manombo, and are likely to influence lemur distribution at these sites?

1.5.2 Chapter 3

Chapter 3 aims to determine how *E. cinereiceps* is responding to forest edge, and what factors may be contributing to that response. This is accomplished by examining possible correlations between distance to forest edge with behavioural variables and vegetation characteristics specific to the diet of this species, and aims to determine what factors, if any, affect this species' distribution. This chapter addresses the following questions:

1. How does *E. cinereiceps* distribute its time spent resting, feeding, traveling, and engaging in social behaviour at varying distances from forest edge?
2. What factors (food availability, habitat structure) may play a role in *E. cinereiceps'* response to forest edge?

CHAPTER 2: LEMUR DENSITY, DISTRIBUTION AND EDGE EFFECTS IN AGNALAZAHA AND MANOMBO

2.1 Introduction

2.1.1 Fragmented Landscapes

The physical characteristics of a forest, and changes in those characteristics, have a strong relationship with species diversity and abundance. They can be measured from small-scale, microclimatic variables to large-scale landscape features, and be a result of either natural of anthropogenic disturbance. One of the most prevalent consequences of deforestation in a tropical environment is the creation of a fragmented mosaic landscape, a process that is ongoing in many tropical forests (Williams 1990, Gade 1996, Britt et al 1999) (see Section 1.2 for a detailed discussion of forest fragmentation). A fragment can be defined simply as an area that differs from its surroundings in its nature or appearance (Kotliar & Wiens 1990). In practice, the existence of fragments is relative to the habitat and spatial requirements of the species being studied (Bowers & Matter 1997). For small- to medium-sized arboreal mammals such as lemurs, effects of forest fragmentation encompass the obvious – a simultaneous loss and alteration of forest habitat as inhospitable, treeless land encroaches on the forest – and the not so obvious, such as incremental changes in microclimate, vegetation structure and food availability (Warry et al 2009). Results in the study of fragment area-density relationships have been diverse (Lovejoy et al 1986, Robinson et al 1992, Bowers & Matter 1997, Onderdonk & Chapman 2000, Cristóbal-Azkarate 2005, Arroyo-Rodríguez & Mandujano 2006) and do not support a general theory of species response to forest fragmentation. Rather, all changes that occur within the forest will affect different species in different ways, depending on their own unique habitat and dietary requirements.

2.1.2 Edge Effects: Relationships Between Species and Edge

On a landscape scale, forest fragmentation results in a reduction in habitat amount, decreasing fragment size, changing fragment shape, and increasing fragment isolation (Fahrig 2003). The consequence of this is a change in the proportion of forest perimeter to forest area (see Chapter 1 Figures 1.2 and 1.3), and therefore a change in the degree to which environmental and climatic conditions from outside the fragment are penetrating into the forest interior, a phenomenon known as edge effects (see Section 1.3 for a detailed discussion of edge effects). A fragment with a small area or a complex shape, for example, will result in a greater proportion of forest edge to interior forest, and these effects alone can reduce the population size of species that respond negatively to forest edge by 10-100% (Ewers & Didham 2007). In contrast, species that tend to prefer forest edge would be expected to increase in population size in complex-shaped fragments (Lidicker 1999, Johnson et al 2002, Lehman et al 2006b).

Edge effects are often quantified by measuring abiotic (climatic) and biotic (botanical) characteristics at intervals from the forest edge into the interior (Murcia 1995), resulting in an estimation of the depth and strength of these effects. Current knowledge of how edge effects vary through space and time is poor and is just one limitation in our ability to construct spatially explicit models of these effects (Ewers & Didham 2007). However, quantifying the demographic variation of certain species with gradient changes from edge to interior in microclimate and vegetation structure may be useful in suggesting which aspects of edge effects are detrimental or beneficial to each species, and to aid in conservation planning. For example, determining an effective reserve size and shape or how wide a forest corridor a species would require would be aided by determining whether the species is avoiding forest edge, and to what extent. This chapter measures the density and edge response of eight lemur species found at Agnalazaha and Manombo in southeastern Madagascar, which include three frugivores (*Varecia variegata editorum* (Manombo only), *E. cinereiceps*, and *C. major*), three folivores (*H. griseus*, *L. jamesi* (Manombo only), and *A. ramantsoavani*), and two insectivores (*M. jollyae*, and *D. madagascariensis*) (taxonomy based on Mittermeier et al 2008) (see Section 1.4.2 for descriptions of each species). In this chapter, "edge response" refers to apparent preference, avoidance or indifference to forest edge based on edge-to-interior distribution patterns, and does not necessarily imply an active behavioural response to edge conditions.

2.2 Research Goals, Hypotheses and Predictions

2.2.1 Research Goals

This chapter will address the following questions:

1. How does lemur diversity and density vary between forest fragments of varying size, shape, forest type, and disturbance levels?
2. How do densities of lemur species at Agnalazaha and Manombo differ from forest edge to interior?
3. What characteristics (abiotic, biotic) correlate with edge-to-interior densities of each lemur species at Agnalazaha and Manombo?

2.2.2 Abiotic Variables

Forest edge in tropical environments is often characterized by a more "open" forest canopy due to a decrease in the size and number of trees (Laurance 1991, Murcia 1995). This canopy openness results in increased light penetration, which in turn can result in elevated temperatures and a decrease in moisture at the edge (Bierregaard et al 1992, Nichol 1994, Murcia 1995, Wilder et al 2005). Edges are also predicted to have increased wind speeds since there is less vegetation to act as a buffer (Bierregaard et al 1992, Murcia 1995). Based on these assumptions, the following predictions are made for the abiotic variables measured:

Prediction 1: Light intensity will increase with increasing proximity to forest edge.

Prediction 2: Temperature will increase with increasing proximity to forest edge.

Prediction 3: Relative humidity will decrease with increasing proximity to forest edge.

Prediction 4: Wind speed will increase with increasing proximity to forest edge.

2.2.3 Vegetation Structure

Quantifying the responses to edge by plant species has been the aim of many edge effects studies (e.g. Chen et al 1993, Aizen & Feinsinger 1994, Laurance et al 1998, Olupot 2009). In addition to increasing canopy openness, forest edge is also characterized by an increase in small tree density, increased tree species richness and diversity, and a decrease in mean tree DBH (Arroyo-Rodriguez & Mandujano 2006, Olupot 2009). These changes in vegetation are likely due to microclimatic conditions at the edge and an increase in anthropogenic disturbance around forest perimeters. The following predictions are made regarding vegetation structure:

Prediction 5: Tree species richness will increase with increasing proximity to forest edge.

Prediction 6: Mean tree height and diameter at breast height (DBH) will decrease with increasing proximity to forest edge.

2.2.4 Anthropogenic Disturbance

In Madagascar, anthropogenic disturbance has led to deforestation on a large scale, and ultimately to population declines and, in some cases, extinction of lemur species (Gade 1996). It is therefore expected that forest sites that show more intense anthropogenic disturbance will also have lower lemur species abundance.

Prediction 7: Lemur species densities will be lower in fragments with more anthropogenic disturbance.

2.2.5 Primate Density and Edge

The ranging behaviours of primate species are generally understood to correlate with resource distribution and food competition (Wrangham 1980). This assumption becomes even stronger in lemurs, where social groups are relatively smaller in size and less socially complex than other primate species (Dunbar 1998), resulting in fewer complications to the model due to social dynamics. For that reason, lemur abundance at Agnalazaha and Manombo is expected to correlate with food availability. For the frugivorous species *V. variegata editorum, E. cinereiceps*, and *C. major*, ranging patterns should be linked to the availability and dispersion of fruit. In general, tree mortality is higher near forest edge in tropical forests (Ferreira & Laurance 1997, Laurance et al 1997, Didham & Lawton 1999), and fruit crops at the edge tend to be lost due to an increase in wind turbulence (Lehman et al 2006b), resulting in greater fruit availability in the forest interior. It is therefore predicted that:

Prediction 8: The primarily frugivorous species *V. variegata editorum, E. cinereiceps* and *C. major* will show a negative response to forest edge.

Since leaves are a ubiquitous food source in tropical forests, densities of the folivorous species *H. griseus*, *L. jamesi* and *A. ramantsoavani* are not predicted to vary significantly with distance to forest edge. Although higher protein levels have been recorded in leaves at newly created forest edges (Ganzhorn 1995), some shade-tolerant plant species maximize protein production in low-light conditions (Mooney et al 2009) or upregulate protein production in response to low-light conditions (Mazzuca et al 2009).

Prediction 9: The folivorous *H. griseus, L. jamesi* and *A. ramantsoavani* will show no response to forest edge.

Although patterns of insect density have not been studied directly in southeastern Madagascar, studies in other tropical forests have shown high densities of arthropods at the forest edge (Lovejoy et al 1986, Passamani & Rylands 2000, Eltz et al 2002). Since *D. madagascariensis* and *M. jollyae* have an abundance of insect prey in their diets, it is predicted that:

Prediction 10: The partly insectivorous *D. Madagascariensis* and *M. jollyae* will show a positive response to forest edge.

2.2.6 Primate Density and Forest Fragmentation

The forest fragments at Agnalazaha and Manombo differ in shape and size. Those fragments with a smaller area and a longer perimeter will be more complex in shape, and will therefore have more edge relative to forest interior.

Prediction 11: Forest fragments that are larger and less complex in shape will support greater densities of species that respond negatively to edge than fragments that are smaller and more complex in shape. Conversely, small and irregularly shaped fragments will support greater densities of species that respond positively to edge.

2.3 Methods

2.3.1 Study Sites

The sites of Agnalazaha (S 23° 11.175' E 47° 43.095') and Manombo (S 23° 01.697' E 47° 43.838') are located on the southeastern coast of Madagascar (see Chapter 1 Figure 1.4). Both sites are known to be high in biodiversity, being home not only to lemurs, but a variety of rodents, carnivores, raptors and invertebrates (Ratsimbazafy 2002). This area is characterized by high rainfall with yearly fluctuations, heaviest during the cyclone season between January and March (Johnson 2002, Ratsimbazafy 2002). This study falls between the cold dry season from June to August (mean rainfall 138 cm, mean temp. 20°C) and the warm dry season from September to November (mean rainfall 115 cm, mean temp. 23°C).

Agnalazaha Forest is comprised of one distinct forest fragment along the coast (ACO) and a larger fragment further inland (AIN). These fragments are separated by an anthropogenic grassland matrix 150 m in width at the closest point. Both fragments are comprised of littoral forest on sandy soils, interspersed with swampy areas and grassland clearings. This site is currently under the management of Missouri Botanical Gardens (MBG), and both fragments are believed to contain six lemur species. The forests at Manombo, located approximately 3 km north of Agnalazaha, consist of four large fragments of lowland and littoral rainforest, surrounded by anthropogenic grassland matrix dotted with small satellite fragments (<100 ha). Of the four main fragments, only two are considered for this study: Parcel I of the Special Reserve (MSR), managed by Madagascar National Parks, and the Classified Forest (MCF), administered by The Department of Water and Forests (DEF). Smaller peripheral fragments were not investigated. Both study fragments are composed of lowland rainforest and are believed to contain eight lemur species. These fragments connect at three separate points ranging from 25-60 m in width, but are treated as distinct fragments as they are largely isolated and differ in their protected status. The most eminent threat to these sites are slash-and-burn agriculture, or *tavy* which is often accompanied by bushfires. Other known threats in the region include clear-cutting, mining, selective logging, and hunting (Johnson & Overdorff 1999, Balko & Underwood 2005, Lehman et al 2006a). All data were collected from June 4 to October 21, 2007.

2.3.2 Fragment Characteristic Measurements

Details of fragment size and shape were calculated using base maps of each site on ArcGIS version 9.3 (see Chapter 1 Figure 1.4). Degree of isolation was not considered in this study, as there was not enough variation among sites. Fragment size measurements included total fragment area (*TA*) in hectares and perimeter length (*P*) in metres. Perimeter measurements included both external perimeter and internal clearings. Shape was calculated using the shape index (SI) formula:

$$SI = \frac{P}{200\left[(\pi TA)^{0.5}\right]}$$ (Patton 1975, Laurance & Yensen 1991)

The shape index will be 1 when the fragment is circular and increase as the fragment becomes more irregular in shape, with any value over 5 being considered highly irregular. The surrounding matrix type of each forest fragment was assessed in the field.

2.3.3 Line Transect Methodology

Line transect methods were used to measure primate density for all eight lemur species found in Agnalazaha and Manombo. A total of seven transects in four forest fragments were surveyed (Table 2.1), and trail lengths varied with the size of the fragment being investigated. In Agnalazaha, all transects were set up along existing trails to limit forest degradation. In this case, the narrowest trails with the least amount of local traffic possible were selected (Figure 2.1a). In Manombo, one existing trail of 2 km (CNR1) was used as a transect, and another transect of 2 km (CNR2) was cut in the northern area of the fragment. Two new transects were also cut in the Classified Forest (CNC1, CNC2), both measuring 2 km (Figure 2.1b). Due to the winding nature of existing trails, all sightings and flag points were analyzed based on their distance to the nearest forest edge using GIS mapping. All newly cut transects ran from the forest edge into the interior of the forest in as perpendicular a direction as possible from the forest edge.

Each transect was marked using flagging tape at 25 m intervals starting at the forest edge. The first tree trunk > 10 cm DBH at the forest edge for each transect was defined as

Table 2.1. Transect characteristics at Agnalazaha and Manombo.

				Number of Repetitions			Total Survey Effort (m)		
Site	**Frag-ment**	**Transect Name**	**Transect Length (m)**	**Day**	**Night**	**All**	**Day**	**Night**	**All**
Agnalazaha	AIN	CHI2/3	1200	17	10	27	20,400	12,000	32,400
		CHI4	1250	22	11	33	27,500	13,750	41,250
	ACO	CHC1	2000	21	10	31	42,000	20,000	62,000
Manombo	MSR	CNR1	2000	11	11	22	22,000	22,000	44,000
		CNR2	2000	9	10	19	18,000	20,000	38,000
	MCF	CNC1	2000	11	14	25	22,000	28,000	50,000
		CNC2	2000	14	8	22	28,000	16,000	44,000

the edge point for the transect (Lehman et al 2006b). Each transect at Agnalazaha was surveyed an average of 30 times during the study period, with a 2:1 ratio of diurnal to nocturnal walks. At Manombo, each transect was surveyed an average of 22 times during the study period, with a 1:1 ratio of diurnal to nocturnal walks.

Figure 2.1a. Transects and sighting points at Agnalazaha.

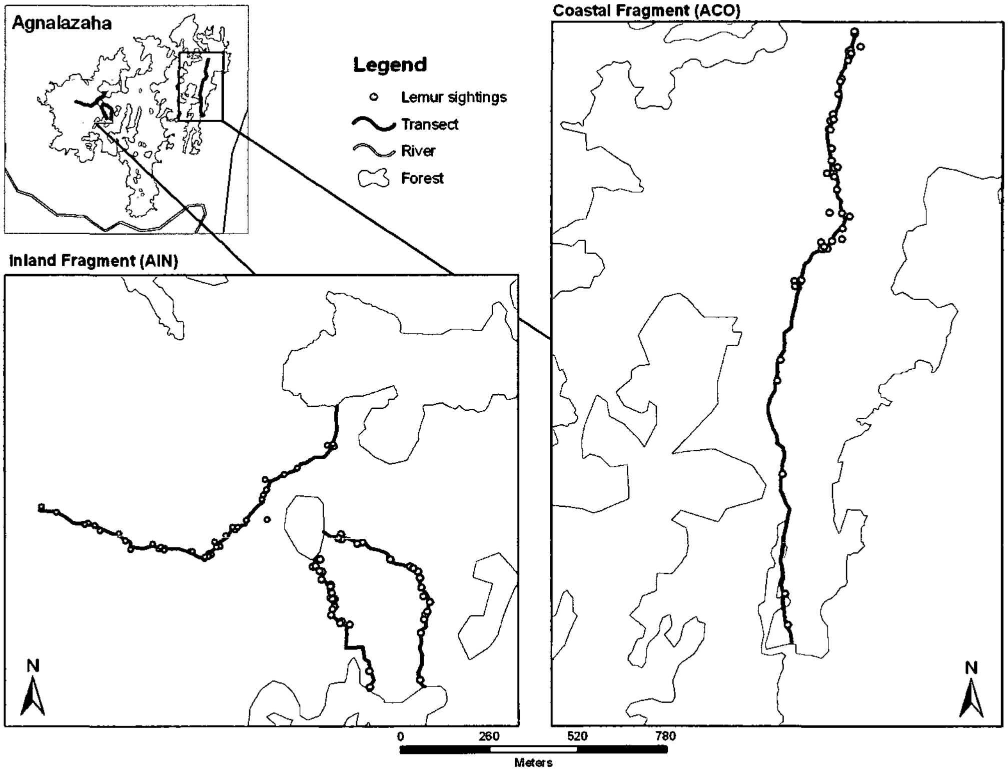
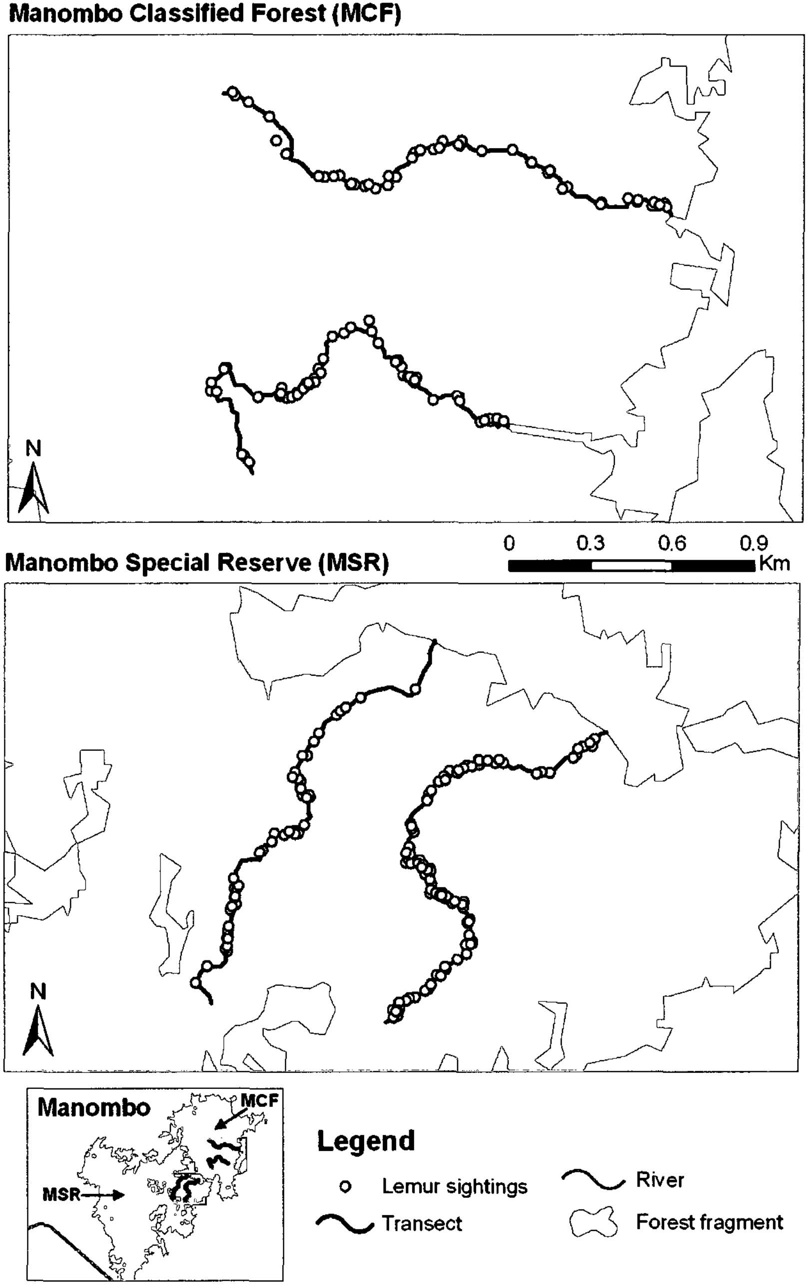


Figure 2.1b. Transects and sighting points at Manombo.



Diurnal walks began between 0700 h and 1100 h and nocturnal walks began between 1800 h and 2300 h. Transect walks occurred 2 to 4 days per week, with between 2 and 6 walks per day and no one transect being walked more than once per day. The two sites were rotated through on a bi-monthly basis, and transect selection was based on a regular order. Starting points for all surveys were rotated between the forest edge and the last flag on the transect to ensure that data were not biased by time of day.

Surveys consisted of walking slowly (approximately 1 km/h) and silently. During each survey, the following were recording at each lemur sighting:

i) Date and time
ii) GPS location
iii) Lemur species
iv) Number of individuals
v) Group composition (age- and sex-class of individuals)
vi) Distance between the observer and the center of the group sighted (m)
vii) Sighting angle (degrees)
viii) Perpendicular distance between transect and the center of the group (m)
ix) Group spread (m)
x) Height in canopy (m)
xi) Method of detection (visual or auditory)
xii) Activity (rest, move, feed, or social)

2.3.4 Abiotic Data Collection

During each survey, abiotic data were collected along transects to assess changes in climatic conditions from forest edge to interior. The following data were collected at each 100 m interval using a light meter (Extech Foot Candle/Lux Light Meter) and portable weather station (SM-19 Skymate Plus): i) light intensity (lux), ii) temperature (°C), iii) relative humidity (%) and iv) wind speed (knots).

2.3.5 Botanical Survey

To evaluate local forest conditions, botanical surveys were conducted at all sites. The objectives of botanical sampling at these sites are to 1) characterize the forest structure and species composition of forest vegetation in forest fragments of differing shape and size, and 2) examine how that structure and species composition varies with distance to forest edge. A 1 ha plot (20 m x 500 m) was established at each site and sub-divided into 20 m x 20 m subplots, for a total of 25 subplots. The plot was positioned in this way to get continuous measurements of forest structure and tree species composition from forest edge to interior. The following data were recorded within each subplot: i) tree species identification (for all trees > 10 cm DBH), ii) number of trees > 10 cm DBH, iii) tree height (m, for all trees > 10 cm DBH), iv) height at first branch (m, for all trees > 10 cm DBH). These data provide preliminary information on forest structure and tree dendrometrics.

2.3.6 Anthropogenic Disturbance

While levels of anthropogenic disturbance at forest sites are often estimated based on species abundance distributions (Hill & Hamer 1998, Watt 1998), a more direct way of assessing forest disturbance is by using visual evidence. This method has the benefit of providing a more quantitative measure of the degree of forest disturbance, rather than simply classifying it as disturbed or undisturbed (Watt 1998), as well as defining the types of disturbance that are occurring. Disturbance data at Agnalazaha and Manombo were collected continuously along transects during daytime surveys. The following instances of disturbance were recorded:

i) Presence/indicators of humans (saw/heard humans, heard wood chopping)
ii) Presence/indicators of cattle (saw cattle, cattle droppings)
iii) Dogs
iv) Clearings > 5 m^2 in diameter
v) Wood chopping sites
vi) Felled trees (either > 10 cm DBH or smaller logs bundled together)
vii) Fires

Disturbance measures i-iii were recorded as the mean number of sightings per km walked. Number of clearings, wood chopping sites, and felled trees were recorded only once at the end of the study. Disproportionate rates of disturbance reported between sites is expected, largely due to the fact that the trails used for transects at Agnalazaha were pre-existing, and therefore in use for activities such as locating and processing forest products. Of the Manombo trails, only one of the four was pre-existing, and was created by lemur researchers rather than local people. Despite this fact, comparisons of disturbance frequencies are still made between the sites since trails were abundant and interconnected throughout Agnalazaha. Those trails that were selected as transects were less frequently utilized, and are believed to provide an accurate representation of this site.

2.3.7 Primate Density

Population density estimates of all lemur species were obtained for each site, each fragment, and each edge distance category using the Whitesides et al (1988) histogram inspection method to determine effective sighting distance and transect area for each species. Effective sighting distance was calculated using the following formula:

$$E = \frac{N_t}{N_f} FD$$

Where E is the effective sighting distance (m), N_t is the total number of sightings, N_f is the number of sightings below the fall-off distance, and FD is the fall-off distance (m) (Whitesides et al 1988). Transect area was then calculated using the following formula:

$$A = \left(\frac{1}{2} S + E\right) L_t$$

Where A is the transect area (m^2), S is the mean group spread (m), E is the effective sighting distance (m), and L_t is the transect length (Whitesides et al 1988). Population density for groups and individuals was calculated by dividing the total number of groups and the total number of individuals sighted during the census by the transect area.

2.3.8 Edge Responses

Data from the primate surveys were used to quantify response to forest edge by each lemur species. The GPS location of all transect flags were recorded using a Garmin GPS 76. These waypoints were then projected onto base maps of each site using ArcGIS version 9.3 (Figures 2.1a and 2.1b). Each lemur sighting was then plotted as a new point along the transect extrapolating from nearest flag, sighting distance, and sighting angle data. All points were then analyzed for their distance to the nearest defined forest edge. Forest edge was defined in two ways: as external edge, which included only the perimeter of each fragment, and as all edge, which included both fragment perimeter and clearings within the fragment (Figures 2.1a and 2.1b). For each flag and sighting point, a distance to external edge (DEE) (m) and distance to any edge (DAE) (m) was output and used to classify each in terms of edge proximity. 100 m distance bins were used as categories.

Each lemur species was analyzed for response to edge by correlating density and distance to forest edge. If a species showed a significant negative relationship with DAE/DEE, they were said to have a positive response to edge. If a species showed a positive relationship with DAE/DEE, they were said to have a negative response to edge. If a species showed no relationship with DAE/DEE, they were said to have no response to forest edge.

2.3.9 Data Analysis

All statistical analyses were executed using SPSS Version 17.0. Mann-Whitney U tests were used to test for differences in abiotic and botanical characteristics between forest fragments and sites, while Chi-Square goodness-of-fit tests were used to test for differences in encounter rates of anthropogenic disturbance and individual and group primate densities between forest fragments and sites. Spearman's rank order correlation tests were used to test for correlations between abiotic and vegetation characteristics, anthropogenic disturbance rates, primate densities, and distance to edge categories. This linear correlation test was used since the sampling area extended only 500 to 1400 m into the forest, a distance within which linear gradient changes in environmental characteristics should be detected without extending too great a distance beyond which edge effects may be occurring (Laurance & Yensen 1991); however, it is important to note that these tests may not be sensitive to non-linear spatial variation. Correlation relationships were classified as weak (r-value from .10 to .29 or -.10 to -2.9), medium (r-value from .30 to .49 or -.30 to -4.9), or strong (r-value from .50 to 1.0 or -.50 to -1.0) (Pallant 2005). In cases where $n < 10$ and the r-value was greater than 0.7 or -0.7 without statistical significance, trends were still inferred as it is likely that non-significance was a result of a small sample size (Ploger & Yasukawa 2003). Nonparametric tests were used in all calculations because data were not normally distributed. Some correlation tests involved multiple tests on the same data. However, corrections to p-values (e.g., the highly conservative Bonferroni correction) were not applied, as these analyses involve small sample sizes (reducing the risk of Type I errors) and are primarily exploratory in nature.

2.4 Results

2.4.1 Fragment Characteristics

On average, the fragments at Agnalazaha had a smaller area relative to perimeter than Manombo and high shape indices. Throughout this study, no GPS waypoints over 650 m from an edge were recorded in Agnalazaha. Forest fragments at Manombo were larger in size but also had high shape indices (Table 2.2). GPS waypoints were recorded at this site up to 1462 m from the edge.

Table 2.2. Fragment shape and size at Agnalazaha and Manombo.

Site	**Fragment**	**Perimeter (km)**	**Total Area (km^2)**	**Shape Index (*SI*)**
Agnalazaha	AIN	70.24	10.63	6.08
	ACO	34.79	3.36	5.35
Manombo	MSR	52.53	15.85	3.72
	MCF	109.14	29.09	5.71

2.4.2 Abiotic Variables

Light intensity, nighttime temperatures and wind speed were significantly higher in Agnalazaha than at Manombo for all times of day. Daytime temperatures and relative humidity differed among fragments but not between sites (Table 2.3).

Table 2.3. Differences between forest fragments in median temperature, relative humidity, wind speed and light intensity at Agnalazaha and Manombo.

Site	Fragment	Light Intensity (lux)	Temperature (°C)			Relative Humidity (%)			Wind Speed (knots)		
		Day	Day	Night	All	Day	Night	All	Day	Night	All
Agnalazaha	AIN	569.6	22.2†	20.9	21.6†	84.2†	86.1	85.2†	.07	.06	.06
	ACO	1089	23.7†	21.9	23.2†	78.3†	85.3	80.4†	.13	.11	.12
	All	810.3††	22.9	21.2††	22.2††	81.4	9.30	83.3	.09††	.08††	0.1††
Manombo	MSR	170.1†	22.4†	19.8†	21.6†	81.8†	81.8†	81.8†	0	0	0
	MCF	227.3†	21.2†	20.8†	21.0†	93.0†	87.8†	90.0†	0	0	0
	All	183.3††	22.1	20.3††	21.4††	84.4	8.00	84.6	0††	0††	0††

† Significant difference in the same category between fragments at the same site using Mann-Whitney U test

†† Significant difference in the same category between sites using Mann-Whitney U test

Light Intensity

Light intensity showed no correlation with distance to edge categories during the day at Agnalazaha or Manombo (Table 2.4). Light intensity was not measured at night.

Table 2.4. Light intensity analyses at Agnalazaha (n=7) and Manombo (n=11) using Spearman's rank order correlation between temperature and distance to forest edge. *p* (2-tailed) < .05

Site	**Time of day**	**DAE**				**DEE**			
		r	*p*	Strength	Trend at edge	*r*	*p*	Strength	Trend at edge
Agnalazaha	Day	-.125	.051		-	-.078	.224		-
Manombo	Day	-.065	.436		-	.089	.286		-

† Significant correlation between light intensity and distance to edge categories using Spearman's rank order correlation

Temperature

Temperature showed only a weak correlation toward warmer temperatures during the day at Agnalazaha using distance to external edge (DEE) categories. At Manombo, daytime temperatures showed a weak positive correlation with distance to all edges (DAE), but a stronger significant negative correlation at night using both DAE and DEE categories (Table 2.5).

Table 2.5. Temperature analyses at Agnalazaha (n=7) and Manombo (n=11) using Spearman's rank order correlation between temperature and distance to forest edge. *p* (2-tailed) < .05

Site	**Time of day**	**DAE**				**DEE**			
		r	*p*	Strength	Trend at edge	*r*	*p*	Strength	Trend at edge
Agnalazaha	Day	-.027	.673		-	-.169	.008†	Weak	Warmer
	Night	.041	.588		-	-.105	.168		-
Manombo	Day	.212	.010†	Weak	Cooler	.131	.113		-
	Night	-.440	.000†	Medium	Warmer	-.431	.000†	Medium	Warmer

† Significant correlation between temperature and distance to edge categories using Spearman's rank order correlation

Relative Humidity

Relative humidity was not significantly correlated with distance to edge categories at Agnalazaha during the day or at night. Results in Manombo showed only a weak correlation towards higher humidity near the forest edge during the day (Table 2.6).

Table 2.6. Relative humidity analyses at Agnalazaha (n=7) and Manombo (n=11) using Spearman's rank order correlation between temperature and distance to forest edge. p (2-tailed) $< .05$

		DAE				**DEE**			
Site	**Time of day**	r	p	Strength	Trend at edge	r	p	Strength	Trend at edge
Agnalazaha	Day	-.067	.295		-	.102	.112		-
	Night	.052	.493		-	.050	.509		-
Manombo	Day	-.235	.004†	Weak	Wetter	-.142	.086		-
	Night	-.014	.892		-	.003	.976		-

† Significant correlation between relative humidity and distance to edge categories using Spearman's rank order correlation

Wind Speed

Wind speed showed weak negative correlations with edge distances at all times of day in Agnalazaha (Table 2.7). At Manombo, wind speed was too low to be recorded over the study period.

Table 2.7. Wind speed analyses at Agnalazaha (n=7) and Manombo (n=11) using Spearman's rank order correlation between temperature and distance to forest edge. p (2-tailed) $< .05$

		DAE				**DEE**			
Site	**Time of day**	r	p	Strength	Trend at edge	r	p	Strength	Trend at edge
Agnalazaha	Day	-.183	.004†	Weak	Windier	-.199	.002†	Weak	Windier
	Night	-.166	.029†	Weak	Windier	-.160	.035†	Weak	Windier

† Significant correlation between wind speed and distance to edge categories using Spearman's rank order correlation

2.4.3 Vegetation Structure

Comparison of Sites and Fragments

The median number of tree species and median tree DBH per subplot were significantly lower in Agnalazaha than in Manombo (Table 2.8). Within Agnalazaha, the median number of trees > 10 cm DBH and median tree DBH were significantly lower in AIN than in ACO, while median tree height was significantly lower in ACO than in AIN. At Manombo, tree abundance and number of species were similar between fragments, but DBH, tree height, and crown height were significantly higher in MCF.

Edge Effects: Tree Density and Species Richness

All botanical data were identical between DEE and DAE categories except in AIN. For this fragment, DEE and DAE results are reported separately in all tables. For ACO, MSR and MCF only DEE results are reported.

Table 2.8. Differences between forest fragments in the median number of trees per subplot, median number of tree species per subplot, median tree DBH per subplot, median tree height per subplot, and median crown height per subplot for all trees > 10 cm DBH at Agnalazaha and Manombo.

Site	**Frag-ment**	**Number of Trees**	**Number of Species**	**DBH (cm)**	**Height (m)**	**Crown Height (m)**
Agnalazaha	AIN	29.56†	15.20	14.20†	9.90†	4.29
	ACO	34.92†	14.64	14.90†	9.44†	3.54
	All	32.24	14.92††	14.60††	9.65	3.88
Manombo	MSR	33.24	18.64	16.00†	8.01†	3.40†
	MCF	33.72	16.28	21.00†	10.92†	4.56†
	All	33.48	17.46††	18.50††	9.45	3.98

† Significant difference in the same category between fragments at the same site using Mann-Whitney U test

†† Significant difference in the same category between sites using Mann-Whitney U test

In AIN, mean number of trees and mean number of species per subplot did not vary significantly with distance to forest edge in the DEE categories. However, mean number of trees did show a weak correlation with DAE categories, with fewer trees closer to the forest edge. These variables did not differ significantly between edge categories in ACO. In Manombo, there were no significant correlations between the number of trees or tree species per subplot and distance to forest edge in MSR. In MCF, number of trees per subplot showed a strong negative correlation with distance to forest edge, and number of tree species per subplot showed a medium negative correlation with distance to forest edge. These results were also evident when data for the two Manombo fragments were combined (Table 2.9).

Edge Effects: Dendrometrics

In Agnalazaha, tree DBH showed a weak negative correlation with distance from forest edge only when considering the site as a whole. Mean tree height consistently showed a weak positive correlation with distance from forest edge at Agnalazaha. Crown height showed a medium-strength correlation with distance from edge in AIN only using DEE categories. There were no significant correlations between tree characteristics and distance to edge at Manombo (Table 2.10).

Table 2.9. Tree density and species richness analysis at Agnalazaha and Manombo (n=5) using Spearman's rank order correlation between mean number of trees > 10 cm DBH and tree species and distance to forest edge. *p* (2-tailed) < .05

		Number of trees per subplot				**Number of species per subplot**			
Site	**Fragment**	*r*	*p*	Strength	Trend at edge	*r*	*p*	Strength	Trend at edge
Agnalazaha	AIN DAE	.429	.032+	Medium	Fewer	.094	.654		-
	AIN DEE	.094	.654		-	-.104	.620		-
	ACO	-.223	.284		-	-.219	.292		-
	All	-.146	.311		-	-.058	.691		-
Manombo	MSR	-.037	.859		-	-.306	.137		-
	MCF	-.609	.001+	Strong	More	-.433	.031+	Medium	More
	All	-.361	.010+	Medium	More	-.382	.006+	Medium	More

+ Significant correlation to distance to edge categories using Spearman's rank order correlation

Table 2.10. Dendrometrics analysis at Agnalazaha and Manombo (n=5) using Spearman's rank order correlation between mean DBH, tree height and crown height for all trees and distance to forest edge. *p* (2-tailed) < .05

		DBH (cm)				**Tree Height (m)**				**Crown Height (m)**			
Site	**Fragment**	*r*	*p*	Strength	Trend at edge	*r*	*p*	Strength	Trend at edge	*r*	*p*	Strength	Trend at edge
Agnalazaha	AIN DEE	-.011	.761		-	.092	.012+	Weak	Shorter	.422	.036+	Medium	Taller
	AIN DAE	.039	.295		-	.115	.002+	Weak	Shorter	.143	.496		-
	ACO	-.049	.150			.191	.000+	Weak	Shorter	.233	.262		-
	All	-.080	.001+	Weak	Larger	.064	.010+	Weak	Shorter	.063	.664		-
Manombo	MSR	.028	.419		-	-.030	.385		-	.231	.266		
	MCF	.061	.075		-	.041	.236			.257	.215		-
	All	.021	.396		-	.029	.235			-.031	.831		-

+ Significant correlation to distance to edge categories using Spearman's rank order correlation

2.4.4 Anthropogenic Disturbance

During census walks at Agnalazaha and Manombo, encounter rates for anthropogenic disturbance were higher at Agnalazaha (Table 2.11). There were no encounters of any anthropogenic disturbance in MSR during the study period. Encounter rates of human presence were significantly higher in AIN than in ACO and MCF. Cattle were seen within the forest only in Agnalazaha. Incidence of dogs was very low or absent at all sites. AIN had the greatest number of clearings and wood chopping sites. Felled trees or log pile encounter rates were similar in both AIN and ACO, and very low or absent at Manombo. Only one live *tavy* fire was seen during transect walks at AIN.

Table 2.11. Anthropogenic disturbance encounter rates at Agnalazaha and Manombo.

Site	**Frag-ment**	**Humans /km**	**Cattle /km**	**Dogs /km**	**Clearings /km**	**Chop sites /km**	**Logs /km**	**Fires /km**
Agnalazaha	AIN	0.88†	0.33	0	0.55	0.40	0.50	0.02
	ACO	0.08†	0.15	0.02	0.25	0.23	0.52	0
Manombo	MSR	0	0	0	0	0	0†	0
	MCF	0.02	0	0.02	0.06	0.06	0.08†	0

† Significant difference between forest fragments using chi-square goodness-of-fit test.

In both Agnalazaha and Manombo, anthropogenic disturbance showed a strong negative correlation with DAE categories. Using DEE categories, no significant correlation was found between disturbance rates and distance to edge in Agnalazaha, but a strong positive correlation was found in MCF (Table 2.12).

Table 2.12. Anthropogenic disturbance analyses at Agnalazaha and Manombo (MCF only) using Spearman's rank order correlation between rates of disturbance and distance to forest edge.

	DAE				DEE			
Site	*r*	*p*	Strength	Trend at edge	*r*	*p*	Strength	Trend at edge
Agnalazaha	-.852	.015†	Strong	More	-.036	.939		-
Manombo	-.602	.023†	Strong	More	.843	.002†	Strong	Less

† Significant correlation between rates of disturbance and distance to edge categories using Spearman's rank order correlation

2.4.5 Primate Density

Only four lemur species were sighted in AIN (the frugivorous *E. cinereiceps* and *C. major,* the folivore *A. ramantsoavani,* and the insectivore *M. jollyae*). Folivorous *H. griseus* was not recorded in AIN during the census but presence was confirmed in this fragment from sightings during other data collection procedures. These five species were also seen along transects in ACO. In Manombo, a total of five lemur species were sighted over the study period (*E. cinereiceps, H. griseus, L. jamesi* (a folivore), *A. ramantsoavani, M. jollyae*). Frugivorous *V. v. editorum* were heard on two occasions during surveys in MCF as well as spotted during *E. cinereiceps* focal follows both in MCF and in MSR, but no sightings were recorded along the transects. Fresh bite marks of insectivorous *D. madagascariensis* were found during botanical sampling in MCF, but this species was never sighted.

Densities of *E. cinereiceps* were not significantly different among fragments or between sites. *Cheirogaleus major* densities also did not vary among fragments in Agnalazaha, and were not sighted in Manombo. Densities of *H. griseus* were low across sites but were significantly higher in Manombo than in Agnalazaha. *Lepilemur jamesi* were found only at Manombo, and densities did not vary among fragments. *Avahi ramantsoavani* density was significantly higher in Manombo than in Agnalazaha but did not differ among fragments within each site. *Microcebus jollyae* densities varied among all fragments and between sites, with increasing density in MSR, ACO, MCF and AIN and higher overall density in Agnalazaha than in Manombo (Table 2.13).

2.4.6 Edge Response of Lemur Density

The relationship between distance to edge and lemur density was investigated using Spearman's rank order correlation (Table 2.14). *Eulemur cinereiceps* density showed a medium-strength negative relationship (positive edge response) with DEE categories when grouping sites together. Looking at each fragment individually, *E. cinereiceps* density had no significant correlation and one negative trend with distance from forest edge. *Cheirogaleus major, A. ramantsoavani* and *L. jamesi* densities all showed no correlation with distance to edge categories. *Microcebus jollyae* density showed a strong negative relationship (positive response) with both DAE and DEE categories at Manombo, and a trend toward a negative edge response with DEE categories at Agnalazaha. Correlation results lumping Manombo and Agnalazaha also supported a strong negative correlation with DAE categories.

Spearman's rank order correlation was used to explore correlations between lemur density and all abiotic, botanical, and disturbance data (Appendix 1 Table A.1.1). *Eulemur cinereiceps* density correlated positively with temperature, wind speed and rates of anthropogenic disturbance in Agnalazaha, and showed a trend toward a negative correlation

Table 2.13. Individual and group densities per km^2 of each lemur species at Agnalazaha and Manombo.

	Agnalazaha						Manombo					
	AIN		ACO		ALL		MSR		MCF		ALL	
Species	**Ind/ km^2**	**Group / km^2**	**Ind/ km^2**	**Group / km^2**	**Ind/ km^2**	**Group / km^2**	**Ind/ km^2**	**Group / km^2**	**Ind/ km^2**	**Group / km^2**	**Ind/ km^2**	**Group / km^2**
V. v. editorum	-	-	-	-	-	-	Pr	Pr	Pr	Pr	Pr	Pr
E. cinereiceps	7.67	2.68	7.20	3.60	7.45	3.11	10.51	2.80	9.47	3.67	9.95	3.26
C. major	0.45	0.45	.32	.21	0.39	0.35	-	-	-	-	-	-
H. griseus	Pr	Pr	0.71	0.71	0.21††	0.21††	5.87	1.07	2.79	2.33	4.23††	1.74††
L. jamesi	-	-	-	-	-	-	44.91	35.35	23.26	17.78	45.73	35.46
A. ramantsoavani	23.29	20.19	35.60	23.73	28.7††	21.8††	48.92	28.99	32.43	19.46	40.7††	25.8††
D. madagascariensis	-	-	-	-	-	-	-	-	Pr	Pr	Pr	Pr
M. jollyae	107.1†	103.3†	51.17†	51.17†	82.5††	80.4††	29.01†	29.01†	66.45†	66.45†	48.2††	48.2††

Pr: No sightings during census period, but presence confirmed

† Significant difference in the same category between fragments at the same site using chi-square goodness-of-fit test

†† Significant difference in the same category between sites using chi-square goodness-of-fit test

Table 2.14. Responses to edge by each lemur species at Agnalazaha (n–7) and Manombo (n–14). p (2-tailed) < .05

	Agnalazaha				Manombo				ALL					
	DAE		DEE		DAE		DEE		DAE		DEE			
Species	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*	**Correlation Strength**	**Response To Edge**
E. cinereiceps	-.75	.053†	-.04	.939	-.50	.067	-.51	.061	-.43	.051	-.45	.040†	Medium	Positive
C. major	-.63	.129	.25	.585	-	-	-	-	-.63	.129	.25	.585		None
H. griseus	-.20	.661	-.20	.661	-.56	.039†	-.21	.482	-.34	.134	-.08	.728	Strong	Positive
L. jamesi	-	-	-	-	.04	.887	.11	.703	.04	.887	.11	.703		None
A. ramantsoavani	-.41	.355	-.25	.589	-.10	.748	-.12	.692	.02	.949	.05	.841		None
M. jollyae	.18	.699	.71	.071†	-.67	.009†	-.68	.007†	-.58	.005†	-.39	.082	Strong	Positive

† Statistically significant or trend correlation by Spearman's rank order correlation

with tree height. In Manombo, *E. cinereiceps* density correlated positively with number of tree species and showed a trend toward negative correlation with DBH. *Hapalemur griseus* densities did not correlate significantly with any variables, but did show trends toward negative correlations with number of trees, number of tree species, DBH, and tree height and positive correlations with crown height at Agnalazaha, and negative correlations with tree height at Manombo. *Lepilemur jamesi* showed trends toward negative correlations with number of trees and DBH at Manombo. *Avahi ramantsoavani* showed trends toward negative correlations with tree height at Agnalazaha and positive correlations with DBH at Manombo. *Microcebus jollyae* density correlated positively with temperature and negatively with number of tree species in Manombo, and showed trends toward negative correlations with tree height at Manombo and positive correlations with DBH at Manombo. *Cheirogaleus major* densities did not correlate significantly with any measured variable.

2.5 Discussion

2.5.1 Fragment Characteristics

The forest fragments at Agnalazaha were smaller in area than those at Manombo, but all fragments had considerably high shape indices. Generally, forest fragment area has been found to significantly alter plant composition and structure (Arroyo-Rodriguez & Mandujano 2006) and wildlife abundance (Winter et al 2000, Wieczkowski 2004), as well as the degree to which edges affect the environment (see Section 1.3). Shape, however, has also been found to be a key factor in influencing these variables (Ewers & Didham 2007).

The responses of plant and animal species based on forest fragment characteristics are further explored in Sections 2.5.2 and 2.5.3.

2.5.2 Edge Effects: Abiotic, Biotic, and Anthropogenic

Abiotic Edge Effects

Overall, abiotic characteristics and vegetation structure appeared to respond irregularly to forest edge. In general, conditions in anthropogenically altered matrix are hotter and drier than those within forested areas, as solar radiation is better able to reach the ground where there is no canopy (Murcia 1995, Gade 1996). This results in higher light intensity, higher temperatures and lower relative humidity at forest edges (Kapos 1989, Chen et al 1993, Matlack 1993). At both Agnalazaha and Manombo, light intensity had no significant relationship with proximity to forest edge showing no support for Prediction 1 (Table 2.15). Temperatures at Agnalazaha were higher than those at Manombo and appeared to be consistent throughout the forest, while at Manombo warmer temperatures were found near forest edge more than in the interior, showing only moderate support for Prediction 2 (Table 2.15). Relative humidity was also consistent at Agnalazaha, while results at Manombo were inconsistent, suggesting only a weak correlation toward higher humidity at the forest edge *contra* Prediction 3 (Table 2.15). Wind speed was the one variable that did vary with distance to forest edge at Agnalazaha, showing some support for Prediction 4 (Table 2.15), although wind was too light to be measurable at Manombo over the study period. Overall, the apparent absence of abiotic edge effects resulting from solar radiation in the matrix and generally ubiquitous climate seen at Agnalazaha is likely related to the typically “open” or non-continuous forest canopy of littoral forests (Bollen & Donati

2005). Murcia (1995) suggests that light intensity may also be interacting with other variables to change patterns of abiotic characteristics with distance to forest edge. For example, an increase in light at a newly created edge may result in a high initial concentration of leaf biomass, creating a peak of canopy closure at the forest edge that would prevent linear correlations from being detected.

Biotic Edge Effects

The median number of trees per subplot was not significantly different between Agnalazaha and Manombo, but was higher in ACO than in AIN. Within Agnalazaha, edge-to-interior correlations of this variable were inconsistent, resulting in only one medium-strength positive relationship. At Manombo, however, medium to strong negative correlations were found, most notably in MCF. Tree stem densities measured in previous studies have been diverse in terms of edge response, as in some cases density increases with proximity to forest edge (Palik & Murphy 1990, Williams-Linera et al 1998, Carvalho & Vasconcelos 1999, Moorman et al 2002, Arroyo-Rodriguez & Mandujano 2006), in others it decreases (Chen et al 1992, Olupot 2009), and in others there is no response (Carvalho & Vasconcelos 1999). Tree species richness is typically higher near the forest edge (Matlack 1994, Foggo et al 2001, Balko & Underwood 2005, Olupot 2009), a characteristic found only in Manombo, where tree species richness was significantly higher overall than in Agnalazaha showing moderate support for Prediction 5 (Table 2.15). Contrasting results in tree density and species richness response at Agnalazaha and Manombo are likely due to differences in tree species compositions between sites, as there may be disparate numbers of edge-tolerant and edge-intolerant species between them.

Differences in fragment size and shape also affects plant composition and structure (Benitez-Malvido 1998, Tabarelli et al 1999, Arroyo-Rodriguez & Mandujano 2006), as well as forest management – the fragments at Manombo have greater protection measures in place, so certain species may not persist in Agnalazaha due to selective logging.

Median tree DBH was significantly higher in Manombo than in Agnalazaha, a disparity that may be expected as littoral forest is characterized by a low canopy and small tree diameters (Bollen & Donati 2005). Within Agnalazaha, mean DBH showed only one weak negative correlation with distance to edge, and no correlations at Manombo. These results are not typical of edge effects, as DBH is usually found to be lower at the forest edge (Carvalho & Vasconcelos 1999, Sizer & Tanner 1999, Chapman & Chapman 2003, Cancino 2005, Olupot 2009). Median tree height did not differ between sites, though correlations with distance to edge at Agnalazaha are more comparable to previous studies, in that there is a weak but consistent positive correlation with distance from forest edge (Unwin 1989, Foggo et al 2001) showing moderate support for Prediction 6 (Table 2.15). No correlation was found between tree height and distance from edge in Manombo. Median crown height also did not differ between sites, and correlations with distance to edge showed a medium-strength negative relationship in AIN only using DEE categories. In general, trees adjacent to edge are expected to have a lower mean DBH, height and crown height, since tree mortality rates at the edge are higher due to the stress of exposure to changes in microclimate, insect attacks, and windfall (Saunders et al 1991). The fact that these trends in tree characteristics were not consistently observed at the study sites suggests that tree size is relatively consistent throughout all of the fragments.

Overall there does not appear to be strong abiotic or biotic edge effects occurring at either Agnalazaha or Manombo. The high variation in results among fragments is not surprising, as forest edges are dynamic in space and time and edge effects can vary according to vegetation structure, time since edge creation, geographical position and forest patch size (Sisk & Margules 1993, Matlack 1994). Agnalazaha and Manombo are part of a landscape that has undergone considerable change, from ongoing forest loss and anthropogenic disturbance within the forest, as well as the effects of Cyclone Gretelle from which the forests are still recovering (Johnson et al, in press). It is also possible that edge effects at these sites are contained within a narrow perimeter zone of the forest edge, and that smaller distance categories or a non-linear correlation analysis may more clearly reveal differences between edge and interior characteristics.

Anthropogenic Edge Effects

In Agnalazaha, the absence of edge effects may also be attributed to the high frequency of anthropogenic disturbance, which has created gaps in the forest caused by selective logging and for creating browse for cattle. Similar conditions have resulted in high variability in forest structure and composition at other tropical forest sites (Kapos et al 1997, Williams-Linera et al 1998), where an increase in disturbance resulted in edge areas becoming wider and increasingly diffuse, making edge effects difficult to measure. According to the "additive edge model", the magnitude of edge effects at any point is equivalent to the sum of edge effects originating from all nearby edges (Malcolm 1994), so smaller internal clearings within the fragments may make it difficult to produce linear correlations with the distance to external edge or distance to all edge (which included large internal clearings) categories used in this study.

2.5.3 Primate Density and Fragmentation Responses

Of the eight lemur species found at Agnalazaha and Manombo, only six were sighted during the census period. The two that were not sighted, *V. v. editorum* and *D. madagascariensis*, were confirmed to be present only in Manombo based on sightings and evidence found outside of census walks. Overall, Manombo had a higher number of lemur species present (except for *C. major* and *M. jollyae*), and this was especially true in MSR. This may imply that conservation efforts at the reserve are effective in conserving those larger-bodied species (*V. v. variegata, E. cinereiceps*) that are most often hunted and that are likely more negatively affected by habitat disturbance because of their body size and a diet that relies less on insects and more on vegetation. Higher densities at Manombo may also be due to a larger forest area, where species are able to maintain larger home ranges. Less intense anthropogenic disturbance at this site may also play a role. For example, the nocturnal *L. jamesi* and *A. ramantsoavani* sleep in the hollows of large trees (Wright 1999, Rasoloharijaona 2008) and are hunted during the day (FB Ralainasolo pers. comm.), and may also be sensitive to any habitat disturbance that may target large trees. High tree species richness at Manombo is another factor that may contribute to high species densities; this characteristic has been found to correlate with higher densities of *Varecia* due to an increase in the probability of year-round fruit availability (Morland 1991, Vasey 2003). Lastly, higher connectivity at Manombo may benefit population densities by increasing gene flow between fragments.

High rates of anthropogenic disturbance at Agnalazaha may account for lower overall lemur densities at this site, supporting Prediction 7. Higher densities of *M. jollyae* and *C. major* at Agnalazaha may indicate that they are resilient to habitat disturbance, or that they benefit from high proportions of forest edge. For example, *M. jollyae* density appears to have a positive relationship with fragment shape, with highest densities in AIN followed by MCF, ACO and MSR. This suggests that *M. jollyae* responds positively to an increase in forest edge relative to total forest area.

2.5.4 Primate Density and Edge Responses

Frugivores

Eulemur cinereiceps showed medium positive response to forest edge when considering both sites as a whole (see Table 2.14), *contra* Prediction 8 (Table 2.15). Correlations between *E. cinereiceps* density and other variables were varied across sites, so possible reasons for edge preference are unclear. In Agnalazaha, *E. cinereiceps* density correlated positively with temperature, wind speed and anthropogenic disturbance, and showed a negative correlation trend with tree height, a possible artifact of higher temperatures, wind speeds and rates of disturbance and shorter trees found at the edge. It is also possible that these variables affect *E. cinereiceps* populations in a positive way, as high temperatures may benefit the species' thermoregulatory processes (Vasey 2004). In addition, high wind speeds and rates of disturbance are likely to occur in less dense areas of the forest where the opportunity for increased exposure to sunlight or an abundance of light-loving plant foods could be driving their ranging behaviours. At Manombo, *E. cinereiceps* density correlated positively with number of tree species, conceivably for the higher possibilities of year-round fruit availability, and showed a trend toward a negative correlation with tree DBH. A study by Lehman et al (2006b) at the eastern rainforest site of Vohibola III Classified Forest reported a neutral response to edge in *E. rubriventer*, another frugivorous *Eulemur* species, further suggesting that frugivorous species are not necessarily affected negatively by edge.

Density correlations for *C. major* also refute Prediction 8, as this species showed no response to forest edge or to any other variables. Lehman et al (2006b) reported a negative response to edge in *C. major* at Vohibola III Classified Forest, a response that covaried strongly with tree diameter (Lehman et al 2006c). Disparity in results may be due to variations in forest characteristics between Vohibola and Agnalazaha, or may be a result of density estimations being calculated at a time when part of the population may still be in torpor.

Folivores

Results for the response to edge by *H. griseus* were inconsistent, showing strong positive response only to all edges in Manombo but no trends elsewhere. *Hapalemur griseus* density also showed no significant correlation to any of the measured abiotic, botanical or disturbance variables, though did show trends toward a negative relationship with tree density, tree species richness, DBH, and tree height and a positive relationship with crown height at Agnalazaha, and a negative relationship with tree height at Manombo. Overall, *H. griseus* appeared to prefer areas of the forest in which trees are relatively small, a possible characteristic of the swamp areas at Agnalazaha in which this species is known to range preferentially (HE Andriamaharoa pers. comm.). Although sightings for this species were few, we can tentatively say that *H. griseus* appears to be unaffected by forest edge, showing some support for Prediction 9 (Table 2.15). This species has also been previously reported to have a neutral response to edge in Vohibola III Classified Forest by Lehman et al (2006b).

Lepilemur jamesi and *A. ramantsoavani* showed no response to edge, also supporting Prediction 9. Lehman et al (2006b) also reported a neutral response to edge in another *Avahi* species, *A. laniger*, at Vohibola III Classified Forest. Like *H. griseus,* densities of these species showed no significant correlation to any other variables, and had higher densities in Manombo (*L. jamesi* is absent from Agnalazaha). These patterns may be due to their folivorous diet, but may also relate to forest type, quality, and fragment protection statuses. There is only 20% overlap of the most common tree species between Agnalazaha and Manombo, so it may simply be that the species at Manombo provide better-quality leaves than those species at Agnalazaha. *Lepilemur jamesi* density also showed trends toward a negative relationship with tree density and DBH at Manombo, while *A. ramantsoavani* density showed trends toward a positive relationship with DBH at Manombo. Disparity in tree size preference between these two species may be due to differences in the feeding habits of these genera, as *Avahi* has been found to use significantly larger trees than *Lepilemur* (Thalmann 2001).

Insectivores

M. jollyae showed a strong positive response to edge in Manombo, and no significant response in Agnalazaha (though a trend toward a negative response to external edge). This could be due to the more ubiquitous edge-type environment in Agnalazaha, which *M. jollyae* should prefer. High densities of *M. jollyae* in AIN, the fragment with the highest shape index, support this theory. Densities of this species also correlated positively with temperature and number of tree species in Manombo. These correlations may be an artifact of temperature and tree density being significantly higher at the forest edge in Manombo and thus not causal. The positive response to forest edge by *M. jollyae* supports Prediction 10 (Table 2.15). The closely related *M. rufus* has also been reported to have a positive response to edge at Vohibola III Classified Forest, perhaps due to an abundance of arthropod prey at the forest edge (Lehman et al 2006b).

Prediction 11 stated that forest fragments that are larger and less complex in shape should support greater densities of species that respond negatively to edge than fragments that are smaller and more complex in shape. Conversely, small and irregularly shaped fragments should support greater densities of species that respond positively to edge (Table 2.15). According to the results of this study, this prediction has some support. Manombo had significantly higher densities of *A. ramantsoavani*, *H. griseus,* and *L. jamesi,* and contained both *V. v. editorum* and *D. madagascariensis*. Although none of these species were found to respond negatively to edge, they were not found to prefer edge overall. In addition, the species with the strongest positive response to edge, *M. jollyae*, had increasing population densities corresponding with increasing fragment shape indices.

Table 2.15. Chapter 2: Predictions and Support

	Prediction	**Supported?**	**Comments**
1	Light intensity will increase with increasing proximity to forest edge.	No	
2	Temperature will increase with increasing proximity to forest edge.	Moderate	Agnalazaha: Weak increase at edge with daytime DEE. Manombo: Medium increase at edge at night.
3	Relative humidity will decrease with increasing proximity to forest edge.	No	Manombo: Weak increase at edge with daytime DAE.
4	Wind speed will increase with increasing proximity to forest edge.	Moderate	Agnalazaha: Weak increase at edge.
5	Tree species richness will increase with increasing proximity to forest edge.	Moderate	Manombo: Medium increase at edge.
6	Mean tree height and diameter at breast height (DBH) will decrease with increasing proximity to forest edge.	Moderate	Agnalazaha: Weak decrease in tree height at edge.
7	Lemur species densities will be lower in fragments with more intense anthropogenic disturbance.	Mostly Yes	Manombo is richer in all lemur species except for *C. major* and *M. jollyae.*
8	The primarily frugivorous species *V. variegata editorum, E. cinereiceps* and *C. major* will show a negative response to forest edge.	No	*E. cinereiceps* appears to respond positively to edge. *C. major* shows no response to edge.
9	The folivorous *H. griseus, L. jamesi* and *A. ramantsoavani* will show no response to forest edge.	Yes	*H. griseus* appears to have no response to edge, but sightings were few. *L. jamesi* and *A. ramantsoavani* show no response to edge.
10	The partly insectivorous *D. Madagascariensis* and *M. jollyae* will show a positive response to forest edge.	Yes	*M. jollyae* responds positively to edge in Manombo, and shows no response in Agnalazaha (but site is theorized to be all edge).
11	Forest fragments that are larger and less complex in shape will support greater densities of species that respond negatively to edge than fragments that are smaller and more complex in shape, which will support greater densities of species that respond positively to edge.	Mostly Yes	Manombo: Higher densities of species with no response to edge. Agnalazaha: Higher densities of *M. jollyae* (who prefer edge), and increasing population density corresponding with increasing fragment SI.

CHAPTER 3: HABITAT USE, RANGING AND EDGE EFFECTS ON THE GRAY-HEADED BROWN LEMURS OF AGNALAZAHA

3.1 Introduction

3.1.1 Edge Effects in a Fragmented Landscape

One of the most prevalent consequences of agriculture and other types of deforestation in a tropical environment is the creation of a fragmented mosaic landscape (Gade 1996, Britt et al 1999). Besides reducing the absolute amount of viable habitat for forest-dwelling species, forest fragmentation may also affect local flora and fauna based on their tolerance to encroaching anthropogenically altered land, or matrix (Saunders et al 1991, Robinson et al 1992, Lynam & Billick 1999). For example, a matrix comprised of grassland or farmland could be considered a hostile landscape for arboreal species that cannot travel effectively over open spaces, or may be more vulnerable to hunters and predators on the ground. Any reluctance to travel between forest fragments could lead to a reduction in home range, reduction in potential food resources, and eventual inbreeding depression in the population (Frankham 1998). Fragmentation in a forest landscape also leads to an increase in the amount of forest edge relative to total forest area.

Forest edge is defined as the boundary between the forest and the surrounding matrix (Malcolm 1994) (see Section 1.3.1). At this boundary, interior parts of the forest become subject to increased penetration of both biotic and abiotic conditions found in the surrounding matrix. This phenomenon is known as edge effects (see Section 1.3 for a detailed discussion). The strength of these effects may differ according to forest type, matrix type, and climate (Newmark 2001), as well as the shape and size of the fragment (see Chapter 1 Figures 1.2 and 1.3). Past studies of edge effects have focused on the demographic responses of species, measuring abundance and distribution of plants and animals in relation to forest edge (Olupot 2004). However, very little research has been conducted on the effects of forest edge on the behaviour of a species. Yahner & Mahan (1997) refer to this unexplored area as the next logical step in understanding species-area relationships, and instrumental in linking behavioural ecology with landscape-level ecological processes. In this chapter, I aim to address this research gap by examining the behavioural responses to forest edge by the lemur species *Eulemur cinereiceps* at the site of Agnalazaha in southeastern Madagascar.

3.1.2 Anthropogenic Disturbance in Southeastern Madagascar

The study of edge effects is of particular relevance in those areas fragmented by active anthropogenic disturbance, as new edges are being continually created. In the tropical forests of Madagascar, agriculture plays a major role in the dynamics of landscape fragmentation (Gade 1996). The dominant method of deforestation is the practice of slash-and-burn agriculture, or *tavy,* which is often accompanied by bushfires. The practice of *tavy* eventually leads to the sterilization of soil, resulting in land that can only support grasses and fire-resistant shrubs (Bollen & Donati 2006). The littoral forests of the southeast are among the ecosystems most threatened by this practice, and are reduced to fragments representing less than 10% of their original area (Ganzhorn et al 2001). Littoral forests grow on sandy soils and occur 2-3 km from the coast at an altitude of 0-20 m (Dumetz 1999). The site of Agnalazaha consists entirely of this type of forest, interspersed with swamps and *tavy* clearings. Anthropogenic threats at this site were ongoing during the study period, and included *tavy* fires, selective logging, and a strong presence of local people and cattle (see Section 2.4.4).

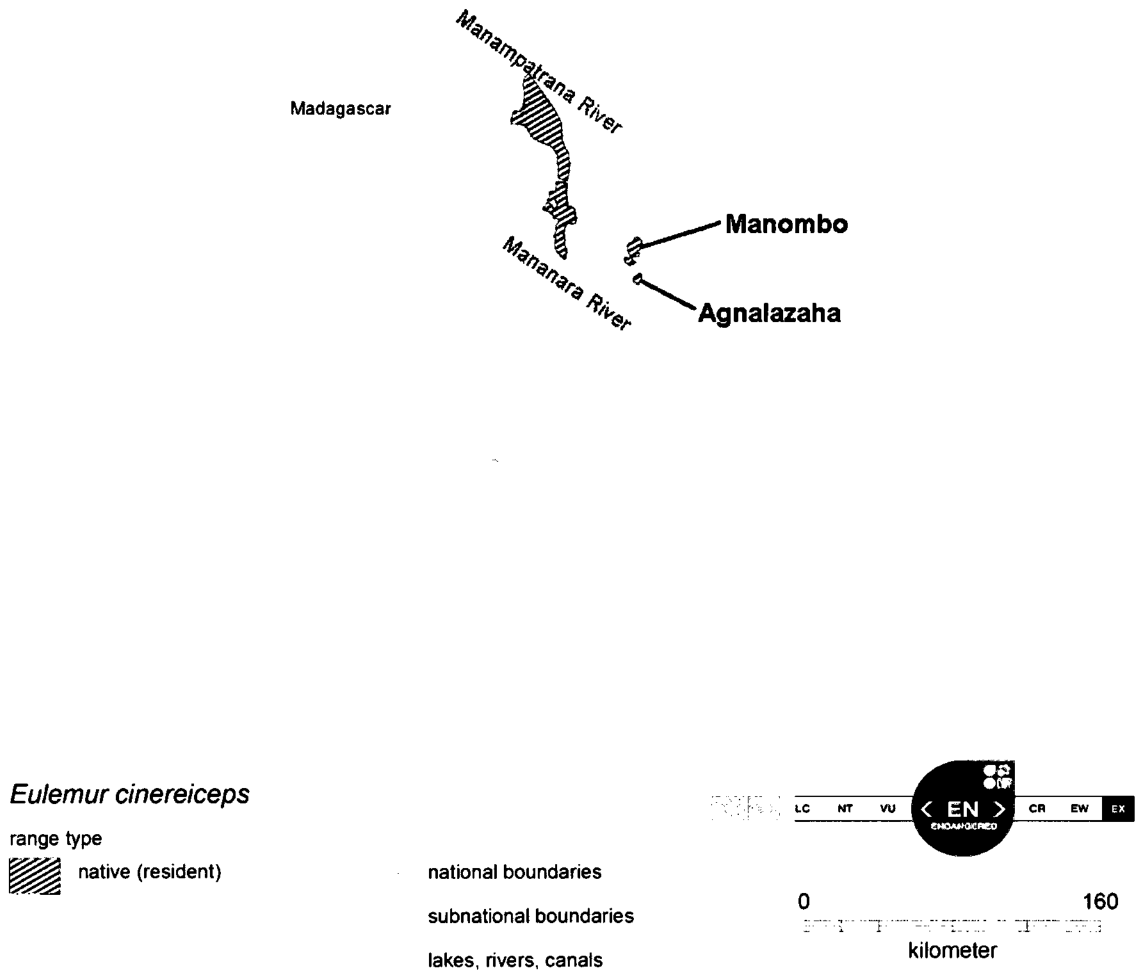
3.1.3 *Eulemur cinereiceps* as a Surrogate Species

Forest fragmentation and edge effects can affect different species in different ways, as some species may be unable to cope with edge conditions while others may thrive. Determining how the flora and fauna in a fragmented forest respond to edge conditions is an important consideration in conservation planning, but further determining *why* a species responds the way that it does will provide greater insight into what aspects of edge effects are likely causative factors in the species' response. This leaves the question of which individual species should be selected in exploring a behavioural response, in a way that will most benefit the study site as a whole.

There are a great variety of conservation planning approaches utilized in evaluating and protecting any particular landscape or species. Surrogate species approaches, such as determining a flagship, focal, keystone, indicator, or umbrella species, are considered effective and allow a focus on one species while supporting many others that populate the same area (Favreau et al 2006). This approach is especially efficient in regions high in biodiversity for which few species-specific data are available. In a fragmented landscape, a good surrogate species should be large (because of the allometric relationship between body size and home range size) (Caro & O'Doherty 1999), and should be one that is sensitive to changes in food availability. This increases the chances that the protection of this species will encompass the protection of species with smaller home ranges and those that rely on patchily distributed food resources.

At the site of Agnalazaha, *E. cinereiceps* was selected to explore a specific species' behavioural response to edge effects for two reasons. Firstly, *E. cinereiceps* is classified by the IUCN as endangered with decreasing numbers (IUCN 2009), a trend exacerbated by ongoing habitat destruction and hunting pressure (Johnson 2002). In total, the range of this species covers only 700 km^2, running along a thin strip of forest from the Mananara River to just north of Manampatrana River in southeastern Madagascar (Irwin et al 2005) (Figure 3.1). The limited range and prevalent anthropogenic threats to *E. cinereiceps* underscore its conservation priority, and understanding this species' responses to anthropogenic disturbance is crucial for its conservation management. Secondly, *E. cinereiceps* is among the larger-bodied frugivorous lemur species in the region, and is likely crucial to ecosystem maintenance through seed dispersal. Their diet consists primarily of fruit, which makes up between 60% and 90% of their total dietary intake, supplemented with leaves, flowers, fungi and insects (Overdorff & Johnson 2003). The local extinction of *E. cinereiceps* would therefore be expected to have a strong impact on forest processes in Agnalazaha, and conservation of this species may be critical in maintaining overall biodiversity. In addition, the frugivorous nature of *E. cinereiceps* makes this species ideal for the study of edge effects, since fruit is patchily distributed and likely affected by the penetration of abiotic conditions from the matrix (Ferreira & Laurance 1997, Laurance et al 1997). Data on *E. cinereiceps'* response to edge effects may be used in conservation plans for Agnalazaha. For example, determining an effective reserve size and shape, or how wide a forest corridor *E. cinereiceps* would require, would be aided by knowing whether the species is avoiding edge, to what extent, and for what reasons.

Figure 3.1. Total range of *E. cinereiceps* (from IUCN 2009)



3.1.4 Research Goals

This chapter examines the behavioural response of *E. cinereiceps* to induced edge resulting from forest fragmentation at Agnalazaha. This is achieved by assessing changes in ranging and feeding patterns as a function of distance to forest edge in order to determine whether *E. cinereiceps* is responding positively, negatively, or neutrally to forest edge, an alternate strategy for determining edge response that will be compared with census results from Chapter 2. These patterns are then correlated with vegetation characteristics of Agnalazaha in an effort to determine what factors, if any, are contributing to *E. cinereiceps'* edge response.

3.2 Hypotheses and Predictions

3.2.1 Ranging and Forest Edge

Since the distribution of primate species is generally understood to correspond with ecological variables and food competition (Wrangham 1980), it is expected that the ranging patterns of *E. cinereiceps* be based on the fulfillment of their dietary needs. *Eulemur cinereiceps* is primarily frugivorous, and so their ranging patterns should be linked to the availability and dispersion of fruit. Since results from Chapter 2 suggest that *E. cinereiceps* prefers to range near forest edges at Agnalazaha, it follows that food availability should be higher for this species near the edge. It is therefore predicted that:

Prediction 1: There will be a negative correlation between time spent overall and distance to forest edge for *E. cinereiceps.*

Prediction 2: There will be a negative correlation between time spent feeding and distance to forest edge for *E. cinereiceps.*

3.2.2 Dietary and Feeding Behaviour Characteristics

Based on the previous assumption that *E. cinereiceps* will spend more time feeding overall at the forest edge, it follows that *E. cinereiceps* should spend more time feeding on fruit at the edge than on other food resources since this species is primarily frugivorous. In turn, *E. cinereiceps* might be expected to resort to a greater variety of foods in parts of the forest where fruit was not abundant. It is therefore predicted that:

Prediction 3: The proportion of fruit eaten by *E. cinereiceps* will correlate negatively with distance to forest edge.

Prediction 4: Dietary diversity of *E. cinereiceps* will correlate positively with distance to forest edge.

Since preferred food resources should be more abundant for *E. cinereiceps* at the forest edge, it follows that the group will not have to cover as large an area at the edge in order for all members to feed simultaneously. It is therefore predicted that:

Prediction 5: Group spread of *E. cinereiceps* while feeding will correlate positively with distance to forest edge.

Prediction 6: Nearest neighbour distance while feeding will correlate positively with distance to forest edge, where the primary food resource is expected to be scarcer.

3.2.3 Home Range

The site of Agnalazaha has a relatively high proportion of forest edge to forest interior, and a high shape index (see Section 2.4.1). Since *E. cinereiceps* has been predicted to range preferentially at the forest edge, it is also predicted that:

Prediction 7: *E. cinereiceps* home ranges at Agnalazaha will be small relative to other *Eulemur* species since their preferred habitat type is abundant at this site.

3.2.4 Food Availability

Food availability for *E. cinereiceps* is calculated as a measure of the presence of fruit that the species is known to include in their diet, and individuals are expected to feed preferentially where fruit availability is highest. It is therefore predicted that:

Prediction 8: Fruit availability will vary negatively with distance to forest edge, since fruit tree density should vary negatively with distance to forest edge.

Prediction 9: Time spent feeding by *E. cinereiceps* will vary positively with fruit availability.

3.3 Methods

3.3.1 Study Animals and Site

The site of Agnalazaha (S 23° 11.175' E 47° 43.095') is located on the southeastern coast of Madagascar (Figure 3.1). This area is characterized by high rainfall with yearly fluctuations, heaviest during the cyclone season between January and March (Johnson 2002, Ratsimbazafy 2002). Data for this study were collected between the cold dry season from June to August (mean rainfall 138 cm, mean temp. 20°C) and the warm dry season from September to November (mean rainfall 115 cm, mean temp. 23°C).

Agnalazaha consists of two distinct forest fragments: ACO, a fragment of forest running along the coastline (3.36 km^2), and AIN, a larger fragment situated further inland (10.63 km^2). These fragments are separated by a grassland matrix, and have large perimeters relative to total area as well as a highly complex shape (see Section 2.4.1). The site of Agnalazaha is currently under the management of Missouri Botanical Gardens

(MBG) in collaboration with local communities, and is home to a wide variety of lemurs, rodents, raptors and invertebrates.

For this study, behavioural data were collected for two *E. cinereiceps* groups in AIN (groups AI1 and AI2). Age and sex composition of each group is indicated in Table 3.1.

Table 3.1. Eulemur cinereiceps group compositions at Agnalazaha.

Group	**No. Adult Males**	**No. Adult Females**	**No. Juvenile Males**	**No. Juvenile Females**	**Total Group Size**
AI1	2	2	2	0	6
AI2	2	1	1	1	5

3.3.2 Focal Animal Sampling

Data collection involved both instantaneous scan and continuous focal animal sampling (Altmann 1974). Groups were followed by one of two primary observers for two to four days every week between June 6 and October 8, 2007. Focal individuals were selected according to a regular rotation of all adult group members, alternating between males and females. Focal observations generally began from 08:30 to 09:00, each lasting two hours with 3 to 4 follows per day. Data were collected on group AI1 during 26 days for a total of 177 observation hours. Group AI2 was also observed during 26 days for a total of 155 observation hours.

State behaviours were recorded at 10-minute intervals, with behaviours categorized as: i) R (rest), ii) F (forage/feed), iii) T (travel), or iv) S (social). A state of travel was considered if the focal animal was moving from tree to tree, or if the animal was stationary but continued a bout of tree-to-tree movement within 10 seconds. Foraging or feeding was defined as picking, holding, biting, chewing, or inspecting a food item either visually or by smelling. If the scan occurring less than 10 seconds after the animal swallowed or dropped a food item, a state of foraging/feeding would still be recorded if the animal continued to forage or feed within 10 seconds. The following data were also recorded at each 10-minute scan interval:

i) Date
ii) Weather (sunny, cloudy or raining)
iii) Temperature (°C)
iv) Relative humidity (%)
v) Time (hh:mm:ss)
vi) GPS location
vii) Forest type (sandy, disturbed sandy, swamp, disturbed swamp)
viii) Group spread (m)
ix) Height of animal in canopy (m)
x) Height of tree (m)
xi) Position in canopy (understory, middle, upper canopy) (tree interior or exposed)
xii) Distance to nearest neighbour (m)

Temperature and relative humidity were recorded using a portable weather station (SM-19 Skymate Plus). GPS waypoints for each scan were recorded using a Garmin GPS 76. Only waypoints with three or more satellite signals and an error of less than 10 m were considered. Group spread was evaluated by having one observer walk frequently from the perceived centre of the group to where no additional animals could be seen. The observer walked perpendicular to the direction of group travel (Chapman & Chapman 2000). Distance to nearest neighbour was recorded as the distance of the nearest animal to the focal animal within 5 metres.

Continuous focal data were taken for all feeding and travel behaviours. Feeding bouts began when the focal animal bit into a food item, and ended after the animal swallowed or dropped the food item and 10 seconds had passed. For each feeding bout by the focal animal, the following data were recorded:

i) Start time (hh:mm:ss)
ii) End time (hh:mm:ss)
iii) GPS location
iv) Plant species (Malagasy vernacular)
v) Plant part consumed (RF: ripe fruit, UF: unripe fruit, ML: mature leaves, YL: young leaves, FL: flower, IN: insect, FU: fungus, or OT: other)
vi) Group spread (m)
vii) Height of animal in canopy (m)
viii) Height of tree (m)
ix) Position in canopy (understory, middle, upper canopy) (tree interior or exposed)
x) Distance to nearest neighbour (m)

Travel behaviour was also recorded continuously, and a GPS waypoint was recorded at the start of each focal follow and again each time a bout of travel ended. Other event behaviours, such as sexual behaviour, scent marking, and response to predators and other disturbances in the forest (vigilance, displays, alarm calls) were also noted throughout follow sessions *ad libitum.*

3.3.3 Edge Use

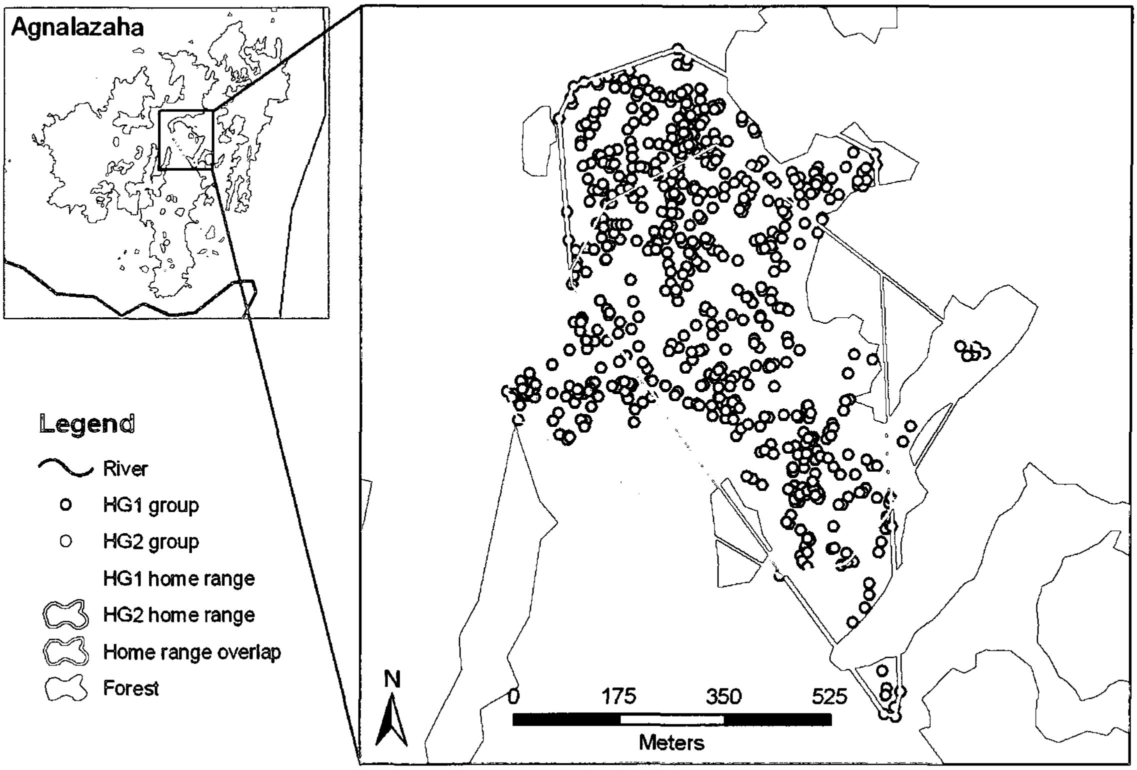
All GPS waypoints recorded during *E. cinereiceps* focal follows were projected onto a base map of Agnalazaha using ArcGIS version 9.3 (Figure 3.2). Each point was then analyzed for distance to the nearest defined forest edge. Forest edge was defined in two ways: as external edge (DEE), which included only the perimeter of each fragment, and as all edge (DAE), which included both fragment perimeter and clearings within the fragment. For each waypoint, DEE (m) and DAE (m) was output and used to classify each in terms of edge proximity. 25 m distance bins were used as categories.

Edge use was examined for all *E. cinereiceps* study groups by calculating mean percentages of time spent resting, feeding, traveling and engaging in social behaviour within distance-to-edge categories (DAE and DEE). Diet composition, dietary diversity, habitat use, vegetation structure and phenology were also calculated for each distance-to-edge category.

3.3.4 Activity Budgets

Activity budgets were constructed for each study group using counts of focal scans in each of the four behaviour categories (R, F, T and S). Each category was expressed as the proportion of overall time spent.

Figure 3.2. GPS waypoints recorded during focal follows of groups AI1 and AI2 in Agnalazaha.



3.3.5 Diet Composition and Diversity

The diet of *E. cinereiceps* was recorded into categories including ripe fruit, unripe fruit, mature leaves, young leaves, flowers, insects, fungus, and other/unknown. For most analyses, each of these food items was placed into one of four major categories: i) fruit, ii) leaves, iii) insects and iv) other. Proportion of each food item present in the *E. cinereiceps* diet was calculated for DAE and DEE as a percentage of total time spent feeding in each distance-to-edge bin.

Dietary diversity was also measured in each distance-to-edge category using the relative proportion time spent feeding on each food item. Diversity scores were calculated for each DAE and DEE category using the following formula:

$$D = \left(\sum_{i=0}^{n} p_i^2 \right)^{-1}$$

where *D* is dietary diversity, *p* is the proportion of time spent feeding in each food category, and *i* is each food category within the total sample (Gautier-Hion 1980). The *D*-value will be greater if individuals spend equal amounts of time feeding on many food items, and lower if individuals spend a disproportionate amount of time feeding on fewer food items. Fruit species diversity was calculated for each DAE and DEE category as the number of fruit species consumed over the study period (Bollen et al 2004).

3.3.6 Habitat Use

Eulemur cinereiceps habitat use was analyzed using the tree height and height of the focal animal in the tree measured during focal scans. Mean heights were then calculated for each distance-to-edge bin.

3.3.7 Travel and Home Range

Home ranges for *E. cinereiceps* were estimated in two ways. First, the Minimum Convex Polygon (MCP) method was used to calculate the area and perimeter of the home ranges of each group, as well as the overlap area between groups AI1 and AI2. This was accomplished by mapping all GPS ranging points onto a 25 m by 25 m grid cell matrix. A minimum convex polygon was then fitted to these points all and grid cells within the polygon were summed. In the second method, home range was calculated a second way using a count of only the grid cells overlapped by the ranging points. These two methods were selected for calculating home range in order to make results comparable to past home range studies in *Eulemur*. These methods do not capture total annual home range size due to the limited study period.

3.3.8 Vegetation and Phenology

To evaluate vegetation structure and fruit availability, a 1 ha plot (20 m x 500 m) was established in AIN and sub-divided into 20 m x 20 m subplots, for a total of 25 subplots. The following data were recorded within each subplot:

i) Tree species identification (Malagasy vernacular and scientific names for all trees > 10 cm DBH)
ii) Number of trees > 10 cm DBH
iii) Tree height (m, for all trees > 10 cm DBH)
iv) Height at first branch (m, for all trees > 10 cm DBH)
v) Crown diameter (m, for all trees > 10 cm DBH)
vi) Crown shape (m, for all trees > 10 cm DBH)

Number of tree species, number of trees, mean DBH, mean tree height, and mean crown volume were calculated for each DAE and DEE category. Crown volume was calculated based on crown shape (conical, prolate, or spheroid). For all botanical measures, distance-to-edge categories used were 100 m deep rather than 25 m deep due to difficulties categorizing the large subplots. This resulted in two DAE categories and five DEE categories.

Fruit phenology was measured four times in the cold, dry season (July 6, 30, August 14, 31) and three times in the warm, dry season (September 14, 28, and October 11, 2009). Trees bearing fruit were scored on a 3-point scale corresponding to the estimated percentage of fruit coverage. Food availability was calculated in each DAE and DEE category as a mean total fruit score for the sum of all fruiting trees. Fruit scores for individual trees were calculated by multiplying the fruit score by crown volume. Only fruit trees observed to be fed on by *E. cinereiceps* during focal follows were included in food availability calculations. Of the 739 trees in the plot, 166 of them were considered food trees.

3.3.9 Data Analysis

All statistical analyses were executed using SPSS Version 17.0. Mann-Whitney U and Kruskal-Wallis tests were used to test for variations in botanical measures and food availability between distance to edge categories, while Chi-Square goodness-of-fit tests were used to test for differences in the raw frequencies of behaviours and time spent feeding in each plant part category between sexes and across study groups. Spearman's rank order correlation tests were used to test for correlations between total time spent by *E. cinereiceps* in each behavioural category, time spent feeding on each food item, dietary diversity, fruit species diversity, and distance to edge categories. This linear correlation test was used since the sampling area extended only 1400 m into the forest, a distance within which linear gradient changes in environmental characteristics should be detected without extending too great a distance beyond which edge effects may be occurring. Spearman's rank order correlation test was also use to test for correlations between vegetation characteristics, food availability, and *E. cinereiceps* ranging patterns while feeding (these correlations were performed using DEE categories only as there were too few DAE categories to perform the test). Correlation relationships were classified as weak (*r*-value from .10 to .29 or -.10 to -2.9), medium (*r*-value from .30 to .49 or -.30 to -4.9), or strong (*r*-value from .50 to 1.0 or -.50 to -1.0) (Pallant 2005). In cases where n < 20 and the *r*-value was greater than 0.7 or -0.7 without statistical significance, trends were still inferred as it is likely that non-significance was a result of a small sample size (Ploger & Yasukawa 2003). Nonparametric tests were used in all calculations because data were not normally distributed.

3.4 Results

3.4.1 Activity Budgets

During focal follows in Agnalazaha, *E. cinereiceps* groups AI1 and AI2 spent the greatest proportion of their time resting (74.30% on average), followed by feeding (10.98%), traveling (8.52%) and engaging in social behaviour (2.46%) (Figure 3.3). The number of focal scans spent resting, traveling, and engaging in social behaviour did not vary significantly between groups AI1 and AI2 (Table 3.2). The number of focal scans spent feeding varied significantly between the females of groups AI1 and AI2. The number of focal scans spent feeding and engaging in social behaviour varied between males and females in AI2. Despite differences in some measures, the ranking in time spent on each activity was fairly consistent between groups and sexes, and the largest proportions of their daily budgets did not differ significantly. For simplicity and to improve sample size, groups and sexes are subsequently combined into a single sample for testing the relationships between behaviour and edge categories

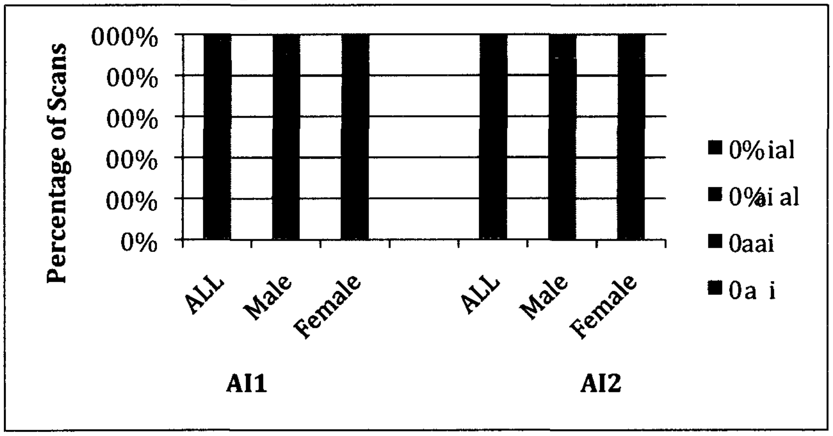
Table 3.2. Proportion of time spent resting, feeding, traveling, and engaging in social behaviour for groups AI1 and AI2 in Agnalazaha based on focal scan data.

Group		**Rest (%)**	**Feed (%)**	**Travel (%)**	**Social (%)**
AI1	Males	77.43	13.03	7.82	1.72
	Females	75.01	11.62††	9.20	4.17
	All	76.15	11.99	8.76	3.10
AI2	Males	74.73	13.93†	9.80	1.54†
	Female	84.52	4.11†/††	8.14	3.23†
	All	78.15	10.44	9.22	2.20

† Significant difference in the same category between sexes in the same group using chi-square goodness-of-fit test on raw frequencies

†† Significant difference in the same category between groups using chi-square goodness-of-fit test on raw frequencies

Figure 3.3. Proportion of time spent resting, feeding, traveling, and engaging in social behaviour for groups AI1 and AI2 in Agnalazaha.



Spearman's rank order correlations using both scan and continuous behavioural data show a strong trend toward more time resting and more time overall spent at forest edges (Table 3.3). In analyses using scan sampling, there is also a strong negative correlation between time spent engaging in social behaviour and DEE categories only. In analyses using continuous focal animal sampling, there are strong negative correlations between time spent traveling and both DAE and DEE categories. No significant correlations were found between time spent feeding and distance to forest edge, though a trend toward a negative relationship is suggested in the continuous data.

Table 3.3. Spearman's rank order correlations between behavioural categories and distance to forest edge. *p* (2-tailed) < .05

	DAE (n=11)				**DEE (n=14)**			
Variable	*r*	*p*	Strength	Trend at edge	*r*	*p*	Strength	Trend at edge
Total No. Scans	-.609	.047†	Strong	More	-.622	.018†	Strong	More
Rest Scans	-.609	.047†	Strong	More	-.600	.023†	Strong	More
Feed Scans	-.487	.128		-	-.467	.092		-
Travel Scans	-.543	.084		-	-.225	.439		-
Social Scans	-.397	.226		-	-.612	.020†	Strong	More
Total Time (continuous)	-.664	.026†	Strong	More	-.543	.045†	Strong	More
Time Feeding	-.600	.051		-	-.434	.138		-
Time Traveling	-.745	.008	Strong	More	-.565	.035†	Strong	More

3.4.2 Diet Composition and Diversity

Fruit (ripe and unripe) accounted for more than 80% of the total diet composition for both males and females in groups AI1 and AI2 (Figure 3.4). During the study, a total of 27 species were consumed by *E. cinereiceps*. Five of these species accounted for 89% of the total fruit diet and were exploited in the majority of edge categories (Table 3.4). The proportion of fruit did not vary significantly between sexes or among groups. The proportion of leaves (young and mature) in the diet was significantly higher for males in AI1 than in AI2, and higher in group AI1 overall. Insect quantity in the diet was significantly higher for males than for females in AI2, and significantly higher for males in AI2 than males in AI1. The proportion of other food items (fungus, nectar, soil) in the diet was significantly higher for females in AI2 than in AI1, and higher in AI2 overall (Table

3.5). As with activity budgets, there are significant differences in some feeding measures between groups and sexes, but the ranking in time spent feeding on each food item was fairly consistent and the largest proportions of their diets did not differ significantly. Thus, groups and sexes are again combined into a single sample for testing the relationships between dietary composition and edge categories

Table 3.4. The top 5 fruit species fed on by AI1 and AI2 at Agnalazaha and their occurrence in each distance-to-edge category.

Species (Malagasy vernacular)	**Proportion of fruit diet (%)**	**DAE Categories**									
		1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**
Randra	36	X	X	X	X	X	X	X	X	X	X
Tsirika	24	X	X	X	X	X	X	X	X	X	X
Voapaky	14	X	X	X	X	X	X	X	X	X	X
Sarivatoa	12	X	X	X	X	X	X	X	X	X	
Farafatrala	3		X							X	

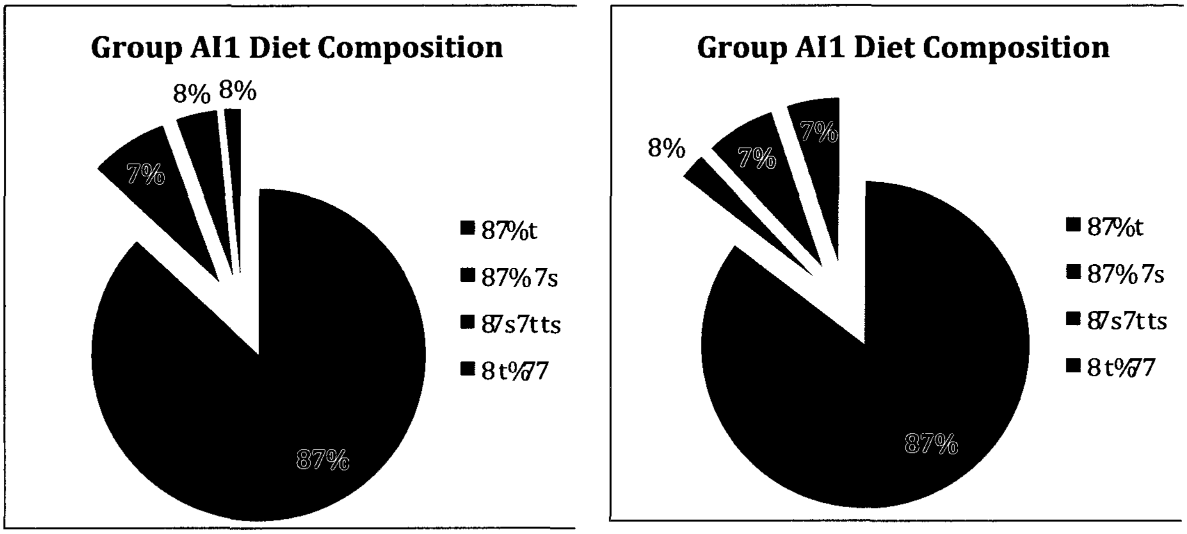
Table 3.5. Proportion of time spent feeding on fruit, leaves, insects, and other food items for groups AI1 and AI2 in Agnalazaha based on continuous focal data.

Group		**Fruit (%)**	**Leaves (%)**	**Insects (%)**	**Other (%)**	**Dietary diversity**	**Fruit sp. diversity**
AI1	Males	88.37	6.98††	3.49††	1.16		14
	Females	85.78	7.84	4.41	1.96††		24
	All	86.97	7.45††	3.99	1.60††	1.14	28
AI2	Males	84.36	2.23††	8.94†/††	4.47		17
	Female	88.89	3.70	0†	7.41††		9
	All	85.41	2.58††	6.87	5.15††	1.09	19

† Significant difference in the same category between sexes in the same group using chi-square goodness-of-fit test on raw frequencies

†† Significant difference in the same category between groups using chi-square goodness-of-fit test on raw frequencies

Figure 3.4. Diet compositions of *E. cinereiceps* groups AI1 and AI2 in Agnalazaha



Using Spearman's rank order test, there were no significant correlations between diet composition and distance-to-edge categories. Dietary diversity and number of fruit species exploited also did not vary with distance to forest edge (Table 3.6).

Table 3.6. Spearman's rank order correlations between diet composition and diversity variables and distance to forest edge. *p* (2-tailed) < .05

	DAE (n=11)				**DEE (n=14)**			
Variable	*r*	*p*	Strength	Trend at edge	*r*	*p*	Strength	Trend at edge
Time fruit	-.600	.051		-	-.418	.156		-
Time leaves	-.147	.667		-	-.077	.802		-
Time insects	-.305	.362		-	-.098	.751		-
Time other	-.467	.147		-	-.520	.069		-
Dietary Diversity	-.269	.424		-	-.118	.700		-
Number Fruit Species	-.535	.090		-	-.417	.157		-

3.4.3 Habitat Use

In testing relationships between habitat use variables and distance to forest edge, a strong negative correlation was found between height of the focal animal with DEE categories, as well as tree height with DEE categories, both heights being higher at the edge

(Table 3.7). Group spread and nearest neighbour distance did not vary with distance to forest edge. No correlations were found in any variable with DAE categories.

Table 3.7. Spearman's rank order correlations between animal height, tree height, group spread, nearest neighbour (NN) distance and distance to forest edge. *p* (2-tailed) < .05

	DAE (n=11)				**DEE (n=14)**			
Variable	*r*	*p*	Strength	Trend at edge	*r*	*p*	Strength	Trend at edge
Animal height	-.327	.326		-	-.538	.047†	Strong	Higher
Tree height	.255	.450		-	-.543	.045†	Strong	Higher
Group Spread	-.227	.502		-	-.143	.642		-
NN distance	.082	.811		-	-.445	.128		-

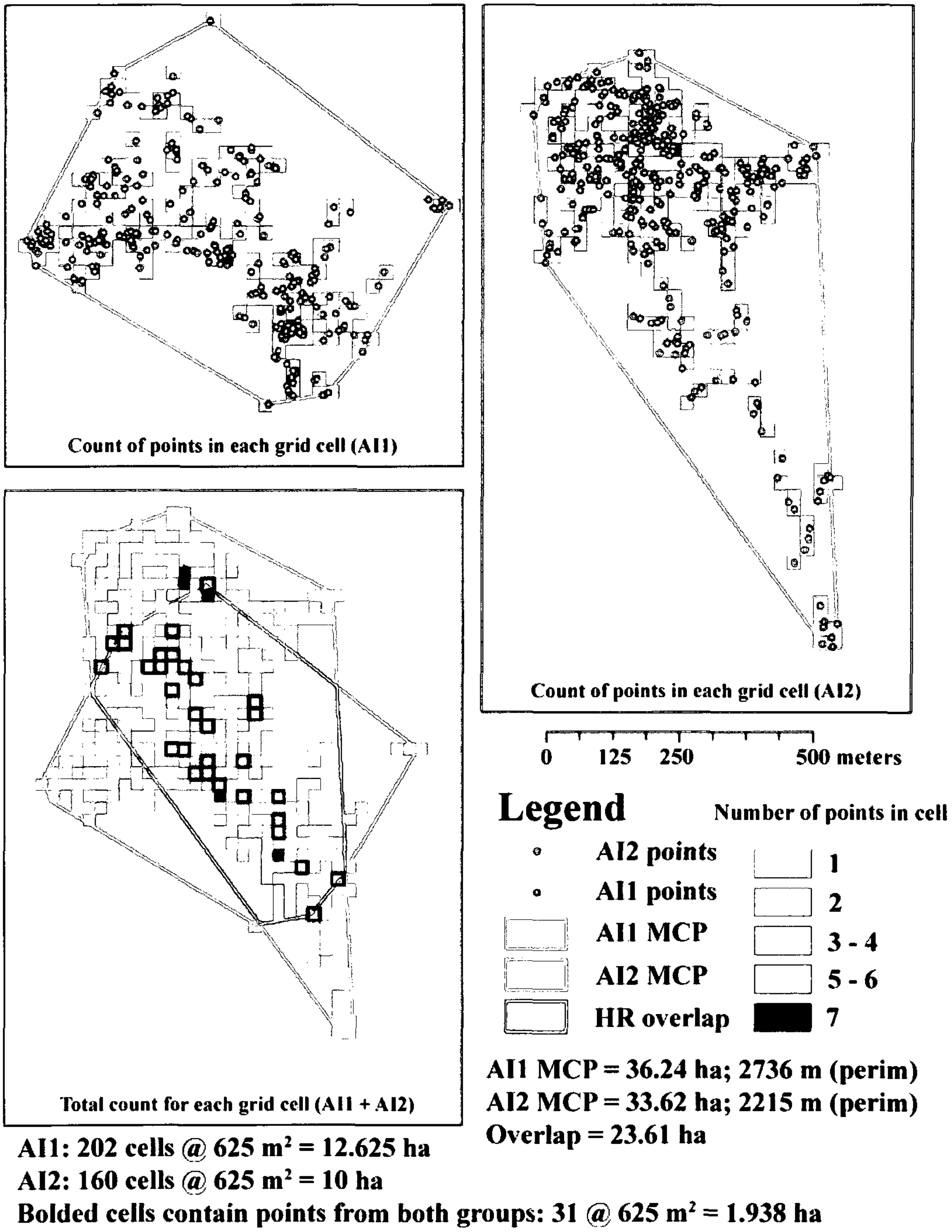
3.4.4 Travel and Home Range

Home ranges for *E. cinereiceps* were very similar between AI1 and AI2 using both the Minimum Convex Polygon (MCP) method and the grid cell count method (Table 3.8, Figure 3.5). Overlap between the home ranges of these two groups was a relatively large area compared to overall home range size.

Table 3.8. Home ranges (HR) and HR overlap for groups AI1 and AI2 using two HR calculation methods.

HR Method	**AI1**	**AI2**	**HR Overlap**
MCP (ha)	36.24	33.62	23.61
Grid Cell Count (ha)	12.63	10	1.94

Figure 3.5. Home ranges and home range overlap of groups AI1 and AI2 using grid cell count and minimum convex polygon (MCP) methods.



AI1 MCP = 36.24 ha; 2736 m (perim)
AI2 MCP = 33.62 ha; 2215 m (perim)
Overlap = 23.61 ha

AI1: 202 cells @ 625 m² = 12.625 ha
AI2: 160 cells @ 625 m² = 10 ha
Bolded cells contain points from both groups: 31 @ 625 m² = 1.938 ha

3.4.5 Vegetation and Phenology

In comparisons between DAE categories, the median number of stems per botanical subplot was significantly higher in the 100 to 200 m category than in the 0 to 100 m category. There were no significant differences between DAE categories in any other botanical variable. In comparisons between DEE categories, the mean crown volume of fruiting trees was significantly larger in the 0 to 100 m category than in the categories ranging from 100 to 500 m from the forest edge (Table 3.9).

Table 3.9. Differences in vegetation characteristics and fruit availability at Agnalazaha using Mann-Whitney U tests between DAE categories and Kruskal-Wallis tests between DEE categories.

	DAE Mann-Whitney U (n=2)		**DEE Kruskal-Wallis (n=5)**	
Variable	*z*	*p*	H	*p*
All Trees				
No. Trees	-2.103	.035†	7.781	.100
No. Species	-.910	.363	5.669	.225
Avg. DBH	-.757	.449	2.885	.577
Avg. Height	-1.165	.244	6.088	.193
Avg. Crown Vol.	-.184	.854	6.421	.093
Fruit Trees				
No. Trees	-1.122	.262	2.332	.675
No. Species	-1.511	.131	2.984	.560
Avg. DBH	-.117	.907	3.231	.520
Avg. Height	-.204	.838	4.557	.336
Avg. Crown Vol.	-.643	.520	12.811	.005†
Cold/dry season fruit availability	-.030	.976	3.311	.507
Warm/dry season fruit availability	-.122	.903	1.632	.803

Spearman's rank order correlations of all tree characteristics with *E. cinereiceps* feedings scans and time spent feeding showed no significant results. However, trends indicating a preference for larger crown volumes were seen using both feeding scans and feeding time. The same analysis using fruit trees in the diet of *E. cinereiceps* also showed no significant correlations, but did suggest trends toward a preference for larger crown volumes and higher fruit availability (Table 3.10).

Table 3.10. Spearman's rank order correlations between *E. cinereiceps* feeding scans and feeding time with botanical measures (n=5, p (2-tailed) < .05)

	Feeding Scans				**Feeding Time**			
Variable	r	p	Strength	Trend at edge	r	p	Strength	Trend at edge
All Trees								
No. Trees	.600	.285		-	.100	.873		-
No. Species	.600	.285		-	-.100	.873		-
Avg. DBH	-.300	.624		-	-.500	.391		-
Avg. Height	-.100	.873		-	-.600	.285		-
Avg. Crown Volume	-.800	.200		Larger	-1.00	-		Larger
Fruit Trees								
No. Trees	-.100	.873		-	-.400	.505		-
No. Species	.400	.505		-	.100	.873		-
Avg. DBH	-.500	.391		-	-.600	.285		-
Avg. Height	-.100	.873		-	-.600	.285		-
Avg. Crown Volume	-1.00	-		Larger	-.800	.200		Larger
Cold/dry season fruit availability	-.400	.600		-	-.800	.200		More
Warm/dry season fruit availability	-1.00	-		More	-.800	.200		More

3.5 Discussion

3.5.1 Activity Budgets

During focal follows at Agnalazaha, *E. cinereiceps* groups spent a large majority of their time resting, followed by feeding, traveling, and engaging in social behaviour. The activity budgets of groups AI1 and AI2 are not unusual, as comparable proportions of time spent on daily activities are found in other *Eulemur* species (Overdorff 1996, Johnson

2002) (Appendix 2 Table A.2.1). In addition, these results are very similar to behavioural data collected on *E. cinereiceps* at the nearby site of Manombo, using similar methodology between October 2006 and December 2007 (Ralainasolo et al 2008) (Appendix 2 Table A.2.1). While Manombo has similar densities of *E. cinereiceps* to Agnalazaha (see Section 2.4.5), the site differs considerably in that it has larger forest fragments (see Section 2.4.1), a higher protection status, and differs in forest type and composition (see Sections 1.4.1 and 2.4.3). This suggests that the characteristics of Agnalazaha (small forest fragments, a high degree of anthropogenic disturbance, littoral forest type) are not altering typical daily activity budgets of *E. cinereiceps*.

Correlations between the total number of scans, rest scans, total time, and time spent traveling with distance to forest edge showed a significantly strong preference of *E. cinereiceps* toward both all edges (DAE) and external edges (DEE), supporting Prediction 1 (Table 3.11). Based on these results, *E. cinereiceps* should be classified as having a positive response to edge, lending further support to results from Chapter 2, which found some evidence of a preference for forest edge based on encounter rates during line transect sampling (see Section 2.4.6). However, no significant correlation was found between feeding scans or time spent feeding with distance to edge categories, *contra* Prediction 2 (Table 3.11).

Hence the patterns seen in *E. cinereiceps'* general activity patterns at this site challenge two major assumptions. Firstly, it was predicted that feeding locations should be affected by distance to forest edge, based on past research that fairly consistently found distinct differences in vegetation between edge and interior forest (MacDougall & Kellman

1992, Benitez-Malvido 1998, Williams-Linera et al 1998, Godefroid & Koedam 2003). There are a number of possible explanations for proximity to forest edge appearing to have no effect on feeding behaviour. For example, the forest fragment in this study is small in area and highly convoluted in shape (see Section 2.4.1), characteristics that may result in the entire fragment being subject to edge conditions that affect fruit tree species abundance or fruiting patterns (see Section 1.3.2). This explanation is supported by the fact that 89% of the fruit species fed on by *E. cinereiceps* were exploited in the majority of distance-to-edge categories. Conversely, it is possible that edge effects at Agnalazaha are contained within a narrow perimeter zone of the forest edge, and that smaller distance categories or a non-linear correlation analysis may more clearly reveal differences between edge and interior feeding behaviours.

The second unsupported assumption is that the general ranging patterns of *E. cinereiceps* would coincide with food availability. In the case of the Agnalazaha groups, strong correlations between resting and traveling with distance to forest edge suggest that there is another reason, unrelated to food availability, that this species might prefer edge. These may include: avoidance of predators that range in the interior (Lahti 2001, Lehman et al 2006b), increased exposure to sunlight or possible warmer temperatures at the edge while resting (MacDougall & Kellman 1992, Nichol 1994, Ostner 2002), or avoidance of anthropogenic disturbances within the forest, such as loggers or fishers present in the swamps (see Section 2.4.4).

3.5.2 Diet Composition and Diversity

The diet of *E. cinereiceps* was found to consist of more than 80% fruit, supplemented with leaves, insects, and occasional fungi, flowers and nectar. These results are consistent with diet compositions of other *Eulemur* species, all showing a heavy reliance on fruit (Overdorff 1993, Dew & Wright 1998, Overdorff & Strait 1998, Johnson 2002, Vasey 2002, Curtis 2004, Tarnaud 2004; 2006, Donati et al 2007, Simmen et al 2007, Tanaka 2007, Ralainasolo et al 2008) (Appendix 2 Table A.2.2). The study groups fed on a total of 27 fruit species during the dry season, considerably more than the 12 fruit species consumed by *E. cinereiceps* at Manombo during a similar time frame (Ralainasolo et al 2008). Between these two sites, *E. cinereiceps* at Agnalazaha had seven fruit species in common with *E. cinereiceps* at Manombo. Six of these species accounted for less than 2% of their total fruit diet and were not fed on within 200 m of the forest edge, and one comprised 24% of the diet and was exploited in all edge categories. This suggests that many of the species fed on in Manombo may only exist in interior forest or in lowland rainforest, accounting for the disparity in fruit species exploited between sites. In comparison to other *Eulemur* species, however, the number of fruit species consumed varies between 10 and 120 species (Overdorff 1993, Johnson 2002, Tarnaud 2004, Donati et al 2007, Simmen et al 2007) (Appendix 2 Table A.2.3), with no clear relationship between number of species and study length, site, or lemur species. This suggests that this characteristic is highly variable in *Eulemur*, which as a genus may be very adaptable to a variety of fruit availability circumstances. Overall, *E. cinereiceps* at Agnalazaha thrive on fruit species whose distribution are not affected by edge.

In assessing correlations between time spent feeding on each food item and distance to forest edge, I found no significant relationship. Dietary diversity and number of fruit species also did not vary with distance to forest edge, *contra* Predictions 3 and 4 (Table 3.11). These results lend further support to the idea that *E. cinereiceps* food items may be evenly distributed throughout this forest, as groups AI1 and AI2 are feeding on the same proportions of plant parts and the same number of fruit species in all parts of the forest. Again, although it has been noted that the ranging patterns of any primate species should be based on fulfilling their dietary requirements (Wrangham 1980), it appears that on the scale of one group's home range, overall distribution relative to forest edge is not being driven by fruit availability. In addition, neither group spread nor nearest neighbour distance while feeding varied with distance to forest edge, *contra* Predictions 5 and 6 (Table 3.11) and contributing to the speculation that proximity to edge does not affect feeding behaviour, as *E. cinereiceps* groups are not required to cover larger areas while feeding simultaneously near the interior.

3.5.3 Habitat Use

A strong negative correlation was found between height of the focal animal and tree height with distance to external edge. This suggests that *E. cinereiceps* prefers taller trees at the external edges of the forest, likely while resting (their primary activity). Vegetation data support this speculation, since tree height was not found to vary with distance to edge (see Section 3.4.5). These results may relate to two previously proposed theories for edge preference in this species. Firstly, the animals may prefer to rest at the forest edge for thermoregulatory purposes, and resting in taller trees further exposes them to sunlight

(Vasey 2004). Secondly, it is possible that *E. cinereiceps* prefers taller trees while resting for the purpose of predator avoidance. However, daytime resting sites in other lemur species have generally been found to range lower in the canopy (Karpanty 2006, Scheumann et al 2007) in order to avoid diurnal raptors, so this explanation is perhaps less probable.

3.5.4 Travel and Home Range

Home range size was very similar between the two *E. cinereiceps* study groups, and home ranges overlapped considerably. This suggests that the territories of groups AI1 and AI2 were not strictly defended during this study period. Home range size may also have been restricted by the small size and very irregular shape of Agnalazaha. However, the genus *Eulemur* is very diverse in terms of home range size, varying between 2.8 to 42.5 ha (using grid cell count method) or 12.0 to 71.8 ha (using MCP method) (Vasey 1997, Curtis & Zaramody 1998, Gould & Overdorff 2002, Johnson 2002, Bayart & Simmen 2005, Tanaka 2007) (Appendix 2 Table A.2.4), so while groups AI1 and AI2 fall closer to the lower end of the scale, their home range size is not exceptionally small, *contra* Prediction 7 (Table 3.11).

3.5.5 Vegetation and Phenology

Analyses of vegetation characteristics produced few significant results. The number of trees greater than 10 cm DBH per subplot was found to be significantly higher nearest to the forest edge (DAE), but this result is weak as there were only two categories for this analysis. Using DEE categories, mean crown volume of fruiting trees was significantly higher closer to the forest edge. This may be due to increased light exposure at the edge, though this does not appear to directly benefit fruit production as fruit availability had no relationship with forest edge in either season, *contra* Prediction 8 (Table 3.11). This result is concurrent with the proposed conclusion that *E. cinereiceps* food resources at Agnalazaha are not affected by edge.

No significant relationships were found in correlations between botanical variables and *E. cinereiceps* feeding behaviour. However, trends were seen toward a preference for larger crown volumes and higher fruit availability while feeding, supporting Prediction 9 (Table 3.11), and the assumption that any species should be expected to feed most where there is the greatest availability of food resources. In light of this, and the fact that the majority of *E. cinereiceps* fruit species were exploited in all distance-to-edge categories, we may conclude that presence of edge is not an influence on overall feeding behaviour in *E. cinereiceps*.

3.5.6 Conclusion

The overall purpose of this chapter has been to determine edge response in *E. cinereiceps*, and the possible causative mechanisms behind this response. Although a strong correlation between ranging patterns and distance to forest edge was found, the reasons are unclear. Activity budget and dietary composition data suggest that food availability likely has no effect on *E. cinereiceps'* response to forest edge. Rather, *E. cinereiceps* appears to prefer edge for resting, and chooses to rest at significantly higher heights in significantly taller trees at the forest edge. It is suggested that this may be for thermoregulatory purposes, but further research exploring light intensity and temperatures at animal height are needed to reach this conclusion.

Table 3.11. Chapter 3: Prediction and Support summary.

	Prediction	**Supported?**	**Comments**
1	There will be a negative correlation between time spent overall and distance to forest edge for *E. cinereiceps*.	Yes	Strong negative correlation between time spent overall and distance to forest edge.
2	There will be a negative correlation between time spent feeding and distance to forest edge for *E. cinereiceps*.	No	
3	The proportion of fruit eaten by *E. cinereiceps* will correlate negatively with distance to forest edge.	No	
4	Dietary diversity of *E. cinereiceps* will correlate positively with distance to forest edge.	No	
5	Group spread of *E. cinereiceps* while feeding will correlate positively with distance to forest edge.	No	
6	Nearest neighbour distance while feeding will correlate positively with distance to forest edge.	No	
7	*E. cinereiceps* home ranges at Agnalazaha will be relatively small.	No	AI1 and AI2 home range sizes fall within the range of other *Eulemur* species.
8	Fruit availability will vary negatively with distance to forest edge.	No	
9	Time spent feeding by *E. cinereiceps* will vary positively with fruit availability.	Yes	Trends showed a preference for areas with high fruit availability while feeding.

CHAPTER 4: FOREST FRAGMENTATION AND EDGE EFFECTS IN SOUTHEASTERN MADAGASCAR: CONCLUSIONS AND IMPLICATIONS FOR CONSERVATION

4.1 Introduction

In the previous chapters, I determined population densities for the lemur species of Agnalazaha and Manombo as a function of distance from forest edge to determine responses to forest fragmentation and edge effects. Abiotic and biotic forest characteristics were also assessed in order to suggest the mechanisms behind edge response, and *E. cinereiceps* ranging, activity budgets and feeding ecology were analyzed in detail to examine the relationships of these variables with forest disturbance more closely in this species. Results were highly varied among species and fragments, demonstrating the complexity among organisms in their interactions with habitat conditions and disturbance, as well as the difficulty in designing reserves to meet the requirements of multiple species. In this chapter, I will further examine these findings in relation to the main study questions.

4.1.1 Chapter 2 Research Questions

1. How does lemur diversity and density vary between forest fragments of varying size, shape, isolation, forest type, and disturbance levels?

Variation was found in population densities among fragments in all species, with the exception of *E. cinereiceps*. Frugivores *V. v. editorum* and *C. major* were found only in Manombo and Agnalazaha, respectively, but comparisons between fragments are unreliable since *V. v. editorum* had no sightings during the census and *C. major* were not found in Manombo possibly due to torpor patterns. Folivores *H. griseus*, *L. jamesi*, and *A. ramantsoavani* had consistently higher densities in Manombo (a lowland rainforest that had a larger area, higher connectivity, and less disturbance), with no differences between MSR and MCF. Insectivore *D. madagascariensis* was found only in MCF (but with no sightings during the census), and *M. jollyae* was found in increasing densities in MSR, ACO, MCF and AIN, showing a positive relationship with increasing fragment shape index, and highest density in the fragment with the highest levels of disturbance.

2. How do densities of lemur species at Agnalazaha and Manombo differ from forest edge to interior?

The frugivorous *E. cinereiceps*, folivorous *H. griseus*, and insectivorous *M. jollyae* all showed some positive response to edge. The relationship was only consistent for *M. jollyae*. Frugivorous/omnivorous *Cheirogaleus major*, folivorous *L. jamesi* and folivorous *A. ramantsoavani* showed no response to forest edge. Frugivorous *V. v. editorum* and insectivorous *D. madagascariensis* were not sighted during surveys.

3. What characteristics (abiotic, biotic) correlate with edge-to-interior densities of each lemur species at Agnalazaha and Manombo?

Eulemur cinereiceps density correlated positively with temperature, wind and habitat disturbance and showed a negative correlation trend with tree height at Agnalazaha, though this was possibly an artifact of increased ranging patterns near forest edge where these characteristics tend to be more pronounced. At Manombo, *E. cinereiceps* density correlated positively with number of tree species, possibly due to an increase of fruit availability in these areas. *Hapalemur griseus* density showed negative correlation trends with tree density, species richness and DBH at Agnalazaha and with tree height at both sites, suggesting a preference for areas of the forest in which trees are relatively small (i.e.

the swamps at Agnalazaha). *Lepilemur jamesi* and *A. ramantsoavani*, two species that share an ecological niche, showed negative correlation trends with tree density and DBH and positive correlation trends with DBH at Manombo, respectively. This is attributed to the documented preference in *Avahi* for larger feeding trees over those of *Lepilemur* (Thalmann 2001). *Microcebus jollyae* density varied positively with temperature and number of tree species in Manombo, though it is unclear whether these variables are causal of density or simply artifacts of higher temperatures and number of tree species near the forest edge at this site. *Cheirogaleus major* densities did not correlate with any of the measured edge effect variables, and *V. v. editorum* and *D. madagascariensis* were not sighted during surveys.

4.1.2 Chapter 3 Research Questions

1. How does *E. cinereiceps* distribute its time spent resting, feeding, traveling, and engaging in social behaviour at varying distances from forest edge?

Eulemur cinereiceps spent significantly more time resting and traveling at the forest edge, and engaging in social behaviour near external edges only. Time spent feeding had no relationship with distance to forest edge. Overall, *E. cinereiceps* spent significantly more time near the forest edge.

2. What factors (food availability, forest structure) may play a role in *E. cinereiceps'* response to forest edge?

Activity budget data suggests that food availability likely has no effect on *E. cinereiceps'* response to forest edge. Rather, *E. cinereiceps* appears to prefer edge for resting, and chooses to rest at higher heights in taller trees at the forest edge. It is speculated that this is for thermoregulatory purposes, since sunlight may be stronger at forest edge and densities of this species were found to correlate positively with temperature in Chapter 2.

4.1.3 Implications of Lemur Response to Forest Fragmentation and Edge Effects

Overall there did not appear to be strong abiotic or biotic edge effects occurring at Agnalazaha or Manombo, a result that may be attributed to the dynamic nature of forest edges or to the scale on which edge effects were measured (see Section 2.5.2). In addition, response to forest fragmentation and edge was shown to be highly variable among the lemur species at these sites. This poses difficulties for making conservation recommendations for these species based on edge effects. Perhaps the most noteworthy finding of this study is that primate ranging patterns as a function of distance from forest edge do not necessarily depend on resource distribution, as *E. cinereiceps* was found to strongly prefer edge in both Chapter 2 and Chapter 3 results, but edge preference was not reflected in feeding behaviour. Most other species also did not conform to predictions regarding diet and edge response. It is therefore important to explore other factors that may be driving lemur distribution and defining habitat viability in addition to resource availability, such as thermoregulatory needs, structural needs (i.e. sleep holes for hibernating species), or predator avoidance.

4.2 Conservation Recommendations

Having conducted research on both landscape-level density patterns for all lemur species and local-level ranging patterns for *E. cinereiceps*, it may come into question whether a surrogate species approach to conservation should be utilized, or if the problem should be approached from a multiple species perspective. Generally, surrogate species approaches, such as determining a flagship, focal, keystone, indicator, or umbrella species, are considered effective and allow conservationists to focus on one species while supporting many others that populate the same area (Favreau et al 2006). This approach is most often used in regions high in biodiversity for which few species-specific data are available. In the case of this study, however, enormous variation in individual species' responses to forest fragmentation and edge effects has been documented, and maintaining an exclusively surrogate species approach to conservation may not be appropriate. I chose to focus on *E. cinereiceps* in this study because this species is globally at higher risk than the other species at Agnalazaha and Manombo, with the exception of *V. v. editorum* (see Section 1.4.2), and unlike *V. v. editorum* these sites represent a significant portion of its total range. However, recent revisions in species taxonomy also suggest that Agnalazaha and Manombo represent the total range of some species (local populations of *C. major* – for which species re-designation is anticipated – and *A. ramantsoavani*) (Mittermeier et al 2008), and updates to their risk statuses are expected. Conversation recommendations here will focus on *E. cinereiceps*, for which more in-depth data on fragment and edge response are available, but will also take into account distribution patterns of other species where appropriate.

4.2.1 Reserve Design

Determining an effective reserve design is a complex issue, in which not only biological but also economic, political and social constraints play a role (Akçakaya 2000).

The optimal reserve system purely in terms of conservation goals would depend solely on ecological considerations, aiming to protect a particular species, a representative set of taxa, or a specific forest area. In this section, I will discuss reserve design based on species habitat requirements in Agnalazaha and Manombo, followed by a discussion of the social and economical considerations that must be made before taking conservation action.

Reserve Size

Generally, large reserves are preferred over small ones because the former are more likely to contain a wider range of environmental conditions, and will be able to better support species that require large home range sizes (Hunter & Gibbs 2007) such as *E. cinereiceps* (~35 ha), *V. v. editorum* (30-70 ha: Ratsimbazafy 2002), and *D. madagascariensis* (females 30-50 ha, males 100-200 ha: Sterling 1993, Andriamasimanana 1994). In addition, large reserves should be able to support larger populations, decreasing the risk of extinction and increasing the base of genetic variation. However, having only one large reserve as opposed to several smaller ones will also increase the risks associated with catastrophes, such as forest fires, which may eradicate entire populations. Therefore, the ideal reserve design would be to have a number of large reserves, and ensure that gene flow is possible between them. A large reserve is considered any fragment greater than 500 ha, since the "core-area model" (Laurance 1991, Laurance & Yensen 1991), used to predict the impacts of edge effects on fragments of varying sizes and shapes, generally suggests that fragments of less than 500 ha are susceptible to elevated disturbance and changes in vegetation structure and composition (Laurance 1991, Ferreira & Laurance 1997). Agnalazaha and Manombo therefore appear to be good candidates for an interconnected system of large reserves, as three of the four fragments already meet the minimum area requirement (with the exception of ACO), and may be close enough to other fragments to make movement between them possible (see Chapter 1 Figure 1.4).

Reserve Shape

One fairly consistent characteristic of large forest fragments is that they tend to be more complex in shape than smaller fragments (Ewers & Didham 2007). This relationship is evident to some extent in Agnalazaha and Manombo, though even the smaller fragments have considerably high shape indices. It has been argued that the complex shapes of large fragments may render them unsuitable for supporting contiguous populations of interior-dwelling species (Tscharntke et al 2002), but this is dependent on the nature of the forest perimeter and the total area available in the interior. In Agnalazaha, the mean shape index is higher than in Manombo although total area is lower, as the forest edge permeates deep into the forest interior whereas the Manombo edge is complex but remains along the outer boundaries of the fragment (see Chapter 1 Figure 1.4: site images are to scale). This has resulted in the forest fragments at Manombo being large and relatively continuous, while still having a high shape index and supporting both species that prefer edge as well as a greater number of species overall. Although the differences are not significant, the highest densities of *E. cinereiceps* (who prefer edge) are found in MSR, which has the lowest shape index and therefore the smallest proportion of edge. This suggests that while *E. cinereiceps* appears to prefer edge in their ranging patterns, a high shape index may not be the most important requirement for the viability of the population. It was speculated that *E. cinereiceps* prefers edge for thermoregulatory purposes, but the persistence of this population will ultimately rely on sufficient resource availability and the ability to interbreed among subpopulations. Therefore the best conservation strategy is not necessarily to focus on reserves with the greatest amount of edge but rather to look to those with a large area and high connectivity that still maintain a relatively high shape index, which will decrease the risk of further fragmentation and increase gene flow while preserving the possible benefits of edge effects. This strategy would also be beneficial to the other lemur species at Agnalazaha and Manombo, as several have large home ranges (listed above) and all were classified as having either a positive or neutral response to edge. One possible way to increase fragment area at Agnalazaha while still maintaining a relatively high degree of edge might be to reforest the large portions of matrix land that are penetrating into the fragments, making them more contiguous while still retaining a complex edge. This will also decrease the chances of the Agnalazaha fragments breaking up any further, which there appears to be a chance of occurring, particularly in AIN (see Chapter 1 Figure 1.4). Planting important *E. cinereiceps* fruiting trees in these areas can improve reforestation by attracting this species and stimulating the seed dispersal they provide (Bollen & Donati 2006).

4.2.2 Corridors

The purpose of forest corridors in conservation planning is to act as pathways for organisms to move between forest fragments (Nasi et al 2008), increasing gene flow among populations. Fragments connected to other habitat patches by corridors have been found to have higher species densities than those that are isolated (Haddad & Baum 1999, Pardini et al 2005, Martensen et al 2008), as was the case at Manombo where densities were higher than at Agnalazaha in every species but one. The presence of corridors has also been found to increase migration into associated fragments, as the increase in forest area leads to a better chance that dispersing individuals in the matrix will encounter them (Bowers & Matter 1997, Haddad & Baum 1999). In addition to the genetic benefits of higher movement rates between fragments, corridors may also be beneficial in increasing the area and changing the shape of a fragment. For example, a corridor will increase the area of a fragment that is far from the edge, increasing the effective area for species that respond negatively to edge (Haddad & Baum 1999), while the corridor itself may act as suitable habitat for species that respond positively to edge.

A possible solution to help preserve important habitat and maintain genetic diversity in lemur populations at Agnalazaha and Manombo is to view these sites jointly in regional conservation plans, by establishing corridor links between forests fragments. For example, a corridor connecting AIN and ACO, which are currently only isolated by 150 m, would be an effective way of increasing movement between these fragments. In addition, the recent discovery of an *E. cinereiceps* group in Manombo's coastal littoral forest (not included in this study) show that this habitat is still viable, and so reforesting the 5 km area between this fragment and Agnalazaha's coastal fragment, which is already sporadically forested, could be a feasible plan for expanding *E. cinereiceps* habitat – though a corridor of this length would be a considerable undertaking. Of the lowland rainforest fragments, MSR and MCF are currently connected at three locations, so movement between these fragments is likely occurring. South of MCF, there is a small private forest containing an *E. cinereiceps* population (HE Andriamaharoa pers. comm.) with an isolation distance of approximately 100 m, which may also be a suitable site for corridor establishment (although there is a river barrier to consider).

When designing forest corridors, it is important to distinguish between structural connectedness and functional connectivity, as creating a strip of forest connecting fragments does not guarantee that they will be utilized for their intended function (Hess & Fischer 2001). For a species such as *E. cinereiceps*, which has been found to travel more frequently within edge, a corridor of moderate width between fragments may be sufficient for dispersal. Laurance and Laurance (1999) have found that arboreal mammals that are not highly sensitive to fragmentation were able to utilize corridors of 20-80 m in width. Previous studies have found that primates are able to adapt to corridor habitats (Singh et al 2001, Zanne et al 2001), so the probability is high that *E. cinereiceps*, a species that prefers edge, as well as the other species at Agnalazaha and Manombo that either prefer or are not affected by edge, will be able to do.

4.2.3 Social and Economic Considerations

In areas such as Agnalazaha and Manombo where surrounding villages rely on extracting forest resources, it is important to foster the good will of local people. This can be cultivated by giving local communities a vested interest in the forest through actions such as allowing a limited degree of forest exploitation, or creating jobs as forest managers and guides (Hunter & Gibbs 2007). This is already taking place at Manombo through Special Reserve management by the System of Protected Areas of Madagascar (SAPM) (formerly ANGAP), which focuses on providing adequate surveillance to halt further degradation and assist in restoration through tree planting and soil conservation measures

(MF Rabotoharifomba pers. comm.), and through Classified Forest management by the Ministry of Environment, Forests and Tourism (MEFT) and local administration by the Interregional Direction of Environment, Forests and Tourism (DREFT), who employ a policy of sustainable use for timber and non-timber forest products. Overall, lemur populations appear to be thriving at this site, although illegal activities within the forest are still occurring. For example, a newly habituated *E. cinereiceps* group disappeared from MCF in December of 2006, coinciding with a time at which administrative presence in the forest was low (FB Ralainasolo pers. comm.). This is why a strong management system must be paired with strong community outreach. The site of Agnalazaha currently has no classification under SAPM, but is under the management of botanical research institution Missouri Botanical Garden (MBG). At this site, enforcement of forest regulations is not focused upon, but rather bringing conservation education to local people and providing alternatives to forest resource extraction, a strategy that has resulted in a decrease in hunting and cutting at this site (R Ludovic pers. comm.).

4.3 New Research Directions

In managing any species' habitat, we cannot be content with simply keeping individuals alive. Rather, importance must be placed on maintaining sufficient genetic variation to allow adaptive responses in the genetic population to any changes or challenges that may occur in that habitat (Schonewald-Cox et al 1983). To do this, reserve planning requires detailed knowledge of the ecology and specific habitat requirements of target species. This study explored the behavioural responses of *E. cinereiceps* to forest fragmentation and edge effects, and has provided a more extensive explanation of the environmental correlates to edge response than data gathered during line transect censuses. More intensive and long-term data would likely offer stronger results. This methodology should therefore be utilized in future studies of edge response, and would be further strengthened in providing suggestions of the causative mechanisms of ranging patterns by analyzing a greater number of abiotic and vegetation variables during focal follows, such as temperature, relative humidity, and light intensity at animal height, and dendrometrics of resting and feeding trees, and by analyzing these characteristics on a finer scale using smaller distance-to-edge categories; this research may be improved by experimental manipulation. Another aspect of fragmentation response that would inform conservation decisions is the ability of species to move through the matrix, and what these patterns of movement are (Bowers & Matter 1997). Quantifying such patterns would be necessary to fully understand metapopulation and source-sink dynamics, and in turn be better able to assess the need for, and potential effectiveness of, forest corridors (Foppen et al 2000).

There are still many questions to answer concerning the response to forest fragmentation and edge effects by the lemur species at Agnalazaha and Manombo. However, unless these forest sites are preserved and restored, there will continue to be a risk of loss of biodiversity. Continuing research on the diverse fragmentation response of primate species will facilitate the development of efficient management strategies for primate conservation in fragmented landscapes.

REFERENCES CITED

Aizen MA, Feinsinger P. 1994. Habitat fragmentation, native insect pollinators, and feral honey bees in Argentine "Chaco Serrano." Ecological Applications 4:378-392.

Akçakaya HR. 2000. Conservation and management for multiple species: Integrating field research and modeling into management decisions. Environmental Management 26:S75-S83.

Altmann J. 1974. Observational study of behavior: Sampling methods. Behavior 49:227-267.

Anderson EM, Boutin S. 2002. Edge effects on survival and behaviour of juvenile red squirrels (*Tamiasciurus hudsonicus*). Canadian Journal of Zoology 80:1038-1046.

Andrainarivo C, Andriaholinirina VN, Feistner A, Felix T, Ganzhorn J, Garbutt N, Golden C, Konstant B, Louis Jr E, Meyers D, Mittermeier RA, Perieras A, Princee F, Rabarivola JC, Rakotosamimanana B, Rasamimanana H, Ratsimbazafy J, Raveloarinoro G, Razafimanantsoa A, Rumpler Y, Schwitzer C, Thalmann U, Wilmé L, Wright P. 2008. *Varecia variegata*. In: IUCN 2009. IUCN red list of threatened species. Version 2009.1. <www.iucnredlist.org>. Downloaded on 27 July 2009.

Andren H, Angelstam P. 1988. Elevated predation rates as an edge effect in habitat islands: Experimental evidence. Ecology 69:544-547.

Andreone F, Vences M, Guarinno FM, Glaw F, Randrianirina JE. 2002. Natural history and larval morphology of *Boophis occidentalis* (Anura: Mantellidae: Boophinae) provide new insights into the phylogeny and adaptive radiation of endemic Malagasy frogs. Journal of Zoology London 257:425-438.

Andriamasimanana M. 1994. Ecoethological studies of free-ranging aye-ayes (*Daubentonia madagascariensis*) in Madagascar. Folia Primatologica 62:37-45.

Andriantompohavana R, Lei R, Zaonarivelo JR, Engberg SE, Nalanirina G, McGuire SM, Shore GD, Andrianasolo J, Herrington K, Brenneman RA, Louis EE. 2007. Molecular phylogeny and taxonomic revision of the woolly lemurs, genus *Avahi* (Primates: Lemuriformes). Museum of Texas Tech University Special Publications 51:1-59.

Arroyo-Rodriguez V, Mandujano S. 2006. Forest fragmentation modifies habitat quality for *Alouatta palliata*. International Journal of Primatology 27(4):1079-1096.

Balko EA, Underwood HB. 2005. Effects of forest structure and composition on food availability for *Varecia variegata* at Ranomafana National Park, Madagascar. American Journal of Primatology 66:45-70.

Bayart F, Simmen B. 2005. Demography, range use, and behavior in black lemurs (*Eulemur macaco macaco*) at Ampasikely, northwest Madagascar. American Journal of Primatology 67:299-312.

Benitez-Malvido J. 1998. Impact of forest fragmentation on seedling abundance in a tropical rain forest. Conservation Biology 12(2):380-389.

Bernstein IS, Balcaen P, Dresdale L, Gouzoules H, Kavanagh M, Patterson T, Neyman-Warner P. 1976. Differential effects of forest degradation on primate populations. Primates 17(3):401-411.

Bierregaard RO, Lovejoy TE, Kapos V, Augusto dos Santos A, Hutchings RW. 1992. The biological dynamics of tropical rainforest fragments. Biological Sciences 42(11):859-866.

Birkinshaw C, Lowry P, Aronson J, Lehavana A, Ludovic R, Andrianjafy M, Rakotoarivony F, Rasolofomirino JJ. 2009. RNC initiatives of the Missouri Botanical Garden – Madagascar. St. Louis: RNC Alliance, Technical Report.

Bollen A, Donati G. 2005. Phenology of the littoral forest of Sainte Luce, southeastern Madagascar. Biotropica 37(1):32-43.

Bollen A, Donati G. 2006. Conservation status of the littoral forest of south-eastern Madagascar: A review. Oryx 40(1):57-66.

Bollen A, Van Elsacker L, Ganzhorn JU. 2004. Relations between fruits and disperser assemblages in a Malagasy littoral forest: A community-level approach. Journal of Tropical Ecology 20:599-612.

Bowers MA, Matter SF. 1997. Landscape ecology of mammals: Relationships between density and patch size. American Society of Mammalogy 78(4):999-1013.

British Columbia Ministry of Forests and B.C. Ministry of Environment, Lands and Parks. 1996. Landscape level biodiversity course workbook. Victoria, B.C.

Britt A, Axel A, Young R. 1999. Brief surveys of two classified forests in Toamasina Province, eastern Madagascar. Lemur News 4:25-27.

Broadbent EN, Asner GP, Keller M, Knapp DE, Oliveira PJC, Silva JN. 2008. Forest fragmentation and edge effects from deforestation and selective logging in the Brazilian Amazon. Biological Conservation 141:1745-1757.

Bruna EM. 2002. Effects of forest fragmentation on *Heliconia acuminata* seedling recruitment in central Amazonia. Oecologia 132:235-243.

Cancino J. 2005. Modelling the edge effect in even-aged Monterey pine (*Pinus radiata* D.Don) stands. Forest Ecology and Management 210:159-172.

Caro TM, O'Doherty G. 1999. On the use of surrogate species in conservation biology. Conservation Biology 13(4):805-814.

Carvalho KS, Vasconcelos HL. 1999. Forest fragmentation in central Amazonia and its effects on litter-dwelling ants. Biological Conservation 91:151-157.

Chapman CA, Chapman LJ. 2000. Interdemic variation in mixed-species association patterns: Common diurnal primates of Kibale National Park, Uganda. Behavioral Ecology and Sociobiology 47:129-139.

Chapman CA, Chapman LJ. 2003. Fragmentation and alteration of seed dispersal processes: An initial evaluation of dung beetles, seed fate, and seedling diversity. Biotropica 35(3):382-393.

Chapman CA, Peres CA. 2001. Primate conservation in the new millennium: The role of scientists. Evolultionary Anthropology 10:16-33.

Chen J, Franklin JF, Spies TA. 1992. Vegetation responses to edge environments in old-growth Douglas-fir forests. Ecological Applications 2(4):387-396.

Chen J, Franklin JF, Spies TA. 1993. Contrasting microclimates among clearcut, edge and interior old growth Douglas-fir forest. Agricultural and Forest Meteorology 63:219-237.

Cibois A, Slikas B, Schulenberg TS, Pasquet E. 2001. An endemic radiation of Malagasy songbirds is revealed by mitochondrial DNA sequence data. Evolution 55(6):1198-1206.

Consiglio T, Schatz GE, McPherson G, Lowry II PP, Rabenantoandro J, Rogers S, Rabevohitra R, Rabehevitra D. 2006. Deforestation and plant diversity of Madagascar's littoral forests. Conservation Biology 20:1799-1803.

Craul M, Chikhi L, Sousa V, Olivieri GL, Rabesandratana A, Zimmermann E, Radespiel U. 2009. Influence of forest fragmentation on an endangered large-bodied lemur in northwestern Madagascar. Biological Conservation 142:2862-2871.

Cristóbal-Azkarate J, Veà JJ, Asensio N, Rodríguez-Luna E. 2005. Biogeographical and floristic predictors of the presence and abundance of mantled howlers (*Alouatta palliata mexicana*) in rainforest fragments at Los Tuxtlas, Mexico. American Journal of Primatology 67:209-222.

Curtis DJ. 2004. Diet and nutrition in wild mongoose lemurs (*Eulemur mongoz*) and their implications for the evolution of female dominance and small group size in lemurs. American Journal of Physical Anthropology 124:234-247.

Curtis DJ, Zaramody A. 1998. Group size, home range use, and seasonal variation in the ecology of *Eulemur mongoz*. International Journal of Primatology 19(5):811-835.

De Santo TL, Willson MF, Sieving KE, Armesto JJ. 2002. Nesting biology of Tapaculos (*Rhinodryptidae*) in fragmented south-temperate rainforests of Chile. Condor 104:482-495.

Dew JL, Wright P. 1998. Frugivory and seed dispersal by four species of primates in Madagascar's eastern rain forest. Biotropica 30(3):425-437.

Diamond J. 1975. The island dilemma: Lessons of modern biogeographic studies for the design of natural reserves. Biological Conservation 7:129-146.

Didham RK, Lawton JH. 1999. Edge structure determines the magnitude of changes in microclimate and vegetation structure in tropical forest fragments. Biotropica 31:17-30.

Donati G, Bollen A, Borgognini-Tarli SM, Ganzhorn JU. 2007. Feeding over the 24-h cycle: Dietary flexibility of cathemeral collared lemurs (*Eulemur collaris*). Behavioral Ecology and Sociobiology 61:1237-1251.

Donovan TM, Lamberson RH, Kimber A, Thompson III FR, Faaborg J. 1995. Modeling the effects of habitat fragmentation on source and sink demography neotropical migrant birds. Conservation Biology 9(6):1396-1407.

Dooley Jr JL, Bowers MA. 1996. Influences of patch size and microhabitat on the demography of two old-field rodents. Oikos 75:543-562.

Douady CJ, Catzeflis F, Kao DJ, Springer MS, Stanhope MJ. 2002. Molecular evidence for the monophyly of Tenrecidae (Mammalia) and the timing of the colonization of Madagascar by Malagasy tenrecs. Molecular Phylogenetics and Evolution 22(3):357-363.

Du Puy DJ, Moat JF. 1998. Vegetation mapping and classification in Madagascar (using GIS): Implications and recommendations for the conservation of biodiversity. In: Huxley DR, Lock JM, Cutler DF, editors. Chorology, taxonomy and ecology of the floras of Africa and Madagascar. Kew: Royal Botanic Gardens. p 97-117.

Dumetz N. 1999. High plant diversity of lowland rainforest vestiges in eastern Madagascar. Biodiversity and Conservation 8:273-315.

Dunbar RIM. 1998. The social brain hypothesis. Evolutionary Anthropology 6:178-190.

Eltz T, Bruhl CA, van derKaars S, Linsenmair KE. 2002. Determinants of stingless bee nest density in lowland dipterocarp forests of Sabah, Malaysia. Oecologia 131:27-34.

Erickson CJ. 1995. Feeding sites for extractive foraging by the aye-aye, *Daubentonia madagascariensis*. American Journal of Primatology 35:235-240.

Ewers RM, Didham RK. 2006. Confounding factors in the detection of species responses to habitat fragmentation. Biological Reviews 81:117-142.

Ewers RM, Didham RK. 2007. The effect of fragment shape and species' sensitivity to habitat edges on animal population size. Conservation Biology 21(4):926-936.

Fahrig L. 2003. Effects of habitat fragmentation on biodiversity. Annual Review of Ecology, Evolution, and Systematics 34:487-515.

Favreau JM, Drew CA, Hess GR, Rubino MJ, Koch FH, Eschelbach KA. 2006. Recommendations for assessing the effectiveness of surrogate species approaches. Biodiversity and Conservation 15:3949-3969.

Ferreira LV, Laurance WF. 1997. Effects of forest fragmentation on mortality and damage of selected trees in Central Amazonia. Conservation Biology 11(3):797-801.

Fichtel C. 2007. Avoiding predators at night: Antipredator strategies in red-tailed sportive lemurs (*Lepilemur ruficaudatus*). American Journal of Primatology 69:611-624.

Fietz J, Ganzhorn JU. 1999. Feeding ecology of the hibernating primate *Cheirogaleus medius*: How does it get so fat? Oecologia 121(2):121-157.

Foggo A, Ozanne CMP, Speight MR, Hambler C. 2001. Edge effects and tropical forest canopy invertebrates. Plant Ecology 153:347-359.

Foppen RPB, Chardon JT, Liefveld W. 2000. Understanding the role of sink patches in source-sink metapopulations: Reed warbler in an agricultural landscape. Conservation Biology 14(6):1881-1892.

Foster J, Gaines MS. 1991. The effects of a successional habitat mosaic on a small mammal community. Ecology 72:1358-1373.

Frankham R. 1998. Inbreeding and extinction: Island populations. Conservation Biology 12(3):665-675.

Franklin AB, Noon BR, George TL. 2002. What is habitat fragmentation? Studies in Avian Biology 25:20-29.

Franklin JF. 1992. Scientific basis for new perspectives in forests and streams. In: Naiman RJ, editor. Watershed management: Balancing sustainability and environmental change. New York: Springer-Verlag. p 25-72.

Gade DW. 1996. Deforestation and its effects in highland Madagascar. Mountain Research and Development 16(2):101-116.

Ganzhorn JU. 1989. Niche separation of seven lemur species in the eastern rainforests of Madagascar. Oecologia 79(2):279-286.

Ganzhorn JU. 1995. Low-level forest disturbances effects on primary production, leaf chemistry, and lemur populations. Ecology 76:2084-2096.

Ganzhorn JU, Lowry PP, Schatz GE, Sommer S. 2001. The biodiversity of Madagascar: One of the world's hottest hotspots on its way out. Oryx 35:346-348.

Gautier-Hion A. 1980. Seasonal variations of diet related to species and sex in a community of *Cercopithecus* monkeys. Journal of Animal Ecology 49:237-269.

Geiser F, Ruf T. 1995. Hibernation versus daily torpor in mammals and birds: Physiological variables and classification of torpor patterns. Physiological Zoology 68:935-966.

Glaw F, Vences M, Ziegler T, Böhme W, Köhler J. 1999. Specific distinctness and biogeography of the dwarf chameleons *Brookesia minima, B. peyrierasi* and *B. tuberculata* (Reptilia: Chamaeleonidae): Evidence from hemipenial and external morphology. Journal of Zoology London 247:225-238.

Godefroid S, Koedam N. 2003. Distribution pattern of the flora in a peri-urban forest: An effect of the city-forest ecotone. Landscape and Urban Planning 65:169-185.

Goodman SM, Benstead JP, editors. 2003. The Natural History of Madagascar. Chicago: The University of Chicago Press.

Gould L, Overdorff DJ. 2002. Adult male scent-marking in *Lemur catta* and *Eulemur fulvus rufus*. International Journal of Primatology 23(3):575-586.

Grassi C. 2006. Variability in habitat, diet, and social structure of *Hapalemur griseus* in Ranomafana National Park, Madagascar. American Journal of Physical Anthropology 131:50-63.

Haddad NM, Baum KA. 1999. An experimental test of corridor effects of butterfly densities. Ecological Applications 9(2):623-633.

Hanski I. 1994. Patch-occupancy dynamics in fragmented landscapes. TREE 9(4):131-135.

Harcourt C. 1991. Diet and behaviour of a nocturnal lemur, *Avahi laniger*, in the wild. Journal of Zoology London 223:667-674.

Hawkins AFA, Goodman SM. 2003. Introduction to the birds. In: Goodman SM, JP Benstead, editors. The Natural History of Madagascar. Chicago: The University of Chicago Press. p 1019.

Hess GR, Fischer RA. 2001. Communicating clearly about conservation corridors. Landscape and Urban Planning 55:195-208.

Hill JK, Hamer KC. 1998. Using species abundance models as indicators of habitat disturbance in tropical forests. Journal of Applied Ecology 35(3):458-460.

Hoffmann M. 2008. *Lepilemur jamesorum*. In: IUCN red list of threatened species. Version 2009.1. <www.iucnredlist.org>. Downloaded on 27 July 2009.

Hokkanen PJ, Kouki J, Komonen A. 2009. Nestedness, SLOSS and conservation networks of boreal herb-rich forests. Applied Vegetation Science 12:295-303.

Hunter ML, Gibbs JP. 2007. Fundamentals of conservation biology, 3rd ed. Malden, MA: Blackwell Publishing Ltd.

Irwin MT, Johnson SE, Wright PC. 2005. The state of lemur conservation in southeastern Madagascar: Population and habitat assessments for diurnal and cathemeral lemurs using surveys, satellite imagery and GIS. Oryx 39:204-218.

IUCN. 2009. IUCN red list of threatened species. Version 2009.1. <www.iucnredlist.org>. Downloaded on 6 August 2009.

Jansa SA, Goodman SM, Tucker PK. 1999. Molecular phylogeny and biogeography of the native rodents of Madagascar (Muridae: Nesomyinae): A test of the single-origin hypothesis. Cladistics 15:253-270.

Johnson R, Fergusen JWH, van Jaarsveld AS, Bronner GN, Chimimba CT. 2002. Delayed responses of small-mammal assemblages subject to afforestation-induced grassland fragmentation. Journal of Mammalogy 83(1):290-300.

Johnson SE. 2002. Ecology and speciation in brown lemurs: White-collared lemurs (*Eulemur albocollaris*) and hybrids (*Eulemur albocollaris* X *Eulemur fulvus rufus*) in southeastern Madagascar. Ph.D dissertation, University of Texas at Austin. 309 p.

Johnson SE. 2006. Evolutionary divergence in the brown lemur species complex. In: Gould L, Sauther ML, editors. Lemurs: Ecology and adaptation. New York: Springer. p189-212.

Johnson SE, Overdorff DJ. 1999. Census of brown lemurs (*Eulemur fulvus* sspp.) in southeastern Madagascar: Methods-testing and conservation implications. American Journal of Primatology 47:51-60.

Johnson SE, Lei R, Martin SK, Irwin MT, Louis EE. 2008. Does *Eulemur cinereiceps* exist? Preliminary evidence from genetics and ground surveys in southeastern Madagascar. American Journal of Primatology 70:372-385.

Johnson SE, Ingraldi C, Ralainasolo FB, Andriamaharoa HE, Birkinshaw CR, Wright PC, Ratsimbazafy JH. 2009. Habitat and population status of white-collared lemurs (*Eulemur cinereiceps*) at Manombo, Madagascar: 10 years of recovery after Cyclone Gretelle [Abstract]. American Journal of Physical Anthropology 138(S48):1-281.

Joly M, Zimmermann E. 2007. First evidence for relocation of stationary food resources during foraging in a Strepsirhine primate (*Microcebus murinus*). American Journal of Primatology 69:1045-1052.

Kapos V. 1989. Effects of isolation on the water status of forest patches in the Brazilian Amazon. Journal of Tropical Ecology 5:173-185.

Kapos V, Wandelli E, Camargo JL, Ganade G. 1997. Edge-related changes in environment and plant responses due to forest fragmentation in central Amazonia. In: Laurance WF, Bierregaard ROJ, editors. Tropical forest remnants ecology, management, and conservation of fragmented communities. Chicago: University Chicago Press. p 33-43.

Kappeler PM, Heymann EW. 1996. Nonconvergence in the evolution of primate history and socio-ecology. Biological Journal of the Linnean Society 59:297-326.

Karpanty SM. 2006. Direct and indirect impacts of raptor predation on lemurs in southeastern Madagascar. International Journal of Primatology 27(1):239-261.

Kotliar NB, Wiens JA. 1990. Multiple scales of patchiness and patch structure: A hierarchical framework for the study of heterogeneity. Oikos 59:253-260.

Lahann P. 2007. Feeding ecology and seed dispersal of sympatric cheirogaleid lemurs (*Microcebus murinus, Cheirogaleus medius, Cheirogaleus major*) in the littoral rainforest of south-east Madagascar. Journal of Zoology 271:88-98.

Lahti DC. 2001. The "edge effect on nest predation" hypothesis after twenty years. Biological Conservation 99:365-374.

Lahti T, Ranta E. 1985. The SLOSS principle and conservation practice: An example. Oikos 44(2):369-370.

Langrad O. 1990. Guide to the birds of Madagascar. New Haven, Connecticut: Yale University Press.

Laurance SG, Laurance WF. 1999. Tropical wildlife corridors: Use of linear rainforest remnants by arboreal mammals. Biological Conservation 91:231-239.

Laurance WF. 1990. Comparative responses of five arboreal marsupials to tropical forest fragmentation. Journal of Mammalogy 71(4):641-653.

Laurance WF. 1991. Edge effects in tropical forest fragmentation: Application of a model for the design of nature reserves. Biological Conservation 57:205-219.

Laurance WF, Yensen E. 1991. Predicting the impacts of edge effects in fragmented habitats. Biological Conservation 55:77-92.

Laurance WF, Bierregaard RO. 1997. Tropical forest remnants: Ecology, management, and conservation of fragmented communities. Chicago: University of Chicago Press.

Laurance WF, Laurance SG, Ferreira LV, Rankin-de Merona JM, Gascon C, Lovejoy TE. 1997. Biomass collapse in Amazonian forest fragments. Science 278:1117-1118.

Laurance WF, Ferreira LV, Rankin-de Merona JM, Laurance SG, Hutchings RW, Lovejoy TE. 1998. Effects of forest fragmentation on recruitment patterns in Amazonian tree communities. Conservation Biology 12:460-464.

Law BS, Lean M. 1999. Common blossom bats (*Syconycteris australis*) as pollinators in fragmented Australian tropical rainforest. Biological Conservation 91:201-212.

Lees DC, Kremen C, Andriamampianina L. 1999. A null model for species richness gradients: Bounded range overlap of butterflies and other rainforest endemics in Madagascar. Biological Journal of the Linnean Society 67:529-584.

Lehman SM, Ratsimbazafy J, Rajaonson A, Day S. 2006a. Ecological correlates to lemur community structure in southeast Madagascar. International Journal of Primatology 27(4):1023-1040.

Lehman SM, Rajaonson A, Day S. 2006b. Edge effects and their influence on lemur density and distribution in southeast Madagascar. American Journal of Physical Anthropology 129:232-241.

Lehman SM, Rajaonson A, Day S. 2006c. Edge effects on the density of *Cheirogaleus major*. International Journal of Primatology 27(6):1569-1588.

Levins R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. Bulletin of the Entomological Society of America 15:237-240.

Lhota S, Junek T, Bartos L, Kubena AA. 2008. Specialized use of two fingers in free-ranging aye-ayes (*Daubentonia madagascariensis*). American Journal of Primatology 70:786-795.

Li L, He X, Li X, Wen Q, He HS. 2007. Depth of edge influence of the agricultural-forest landscape boundary, Southwest China. Ecological Research 22:774-783.

Lidicker WZ. 1999. Responses of mammals to habitat edges: An overview. Landscape Ecology 14:333-343.

Linares MC, Soto-Calderón ID, Lees DC, Anthony NM. 2009. High mitochondrial diversity in geographically widespread butterflies of Madagascar: A test of the DNA barcoding approach. Molecular Phylogeny and Evolution 50:485-495.

Louis Jr EE, Coles MS, Andriantompohavana R, Sommer JA, Engberg SE, Zaonarivelo JR, Mayor MI, Brenneman RA. 2006a. Revision of the mouse lemurs (*Microcebus*) of eastern Madagascar. International Journal of Primatology 27(2):347-389.

Louis Jr EE, Engberg SE, Lei R, Geng H, Sommer JA, Randriamampionona R, Randriamanana JC, Zaonarivelo JR, Andriantompohavana R, Randria G, Prosper, Ramaromilanto B, Rakotoarisoa G, Rooney A, Brenneman RA. 2006b. Molecular and morphological analyses of the sportive lemurs (family Megaladapidae: genus *Lepilemur*) reveals 11 previously unrecognized species. Museum of Texas Tech University Special Publications 49:1-47.

Lovejoy TE, Bierregaard Jr RO, Rylands AB, Malcolm JR, Quintela CE, Harper LH, Brown KS Jr. 1986. Edge and other effects of isolation on Amazon forest fragments. In: Soule ME, editor. Conservation biology: The science of scarcity and diversity. Sunderland, Massachusetts: Sinauer. p 257-285.

Lynam AJ, Billick I. 1999. Differental responses of small mammals to fragmentation in a Thailand tropical forest. Biological Conservation 91:191-200.

MacArthur RH, Wilson EO. 1967. The theory of island biogeography. Princeton, NJ: Princeton University Press.

MacDougall A, Kellman M. 1992. The understorey light regime and patterns of tree seedlings in tropical riparian forest patches. Journal of Biogeography 19:667-675.

Malcolm JR. 1994. Edge effects in central Amazonian forest fragments. Ecology 75(8):2438-2445.

Martensen AC, Pimentel RG, Metzger JP. 2008. Relative effects of fragment size and connectivity on bird community in the Atlantic rain forest: Implications for conservation. Biological Conservation 141:2184-2192.

Matlack GR. 1993. Microenvironment variation within and among deciduous forest edge sites in the eastern United States. Biological Conservation 66:185-194.

Matlack GR. 1994. Vegetation dynamics of the forest edge: Trends in space and successional time. Journal of Ecology 82:113-123.

Mazzuca S, Spadafora A, Filadoro D, Vannini C, Marsoni M, Cozza R, Bracale M, Pangaro T, Innocenti AM. 2009. Seagrass light acclimation: 2-DE protein analysis in Posidonia leaves grown in chronic low light conditions. Journal of Experimental Marine Biology and Ecology 374(2):113-122.

Mesquita RCG, Delamonica P, Laurance WF. 1999. Effect of surrounding vegetation on edge-related tree mortality in Amazonian forest fragments. Biological Conservation 91:129-134.

Mittermeier RA, Konstant WR, Hawkins F, Louis Jr EE, Langrand O, Ratsimbazafy J, Rasoloarison R, Ganzhorn JU, Rajaobelina S, Tattersall I, Meyers DM. 2006. Lemurs of Madagascar, 2nd ed. Washington, D.C.: Conservation International.

Mittermeier RA, Ganzhorn JU, Konstant WR, Glander K, Tattersall I, Groves CP, Rylands AB, Hapke A, Ratsimbazafy J, Mayor MI, Louis Jr EE, Rumpler Y, Schwitzer C, Rasoloarison RM. 2008. Lemur diversity in Madagascar. International Journal of Primatology 29:1607-1656.

Mooney EH, Tiedeken EJ, Muth NZ, Niesenbaum RA. 2009. Differential induced response to generalist and specialist herbivores by Linderabenzoin (*Lauraceae*) in sun and shade. Oikos 118(8):1181-1189.

Moorman CE, Guynn Jr DC, Kilgo JC. 2002. Hooded warbler nesting success adjacent to group-selection and clearcut edges in a southeastern bottomland forest. The Condor 104:366-377.

Morland HJ. 1991. Social Organization and ecology of black and white ruffed lemurs (*V. Variegata variegata*) in lowland rain forest, Nosy Mangabe, Madagascar. Ph.D dissertation, Yale University, New Haven. 419 p.

Murcia C. 1995. Edge effects in fragmented forests: Implications for conservation. Trends in Ecology and Evolution 10(2):58-62.

Mutschler T. 1999. Folivory in a small-bodied lemur: The nutrition of the Alaotran gentle lemur (*Hapalemur griseus alaotrensis*). In: Rakotosaminanana B, Rasamimanana H, Ganzhorn JU, Goodman S, editors. New directions in lemur studies. New York: Kluwer Academic/Plenum Publishers. p 2221-2239.

Myers N, Mittermeier RA, Mittermeier CG, da Fonseca GAB, Kent J. 2000. Biodiversity hotspots for conservation priorities. Nature 403:853-858.

Namba T, Umemoto A, Minami E. 1999. The effects of habitat fragmentation on persistence of source-sink metapopulations in systems with predators and prey or apparent competitors. Theoretical Population Biology 56:123-137.

Nasi R, Koponen P, Poulsen JG, Buitenzorgy M, Rusmantoro W. 2008. Impact of landscape and corridor design on primates in a large-scale industrial tropical plantation landscape. Biodiversity and Conservation 17:1105-1126.

Newmark WD. 2001. Tanzanian forest edge microclimatic gradients: Dynamic patterns. Biotropica 33(1):2-11.

Nichol JE. 1994. An examination of tropical rain forest microclimate using GIS modeling. Global Ecology and Biogeography Letters 4(3):69-78.

Olivieri G, Zimmermann E, Randrianambinina B, Rasoloharijaona S, Rakotondravony D, Guschanski K, Radespiel U. 2007. The ever-increasing diversity in mouse lemurs: Three new species in north and northwestern Madagascar. Molecular Phylogenetics and Evolution 43:309-327.

Olupot W. 2004. Edge effects on trees and large mammal distribution. In: Olupot W. Boundary edge effects in Bwindi Impenetrable National park: A report. Uganda: Institute of Tropical Forest Conservation. p 127-186.

Olupot W. 2009. A variable edge effect on trees of Bwindi Impenetrable National Park, Uganda, and its bearing on measurement parameters. Biological Conservation 142:789-797.

Onderdonk DA, Chapman CA. 2000. Coping with forest fragmentation: The primates of Kibale National Park, Uganda. International Journal of Primatology 21(4):587-611.

Orsini L, Koivulehto H, Hanski I. 2007. Molecular evolution and radiation of dung beetles in Madagascar. Cladistics 23:145-168.

Ostner J. 2002. Social thermoregulation in redfronted lemurs (*Eulemur fulvus rufus*). Folia Primatologica 73(4):175-180.

Overdorff DJ. 1993. Similarities, differences, and seasonal patterns in the diets of *Eulemur rubriventer* and *Eulemur fulvus rufus* in the Ranomafana National Park, Madagascar. International Journal of Primatology 14(5):721-753.

Overdorff DJ. 1996. Ecological correlates to activity and habitat use of two prosimian primates: *Eulemur rubriventer* and *Eulemur fulvus rufus* in Madagascar. American Journal of Primatology 40:327-342.

Overdorff DJ, Strait SG, Telo A. 1997. Seasonal variation in activity and diet in a small-bodied folivorous primate, *Hapalemur griseus*, in southeastern Madagascar. American Journal of Primatology 43:211-223.

Overdorff DJ, Strait SG. 1998. Seed handling by three prosimian primates in southeastern Madagascar: Implications for seed dispersal. American Journal of Primatology 45:69-82.

Overdorff DJ, Johnson SE. 2003. *Eulemur*, true lemurs. In: Goodman SM, Benstead JP, editors. The natural history of Madagascar. Chicago: University of Chicago Press. p 1320-1324.

Palik BJ, Murphy PG. 1990. Disturbance versus edge effects in sugar maple-beech forest fragments. Forest Ecology and Management 32:187-202.

Pallant J. 2005. SPSS survival manual: A step by step guide to data analysis using SPSS for Windows (version 12), 2nd ed. Crows Nest, Australia: Allen & Unwin.

Pardini R, de Souza SM, Braga-Neto R, Metzger JP. 2005. The role of forest structure, fragment size and corridors in maintaining small mammal abundance and diversity in an Atlantic forest landscape. Biological Conservation 124:253-266.

Passamani M, Rylands AB. 2000. Home range of a Geoffroy's marmoset group, *Callithrix geoffroyi* (primates, Callitrichidae) in south-eastern Brazil. Revista Brasileira de Biologia 60:275-281.

Patton DR. 1975. A diversity index for quantifying habitat "edge". Wildlife Society Bulletin 3:171-173.

Peters HA. 2001. *Clidemia hirta* invasion at the Pasoh Forest Reserve: An unexpected plant invasion in an undisturbed tropical forest. Biotropica 33:60-68.

Ploger BJ, Yasukawa K. 2003. Introduction to statistics. In: Ploger BJ, Yasukawa K, editors. Exploring animal behavior in laboratory and field: An hypothesis-testing approach to the development, causation, function, and evolution of animal behavior. San Diego: Academic Press. p 415-447.

Poux C, Madsen O, Marquard E, Vieites DR, deJong WW, Vences M. 2005. Asynchronous colonization of Madagascar by the four endemic clades of primates, tenrecs, carnivores, and rodents as inferred from nuclear genes. Systematic Biology 54(5):719-730.

Pulliam HR. 1988. Sources, sinks, and population regulation. American Naturalist 132(5):652-661.

Rabarivola C, Prosper P, Zaramody A, Andriaholinirina N, Hauwy M. 2007. Cytogenetics and taxonomy of the genus *Hapalemur*. Lemur News 12:46-49.

Ralainasolo FB, Ratsimbazafy JH, Stevens NJ. 2008. Behavior and diet of the critically endangered *Eulemur cinereiceps* in Manombo forest, southeast Madagascar. Madagascar Conservation and Development 3(1):38-43.

Ramanamanjato JB, Ganzhorn JU. 2001. Effects of forest fragmentation, introduced *Rattus rattus* and the role of exotic tree plantations and secondary vegetation for the conservation of an endemic rodent and a small lemur in littoral forests of southeastern Madagascar. Animal Conservation 4:175-183.

Rasoloharijaona S, Randrianambinina B, Zimmermann E. 2008. Sleeping site ecology in a rain-forest dwelling nocturnal lemur (*Lepilemur mustelinus*): Implications for sociality and conservation. American Journal of Primatology 70:247-253.

Ratsimbazafy HJ. 2002. On the brink of extinction and the process of recovery: Responses of black-and-white ruffed lemurs (*Varecia variegata variegata*) to disturbance in Manombo forest, Madagascar. Ph.D dissertation, SUNY-Stony Brook, NY. 190 p.

Raxworthy CJ, Nussbaum RA. 1995. Systematics, speciation and biogeography of the dwarf chameleons (*Brookesia*; Reptilia, Squamata, Chamaeleontidae) of northern Madagascar. Journal of Zoology London 235:525-558

Robinson GR, Holt RD, Gaines MS, Hamburg SP, Johnson ML, Fitch HS, Martinko EA. 1992. Diverse and contrasting effects of habitat fragmentation. Science 257(5069):524-526.

Saunders DA, Hobbs RJ, Margules CR. 1991. Biological consequences of ecosystem fragmentation: A review. Conservation Biology 5(1):18-32.

Schatz GE. 2001. Generic tree flora of Madagascar. Missouri Botanical Garden and Royal Botanical Gardens, Kew. 490 p.

Scheumann M, Rabesandratana A, Zimmermann E. 2007. Predation, communication, and cognition in lemurs. In: Gursky S, Nekaris A, editors. Primate anti-predator strategies. New York: Karger. p 100-127.

Schlaepfer MA. 2003. Successful lizard eggs in a human-disturbed habitat. Oecologia 137:304-311.

Schmid J, Kappeler PM. 1994. Sympatric mouse lemurs (*Microcebus* spp.) in western Madagascar. Folia Primatologica 63:162-170.

Schonewald-Cox C, Chambers S, MacBryde B, Thomas L. 1983. Genetics and conservation: A reference for managing wild animal and plant populations. Menlo Park, CA: Benjamin Cummings Publ. Co.

Secretariat of the Convention on Biological Diversity. 2006. Global Biodiversity Outlook 2. Montreal, Quebec.

Simberloff DS, Abele LG. 1976. Island biogeography theory and conservation practice. Science 191:285-286.

Simmen B, Bayart F, Marez A, Hladik A. 2007. Diet, nutritional ecology, and birth season of *Eulemur macaco* in an anthropogenic forest in Madagascar. International Journal of Primatology 28:1253-1266.

Simons EL, Meyers DM. 2001. Folklore and beliefs about the aye aye (*Daubentonia madagascariensis*). Lemur News 6:11-16.

Singh M, Kumara HN, Kumar MA, Sharma AK. 2001. Behavioural responses of lion-tailed macaques (*Macaca silenus*) to a changing habitat in a tropical rain forest fragment in the Western Ghats, India. Folia Primatologica 72:278-291.

Sisk TD, Margules CR. 1993. Habitat edges and restoration: Methods for quantifying edge effects and predicting results of restoration efforts. In: Saunders DA, Hobbs RJ, Ehrlich PR, editors. Nature conservation 3: Reconstruction of fragmented ecosystems, global and regional perspectives. Sydney: Surrey Beatty & Sons. p 57-69.

Sisk TD, Haddad NM, Ehrlich PR. 1997. Bird assemblages in patchy woodlands: Modeling the effects of edge and matrix habitats. Ecological Applications 7(4):1170-1180.

Sizer N, Tanner EVJ. 1999. Responses of woody plant seedlings to edge formation in a lowland tropical rainforest, Amazonia. Biological Conservation 91:135-142.

Skole DL, Tucker C. 1994. Tropical deforestation and habitat loss fragmentation in the Amazon: Satellite data from 1978-1988. Science 260:1905-1910.

Smith AP, Horning N, Moore D. 1997. Regional biodiversity planning and lemur conservation with GIS in western Madagascar. Conservation Biology 11(2):498-512.

Sork VL. 1983. Distribution of pignut hickory (*Carya glabra*) along a forest to edge transect, and factors affecting seedling recruitment. Bulletin of the Torrey Botanical Club 110:494-506.

Sterling E. 1993. Behavioral ecology of the aye-aye (*Daubentonia madagascariensis*) on Nosy Mangabe, Madagascar. Ph.D dissertation, Yale University, New Haven, CT. 232 p.

Sterling E. 1994. Aye-ayes: Specialists on structurally defended resources. Folia Primatologica 62:142-154.

Tabarelli M, Mantovani W, Peres CA. 1999. Effects of habitat fragmentation on plant guild structure in the montane Atlantic forest of southeastern Brazil. Biological Conservation 91:119-127.

Tabarelli M, Lopes AV. 2008. Edge-effects drive tropical forest fragments towards an early-successional system. Biotropica 40(6):657-661.

Tanaka M. 2007. Habitat use and social structure of a brown lemur hybrid population in the Berenty Reserve, Madagascar. American Journal of Primatology 69:1189-1194.

Tarnaud L. 2004. Ontogeny of feeding behavior of *Eulemur fulvus* in the dry forest of Mayotte. International Journal of Primatology 25(4):803-824.

Tarnaud L. 2006. Feeding behavior of lactating brown lemur females (*Eulemur fulvus*) in Mayotte: Influence of infant age and plant phenology. American Journal of Primatology 68:966-977.

Tattersall I. 1982.The primates of Madagascar. New York: Columbia University Press.

Thalmann U. 2000. Lemur diversity and distribution in western Madagacar: Inferences and predictions using a cladistic approach. In: Lourenço WR, Goodman SM, editors. Diversité et endémisme à Madagascar. Paris: Mémoires de la Société de Biogéographie. p 191-202.

Thalmann U. 2001. Food resource characteristics in two nocturnal lemurs with different social behavior: *Avahi occidentalis* and *Lepilemur edwardsi*. International Journal of Primatology 22(2):287-324.

Thomas JW, Maser C, Rodiek R. 1979. Edges. In: Thomas JW, editor. Wildlife habitats managed forests: The Blue Mountains of Oregon and Washington. Washington, D.C.: Wildlife Management Institute.

Tscharntke T, Steffan-Dewenter I, Kruess A, Thies C. 2002. Characteristics of insect populations on habitat fragments: A mini review. Ecological Research 17:229-239.

Unwin GL. 1989. Structure and composition of the abrupt rainforest boundary in the Herberton Highland, North Queensland. Australian Journal of Botany 37:413-428.

Vasey N. 1997. Community ecology and behavior of *Varecia variegata rubra* and *Lemur fulvus albifrons* on the Masoala Peninsula, Mdagascar. Ph.D dissertation,Washing University, St. Louis.

Vasey N. 2002. Niche separation in *Varecia variegata rubra* and *Eulemur fulvus albifrons:* II. Intraspecific patterns. American Journal of Physical Anthropology 118:169-183.

Vasey N. 2003. *Varecia*, ruffed lemurs. In: Goodman SM, Benstead JP, editors. The natural history of Madagascar. Chicago: University of Chicago Press. p 1332-1336.

Vasey N. 2004. Circadian rhythms in diet and habitat use in red ruffed lemurs (*Varecia rubra*) and white-fronted brown lemurs (*Eulemur fulvus albifrons*). American Journal of Primatology 124:353-363.

Vasey N. 2005. New developments in the behavioral ecology and conservation of ruffed lemurs (*Varecia*). American Journal of Primatology 66:1-6.

Wade TG, Riitters KH, Wickham JD, Jones KB. 2003. Distribution and causes of global forest fragmentation. Conservation Ecology 7(2):7.

Warry FY, Hindell JS, Macreadie PI, Jenkins GP, Connolly RM. 2009. Integrating edge effects into studies of habitat fragmentation: A test using meiofauna in seagrass. Oecologia 159:883-892.

Watkinson AR, Sutherland WJ. 1995. Sources, sinks and pseudo-sinks. Journal of Animal Ecology 64:126-130.

Watt AD. 1998. Measuring disturbance in tropical forests: A critique of the use of species-abundance models and indicator measures in general. Journal of Applied Ecology 35(3):467-469.

Whitesides GH, Oates JF, Green SM, Kluberdanz RP. 1988. Estimating primate densities from transects in a west African rain forest: A comparison of techniques. Journal of Animal Ecology 57(2):345-367.

Wieczkowski J. 2004. Ecological correlates of abundance in the Tana Mangabey (*Cercocebus galeritus*). American Journal of Primatology 63:125-138.

Wilder SM, Abtahi AM, Meikle DB. 2005. The effects of forest fragmentation on densities of white-footed mice (*Peromyscus leucopus*) during the winter. American Midland Naturalist 153(1):71-79.

Williams M. 1990. Transformations of the global environment: Forests. In: Turner BL, Clark WC, Kates RW, Richards FJ, Mathews JT, Meyer WB, editors. The Earth as transformed by human action: Global and regional changes in the biosphere over the past 300 years. Cambridge: Cambridge University Press. p 179-202.

Williams-Linera G, Dominguez-Gastelu V, Garcia-Zurita ME. 1998. Microenvironment and floristics of different edges in a fragmented tropical rainforest. Conservation Biology 12(5):1091-1102.

Winter M, Johnson DH, Faaborg J. 2000. Evidence for edge effects on multiple levels in tallgrass prairie. Condor 102:256-266.

Wirta H, Orsini L, Hanski I. 2008. An old adaptive radiation of forest dung beetles in Madagascar. Molecular Phylogenetics and Evolution 47:1076-1089.

Wollenberg KC, Vieites DR, van der Meijden A, Glaw F, Cannatella DC, Vences M. 2008. Patterns of endemism and species richness in Malagasy Cophyline frogs support a key role of mountainous areas for speciation. Evolution 62:1890-1907.

Wrangham RW. 1980. An ecological model of female-bonded primate groups. Behavior 75:262-300.

Wright PC. 1999. Lemur traits and Madagascar ecology: Coping with an island environment. Yearbook of Physical Anthropology 42:31-72.

Wright PC, Martin LB. 1995. Predation, pollination and torpor in two nocturnal primates: *Cheirogaleus major* and *Microcebus rufus* in the rain forest of Madagascar. In: Alterman L, Doyle G, Izard MK, editors. Creatures of the dark. New York: Plenum. p 45-60.

Yahner RH, Mahan CG. 1997. Behavioral considerations in fragmented landscapes. Conservation Biology 11(2):569-570.

Young AG, Boyle TJ. 2000. Forest fragmentation. In: Young AG, Boshier D, Boyle TJ, editors. Forest conservation genetics: Principles and practice. Australia: Csiro Publishing. p 123-134.

Zanne AE, Keith B, Chapman CA, Chapman LJ. 2001. Protecting terrestrial mammal communities: Potential role of pine plantations. African Journal of Ecology 39:399-401.

APPENDIX 1: CHAPTER 2

Table A.1.1 Spearman's rank order correlations between lemur density and temperature, relative humidity, wind speed, light intensity, number of trees > 10 cm DBH, number of tree species > 10 cm DBH, mean tree DBH, tree height, crown height, and encounters of anthropogenic disturbance at Agnalazaha and Manombo. *r*-value refers to the direction and strength of the correlation. *p* (2-tailed) < .05

	Temperature				**Relative Humidity**				**Wind Speed**				**Light Intensity**			
	Agnalazaha		**Manombo**		**Agnalazaha**		**Manombo**		**Agnalazaha**		**Manombo**		**Agnalazaha**		**Manombo**	
Species	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*
E. cinereiceps	.906	.005†	.001	.997	-.433	.331	.297	.303	.818	.025†	-	-	.374	.408	.510	.062
C. major	.111	.812	-	-	-.411	.359	-	-	.000	1.00	-	-	-	-	-	-
H. griseus	.612	.144	-.059	.841	.204	.661	.013	.965	.424	.344	-	-	.000	1.00	.356	.212
L. jamesi	-	-	.115	.696	-	-	.167	.568	-	-	-	-	-	-	-	-
A. ramantsoavani	.090	.848	.113	.701	.100	.831	.125	.669	-.206	.658	-	-	-	-	-	-
M. jollyae	-.144	.758	.575	.031†	.300	.513	.267	.355	-.618	.139	-	-	-	-	-	-

† Significant or trend correlation to distance to edge categories using Spearman's Rank Order Correlation

Table A.1.1 (contd.)

	Number of trees				**Number of tree species**				**DBH**				**Tree height**			
	Agnalazaha		**Manombo**		**Agnalazaha**		**Manombo**		**Agnalazaha**		**Manombo**		**Agnalazaha**		**Manombo**	
Species	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*
E. cinereiceps	-.500	.667	.500	.391	-.500	.667	.900	.037†	.500	.667	-1.00	-†	-1.00	-†	.400	.505
C. major	.500	.667	-	-	.500	.667	-	-	-.500	.667	-	-	-.500	.667	-	-
H. griseus	-.866	.333†	-.154	.935	-.866	.333†	-.051	.935	.866	.333†	.205	.741	-.866	.333†	-.821	.089†
L. jamesi	-	-	-.800	.104†	-	-	-.300	.624	-	-	-.100	.873†	-	-	.000	1.00
A. ramantsoavani	-.500	.667	-.400	.505	-.500	.667	-.600	.285	.500	.667	.700	.188†	-1.00	-†	-.100	.873
M. jollyae	-.500	.667	-.500	.391	-.500	.667	-.900	.037†	.500	.667	1.00	-†	-1.00	-†	-.400	.505

† Significant or trend correlation to distance to edge categories using Spearman's Rank Order Correlation

Table A.1.1 (contd.)

Species	Crown height				Anthropogenic disturbance			
	Agnalazaha		Manombo		Agnalazaha		Manombo	
	r	*p*	*r*	*p*	*r*	*p*	*r*	*p*
E. cinereiceps	.500	.667	.300	.624	.818	.025†	.375	.186
C. major	-.500	.667	-	-	.538	.212	-	-
H. griseus	.866	.333†	-.667	.219	.212	.648	.475	.086
L. jamesi	-	-	-.400	.505	-	-	-.285	.324
A. ramantsoavani	.500	.667	.000	1.00	.299	.515	-.087	.769
M. jollyae	.500	.667	-.300	.624	-.262	.571	.029	.922

† Significant or trend correlation to distance to edge categories using Spearman's Rank Order Correlation

APPENDIX 2: CHAPTER 3

Table A.2.1. Summary of activity budgets in the genus *Eulemur*.

Species	**Site**	**Rest (%)**	**Feed (%)**	**Travel (%)**	**Social (%)**	**Citation**
E. cinereiceps	Agnalazaha	76	12	9	3	Present study
		78	10	9	2	Present study
	Manombo	41.1	11.8	11.6	31.8	Ralainasolo et al 2008
	Vevembe	76.6	14.0	7.2	2.3	Johnson 2002
E. fulvus rufus x *cinereiceps*	Andringitra	71.9	11.4	14.2	2.6	Johnson 2002
		64.8	18.5	16.2	0.6	Johnson 2002
E. fulvus rufus	Ranomafana	47	19	31	3	Overdorff 1996
E. macaco	Ampasikely	30-33	15-16	32	n/r	Bayart & Simmen 2005
E. rubriventer	Ranomafana	54	20	21	5	Overdorff 1996

n/r: Not reported

Table A.2.2. Summary of diet compositions in the genus *Eulemur*.

Species	**Site**	**Fruit (%)**	**Leaves (%)**	**Flowers (%)**	**Insects (%)**	**Other (%)**	**Citation**
E. cinereiceps	Agnalazaha	86.19	5.02	n/r	5.43	3.38	Present study
	Manombo	67.86	26.79	1.79	n/r	3.58	Ralainasolo et al 2008
E. collaris	Sainte Luce	78.5	4.4	14.0	2.6	0.7	Donati et al 2007
E. fulvus	Pointe Saziley	71.3	24.4	4.4	n/r	n/r	Tarnaud 2006
		60+	n/r	9	n/r	n/r	Tarnaud 2004
	Ranomafana	60	n/r	n/r	n/r	n/r	Dew & Wright 1998
E. fulvus albifrons	Andranobe	68.89	11.78	13.06	n/r	6.26	Vasey 2002
E. fulvus rufus	Ranomafana	79	n/r	n/r	n/r	n/r	Overdorff & Strait 1998
		92	n/r	n/r	n/r	n/r	Overdorff 1996
		66.8	23.4	4	n/r	6.8	Overdorff 1993
E. fulvus rufus x *collaris*	Berenty	83.0	4.3	11.4	n/r	1.3	Tanaka 2007
E. macaco	Ampasikely	69-73	10-12	13-16	n/r	0-7	Simmen et al 2007
E. mongoz	Anjamena	63-65	8-21	3-6	0-2	5-26	Curtis 2004
E. rubriventer	Ranomafana	80	n/r	n/r	n/r	n/r	Overdorff & Strait 1998
		92	n/r	n/r	n/r	n/r	Overdorff 1996
		88.9	n/r	n/r	n/r	n/r	Dew & Wright 1998
		80.6	13.6	3.1	n/r	2.7	Overdorff 1993

n/r: Not reported

Table A.2.3. Summary of number of fruit species utilized by the genus *Eulemur*.

Species	**Site**	**Length of Study**	**# Fruit Species**	**Citation**
E. cinereiceps	Agnalazaha	4 months	27	Present study
	Manombo	5 months	12	Ralainasolo et al 2008
	Vevembe	4 months	96	Johnson 2002
E. fulvus rufus x *cinereiceps*	Andringitra	8 months	27	Johnson 2002
		8 months	69	Johnson 2002
E. collaris	St. Luce	1 year	120	Donati et al 2007
E. fulvus	Pointe Saziley	10 months	~10	Tarnaud 2004
E. fulvus rufus	Ranomafana	13 months	104	Overdorff 1993
E. macaco	Ampasikely	2 months?	> 104	Simmen et al 2007
E. rubriventer	Ranomafana	13 months	96	Overdorff 1993

Table A.2.4. Summary of home range sizes in the genus *Eulemur*.

Species	**Site**	**Home Range (ha)**		**Citation**
		MCP	**Grid Cell**	
E. cinereiceps	Agnalazaha	36.2	12.6	Present study
		33.6	10.0	Present study
	Vevembe	64.3	33.5	Johnson 2002
E. fulvus rufus x *cinereiceps*	Andringitra	71.8	42.5	Johnson 2002
		12.0	8.8	Johnson 2002
E. fulvus rufus x *collaris*	Berenty	22.6	18.1	Tanaka 2007
		16.8	12.1	Tanaka 2007
E. fulvus rufus	Ranomafana	>100	n/r	Gould & Overdorff 2007
	Kirindy	23.0	n/r	Scholz & Kappeler 2004
		35.7	n/r	Scholz & Kappeler 2004
E. fulvus albifrons	Andranobe	n/r	13.1	Vasey 1997
E. macaco macaco	Ampasikely	14.4 – 23.8	n/r	Bayart & Simmen 2005
E. mongoz	Anjamena	n/r	2.8 – 2.9	Curtis & Zaramody 1998

n/r: Not reported