Determinants of Abundance and the Distribution of Primates in Northern Madagascar

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Abstract of the Dissertation

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Finding consistent causalities for patterns of wildlife abundance and distribution in the natural world is a central goal of ecology. Insights into how energy and biomass is distributed at particular trophic levels provide important clues towards understanding mechanisms for community structure. Among primates, the lemurs of Madagascar represent a fascinating case study for inquiry given the absence of many other animal taxa; a pattern that reflects a unique biogeographic history. A variety of factors have been proposed to influence community structure in nature and among these empirical work with primates has highlighted in particular, the role that resource availability, predation, competition and evolutionary history play in driving such complex phenomena. Despite the utility of this contextual framework, human population trends in Madagascar exceed a 3% annual growth rate, a pattern that reflects a growing interface between humans and wildlife. Increasingly, researchers that are interested in primate community structure are being challenged to separate the dynamic and often synergistic role that humans have to play in determining the abundance of wild primate populations from the more natural characteristics of the environment.

This dissertation evaluates patterns of primate abundance and distribution across a dynamic and heavily fragmented landscape characterized by a variety of human activities, including agriculture, selective logging, stock grazing, large scale fires and hunting. The primary objectives of the dissertation are threefold: (1) evaluate the reliability of density estimates for primates using a widely accepted method, the line transect method, (2) assess the influence of natural and anthropogenic factors in determining the population densities of different lemur species within a diurnal primate community and (3) assess the influence of natural and anthropogenic factors in determining occupancy patterns of primates across a fragmented landscape. To meet these aims I gathered data on a diurnal primate community in three protected areas, the Analamerana Special Reserve, Ankarana National Park and the Andrafiamena-Andavakoera Forest Corridor, all located in the Diana region, Antsiranana Province of northern Madagascar. The results first demonstrate that the role of imperfect detection in biasing density estimates can be largely reconciled by collecting data on patterns of detectability in the different primate species sampled. Using adjusted counts however only marginally improved the accuracy of density estimates for one species from the current sample, suggesting that contemporary criticism over the use of line transect methods with primates may be overstated. Second, lemur population densities were most influenced by patterns of resource availability and quality as well as interactive effects at the community level. Notably, folivorous lemurs showed a strong preference for habitats that occur on specific geological formations where the top ten dry season foods were most abundant. Low level to moderate disturbances further optimized the habitat for folivores and reinforced the importance of the role of leaf quality in driving folivorous primate abundance. Frugivorous primates were also apparently uninfluenced by the spatial attributes of forest fragments but showed some evidence of preference for habitats with more abundant resources. Nonetheless the strongest relationship among frugivorous primates involved the tendency for the densities of the two sympatric species to track one another. The result suggests that there may be benefits to the polyspecific associations that have been described for these two species and indicates that the frugivores are likely targeting similar resources not measured here. (3) Finally the results from studies of occupancy patterns indicate that despite difficulties with modeling species richness or patterns of incidence for all species, some taxa show very clear responses to some easily quantified characteristics of the landscape. In particular the most frugivorous taxon shows a strong preference for forests of a threshold size. These large forest patches are likely to provide a greater abundance of the rare and patchily distributed resources that form a mainstay of the diet. Similarly folivorous lemurs also show a strong preference for the habitats where their preferred resources are most abundant, but also where heavy pressure on the environment from humans is minimized.

On the whole these results provide some on-going support for the resource concentration hypothesis whereby species are primarily limited by the availability of palatable resources. The results also highlight the potential importance of interactive effects at the community level and specifically the role of polyspecific associations in structuring the northern Malagasy primate communities. Finally the findings also demonstrate a general resilience of lemurs to the process of fragmentation, a response that reflects congruence with the energy frugality hypothesis of Wright (1999) which postulates that lemurs have evolved under selective pressure for traits that confer efficiency in coping with a harsh and unpredictable environment.

For my parents,

Vivian and Harold Banks.

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CHAPTER ONE:

Introduction

Background

At the center of fundamental work in ecology is the attempt to understand the most pivotal factors in driving the abundance and distribution of different organisms. Among the Order Primates, scientists have largely focused on four overarching categories including (1) food resources and more specifically the quantity and quality of resources, (2) predation, (3) inter-specific competition and (4) disease. Extrinsic factors, such as those emerging from the influence of anthropogenic activities are, in general, adequately expressed under these four categories. Nonetheless it remains a substantial challenge for research to disentangle these proximate mechanisms from the noise created through the full variety and magnitude of effects that humans currently impose on primate populations worldwide (Struhsaker 1999). Furthermore in the current age of increasingly frequent human and non-human primate contact and interaction, a robust theoretical framework for better understanding the similiarities and differences across primate communities should attempt to take these factors into account and identify their relative levels of importance (Fleagle et al. 1999).

The current study evaluates the role of natural ecology and anthropogenic factors in determining the abundance and distribution of primates in forest fragments of the Ankarana National Park, the Analamerana Special Reserve and the Andrafiamena-Andavakoera Forest Corridor in the Diana region of northern Madagascar. I studied members of the diurnal primate community found in these three protected areas in 45 forest fragments of variable spatial configuration, habitat structure, floral composition, and disturbance intensity by quantifying differences in population density and occurrence across the landscape. It is important to note that despite the large number of factors considered using this framework, the design is not an attempt at providing a truly comprehensive approach towards understanding patterns of abundance and distribution within this primate community. In particular, abiotic factors such as soil fertility, climate, topography and altitude have also received support in the literature but were not considered here. This initial stage of inquiry was instead primarily concerned with isolating the major ecological factors that have produced existing population patterns. It is also worth noting that there are other measures of population success that should also be considered above and beyond primate population abundance and distribution, including the study of physiological health, demographic rates and behavioral shifts within primate populations occupying dynamic environments (Strier et al. 2006; Irwin et al. 2010a; Strier and Ives 2012).

Madagascar's diverse radiation of primates provides a suitable backdrop in which to examine such processes, given the substantial role that humans are presumed to have played in the historical modification and loss of forested habitats (Burney 1999; Burney et al. 2003a; Crowley 2010; Dewar and Richard 2012). Despite this widespread view, several recent studies have highlighted the importance of considering regional differences and alternative scenarios in attempts to characterize this dynamic relationship (Kull 2000; Virah-Sawmy et al. 2010; Dewar et al. 2013). Nonetheless, at the turn of the century early European explorers frequently included often scornful accounts of extensive on-going deforestation, particularly in the humid east and the highlands of Madagascar as part of their detailed notes describing the vast biological wealth of the island (Perrier de la Bâthie 1921; Humbert 1927). In more recent times and with the advent of remote sensing technologies and standardized analyses of changes in forest cover, the extent of habitat loss for lemurs and the country's primarily forest dependent taxa has been further clarified. While differences in the precise estimates of deforestation have remained, one result that is consistent across these more recent studies indicates probable loss of at least 70% of the original primary vegetation (Green and Sussman 1990; Myers et al. 2000; Harper et al. 2007). The implications of these findings for lemurs are reflected in the results of a July 2012, meeting of the Species Survival Commission (SSC) where over 94% of the island's entirely endemic primate fauna were classified as either threatened, endangered or critically endangered by the World Conservation Union (IUCN); (Schwitzer et al. 2013).

In the extreme north of Madagascar the situation for lemurs appears similarly aggravated by such factors given that the conservation status of primate taxa follows a familiar pattern. Of the diurnal primates that are the subject of this work both *Eulemur coronatus* and *Eulemur sanfordi* are considered endangered, *Hapalemur occidentalis* is classified as vulnerable and the elusive Perrier's sifaka, *Propithecus perrieri*, critically endangered by the IUCN. Noctural primates are similarly threatened with three out of the five known taxa recently assigned endangered status (Schwitzer et al. 2013). Not only are lemurs threatened with on-going habitat loss and the fragmentation of remaining habitat through slash-and-burn agriculture and wildfires of anthropogenic origin but in many areas selective logging, mining, charcoal production and hunting have also been implicated in depressing lemur populations (Banks et al. 2007; Quéméré et al. 2010a). Nonetheless, and only with the exception of hunting, habitat loss and fragmentation are widely acknowledged as posing the greatest threats to wild primate populations (Cowlishaw and Dunbar 2000; Chapman and Peres 2001; Godfrey and Irwin 2007; Arroyo-Rodríguez and Mandujano 2009). Certainly it is these three factors together that are commonly evoked to explain the relatively recent disappearance of Madagascar's subfossil lemurs (Perez et al. 2005; Godfrey and Irwin 2007; Muldoon 2010), so it is expected that they remain active in playing a major role in limiting populations of extant lemurs.

In addition to the prevalence of these threats in Madagascar and their general association with primate declines, comparative work has shown how susceptibility to extinction bears a strong phylogenetic signal (Purvis et al. 2000; Purvis et al. 2005). So an important question involves whether or not levels of relatedness between Madagascar's extinct subfossil lemurs and the extant primate fauna are sufficient to provide a reliable signal of future susceptibility to extinction. Despite the utility of identifying the phylogenetic signal for conservation, the inability of taxonomy to consistently serve as a proxy for ecology, may provide important clues for understanding the extinction process (Jernvall and Wright 1998; Godfrey and Irwin 2007). Accordingly it remains imperative that ecological datasets addressing patterns of response to site-specific threats in primates be made available for an increasing number of taxa to more accurately model extinction risk (Cowlishaw et al. 2009). Furthermore, it is critical that the intensity of threat also be evaluated within the appropriate context to avoid characterizing patterns of response on strictly qualitative assessments of population pressure (Ganzhorn 1995; Irwin et al. 2010b).

Although high levels of primate endangerment and the prevalence of influences from humans on wildlife in northern Madagascar distinguish it as an ideal setting to investigate the role of these factors in driving extinction risk among lemurs, there is the issue of whether or not habitat loss and fragmentation in northern Madagascar reflect human impacts or are instead artifacts of the island's history of climate change (Kull 2000; Virah-Sawmy 2009; Virah-Sawmy et al. 2010). This distinction is important to make because forest loss and fragmentation of a distant natural as opposed to a recent anthropogenic origin would be predicted to have previously altered selective pressures on the traits that confer success in forest fragments for lemurs (Ewers and Didham 2006). Indeed there have been provocative arguments raised addressing these matters for northern Madagascar and the likely consequences for primates (Quéméré et al. 2012), but both floral and faunal evidence suggest that the emergence of truly open habitats in northern Madagascar is primarily associated with the arrival and proliferation of humans in Madagascar (Jungers et al. 1995; Burney et al. 2003b; Burney et al. 2004). Furthermore, despite evidence for changes in the extent of forest cover in northern Madagascar having been convincingly argued for the late Quaternery period (Rakotoarisoa et al. 2013), studies of the structural composition of grasslands (Burney et al. 2004) and patterns of natural regeneration along the ecotone between savanna and forest in Madagascar (Pareliussen et al. 2006) indicate that the drying events associated with these vegetation shifts would have eventually given rise to wooded grasslands or a grassland/woodland mosaic and not the open savannas that characterize much of the north today (Lowry et al. 1997; Bond et al. 2008; Rakotoarisoa et al. 2013). These arguments are further supported through consideration of the role that the repeated burning of savanna for pasture and agriculture has on soil-nutrient dynamics, the existing seed bank and the spread of pyrogenic communities into areas incapable of naturally supporting a fire regime (Burney 1996; Goodman 2013). The extirpation of Madagascar's largely herbivorous megafauna must also be implicated in changes to the predominant fire ecology and vegetational shifts given the role that these large grazers and browsers would have played in reducing the fuel loads that predispose forests and other wooded habitats to fire (Burney 2003; Burney et al. 2003b; Cochrane 2003).

While fragmented habitats are generally considered to present most primates with substantial challenges (Fahrig 2003; Ganzhorn et al. 2003; Marsh 2003; Marsh and Chapman 2013, Arroyo-Rodríguez and Mandujano 2009) they also present an important opportunity for scientists and wildlife managers to evaluate regional differences in population status as a function of numerous factors. In particular, as well as variability in spatial dimension (i.e. size, shape and isolation) forest fragments often vary in characteristic ways with respect to habitat structure, tree species composition, and patterns of on-going human disturbance (Fahrig 2003), yet few studies with primates have considered this full complement of factors and how they covary in their analyses (Ganzhorn et al. 2003). In Madagascar, the majority of fragmentation studies with primates have focused on factors related to the role that the spatial arrangement of fragments within landscapes has on lemur distribution and genetic diversity (Ganzhorn et al. 2003; Schad et al. 2004; Quéméré et al. 2010b). Other research has considered differences in the behavioral adaptations of primate groups in forest fragments and continuous forest (Irwin 2007b; Irwin 2007a; Irwin 2008). Finally, Lehman and colleagues have adopted a rigorous approach towards evaluating primate responses to edge effects, a major consequence of fragmentation (Laurance and Yensen 1991; Murcia 1995; Fahrig 2003), by studying differences in lemur abundance along the fringes of forests and contrasting the findings with results from more interior habitats (Lehman et al. 2006a; Lehman et al. 2006c; Lehman 2007). Nonetheless, clear gaps in previous research with lemurs in fragmented habitats and most notably approaches that consider a more comprehensive range of the natural and anthropogenic factors known to limit lemur populations, as well as studies that address differences in the degree of fragmentation within the landscape as opposed to using the qualitative dichotomy of “fragmented” versus “continuous” currently limit our ability to draw firm conclusions regarding the influence of habitat fragmentation on lemur populations. This dissertation is a first attempt to understand these factors in a scientifically rigorous way.

Additional gaps include determining which measures of population status are capable of clearly and reliably capturing patterns of population response in primate communities. Fragmentation studies in Madagascar have almost exclusively focused on patterns of primate species incidence in forest fragments, but what additional information might be gained by studying patterns of abundance in forest patches? Indeed cost and time limitations generally preclude more detailed studies of primate density in an adequate number of fragments to discern patterns of response to habitat fragmentation (Arroyo-Rodríguez and Mandujano 2009). Although a few recent studies have made valuable gains in an attempt to fill these gaps (Quéméré et al. 2010a; Salmona et al. 2013), the estimation of wildlife population density is subject to a variety of caveats (Marques et al. 2007; Marshall et al. 2008) that are rarely addressed in a systematic way. These considerations should be of particular importance for Madagascar’s primate fauna given their high levels of endangerment and the need to base future management decisions on reliable indicators of population abundance. This study adopts a rigorous approach to this issue by taking into account temporal, behavioral, and other sampling biases known to influence the detectability of primates (Plumptre and Cox 2006). Furthermore, both patterns of primate incidence and population density are considered thereby enabling an evaluation of the level of resolution required to identify limits to primate persistence in the remaining landscape.

In addition to these limitations, previous studies of primate densities in the fragmented habitats of Madagascar have often focused exclusively on the populations of a single species (Irwin 2006; Craul et al. 2009; Quéméré et al. 2010a; Salmona et al. 2013). That such results are of value for theory and conservation is certainly irrefutable, yet the opportunity to estimate the population densities of multiple primate species from the same regional community should also offer insights into patterns of community structure, interspecific interaction as well as the dynamics of extinction risk for primate assemblages and not just single species (Chapman and Peres 2001). In northern Madagascar these research endeavors should be considered timely given what has previously been described for these communities. For example, polyspecific associations have been used to characterize the behavior of the region's two most frugivorous diurnal primates, *Eulemur sanfordi* and *Eulemur coronatus* (Freed 1996; Freed 2006). Although the relatively recent extirpation of Madagascar's primate megafauna may help to explain this pattern (Ganzhorn 1997) quantitative evidence at the population level has yet to be presented where the benefits and costs for each of these taxa are clearly outlined. Accordingly one major aim of this dissertation is to clarify this issue as well as the potential for interaction at the level of the community by studying the abundance and distribution of all potentially competing members of the diurnal primate community known from the extreme north of Madagascar.

Natural Determinants of Primate Abundance: Food Resources and the Quality and Quantity of Food

The importance of food resources in determining primate abundance has been considered from the perspective of the diversity of potential food species (Ganzhorn et al. 1997), the structural diversity of habitats (Bourlière 1985; Terborgh and Van Schaik 1987; Ganzhorn et al. 1997), nutritional value of foods (Waterman et al. 1988; Oates et al. 1990a; Ganzhorn 1992; Chapman et al. 2004) the productivity (Stevenson 2001)and seasonality of habitats (Ganzhorn 1999b), and interspecific resource competition (Ganzhorn 1993b; Struhsaker 1997; Ganzhorn 1999a). Food resources have regularly been used to explain differences in abundance and distribution among Madagascar's primate fauna (Ganzhorn 2002; Balko and Underwood 2005; Grassi 2006; Lehman 2007; Irwin 2008) and findings elsewhere with primates that provide evidence for a strong relationship between heightened foraging efficiency, physiological adaptations of the primate gut, access to highly nutritious foods and elevated population densities reinforces the fundamental importance of food resources in determining primate abundance (Janson and Chapman 1999).

Tree Species Diversity

A high diversity of tree species, through a staggered and divergent phenology is posited to augment the availability of foods for primates at any one time, effectively raising the capacity of the environment to support either a greater number of primate species or higher densities of species (Oates et al. 1990a). In support of this argument Ganzhorn et al. (1997) found a positive trend for both primate abundance and species richness to increase with tree species diversity in northern Madagascar. There was a "dilution effect" however, and at the highest levels of tree species diversity, both primate species richness and abundance declined (Tilman 1982). This finding suggests that in habitats that support very high tree species diversity, key resources become scarce and more patchily distributed for primates, thereby limiting access to food to meet minimum energy requirements.

Despite the apparent generality of this relationship, one recent study of *Propithecus diadema* in forest fragments demonstrated that this species occurs at higher densities in areas of lower plant species richness (Irwin 2008). The author highlights the widespread availability of a single keystone resource in areas of low plant species richness as a likely explanation for this pattern. A similar relationship was found for many of the primates that occur in the Lopé Reserve, Gabon (Tutin and White 1999) where forest fragments of lower tree species diversity supported higher densities of primates. It is nonetheless important to note that these results could also indicate an overcrowding of forest fragments, at least in the short term (Irwin 2008; Irwin et al. 2010a). Rovero and Struthsaker (2007) found that the density of only one of four diurnal primates increased in areas of higher tree species diversity along sections of the same transect in Udzungwa Mountains of Tanzania. These results highlight that the relationships found by Ganzhorn et al. (1997) are likely to operate at the level of individual species yet do not necessarily affect whole communities.

Forest Structural Diversity

Some workers have argued that habitats characterized by high structural diversity may offer primates a greater number of distinct microhabitats for feeding, travel and resting, and as a result could raise the carrying capacity to support higher numbers of primates (Bourlière 1985; Ganzhorn et al. 1997; Peres 1997). In the case of the folivorous *Alouatta*, greater structural diversity and a more discontinuous canopy characterized preferred habitats for this genus (Peres 1997). Emergent trees and exposure of more of the plant biomass to direct sunlight translates into increases in plant growth, including increases in fruit production and immature foliage (Ganzhorn 1992; Ganzhorn 1995), both of which form the staples of many primate diets. (Schwarzkopf and Rylands 1989) provide complementary evidence from Amazonia where primate species richness tracked the structural diversity of five forest fragments there. The authors argued that not only did the presence of canopy gaps promote plant growth in the fragments, thereby increasing several primate foods, but abundant lianas may have facilitated the vertical clinging and leaping form of locomotion exhibited by many primates there. Furthermore, there may be an upper limit on the size or other attributes of the trees used for locomotion as shown in a study on patterns of locomotion in *Lepilemur ruficaudatus* in habitats both affected and unaffected by logging (Ganzhorn 1993a).

Leaf Quality

Three components of leaf chemistry are distinguished when considering the quality of leaves as food for folivorous primate species – digestibility, mineral levels and protein-to-fiber ratios (Milton 1979). Secondary compound levels (i.e. tannins and alkaloids) and fiber concentrations relate to digestibility by impeding the digestion of leaves in herbivores, although a more general role for secondary compounds in this process is only beginning to be elucidated (Silanikove et al. 2001; Felton et al. 2009). A high digestibility of leaves may reduce the metabolic costs of lactation, increasing the growth and survival of infants and thereby shortening inter-birth intervals (Lee 1987; Koenig et al. 1997) and raising the intrinsic rate of increase of the population (Chapman et al. 2004).

Mineral levels are concerned with the amounts of potassium, phosphorus, sodium, calcium, zinc and magnesium in leaves. Higher survivability and shorter inter-birth intervals are found in primate populations not limited by mineral deficiencies (Oates 1978; Rode 2003; Rothman et al. 2006; Fashing et al. 2007). Furthermore, a number of studies with primates have documented how mineral content in food items appears to influence food choice (Oates 1978; Rode 2003; Rothman et al. 2006).

Protein-to-fiber ratios are often used as an index of leaf quality for folivores that must meet threshold levels in protein uptake to satisfy basic nutritional requirements. In contrast, increasing fiber levels largely inhibit protein uptake (Chapman et al. 2002). In light of the constraints on primate diets a positive relationship has been found between the protein-to-fiber ratio of mature leaves and the biomass of folivorous lemurs in the forests of Madagascar (Ganzhorn 1992). This relationship has also been shown to reliably predict folivorous primate biomass in many other areas (Milton 1979; Oates et al. 1990b; Peres 1997; Milton 1998), as well as the biomass of other mammalian folivores (Emmons 1984). These patterns are indeed upheld even within sites of the same forest (Chapman *et al.* 2002). Nonetheless, the use of the protein-to-fiber ratio has fallen under growing criticism owing largely to the inability of this measure to integrate the role of energy and secondary compounds in explaining differences in folivorous primate biomass (Chapman et al. 2010a; Chapman et al. 2010b; Gogarten et al. 2012; Wallis et al. 2012).

Ganzhorn et al. (1999) argue that the production of high quality leaves for primates in Madagascar's forests is heavily limited by the availability of minerals, many of which are found at low levels in the acidic soils that characterize Madagascar's evergreen rainforests. This pattern may largely be the result of topography and the fact that the majority of Madagascar's remaining evergreen forests persist primarily on steep slopes, where the leaching of minerals should be high in response to heavy rainfall in these areas (Ganzhorn et al. 1999) Alternatively, the leaves of drier and more deciduous formations are metabolically distinct from evergreen forests where plants must invest less in growth and more in secondary compounds to limit the loss of leaves to herbivore predators. In more seasonal forests, the life span of leaves is much shorter than for evergreen habitats, reflecting higher metabolic rates and higher protein contents (Coley and Barone 1996; Janson and Chapman 1999; van Schaik et al. 2005).

Large Food Tree Density

The density or abundance of food trees and their distribution within an area can influence the density of primate species, by increasing the overall abundance of food and increasing the carrying capacity of the environment (Oates et al. 1990a; Chapman and Chapman 1999; Arroyo-Rodríguez et al. 2007). (Davies 1994) for example, found a positive correlation between the density of leguminous trees and the biomass of colobus monkeys in Asia. (Stevenson 2001) also found a strong correlation between the density of large fruit trees and frugivorous primate biomass among Neotropical sites. Low densities of the most important food trees may force animals to expend suboptimal amounts of energy to travel between food patches to meet their nutritional requirements (Janson and Chapman 1999). While some studies have highlighted a clear relationship between average tree size and fruit production (Ganzhorn 1995), knowledge of the actual fruit trees used by primates, should provide a more informative measure regarding the impact of large trees on primate populations (Lehman 2007; Rovero and Struhsaker 2007).

Although knowledge of site-specific large tree density provides a useful proxy for overall productivity, a number of workers have argued that limitations on population size are set by the period of lowest food availability (Janson and Chapman 1999). Primates may ultimately depend on the density of fall-back foods or keystone resources during periods when preferred foods are scarce or unavailable (Terborgh 1984; Marshall and Wrangham 2007; Marshall et al. 2009). Keystone resources are described as those with limited inter-annual availability and a high rate of consumption by resource limited animal populations (Gautier-Hion and Michaloud 1989). Irwin (2008) found that diademed sifakas (*Propithecus diadema*) use a hemiparasitic mistletoe species (*Bakerella clavata*) with an extended phenology during the lean dry season in the continuous rainforests of Tsinjoarivo, Madagascar. In fragmented forests, the absence of preferred fruit trees forces sifakas to depend on this plant species year-round, further suggesting that the densities of particular plant species can be critically important in determining population size. Accordingly Irwin (2008) focused on areas that support both high densities of mistletoes and large fruit trees in his recommendations for the conservation of diademed sifakas.

Approaching the concept of keystone resources from a different perspective, Wright *et al.* (2005) noted that in the rainforests of Ranomafana National Park in Madagascar, *Propithecus edwardsi* tracks the increasing availability of a large breadth of fruit species during the wet season to coincide with peak lactation. So instead of the classic interpretation of lower quality keystone resources, here lemurs are found to rely on high quality keystone resources during the periods of lactation and weaning to ensure that reproduction will succeed. Loggers tend to target preferred lemur fruit trees (Balko and Underwood 2005), and it has been suggested that this may adversely affect sifaka reproductive success and population levels years after logging (Wright et al. 2005). In support of this hypothesis, (White et al. 1995) found that the frugivorous *Varecia variegata variegata* was extirpated from sites where loggers had dramatically influenced the abundance of common fruit trees.

Phenology

Productivity and seasonality are fundamental components to any consideration of phenological patterns. The overall abundance of food resources in a habitat is characterized by its productivity. As mentioned previously, a higher primary productivity may support a higher primate biomass (Janson and Chapman 1999). In addition to productivity, a habitat's seasonality describes variation in food production over an annual cycle. The role of seasonality has implications for the quality of browse available for folivorous primates (Janson and Chapman 1999; van Schaik et al. 2005). Folivorous lemur biomass in Madagascar has been shown to increase with increasing seasonality (Ganzhorn 1992) and Peres (1997) used a related argument to explain elevated *Alouatta* densities in Amazonian areas with more pronounced dry seasons. In contrast to the situation for folivores, frugivorous primate densities may be limited in more seasonal habitats where the period of peak fruit production and peak flush may coincide (van Schaik et al. 2005). This scenario is upheld by arguments in support of the importance of fallback resources during the most resource limiting periods. The suggestion here is that high quality fallback resources (e.g. the flush of young nutritious leaves) are scarce in seasonal habitats and primates that rely on flush as fallback are likely to encounter greater difficulties with meeting minimum energy requirements during these periods.

Resource Competition

Competition is described as a phenomenon in which two or more individuals, species or populations seek to use the same resources (Gause 1934a; Gause 1934b). Ecological theory postulates that the potential for competition is greatest among closely related species that share the same functional characteristics (e.g. members of the same dietary guild; (Heymann and Buchanan-Smith 2000). In support of this principle, Ganzhorn (1997) has shown how species interactions play a major role in shaping primate community structure in Madagascar with members of the different trophic guilds showing a strong tendency to be equally represented across communities. While such findings highlight the potential for interspecific competition to exert strong selective pressures on membership in primate communities, many closely related species are able to coexist through patterns of niche diversification. Niche diversification might be achieved when certain species accept a greater breadth of items in the diet, or items of lower quality (Ganzhorn 1993b; Porter 2001; Haugaasen and Peres 2009).

Given the variable response of many primates to the presence of potential competitors and the caveats associated with demonstrating competition (Ganzhorn 1993b; Ganzhorn 1999a), some workers have focused on the concept of density compensation to highlight the potential importance of interspecific competition in structuring communities. Some authors have suggested that the phenomenon of density compensation may help to explain rises in the population densities of small-bodied species in habitats where large-bodied primates have been extirpated by hunters (Peres and Dolman 2000). The absence of strong evidence that small and large-bodied primates typically select the same resources in habitats may be reflected in the absence of evidence that the densities of large species were not entirely offset by smaller ones (Peres 1999). A second study attempted to address this problem by investigating differences in the quality of food items for two sympatric folivores in the dry forests of western Madagascar (Ganzhorn 1993). One of these folivores, *Lepilemur ruficaudatus* consistently choose lower quality leaves when the sympatric *Avahi* was present. Although densities were not measured in the two habitats, the fact that *Lepilemur* is forced to accept a lower quality diet should translate into reduced fertility, a lower birth rate and decreases in population density. Nonetheless, each of these studies further reinforces the strong impact that competitive interactions can have in shaping the distribution of biomass within primate communities.

Anthropogenic Determinants of Primate Abundance: Habitat Fragmentation

Data on population densities in fragmented landscapes can be used to quantify patterns of abundance relative to variable habitat characteristics since fragments often differ in their spatial, geometric, structural and vegetative composition as well as predominant disturbance regimes. Among primate species there is evidence for mixed responses to these differences (Ganzhorn 2000; Onderdonk and Chapman 2000; Umapathy and Kumar 2000a; Umapathy and Kumar 2000b; Ganzhorn et al. 2000 ; Ganzhorn et al. 2003; Gilbert 2003; Anderson et al. 2007) yet few studies from Madagascar have used an integrative approach towards examining the likely synergy that exists between these factors. Nevertheless, one major limitation with many fragmentation studies involves an inability to separate the effects of fragmentation per se (i.e. the spatial configuration, structure, and population dynamics of habitats) from that of forest loss (Fahrig 2003).

Fragment Size, Shape and Isolation

The area of a forest fragment is an important determinate of primate abundance because it relates directly to the carrying capacity of the environment. Small populations are also increasingly vulnerable to extinction due to the effects of genetic, demographic and environmental stochasticity (Soule and Wilcox 1980; Soulé 1987; Simberloff 1988; Boyce 1992; Young and Clarke 2000). Work with primates has shown that few generalizations are available to accommodate the full diversity of responses exhibited by members of the primate order, however examining primate responses by functional guild has illuminated many more distinctive patterns. In particular, frugivorous primates that rely on patchily distributed fruit trees are more likely to occupy large home ranges and show greater sensitivity to variability in fragment size (Balko and Underwood 2005). Alternatively, folivorous primates are not faced with the same constraints in locating palatable food given that leaf availability does not vary as dramatically with changes in fragment size (Powzyk and Mowry 2003)as does fruit. Given the importance of acknowledging these differences among different functional guilds it is perhaps no surprise that many studies have commonly reported that fragment area shares a positive relationship with the abundance and/or density of certain primate species (Medley 1993; Estrada and Coates-Estrada 1996; Chiarello and de Melo 2001; Wieczkowski 2004) while others have reported either a negative pattern (Rylands and Keuroghlian 1988; Gilbert 2003), no relationship at all (Onderdonk and Chapman 2000), or variable results across species (Tutin et al. 1997).

In considering individual forest fragments, the degree of isolation from other forested habitat patches is also presumed to influence patterns of primate abundance because large inter-fragment distances may limit the ability of a local population to avoid local extinction through recolonization (i.e. the rescue effect; (Brown and Kodric-Brown 1977; Laurance et al. 2002). Additionally, the age at which a forest fragment became isolated may be important for the density of primates it can support because the quality of habitat may deteriorate progressively over time due to both natural and anthropogenic effects (Gillespie and Chapman 2006). The role of isolation distance has provided contrasting results relative to the responses of many primates, with some studies indicating a positive (Estrada and Coates-Estrada 1996) relationship, and the majority of studies providing no general pattern (Lawes et al. 2000; Dehgan 2003). The results from studies of the age of isolation on primate abundance are equally fraught with contradiction (Estrada and Coates-Estrada 1996; Ganzhorn et al. 2000 ; Chiarello and de Melo 2001; Fahrig 2003; Ewers and Didham 2006). Despite these disparities, efforts to assess the dispersal capacities of different primate species have yielded more informative results (Arroyo-Rodríguez and Mandujano 2009) with analysts devising strategies to model these patterns based on existing knowledge of the species in question (Tischendorf et al. 2003).

The influence of fragment geometry (i.e. shape) on patterns of primate abundance has only recently begun to receive greater attention in the primate literature despite a growth in the theory aimed at quantifying some of the expected responses in wildlife (Fahrig 2003; Ewers and Didham 2006). Forest fragments with convoluted shapes are widely presumed to confer mostly negative impacts on primate populations given the role of edge effects in modifying plant species diversity and the structure of vegetation (Murcia 1995; Laurance et al. 1998; Laurance et al. 2000; Laurance et al. 2002; Lehman 2007). In particular, forests with extensive edges are expected to experience heightened mortality among large trees and dessication-sensitive plants, as well as proliferation of disturbance loving pioneer and successional species (Laurance et al. 2002). Despite these drastic changes to floristic composition and structure in fragments with complex shapes some primates have been shown to respond positively to edges or exhibit no consistent response at all (Lehman et al. 2006b; Anzures-Dadda and Manson 2007). The abundance of secondary plant species along forest edges has been used to explain similarities between species that are tolerant of disturbed areas and those that frequently use edge habitats (Arroyo-Rodríguez and Dias 2010). Additionally the successional nature of floristic composition along forest edges (Laurance et al. 2006) is consistent with a plant physiology that places a greater emphasis on plant growth than plant defenses. The result can translate into increases in the availability of young foliage and fruits along edges (Ganzhorn 1995)but in general increases in the relative amount of edge in fragments tend to reduce the basal area and quality of resources for primates (Arroyo-Rodríguez and Mandujano 2006; Lehman 2007; Irwin 2008).

Human Impacts: Agriculture, Stock grazing, Selective logging, Hunting and Fire

Humans are increasingly coming into contact with non-human primates as the world’s total human population continues to expand with the highest growth rates occurring in countries that support primate populations (Chapman and Peres 2001; Chapman and Lawes 2003; Lehman et al. 2005). Prominent human activities in habitats where primates occur include hunting, mechanized logging, introduction of exotic plant species, habitat modification through agriculture and increases in the incidence of fires (Ganzhorn 1995; Peres 1999; Tan 1999; Chapman et al. 2000; Peres et al. 2003; Lehman et al. 2005; Lehman 2006; Golden 2009).

Human activities including agriculture and hunting play a major role in limiting primate populations not only by reducing available habitat and culling population numbers but also by disrupting the social cohesion of groups and forcing primates to shift to suboptimal diets. Research in Madagascar has shown that agriculture and other domestic activities in close proximity to human settlements place upper limits on primate population numbers and primate diversity (Smith et al. 1997; Lehman 2006). In contrast, some disturbances that are responsible for opening gaps in forest and encouraging new growth, such as low intensity selective logging may improve the quality of the habitat for some primates (Ganzhorn 1995; Chapman et al. 2000). Diet may provide the greatest insights into how different primate species will respond to pressures from selective logging (Herrera et al. 2011). Although research into the role of logging in structuring primate communities has offered some support for the compatibility of human activities with wildlife management, the majority of logging in areas that support primates is of high intensity and likely results in food shortages and increased levels of hunting (Chapman and Peres 2001).

Smith et al. (1997) have provided evidence from western Madagascar that habitats situated in close proximity to human settlements are likely to support less species rich communities of primates. The authors found that activities such as agriculture, stock grazing and hunting increase incrementally in close proximity to human settlements. Stock grazing in Madagascar is often associated with the annual burning back of savanna to provide palatable shoots and herbaceous growth to support cattle (Kull 2000). These fires commonly spread into forested areas, and may threaten primate populations with death from smoke asphyxiation, loss of fruiting crops and heightened tree mortality causing food shortages (Peres et al. 2003). Indeed the role of human activities in exacerbating the potential for fire has many levels and selectively logged forests are more susceptible to fire than are primary forests (Barlow and Peres 2004). The impact of human populations on primate habitats also extends to the introduction of invasive plant and animal species (Ganzhorn 2003; Grassi 2006). Simmen et al. (2007), for example suggest that black lemurs (*Eulemur macaco macaco*) in Ampasikely, Madagascar suffer reduced protein intake by specializing on introduced and cultivated plant species while using few alternative resources that might otherwise assist individuals in meeting nutritional requirements. The authors highlight higher densities in more pristine habitats containing a full complement of native plant species (Simmen et al. 2007). Alternatively Grassi (2006) has shown how bamboo lemurs (*Hapalemur griseus griseus*) at Ranomafana National Park reached their highest densities in areas where the introduced Chinese guava (*Psidium cattleyanum*) was used as a top food source.

Study Site and Subjects

This study took place in three protected areas of the Diana Region of the Antsiranana Province, northern Madagascar from 14 July 2003 to 14 July 2012 (Figure 1; for site names please see Table 1). Data included in the current dataset includes the subset of data presented in Banks et al. (2007). Primate abundance and distribution were studied within isolated forest fragments of the Analamerana Special Reserve (hereafter Analamerana: S12°46'34.30", E 49°29'6.34, area: 34,700 ha) the Ankarana National Park (hereafter Ankarana: S 12°53'34.25", E 49° 8'12.05", area: 18,225 ha) and the Andrafiamena-Andavakoera Forest Corridor (hereafter Andrafiamena approximate geographic center: S12°58'53.07", E 49°18'5.39", area: 85,000 ha), a newly gazetted IUCN, category V landscape.

The region supports four diurnal primate species including two frugivorous species, *Eulemur coronatus* (average body mass: 1.18 kg) and *Eulemur sanfordi* (average body mass: 1.85 kg), one bamboo specialist, *Hapalemur occidentalis* (average body mass: 1.03 kg) and one folivore-frugivore, *Propithecus perrieri* (average body mass: 4.48 kg). The three protected areas support several forest types including dry deciduous forest characterized by *Hildegardia*, *Dalbergia* and *Commiphora*, semi-evergreen forest characterized by *Diospyros sp*., *Pandanus spp*., *Grewia spp*. and members of the family, Sarcolaenaceae, *Uapaca* forests above 600m and dominated by *Uapaca aff. ferruginea* as well as xeric scrub forest characterized by *Adenia*, *Aloe* and *Euphorbia*.

In collaboration with the Henry Doorly Zoo research teams also followed four family groups of the Perrier's sifaka (*Propithecus perrieri*), between May of 2008 and May of 2011, to collect data on dietary diversity and ranging patterns. All of the groups followed occurred at Andrafiamena at the site of Anjahankely (S 12°54'27.65" E 49°18'48.99"). Group size varied from one to seven adult individuals (standard error: ± 0.06). We recorded seven births and eight deaths during the four-year period.

Overview of Thesis Chapters

In this section I provide a brief summary of the objectives for each chapter in the thesis. A detailed overview of the theoretical background for each chapter is provided in the chapters themselves.

In chapter two I attempt to evaluate the role of covariates to detectability in line transect surveys in biasing estimates of primate population density. I review the sources of bias that have received the most attention in the literature and examine the influence of these variables on the distribution of perpendicular sighting distances (used here as a proxy for detectability) for all members of the diurnal primate community in northern Madagascar. Using generalized linear mixed models and model averaging, I assess the magnitude of effect and relative importance of all covariates in determining detectability for each species. Relying on the results from these analyses the detection function is modeled as a function of both distance and one or more additional covariates using the multiple covariate distance sampling engine in the Distance 6.0 software package, allowing density to be estimated for each lemur species. The density estimates are then compared with the results from an analysis of the same data, but the detection function is instead modeled as a function of distance alone (i.e. conventional method). The principal aim of this comparison is to determine if the accuracy and precision of density estimates are substantially improved by adjusting for detectability on line transects. The results have implications for improving the reliability of results in line transect surveys and in providing informed recommendations for the management of wild primate populations.

In chapter three of the thesis I estimate population density for three diurnal lemurs of the Diana region in eleven forest fragments of varying size, spatial geometry, disturbance history, and geology. Using generalized linear mixed models and model averaging techniques I evaluate the magnitude and direction of effect for natural and anthropogenic drivers of primate abundance following prominent theory in the primatological literature. In particular I evaluate the role of the spatial attributes of forest fragments, the influence of logging and other low intensity disturbances, as well as large scale fires, hunting and the abundances of potential competitors in determining primate population numbers. As a confirmatory analysis, I remove variables characterizing the spatial attributes of fragments and replace these with detailed information regarding characteristics of the habitat in each fragment via the use of botanical plots situated at all sites. Using behavioral data I also integrate data on the diet and availability of preferred foods for one of the members of this diurnal primate community (i.e. *P. perrieri*) in an effort to better assess the influence of food resources on the abundance of this species.

Chapter four combines presence absence data for four diurnal lemur species in 45 forest fragments with an analysis of the spatial attributes of all forest fragments. I once again use a model averaging procedure based on the use of generalized mixed models as a central paradigm for this analysis. I evaluate the role of geology, fragment size, shape and isolation as well as an index for disturbance in driving species distribution patterns. In particular, I assess whether classic species-area relationships and other aspects of island biogeography theory are relevant in outlining generalizable patterns of species richness across this sample of dry deciduous and semi-evergreen forest fragments. Finally I use trophic categories as a functional grouping to generate predictions regarding the occurrence of individual primate species within this sample of forest fragments.

I conclude the thesis with a chapter summarizing and synthesizing the key results from chapters 2-4 and offer suggestions for future studies of primate abundance and distributional patterns. I also frame the results in the context of recommendations for future wildlife management and primate conservation. Major questions include 1) which of the factors known to influence detectability in line transect surveys are a consistent source of bias in estimating lemur densities and how can this information be used to improve future surveys with primates, 2) how important are human factors in determining the abundance, occupancy and species richness patterns of primate communities occurring in the fragmented forests of northern Madagascar and can the results be used to help predict future impacts from human-nonhuman primate interactions on the survival prospects for these lemurs, 3) can presence absence studies serve as a useful surrogate for more detailed studies of primate abundance and 4) what possible directions for future research should be prioritized in the interest of filling the gaps from this study and contributing to the conservation of Madagascar's highly threatened northern primate fauna.

References

Anderson J, Cowlishaw G, Rowcliffe JM (2007) Effects of Forest Fragmentation on the Abundance of *Colobus angolensis palliatus* in Kenya's Coastal Forests. International Journal of Primatology 28:637–655

Anzures-Dadda A, Manson RH (2007) Patch- and landscape-scale effects on howler monkey distribution and abundance in rainforest fragments. Animal Conservation 10:69–76

Arroyo-Rodríguez V, Dias P (2010) Effects of habitat fragmentation and disturbance on howler monkeys: a review. American Journal of Primatology 72:1-16

Arroyo-Rodríguez V, Mandujano S (2006) Forest Fragmentation Modifies Habitat Quality for *Alouatta palliata*. International Journal of Primatology 27:1079-1096

Arroyo-Rodríguez V, Mandujano S (2009) Conceptualization and Measurement of Habitat Fragmentation from the Primates' Perspective. International Journal of Primatology 30:497–514

Arroyo-Rodríguez V, Mandujano S, Benítez-Malvido J, Cuende-Fanton C (2007) The Influence of Large Tree Density on Howler Monkey (*Alouatta palliata mexicana*) Presence in Very Small Rain Forest Fragments. Biotropica 39:760–766

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

Banks MA, Ellis ER, Antonio, Wright PC (2007) Global population size of a critically endangered lemur, Perrier's sifaka. Animal Conservation 10:254-262

Barlow J, Peres CA (2004) Ecological responses to el Niño-induced surface fires in central Brazilian Amazonia: management implications for flammable tropical forests. Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences 359:367-380

Bond WJ, Silander Jr. JA, Ranaivonasy J, Ratsirarson J (2008) The antiquity of Madagascar's grasslands and the rise of C 4 grassy biomes. Journal of Biogeography 35:1743–1758

Bourlière F (1985) Primate communities: Their structure and role in tropical ecosystems. International Journal of Primatology 6:1–26

Boyce MS (1992) Population viability analysis. Annual Review of Ecology and Systematics 23:481-506

Brown J, Kodric-Brown A (1977) Turnover rates in insular biogeography: Effect of immigration on extinction. Ecology 58:445-449

Burney DA (1996) Climate Change and Fire Ecology as Factors in the Quaternary Biogeography of Madagascar. In: Lourenço W (ed) Biogéographie de Madagascar. ORSTROM, Paris, pp 49-58

Burney DA (2003) Madagascar's prehistoric ecosystems. In: Goodman S, Benstead J (eds) The Natural History of Madagascar. Univ. Chicago Press, Chicago, pp 47-51

Burney DA, Burney L, Godfrey LR, Jungers WL, Goodman SM, Wright H, Jull A (2004) A chronology for late prehistoric Madagascar. Journal of Human Evolution 47:25-63

Burney DA, James H, Grady F, Rafamantanantsoa J-G, Ramilisonina, Wright H, Cowart J (2003a) Environmental change, extinction and human activity: evidence from caves in NW Madagascar. Journal of Biogeography 24:755-767

Burney DA, Robinson G, Burney L (2003b) Sporormiella and the late Holocene extinctions in Madagascar. Proceedings of the National Academy of Sciences of the United States of America 100:10800-10805

Burney DA (1999) Rates, patterns, and processes of landscape transformation and extinction in Madagascar. In: Extinctions in near time: causes, contexts, and consequences, pp 145-164

Chapman CA, Chapman LJ, Jacob AL, Rothman JM, Omeja P, Reyna-Hurtado R, Hartter J, Lawes MJ (2010a) Tropical tree community shifts: Implications for wildlife conservation. Biological Conservation 143:366–374

Chapman CA, Chapman LJ, Naughton-Treves L, Lawes MJ, McDowell L (2004) Predicting folivorous primate abundance: validation of a nutritional model. American Journal of Primatology 62:55-69

Chapman CA, Lawes MJ (2003) Primate survival in community-owned forest fragments: Are metapopulation models useful amidst intensive use. In: Marsh LK (ed) Primates in Fragments: Ecology and Conservation. Springer, New York, pp 63-77

Chapman CA, Struhsaker T, Skorupa J, Snaith T, Rothman J (2010b) Understanding long-term primate community dynamics: implications of forest change. Ecological Applications 20:179-191

Chapman CA, Balcomb SR, Gillespie TR, Skorupa JP, Struhsaker TT (2000) Long-Term Effects of Logging on African Primate Communities: a 28-Year Comparison From Kibale National Park, Uganda. Conservation Biology 14:207-217

Chapman CA, Chapman LJ (1999) Implications of small scale variation in ecological conditions for the diet and density of red colobus monkeys. Primates 40:215-231

Chapman CA, Chapman LJ, Bjorndal KA, Onderdonk DA (2002) Application of protein-to-fiber ratios to predict colobine abundance on different spatial scales. International Journal of Primatology 23:283-310

Chapman CA, Peres CA (2001) Primate conservation in the new millennium: The role of scientists. Evolutionary Anthropology 10:16–33

Chiarello AG, de Melo FR (2001) Primate population densities and sizes in Atlantic forest remnants of northern Espirito Santo, Brazil. International Journal of Primatology 22:379-396

Cochrane M (2003) Fire science for rainforests. Nature 421:913-919

Coley P, Barone J (1996) Herbivory and plant defenses in tropical forests. Annual Review of Ecology and Systematics 27:305-335

Cowlishaw G, Dunbar RIM (2000) Primate Conservation Biology. University of Chicago Press: 498 pp.

Cowlishaw G, Pettifor R, Isaac N (2009) High variability in patterns of population decline: the importance of local processes in species extinctions. Proc. R. Soc. Lond. B 276:63-69

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

Crowley BE (2010) A refined chronology of prehistoric Madagascar and the demise of the megafauna. Quaternary Science Reviews 29:2591-2603

Davies A (1994) Colobine populations. In: Davies A, Oates J (eds) Colobine Monkeys: Their Ecology, Behaviour and Evolution. Cambridge University Press, Cambridge, UK, pp 285-310

Dehgan A (2003) The Behavior of Extinction: Predicting the Incidence and Local Extinction of Lemurs in Fragmented Habitats of Southeastern Madagascar. In. University of Chicago, Chicago, IL, pp 248

Dewar R, Radimilahy C, Wright H, Jacobs Z, Kelly G, Berna F (2013) Stone tools and foraging in northern Madagascar challenge Holocene extinction models. Proceedings of the National Academy of Sciences of the United States of America 110:12583-12588

Dewar R, Richard A (2012) Madagascar: A History of Arrivals, What Happened, and Will Happen Next. Annual Review of Anthropology 41:495–517

Estrada A, Coates-Estrada R (1996) Tropical rain forest fragmentation and wild populations of primates at Los Tuxtlas, Mexico. International Journal of Primatology 17:759-783

Ewers R, Didham R (2006) Confounding factors in the detection of species responses to habitat fragmentation. Biological Reviews of the Cambridge Philosophical Society 81:117-142

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

Fashing PJ, Dierenfeld ES, Mowry CB (2007) Influence of Plant and Soil Chemistry on Food Selection, Ranging Patterns, and Biomass of *Colobus guereza* in Kakamega Forest, Kenya. International Journal of Primatology 28:673-703

Felton AM, Felton A, Lindenmayer DB, Foley WJ (2009) Nutritional goals of wild primates. Functional Ecology 23:70-78

Fleagle JG, Janson CH, Reed KE (1999) Primate communities. Cambridge University Press, Cambridge, UK

Freed BZ (2006) Polyspecific Associations of Crowned Lemurs and Sanford's Lemurs in Madagascar. In: Gould L, Sauther M (eds) Lemurs. Springer Science, New York, NY, pp 111-131

Freed BZ (1996) Co-occurrence among crowned lemurs (*Lemur coronatus*) and Sanford's lemurs (*Lemur fulvus sanfordi*) of Madagascar. In: Department of Anthropology. Washington University, pp 450

Ganzhorn JU, Goodman SM, Dehgan A (2003) Effects of Forest Fragmentation on Small Mammals and Lemurs. In: Goodman S, Benstead J (eds) The Natural History of Madagascar. University of Chicago Press, Chicago, pp 1228-1234

Ganzhorn JU (1992) Leaf chemistry and the biomass of folivorous primates in tropical forests. Oecologia 91:540-547

Ganzhorn JU (1993) Flexibility and constraints of Lepilemur ecology. In: Kappeler PM, Ganzhorn JU (eds) Lemur social systems and their ecological basis. Springer, Gôttingen, pp 153-166

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

Ganzhorn JU (1997) Test of Fox's assembly rule for functional groups in lemur communities in Madagascar. Journal of Zoology 241:533-542

Ganzhorn JU (1999a) Body mass, competition and the structure of communities. In: Fleagle J, Janson C, Reed K (eds) Primate Communities. Cambridge University Press, Cambridge, UK, pp 141-157

Ganzhorn JU (1999b) Body mass, competition and the structure of primate communities. In: Primate Communities, pp 141-157

Ganzhorn JU (2000a) Vertebrate species in fragmented littoral forests of Madagascar. In: Lourenço W, Goodman S (eds) Diversité et Endémisme à Madagascar. Mémoires de la Societé de Biogéographie, Paris, pp 155-164

Ganzhorn JU (2002) Distribution of a folivorous lemur in relation to seasonally varying food resources: integrating quantitative and qualitative aspects of food characteristics. Oecologia 131:427–435

Ganzhorn JU (2003) Effects of introduced Rattus rattus on endemic small mammals in dry deciduous forest fragments of western Madagascar. Animal Conservation 6:147–157

Ganzhorn JU, Goodman SM, Ramanamanjato JB, Ralison J, Rakotontravony D, Rakotosamimanana B (2000b) Effects of fragmentation and assessing minimum viable populations of lemurs in Madagascar. In: Rheinwald G (ed) Isolated Vertebrate Communities in the Tropics. 4th Int. Symp., Bonn, Germany, pp 265–272

Ganzhorn JU, Malcomber S, Andrianantoanina O, Goodman SM (1997) Habitat Characteristics and Lemur Species Richness in Madagascar. Biotropica 29:331-343

Ganzhorn JU, Wright PC, Ratsimbazafy J (1999) Primate communities: Madagascar. In: Fleagle J, Janson C, Reed K (eds) Primate Communities. Cambridge University Press, Cambridge, UK, pp 75-89

Gause G (1934a) Experimental analysis of Vito Volterra's mathematical theory of the struggle for existence. Science

Gause G (1934b) The struggle for existence. Williams and Wilkins, Baltimore

Gautier-Hion A, Michaloud G (1989) Are figs always keystone resources for tropical frugivorous vertebrates? A test in Gabon. Ecology 70:1826-1833

Gilbert KA (2003) Primates and fragmentation of the Amazon forest. In: Marsh LK (ed) Primates in Fragments: Ecology and conservation. Springer, New York, NY, pp 145-157

Gillespie TR, Chapman CA (2006) Prediction of parasite infection dynamics in primate metapopulations based on attributes of forest fragmentation. Conservation Biology 20:441-448

Godfrey LR, Irwin MT (2007) The evolution of extinction risk: past and present anthropogenic impacts on the primate communities of Madagascar. Folia Primatologica 78:405-419

Gogarten JF, Guzman M, Chapman CA, Jacob AL, Omeja PA, Rothman JM (2012) What is the predictive power of the colobine protein-to-fiber model and its conservation value? Tropical Conservation Science 5:381-393

Golden CD (2009) Bushmeat hunting and use in the Makira Forest, north-eastern Madagascar: a conservation and livelihoods issue. Oryx 43:386–392

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

Green G, Sussman R (1990) Deforestation history of the eastern rain forests of madagascar from satellite images. Science 248:212-215

Harper GJ, Steininger MK, Tucker CJ, Juhn D, Hawkins F (2007) Fifty years of deforestation and forest fragmentation in Madagascar. Environmental Conservation 34:325–333

Haugaasen T, Peres C (2009) Interspecific primate associations in Amazonian flooded and unflooded forests. Primates 50:239-251

Herrera JP, Wright PC, Lauterbur E, Ratovonjanahary L, Taylor LL (2011) The Effects of Habitat Disturbance on Lemurs at Ranomafana National Park, Madagascar. International Journal of Primatology 32:1091–1108

Heymann EW, Buchanan-Smith HM (2000) The behavioural ecology of mixed-species troops of callitrichine primates. Biological Reviews 75:169-190

Humbert H (1927) La destruction d'une flore insulaire par le feu: principaux aspects de la végétation à Madagascar, documents photographiques et notices. Memoires de l'Academic Malagache Fascicule V

Irwin M, Junge R, Raharison J-L, Samonds K (2010a) Variation in physiological health of diademed sifakas across intact and fragmented forest at Tsinjoarivo, Eastern Madagascar. American Journal of Primatology 72:1013-1025

Irwin MT, Wright PC, Birkinshaw C, Fisher BL, Gardner CJ, Glos J, Goodman SM, Loiselle P, Rabeson P, Raharison J-L (2010b) Patterns of species change in anthropogenically disturbed forests of Madagascar. Biological Conservation 143:2351–2362

Irwin MT (2006) Ecological impacts of forest fragmentation on diademed sifakas (*Propithecus diadema*) at Tsinjoarivo, eastern Madagascar: Implications for conservation in fragmented landscapes. In: Department of Anthropology. Stony Brook University, ProQuest, pp 433

Irwin MT (2007a) Feeding Ecology of *Propithecus diadema* in Forest Fragments and Continuous Forest. International Journal of Primatology 29:95–115

Irwin MT (2007b) Living in forest fragments reduces group cohesion in diademed sifakas (*Propithecus diadema*) in eastern Madagascar by reducing food patch size. American Journal of Primatology 69:434-447

Irwin MT (2008) Diademed Sifaka (*Propithecus diadema*) Ranging and Habitat Use in Continuous and Fragmented Forest: Higher Density but Lower Viability in Fragments? Biotropica 40:231–240

Janson CH, Chapman CA (1999) Resources and primate community structure. In: Primate communities. Cambridge University Press, Cambridge, UK, pp 237-267

Jernvall J, Wright PC (1998) Diversity components of impending primate extinctions. Proceedings of the National Academy of Sciences of the United States of America 95:11279-11283

Jungers W, Godfrey L, Simons E, Chatrath P (1995) Subfossil *Indri indri* from the Ankarana Massif of northern Madagascar. American Journal of Physical Anthropology 97:357-366

Koenig A, Borries C, Chalise MK, Winkler P (1997) Ecology, nutrition, and timing of reproductive events in an Asian primate, the Hanuman langur (*Presbytis entellus*). Journal of Zoology 243:215-235

Kull C (2000) Deforestation, erosion, and fire: degradation myths in the environmental history of Madagascar. Environment and History Vol. 6:423-450

Laurance W, Delamônica P, Laurance S, Vasconcelos H, Lovejoy T (2000) Rainforest fragmentation kills big trees. Nature Vol. 404:836

Laurance WF, Lovejoy TE, Vasconcelos HL, Bruna EM, Didham RK, Stouffer PC, Gascon C, Bierregaard RO, Laurance SG, Sampaio E (2002) Ecosystem Decay of Amazonian Forest Fragments: a 22-Year Investigation. Conservation Biology 16:605-618

Laurance W, Ferreira L, Rankin-de J (1998) Rain forest fragmentation and the dynamics of Amazonian tree communities. Ecology 79:2032-2040

Laurance W, Nascimento H, Laurance S, Andrade A, Fearnside P, Ribeiro J, Capretz R (2006) Rain forest fragmentation and the proliferation of successional trees. Ecology 87:469-482

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

Lawes M, Mealin P, Piper S (2000) Patch Occupancy and Potential Metapopulation Dynamics of Three Forest Mammals in Fragmented Afromontane Forest in South Africa. Conservation Biology 14:1088-1098

Lee PC (1987) Nutrition, fertility and maternal investment in primates. Journal of Zoology 213:409-422

Lehman SM (2006) Effects of Transect Selection and Seasonality on Lemur Density Estimates in Southeastern Madagascar. International Journal of Primatology 27:1041-1057

Lehman SM (2007) Spatial variations in *Eulemur fulvus rufus* and *Lepilemur mustelinus* densities in Madagascar. Folia Primatologica 78:46-55

Lehman SM, Rajaonson A, Day S (2006a) 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 (2006b) Lemur responses to edge effects in the Vohibola III classified forest, Madagascar. American Journal of Primatology 68:293-299

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

Lehman SM, Ratsimbazafy J, Rajaonson A, Day S (2005) Decline of *Propithecus diadema edwardsi* and *Varecia variegata variegata* (Primates: Lemuridae) in south-east Madagascar. Oryx 40:108-111

Lowry PP, Schatz GE, Phillipson PP (1997) The classification of natural and anthropogenic vegetation in Madagascar. In: Goodman S, Patterson BD (eds) Natural Change and Human Impact in Madagascar. Smithsonian Institution Press, Washington, D.C., pp 93-123

Marques TA, Thomas L, Fancy SG, Buckland ST (2007) Improving estimates of bird density using multiple-covariate distance sampling. The Auk 124:1229-1243

Marsh LK (2003) Primates in Fragments: Ecology in Conservation. Kluwer Academic/Plenum Publishers New York

Marsh LK, Chapman CA (2013) Primates in Fragments: Complexity and Resistance. Springer, New York

Marshall A, Boyko C, Feilen K, Boyko R, Leighton M (2009) Defining fallback foods and assessing their importance in primate ecology and evolution. American Journal of Physical Anthropology 140:603-614

Marshall AJ, Wrangham RW (2007) Evolutionary Consequences of Fallback Foods. International Journal of Primatology 28:1219-1235

Marshall AJ, Lovett JC, White PC (2008) Selection of line-transect methods for estimating the density of group-living animals: lessons from the primates. American Journal of Primatology 70:452-462

Medley K (1993) Primate Conservation along the Tana River, Kenya: An Examination of the Forest Habitat. Conservation Biology 7:109-121

Milton K (1979) Factors influencing leaf choice by howler monkeys: a test of some hypotheses of food selection by generalist herbivores. American Naturalist 114:362-378

Milton K (1998) Physiological ecology of howlers (*Alouatta*): energetic and digestive considerations and comparison with the Colobinae. International Journal of Primatology 19:513-548

Muldoon K (2010) Paleoenvironment of Ankilitelo Cave (late Holocene, southwestern Madagascar): implications for the extinction of giant lemurs. Journal of Human Evolution 58:338-352

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

Myers N, Mittermeier R, Mittermeier C, da Fonseca G, Kent J (2000) Biodiversity hotspots for conservation priorities. Nature 403:853-858

Oates J (1978) Water-plant and soil consumption by guereza monkeys (*Colobus guereza*): a relationship with minerals and toxins in the diet? Biotropica 10:241-253

Oates J, Whitesides G, Davies A, Waterman P (1990a) Determinants of variation in tropical forest primate biomass: new evidence from West Africa. Ecology 71:328-343

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

Pareliussen I, Olsson EGA, Armbruster WS (2006) Factors Limiting the Survival of Native Tree Seedlings Used in Conservation Efforts at the Edges of Forest Fragments in Upland Madagascar. Restoration Ecology 14:196-203

Peres CA (1997) Effects of habitat quality and hunting pressure on arboreal folivore densities in neotropical forests: a case study of howler monkeys (*Alouatta* spp.). Folia Primatologica 68:199-222

Peres CA (1999) Effects of subsistence hunting and forest types on the structure of Amazonian primate communities. In: Fleagle J, Janson C, Reed K (eds) Primate Communities. Cambridge University Press, Cambridge, UK, pp 268-284

Peres CA, Barlow J, Haugaasen T (2003) Vertebrate responses to surface wildfires in a central Amazonian forest. Oryx 37:97-109

Peres CA, Dolman PM (2000) Density compensation in neotropical primate communities: evidence from 56 hunted and nonhunted Amazonian forests of varying productivity. Oecologia 122:175-189

Perez V, Godfrey L, Nowak-Kemp M, Burney D, Ratsimbazafy J, Vasey N (2005) Evidence of early butchery of giant lemurs in Madagascar. Journal of Human Evolution 49:722-742

Perrier de la Bâthie H (1921) La Végétation Malagache. In: Annals du Musée Colonial de Marseille, pp 1-266

Plumptre A, Cox D (2006) Counting primates for conservation: primate surveys in Uganda. Primates 47:65-73

Porter L (2001) Benefits of polyspecific associations for the Goeldi's monkey (Callimico goeldii). American Journal of Primatology 54:143-158

Powzyk J, Mowry C (2003) Dietary and Feeding Differences Between Sympatric *Propithecus diadema diadema* and *Indri indri*. International Journal of Primatology 24:1143-1162

Purvis A, Cardillo M, Grenyer R, Collen B (2005) Correlates of extinction risk: phylogeny, biology, threat and scale. In: Purvis A, Gittleman JL, T. B (eds) Phylogeny and Conservation pp 295-316

Purvis A, Gittleman J, Cowlishaw G, Mace G (2000) Predicting extinction risk in declining species. Proc. R. Soc. Lond. B 267:1947-1952

Quéméré E, Amelot X, Pierson J, Crouau-Roy B, Chikhi L (2012) Genetic data suggest a natural prehuman origin of open habitats in northern Madagascar and question the deforestation narrative in this region. Proceedings of the National Academy of Sciences of the United States of America 109:13028-13033

Quéméré E, Champeau J, Besolo A, Rasolondraibe E, Rabarivola C, Crouau-Roy B, Chikhi L (2010a) Spatial variation in density and total size estimates in fragmented primate populations: the golden-crowned sifaka (*Propithecus tattersalli*). American Journal of Primatology 72:72-80

Quéméré E, Crouau-Roy B, Rabarivola C, Louis E, Chikhi L (2010b) Landscape genetics of an endangered lemur (*Propithecus tattersalli*) within its entire fragmented range. Molecular Ecology 19:1606-1621

Rakotoarisoa JE, Raheriarisena M, Goodman S (2013) Late Quaternary climatic vegetational shifts in an ecological transition zone of northern Madagascar: insights from genetic analyses of two endemic rodent species. Journal of Evolutionary Biology 26:1019-1034

Rode KD (2003) Mineral resource availability and consumption by colobus in Kibale National Park, Uganda. International Journal of Primatology 24:541-573

Rothman J, Van Soest P, Pell A (2006) Decaying wood is a sodium source for mountain gorillas. Biology Letters 2:321-324

Rovero F, Struhsaker T (2007) Vegetative predictors of primate abundance: utility and limitations of a fine-scale analysis. American Journal of Primatology 69:1242-1256

Rylands A, Keuroghlian A (1988) Primate populations in continuous forest and forest fragments in central Amazonia. Acta Amazonica 18:291-307

Salmona J, Rasolondraibe E, Jan F, Besolo A (2013) Conservation Status and Abundance of the Crowned Sifaka (*Propithecus coronatus*). Primate Conservation Published electronically prior to print

Schad J, Sommer S, Ganzhorn JU (2004) MHC Variability of a Small Lemur in the Littoral Forest Fragments of Southeastern Madagascar. Conservation Genetics 5:299–309

Schwarzkopf L, Rylands AB (1989) Primate species richness in relation to habitat structure in Amazonian rainforest fragments. Biological Conservation 48:1-12

Schwitzer C, Mittermeier RA, Davies N, Johnson S, Ratsimbazafy J, Razafindramanana J, Louis Jr. EE, Rajaobelina S (2013) Lemurs of Madagascar: A Strategy for Their

Conservation 2013–2016. SSC Primate Specialist Group, Bristol Conservation and Science Foundation, and Conservation International, Bristol, UK

Silanikove N, Perevolotsky A, Provenza FD (2001) Use of tannin-binding chemicals to assay for tannins and their negative postingestive effects in ruminants. Animal Feed Science and Technology 91:69-81

Simberloff D (1988) The contribution of population and community biology to conservation science. Annual Review of Ecology and Systematics 19:473-511

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

Smith AP, Horning N, Moore D (1997) Regional Biodiversity Planning and Lemur Conservation with GIS in Western Madagascar. Conservation Biology 11:498–512

Soulé ME (1987) Viable populations for conservation. Cambridge University Press, Cambridge, UK.

Soule ME, Wilcox BA (1980) Conservation biology. An evolutionary-ecological perspective. Sinauer Associates, Inc., The University of California

Stevenson P (2001) The relationship between fruit production and primate abundance in Neotropical communities. Biological Journal of the Linnean Society 72:161-178

Strier K, Boubli J, Possamai C, Mendes S (2006) Population demography of Northern muriquis (*Brachyteles hypoxanthus*) at the Estação Biológica de Caratinga/Reserva particular do Patrimônio Natural-Felìciano Miguel Abdala, Minas Gerais, Brazil. American Journal of Physical Anthropology 130:227-237

Strier K, Ives A (2012) Unexpected demography in the recovery of an endangered primate population. PLoS ONE 7: e44407:1-11

Struhsaker T (1999) Primate communities in Africa: The consequence of long-term evolution or the artifact of recent hunting? In: Fleagle J, Janson, C, Reed, KE (ed) Primate Communities. Cambridge University Press, Cambridge, UK, pp 289-294

Struhsaker TT (1997) Ecology of an African Rain Forest: Logging in Kibale and the Conflict between Conservation and Exploitation. University Presses of Florida, Gainesville, Florida

Tan CL (1999) Group composition, home range size, and diet of three sympatric bamboo lemur species (genus *Hapalemur*) in Ranomafana National Park, Madagascar. International Journal of Primatology 20:547-566

Terborgh J (1984) Five New World primates: a study in comparative ecology. Princeton University Press, Princeton, NJ

Terborgh J, Van Schaik CP (1987) Convergence vs. nonconvergence in primate communities. In: Gee P, Giller P (eds) Organisation of Communities. Blackwell Scientific, Oxford, UK

Tilman D (1982) Resource Competition and Community Structure. Princeton University Press, Princeton, NJ

Tischendorf L, Bender DJ, Fahrig L (2003) Evaluation of patch isolation metrics in mosaic landscapes for specialist vs. generalist dispersers. Landscape Ecology 18:41-50

Tutin C, Ham R, White L, Harrison M (1997) The primate community of the Lopé Reserve, Gabon: diets, responses to fruit scarcity, and effects on biomass. American Journal of Primatology 42:1-24

Tutin C, White L (1999) The recent evolutionary past of primate communities: Likely environmental impacts during the past three millennia. In: Fleagle J, Janson C, Reed K (eds) Primate Communities. Cambridge University Press, Cambridge, UK, pp 220-236

Umapathy G, Kumar A (2000a) The demography of the lion-tailed macaque (*Macaca silenus*) in rain forest fragments in the Anamalai Hills, South India. Primates 41:119-126

Umapathy G, Kumar A (2000b) The occurrence of arboreal mammals in the rain forest fragments in the Anamalai Hills, south India. Biological Conservation 92:311-319

van Schaik C, Madden R, Ganzhorn J (2005) Seasonality and primate communities. In: Brockman D, van Schaik C (eds) Seasonality in Primates: Studies of Living and Extinct Human and Non-Human Primates. Cambridge University Press, Cambridge, UK, pp 445-463

Virah-Sawmy M (2009) Ecosystem management in Madagascar during global change. Conservation Letters 2:153-170

Virah-Sawmy M, J. Willis K, Gillson L (2010) Evidence for drought and forest declines during the recent megafaunal extinctions in Madagascar. Journal of Biogeography 37:506–519

Wallis I, Edwards M, Windley H, Krockenberger A, Felton A, Quenzer M, Ganzhorn J, Foley W (2012) Food for folivores: nutritional explanations linking diets to population density. Oecologia 169:281-291

Waterman PG, Ross JAM, Bennett EL, Davies AG (1988) A comparison of the floristics and leaf chemistry of the tree flora in two Malaysian rain forests and the influence of leaf chemistry on populations of colobine monkeys in the Old World. Biological Journal of the Linnean Society 34:1-32

White FJ, Overdorff DJ, Balko EA, Wright PC (1995) Distribution of Ruffed Lemurs (*Varecia variegata*) in Ranomafana National Park, Madagascar. Folia Primatologica 64:124-131

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

Wright P, Volonlontiana R, Razafindratsita V, Pochron S, Jernvall J (2005) The Key to Madagascar Frugivores. In: Dew JL, Boubli JP (eds) Tropical Fruits and Frugivores: The Search for Strong Interactors. Springer, Dordrecht, Netherlands, pp 121-138

Young A, Clarke G (2000) Genetics, demography and viability of fragmented populations. Cambridge University Press, Cambridge, UK

CHAPTER TWO:

Covariates to Modeling Detection in a Community of Primates from Northern Madagascar

Abstract

Obtaining reliable estimates of population size using line transect and complementary recce sampling methods for wild primate populations requires that analysts account for biases that originate from a variety of sources. These include those related to the design of the survey as well as the imperfect detection of primates on survey routes owing to seasonal, habitat-specific, and behavioral differences. Previous evidence from other primate communities suggests that sampling and temporal effects such as observer experience and seasonal differences in forest visibility respectively are frequently found to influence detectability in line transect surveys. I tested several hypotheses addressing the role of sampling, temporal, demographic, habitat-specific and anthropogenic factors in determining the detectability of four diurnal primates from the primate community of extreme northern Madagascar. I also assessed the impact that adopting corrections for observed patterns of bias has on the precision of density estimates by including information about covariates to detectability in subsequent analyses conducted using the Distance 6 © software package. Contrary to expectations, accounting for sampling effects (i.e. observer experience) in modeling the detection process for three diurnal lemur species only explained limited variation in this sample and only in conjunction with other factors did it marginally improve the precision of density estimates for one species, *E. coronatus*. In general, and despite limited improvements in the precision of all density estimates, the determinants of detectability varied widely across all species, lending support to recent calls for researchers to integrate the concept of imperfect detection into estimating primate densities by evaluating the role of multiple covariates in driving the detection process. The lack of improvement in the precision of density estimates is attributed to measures initially taken to address possible sampling biases through the design of the surveys.

Introduction

Reliable estimates of population size play an indispensable role in driving our understanding of many of the most fundamental ecological patterns but they are also central to the decision making process that determines how wildlife populations will be managed for conservation (Mitani et al. 2000; Lehman 2006; Ogutu et al. 2006; Plumptre and Cox 2006; Marques et al. 2007). Indeed changes in population size and trends in the population levels of wildlife often form the foundation for biodiversity policy in many countries (Petrovan et al. 2011). Despite widespread recognition concerning the importance of these measures in the assessment of species conservation status, only more recently have specialists attempted to devise solutions for the sources of bias known to complicate biological inference in such studies (Alldredge et al. 2006; Marques et al. 2012b; Renato et al. 2012). A broader range of statistical techniques to better accommodate ecological datasets (e.g. (Bolker et al. 2009; Zuur et al. 2009; Burnham et al. 2010) has no doubt played an important role in stimulating calls for greater transparency over the levels of precision and accuracy appearing in published studies. While greater scrutiny over the reliability of such results addresses empirical shortcomings and should improve the application of ecological theory, wildlife managers are also faced with issues of cost and practicality in determining which approaches will be of the greatest value.

There are numerous methods available for estimating wildlife abundance (for overviews see Williams et al. 2002, Milner-Gulland and Rowcliffe 2008, Setchell and Curtis 2011). However, the methods typically accessible to wildlife managers and from which absolute measures of population size are derived consist primarily of survey methods (e.g. line and point transects, mark-recapture methods). Despite synonymy in the biological literature, none of these methods are accurately described as censuses since a complete count of all individuals from an entire population is rarely possible. Alternatively a complete count can be performed over predefined sampling units. Surveys instead involve sampling a subset of the target population over a known or estimated area of coverage and extrapolating to the larger population from which the sample is considered to be representative (Williams et al. 2002). Line and point transect surveys continue to grow in popularity, likely a result of their relevance in a variety of contexts and to numerous species (e.g. terrestrial mammals: Ogutu et al. 2006, marine mammals: Williams and Thomas 2009, reptiles: Anderson et al. 2001, amphibians: Schmidt 2003, plants: Buckland et al. 2007, indirect sign: Stephens et al. 2006) and the growing availability of powerful software packages for analysis. An additional method is “mark-recapture” that involves capturing a sample of the target population, and marking those individuals so that they can be easily identified during recaptures. The ratio of marked to unmarked individuals during subsequent captures can be used to estimate population size (Williams et al. 2002). Options for the analysis of mark-recapture data are extensive, and while many of the same software packages can be used as with the other survey methods, the associated costs and practicality of these methods for use with certain taxa precludes more widespread use. On the whole each of these methods are related and they are commonly referred to using the umbrella term, “distance sampling”. Target species can be sampled through direct encounters or the detection of indirect sign, such as dung or nests. To address the influence of detectability on the abundance estimates of primates I chose to focus on the most widely used method for this Order of mammals, line transect sampling.

Primates are an appropriate group for examining patterns of variability in abundance estimates, as they are large, arboreal, form groups, and are often noisy and diurnal. They are among the most threatened groups of animals and have recently been labeled a global conservation priority (Schipper et al. 2008). Furthermore, patterns of primate density across the landscape provide insights into the functioning of ecosystems and the importance of particular ecological phenomena in structuring wildlife communities (Bourlière 1985; Fleagle et al. 1999; Chapman et al. 2010). Among those species comprising the diurnal primate community that provides the subject for this chapter, the Perrier’s sifaka (*Propithecus perrieri*) is a critically endangered lemur, and has previously been estimated to have a population of less than 2000 individuals (Banks et al. 2007). Other lemurs of this community include the IUCN vulnerable status northern bamboo lemur (*Hapalemur occidentalis*), and the endangered Sanford’s

(*Eulemur sanfordi*) and crowned (*Eulemur corontaus*) lemurs (Schwitzer et al. 2013). Furthermore, the region supporting this community of primates is home to a variety of threatened and endemic wildlife from other groups (avifauna: Raherilalao 2007, reptiles and amphibians: Razafimaharatra 2007, flora: Letsara 2007), a designation prompting the creation of a new IUCN category V protected area (i.e. Andrafiamena-Andavakoera Forest Corridor) in October of 2008. It is important as habitats are reduced to understand the determinants of population density, especially with highly threatened groups such as the primates where the loss of species could lead to a cascade of downward effects on the entire ecosystem (Terborgh and Estes 2010; Chapman et al. 2012; Laurance et al. 2012). Accuracy in estimating population densities could mean the extinction or survival of Perrier's sifakas, a species whose removal as a large, primary consumer might dramatically influence the region's ecosystem structure (Petrovan et al. 2011; Wright et al. 2011; Chapman et al. 2012).

Studies of primate density are abundant in the literature and growing interest in survey methods for wildlife has recently seen a surge in the number of workers who have provided guidelines for the design and analysis of surveys with primates (Hassel-Finnegan et al. 2008; Marshall et al. 2008; Buckland et al. 2010a). Much of the focus has shifted towards identifying known sources of variability in estimating primate abundance (e.g. Marshall et al. 2008) and adopting a conservative stance with regards to the potential for biological inference (Mitani et al. 2000; Rovero et al. 2006). Additionally the number of novel methods proposed for sampling primate populations has increased (e.g. Hanya et al. 2003, Savage et al. 2010) yet, despite often elegant alternatives, line-transect methodology remains the most widely used method and is generally considered to be the most practical approach available for primates (Plumptre 2000b; Rovero et al. 2006). Given the widespread use of line transect methodology with primates and persistent concerns over common sources of bias, it is surprising that greater attention has not centered on finding *post hoc* remedies for controlling bias during the analysis stage.

Line transect methodology has been rigorously outlined elsewhere (NRC 1981; Peres 1999; Buckland et al. 2001) yet differences in the way that key parameters have been measured in comparative studies with primates has stimulated considerable debate (Plumptre and Cox 2006; Hassel-Finnegan et al. 2008; Buckland et al. 2010b). Indeed competing approaches have emerged to accommodate variable patterns in the spatial distribution of primate groups, low visibilities and other violations of key assumptions (Marshall et al. 2008; Buckland et al. 2010a). While this chapter is not an attempt to find consensus over which of the available methods provides the most reliable framework for wildlife surveys (a topic which has been addressed at length elsewhere, e.g. Marshall et al. 2008; Fashing and Cords 2000; Buckland et al. 2010b), emphasis here is instead placed on addressing common sources of variability in primate abundance estimates and how to address them as part of the final analysis. The implications of this exercise should help to inform future studies, particularly where absolute estimates of abundance are the aim, yet an inability to control sources of heterogeneity in the data clouds reliable biological inference.

While much of the heterogeneity in abundance estimates from line transects can be controlled for through the design of the sampling regime, wildlife programs are often interested in monitoring species over long periods during which the seasons change, as do personnel and their motivations for monitoring wildlife. Additionally habitat disturbances or losses may occur and lapses in funding may create gaps in the data. These and other developments may introduce bias into the sampling regime and without quantitative information on the factors that covary with the detectability of the target species, these effects can't be distinguished from other variables that honestly reflect the biological process of interest. To understand more about how such factors influence estimates of density in wildlife populations, we have to understand what are the components of a density estimate.

As stated in Buckland et al. (2004).

> " … there are three categories of parameter estimated in conventional distance sampling: those relating to the encounter rate *n/L*, those relating to the detection function *g*(*y*), and those relating to mean cluster size *E*(*s*)."

Although the influence of bias on any of these parameters could translate into large differences in abundance estimates, the detection function (i.e. the distribution of sighting distances) is unique in characterizing the probability of seeing an object given its distance from the survey route. In principle, objects are less likely to be detected at increasing distances from the survey route (Buckland et al. 2001). Alternatively the other parameters are concerned directly with abundance and implicitly it is only the perpendicular distance of the object from the transect that determines its probability of detection (Marques and Buckland 2004). Meeting this assumption of constant detectability however can be easily violated since detecting an object might also vary as a function of many factors, including observer motivation, weather conditions, habitat differences, etc. (Marques et al. 2007). To relax this assumption and address these sources of bias, detectability might instead be modeled as a function of these covariates as well as its distance from the survey route. Accordingly, in the preceding analyses I will use a novel dataset to model the influence of covariates on detection patterns in a community of diurnal Malagasy primates, treating perpendicular sighting distances as the response variable. After assessing the role of covariates in driving the detection process, densities will be calculated for all primates using both conventional methods as well as those that, through knowledge of covarying factors, adjust for imperfect detection.

While historically researchers have acknowledged potential sources of variability aside from the distance at which an object (e.g. an individual or group of the target species) is detected (Defler and Pintor 1985; Johns 1985a; Brockelman and Ali 1987), only more recently has there been a concerted attempt by specialists to address the impact that these factors have on population estimates. To control for the effect of these factors, detectability can be modeled as a function of not only distance, but also of any factors found to covary with sighting distances. This is accomplished by allowing covariates to affect either the scale or shape of the detection function (Marques et al. 2007). In the case of a detection function modeled by perpendicular distance alone (i.e. conventional detection function or CDF), a key function (e.g. half-normal, hazard-rate and uniform functions are widely used; see Buckland et al. 2001 for an overview) that captures the overall shape of the distribution of perpendicular distances is fitted. Where changes to the scale of the function provide an improved fit, adjustments such as those described by cosine and polynomial terms can be added. The result is a multiple covariate detection function (MCDF). While a parameter must be added for each level of a factor covariate, non-factor covariates do not have the same limitation and optimize parsimony in reducing bias in the density estimate. As with the scale and shape parameters that describe the CDF, those used in modeling a MCDF are specified using maximum likelihood methods (Marques et al. 2007).

Fortunately modeling detectability as a function of multiple covariates is now automated as part of the software package, Distance 6.0 © referred to in the literature as multiple covariate distance sampling (MCDS). Here the analyst includes covariate values for each repetition (or other relevant unit of measurement) of the survey. The use of MCDS attempts to either reduce bias in cases where the true detection function differs by stratum (e.g. habitat type, year, season, observer A vs observer B, etc.) or to increase precision. One option for reducing bias would be to assign a detection function for each relevant strata in which the survey was conducted, yet the number of observations per strata may be insufficient to achieve desired precision. Although a MCDF represents a less parsimonious alternative, it may greatly improve precision by allowing all of the observations to be pooled. This trade-off is considered to be a model selection problem, and can be resolved using a maximum likelihood framework (Marques and Buckland 2004; Marques et al. 2007). In cases where several competing models can be fit to the data an information-theoretic approach based on model selection criteria such as Akaike's Information Criterion (AIC) can be implemented. To evaluate the advantages of MCDS methods the detection function should be specified both with and without using relevant covariates, the former using the MCDS engine and the latter with the CDS engine, both included as part of the Distance 6.0 software package (Thomas et al. 2010).

A number of sources of variability are suspected to commonly influence primate population density estimates. In previous studies of covariates to primate detection, a number of workers have highlighted the potential bias arising from differences in observer ability (Whitesides et al. 1988; Rovero et al. 2006; Marshall et al. 2008). Indeed even line transects conducted from aircraft, from which large game animals are more easily detected, have been shown to be susceptible to similar effects when observer motivation, fatigue and experience are taken into account (Ransom 2012). Efforts to control variation in primate detection arising from observer differences first requires that observers undergo training, evaluate inter-observer reliability during the course of the study, conduct surveys simultaneously with multiple observers or alternatively, limit the total number of observers that participate in the study (Rovero et al. 2006). Owing to management considerations there are circumstances in which these corrections are impractical, often forcing analysts to acknowledge the potential for these differences to introduce bias into the analysis thereby restricting the depth of inference that can be drawn from the study. Both Mitani et al. (2000) and Rovero et al. (2006) found that the estimated distances of primate group sightings in their surveys of two African forests where a community of five diurnal primates was supported differed significantly among observers. Now one obvious fix to these discrepancies with multi-observer data is to measure distances to the nearest tenth of a meter, a provision easily accommodated through the use of a laser rangefinder or meter tape. Nonetheless observer differences might still persist if errors are associated with the measurements of certain observers or if observers differ in their ability to simply detect primates along the transect. **Based on previous accounts in the literature highlighting strong observer differences in estimating sighting distances for primates, I predict that the distribution of sighting distances for all primates encountered in the Diana region will differ among observers and observer identity will be an important predictor of detectability.**

An additional observer effect might be exerted on the distribution of sighting distances if the number of observers participating varies from survey to survey. Although walking transects with multiple observers may increase the chance of detecting primates (Plumptre and Cox 2006), the guideline to use stealth in searching for primates (Ross and Reeve 2003) might be compromised as the number of observers increases (Marshall et al. 2008). Both of these scenarios could translate into differences in perpendicular sighting distances. Borries et al. (2002) nonetheless found no differences in the number of primate sightings recorded by either a single or pairs of observers on line-transects in the dry evergreen forests of the Phu-Khieo Wildlife Sanctuary in Thailand, where seven diurnal primates occur. Furthermore, it seems that where multiple observers are trained to move as a cohesive group and coordinate their activities (Buckland et al. 2010a) as adopted here, few differences in detectability would be expected. **Accordingly I predict that there will be no differences in the distribution of sighting distances between single and multi-observer surveys.**

Other examples of variability arising from sampling effects in line transect surveys includes the use of pre-existing trails as opposed to transects systematically prepared using a compass bearing (Johnson and Overdorff 1999; Lehman 2006). During the current study the majority of survey routes (i.e. 63%) were prepared following a strict compass bearing and are considered as transects. Pilot studies, also included in the analyses presented here, did incorporate the use of pre-existing research trails, although these were originally cut for the purpose of surveying primates in the area (e.g. Hawkins et al. 1990) and were found to have been situated in a manner consistent with the random stratified approach we implemented elsewhere. Nevertheless, these routes were not prepared from compass bearings and will hereafter be referred to as recce trails (Walsh and White 1999; Plumptre 2000a).

As a more extreme example of the potential effects of using non-randomized survey routes Hilário et al. (2012) found differences in estimates of strip width and population density for two diurnal primates when using roads as opposed to recce trails in southeastern Brazil. Although roads are expected to expose animals to a greater breadth of effects and at higher intensities than on forest trails (Trombulak and Frissell 2000) a similar argument might be made for potential differences between animal presence along recce trails and straight line transects. While there are examples in the primate literature where differences in the selection of survey routes did not influence density estimates for some primates (Lehman 2006) other workers have urged for their careful consideration (Buckland et al. 2010a). The non-random placement of transects is discouraged on the grounds that transects will have a greater chance of sampling either unusually high or low abundance areas and thereby introduce bias into the sample and distort any forthcoming biological inference (Buckland et al. 2001). Furthermore, in the case of pre-existing trails, biases may also arise owing to primate avoidance behaviors driven by the conspicuous presence of human activities along footpaths including the removal of preferred primate food resources (Arrigo-Nelson and Wright 2004; Lehman 2006). Marques et al. (2012) suggest an elegant correction for cases where such discrepancies arise, however in the present study the use of reconnaissance work, satellite imagery and other spatial layers of landscape features (i.e. elevation, vegetation, slope) enabled us to adopt a random stratified sampling approach to transect and recce placement that was aimed at addressing these concerns. Given the provisions made for reducing bias that are associated with the sampling design used here and n**oting especially previous studies with lemurs where trails used by local populations and transects prepared from straight line compass bearings yielded similar density estimates (i.e. Lehman 2006), I predict that the distribution of sighting distances on recce trails will not differ from that on straight line transects.**

Temporal heterogeneity can also lead to considerable bias in line transect surveys with primates. The time of day in which the survey is conducted is considered an important aspect of sampling design and surveying when the target species is known to be most active is generally recommended (NRC 1981; Ross and Reeve 2003). This caveat becomes particularly relevant when sampling primates using auditory cues such as the morning songs of gibbons (Hylobatidae) or *Indri indri* (Indriidae; Brockelman and Ali 1987). None of the species found in the Diana region are known to use temporally restricted loud songs as part of their behavioral repertoire and our sampling protocols did not rely on detecting primates in this manner. Nevertheless, bimodality of the diel activity pattern has been described in a number of primate species, including members of the same primate genera that were sampled in this study (*Propithecus*: Erkert and Kappeler 2004 and *Eulemur*: Kappeler and Erkert 2003). Certainly such an activity pattern has the potential to influence the detectability of primates throughout the day with sightings predicted to decrease along with the midday heat. Nonetheless, standard guidelines for primate surveys tend to specify that the morning and late afternoon hours are the best times for sampling (e.g. Ross and Reeve 2003) and we have followed those recommendations here. **Given the sampling regime adopted here is aimed at minimizing bias originating from variation in daily activity patterns associated with the bimodality in activity pattern previously documented for *Propithecus* and *Eulemur* I predict that there will be no difference in the distribution of sighting distances recording during mornings and afternoons.**

Other examples of introducing systematic bias through temporal heterogeneity in primate detectability involves cases where seasonal differences drive variability in the conspicuousness of primates and visibility along paths in dense forest. In such cases one must address whether or not samples from multiple seasons are independent and can be pooled for analysis. Firstly, the shedding of leaves during the dry season by a variety of tree species in tropical deciduous forest might be expected to improve the visibility of lemurs along survey routes. Nonetheless, in Madagascar dry periods confront many lemurs with resource scarcity (Overdorff 1996; Scholz and Kappeler 2004; Irwin 2008), thereby forcing species to conserve energy by becoming less active (Wright 1999; Wright et al. 2005) and as a result, less visible (Lehman 2006). Elsewhere increasing daily activity levels instead requires that primates compensate for the scarcity of preferred resources by engaging in lengthier feeding bouts on lower quality fallback foods (Hemingway and Bynum 2005) and as a result increasing detectability. Similarly, the response might include traveling further to gain access to isolated high quality resources, (Hemingway and Bynum 2005), making primates more conspicuous on transect surveys. However, in Madagascar, frugivorous lemurs spend the driest months conserving energy by resting (Meyers and Wright 1993; Wright et al. 2005; Wright 2007) and not investing greater energy towards feeding on various fallback foods such as the figs that sustain primates in other areas (Meyers and Wright 1993; Tutin et al. 1997; Vogel et al. 2009). The energy conservation or energy frugality hypothesis (Wright 1999) has been used to explain reproductive strategies in Malagasy lemurs (Meyers and Wright 1993) and has been shown to exert a strong evolutionary force on their ecology (Dewar and Richard 2012). In support of this, Lehman (2006) has shown how seasonal patterns can play a strong role in the detectability of several lemur species along line transects and bias density estimates in Madagascar. Using a dataset from several humid rainforest sites in southeastern Madagascar the author highlights modalities in detection that tracked periods of heightened fruit availability. **In light of previous support for the energy conservation hypothesis elsewhere in Madagascar I predicted that lemurs will be less detectable and the distribution of perpendicular distances will be negatively associated with dry season samples and therefore the period of lowest food availability.**

Johns (1985) provided evidence for a negative relationship between habitat disturbance and primate detectability in a community of Malaysian primates and highlighted cryptic behavior and reduced calling rates in some species. Other workers have suggested structural mechanisms for changes in visibility that may track disturbances at various successional stages of the regenerating vegetation (Mitani et al. 2000). Logging pressure for example, opens gaps in forest canopies and initially increases visibility before emerging undergrowth fills gaps, causing reduced visibility along survey routes. In the eastern rainforests, logged habitats at various successional stages (50 or 150 ya) were found to possess a reduced number of stems and a larger number of smaller understory pioneer and invasive species (Brown and Gurevitch 2004). Along transects visibility might increase immediately following disturbance owing to the removal of vegetation but once the regenerating habitat reaches a certain height, sighting distances would be expected to diminish (Mitani et al. 2000). In the case of the forests that are the subject of this study, logging intensity was highest anywhere between five to ten years ago (Ranirison P, pers.comm.). Chapman et al. (2000) attributed apparent declines in four out of the five diurnal primates sampled during two periods at Kibale National Park in Uganda to changes in visibility resulting from regeneration of the under-storey following heavy selective logging. **Both relatively recent impacts from selective logging within the study region in addition to the finding that changes in visibility following logging often reduce the detectability of primates is supported by the following prediction: lemurs will be less detectable and perpendicular distance will exhibit a negative relationship with disturbance.**

In distance sampling surveys with primates, the unit of interest is the cluster and not the larger social group. Noting the tendency of primates to frequently form smaller sub-groups than their complete social unit, the term cluster here only refers to those individuals that are visible and form a well-defined group at the time of detection (Plumptre and Cox 2006). Owing to the potential for a strong size-bias where larger clusters are more detectable at greater distances from the line than are smaller ones, experts suggest as an alternative to using mean cluster size in density estimation, by allowing “mean cluster size to vary as a continuous function throughout the survey region” (Buckland et al. 2001). Although uncommon, the potential for this bias is increasingly being recognized in studies with primates (Waltert et al. 2008; Brenneman et al. 2011) where the authors have stratified cluster size for primates by site identity, habitat type or survey route. While lemur group sizes generally tend to be small (Wright 1999) and there is less variation in group size than for other primates and group living species such as large terrestrial herbivores (Ogutu et al. 2006), fission-fusion dynamics are well documented in many primates (Aureli et al. 2008), including *Eulemur coronatus*, one of the primates studied here. **Given the more recent warnings encouraging analysts to evaluate the potential influence of size bias before modeling detectability and estimating population density, and particularly in the case of socially flexible animals such as primates, I predict that the distribution of sighting distances will exhibit a positive size bias for larger clusters.**

Different habitat types might also influence detectability for primates in cases where the structural properties of these habitats differ (Mitani et al. 2000). The dry forests of Madagascar are generally shorter in height than the rain forests that extend along the island’s east coast (Ganzhorn et al. 1999). The substrates available for use by primates should increase as average forest height and canopy heterogeneity increases, making primates less detectable than in shorter forests. Forests that occur within the study region fall within the transition zone between the humid forests of eastern Madagascar and the drier more deciduous formations that characterize the west (Humbert and Cours-Darne 1965). Meyers (1993) noted in his study of the golden crowned sifaka (*Propithecus tattersalli*) at Daraina (found within 75 kilometers to the south of the study sites presented here), that forests falling within the transition zone between Humbert’s Eastern and Western domains vary from between 10 to 50% deciduousness of the trees. He broadly described forests along this continuum as evergreen, intermediate and deciduous. He highlighted differences in phenology, species composition and forest structure as grounds for such a distinction. The role of topography and altitudinal differences between sites were used to explain differences in the groundwater regime and hence the variation in habitat structure and plant species composition.

Forests within the current study occur on one of two substrate types, including exposed Mesozoic limestone karst formations and Precambian sandstones (Buřivalová 2011). A preliminary study of habitat differences suggests that while there is quite similar level of tree species diversity across the two substrates, tree species composition and forest structure differed pronouncedly (Buřivalová 2011). Of the 453 total tree species recorded only 20 were shared between limestone and sandstone forests. Additionally, forest heights, heterogeneity of the canopy and the above ground wood volume were found to differ between the two forest types. A greater maximum canopy height, and height difference ratio in sandstone forests suggests that on average, these forests are more structurally complex. The author was unable to include data from disturbed forest plots on limestone substrates and used this discrepancy to explain marginally higher average canopy heights in limestone forests. Evaluation of average canopy height in both intact and disturbed sandstone forest plots indeed highlight a significant trend for lower canopy heights in disturbed sandstone forests. Based on these results limestone forests were interpreted to be less structurally complex than sandstone forests and lower average canopy heights and a more homogenous canopy with fewer horizontal understory layers exemplifies this difference. **Therefore I predict that the greater structural complexity of sandstone forests is consistent with lower detectability for primates in these habitats**.

Methods

Study Sites

Local research teams including the members of protected area personnel and I collected data on lemur abundance in twelve forest fragments falling within the Diana Region of the Antsiranana Province, northern Madagascar from 14 July 2003 to 14 July 2012 (Figure 1; for site names please see Table 1). Study sites were situated in one of three different protected areas, although one of these areas was only recenlty elevated to provisional protected status in October of 2008 (Buřivalová 2011). The two easternmost sites occur within the Analamerana Special Reserve (34,700 ha; hereafter Analamerana) and to the northwest two sites from the Ankarana National Park (hereafter Ankarana) are represented (18,225 ha). Centrally within the complete study region sites are found within the Andrafiamena-Andavakoera Forest Corridor (hereafter Andrafiamena), a newly gazetted IUCN category V landscape (85,000 ha). The protected landscape/seascape category was designated in the interest of integrating management considerations for conservation with traditional practices of local populations such as farming and hunting. Nature conservation is typically overseen by an entity that also provides infrastructure to support “for profit” activities as well as facilitating management objectives outlined by surrounding communities.

Using multiple Landsat scenes (170/69, 158/69) we selected forest fragments to provide a representative sample of fragment sizes, isolation, geometry, disturbance history and protected status for the study region. Forests were surrounded primarily by a matrix of grasslands and often dominated by the following grasses (i.e. Poaceae), *Aristida rufescens, Hyparrhenia sp.*, *Trachypogon spicatus* (Letsara 2007).

Climatology data is scarce for the study region, but broadly speaking study sites are located within Humbert and Cour Darne’s (1965) western biogeographic domain of dry, dense forest, later referred to as deciduous, seasonally dry, western forest (Du Puy and Moat 1996; Du Puy and Moat 2003). A climate model for the study region provides a mean annual rainfall of 1500 mm (Jury 2003), which is comparable to rainfall amounts, recorded in Ankarana (i.e. 1800 – 2000 mm; Cardiff and Befourouak 2003), an area characterized by five wet months annually. Buřivalová (2011) reports annual rainfall data of 1785 mm for the village of Betsiaka before the year of 1975, a location that falls within the southern boundaries of the Andrafiamena-Andavakoera Forest Corridor.

There are a variety of habitat types that have been recorded within Ankarana (Fowler et al. 1989; Hawkins et al. 1990; Cardiff and Befourouack 2003) where recce surveys of primates were conducted for the current study during 2004. Assessments of forested habitat in the areas bordering Ankarana and stretching east into Andrafiamena and Analamerana highlighted both topographic and edaphic differences as major distinguishing characteristics (Lehman and Mayor 2004; Buřivalová 2011). In particular slopes harbor species characteristic of Humbert's (1965) Western Domain of dry deciduous forests including, *Commiphora, Hildegardia* and *Dalbergia,* while species more representative of the more humid Eastern Domain such as *Canarium*, *Eugenia* and *Diospyros* are frequently recorded in valleys and more riparian areas. Similar dichotomies have been framed in terms of the geology of the region. Forests occur along one of two substrate types, a Mesozoic limestone plateau and sedimentary sandstones originating from Precambrian basement rock (Buřivalová 2011). Between the two substrate types, only 4% of tree species were shared. In general, and consistent with Meyers (1993) explanation for varying degrees of deciduousness in forests of the Daraina region, groundwater regimes are likely to differ greatly across these habitat types. Forests on slopes and on the exposed limestone outcrops that characterize the protected areas of Analamerana and Ankarana are more water deprived and support a more deciduous formation of forest characterized by trees adapted to water scarcity (e.g. *Adasonia*, *Hildegardia*, *Commiphora* and *Pachypodium*). Alternatively, forests on sandstone support more evergreen species such as *Eugenia*, *Sarcolaena*, *Uapaca* and *Dypsis* (Banks unpbl data).

Primate Surveys: Recce vs Line Transect

We used standardized line transect techniques (Buckland et al. 2001) to sample primate populations in northern Madagascar (Diana Region, Antsiranana Province) and prepared 32 transects in eleven isolated forest fragments from June of 2003 to June of 2012. In 2003 and 2004 our surveys were restricted to three month sampling periods (Banks et al. 2007) while in 2007 we initiated a long-term sampling regime that extended over five years.

During the pilot studies of 2003-04 we adopted a protocol that was restricted to sampling along survey routes left by previous researchers (see Hawkins et al. 1990), hereafter referred to as recce trails. Time limitations and restrictions under the management of the protected areas during this period precluded fashioning survey routes from strict compass bearings. We also limited our sampling to forests within Analamerana and Ankarana. However, by April of 2007 surveys were conducted only in Analamerana and Andrafiamena and instead of recce trails, standardized line transects were prepared from strict compass bearings. Within the total sample including data from all three protected areas, there were twelve recce trails and 20 line-transects. Both recce trails and line transects were selected following a random stratified design so that inferences regarding the larger forest areas could be made through extrapolation. In the case of one transect used to sample Ankarana however, the trajectory of the recce trail used passed alongside a popular tourist area and in close proximity to a provisioning site. Surveys avoided the areas where animals are provisioned and although animals never approached observers, primate densities could be artificially elevated as a result of the proximity of provisioning. Accordingly, inferences regarding total primate population sizes within Ankarana are restricted to only the areas covered during our surveys and the sample was not used to extrapolate to the greater extent of the reserve.

Additionally during the project's first field season we walked some transects during late afternoon hours (14:30-17:30). Otherwise primates were typically surveyed during mornings (6:00 – 12:30) but never during the middle of the day (12:30-14:00). Transects varied from between 0.5 and 4.3 km in length, but on average a total of 3.6 km were walked during any morning or afternoon sampling period. We walked transects at an average of 1.2 km/hr. A combination of available satellite imagery, topographic and vegetation maps were used to choose the trajectory of all survey routes. Aside from the recce trails used by previous researchers we did not use trails left by humans, bush pigs or cattle to assist us in the placement of transects in any way. We were unable to use a systematic sampling scheme based on a series of randomly situated parallel lines owing to both protected area regulations and logistical considerations. This is a scenario that is likely to be duplicated in other projects involving surveys for primates.

When primates were encountered we recorded the species and the number of conspecific individuals that were clearly visible and maintained inter-individual distances of ≤ 50 m. All survey routes were measured with a tape measure and marked at 25 m intervals using flagging tape. Positions along survey routes where primates were encountered were measured using a laser rangefinder and the 25 m interval flags. We measured the distance from the location of the sighting to the center of the group using the laser rangefinder and measured the sighting angle relative to the trail using a precision compass. With basic trigonometry, the latter two measurements were then used to calculate perpendicular sighting distances. Densities were calculated using the Distance 6.0 software package.

Disturbance and Hunting

During transect walks we recorded information from signs and direct encounters with light to moderate forest disturbances. These included cut tree stumps, encounters and sign from wild boar (*Potachamerus larvatus*), cattle (*Bos indicus*), and encounters and signs (e.g. campfires, holes for precious stone prospecting) from people. Our survey effort was recorded as the number of kilometers walked, allowing us to provide an index of disturbance. Alternatively, all direct and indirect (i.e. traps) signs of hunting were recorded and considered to provide evidence of hunting at sites. Hunting was entered as a binomial variable (i.e. presence or absence) in all subsequent analyses. Similarly, evidence of heavy disturbance from large-scale fire (i.e. ≥ 0.5 ha) was also recorded as presence/absence variable.

Fragment Area, Geology and Forest Loss

I estimated forest loss for all forest fragments by deriving a supervised classification of forest and non-forest vegetation classes using the software package ERDAS Imagine 8.6© and Landsat 7 imagery. Images from the dry seasons in 1994 and 2003 were compared and forest areas were calculated in ArcMap 10 ©. I used the simplified geological classification provided in Du Puy and Moat (1996) to distinguish between forests on sandstone and limestone.

Statistical Tests

During the exploratory phase of the analysis efforts were made to model perpendicular sighting distances for each lemur species using linear regression techniques, yet an evaluation of the residuals at all levels of the explanatory variables revealed departures from normality for all lemur species. To avoid changing the nature of the ecological relationship between the explanatory variables and the response variable I abandoned the use of classical linear regression and did not perform any transformations on the data (Zuur et al. 2009). Additionally, consistent differences in the shape and scaled distribution of variables chosen for inclusion in the models derived for each species precluded the use of non-parametric tests. I instead used generalized linear mixed modeling (GLMM) techniques. This approach allows one to use alternatives to the normal distribution to model the response variable (Zuur et al. 2009). The poisson distribution is commonly used to approximate count data, such as those analyzed here, and was considered appropriate for the modeling process. All analyses were performed at the level of individual sightings with lemurs..

Another advantage of a generalized mixed modeling approach is that an underlying correlation structure can be maintained between observations through the inclusion of variables using a nested and crossed effects framework (Zuur et al. 2009). To adopt such a framework for the current study, the identity of study sites, transects surveyed, in addition to the year of the survey were treated as random effects in all candidate models. Not only will this structure improve inference for the biological questions being addressed but it also addresses the issue of collinearity among variables. In particular, the issue of spatial correlation between sites and transects, and that of temporal correlation between years are controlled for by treating these effects as random and isolating their effects from those including in the fixed effects component of the models. I further elaborated this approach by treating the variable, "transect" as a random effect nested within the variable "site". Multi-collinearity among the remaining explanatory variables was addressed by evaluating variance inflation factors (VIF). Following Chatterjee and Hadi (2013) I ensured that VIF values were well below 10 (i.e. ≤ 4.8) for all exploratory analyses, a value at which collinearity is no longer considered a problem. Incidentally, in the final, "hypothesis" testing stage of analysis (described more below) VIF factors fell between the values of 1 and 2.6 in the models for all species.

The information-theoretic paradigm (Burnham and Anderson 2002) was used to select between alternative models in all stages of the analysis. Alternative models were specified based on the various hypotheses posited to best explain variability in primate detectability. In the exploratory stage of the analysis, subsets of the explanatory variables were assigned to different functional groups in support of the various hypotheses presented earlier. Functional groups included, (1) temporal effects (AM vs. PM or wet vs. dry season surveys), (2) species demography (cluster size, encounter rate, and the number of adult females), (3) disturbance effects (transect and site disturbance, forest loss), (4) sampling effects (strict transects vs. recce trails, number of observers) and (5) habitat type effects (limestone vs sandstone forests). Along with the crossed, nested structure described above, global models from an "exploratory phase" were formulated to represent the unique contribution of explanatory variables from one of the four functional groups to variance in the distribution of sighting distances. An example of one of the candidate models, in this case the exploratory global model representing the functional group for temporal effects, is provided below:

$$\begin{aligned}
&\textit{Perpendicular Distance}_{(ist)uv} \bullet \text{Poisson}(\mu_{(ist)uv}) \square\ \text{E}(\textit{Perpendicular Distance}) \bullet \mu_{(ist)uv} \\
&\eta_{(ist)uv} = \beta_1 \times \text{Time}_{(ist)uv} + \beta_2 \times \text{Season}_{(ist)uv} + \beta_3 + a_{(ist)uv} \\
&a_{(ist)uv} = N(0, \sigma_a^2) \\
&\log(\mu_{(ist)uv}) = \eta_{(ist)uv}
\end{aligned}$$

The perpendicular distance for observation i, along transect t, nested within site s, and crossed over year u, and observer v, is Poisson distributed with mean, $\mu_{(ist)uv}$ is specified in the first line of the notation. The linear predictor function is provided in subsequent lines and includes the unknown regression parameters ($\beta_{1\ldots}\ \beta_n$) and the fixed effects, (Time; i.e. AM vs PM survey and Season; i.e. dry or wet season survey). The link between the expected value of, *Perpendicular Distance*, $\mu_{(ist)uv}$ and the systematic component $\eta_{(ist)uv}$, is the log-link: $\log(\mu_{(ist)uv}) = \eta_{(ist)uv}$. This link between the mean of $\textit{Perpendicular Distance}_{(ist)uv}$, and the predictor function $\eta_{(ist)uv}$, ensures that the fitted values are always non-negative (Zuur et al. 2009). Overdispersion was an issue for all of the models evaluated. As a result an individual level random effect was fitted, and perpendicular distance and the generalized structure of models followed a poisson log normal distribution.

It is important to note that during the exploratory stage of analysis I did not include explanatory variables from competing hypothesis in specifying the global model for each functional group. The aim of the exploratory phase was to identify explanatory variables from each functional group that were the most informative in capturing patterns of variance in the distribution of sighting distances. Of the eleven variables retained for analysis after meeting criteria for collinearity we considered a total of 23 models for all species across all functional groups. The absence of any strong a priori biological support for interactions precluded their inclusion.

The use of Kullback-Liebler information (e.g. Akaike Information Criteria; Anderson and Burnham 2002; Kullback and Leibler 1951) provides a criterion to compare competing models (Burnham and Anderson 2002) by combining likelihood theory and the principle of parsimony in statistics. Model selection is therefore aimed at minimizing bias and maximizing parsimony to isolate the "best approximating" model or models. AIC criteria is defined as

$$\text{AIC} = -2\text{L} + 2\text{K},$$

where L is equal to the maximum likelihood of the model and K is the number of parameters in the model (Akaike 1973). The role of parsimony can be applied to a set of competing models that were derived from the same dataset by comparing their AIC values and selecting the model with the lowest AIC. Since several models were considered in the two phases of the analysis, the probability of any one model being the best model was evaluated by calculating the Akaike weights for all models in a 95% confidence set. Akaike weights consider the differences in AIC values for all candidate models relative to the most parsimonious (i.e. the model with the lowest AIC value) in the set (Rhodes et al. 2009). Through the comparison of AIC weights a 95% confidence set of models are produced for each species. The comparison of AIC ratios between models (i.e. evidence ratios) enables the analyst to consider the relative support for one model over another (Rhodes et al. 2009). The GLMMs for all stages of the analysis were specified using the lme4 package (Bates and Maechler 2010) while Akaike weights were derived using the AED package (Zuur et al. 2009). All stages of the analysis were performed in R (R Core Development Team 2013).

During the exploratory phase I generated a 95% confidence set for all 23 models that were fitted using only variables from each of the functional groups. This exploratory phase could be considered as approach towards refining an *a priori* hypothesis set (Dochtermann and Jenkins 2010). I implemented a criterion for the inclusion of variables in the second phase of analysis based on their reoccurrence in competing models from the 95% confidence set. When an explanatory variable was represented in at least half of the models in the 95% confidence set it was then included in the second, hypothesis-testing phase of the analysis. A null model was also fitted to the data by excluding all explanatory variables. The null model was used to assess whether the explanatory variables from a particular functional group were important in explaining the distribution of perpendicular sighting distances. In cases where the null model provided superior fits to the data relative to alternative models and therefore explained more of the variation, I considered the role of the associated explanatory variables less informative (Rhodes et al. 2009) in modeling sighting distances and they were no longer considered in the subsequent stages of analysis. Given the large number of models being considered (n = 23) the rationale behind this procedure is primarily concerned with reducing the initial number of models and minimizing overparameterization (Burnham and Anderson 2002). The null model can therefore be used as a means of identifying whether or not the candidate models are in fact appropriate, and particularly in cases where there is equal support for both the null and the other candidate models the results indicate that the causal factors of biological interest have not been captured by the existing survey design (Dochtermann and Jenkins 2010).

Once the most informative explanatory variables had been isolated from each functional group, the second phase of analysis began by specifying a global model that included all of the variables from the competing functional groups. The global model was standardized following the Gelman approach (Gelman 2008) and was used to generate a full subset of competing models (Grueber et al. 2011). This was performed using all combination of variables and the dredge function from the MuMIn (i.e. Multimodel Inference; Bartón 2012) package in R (R Core Development Team 2013). A second 95% confidence set of models was then produced for each species from the standardized global model and model averaging was performed via the MuMIn package so that the estimates for the parameter attributed to each explanatory variable could be compared and interpreted (Grueber et al. 2011). Although the information arising from interactions between predictor variables can be lost by deriving parameter estimates using model averaging, this problem can be largely reconciled by centralizing predictors (Gelman 2008; Holger 2010), an approach also adopted here. I considered a relative importance (RI) value of 0.5 or greater for any variable as grounds for inclusion as a covariate in the subsequent calculation of density for each species using the multi-covariate distance sampling engine (MCDS) in Distance 6.0. A variable's relative importance is determined by summing the Akaike weights for all models that include that variable as part of the 95% confidence set (Anderson et al. 2001b). Roughly speaking, the relative importance describes the reoccurrence of the variable in the 95% confidence set. A relative importance of 0.5 translates into an occurrence of that variable in half of the 95% set of top models.

Estimating Primate Densities using Conventional (CDS) and Multiple Covariate Distance Sampling Techniques (MCDS)

I performed all analyses using the Distance version 6.0 © software (Thomas et al. 2010). Based on exploratory analyses and both visual and statistical evaluation of chi-square and Kolmogorov-Smirnov goodness of fit tests final analyses were performed with ungrouped data and at a truncation distance of 50 m for all species. I considered changing the scale of the detection function through the inclusion of one or more adjustment terms if the resultant model achieved a superior fit via a comparison of AIC values. In the case of detection functions formulated from both CDS and MCDS techniques the data were pooled across the eleven sites from which observations were available for analysis.

Variance was estimated both analytically via the delta method and through a bootstrap resampling procedure where individual repetitions of transects (b=400) were treated as the unit of analysis. The percent coefficient of variation (%CV) is provided for each method. The decision to use 400 resamples in the bootstrap procedure was chosen by following Buckland et al.'s (2001) guidelines for yielding reliable confidence intervals. In selecting final density estimates only the bootstrap %CV were considered. The goal of this exercise was to derive the most precise estimates of density given the data at hand. The guideline provided in Anderson and Burnham (2002) was followed whereby differences in AIC (ΔAIC) greater than 5 were considered to provide strong exclusive support for a particular model. Alternatively ΔAIC values that falling between 2-4 provided more equivocal support and those less than 2 were considered indicative of only weak support. In cases where a model offered only weak or equivocal support through these comparisons the model with the lowest %CV was selected as the "best" compromise between bias and parsimony in estimating population density for that species.

Results

Model Averaging: Determinants of Lemur Detectability

We walked a total of 1234 kilometers on 32 transects spread across eight dry deciduous and three semi-evergreen forest fragments during the course of the nine year study. Characteristics describing particular site attributes are presented in Table 2.1. Following truncation of all outliers, 430 observations with *Eulemur coronatus*, 172 observations with Sanford's brown lemurs (*Eulemur sanfordi*) and 158 observations with the Perrier's sifaka (*Propithecus perrieri*) were used in the analysis. There was an insufficient number of observations to model the global detection function (i.e.≤ 60 observations; Buckland et al. 2001) for *Hapalemur occidentalis* and this species will no longer be considered in the subsequent analyses.

Detectability in *E. coronatus* varied as a function of differences in observer experience. As a predictor variable, observer experience had the greatest relative importance for this species and its representation was ubiquitous in the 95% confidence set of models (Table 2.2). The finding highlights the tendency of less experienced observers to record observations with *E. coronatus* at greater distances from the survey route than do observers with at least a month of experience sampling primate population levels on line transects and recce trails (Figure 2.2A).

After evaluating the confidence intervals for all parameter estimates with *E. coronatus* the only additional predictor variables that exhibited a clear direction of effect and were represented in more than half of the models from the 95% confidence set included the season and the disturbance index, variables with 74% and 75% relative importance to observer experience in modeling detectability. These results indicate that there was a slight tendency for individuals of this species to be detected at greater distances in wet rather than dry months (Figure 2.2C). The negative relationship with disturbances along survey routes also reveals that *E. coronatus* were less detectable in more disturbed forests (Figure 2.2B). Alternatively, the low relative importance in modeling detectability for the remaining variables, cluster size and time of day (0.36 and 0.39) and the fact that the confidence intervals for these variables include the value of zero, makes it difficult to more definitively assign positive or negative values to their effects and to argue that these factors ultimately affect the probability of detecting *E. coronatus*.

None of the potential covariates to primate detectability, whether associated with sampling, temporal, demographic, habitat or disturbance-related effects proved informative in modeling the distribution of sighting distances for *E. sanfordi*. Indeed it was the null model including only the underlying random effects structure that had the lowest AIC of all models during the exploratory phase. Site level differences (Figure 2.3) however, accounted for more of the variance in detectability (Variance = 0.04; see Table 2.4) for *E. sanfordi* than in any other lemur.

There was a bias for larger groups of the species, *Propithecus perrieri* to be detected at small distances from the survey route (Figure 2.6). Although cluster size appeared in a large proportion of the 95% confidence set of models and had the highest relative importance (RI = 0.61; Table 2.6) the fact that the confidence intervals for this parameter estimate include the value of zero indicates considerable uncertainty over the use of cluster size in predicting *P. perrieri* detectability. Similar ambiguity was encountered through an examination of the two remaining predictors (i.e. survey route and substrate type) that were retained from the exploratory phase of the analysis. Neither variable exhibited a clear direction of effect (Table 2.6) or was represented in more than half of the models in the 95% confidence set (RI: 0.47 and 0.28 respectively).

Multi-Covariate Distance Sampling (MCDS) Results

The results of the CDS and MCDS analyses for all species are presented in Tables 3, 5 and 7. Exploratory analyses indicated that a truncation point of 50 m offered the best compromise between parsimony and setting limitations on the amount of data that needed to be discarded to reliably conduct the analysis (i.e. sample size limitations; Buckland et al. 2001). By selecting a truncation distance the need to apply an unwieldy number of adjustment terms to fit outliers at the tail of the distribution of sighting distances is minimized (Thomas et al. 2010). Furthermore, outliers at the tail of the distribution are unlikely to reflect the same detection process that characterizes encounters at shorter distances (Buckland et al. 2001) and may reflect uncommon scenarios of increased vantage along survey routes including greater visibility in large forest openings or along ridgetops. Incidentally adjustment terms were not required in estimating abundance for any of the species studied here and scaling the detection function using such methods provided no improvements in AIC values.

The results of the CDS and MCDS analyses for *E. coronatus* are presented in Table 2.3. The hazard rate model with no adjustment terms provided the best model for both CDS and MCDS analyses. The MCDS analysis fitting the three covariates with the highest relative importance in modeling detectability (i.e. observer experience = OBS, transect disturbance = TRN DST and season = SEA) offered the best trade-off between bias and precision. This model had the lowest AIC value and a %CV (coefficient of variation) nearly identical to that of the other analyses. The fact that it maintained the lowest AIC despite having a large number of parameters reinforces that it provides the best fit to the data. Nevertheless both the CDS and MCDS approaches to the analysis provided very similar density estimates (i.e. 0.31 and 0.32 individuals/ha respectively) and levels of precision (%CV = 31.1 and 31.9 respectively) for *E. coronatus*. It is indeed the lack of fit to the data using the CDS detection function (ΔAIC > 4) that distinguishes this approach as inferior to the complementary MCDS techniques. Both multi-covariate detection functions fitted to OBS, TRN DST and SEA as well as a more parsimonious model that considered only OBS and SEA had the lowest AICs and offered improvements over both the CDS approach and all alternative MCDS models (ΔAIC < 2).

Attempts to average the effects of potential covariates to detectability in *E. sanfordi* revealed few strong relationships and only site level differences (i.e. SITE) appeared to influence the distribution of sighting distances for this species. Entering SITE as a factor covariate in subsequent efforts to model the detection function was performed to allow comparison with CDS methods that model detection as function of the distribution of sighting distances alone. The results of this analysis are presented in Table 2.5. Visual examination of the differences between the cumulative and empirical distribution functions through the Kolmogorov-Smirnov statistic (Figure 2.4) reveals that CDS methods provide a superior fit to those offered by MCDS methods. Strikingly the MCDS methods offered greater precision in modeling *E. sanfordi* detectability (Table 2.5; CDS %CV = 30.9, MCDS (SITE) %CV = 10.3). Despite this discrepancy, evaluating the criteria for model fit revealed a ΔAIC > 10, a further indication that the inability to fit the data adequately to the MCDS model is primarily what distinguishes the two approaches.

Table 2.7 summarizes the results of CDS and MCDS analyses for *P. perrieri*. The best compromise between bias and precision was marginally offered by the MCDS analysis where detection was modeled as a function of cluster size (i.e. lowest AIC value of all models). Nonetheless CDS methods offered a comparable fit to the data and a ΔAIC value of well below 2 indicates that there are limited differences in the ability of either CDS or MCDS methods to fit the data on hand. The inclusion of the covariates, substrate type (i.e. forest type = SUB), and survey route (SUR) did not offer any improvements in model fit over CDS methods (Table 2.7) although the ΔAIC did not exceed a value of 2 suggesting that competing approaches were comparable in terms of model fit. The primary difference uncovered in modeling *P. perrieri* sighting distances using CDS and MCDS methods was the precision of the associated analyses. The CDS analysis offered a more precise estimate of population density than the best fitting MCDS analysis, CLU (%CV = 9.7, 34.24 respectively). Although two separate MCDS analyses fitted with the covariates SUB and SUR respectively provided comparable precision and the ΔAIC was right at the boundary delimiting more equivocal support over the best fitting models (ΔAIC = 1.93 and 1.97 respectively). Once density estimates were selected for each species based on the Kullback-Leiber criteria outlined in the statistical methods section, it can be shown that *Eulemur sanfordi* had the greatest variation in density across the eleven sites (range = 0.09 – 2.05 ind/ha; Figure 2.7) while *P. perrieri* observed more modest variation (range = 0.01 – 0.44 ind/ha).

Discussion

There was somewhat limited support from ecological theory in describing patterns of detectability across primates from this northern Malagasy diurnal primate community. Although some of these results followed expectations, there were no patterns that were widely observed across all species. This finding is consistent with results from the Mwanihana Forest, Udzungwa Mountains Tanzania where differences in demography and behavior were used to explain variable detection patterns across the five species of diurnal primates found there (Rovero et al. 2006). Furthermore, while Johns and Skorupa (1987) highlighted reduced calling rates and cryptic behavior in several species as a behavioral response to logging and an increased frequency of encounter with humans among primates, this response was not universal across all members of the primate community. Nijman and Nekaris (2012) provide evidence that antipredator strategies such as cryptic behaviors can even be quite variable among closely related taxa.

Despite few consistent findings across the lemur species sampled here, some results did follow expectations from prominent ecological theory. In particular, variability in observer experience did result in differences in patterns of detection for *E. coronatus*. This finding indicates that inexperienced observers frequently miss sightings with this species occurring close to the survey route. The results are consistent with knowledge of *E. coronatus* behavior and especially the tendency of this species to use cryptic behaviors through freeze tactics and a dull pelage coloration (Banks et al. 2007) to escape detection by human observers (Nijman and Nekaris 2012). Crypticity among other *Eulemur sp*. is also known from elsewhere in Madagascar (Banks et al. 2007; Karpanty and Wright 2007) so it is somewhat surprising that we did not see a similar effect in the distribution of sighting distances for *Eulemur sanfordi*. Rovero et al. (2006) highlighted shyness and the ability to use dense vegetation for concealment to explain the paucity of sightings with *Papio cynocephalus*, behavioral tendencies that are not inconsistent with the behavioral ecology of *E. coronatus* (Freed 2007, Banks pers.obs.). If certain lemurs are using cryptic behaviors to avoid detection by human observers, a systematic bias relative to how these species are being detected on recce and line transect surveys should be apparent. Since freeze tactics have been previously used to characterize cryptic *Eulemur* behaviors during line transect surveys in northern Madagascar (Banks et al. 2007), a disproportionate number of encounters triggered through sight alone might be expected. So to address the potential for bias in estimating the densities of primates known to exhibit cryptic behaviors, future surveys should always include information about the mode of detection (e.g. sight, sound or smell) so that this factor can also be further considered as a potential covariate to detectability (Borries et al. 2002).

It is also known that within group spatial cohesiveness in *E. coronatus* is highly variable and subgrouping seems to be driven primarily by the foraging benefits that fission-fusion dynamics confer for this species (Freed 2006). Nijman and Nekaris (2012) also noted that across Southeast Asia, *Presbytis* species that support small groups sizes (i.e. < 5 individuals) were inconspicuously colored and often used crypticity to avoid detection by human observers. *E. coronatus* foraging subparties are similarly small (i.e. 2 – 4 individuals; Freed 1996) presumably exposing this species to greater risks from predation. The relatively dull coloration of *E. coronatus* provides a means to effectively blend into the backdrop of deciduous vegetation that broadly characterizes forests of the Diana region. Furthermore, *E. coronatus* often forages in treelets and dense tangles of vegetation (Freed 2006) where visual detection is likely to be obstructed.

The absence of strong support for other sampling effects as strong drivers of detectability in this diurnal primate community is consistent with the few examples that exist from elsewhere in Madagascar. Johnson and Overdorff (1999) found that estimates of the density of brown lemurs (*Eulemur fulvus rufus*, now *Eulemur rufifrons*; Mittermeier et al. 2010) in Ranomafana National Park using existing trails provided results comparable to the true density. This comparison was possible due to long-term data from direct counts with groups of *E. rufifrons* at this site. The authors also obtained comparable estimates of density through the use of shorter segments of longer transects, a finding that further supports the suggestion that sampling effects may indeed contribute little to variation in lemur detection.

Lehman (2006) found only one example among a community of five primate species in southeastern Madagascar where lemurs were influenced by whether existing trails or cut transects were used to conduct line transect surveys. He suggested that the affected species, *Hapalemur griseus griseus* was repelled from existing trails owing to the removal of its preferred food species there. Indeed this taxon specializes on giant bamboo (*Cathariostachys madagascariensis*), which comprises over 70% of its annual diet, making it easy to explain differences in its patterns of detection. While one species from the diurnal primate community of the Diana region, *Hapalemur occidentalis* does meet similar requirements for dietary specialization (e.g. see Ganzhorn et al. 1999), there was no evidence of the selective removal of bamboo along existing trails here. While there were problems related to the detection of *Hapalemur* (discussed below) in this sample clearly they do not apply here nor do they find analogues with the remaining diurnal primates from this community. Coupled with the evidence presented for the southeast, these new results from Madagascar's north lend support to the notion that existing trails may provide reliable and comparable density estimates to those on cut transects.

Sighting distances also varied between the dry and wet seasons for *E. coronatus* (Figure 2C), lending support to the energy conservation hypothesis of Wright (1999). Wet season sightings were on average further from the transect line, indicating a broader shoulder for the detection function and hence, greater detectability. Notably there is no indication that animals close to the transect line were being missed during wetter periods, thereby driving average sighting distances upwards, since the lower bounds of confidence intervals for sighting distances were roughly the same in both seasons (Figure 2C). Elsewhere in the Diana region, *E. coronatus* has been observed to experience temporary food shortages, but the strongest shifts in food availability occurred during wetter periods (Freed 2007). Despite this trend, and contrary to the energy conservation hypothesis, *E. coronatus* coped with these shortages by forming associations with sympatric *E. sanfordi* and foraged for longer periods on the fruits and flowers of small trees, treelets, and non-trees that require greater time and effort to exploit (Freed 1996). Therefore, while it is still possible that the activity pattern for *E. coronatus* changes seasonally, these changes are perhaps best characterized by increases in foraging that coincide with the wet season when resources are less accessible, thereby making the lemurs more conspicuous to observers.

It is unclear however whether actual shifts in activity are also observed in the sites sampled as part of the current study. Indeed the superabundant dry season food resources used by *E. coronatus* in the Freed (1996) study, such as *Leea spinea* either were not recorded or were rare in botanical plots situated across the eleven study sites described here (Banks unpbl data). Accordingly it remains plausibe that *E. coronatus* might use an energy conserving strategy during the dry season at sites where superabundant resources are rare, thereby explaining lower detection during these periods. Additionally, it is important to note that the magnitude of effect for season was modest when compared to other important covariates to *E. coronatus* detectability (Table 2). The indication here of course being that seasonal differences have, in general, a more limited impact on the detectability of *E. coronatus* than do other factors.

E. coronatus was also less detectable in more disturbed habitats. This finding is consistent with research showing that primates are often less visible in disturbed habitats where forest regeneration has recently taken place (e.g. Chapman et al. 2000). Indeed in the most disturbed habitats sampled here this species was never detected at distances greater than 10 m from the transect line. Burivalova (2011) also found lower average tree heights and lower densities of the largest trees in disturbed forests in the Diana region. This finding suggests that following the removal of large trees characteristic of structurally more intact forest, regenerating vegetation is likely to reduce visibility and the detectability of lemurs.

Cluster size proved to be the only consistent determinant of *P. perrieri* detectability in forests of the Diana region. This size-bias however operated in the opposite direction from what was expected from popular ecological theory (Otto and Pollock 1990). In particular, sightings with larger clusters should have a greater probability of detection at greater distances than do smaller clusters. In this study however, larger groups of *P. perrieri* showed a bias for greater detection at shorter distances. I attribute this difference to behaviors previously noted for *P. perrieri* and specifically the tendency at large group sizes to approach observers using defensive postures (Banks et al. 2007). Large group size has been shown to reduce predation risk in a variety of taxa. Furthermore the reliance of many predators on surprise and the tendency to abort hunting attempts if detected by the targeted prey (Treves and Palmqvist 2007) makes alarm calling, mobbing and otherwise demonstrating awareness of a potential threat a potentially adaptive anti-predator strategy, particularly for a large-bodied species such as *Propithecus* (Heymann and Buchanan-Smith 2000). It is somewhat anomalous however that data on group size and predation in *Propithecus edwardsi* at Ranomafana did not support the hypothesis that larger groups were less vulnerable to predation (Wright 1998). Nonetheless it is interesting to note that Wright (1998) emphasized considerable behavioral plasticity in *Propithecus* as a strategy for dealing with different types of predators and perhaps the responses to humans recorded here highlight a greater range to the taxon’s predator-specific behaviors than previously thought. Indeed the majority of encounters between the members of local communities and Perrier’s sifakas appear to be driven by fear and subsequent flight on the part of humans (Banks pers.obs.). Taboos that protect *Propithecus* may still exist in some parts of the species’ range but transient migration from other ethnic groups and shifts in traditional beliefs suggest that there is the potential for *Propithecus* to exhibit anti-predatory behaviors in the presence of humans (Meyers and Ratsirarson 1989; Banks et al. 2007).

I found no support for the role of sampling, temporal, demographic, habitat-related or anthropogenic effects in determining patterns of detection in *E. sanfordi*. In fact, site-level differences provided the greatest insight into patterns of detection in this species. Site-level differences in detectability were treated as a random effect in all analyses and accounted for near-zero levels of variance in the models for the other two diurnal species. The variance attributed to site-level differences in *E. sanfordi* models was nonetheless low (i.e. 0.04) and these differences did not translate into improved fits to the line transect data (i.e. greater accuracy) when “site” was used as a covariate in approximating the detection function for this species. However the MCDS calculated density was considerably more precise (i.e. % CV = 10.3 vs. 30.9 in the MCDS and CDS methods respectively). Sites were not sampled equally so this difference could be an artifact of sample size limitations. It is interesting to note that the density estimates were similar for both methods (0.09 and 0.06 for CDS and MCDS methods respectively). At present however, more information on these site-level differences would be needed to make better inferences regarding the true nature of these discrepancies. Until such data are available, estimates of *E. sanfordi* population density that are derived from specifying a global detection function across sites should be treated with greater caution.

Modeling detectability was not possible for *Hapalemur*, a species that was seen less than 10 times during all recce and transect walks. Indeed preferred foods for this species (i.e. primarily bamboos, Poaceae) were patchily distributed at study sites and despite efforts to sample these habitats proportional based on their representation throughout the habitat, crypticity and evasive behaviors in *Hapalemur* are known to further confound detection of this species (Karpanty and Wright 2007). Furthermore, most bamboos in northern Madagascar (i.e. *Valiha sp*.) appear to favor degraded areas, either previously influenced by fire or serving successional roles in steep areas that are prone to landslides (Dransfield 2003; Buřivalová 2011). In the future, attempts to collect information on *Hapalemur* population levels should implement alternatives to standard line transect sampling, such as the use of sweep samples across patches of small and large culm bamboo (Arrigo-Nelson and Wright 2004).

In addition to making the appropriate provisions for the sources of bias associated with detecting highly specialized members of the genus *Hapalemur*, future surveys should also attempt to better address the role of cathemerality in influencing detection probabilities for many of the primates surveyed here. In fact, cathemerality has been described in a few eastern populations of *Hapalemur griseus* (Tan 2000; Vasey 2000; Ratsirarson and Ranaivonasy 2002) as well as *Hapalemur aloatrensis* (Mutschler 2003), although evidence from *Hapalemur occidentalis* elsewhere in northern Madagascar supports a diurnal activity cycle (Colquhoun 1993). Nonetheless cathemerality characterizes the activity cycle, at least to some degree in all of the *Eulemur* species (Overdorff and Johnson 2003), two of which were studied here. In addition to introducing bias by sampling during periods of potential inactivity for *Eulemur* (Müller et al. 2000), a number of cathemeral primates have also been found to exhibit cryptic behaviors (Colquhoun 2007) that may also influence their detectability during line transect surveys. There is indeed some evidence that this may have occurred during the current study and by comparing differences in precision for the two cathemeral *Eulemur* species (i.e. range in % CV = 30.1 - 31.2) and the strictly diurnal *Propithecus perrieri* (i.e. % CV = 9.7) it is apparent that density estimates for cathemeral primates are considerably less precise. The finding is particularly stark when taking into account the relatively small number of observations recorded with *Propithecus* (n = 158) relative to *E. coronatus* (n = 340) and *E. sanfordi* (n = 172) despite identical survey effort with all species. Given the absence of a *tapetum lucidum* (Richard and Dewar 1991) and therefore a reliable means for detecting *Eulemur* species at night, it may be that either additional survey effort is required to improve the precision of estimates with cathemeral species (Müller et al. 2000), or that line transect methodology simply presents an ineffective sampling design for cathemeral primates. To better understand the role of cathemerality in influencing primate detectability, future population surveys of *Eulemur* species should attempt to cross check density estimates from line transect surveys with studies based on complete counts or focal group studies of home range (Marshall et al. 2008).

A second complementary objective in modeling covariates to primate detection in this study was to determine if such insights would lead to more reliable density estimates. Indeed knowledge of covariates to detectability in a wildlife survey and their magnitude of effect allow the analyst to consider many more alternatives to improve reliability than he or she would if these factors were ignored. The possibility of modeling detection as a function of covariates using the popular software package, Distance ©, makes such precautionary measures an attractive option for theorists and managers of wildlife populations alike. Surprisingly however, the results from this study do not reveal a marked improvement in the accuracy or precision of density estimates whether modeling detection as a function of covariates and sighting distances or using the distribution of sighting distances alone. In this study in only one of the three diurnal primates (i.e. *E. coronatus*) did MCDS methods offer some improvement over the conventional methods (CDS) and these improvements were modest at best. In fact, both density estimates and their associated levels of precision were nearly identical when the most parsimonious models using either method were compared for this species (Table 2).

Even proponents of MCDS methods acknowledge that infrequently do density estimates derived using a MCDF yield results that contrast starkly with those derived using more conventional methods (Marques et al. 2007; Marques, pers.comm.). The reasoning behind this is that the standard methods for modeling detectability are, as long as the assumptions of line transect methodology are met, “pooling robust” (Buckland et al. 2001; Marques et al. 2007). Primate surveys are nonetheless often confronted with scenarios where making exceptions to the strict assumptions of line transect methodology are required, and whether these assumptions can actually be relaxed is an on-going debate in the primate literature (Hassel-Finnegan et al. 2008; Buckland et al. 2010b). The results of this study suggest that line transect methods may indeed remain robust to many of the sources of bias commonly introduced when working with primate populations. In particular, sampling effects had a limited impact on lemur detectability and much of the recent call for strict, systematic sampling regimes may in fact be overstated for primates. As with the well-known study by Whitesides et al. (1988), as well as earlier visits to the study areas presented here (Banks et al. 2007) and other prominent studies with lemurs (e.g. Johnson and Overdorff 1999, Lehman 2006) the role of sampling effects probably has a much more limited impact on the results from primates surveys than has been suggested by statisticians and modeling experts (e.g. Buckland et al. 2010b). Observer differences however remain a consistent source of bias in wildlife studies and initiatives where pooling data from multiple observers is an objective should always plan to evaluate the role that this important factor has on density estimates.

Despite a generally weak relationship between sampling effects and patterns of bias in density estimates the results of the current study certainly do not provide support for an approach that ignores the influence of these and other covariates to primate detectability altogether. Authors have previously shown how seasonality, species-specific behaviors and demography, as well as disturbances (Nijman 2001; Lehman 2006; Waltert et al. 2008) can provide less reliable results and these findings are, to a certain degree, upheld by the results of this study. Seasonality (*E. coronatus*) as well as the behavioral tendencies of certain species (*E. coronatus* and *P. perrieri*) had an influence on estimates of primate density. The nature of these effects and their magnitude had a limited impact on model accuracy and precision. Site-level differences in *E. sanfordi* detectability represented a source of bias that could not effectively be controlled for using methods that take such variability into account. This result emphasizes that for some taxa, and particularly rare species such as this one, increased sampling efforts may remain the primary means for deriving more reliable estimates of abundance. Nevertheless it is interesting to note that MCDS methods did not translate into more accurate results for this lemur, although they may improve estimates by increasing precision (Table 4). By evaluating these differences researchers studying wildlife abundance theory as well as managers of wildlife populations gain important insights into the full suite of factors driving abundance patterns in their datasets. Without evaluating the difference between adjusted and unadjusted counts, analysts are left only to speculate regarding any biological inference associated with their results. If the goal of the survey is to inform the management of a highly endangered species such as *P. perrieri*, the manner in which the results are interpreted could influence the survival prospects for the species.

Tables and Figures

Table 2.1. Site attributes for eleven forest fragments in northern Madagascar. Symbols are represented in Figure 2.1. Protected status includes category V IUCN protected landscapes (cat. V), Special Reserves (SR) and National Parks (NP). The area of each fragment is provided in hectares along with the total distance of transects walked over the course of the study in kilometers. The substrate type is categorized as either limestone karst (L) or Precambrian sandstones (S). Forest loss is quantified as the percentage of forest lost, May 1994 – June 2003. The intensity of pressure is provided as a measure of the number of disturbances observed over the course of the study per km of survey route traversed. Predator abundance is the relative abundance of *Sanzinia madagascariensis*, *Acrantophis madagascariensis*, *Polyboroides radiatus*, *Accipter hentsii* and *Buteo brachypterus* as measured in number per km of transect walked.

Site Name	Map Symbol	Protected Status	Area (km^2)	Distance Walked (km)	Substrate Type	Forest Loss	Pressure	Predator Abundance
Ampondrabe	C	cat. V	5.0	120	L	0.83	0.10	0.03
Mahanoro	G	cat. V	4.2	155	S & L	0.83	0.07	0
Ambatovazaha	A	cat. V	12.1	133	S	0.52	0.04	0.02
Madiromasina	F	cat. V	1.1	100	L	0.49	0.05	0
Antsahabe	H	cat. V	4.64	105	L	0.12	0.05	0.01
Analamerana E	E	SR	124.0	262	L	0.05	0	0
Andampibe	D	SR	7.6	51	S	0.52	0	0
Analamerana W	B	SR	90.9	225	L	0.17	0	0
Ankarana W	K	NP	100.8	32	L	0	0.06	0
Ankarana E	J	NP	19.6	36	L	0.17	0.17	0
Ambery	I	cat. V	6.2	16	L	0.88	0.19	0

Table 2.2. Summary of model averaging results for *Eulemur coronatus* from phase2, 95% confidence set of models. Parameter estimates and associated standard errors along with the lower and upper confidence intervals are presented. The relative importance of each parameter is also included, a measure of the reoccurrence of each variable across the 95% confidence set of models.

Parameter	Estimate	Std. Error	Lower CI	Upper CI	Relative Importance
(Intercept)	2.05	0.04	1.96	2.14	
Observer	0.56	0.20	0.17	0.96	1.00
Season	0.18	0.08	0.01	0.34	0.74
Transect Disturbance	-0.22	0.09	-0.41	-0.02	0.75
Cluster Size	0.07	0.07	-0.07	0.22	0.36
Time of Day	-0.12	0.11	-0.34	0.09	0.39

Table 2.3. CDS and MCDS results representing unadjusted and adjusted counts respectively for *Eulemur coronatus* across eleven sites in northern Madagascar. Conventional distance sampling (CDS) analyses were performed using a pooled detection function, f(0) whereas multiple covariate distance sampling (MCDS) analyses modeled detectability as a function of the following covariates, OBS = observer, TRN DST = transect disturbance, and SEA = season. The key function used for all analyses was the hazard rate function with polynomial adjustment terms (see Buckland et al. 2001 for a description of all available key function terms). Incidentally no change in scale was required to achieve a superior fit of the data, so no adjustment terms were used in any of the models. Variance was estimated analytically using the delta method and via a bootstrap resampling procedure (b = 400) that treated each repetition of the transect as the unit for analysis. The %CV is provided for both methods. The model for which support was considered the greatest is indicated in bold print.

Covariates	Number of parameters	ΔAIC	AIC	Density Estimate 95% CIs	%CV	Bootstrap Density 95% CIs	Bootstrap %CV
				Eulemur coronatus			
				CDS: f(0) pooled			
-	2	5.1	2805.1	0.31 (0.2-0.49)	19.13	0.35 (0.21-0.57)	31.07
				MCDS			
OBS + TRN DST + SEA	**16**	**0**	**2799.9**	**0.32 (0.21-0.51)**	**19.23**	**0.36 (0.22-0.58)**	**31.89**
OBS + SEA	4	1.5	2801.4	0.32 (0.21-0.49)	19.17	0.35 (0.21-0.58)	31.64
SEA + TRN DIS	10	4.6	2804.5	0.32 (0.20-0.50)	19.23	0.36 (0.22-0.59)	31.35
SEA	3	5.2	2805.1	0.31 (0.2-0.49)	19.16	0.34 (0.21-0.56)	33.1
TRN DST	14	6.6	2806.5	0.31 (0.19-0.49)	19.22	0.35 (0.22-0.58)	31.93
OBS + TRN DST	15	6.7	2806.6	0.32 (0.20-0.50)	19.23	0.36 (0.22-0.59)	30.97
OBS	3	12.6	2812.5	0.3 (0.19-0.47)	19.16	0.35 (0.21-0.57)	32.51

Table 2.4. Variances and standard deviations for the random effects in the null model for *Eulemur sanfordi*. The Individual Level Random Effect is fitted to account for overdispersion and is part of the underlying structure for all candidate models. The remaining random effects include the identity of the transect as a nested effect within the identity of the site, in addition to year and site which are included as crossed effects.

Random Effects	Variance	Standard Deviation
Individual Level Random Effect	0.46	0.68
Transect (Site Level Nested Effect)	0	0
Site	0.04	0.19
Year	0	0

Table 2.5. CDS and MCDS results representing unadjusted and adjusted counts respectively for *Eulemur sanfordi* across eleven sites in northern Madagascar. Conventional distance sampling (CDS) analyses were performed using a pooled detection function, f(0) whereas multiple covariate distance sampling (MCDS) analyses modeled detectability as a function of the covariate for site identity (SITE). The key function used in all analyses was the hazard rate function. The addition of adjustment terms was not found to improve the fit of the models to the data. Variance was estimated analytically using the delta method and via a bootstrap resampling procedure (b = 400) that treated each repetition of the transect as the unit for analysis. The %CV is provided for both methods. The model for which support was considered the greatest is indicated in bold print.

Covariates	Number of parameters	ΔAIC	AIC	Density Estimate	%CV	Bootstrap Density	Bootstrap %CV
				Eulemur sanfordi			
				CDS: f(0) pooled			
	2	**0**	**1093.6**	**0.084 (0.051-0.14)**	**25.34**	**0.09 (0.05-0.15)**	**30.87**
				MCDS			
SITE	13	13.2205	1106.8	0.056 (0.044-0.072)	12.71	0.06 (0.05-0.07)	10.28

Table 2.6. Summary of model averaging results for *Propithecus perrieri* from 95% confidence set of models

Parameter	Estimate	Std. Error	Lower CI	Upper C	Relative Importance
Intercept	2.19	0.07	2.05	2.32	
Cluster Size	-0.22	0.13	-0.48	0.04	0.61
Survey Route	-0.24	0.16	-0.55	0.07	0.47
Substrate	-0.11	0.17	-0.43	0.22	0.28

Table 2.7. CDS and MCDS results representing unadjusted and adjusted counts respectively for *Propithecus perrieri* across eleven sites in northern Madagascar. Conventional distance sampling (CDS) analyses were performed using a pooled detection function, f(0) whereas multiple covariate distance sampling (MCDS) analyses modeled detectability as a function of the following covariates, including cluster size (CLU), substrate type (SUB), and survey route type (SUR). The key function used in all analyses was the half normal function. The addition of adjustment terms was not found to improve the fit of the models to the data. Variance was estimated analytically using the delta method and via a bootstrap resampling procedure (b = 400) that treated each repetition of the transect as the unit for analysis. The %CV is provided for both methods. Use of the delta method is unavailable for calculating variance when cluster size is included as a covariate in MCDS analyses. The model for which support was considered the greatest is indicated in bold print.

Covariates	Number of parameters	ΔAIC	AIC	Density Estimate	%CV	Bootstrap Density	Bootstrap %CV
Propithecus perrieri							
CDS: f(0) pooled							
	2	**0.034**	**1063.3**	**0.06 (0.04-0.07)**	**12.53**	**0.06 (0.05-0.07)**	**9.68**
MCDS							
CLU	2	0	1063.3	-	-	0.1 (0.041-0.18)	34.24
CLU + SUB	3	1.79	1065.1	-	-	0.1 (0.05-0.18)	35.18
SUB	2	1.93	1065.2	0.056 (0.04-0.07)	12.71	0.06 (0.05-0.07)	10.28
SUR	2	1.97	1065.2	0.056 (0.04-0.07)	12.71	0.06 (0.05-0.07)	9.95
CLU + SUR	3	1.98	1065.3	-	-	0.1 (0.05-0.18)	35.12
CLU + SUB + SUR	4	3.72	1067.0	-	-	0.1 (0.45-0.17)	35.62
SUB + SUR	3	3.93	1067.2	0.056 (0.044-0.072)	12.72	0.06 (0.05-0.07)	10.03

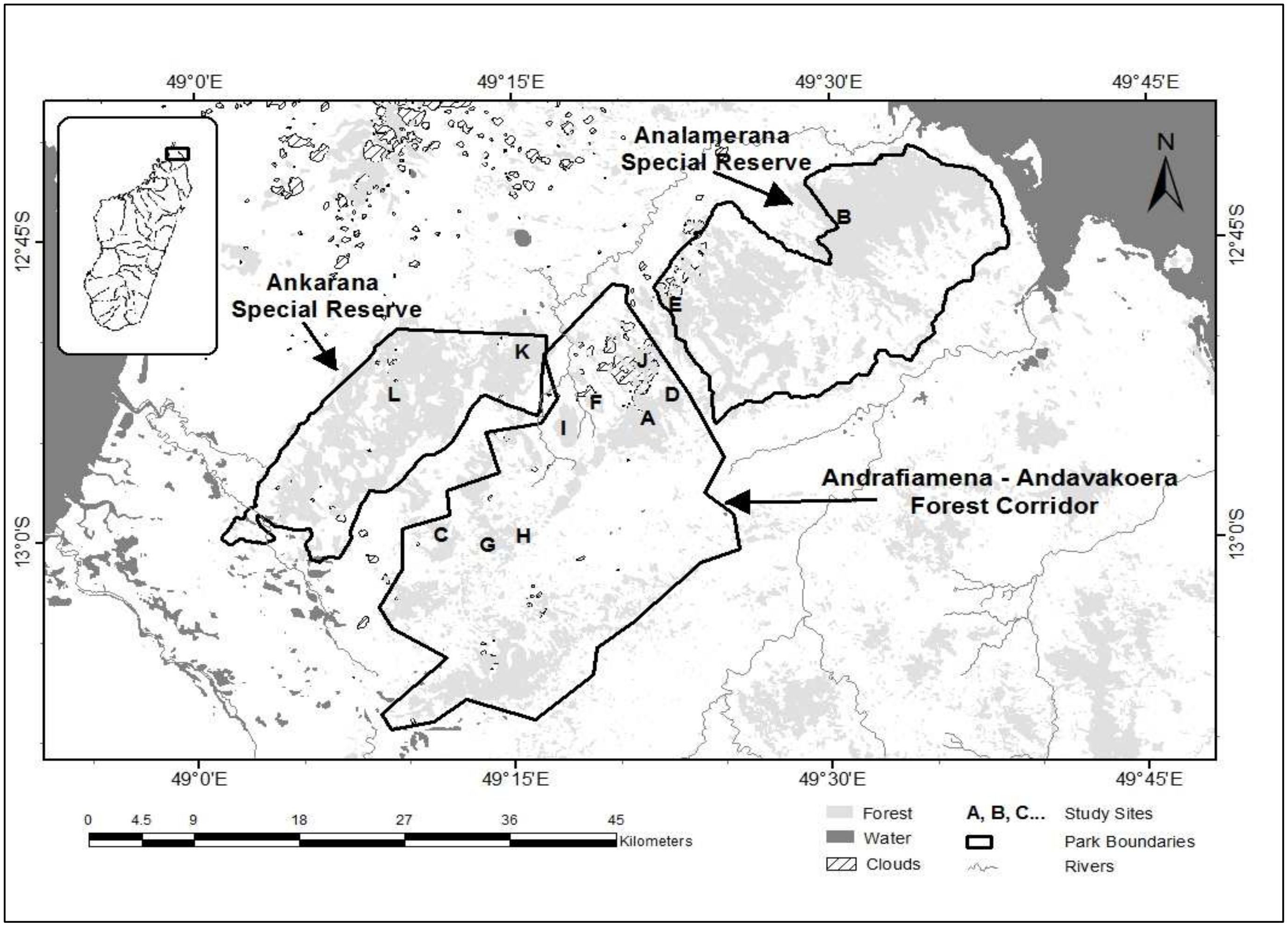

Fig. 2.1. A map of the study region with protected area boundaries for the Ankarana Special Reserve, the Analamerana Special Reserve and the Andrafiamena –Andavakoera Forest Corridor indicated. See Table 2.1. for site names.

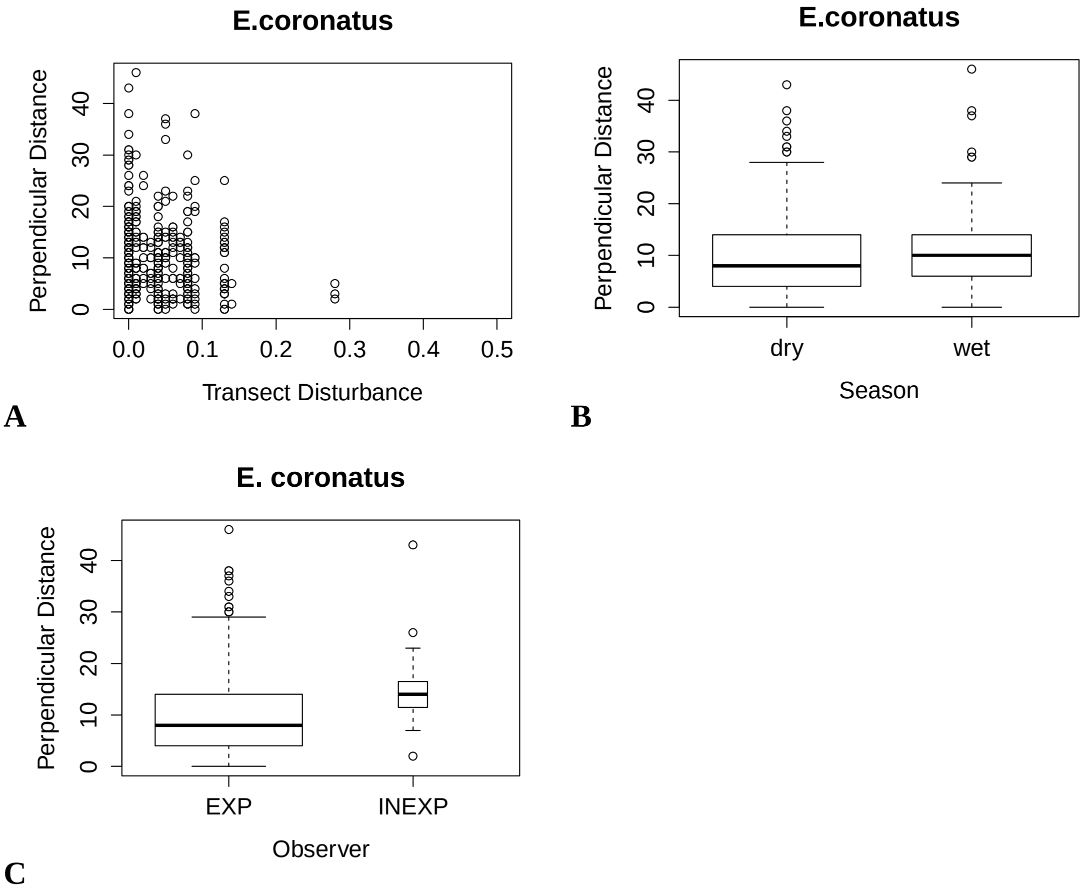

Figure 2.2. Perpendicular distance as a function of three covariates, A: Transect Disturbance, B: Observer Experience and C: Season. Transect Disturbance is measured as the number of encounters with humans, cattle, wild boar and traces of human activity such as fire, selective logging, harvesting of roots, honey medicines and mining per kilometer of transect walked; Observer experience: EXP= experienced, INEXP = inexperienced; Season: Dry or Wet) with the highest relative importance in a 95% confidence set of GLMMs for *Eulemur coronatus*. In figures B and C the width of the boxplots is proportional to the sample size per level, the horizontal lines in each box are the medians, the boxes define the hinge (i.e. 25% -75% quartile) and the lines outside the box are 1.5 times the hinge.

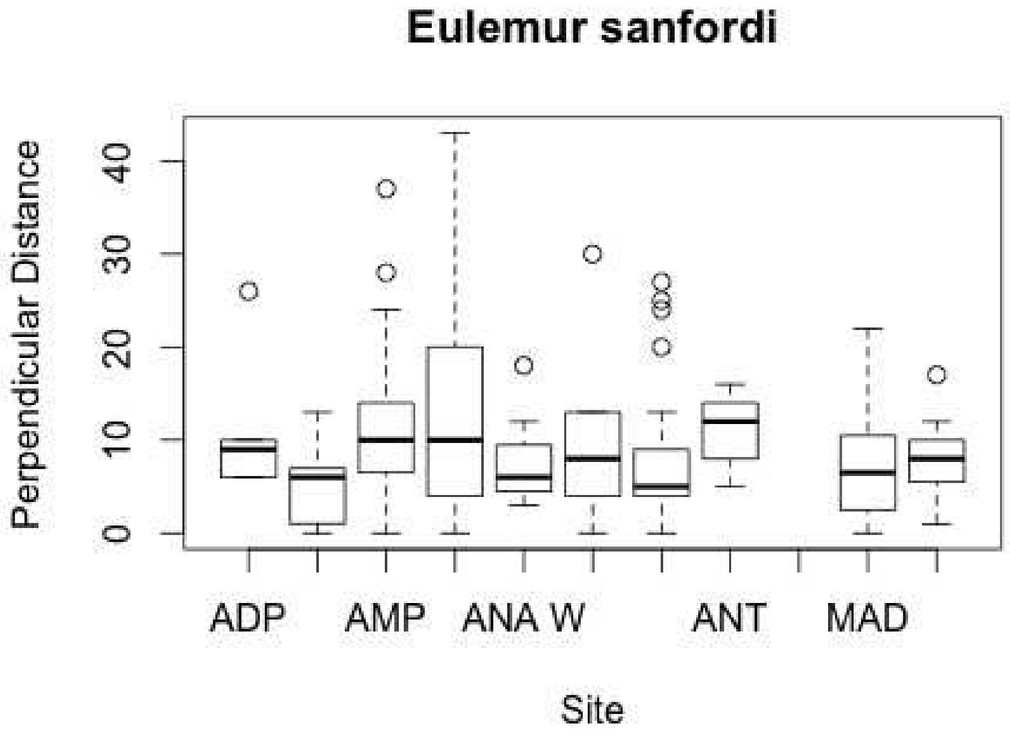

Figure 2.3. Site level variation in the distribution of perpendicular sighting distances for *Eulemur sanfordi*.

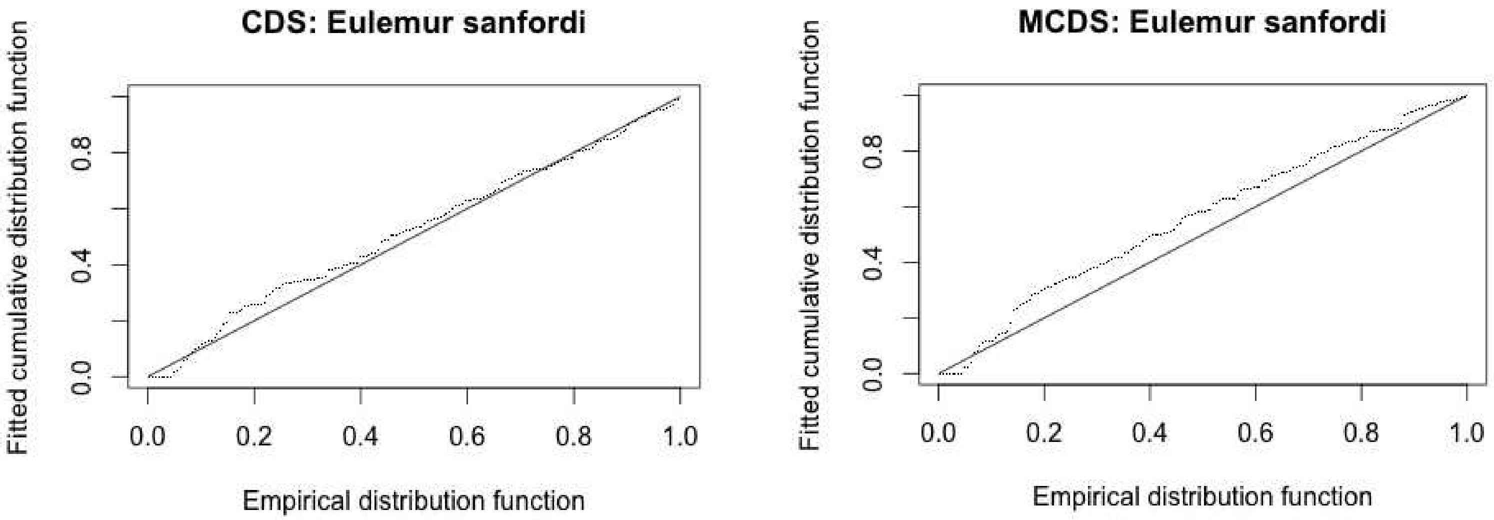

Figure 2.4. Differences in the Kolmogorov-Smirnov cumulative distribution function and the empirical distribution function in complementary CDS and MCDS analyses with *Eulemur sanfordi*.

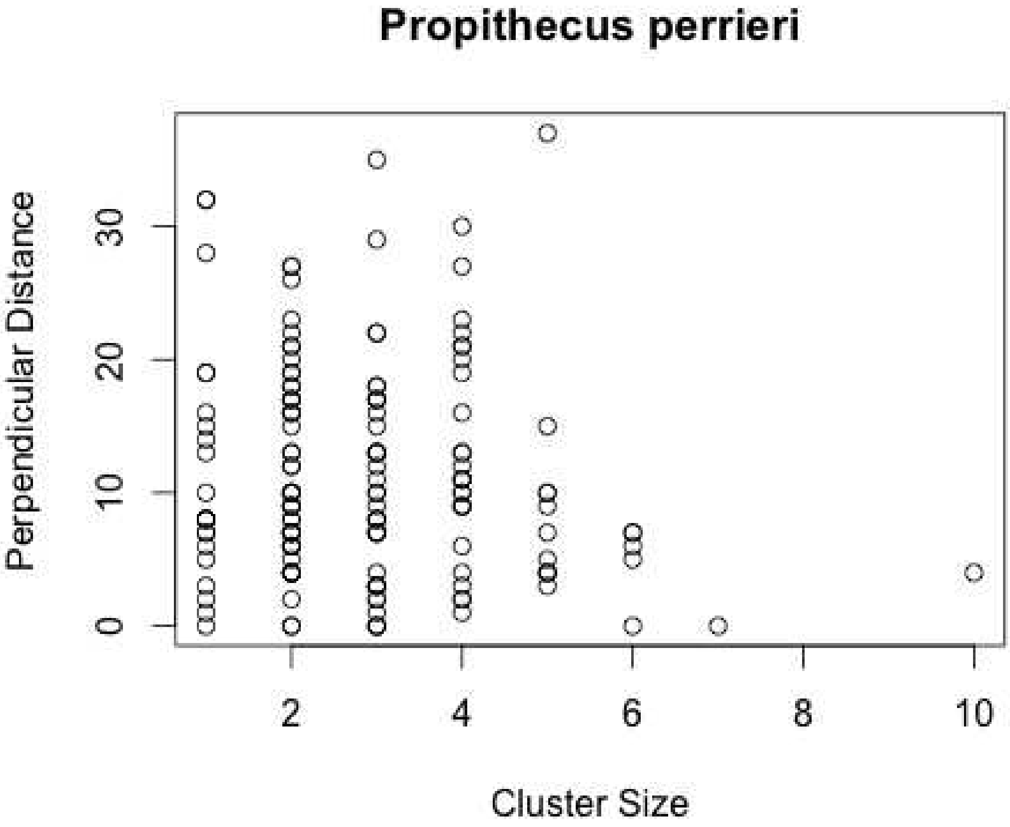

Fig. 2.5. Perpendicular distance plotted as a function of cluster size in *Propithecus perrieri*

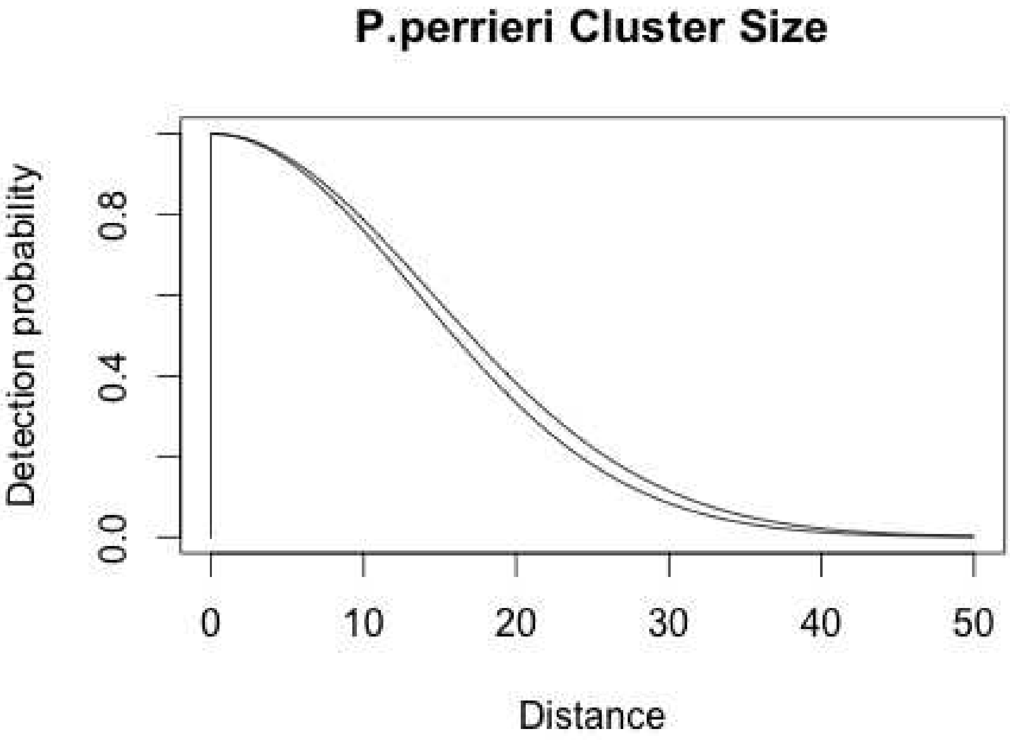

Fig. 2.6. Detection functions for *Propithecus perrieri* modeled as a function of the covariate, cluster size. The plot depicts the effect of two cluster sizes on the detection function. The higher line represents a cluster size of 3 while the lower line represents a cluster size of 4 demonstrating that larger groups are less detectable at greater distances from the line than smaller ones.

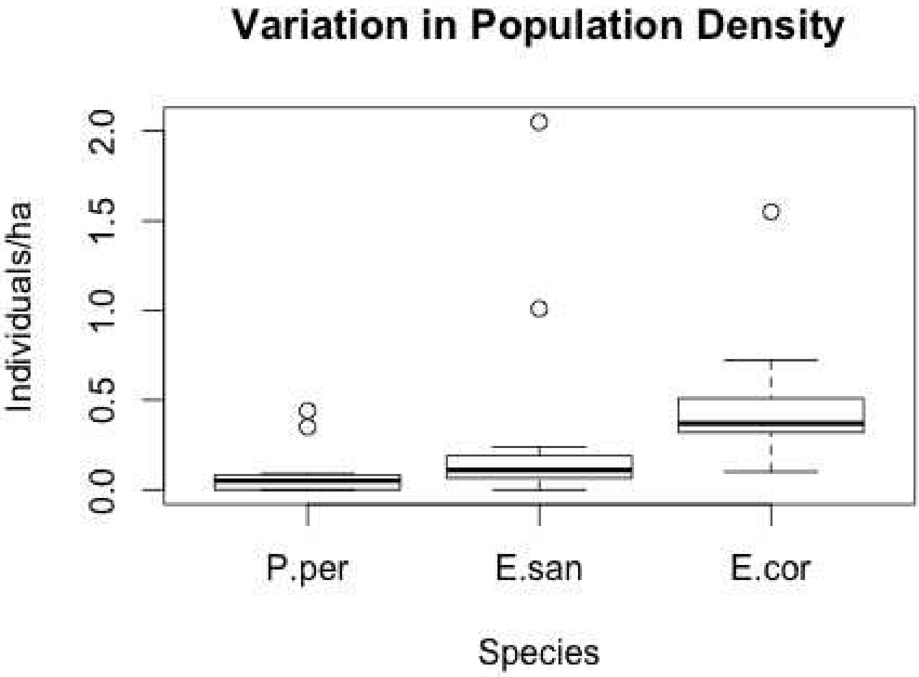

Fig. 2.7. Variation in population density for three primate species (*Eulemur coronatus*, *Eulemur sanfordi*, and *Propithecus perrieri*) across eleven forest fragments in northern Madagascar.

References

Akaike H (1973) Information theory and an extension of the maximum likelihood principle. Akademinai Kiado:267-281

Alldredge MW, Pollock KH, Simons TR, Johnson D (2006) Estimating detection probabilities from multiple-observer point counts. The Auk 123:1172-1182

Anderson D, Burnham K (2002) Avoiding pitfalls when using information-theoretic methods. The Journal of Wildlife Management 66:912-918

Anderson DR, Burnham KP, Lubow BC, Thomas L, Corn PS, Medica PA, Marlow RW (2001a) Field trials of line transect methods applied to estimation of desert tortoise abundance. The Journal of Wildlife Management 65:583-597

Anderson DR, Link WA, Johnson DH, Burnham KP (2001b) Suggestions for Presenting the Results of Data Analyses. The Journal of Wildlife Management 65:373-378

Arrigo-Nelson S, Wright P (2004) Survey results from Ranomafana National Park: new evidence for the effects of habitat preference and disturbance on the distribution of Hapalemur. Folia Primatologica 75:331-334

Aureli F, Schaffner CM, Boesch C, Bearder SK, Call J, Chapman CA, Connor R, Di Fiore A, Dunbar RIM, Henzi SP (2008) Fission Fusion Dynamics. Current Anthropology 49:627-654

Banks MA, Ellis ER, Antonio, Wright PC (2007) Global population size of a critically endangered lemur, Perrier's sifaka. Animal Conservation 10

Bates D, Maechler M (2010) lme4: Linear mixed-effects models using S4 classes. R package. In, Version 0.999375–34 edn

Bolker B, Brooks M, Clark C, Geange S, Poulsen J, Stevens MH, White J-S (2009) Generalized linear mixed models: a practical guide for ecology and evolution. Trends in ecology & evolution 24:127-135

Borries C, Larney E, Kreetiyutanont K, Koenig A (2002) The diurnal primate community in a dry evergreen forest in Phu Khieo Wildlife Sanctuary, Northeast Thailand. Natural History Bulletin Siam Society 50:75-88

Bourlière F (1985) Primate communities: Their structure and role in tropical ecosystems. International Journal of Primatology 6

Brenneman RA, Johnson S, E. , Bailey C, A. , Ingraldi C, Delmore KE, Wyman TM, Andriamaharoa HE, Ralainasolo FB, Ratsimbazafy JH, Louis EE (2011) Population genetics and abundance of the Endangered grey-headed lemur Eulemur cinereiceps in south-east Madagascar: assessing risks for fragmented and continuous populations. Oryx 46:298-307

Brockelman W, Ali R (1987) Methods of surveying and sampling forest primate populations. In: Marsh CW, Mittermeier RA (eds) Primate conservation in the tropical rain forest. Alan R. Liss, Inc., New York, NY, pp 23-62

Brown K, Gurevitch J (2004) Long-term impacts of logging on forest diversity in Madagascar. Proceedings of the National Academy of Sciences of the United States of America 101:6045-6049

Buckland S, Borchers D, Johnston A, Henrys P, Marques T (2007) Line transect methods for plant surveys. Biometrics 63:989-998

Buckland ST, Anderson DR, Burnham KP, Laake JL, Borchers DL, Thomas L (2001) Introduction to Distance Sampling. Oxford University Press, Oxford, UK

Buckland ST, Anderson DR, Burnham KP, Laake JL, Borchers DL, Thomas L (2004) Advanced distance sampling. Oxford University Press, Oxford, UK

Buckland ST, Plumptre AJ, Thomas L, Rexstad EA (2010a) Design and Analysis of Line Transect Surveys for Primates. International Journal of Primatology 31:833-847

Buckland ST, Plumptre AJ, Thomas L, Rexstad EA (2010b) Line Transect Sampling of Primates: Can Animal-to-Observer Distance Methods Work? International Journal of Primatology 31:485–499

Buřivalová Z (2011) Remote Sensing of Vegetation in Conservation: A Case Study from the Dry and Transitional Forests of Andrafiamena, Northern Madagascar. In: Université de Geneve and Conservatoire et Jardin Botanique de la Ville de Geneve. Université de Geneve, Geneva, Switzerland, pp 89

Burnham K, Anderson D (2002) Model selection and multi-model inference: a practical information-theoretic approach. Springer-Verlag, New York, NY

Burnham KP, Anderson DR, Huyvaert KP (2010) AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. Behavioral Ecology and Sociobiology 65:23-35

Cardiff S, Befourouack J (2003) The Reserve Spéciale d'Ankarana. In: Goodman SM, Benstead JP (eds) The Natural History of Madagascar. University of Chicago Press, Chicago, IL, pp 1501-1507

Chapman C, Bonnell TR, Gogarten JF, Lambert JE, Omeja PA, Twinomugisha D, Wasserman MD, Rothman JM (2012) Are Primates Ecosystem Engineers? International Journal of Primatology 34

Chapman C, Struhsaker T, Skorupa J, Snaith T, Rothman J (2010) Understanding long-term primate community dynamics: implications of forest change. Ecological Applications 20:179-191

Chapman CA, Balcomb SR, Gillespie TR, Skorupa JP, Struhsaker TT (2000) Long-Term Effects of Logging on African Primate Communities: a 28-Year Comparison From Kibale National Park, Uganda. Conservation Biology 14:201-217

Chatterjee S, Hadi AS (2013) Regression analysis by example. John Wiley & Sons, Inc., Hoboken, NJ

Colquhoun IC (1993) The socioecology of Eulemur macaco: A preliminary report. In: Kappeler PM, Ganzhorn JU (eds) Lemur social systems and their ecological basis. Plenum Press, New York, pp 11-23

Colquhoun IC (2007) Anti-Predator Strategies of Cathemeral Primates: Dealing with Predators of the Day and the Night. In: Gursky SL, Nekaris K (eds) Primate Anti-predator Strategies. Springer, New York, NY., pp 146-172

Defler TR, Pintor D (1985) Censusing primates by transect in a forest of known primate density. International Journal of Primatology 6

Dewar R, Richard A (2012) Madagascar: A History of Arrivals, What Happened, and Will Happen Next*. Annual Review of Anthropology

Dochtermann NA, Jenkins SH (2010) Developing multiple hypotheses in behavioral ecology. Behavioral Ecology and Sociobiology 65:37-45

Dransfield S (2003) Poaceae, Bambuseae, Bamboos In: Goodman SM, Benstead JP (eds) The Natural History of Madagascar. Chicago University Press, Chicago, IL, pp 467-471

Du Puy DJ, Moat J (1996) A refined classification of the primary vegetation of Madagascar based on the underlying geology: using GIS to map its distribution and to assess its …. In: Lourenço WR (ed) Proceedings of the International Symposium on the

Biogeography de Madagascar. Editions de l'ORSTROM, Paris, Paris, France, pp 205-218 + 3 maps

Du Puy DJ, Moat J (2003) Using Geological Substrate to Identify and Map Primary Vegetation Types in Madagascar and the Implications for Planning Biodiversity Conservation. In: Goodman SM, Benstead JP (eds) The Natural History of Madagascar. University of Chicago Press, Chicago, IL, pp 51-66

Erkert HG, Kappeler PM (2004) Arrived in the light: diel and seasonal activity patterns in wild Verreaux?s sifakas (Propithecus v. verreauxi; Primates: Indriidae). Behavioral Ecology and Sociobiology 57:174-186

Fashing P, Cords M (2000) Diurnal primate densities and biomass in the Kakamega Forest: an evaluation of census methods and a comparison with other forests. American Journal of Primatology 50:139-152

Fleagle JG, Janson C, Reed K (1999) Primate communities. Cambridge University Press, Cambridge, UK

Fowler SV, Chapman P, Checkley D, Hurd S, McHale M, Ramangason GS, Randriamasy JE, Stewart P, Walters R, Wilson JM (1989) Survey and management proposals for a tropical deciduous forest reserve at Ankarana in northern Madagascar. Biological Conservation 47:297-313

Freed B (2006) Polyspecific Associations of Crowned Lemurs and Sanford's Lemurs in Madagascar. In: Gould L, Sauther M (eds) Lemurs. Springer Science, New York, NY, pp 111-131

Freed BZ (1996) Co-occurrence among crowned lemurs (Lemur coronatus) and Sanford's lemurs (Lemur fulvus sanfordi) of Madagascar. In: Department of Anthropology. Washington University, pp 450

Ganzhorn JU, Wright PC, Ratsimbazafy J (1999) Primate communities: Madagascar. In: Fleagle J, Janson C, Reed K (eds) Primate Communities. Cambridge University Press, Cambridge, UK, pp 75-89

Gelman A (2008) Scaling regression inputs by dividing by two standard deviations. Statistics in medicine 27:2865-2873

Grueber C, Nakagawa S, Laws R, Jamieson I (2011) Multimodel inference in ecology and evolution: challenges and solutions. Journal of Evolutionary Biology 24:699-711

Hanya G, Yoshihiro S, Zamma K, Kubo R, Takahata Y (2003) New method to census primate groups: estimating group density of Japanese macaques by point census. American Journal of Primatology 60:43-56

Hassel-Finnegan HM, Borries C, Larney E, Umponjan M, Koenig A (2008) How Reliable are Density Estimates for Diurnal Primates? International Journal of Primatology 29

Hawkins AFA, Chapman P, Ganzhorn JU, Bloxam QMC, Barlow SC, Tonge SJ (1990) Vertebrate Conservation in Ankarana special reserve, Northern Madagascar. Biological Conservation 54:83-110

Hemingway CA, Bynum N (2005) The influence of seasonality on primate diet and ranging. In: Brockman DK, van Schaik CP (eds) Seasonality in primates: Studies of living and extinct human and non-human primates. Cambridge University Press, Cambridge, UK, pp 57-105

Heymann E, Buchanan-Smith H (2000) The behavioural ecology of mixed-species troops of callitrichine primates. Biological Reviews of the Cambridge Philosophical Society 75:169-190

Hilário R, Rodrigues F, Chiarello A, Mourthé I (2012) Can roads be used as transects for primate population surveys? Folia Primatologica 83:47-55

Holger S (2010) Simple means to improve the interpretability of regression coefficients. Methods in Ecology and Evolution 1:103-113

Humbert H, Cours-Darne G (1965) Carte Internationale de Tapis Vegetale: Madagascar, 1:1,000,000. Travaux de la Section Scientifique et Technique de l'Institut Français de Pondichéry (hors serie), Toulouse, France

Irwin MT (2008) Diademed Sifaka (Propithecus diadema) Ranging and Habitat Use in Continuous and Fragmented Forest: Higher Density but Lower Viability in Fragments? Biotropica 40:231-240

Johns A, D. (1985a) Differential detectability of primates between primary and selectively logged habitats and implications for population surveys. American Journal of Primatology 8

Johns A, Skorupa J (1987) Responses of rain-forest primates to habitat disturbance: a review. International Journal of Primatology 8:157-191

Johns AD (1985b) Differential detectability of primates between primary and selectively logged habitats and implications for population surveys. American Journal of Primatology 8:31-36

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

Jury MR (2003) The Climate of Madagascar. In: Goodman SM, Benstead JP (eds) The Natural History of Madagascar. University of Chicago Press, Chicago, IL, pp 75-85

Kappeler PM, Erkert HG (2003) On the move around the clock: correlates and determinants of cathemeral activity in wild redfronted lemurs (Eulemur fulvus rufus). Behavioral Ecology and Sociobiology 54:359-369

Karpanty S, Wright PC (2007) Predation on lemurs in the rainforest of Madagascar by multiple predator species: observations and experiments. In: Gursky SL (ed) Primate anti-predator strategies. Springer, New York, NY., pp 77-99

Kullback S, Leibler RA (1951) On information and sufficiency. The Annals of Mathematical Statistics 22:79-86

Laurance W, Useche D, Rendeiro J, Kalka M, Bradshaw C, Sloan S, Laurance S, Campbell M, Abernethy K, Alvarez P, Arroyo-Rodriguez V, Ashton P, Benítez-Malvido J, Blom A, Bobo K, Cannon C, Cao M, Carroll R, Chapman C, Coates R, Cords M, Danielsen F, De Dijn B, Dinerstein E, Donnelly M, Edwards D, Edwards F, Farwig N, Fashing P, Forget P-M, Foster M, Gale G, Harris D, Harrison R, Hart J, Karpanty S, Kress W, Krishnaswamy J, Logsdon W, Lovett J, Magnusson W, Maisels F, Marshall A, McClearn D, Mudappa D, Nielsen M, Pearson R, Pitman N, van der Ploeg J, Plumptre A, Poulsen J, Quesada M, Rainey H, Robinson D, Roetgers C, Rovero F, Scatena F, Schulze C, Sheil D, Struhsaker T, Terborgh J, Thomas D, Timm R, Urbina-Cardona J, Vasudevan K, Wright S, Arias-G J, Arroyo L, Ashton M, Auzel P, Babaasa D, Babweteera F, Baker P, Banki O, Bass M, Bila-Isia I, Blake S, Brockelman W, Brokaw N, Brühl C, Bunyavejchewin S, Chao J-T, Chave J, Chellam R, Clark C, Clavijo J, Congdon R, Corlett R, Dattaraja H, Dave C, Davies G, Beisiegel B, da Silva R, Di Fiore A, Diesmos A, Dirzo R, Doran-Sheehy D, Eaton M, Emmons L, Estrada A (2012) Averting biodiversity collapse in tropical forest protected areas. Nature 489:290-294

Lehman SM (2006) Effects of Transect Selection and Seasonality on Lemur Density Estimates in Southeastern Madagascar. International Journal of Primatology 27

Lehman SM, Mayor M (2004) Dietary patterns in Perrier's sifakas (Propithecus diadema perrieri): a preliminary study. American Journal of Primatology 62:115-122

Letsara R (2007) Inventaire rapide de la flore et de la vegetation du corridor forestier d'Andrafiamena. In: Conservation International Rapid Assessment Program Report, Alexandria, VA

Marques FFC, Buckland S (2004) Covariate models for the detection function. In: Buckland ST, Anderson DR, Burnham KP, Laake JL, Borchers DL, Thomas L (eds) Advanced Distance Sampling. Oxford University Press, Oxford, UK, pp 31-47

Marques T, Thomas L, Fancy S, Buckland S (2007) Improving estimates of bird density using multiple-covariate distance sampling. The Auk

Marques TA, Buckland ST, Bispo R, Howland B (2012a) Accounting for animal density gradients using independent information in distance sampling surveys. Statistical Methods & Applications 22:67-80

Marques TA, Buckland ST, Bispo R, Howland B (2012b) Accounting for animal density gradients using independent information in distance sampling surveys. Statistical Methods & Applications 22

Marshall A, Lovett J, White P (2008) Selection of line-transect methods for estimating the density of group-living animals: lessons from the primates. American Journal of Primatology 70:452-462

Meyers D, Ratsirarson J (1989) Distribution and conservation of two endangered sifakas in northern Madagascar. Primate Conservation 10:81-86

Meyers DM (1993) The effects of resource seasonality on behavior and reproduction in the golden-crowned sifaka (Propithecus tattersalli, Simons, 1988) in three Malagasy forests. In: Department of Biological Anthropology and Anatomy. Duke University, Durham, NC, pp 230

Meyers DM, Wright PC (1993) Resource tracking: food availability and Propithecus seasonal reproduction. In: Lemur social systems and their ecological basis. . Plenum Press, New York, NY., pp 179-192

Milner-Gulland E, Rowcliffe J (2007) Conservation and sustainable use: a handbook of techniques. Oxford University Press, Oxford, UK

Mitani JC, Struhsaker TT, Lwanga JS (2000) Primate community dynamics in old growth forest over 23.5 years at Ngogo, Kibale National Park, Uganda: implications for conservation and census methods. International Journal of Primatology 21:269-286

Mittermeier RA, Louis EE, Richardson M, Schwitzer C, Langrand O, Rylands AB, Hawkins F, Rajaobelina S, Ratsimbazafy J, Rasoloarison R, Roos C, Kappeler PM, MacKinnon J (2010) Lemurs of Madagascar. Conservation International, Arlington, VA.

Müller P, Velo A, Raheliarisoa E-O, Zaramody A, Curtis DJ (2000) Surveys of sympatric lemurs at Anjamena, north-west Madagascar. African Journal of Ecology 38:248-257

Mutschler T (2003) Alaotran gentle lemur: Some aspects of its behavioral ecology. Evolutionary Anthropology: Issues, News, and Reviews 11:101-104

Nijman V (2001) Effects of behavioural changes due to habitat disturbance on density estimation of rain forest vertebrates, as illustrated by gibbons (primates: Hylobatidae). In: Hillegers PJM, de Iongh HH (eds) The Balance between Biodiversity Conservation and Sustainable Use of Tropical Rain Forests: Workshop Proceedings Tropenbos, Wageningen, Netherlands, pp 217-225

Nijman V, Nekaris K (2012) Loud calls, startle behaviour, social organisation and predator avoidance in arboreal langurs (Cercopithecidae: Presbytis). Folia primatologica 83:274-287

NRC (1981) Techniques for the study of primate population ecology. National Academy Press., Washington, DC

Ogutu JO, Bhola N, Piepho HP, Reid R (2006) Efficiency of strip- and line-transect surveys of African savanna mammals. Journal of Zoology 269:149–160

Otto MC, Pollock KH (1990) Size bias in line transect sampling: a field test. Biometrics 46:239-245

Overdorff D, Johnson SE (2003) *Eulemur*, true lemurs. In: Goodman SM, Benstead JP (eds) The Natural History of Madagascar. Chicago University Press, Chicago, IL, pp 1320-1324

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

Peres C (1999) General guidelines for standardizing line-transect surveys of tropical forest primates. Neotropical Primates 7:11-16

Petrovan S, Ward A, Wheeler P (2011) Detectability counts when assessing populations for biodiversity targets. PloS one 6:e24206

Plumptre A, Cox D (2006) Counting primates for conservation: primate surveys in Uganda. Primates 47:65-73

Plumptre AJ (2000a) Monitoring mammal populations with line transect techniques in African forests. Journal of Applied Ecology 37:356-368

Plumptre AP (2000b) Monitoring mammal populations with line transect techniques in African forests. Journal of Applied Ecology 37

R Core Development Team (2013) R: Language and Environment for Statistical Computing. In. R Foundation for Statistical Computing, Vienna, Austria

Raherilalao MJ (2007) Les oiseax de la forêt sèche, semi-caducifoliée d'Ampatsona, Andrafiamena. In: Conservation International Rapid Assessment Program Report, Alexandria, VA

Ratsirarson J, Ranaivonasy J (2002) Ecologie des Lémuriens dans la forêt littorale de Tampolo. Lemur News 7:26-30

Razafimaharatra B (2007) Reptiles et amphibiens de la forêt d'Andrafiamena. In: Conservation International Rapid Assessment Program Report, Alexandria, VA

Renato H, Flávio R, Adriano C, Italo M (2012) Can roads be used as transects for primate population surveys? Folia Primatologica 83:47-55

Rhodes JR, McAlpine CA, Zuur AF, Smith GM, Ieno EN (2009) GLMM Applied on the Spatial Distribution of Koalas in a Fragmented Landscape. In: Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (eds) Mixed Effects Models and Extensions with R. Springer, New York, NY.

Richard AF, Dewar RE (1991) Lemur ecology. Annual Review of Ecology and Systematics 22:145-175

Ross C, Reeve N (2003) Survey and census methods: population distribution and density. In: Setchell JM, Curtis DJ (eds) Field and Laboratory Methods in Primatology. Cambridge University Press, Cambridge, UK, pp 90-109

Rovero F, Struhsaker TT, Marshall AR, Rinne TA, Pedersen UB, Butynski TM, Ehardt CL, Mtui AS (2006) Abundance of Diurnal Primates in Mwanihana Forest, Udzungwa Mountains, Tanzania. International Journal of Primatology 27:675-697

Savage A, Thomas L, Leighty K, Soto L, Medina F (2010) Novel survey method finds dramatic decline of wild cotton-top tamarin population. Nature communications 1:30

Schipper J, Chanson J, Chiozza F, Cox N, Hoffmann M, Katariya V, Lamoreux J, Rodrigues A, Stuart S, Temple H, Baillie J, Boitani L, Lacher T, Mittermeier R, Smith A, Absolon D, Aguiar J, Amori G, Bakkour N, Baldi R, Berridge R, Bielby J, Black P, Blanc J, Brooks T, Burton J, Butynski T, Catullo G, Chapman R, Cokeliss Z, Collen B, Conroy J, Cooke J, da Fonseca G, Derocher A, Dublin H, Duckworth J, Emmons L, Emslie R, Festa-Bianchet M, Foster M, Foster S, Garshelis D, Gates C, Gimenez-Dixon M, Gonzalez S, Gonzalez-Maya J, Good T, Hammerson G, Hammond P, Happold D, Happold M, Hare J, Harris R, Hawkins C, Haywood M, Heaney L, Hedges S, Helgen K, Hilton-Taylor C, Hussain S, Ishii N, Jefferson T, Jenkins R, Johnston C, Keith M, Kingdon J, Knox D, Kovacs K, Langhammer P, Leus K, Lewison R, Lichtenstein G, Lowry L, Macavoy Z, Mace G, Mallon D, Masi M, McKnight M, Medellín R, Medici P, Mills G, Moehlman P, Molur S, Mora A, Nowell K, Oates J, Olech W, Oliver W, Oprea M, Patterson B, Perrin W, Polidoro B, Pollock C, Powel A, Protas Y, Racey P, Ragle J, Ramani P, Rathbun G (2008) The status of the world's land and marine mammals: diversity, threat, and knowledge. Science 322:225-230

Schmidt B (2003) Count data, detection probabilities, and the demography, dynamics, distribution, and decline of amphibians. Comptes rendus biologies 326 Suppl 1:24

Scholz F, Kappeler PM (2004) Effects of Seasonal Water Scarcity on the Ranging Behavior of Eulemur fulvus rufus. International Journal of Primatology 25:599-613

Schwitzer C, Mittermeier RA, Davies N, Johnson S, Ratsimbazafy J, Razafindramanana J, Louis Jr. EE, Rajaobelina S (2013) Lemurs of Madagascar: A Strategy for Their Conservation 2013–2016. SSC Primate Specialist Group, Bristol Conservation and Science Foundation, and Conservation International, Bristol, UK

Setchell JM, Curtis DJ (2011) Field and laboratory methods in primatology: a practical guide. Cambridge University Press

Stephens PA, Zaumyslova OY, Miquelle DG, Myslenkov AI, Hayward GD (2006) Estimating population density from indirect sign: track counts and the Formozov–Malyshev–Pereleshin formula. Animal Conservation 9

Tan C (2000) Behavior and ecology of three sympatric bamboo lemur species (Genus: Hapalemur) in Ranomafana National Park, Madagascar. . In: Anthropology. The State University of New York at Stony Brook, Stony Brook, NY.

Terborgh J, Estes JA (2010) Trophic cascades: predators, prey, and the changing dynamics of nature. Island Press, Washington, DC

Thomas L, Buckland S, Rexstad E, Laake J, Strindberg S, Hedley S, Bishop J, Marques T, Burnham K (2010) Distance software: design and analysis of distance sampling surveys for estimating population size. The Journal of Applied Ecology 47:5-14

Treves A, Palmqvist P (2007) Reconstructing hominin interactions with mammalian carnivores (6.0–1.8 Ma). In: Gursky SL, Nekaris K (eds) Primate anti-predator strategies. Springer, New York, NY., pp 355-381

Trombulak SC, Frissell CA (2000) Review of Ecological Effects of Roads on Terrestrial and Aquatic Communities. Conservation Biology 14:18-30

Tutin C, Ham R, White L, Harrison M (1997) The primate community of the Lopé Reserve, Gabon: diets, responses to fruit scarcity, and effects on biomass. American Journal of Primatology 42:1-24

Vasey N (2000) Niche separation in Varecia variegata rubra and Eulemur fulvus albifrons: I. Interspecific patterns. American journal of physical anthropology 112:411-431

Vogel E, Haag L, Mitra-Setia T, van Schaik C, Dominy N (2009) Foraging and ranging behavior during a fallback episode: Hylobates albibarbis and Pongo pygmaeus wurmbii compared. American Journal of Physical Anthropology 140:716-726

Walsh PD, White LJT (1999) What It Will Take to Monitor Forest Elephant Populations. Conservation Biology 13:1194-1202

Waltert M, Abegg C, Ziegler T, Hadi S, Priata D, Hodges K (2008) Abundance and community structure of Mentawai primates in the Peleonan forest, north Siberut, Indonesia. Oryx 42:375-379

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

Williams BK, Nichols JD, Conroy MJ (2002) Analysis and management of animal populations: modeling, estimation, and decision making. Academic Press, San Diego, CA

Williams R, Thomas L (2009) Cost-effective abundance estimation of rare animals: Testing performance of small-boat surveys for killer whales in British Columbia. Biological Conservation 142:1542-1547

Wright P (1999) Lemur traits and Madagascar ecology: coping with an island environment. American Journal of Physical Anthropology 42:31-72

Wright P (2007) Considering climate change effects in lemur ecology and conservation. In: Gould L, Sauther ML (eds) Lemurs: Ecology and Adaptation. Springer, New York, NY, pp 385-401

Wright P, Tecot S, Erhart E, Baden A, King S, Grassi C (2011) Frugivory in four sympatric lemurs: implications for the future of Madagascar's forests. American Journal of Primatology 73:585-602

Wright PC (1998) Impact of predation risk on the behaviour of Propithecus diadema edwardsi in the rain forest of Madagascar. Behaviour 135:483-512

Wright PC, Razafindratsita VR, Pochron ST, Jernvall J (2005) The key to Madagascar frugivores. In: Dew JL, Boubli JP (eds) Tropical fruits and frugivores: The search for strong interactors. Springer, Dordrecht, Netherlands, pp 121-138

Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009) Mixed effects models and extensions in ecology with R. Springer, New York, NY.

CHAPTER THREE:

Factors Driving Abundance in Three Diurnal Primate Species in the Dry Deciduous and Semi-Evergreen Forests of Northern Madagascar

Abstract

Increasingly, wild primates are coming into contact with human populations and attempts to distinguish the influence of human activities from natural variability in the environment in determining primate abundance represents an important challenge for research aimed at refining ecological theory and providing informed management plans for conservation. The diurnal primates of northern Madagascar are exposed to a variety of human activities including fragmentation of their habitat through large-scale fires, selective logging, habitat clearing for charcoal production, swidden agriculture and clearing to support stock grazing. In some areas hunting may also influence primate populations. I use multivariate statistical techniques and model averaging to compare the role of these factors along with natural characteristics of the environment including habitat type, tree dendrometrics, the spatial attributes of forest fragments and interactive effects at the community level in driving abundance in three primate species, *Propithecus perrieri*, *Eulemur sanfordi* and *Eulemur coronatus* across eleven forest fragments from this region. I use differences in species attributes including dietary preferences, body size and capacity for dispersal to generate predictions under prominent ecological theory. The results indicate that differences in resource availability provide the most likely explanation for patterns of primate abundance within this community. Findings from two species that form mixed-species associations (i.e. *E. coronatus* and *E. sanfordi*) suggests mutual benefits for these taxa, likely through increased foraging although the potential role of environmental filtering in augmenting sympatric population densities can't be rejected. Alternatively, *Propithecus* populations were most strongly influenced by the substrate type supporting the predominant vegetation. Further, population abundance in this species was positively affected by small to moderate disturbances while large-scale fires clearly depressed *Propithecus* numbers. Finally, the abundance of the top ten dry season food species was also an important predictor of population density for *P. perrieri*. The results reinforce previous theories suggesting that as an adaptive radiation lemurs may have evolved under selective pressure for traits that confer resilience to harsh conditions and an unpredictable environment. While humans impose local threats potentially analogous to the challenges of this highly variable climate, habitat loss is advancing rapidly in this region and could lead to future extirpations of lemur populations.

Introduction

Studies of wildlife abundance provide a central framework for a great deal of ecological theory. Understanding the factors that limit wildlife abundance and distributional patterns allows us to form links between pattern and process in the natural world (Wiens and Moss 2005). One theoretical application for studies of primate abundance is their use in gaining insights into mechanisms for community structure

(Bourlière 1985; Reed and Fleagle 1995; Ganzhorn et al. 1997; Fleagle et al. 1999). Indeed even the somewhat anomalous finding that total primate community biomass finds consistent correlates across geographic regions despite wide variation in species composition, habitat type and climate suggests that some underlying mechanisms should exist for all primate communities (Fleagle et al. 1999). Studying these and related processes in the context of individual primate communities may help to shed light on, as of yet, poorly known causalities that find broad application across the primate Order. In particular and despite important gains from previous work (e.g. Waterman et al. 1988, Stevenson 2001), broadly speaking, the determinants of primate abundance remain poorly understood (Janson and Chapman 1999). Furthermore, in the case of the all too familiar scenario where primates have been heavily influenced by habitat change and human disturbances the results will provide valuable insights into developing new strategies for the conservation of not only individual species or guilds but entire communities of primates.

To contribute to our understanding of the mechanisms involved in shaping patterns of abundance in primate communities, in this chapter I attempt to assess the role of the natural environment and humans in determining patterns of primate abundance in eleven forest fragments of variable disturbance history, spatial attributes, habitat characteristics and primate composition in the Diana region of northern Madagascar. The region supports four diurnal primate species including two frugivorous species, *Eulemur coronatus* (average body mass: 1.18 kg) and *Eulemur sanfordi* (average body mass: 1.85 kg), one bamboo specialist, *Hapalemur occidentalis* (average body mass: 1.03 kg) and one folivore-frugivore, *Propithecus perrieri* (average body mass: 4.48 kg; data from Terranova and Coffman 1997 and Louis and Banks, unpublished results). In heavily human influenced landscapes, how do the different species from this community respond to human pressures when controlling for differences in natural ecology? Furthermore, what insights into the determinants of community structure can we gain by better understanding correlates to lemur abundance in several forest fragments differing in spatial dimension, habitat characteristics and abiotic environmental variables?

In previous studies what have been the principal factors that determine the numbers of individual primate species in the wild? Indeed the answer to this question relative to the number and intensity of different factors relies heavily on the defining characteristics of the study system, but the many of the most widespread determinants of abundance are represented under one of the following four major groupings, including: (1) food resources related to food availability and/or quality, (2) interspecific competition, (3) predation and (4) disease (Fleagle et al. 1999). It is important to note that a major weakness of this framework is that it ignores abiotic factors associated with environmental conditions. Still it is presumed that adopting this approach here is adequately comprehensive for initial investigations into the determinants of abundance in extant primate populations. Notably, all of the forest fragments included in the forthcoming analyses are situated within a maximum inter-fragment distance of 38 km, are not separated by any major geographical features, observe broadly similar climates and do not exceed 760 m in elevation. Nonetheless and despite these regional similarities, many abiotic factors vary over small spatial scales (e.g. edaphic, topographic, and hydrogeological differences) and the goal of this analysis is not to obscure the potential for these differences to influence primate abundance. To clarify, the major aim of using this framework however is to primarily evaluate the role of **biotic** factors in determining primate abundance. The role of fragmentation, habitat change and disturbance add another yet another dimension of determinants however one could envision how the impacts of disturbance are typically expressed relative to the effect that is exerted upon one of the four biotic factors above.

Through studies of patterns of primate abundance across a dynamic and heterogeneous landscape, is it also possible to gain insights into the determinants of community structure? Fragmented landscapes present research with a particularly ripe opportunity to evaluate differences in primate species composition across forest fragments that differ in many of the four biotic factors described above thereby allowing researchers to test hypotheses that concern the structuring of primate communities. , The use of functional groupings (e.g. trophic guilds, body size differences and dispersal abilities) has been informative in outlining patterns of species assembly in the lemur communities of Madagascar (Ganzhorn 1997). Ganzhorn (1997) used Fox's assembly rule (Fox 1987) to characterize primate community structure throughout much of Madagascar. This assembly rule postulates that species from different functional groups are more likely to be represented equally within communities before new species representing those same functional groups are duplicated within that community. The implications that such a distinct structuring mechanism should have on patterns of species turnover and the dynamics of extinction suggests that studies of abundance may provide some insights into how communities change over time. For example, by comparing forest fragments where several frugivorous primates that are likely to compete for resources persist with those where only a few are present, do we find that the phenomenon of density compensation applies? The ability to compare the abundance of these primates in different forest fragments presents an opportunity to test the potential role of these interactive effects at the community level (Peres and Dolman 2000; Chapman and Peres 2001).

In Madagascar there has been considerable success with finding ecological correlates to primate abundance through the quantity (Balko and Underwood 2005) and quality (Ganzhorn 1992; Ganzhorn 1995) of food resources. In general, folivorous monkeys appear to be more sensitive to differences in leaf quality rather than leaf production (Oates et al. 1990; Koenig et al. 1997) and this relationship also holds for folivorous strepsirhines in Madagascar (Ganzhorn 1992; Ganzhorn 1995; Ganzhorn 2002). Alternatively, studies of the role of food resources in driving frugivorous lemur numbers have been best explaining in terms of factors that augment fruit availability and production (White et al. 1995; Wright et al. 2005; Potts et al. 2009). Therefore both natural and human induced factors that lead to higher leaf quality are predicted to lead to increases in folivorous primate densities (Waterman et al. 1988; Oates et al. 1990), whereas factors that lead to increases in fruit production are expected to follow increases in frugivorous primate numbers (Stevenson 2001). In fragmented habitats for example, small and irregularly shaped fragments are known to possess fewer large trees, have reduced basal areas and canopy volumes (Laurance et al. 2000; Laurance et al. 2002; Godfrey and Irwin 2007). **Accordingly it is predicted that smaller and more irregularly shaped forest fragments will support reduced numbers of primate**

frugivores. The loss or absence of large trees is less likely to affect the availability of food for folivores (Ganzhorn 2002; Norconk et al. 2003; Powzyk and Mowry 2003). In fact the greater prevalence of edge effects in small fragments that are characterized by complex shapes may balance the effects of dessication through increases in leaf quality. This response is expected owing to the finding that increases in leaf quality are often coincident with the higher light levels and increased space for new growth that occurs along forest edges (Ganzhorn 1995; Lehman 2007). **Folivore densities are therefore not predicted to vary in response to changes in the size and shape of forest fragments.**

As forest fragments become more isolated there is a reduced probability of colonization by a dispersing animal (Hanski 1999). In the Diana region of northern Madagascar forest fragments are separated primarily by savanna but to a lesser degree by *Eucalyptus* plantations and agricultural fields. Although one of the primate species from this study system, *P. perrieri* is known to enter savanna habitat to visit isolated food trees (i.e. *Sclerocaryan* sp and *Mangifera indica* flowers and fruit), this species has never been observed to spend prolonged periods in such areas and always returns to closed canopy forests following feeding bouts in these open habitats. None of the other three diurnal species has ever been observed to cross open areas to reach fruit trees or to access neighboring forest during the nine years of study (Banks pers.obs). However, Freed (2007) noted that *E. coronatus* were willing to use many of the shrubs and small successional bushes that border agricultural fields in dry deciduous forests north of the Montagne d'Ambre National Park and some 70 kilometers north of the site discussed here. Nevertheless, matrix habitats were not used for food, social interaction, resting or travel by either *Eulemur* species or *Hapalemur* in this study.

Isolated forests are less likely to affect species from particular trophic guilds but should instead be better predicted using a measure of, where possible, local species-specific dispersal capacity (Tischendorf et al. 2003; Arroyo-Rodríguez and Mandujano 2009; Beaudrot and Marshall 2011). Deghan (2003) found that *Propithecus edwardsi* rarely crossed open areas of a few tens of meters and used this limited capacity for dispersal to explain low levels of occupancy in evergreen forest fragments in southeastern Madagascar. Since the two *Eulemur* species and *H. occidentalis* have never been observed to cross matrix habitat to reach neighboring forest in the study region, following Tischendorf et al. (2003) these species are considered dispersal specialists or dispersal limited species. Given that several fragments are found within the distances at which *P. perrieri* has previously been recorded traversing open areas, this species is considered a dispersal generalist or generalized disperser. Species with greater capacities for dispersal are less likely to be sensitive to forest isolation as a barrier to dispersal into new areas (Arroyo-Rodríguez and Dias 2010). **I predict that specialist dispersers such as *E. coronatus*, *E. sanfordi* and *H. occidentalis* will have higher densities in less isolated habitats while there should be no effect of isolation on the population density of the generalized disperser, *P. perrieri* in forest fragments of the Diana region.**

The role of disturbances (i.e. large scale fires, selective logging and other extractive activities) in shaping patterns of primate abundance overlaps with much of the theory set forth in describing folivorous and frugivorous primate responses to fragmented habitats. Food resources are expected to diminish for frugivorous primates in disturbed and fire prone habitats while food quality is expected to increase for folivorous in habitats characterized by these pressures. Peres et al. (2003) found substantial losses of maturing fruit crops through direct burning or from spontaneous abortions through heat stress as well as heightened mortality of large trees in Amazonian forest recently affected by large-scale fire. These changes are expected to reduce food for frugivores and depress population densities. Although fires increase the relative proportion of forest edge and may improve the quality of foraging opportunities for folivores, these events can dramatically increase fire canopy openness and fire-induced mortality of trees (Cochrane and Laurance 2002), changes that have been used to explain decreases in folivore abundance (Ganzhorn 1995, Irwin et al. 2010). The opening of forest gaps as a consequence of small to moderate human disturbances leads to increased growth of foliage in forest understorey and improved food quality for folivores (Oates et al. 1990; Ganzhorn 1995; Chapman et al. 2004). Selective logging and other extractive activities tend to reduce food availability for frugivores in Madagascar (Balko and Underwood 2005; Wright et al. 2005) while foods for folivores should increase in quality (Ganzhorn 1995). **In light of these patterns I predict that frugivorous lemurs will have lower densities in forests with an increasing presence of large-scale fires and human disturbances. Folivorous lemurs densities are not predicted to be influenced by small to moderate human disturbances but abundance is predicted to decrease in the increasing presence of fire.**

Given that the spatial attributes of forest fragments and patterns of disturbance often serve as a reliable proxy for prevailing habitat characteristics at a site (Arroyo-Rodríguez and Mandujano 2006) many of the same predictions can also be framed as confirmatory hypotheses by modeling abundance patterns as a function of habitat variables. Therefore, in general frugivores should be sensitive to habitat characteristics that reflect a greater abundance of resources (i.e. larger and higher density of large trees, larger crowns, taller trees; Stevenson 2001) while folivores should show little response to these factors since they share little relationship with differences in leaf quality. **Based on these lines of evidence I predict that frugivore densities will increase as a function of large tree size (i.e. DBH), large tree densities, large tree heights and large crowns. No differences in the densities of more folivorous primates are predicted as a function of these variables.**

Other habitat characteristics that might be used to predict patterns of primate abundance do intersect with the hypotheses presented above. Notably the deciduousness of the vegetation has been used to explain differential investments in plant leaf defenses, growth and protein content. Emphasis is placed largely on the production of plant defenses in the long-lived leaves of more evergreen forests while growth and protein content are targeted by the more ephemeral and metabolically accelerated leaves of dry deciduous forests (Janson and Chapman 1999; van Schaik et al. 2005). **Accordingly I predict that the folivore densities will be higher in dry deciduous forests on limestone substrate than in the semi-evergreen transitional forests that occur on sandstone substrate within the targeted study region.** The relationship between deciduousness and fruit production may be less direct but there is evidence suggesting that evergreen forests from the eastern escarpment experience more irregular patterns of fruiting due to poor levels of exchangeable minerals in soil and poor soil fertility (Ganzhorn et al. 1999; Wright 1999; Wright et al. 2005). **As such I predict that frugivore densities will also be higher in dry deciduous forests than in semi-evergreen forests.**

In addition to structural attributes of the habitat and levels of leaf deciduousness, estimating the availability of top foods has also been found to play an important role in limiting primate population levels elsewhere (Balko and Underwood 2005; Arroyo-Rodríguez and Mandujano 2006). Given the conservation importance of documenting these patterns for the most threatened primate taxa I decided to focus these efforts on one species, the critically endangered Perrier's sifaka (*Propithecus perrieri*). **I predict that *Propithecus* densities will increase as the density of their top ten dry season food trees increases.**

Ganzhorn's (1997) test of Fox's assembly rule among several lemur communities across Madagascar highlights the likely importance of species interactions in structuring Madagascar's primate communities. The model requires that species from the same functional groups (e.g. trophic guilds) hold the greatest potential to compete with one another so functional groups should be equally represented, in terms of the numbers of species. Indeed morphological and physiological similarities can result related species concentrating on many of the same foods, particularly during periods of resource scarcity when competition should increase as sympatric primates are often forced to converge on "fallback" foods (Terborgh 1984; Marshall and Wrangham 2007; Marshall et al. 2009). Despite this potential for competition, closely related sympatric primates are expected to have undergone varying degrees of niche separation to enable coexistence (Haugaasen and Peres 2009). In addition to niche separation, some sympatric species are able to counter the costs from interspecific competition through the gains they can receive by forming polyspecific associations (Porter 2001; Stensland et al. 2003; Heymann and Buchanan-Smith 2007). The majority of benefits emerging from these mixed species associations fall into one of two functional contexts, (1) increased protection from potential predators (Noë and Bshary 1997) or (2) improved foraging efficiency and food intake (Porter and Garber 2007).

Freed (1996, 2007) found that *E. sanfordi* and *E. coronatus* frequently associate in the dry deciduous and evergreen forests of the Diana region in northern Madagascar. His findings suggest that the two closely related species benefit from associations during times of resource scarcity and gain access to foods at levels of the vertical strata that they would otherwise ignore. The lack of agonism during these associations and the fact that resources were rarely if ever completely exhausted by either species (Freed 2006) suggests that mixed feeding associations consistently offer improved opportunities for food to both species. Indeed this finding seems consistent with the notion that primates forming polyspecific associations confer benefits from these associations that should outweigh the costs inevitably arising from any competition between species (Porter 2001; Heymann and Buchanan-Smith 2007). Following this line of reasoning and the theoretical underpinnings of polyspecific associations in general, at least one of the two sympatric *Eulemur* species occurring within the study region discussed here should be expected to benefit from such associations. In studies with mixed species assocatiations between callitrichid species, Norconk (1990) found that population densities were higher for one of the two primates, *Saguinus fuscicollis*, in areas where associations with *Saguinus mystax* were common. Furthermore, *S. fusicicollis* densities declined after extensive trapping programs aimed at removing several *S. mystax* individuals five years earlier (Glander et al. 1984). Finally, Chapman and Chapman (2000) show that the occurrence of mixed species associations between diurnal primates at Kibale National Park in Uganda were positively related to the densities of the species that formed associations. Freed (2006) suggests that strong vertical separation in habitat use (Buchanan-Smith 1999) between *E. sanfordi* and *E. coronatus* and the fact that neither species depletes their conspecific's resources increases the chances that both species benefit from polyspecific associations through increased foraging efficiency. **Accordingly, I predicted that the population densities of both *Eulemur* species will increase at higher densities of their sympatric congeneric.**

Noting once again the importance of species interactions in shaping the structure of Madagascar's primate communities (Ganzhorn 1997; Ganzhorn 1999) hunting might also be expected to release certain species from competition with one another through the phenomenon of density compensation (MacArthur et al. 1972; Peres and Dolman 2000). Indeed three of the four diurnal species, including *E. sanfordi*, *E. coronatus* and *P. perrieri* are expected to obtain a substantial proportion of their diet from fruits. Wright et al. (2005) have demonstrated how fruit may be a limiting factor for many lemurs and that the season of greatest fruit availability coincides with the period of lactation and weaning. It is likely that even folivorous-frugivorous lemurs such as *Propithecus* would be willing to compete for such ephemeral resources given their importance to reproductive success. In forests that support primates human hunters have been shown to target the largest animals to ensure the greatest returns from hunting effort (Peres 1999; García and Goodman 2003; Golden 2009). **I predict that the density of large bodied species will therefore decrease at sites affected by hunting. Owing to the proposed importance of interspecific competition in structuring Malagasy primate communities I also predict that through the phenomenon of density compensation the densities of smaller bodied species will increase at sites affected by hunting.**

Methods

Study Sites

I collected data on lemur abundance in twelve forest fragments falling within the Diana Region of the Antsiranana Province, northern Madagascar from 14 July 2003 to 14 July 2012 (Figure 3.1; for site names please see Table 3.1). Data included in the current dataset includes the subset of data presented in Banks et al. (2007). Study sites were situated in one of three different protected areas, although one of these areas was only recently elevated to "provisional" protected status as of October of 2008 (Buřivalová 2011). The three easternmost fragments occur within the Analamerana Special Reserve (hereafter Analamerana: S12°46'34.30", E 49°29'6.34, area: 34,700 ha) and to the northwest two forest fragments from the Ankarana National Park (hereafter Ankarana: S 12°53'34.25", E 49° 8'12.05", area: 18,225 ha) are represented. Sites situated centrally within the study region (n = 7) are found within the Andrafiamena-Andavakoera Forest Corridor (hereafter Andrafiamena approximate geographic center: S12°58'53.07", E

49°18'5.39", area: 85,000 ha), a newly gazetted IUCN, category V landscape. The protected landscape/seascape category was designated in the interest of integrating management considerations for conservation with traditional practices such as farming and hunting. Nature conservation is typically overseen by an entity that also provides infrastructure to support certain, controlled, “for profit” activities as well as facilitating management objectives outlined by surrounding communities.

Using two Landsat 7 scenes (170/69, 158/69) we selected eleven forest fragments to provide a representative sample of fragment sizes, degrees of isolation, geometry, disturbance history and protected status for the study region (Table 3.1). Forests were surrounded primarily by a matrix of grasslands dominated by the following grasses (i.e. Poaceae), *Aristida rufescens*, *Hyparrhenia* sp., *Trachypogon spicatus* (Letsara 2007). Cultivated lands are also intermixed with the savanna matrix, frequently at the foothills of the region’s mountains. These include dry rice paddies, crops of cassava, small produce gardens, and plantations of *Eucalyptus* sp. Although one of the primate species studied here is known to cross open areas of savanna to reach isolated food trees (e.g. *Mangifera indica*, *Scelerocaryan* sp.) these feeding bouts are abbreviated events and always followed by a return to the closed canopy of forested habitat (i.e. open areas are not used as sleep sites or breeding grounds but exclusively for feeding). None of the other three diurnal primates observed during the nine-year study period were ever found to come to the ground to cross open areas.

The perimeters of forest fragments were measured by ground truthing forest borders with a Visiontac^{TM} V-GPS Data Logger and evaluating the concordance with satellite imagery available free-of-charge from the Google Earth © software package. All forest fragments were separated by at least 100m from any neighboring forested habitat. The elevational range for the study sites falls between 50 and 760m above sea level. Elevation seems to only have an effect on vegetation above 600m (Buřivalová 2011), a circumstance that only presented itself for semi-evergreen forests. Here tree species composition is dominated by the species, *Uapaca aff. ferruginea* (Euphorbiaceae), yet preliminary studies (e.g. Ratelolahy 2007) reveal that this vegetation type does not pose any limits to diurnal primate species presence here. Additionally, the upper altitudinal limit for diurnal primates within the region Diana with the exception of *Hapalemur occidentalis* is well above the elevation of the highest peaks at 760 m (Freed 1996; Goodman and Ganzhorn 2004b; Goodman and Ganzhorn 2004a). In dry deciduous forests across the study region the highest elevation is at 583m and no *Uapaca* or otherwise heavily species dominated habitats are known to occur. In the easternmost portions of Analamerana however, and within a few kilometers of the coast habitats become pronouncedly drier, more xeric and succulent in vegetative composition. The dominance of *Euphorbia*, *Adansonia*, *Aloe* and *Adenia spp*. along with other species adapted to severe water stress is strikingly apparent (Banks pers.obs.). Although reconnaissance missions were performed in these areas, no systematic surveys were performed here.

Climatology data is scarce for the study region, but based on existing phytogeographic classifications for Madagascar, sites are considered as falling within Humbert and Cour Darne’s (1965) western biogeographic domain of dry, dense forest.

The initial divisions outlined by the authors have largely been retained but have undergone revision using remote sensing techniques that integrate information on soil, elevation, and meteorological clines (Gautier and Goodman 2003). As a result the study sites presented in this work have been further described as deciduous, seasonally dry, western forest (Du Puy and Moat 2003). A climate model for the study region provides a mean annual rainfall of 1500 mm (Jury 2003), which is comparable to rainfall amounts recorded for Ankarana and nearby localities (e.g. Ankarana: 1800 – 2000 mm; Cardiff and Befourouak 2003, Ambilobe (20 km south of Ankarana): average = 2075mm and Betsiaka (15 km south from the geographic center of Andrafiamena): average = 1785mm), areas that are all characterized by five wet months annually.

Botanical descriptions for some of the areas included in our surveys are also limited, however some workers have described the predominant habitat types within Ankarana and Analamerana (Fowler et al. 1989; Hawkins et al. 1990; Cardiff and Befourouack 2003). More recently research has expanded into the areas that fall in between these two reserves (i.e. Andrafiamena) and some preliminary descriptions of the vegetation have been undertaken (Letsara 2007; Buřivalová 2011). The topography and geology of these areas has featured prominently in the newer assessments. Authors have highlighted how slopes tend to harbor species characteristic of Humbert and Cour Darne's (1965) Western Domain of dry deciduous forests including, *Commiphora*, *Hildegardia* and *Dalbergia.* Species representative of the more humid Eastern Domain such as *Canarium*, *Eugenia* and *Diospyros* are typically recorded in valleys and more riparian areas.

An even more striking dichotomy regarding Madagascar's remaining vegetation has been posited relative to geological differences (Du Puy and Moat 2003). In particular, Du Puy and Moat (2003) summarized patterns of plant species distribution by relying on the relationship that has been demonstrated between substrate type and structural and compositional differences among Malagasy forests. Broadly speaking, forests within the study region occur along one of two substrate types, a Mesozoic limestone plateau and sedimentary sandstones originating from Precambrian basement rock (Buřivalová 2011). The Andrafiamena chain separates the study region into a northern and southern sector characterized by limestone karst and sandstone formations respectively.

Perhaps not surprisingly given the relationship between substrate and habitat types, landscape level studies controlling for the effect of the environment (e.g. rainfall, elevation, latitude etc.) have also highlighted the importance of the role that substrate plays in driving differences in peak deciduousness across tropical forests (Bohlman 2010). Indeed previous descriptions of regional differences in habitat type in northern Madagascar have long acknowledged geological differences and emphasized varying degrees of deciduousness (e.g. xerophytic thicket on karst, dry deciduous forest, semi-evergreen canopy forest on basalt, and transitional forests; Fowler et al. 1989, Hawkins et al. 1990, Cardiff and Befourouack 2003). Forests that occur within the study region and are examined here have also been separated using similar criteria falling broadly into either dry deciduous or semi-evergreen transitional formations (Buřivalová 2011).

Relative to species composition, Buřivalová (2011) sampled large trees in forested habitats found on both substrates and determined that only 4% of the species were shared. In general, and consistent with Meyers' (1993) explanation for varying degrees of deciduousness in forests of the Daraina region, groundwater regimes are likely to differ greatly across different geological formations. Forests on the exposed limestone outcrops that characterize the protected areas of Analamerana and parts of Ankarana have a shallow, alkaline soil layer, are more water deprived and support a more xeric and deciduous vegetation (Fowler et al. 1989). Trees in the driest areas are characterized by strong resilience to water scarcity (e.g. *Adenia*, *Aloe* and *Euphorbia* on xerophytic thicket, *Adasonia*, *Hildegardia*, *Commiphora* and *Pachypodium* in dry deciduous forests). When controlling for differences in topography, species typical of the limestone forest include *Diospyros spp*., *Xylopia bemarivensis*, *Norhonia spp*., *Coffea spp*., *Commiphora sp*., *Cynometra sp*., *Hildegardia sp.* and closely related members of the Sapotaceae family such as *Mimusops* and *Faucherea sp*. Alternatively, in the semi-evergreen forests that occur on sandstone, trees are less water deprived and many more cogeners from the eastern rainforest are present. In these forests, the representative tree species include *Sarcolaena condonochlamys*, *Schizolaena viscosa*, *Sapotaceae sp*., *Diospyros spp*., *Uapaca spp*., *Pandanus sp*. *Grewia spp*. and *Bathiorhamus cryptophorus* and *Dypsis madagascariensis* (Banks unpubl. data). Structurally the two forest types have also been found to differ relative to the homogeneity of the canopy, the above ground biomass and tree size diversity (Buřivalová 2011).

Primate Surveys

We used standardized line transect techniques (Buckland et al. 2001) to sample primate populations in northern Madagascar (Diana Region, Antsiranana Province) and prepared 32 transects in eleven isolated forest fragments from June of 2003 to June of 2012. In 2003 and 2004 our surveys were restricted to shorter three month sampling periods (Banks et al. 2007) while in 2007 we initiated a long-term sampling regime that extended over five years.

During the pilot studies of 2003-04 we adopted a protocol that was restricted to sampling along survey routes left by previous researchers (see Hawkins et al. 1990). Our selection of survey routes was further informed using available vegetation maps and extensive reconnaissance of forest fragments. We attempted to ensure that all of the relevant microhabitats *within* individual forest fragments were represented proportionally along survey routes (i.e. bamboo forest, riparian forest, slope forest, *Uapaca* forest, primary and secondary vegetation). Political and logistical considerations during these periods precluded fashioning survey routes from strict compass bearings. We also limited our sampling to forests within Analamerana and Ankarana during this initial period.

By April of 2007 we focused our primate surveys exclusively on Analamerana and the recently (i.e. 2008) gazetted Category V IUCN protected landscape, Andrafiamena. Primate surveys during this period made use of strict compass bearing transects but were consistently prepared following the random stratified design described above. To address differences between the two survey periods (e.g. seasonal, observer, behavioral etc.) and across sites (e.g. habitat, demography, disturbance regimes etc.) I examined the role of various covariates in driving the detection process. The individual primate detection functions used to calculate primate densities were modeled as a function of covariates in cases where differences in the Kullback-Leiber information (i.e. AIC) for competing models indicated strong support for one model over another (Burnham and Anderson 2002; ΔAIC > 5)

Observers used stealth to detect lemurs by advancing slowly along transects at approximately 1.2 km/hour. When primates were encountered we recorded the species and the number of individuals forming a well-defined group (i.e. maintaining an inter-individual distance of ≤ 25m). Transects were measured using a Keson © 30m tape measure and marked at 25 m intervals using flagging tape. Positions along transects where primates were encountered were measured using a laser rangefinder and the 25 m interval flags. In cases where distances could not be registered using a rangefinder they were measured using the tape measure. Observers measured the distance from the location of the sighting to the center of the group and measured the sighting angle relative to the trail using a precision compass. With basic trigonometry, the latter two measurements were then used to calculate perpendicular sighting distances. Densities were calculated using the conventional distance sampling and multiple covariate distance sampling engines from the DISTANCE 6.0 © software package (Thomas et al. 2010). We truncated distances for analyses after examining histograms of the data (Buckland et al. 2001). The distribution of sighting distances for all species across the eleven forest fragments was only found to covary with site identity for *E. sanfordi* (Banks chapter 1, this volume). Following efforts to model the detection function for *E. sanfordi* using site identity as a covariate, I found only equivocal support for the role of site level differences in driving patterns of detection in this species (Banks, chapter 1, this volume). Accordingly a global detection function was fitted to the data for each species across sites, thus enabling reliable density estimation for sites that did not achieve the recommended number of sightings (Buckland et al. 2001; Marques et al. 2007) and thereby permitting comparison of the complete dataset.

Behavioral Follows: Propithecus perrieri

To investigate patterns of dietary diversity in one of the primates that occurs within the Diana region, a collaboration with Omaha's Henry Doorly Zoo & Aquarium (OHDZA) was formed to enable behavioral follows with family groups of the species, *Propithecus perrieri*. Between May 9-26 of 2008, a team from the OHDZA, led by PhD conservation geneticist, Brandon Sitzman, safely immobilized 18, healthy individuals from five Perrier's sifaka (*Propithecus perrieri*) social groups in the forests of Ampantsona, Province of Antsiranana, Diego II district, CR Anivorano-Nord, Fokontany of Andrafiabe (S 12°54'27.65" E 49°18'48.99"). All immobilized sifakas were provided with radio collars to assist in individual identification and with locating groups for systematic behavioral studies.

I used an instantaneous focal sampling protocol with an all occurrence sampling procedure for feeding bouts during half and full day behavioral follows. Attempts were made to visit all groups at least once per month. I recorded the length of all feeding bouts, plant species and plant part ingested. One of the five groups suffered heavy predation, most likely from *Cryptoprocta ferox* in late May 2008, and no radio collared individuals remained to facilitate further contacts with this group. Accordingly we abandoned behavioral follows with this group and concentrated on the remaining four groups. Focal animals from all four groups were alternated on a cyclical basis but only the behaviors of adult (> 1 year age based on tooth wear and age estimates provided by HDZ) individuals were recorded. Top foods in the *Propithecus* diet were only tabulated for the dry season (April 15 – November 15). I prepared voucher specimens of all food species which were subsequently identified by trained botanists at the Parc Biologique et Zoologique de Tsimbazaza and at the California Academy of Sciences, both located on the grounds of the National Park in Tsimbazaza.

Disturbance, Hunting and Large Scale Fires

During transect walks we recorded information from signs and direct encounters with forest disturbances. These included cut tree stumps, encounters and sign from wild boar (*Potachamerus larvatus*) and cattle (*Bos indicus*), as well as direct encounters with people and their signs (e.g. fire and tree damage associated with extraction of wild honey, remains from temporary camps, etc.). Subsequently disturbance was quantified as an index relative to number of disturbances recorded per km of walked transect. Similarly, all direct and indirect (i.e. traps) signs of hunting were recorded and were used to provide evidence of the presence or absence of hunting at sites. Hunting was entered as binary data in all subsequent statistical analyses (see below).

The influence of large-scale fires on forest fragments was also entered into the multi-modeling analysis framework (described below) as binary data, depicting presence or absence at focal sites. Observers compiled these data as part of efforts to build a regional database documenting the frequency of fire across the landscape. The initiative is overseen by the National Park Service (MNP; Madagascar National Parks) who have administrative authority over Analamerana and Ankarana as well as NGO Fanamby, the administrative authority for Andrafiamena. Fires were considered large scale if they penetrated forests and resulted in damage totaling at least 0.5 ha of the vegetation. Damage from fire was assessed by recording the perimeter of fire-affected areas using GPS Data Loggers and subsequent calculation of affected areas using the Spatial Analyst extension in ArcMap 10 © ESRI 2013.

Fragment Spatial Attributes, Geology and Forest Loss

I estimated forest loss for all forest fragments (please note that the term fragment, patch and site are used interchangeably throughout all subsequent text) by deriving a supervised classification of forest and non-forest vegetation classes using the software package ERDAS Imagine 8.6© and various Landsat 7 images downloaded from the Global Land Cover Facility (GLCF; University of Maryland). The inclusion of Images from the dry seasons in 1994 (i.e. June) and 2002 (i.e. May) were compared and fragment area was calculated for each forest patch using the spatial analysis extension in ESRI © ArcMap 10 software package. We imported the simplified geological classification provided in Du Puy and Moat (1996) as a shapefile using ESRI ArcMap 10 software and georeferenced the layer using conspicuous landmarks visible in the supervised classifications of regional vegetation. The resultant layers of regional geology and vegetation were then used to distinguish between forests on sandstone and limestone.

Fragment shapes were quantified using the shape index (SI) of Forman and Godron (1981). Although the perimeter-to-area ratio is widely used in landscape ecology, by holding patch shape constant, an increase in patch size results in an increase in this ratio (McGarigal and Marks 1995). The SI addresses this source of bias by measuring the complexity of fragment shape relative to that of a standard shape (e.g. circle, square) of the same size. In mathematical terms, the shape index is equal to the perimeter of the target fragment divided by the square root of the fragment's area. This term is multiplied by a constant to adjust for an equally sized, shape, standard. In general the index is equal to one when the fragment approximates a standard shape and increases without limit as shapes become more complex.

Fragment isolation was measured as a function of remaining habitat within a predefined radius of the target fragment using the proximity index (PI) of Gustafson and Parker (1994). Accordingly both the size and proximity of neighboring fragments are taken into account. The search radius for available habitat was defined based on preliminary information from casual observations during the nine years of study as well as local knowledge regarding each species' dispersal capabilities within available matrix habitat. Matrix habitats were considered to be equal and consisted primarily of either savanna or human and agricultural settlements. Although the potentially different roles of various parts of the matrix were ignored, these habitats are widely considered as inhospitable for most primates (Arroyo-Rodríguez and Mandujano 2009). There is scant evidence for the small to medium sized arboreal quadrupeds (i.e. *Hapalemur occidentalis*. and *Eulemur* spp.) of this primate community coming to the ground to cross open areas (Banks, pers.obsv). As a result I used a smaller search radius (250 m) for these species than for *Propithecus perrieri*, which has been seen crossing areas of savanna at distances up to 600m to reach isolated *Sclerocaryan sp*. trees and neighboring forest (Lehman and Mayor 2004, Banks, pers.obsv.). When modeling the determinants of total primate biomass, the PI was considered simultaneously at three different scales (i.e. 250, 500 and 1000m radii from the focal patch) in an effort to identify the most relevant threshold distance for quantifying isolation across the diurnal primates from this community. To reduce multicollinearity between the different isolation parameters, new variables were created using linear combinations of the original variables (Chatterjee and Hadi 2013). The PI was calculated as the summed area of all neighboring forest fragments within the search radius of the target fragment, divided by the distance of each neighboring patch from the target fragment.

Forest Structural and Diversity Attributes

Forest structure was measured in 1000m^2 plots (n = 104) across eleven focal forest fragments (mean = 8.7, sd = 7) situated within the study region. Within plots trees with a diameter at breast height (1.2m; DBH) of ≥ 10cm were measured. Field teams measured the DBH of trees to the nearest cm using a metric steel diameter tape, tree heights were measured to the nearest meter using a laser rangefinder (measurements were corrected to the height and angle of the observer's vantage point) and/or measuring poles and tree crowns were measured using measuring poles. The density of large trees was calculated as the number of trees ≥ 10 cm DBH in the site- specific sampling area. This proportionate representation of large trees was then converted to the number of large trees per square kilometer.

The top ten dry season food species for *Propithecus perrieri* were identified for limestone and sandstone habitats in botanical plots after referring to the data in Lehman and Mayor (2004; n = 1217 individual feeding records (IFR)) and Banks et al. (unpub.data, n = 279 IFRs) for each of the respective substrate types. Voucher plant specimens were prepared at all sites and plant identifications were performed by Madame Rahelivolana Elisette at le Departèment Botanique at the National Park in Tsimbazaza, Antananarivo, Madagascar and by Letsara Rokiman at the California Academy of Sciences Botanical Department, also located on the National Park grounds in Tsimbazaza. Inclusion of IFRs required that the data were restricted to periods from April 16 – November 14 of any sampled year. Climate data from both the Daraina (Meyers 1993) and Betsiaka (Buřivalová 2011) regions just to the south of Andrafiamena are in support of a dry season delineated by the above period. Patterns of *Propithecus* dietary diversity were studied by Lehman and Mayor (2004) during the dry season of 1998 whereas data from the study by Banks et al. (unpubl.data) extended over three consecutive dry seasons (2009-2011).

Statistical Tests

The role of fragment attributes (i.e. patch size, patch, shape and patch isolation), anthropogenic influences (i.e. extractive disturbances, large scale fires, hunting and forest loss) and natural ecology (i.e. habitat type, forest structural attributes and inter-specific competition) in driving primate population densities within a diurnal primate community in northern Madagascar were evaluated using model averaging techniques (Burnham and Anderson 2002) under a generalized linear mixed model (GLMMs; Bolker et al. 2009) framework. All GLMMs were fit to a Poisson distribution. Potential overdispersion was evaluated using the *stats* package for the R statistical computing environment software, version 3.0. A list and summarized description of all explanatory variables considered is provided in Table 2.

A multimodel averaging procedure was chosen for its flexibility in simultaneously evaluating the relative support for competing hypotheses (Grueber et al. 2011). The basis for the averaging of parameter estimates relies is found in information theory (i.e. IT approach), or the use of Kullback-Leiber information such as Akaike's criterion (i.e. AIC) to identify a best set of candidate models. Models are ranked and weighted by balancing the uncertainty associated with fitting a particular model to the data (i.e. using maximum likelihood methods or random-sum-of-squares residuals) with the information that is lost by reducing the number of parameters in the interest of parsimony (Symonds and Moussalli 2010).

Given the relatively small number of observations (i.e. n = 32 transects) in the dataset and the large number of factors predicted to drive population levels in this relatively unknown study system, a multi-stage approach of model selection was adopted.

One of the greatest criticisms of current use of the IT approach is the inclusion of too many models in the model selection process (Anderson and Burnham 2002). Given the large number of putative predictor variables and the ultimate goal of producing a predictive model through multimodel inference, I chose to employ an all subset strategy (Dochtermann and Jenkins 2011). Hypotheses were formulated for the dataset only if some *a priori* support was found in the literature or ecological theory dictated its evaluation in the absence of better data. Problems of multi-collinearity were addressed by evaluating variance inflation factors (VIF) and associated correlation matrices for all explanatory variables. Data were fit to the model once the VIFs for all predictor variables were well below the value of 10 (Chatterjee and Hadi 2013).

A set of competing models representing all potential combinations of the explanatory variables from a standardized version of the global model was perfomed using the *dredge* function, implemented in the *MuMIn* package (Bartón 2012) for the R software environment (R Core Development Team 2013). A 95% confidence set was derived from the resultant set of models by isolating only models with a cumulative Akaike weight of 0.95. Akaike weights are calculated based on the difference in AIC (i.e. ΔAIC) between a candidate model and the model with the lowest AIC (i.e. the best approximating model). Model parameters were then averaged using the *model.average* function, as implemented in the *MuMIn* package (Bartón 2012). The relative importance (RI) of the various predictors was determined by evaluating the proportionate representation of a particular predictor within the 95% confidence set. Put another way, an explanatory variable with a RI of 0.75 appears in three quarters of the models from the 95% confidence set.

A subsequent stage to this part of the analysis was initiated after evaluating the model averaging results from the steps outlined. Data were fit to a new global model that was specified using only explanatory variables that were represented in 50% of the models from the initial 95% confidence set. Global models from the second phase of analysis were also evaluated for problems of multicollinearity using the protocols described above, however a more stringent VIF cut-off of ≤2.5 was adopted to determine the inclusion of predictor variables (Zuur et al. 2009). Model averaging was performed on a 95% confidence set of models as derived from the newly parameterized global model following the steps described above.

A confirmatory stage of analysis was implemented to further assess available support for the various hypotheses considered. Notably, many of the explanatory variables associated with the spatial characteristics of forest fragments and considered in the first stage of the analysis were expected to share a strong association with indices of habitat availability for primates. The literature on primate responses to fragmentation reveals that many patterns are intrinsically linked to specific habitat attributes (i.e. the structural composition of habitats). To minimize problems of multicollinearity and model convergence during the first two phases of the analysis I considered the role of fragment spatial attributes (i.e. size, shape and isolation) separately from the structural attributes (i.e. large tree density, average large tree DBH, average large tree height, and average crown diameter) of forests within fragments. Structural attributes were only considered during the final confirmatory stage of analysis and were subjected to the model averaging procedure described earlier. Confirmatory models were specified through the inclusion of explanatory variables isolated during the second phase of model selection along with the structural attribute variables. Confirmatory analyses represent an approach towards data simplification and can be conducted with datasets acquired independently or data initially withheld from analysis (Hurvitch and Tsai; cited in Dochtermann and Jenkins 2011).

Results

We walked a total of 1234 kilometers on 32 transects spread across 11 dry deciduous and semi-evergreen forest fragments during the course of the nine year study. A map of all forest fragments is provided in Figure 3.1. All hypotheses considered in the forthcoming analysis and whether or not the predictions based on prominent theory in primate ecology were upheld are listed in Table 3.1. General site-specific variables for the eleven forest fragments evaluated are presented in Table 3.2. A description of the explanatory variables used to model primate densities is provided in Table 3.3. A table of summary statistics for the spatial and habitat characteristics of all sites is presented in Tables 3.4 and 3.5. Additionally Table 3.5 presents data on primate densities and the total primate biomass at all sites as calculated in Distance 6.0 ©. *Hapalemur occidentalis* was encountered infrequently during line transect surveys and we did not meet the minimum number of sightings (i.e. ≥ 40) recommended to reliably estimate its population levels (Buckland et al. 2001). Data are instead presented exclusively for the lemurs with an adequate number of sightings including *Eulemur sanfordi*, *Eulemur coronatus,* and *Propithecus perrieri*.

The results of model averaging for the three diurnal primates in the eleven forest fragments are presented in Tables 3.7-3.10. I was forced to remove both the shape index and forest loss as explanatory variables in all models as a result of high multicollinearity. These variables shared strong correlations with fragment area. The relationship between the shape index and forest area was strongly negative. This pattern indicates that fragment shapes in the Diana region increase in complexity at greater fragment sizes. Forest loss was also negatively associated with fragment area, an indication that the smallest fragments have historically suffered the greatest losses in forest coverage.

The results of model averaging for *P. perrieri* when structural indices of the habitat are excluded revealed that three variables were important predictors of the species' abundance, including substrate type, large-scale fire and human disturbance (Table 3.7). In fact with RIs of ≥ 0.84 all three variables were present in more than three quarters of the models from the 95% confidence set. Note that the estimates for each parameter are standardized and can be directly compared (Grueber et al. 2011). Substrate type had the largest magnitude of effect (i.e. Estimate: 3.33) and was ubiquitous in the 95% confidence set (i.e. RI: 1.0). The positive direction of effect indicates that *P. perrieri* abundance increases in forests occurring on sandstone substrates (Figure 3.2). Large-scale fire and human disturbances had 84 and 86% relative importance to substrate type respectively. The effect of large-scale fire was negative while human disturbances had a positive effect on *P. perrieri* population density (Table 3.7).

Confirmatory analyses conducted through the inclusion of variables quantifying the structural characteristics of the habitat reveal that average tree size, the abundance of the top ten dry season foods are also important predictors of *P. perrieri* population density (Table 3.8). Substrate type, patch size and shape were removed as predictors owing to high multi-collinearity. Large scale-fires and human disturbances are confirmed as important predictors and are represented in all of the models from the 95% confidence set (Table 3.8). Large-scale fires negatively influence *Propithecus* population numbers while small to moderate human disturbances have a positive effect on abundance patterns in this species (Figure 3.3). Crown diameter and tree height were also represented in the 95% confidence set of models, but both the magnitude of effect was lower than for the other variables. Furthermore, by evaluating the confidence intervals for these parameter estimates it is unclear whether there is a positive or negative direction of effect. The variable with the largest effect size is average tree size (Estimate: -2.66; Table 3.8) and the negative direction of effect indicates that population density increases as average tree size decreases. Average tree size had a strong pairwise correlation with substrate type (Pearson's r = 0.73) indicating that larger trees on average are found on limestone substrate (Figure 3.4).

The next largest effect size in the model for *P.perrieri* density is represented by the abundance of the top ten dry season food species (Table 3.8; Estimate: 1.25). Substrate type (which was removed from this stage of the analysis to reduce multicollinearity) did appear to share a strong relationship with the abundance of the top ten dry season food species (Figure 3.5) although the pairwise correlation for these two variables was relatively modest (Pearson's r = 0.52). In fact only fragment size consistently predicts the abundance of the top ten dry season *Propithecus* foods and appears in 87% of the models from a 95% confidence set formulated using an analogous procedure this is not presented here.

The results of model averaging for *E. coronatus* during the confirmatory stage of analysis (i.e. habitat characteristics are included and remaining explanatory variables exhibiting high multicollinearity such as substrate type, patch size and shape were removed) reveal that both the proximity index (PI) and the density of the sympatric *E. sanfordi* (Figure 3.6) are important predictors of *E. coronatus* density and appear in more than 50% of the models from a 95% confidence set (Table 3.9; RIs = 1.0 and 0.61 respectively). Remaining variables exhibit smaller effect sizes than does the PI and density of *E. sanfordi* as predictor variables and there is no clear direction of effect (Table 3.9). This species shows a negative effect of the proximity index at 250 m (see Figure 3.7 for a description of the proximity index taken at different threshold distances) and a positive effect of *E. sanfordi* abundance (Table 3.9).

Finally results for *E. sanfordi* show many of the same patterns as for *E. coronatus*. In particular, both the PI and *E. coronatus* density are important predictors of *E. sanfordi* abundance (RI = 0.86 and 1.0 respectively; Table 3.10) and exhibited negative and positive directions of effect respectively. Additionally however, large tree density was also an important predictor and had 94% importance relative to *E. coronatus* density despite having a smaller effect size than the other two predictors (Table 3.10). Average tree height and size (i.e. DBH) were also present in the 95% confidence set but their RIs were comparatively low (i.e. range = 0.25 – 0.36) and there was no clear direction of effect for either variable.

Discussion

Relative lack of support for the resource concentration hypothesis and for any strong role of habitat in driving frugivore densities may be a result of the generalist ecological and behavioral strategies adopted by *Eulemur* species throughout Madagascar (Overdorff and Johnson 2003; Johnson 2006). The two *Eulemur* species sampled here are known to actively use flowers as fallback foods during the lean dry season (Freed 1996) and *E. coronatus* demonstrated even greater dietary flexibility than its conspecific by frequently feeding in non-trees and treelets, showing a less exclusive preference for tall or mid-sized trees. It is interesting to note that among *Eulemur* species, *E. sanfordi* has one of the least diversified diets and their limited dependency on secondary food items (9% of total diet) in a detailed study of polyspecific associations between *E.sanfordi* and *E. coronatus* (Freed 1996) is the lowest for any *Eulemur* sp (Johnson 2006). Indeed the diet of *E. sanfordi* was comprised of greater than 60% ripe fruit regardless of the season in this study. This distinction as more of a ripe fruit specialist may help to explain why *E. sanfordi* population densities are consistently predicted using a measure of large tree abundance (i.e. ≥ 10cm DBH) in the forest fragments sampled here (Table 3.10).

I did not find frugivorous primates to be more abundant in deciduous rather than semi-evergreen forest fragments despite some evidence for this pattern in a previous comparison of eastern humid evergreen and western dry deciduous forests in Madagascar (Ganzhorn et al. 1999). The proposed mechanism for this is greater predictability of fruiting in dry deciduous forests where limited rainfall and flat topography limits the leaching of nutrients and hence augments the availability of energy for plant growth. Given that all sites are located within the same study region suggests that rainfall differences are unlikely to separate dry deciduous and semi-evergreen forests in northern Madagascar. Topography might be more likely to account for the lack of relationship since presumably sites contain areas of more irregular relief than at Kirindy where Ganzhorn et al. (1999) performed their dry forest assessments. In particular, elevation varies substantially (i.e. 2-568m) across the dry deciduous forests that characterize both Ankarana and Analamerana. Nonetheless, the range in elevation for remaining semi-evergreen forests on sandstone substrate is even greater (40 – 760 m). Ganzhorn et al. (1999) show that the exchangeable minerals in the wet forests from their sample (Ranomafana) were much more depauperate than in deciduous forest (Kirindy). Perhaps the reverse situation is true for deciduous forests in northern Madagascar since these formations are typically associated with large limestone outcrops and a shallow soil layer (Cardiff and Befourouack 2003). Whether forests on limestone are more mineral deficient will nonetheless have to await chemical analyses of the soil. The absence of any strong relationship could also be the result of having poorly defined “deciduous” and “semi-evergreen” forests in this study and future research should consider using phenological surveys to better distinguish between these two forest types.

Consistent with my predictions, evidence that sympatric *Eulemur* densities consistently covary with one another in a positive direction may be a sign that the two species are benefiting from the polyspecific associations that have been documented elsewhere in the Diana region (Freed 1996). The magnitude of effect of sympatric *Eulemur* density in either species' model was strongest when predicting *E. sanfordi* densities and was more important in modeling abundance for this species than it was for *E. coronatus*. This pattern is likely to be a product of the foraging benefits that these associations have been hypothesized to confer in areas where these species range together (Freed 2006) but it is not entirely clear as to why *E. sanfordi,* may obtain greater benefits from these associations. In a comparison of brown lemur species, Johnson (2006) contends that although brown lemurs are widely considered as dietary generalists, *E. sanfordi* stand out for consuming fewer secondary items than the other brown lemur species. This less flexible diet may limit opportunities for *E. sanfordi* to achieve high population densities in the absence of the foraging benefits they experience by associating with *E. coronatus*. *E. sanfordi* diets seem to be more confined by demands for ripe fruits than the smaller *E. coronatus* which accepts more unripe fruits, flowers and other fallback resources in their annual diets. The generalist dietary strategy of *E. coronatus* could mean that the information gained from association with *E. sanfordi* regarding the location of food is less productive for their populations than is the presence of *E. coronatus* for *E. sanfordi*. Nonetheless, *E. coronatus* range farther on average than *E. sanfordi* (Freed 1996) suggesting that they may have greater opportunities to parasitize information from *E. sanfordi* regarding feeding locations given their interactions with the environment on a larger scale. Finding greater evidence for the nature of foraging benefits gained through association between these two species awaits new data on patterns of food intake in low- and high-density habitats.

Mixed species interactions have also been shown to confer benefits beyond the advantages experienced through foraging. Anti-predator benefits have also received considerable attention in the literature (Noë and Bshary 1997; Chapman and Chapman 2000), and increases in the number of individuals forming a cohesive group are expected to minimize per capita risks from predation through the dilution effect (Hamilton 1971). Freed (2006) noted however that *E. coronatus* was willing to form small, foraging sub-groups and both species fed at times and in areas unlikely to expose them to substantial predation threats. Furthermore, mortality from predation was probably low in this study (Freed 1996). Nonetheless, both species would respond to each other's raucous alarm calls, and associations were often formed to facilitate opportunities for the young of both species to interact and play, presumably the result of greater vigilance from adults of both species (Freed 2006).

An alternative interpretation of the positive relationship between the abundances of the two *Eulemur* species studied here involves the recognition that high evolutionary relatedness generally translates into high ecological similarity (Fleagle and Reed 1999; Kamilar and Guidi 2010) and may confer tolerance for similar environmental conditions. This phenomenon of environmental filtering suggests that species are only capable of inclusion within a community if their morphologies, physiologies and life history traits are compatible with existing environmental and habitat characteristics (McGill et al. 2006). Muldoon and Goodman (2010), in an examination of non-volant Malagasy mammalian community structure, found strong support for an ecoregion model postulating that species ranges are sorted ecologically along environmental gradients but show that the results do not exclude the possibility of a more secondary role for historical processes. Kamilar (2009), using a cross-continental comparison of primate communities found that both historical and environmental factors are important in structuring extant primate communities. The suggestion that the structure of extant Malagasy primate assemblages are an artifact of primarily historical processes relies on the role of extinction and migration to explain current patterns (Ganzhorn 1998; Kamilar 2009).

Ganzhorn (1998) for example noted the absence of a distance effect in attempting to explain primate community similarity in the humid eastern forests of Madagascar. In addition to the selective extinction of primates vulnerable to late Quaternary climatic vicissitudes, authors have also stressed that broader elevational ranges among eastern lemur species would have enabled migration along the headwaters of rivers into areas that would have otherwise been inaccessible during drier periods (Wilmé et al. 2006; Muldoon and Goodman 2010; Markolf and Kappeler 2013). In contrast, western lemur species (including the subset sampled here) do not have the same tolerance for higher elevations and the distribution of micro-endemic primate fauna in western Madagascar tracks the distribution of rivers more closely than in the east (Goodman and Ganzhorn 2004a). It is plausible that historical processes and as a result taxonomic similarity contribute to structuring primate communities in northern Madagascar. If this were the case, facilitation through polyspecific associations might serve as a better explanation for covariance between sympatric *Eulemur* densities than does environmental filtering. The two explanations are not mutually exclusive however and it seems more likely that both the environment and historical factors have played some role. Most studies of the potential structuring mechanisms for primate communities emphasize habitat and the importance of environmental factors in contributing more to variation in the structure of extant primate communities than do historical factors (Kamilar 2009; Kamilar and Muldoon 2010; Muldoon and Goodman 2010). These findings urge for greater consideration of environmental factors in comparative studies of primates and suggest that the role of environmental filters may provide a particularly strong alternative hypothesis for explaining covariance among *E. coronatus* and *E. sanfordi* densities in this study.

One result that falls counter to my predictions for the two *Eulemur* species is that both species were found exhibit a positive effect of isolation on population density (Tables 3.9 and 3.10). If *E. sanfordi* and *E. coronatus* are dispersal limited as assumed based on casual observation and local knowledge for this analysis, population densities would be expected to be lower in more isolated habitats reflecting lower rates of colonization. The result could be an artifact of patterns of historical retreat into isolated refugia during climatic fluctuations of the late Quaternary and Holocene (Wilmé et al. 2006; Markolf and Kappeler 2013). Elevated abundance in more isolated forest fragments could reflect that in the absence of neighboring sites for dispersal *E. sanfordi* densities have reached an upper level to the carrying capacity of the habitat. Home range sizes would be at minimum levels and individuals are more tightly packed than in less isolated forests where dispersal between neighboring fragments is possible. Alternatively however, the result may instead expose one of the methodological limitations of conducting landscape analyses at lower spatial resolutions (i.e. 30 m). In particular, images do not capture the thin bands of discontinuous riparian forests connecting otherwise isolated (i.e via savanna or agricultural fields) forest patches. The importance of riparian habitats for lemur dispersal has not yet been properly investigated with the current design and highlights a gap to fill in future research with this primate community (Arroyo-Rodríguez and Mandujano 2009).

Freed (1996) also found that *E. coronatus* was adept at using small trees and treelets for food and as supports while foraging. Similarly during periods of food scarcity, *E. sanfordi* would associate with groups of *E. coronatus* to better locate fruits growing in smaller plants at lower levels of the forest. This finding along with the observation that both *Eulemur* species are frequently found in the sparse vegetation of discontinuous riparian forests in the otherwise open and isolated areas bordering villages (Banks, pers. obs.) suggests that the two species may use riparian forests regularly as corridors to larger more continuous habitats. *Propithecus* have been recorded using these habitats during the behavioral studies of Lehman and Mayor (2004) and Banks and Antonio (unpublished data). The *Propithecus* social groups in these studies range regularly into an isolated band of riparian forests but well removed from human settlements, a landscape feature that the species may avoid (Chapter 4). Increasingly, researchers in tropical areas are emphasizing the importance of riparian forests for preserving primate diversity (Gautier-Hion and Brugière 2005; Lees and Peres 2008) and future work on the abundance and distribution of primates in northern Madagascar should also attempt to consider the role of riparian forests in facilitating *Eulemur* dispersal.

I found some support for the leaf quality hypothesis of Waterman et al. (1988) and Oates et al. (1990) through a comparison of *Propithecus* abundance in disturbed habitats and more pristine habitats. Other *Propithecus* species have also been shown to exhibit some tolerance for both disturbed and edge habitats (Ganzhorn 1995; Lehman et al. 2006). In this study light to moderate human disturbances augmented population densities of *Propithecus* (Figure 3.3). However heavy disturbance through extensive removal of the canopy results in substantially lower *Propithecus* abundance (Ganzhorn 1995). Similarly *Propithecus* abundance was negatively associated with the recent influence of large-scale fire (Figure 3.3). Large-scale surface fires in tropical forests result in dramatic reductions in canopy cover and greatly raise mortality in large trees over an extended period (Cochrane et al. 1999; Cochrane 2003; Peres et al. 2003). Forest loss from large surface fires was commonly ≥ .01 km^2 in the Diana region (Banks pers.obs) and recurrent fires at sites were coincident with the season of heaviest tradewinds (late Sept – early Nov). These changes in forest structure would be expected to affect nearly all primates adversely in the Diana region given their almost exclusive arboreality. At weights frequently exceeding 5 kilograms, *P. perrieri* and other vertical clingers and leapers are likely to favor large vertical substrates for locomotion (Ganzhorn 1992; Ganzhorn 1993). Large scale surface fires are capable of removing up to 95% of all stems ≥ 1 cm DBH (Cochrane et al. 1999). While the species is willing to come to the ground to cross open areas they face greater predation risks from dogs and other terrestrial predators in doing so. These costs may outweigh the gains of foraging on the young nutritious foliage and successional vegetation that characterizes forests recently recovering from fire (Peres et al 2003). Large-scale fires are more representative of the heavy disturbances that were highlighted in the Ganzhorn (1995) study for their role in depressing primate populations in general (Irwin et al. 2010). Why the two frugivores don't exhibit a similar response, particularly given their greater reliance on fleshy fruits and rare food resources unfortunately can't be reconciled with the data on hand. Furthermore, also contrary to predictions, frugivores did not exhibit a negative response to light to moderate disturbances along survey routes and disturbance explained sufficient variation in the abundance of these two species to be included in the 95% confidence set of models (Tables 3.9 and 3.10).

Along with support for the leaf quality hypothesis, *Propithecus* densities were shown to respond positively to differences in the abundance of their top ten dry season foods. Despite the expectation that frugivores would be most sensitive to differences in habitat productivity, these results provide some support for the resource concentration hypothesis (Root 1973) in the folivorous-frugivorous, *P. perrieri*. Measures of the top ten foods for other folivorous-frugivorous taxa, most notably *Alouatta* spp. in Central America and the Neotropics, has proven to be a useful predictor of habitat quality in this genus (Cristóbal-Azkarate et al. 2005; Arroyo-Rodríguez and Mandujano 2006) and the examples extend to even more folivorous taxa (Chapman and Chapman 1999). It is interesting to note that the habitat specific top ten resources for *P. perrieri* were proportionally more abundant in semi-evergreen forests on sandstone than in dry deciduous forests that occur on limestone outcrops (Figure 3.5). Given the absence of a theorized mechanism for higher leaf quality in semi-evergreen habitats over more deciduous ones, it remains a major goal for future research to determine ultimately how important the abundance of preferred food species is during periods of food scarcity in determining folivorous primate densities in the Diana region.

Another unexplained pattern that emerged from modeling *P. perrieri* abundance as a function of habitat characteristics was the clear, strong negative effect with the average DBH of trees in 500 and 1000 m^2 botanical plots. *Propithecus* abundance was also negatively related to average tree heights and crown diameters across sites, but the direction of both effects were unclear after examining the results from performing model averaging on a top set of models (Table 3.8). It is uncertain why this species would accept smaller trees as a characteristic of its preferred habitats although the role of substrate type in driving *P. perrieri* densities appears to provide the most important clue. Trees were on average larger in limestone than sandstone forests (Figure 3.4) and sandstone forests contain larger numbers of *P. perrieri* dry season top food species (Figure 3.5).

Also contrary to expectations, folivorous-frugivorous primate (i.e. *Propithecus*) numbers did not increase in more deciduous forests and were actually orders of magnitude greater in semi-evergreen transitional forests on sandstone substrates. This result refuted any support for the seasonality-deciduousness hypothesis of van Schaik et al. (2005) although chemical analyses (Rothman et al. 2011) would be required to confirm the *a priori* assumption that dry, deciduous forests in the Diana region have higher quality leaves on average than do semi-evergreen forests. Leafy plants in more evergreen forests are expected to invest greater energy into plant chemical defenses and less into protein and growth than more deciduous forests (Janson and Chapman 1999).

Folivorous primate food selection based on leaf quality has already been demonstrated on several continents (Oates et al. 1990: Africa, Milton 1979, Peres 1997: Central America and Amazonia respectively, Ganzhorn 1992: Madagascar), and in Asian colobines there is even evidence of female primates contesting for higher quality foliage (Koenig et al. 1997). As mentioned above, rainfall was roughly comparable across sites in this study and therefore it offers an unlikely mechanism for any differences in leaf quality across the two substrate types. It is possible however that the shallow, weathered soils that support deciduous forest along heavily exposed limestone outcrops in this region are more nutrient deficient (see Janson and Chapman 1999). Indeed the vegetation in areas where such outcrops predominate have been best characterized as xeric succulent scrub and dry thicket (Cardiff and Befourouack 2003). Alternatively and as mentioned above there may have been limited differences in leaf quality between the two habitat types owing to broadly similar climatic conditions and increases in folivore density in semi-evergreen forests may be down to differences in food availability.

Finally no evidence was uncovered for the role of hunting in differentially depressing larger-bodied primate species. Indeed hunting did not appear to exhibit a strong effect on primate populations in the Diana region despite the detection of snares, slingshots, and even in one instance the recovery of *Eulemur* carcasses being prepared for consumption at the campsite of a group of illegal charcoal squatters. Most hunting in Madagascar in protected areas is however, known to be an extremely cryptic enterprise (García and Goodman 2003; Golden 2009) and the methods employed here may have not been sufficient to accurately index variability in hunting pressure across sites. Nevertheless the reactions from lemurs in response to the presence of human observers did not suggest hunting pressure with projectile weapons during our surveys at most sites, including those where snares and the remains of slingshots have been found. This finding may be the result of the more widespread observance of a regional taboo that warns against the consumption of lemurs, and particularly *P. perrieri,* a species believed to share a close relationship with the ancestors of humans. In particular many Antakarana believe that these animals may harbor the spirits of deceased ancestors that have been buried in the sacred forests where these animals often reside (Norbert Guitot, pers.comm). Hunting seems to be performed primarily by the members of immigrant populations, including those from the central highlands engaged in charcoal production and slash-and-burn agriculture, and miners from throughout northern Madagascar and elsewhere in the country.

Tables and Figures

Table 3.1. Functional groups and hypotheses tested relative to proposed determinants of abundance in the diurnal primates of the Diana region, northern Madagascar. Predictions offered are based on theory in primate behavioral ecology and individual species characteristics. Proposed relationships and empirical evidence (EE) from the current study are presented: +positive relationship; ±no relationship; -negative relationship.

Patch-Specific Attributes	Predictions	Species	Proposed Relationship	EE
Spatial				
Patch Size and Shape	Through greater food availability, larger and less irregularly shaped patches support more individuals of frugivorous species than do smaller ones (Johns and Skorupa 1987, Godfrey and Irwin 2007)	*E. sanfordi*	+	±
		E. coronatus	+	±
	Folivorous primate densities do not vary in response to changes in the size and shape of forest fragments given the relatively high abundance and availability of leaves (Ganzhorn 1995, Lehman 2007)	*P. perrieri*	±	±
		H. occidentalis	±	NA
Patch Isolation	More isolated fragments support lower densities of dispersal limited species than do more highly connected fragments (Deghan 2003)	*E. sanfordi*	-	+
		E. coronatus	-	+
		H. occidentalis	-	NA
	Generalized dispersers are not influenced by the degree of isolation characterizing forest fragments (Deghan 2003)	*P. perrieri*	±	±
Human Activities				
Large-scale Fire and Human Disturbance	Frugivorous primates have lower densities in forests affected by fire and low to moderate human disturbances as a consequence of reduced fruit availability (Peres et al. 2003)	*E. sanfordi*	-	±
		E. coronatus	-	±

	Leaf quality increases along the edges of forest created through small to moderate human disturbances and folivorous primate densities are not affected (Ganzhorn 1995; Lehman 2007)	*P. perrieri*	±	+
		H. occidentalis	±	NA
	Folivorous primate densities decrease with the increasing presence of large-scale fires and other heavy disturbances (Irwin et al. 2010)	*P. perrieri*	-	-
		H. occidentalis	-	NA
Hunting	The density of large bodied primates decrease in areas with hunting pressure as a consequence of human hunter preference for large species (Golden 2009)	*P. perrieri*	-	±
	Through the phenomenon of density compensation the densities of smaller bodied primates increases in areas experiencing hunting pressure (Peres and Dolman 2000)	*E. sanfordi*	+	±
		E. coronatus	+	±
		H. occidentalis	+	±
Forest Structural Characterisitics				
Large Tree Density, Avg. Tree Size, Avg. Tree Height, Avg. Crown Diameter	Given greater fruit availability frugivorous primate densities increase in forests with higher densities of large trees, larger on average tree size, height and crown diameters (Stevenson 2001)	*E. sanfordi*	+	+
		E. coronatus	+	±
	Relatively high abundance and availability of leaves in lemur habitats on average means that folivorous primate densities are not affected by changes in tree dendrometrics (Lehman 2007)	*P. perrieri*	±	-
		H. occidentalis	±	NA

Major Dry Season Food Tree Density	Primate densities will increase as the density of top ten dry season food trees increases (Balko and Underwood 2005)	*P. perrieri*	+	+
Habitat Seasonality				
Tree deciduousness	Irregularity in fruiting in more evergreen habitats has a negative effect on frugivorous primate densities (Ganzhorn et al. 1999)	*E. sanfordi*	+	±
		E. coronatus	+	±
	Higher quality foliage in more deciduous forests is consistent with a positive relationship between folivorous primate density and forest deciduousness.	*P. perrieri*	+	-
Interactive Effects				
Polyspecific Associations	Through increased foraging efficiency the densities of *E. sanfordi* and *E. coronatus* are positively associated (Freed 2006).	*E. sanfordi*	+	+
		E. coronatus	+	+

Table 3.2. Site attributes for eleven forest fragments in northern Madagascar. Symbols are represented in Figure 1. Protected status includes category V IUCN protected landscapes (cat. V), Special Reserves (SR) and National Parks (NP). The area of each fragment is provided in hectares along with the total distance of transects walked over the course of the study in kilometers. The substrate type is categorized as either limestone karst (L) or Precambrian sandstones (S). Forest loss is quantified as the percentage of forest lost, May 1994 – June 2003. The intensity of pressure is provided as a measure of the number of disturbances observed over the course of the study per unit effort of total search time.

Site Name	Map Symbol	Protected Status	Area (km^2)	Distance Walked (km)	Substrate Type	Forest Loss	Pressure
Ampondrabe	C	cat. V	5.1	120	L	0.83	0.10
Mahanoro	G	cat. V	4.2	155	S & L	0.83	0.07
Ambatovazaha	A	cat. V	12.1	133	S	0.52	0.04
Madiromasina	F	cat. V	1.1	100	L	0.49	0.05
Antsahabe	H	cat. V	4.6	105	L	0.12	0.05
Analamerana E	E	SR	124.0	262	L	0.05	0
Andampibe	D	SR	7.59	51	S	0.52	0
Analamerana W	B	SR	90.9	225	L	0.17	0
Ankarana W	K	NP	100.8	32	L	0	0.06
Ankarana E	J	NP	19.6	36	L	0.17	0.17
Ambery	I	cat. V	6.2	16	L	0.88	0.19

Table 3.3. Description of the explanatory variables used to model primate densities in this study.

Variable Name	Description
Fragment Spatial Attributes	
Area	Fragment surface area (km2)
Shape Index (SI)	Fragment perimeter (m) divided by the square root of fragment area (km2), adjusted by a constant to simulate a square or circular standard.
Proximity Index (PI)	Sum of fragment area (km2) divided by the nearest edge-to-edge distance squared between the focal fragment and adjacent fragments of the same vegetation class as long as their edges are within a predifined search radius (e.g. 250, 500 and 1000m) of the focal fragment.
Anthropogenic Factors	
Reserve	Protected Area status (either National Park (NP), Special Reserve (SR) or IUCN Category V Seascape/Landscape (CAT5)
Fire	Site specific presence/absence of large scale fire (>0.5ha) during the course of study (6/2003 - 6/2012)
Hunting	Site specific presence/absence of hunting or its signs (traps, slingshots, bullet shells).
Disturbance	Transect specific disturbance index = sum of cut tree stumps and encounters with domestic or invasive animals, humans and their signs divided by the total distance (km) walked for each transect
Forest Loss	Percentage of site specific forest coverage (km) lost during period from 6/1994 - 5/2002.
Natural Ecology	
Substrate	Site specific categorical variable representing one of two states, either limestone or sandstone
Top Ten *Propithecus* Foods	Number of trees from the top ten dry season food species for *Propithecus perrieri* per km^2.
Large Tree Density	Number of trees with DBH ≥ 10 cm per km^2
Average Tree DBH	Average DBH of trees ≥ 10 cm diameter per km^2.
Average Tree Height	Average height of trees ≥ 10 cm diameter per km^2
Propithecus density	Number of individuals (*Propithecus*) per km^2
E. coronatus density	Number of individuals (*E. coronatus*) per km^2
E. sanfordi density	Number of individuals (*E. sanfordi*) per km^2

Table 3.4. Summary table of spatial attributes for eleven forest fragments, measured at the patch level, Region Diana, Northern Madagascar. The forest type relative to the degree of deciduousness is also provided. In general semi-evergreen forests occur on sandstone substrates and dry deciduous forests are characteristic of limestone substrates

Site	Area	Shape Index (SI)	Proximity Index (PI; 250m)	PI (500m)	PI (1000m)	Forest Type
AMB	17.71	4.27	477	1855	1862	Semi-Evergreen
GRO	5.20	3.19	5070	5074	5079	Dry Deciduous
AMP	5.97	4.43	49	50	68	Dry Deciduous
ANA E	124.0	6.15	1985	1997	2002	Dry Deciduous
ANA W	90.87	9.17	3045	3073	3078	Dry Deciduous
ADP	4.62	2.4	3332	3357	3359	Semi-Evergreen
ANK E	25.64	6.49	0	7	195	Dry Deciduous
ANK W	121.84	7.61	84	93	154	Dry Deciduous
ANT	5.38	2.05	2	2	9	Dry Deciduous
MAD	1.28	2.84	10	103	103	Dry Deciduous
MAH L	4.58	3.8	374	376	378	Dry Deciduous
MAH S	2.61	3.44	327	333	334	Semi-Evergreen

Table 3.5. Summary of habitat and other natural ecological characteristics for eleven forest fragments, measured at both the level of the patch and transect, Region Diana, Northern Madagascar. Estimated primate densities are provided for three diurnal lemurs as the number of individuals per km^2. The upper and lower 95% confidence intervals for these estimates are bound by parentheses. Substrate type: S = sandstone, L = limestone.

Site	Transect Label	Substrate Type	Large Tree Density (indiv/km^2)	DBH (cm)	Height (m)	Crown Diameter (m)	*P. perrieri* Density (indiv/km^2)	*E. coronatus* Density (indiv/km^2)	*E. sanfordi* Density (indiv/km^2)	Total Diurnal Primate Biomass (kg)
AMB	AMB A	S	76313	17	12	NA	32.2 (24.2, 42.9)	41.6 (29.4, 58.9)	17.9 (9.8, 32.8)	226
GRO	GRO A	L	45000	19	11	3	0	14.6 (0.07, 3029.5)	0	18
GRO	GRO B	L	45000	19	11	3	20.9 (4.0, 108.3)	0	0	94
AMP	KIJ A	L	99200	29	10	3	0	43.8 (19.3, 99.9)	197.0 (120.9, 321.1)	417
AMP	AMP A	L	99200	29	10	3	0.5 (0.1, 2.5)	44.0 (24.0, 80.9)	88.1 (44.8, 173.4)	215
AMP	AMP B	L	99200	29	10	3	1 (0.2, 4.6)	113.5 (61.8, 208.6)	84.9 (37.4, 192.9)	296
AMP	AMP C	L	99200	29	10	3	0	77.3 (39.2, 152.7)	53.4 (21.2, 134.8)	189
ANA E	ANA A	L	66696	18	11	2	4 (0.3, 49.1)	25.2 (9.8, 65.1)	0	47
ANA E	APM A	L	66696	18	11	2	0.5 (0.1, 2.5)	9.1 (0.4, 227.4)	0	11
ANA E	ALB A	L	66696	18	11	2	2.6 (0.3, 27.4)	25.7 (7.5, 89.1	16.8 (6.3, 44.9)	76
ANA E	ALB B	L	66696	18	11	2	2.5 (0.5, 12.9)	8.2 (0.001, 479.5)	0	18
ANA E	ALB C	L	66696	18	11	2	1.5 (0.3, 8.0)	20.4 (7.7, 54.0)	19.1 (6.0, 60.9)	68
ANA E	ALB D	L	66696	18	11	2	4.8 (1.8, 13.1)	26.7 (15.3, 46.6)	4.4 (0.6, 31.6)	62
ANA W	ADB A	L	89667	16	12	5	6 (1.8, 19.6)	35.7 (18.0, 70.8)	2.7 (0.5, 14.1)	75
ANA W	ANK A	L	89667	16	12	5	3.8 (1.5, 9.5)	18.1 (9.8, 33.5)	1.5 (0.3, 7.9)	43

ANA W	ANK B	L	89667	16	12	5	7.6 (4.2, 13.8)	48.5 (33.7, 69.7)	6.1 (15.7, 23.9)	103
ADP	ADP A	S	114449	17	11	2	31 (18.7, 52.8)	26.5 (13.3, 53.1)	6.7 (2.2, 20.6)	184
ADP	ADP B	S	114449	17	11	2	20 (41.5, 100.5)	47.9 (18.0, 127.5)	10.9 (0.007, 15605)	166
ANK E	NOS D	L	35000	18	10	5	0	106.4 (9.7, 1169.9)	37.3 (7.2, 193.8)	193
ANK E	SBO A	L	35000	18	10	5	0	57.3 (29.1, 112.9)	23.3 (5.0, 110.2)	110
ANK E	NOS C	L	35000	18	10	5	0	13.6 (0.02, 9684.7)	6.2 (1.2, 32.0)	28
ANK W	ANI A	L	38600	24	13	6	0	162.4 (105.2, 250.5)	211.3 (131.2, 340.1)	581
ANK W	DRV C	L	38600	24	13	6	0	22.1 (0.007, 665.6)	0	26
ANK W	DRV D	L	38600	24	13	6	0	173.7 (29.2, 1033.4)	34.4 (6.6, 178.9)	268
ANT	ANT A	L	101415	21	11	2	0	35.1 (20.8, 59.3)	14.3 (5.2, 39.8)	67
ANT	ANT B	L	101415	21	11	2	0	41.3 (21.4, 80.0)	6.8 (0.01, 3265.1)	61
MAD	MAD A	L	106333	16	11	3	3.3 (0.9, 11.8)	58.9 (29.5, 117.6)	37.7 (12.8, 110.7)	153
MAD	MAD B	L	106333	16	11	3	8.9 (2.2, 35.2)	42.4 (20.4, 88.1)	11.9 (1.1, 125.4)	112
MAD	MAD C	L	106333	16	11	3	0.7 (0.1, 3.3)	61.8 (35.3, 108.3)	28.0 (9.6, 82.1)	129
MAH L	MAH A	L	105000	21	10	3	2.8 (1.0, 7.6)	36.2 (22.4, 58.4)	15.8 (7.3, 34.2)	85
MAH S	MAH B	S	73750	16	9	2	7.2 (4.2, 13)	43.6 (30.0, 63.4)	3.9 (1.0, 15.2)	91
MAH S	MAH C	S	73750	16	9	2	66.7.7 (2.8, 16)	333.03.0 (16.6, 65.6)	1212.1.1 (0.8, 195.3)	92

Table 3.6. Summary table of anthropogenic factors influencing eleven forest fragments, measured at the level of the transect, Region Diana, Northern Madagascar. Fire and hunting were considered as presence absence variables in all models of primate density. Disturbances are indexed as the number of cut stems, encounters with humans and/or domesticated animals for every kilometer of primate survey conducted along survey routes. The top ten *Propithecus* foods were enumerated at the number of stems of preferred dry season food species per km^2.

Site	Transect Label	Reserve	Fire	Hunting	Disturbance (per km^{-1})	Proportion of Total Forest Loss (1994 – 2002)	Top Ten *Propithecus* Foods
AMB	AMB A	Cat 5	Fire	Hunt	0.01	0.52	NA
GRO	GRO A	Cat 5	Fire	No Hunt	0.14	0.88	5500
GRO	GRO B	Cat 5	No Fire	No Hunt	0.5	0.88	5500
AMP	KIJ A	Cat 5	Fire	Hunt	0.07	0.83	9042
AMP	AMP A	Cat 5	Fire	Hunt	0.05	0.83	9042
AMP	AMP B	Cat 5	Fire	Hunt	0.04	0.83	9042
AMP	AMP C	Cat 5	Fire	Hunt	0	0.83	9042
ANA E	ANA A	SR	No Fire	Hunt	0.08	0.05	2477
ANA E	APM A	SR	No Fire	No Hunt	0	0.05	2477
ANA E	ALB A	SR	No Fire	Hunt	0	0.05	2477
ANA E	ALB B	SR	No Fire	Hunt	0	0.05	2477
ANA E	ALB C	SR	No Fire	No Hunt	0	0.05	2477
ANA E	ALB D	SR	No Fire	No Hunt	0	0.05	2477
ANA W	ADB A	SR	No Fire	No Hunt	0	0.17	2583
ANA W	ANK A	SR	No Fire	No Hunt	0	0.17	2583
ANA W	ANK B	SR	No Fire	No Hunt	0	0.17	2583
ADP	ADP A	SR	No Fire	No Hunt	0.03	0.52	3918
ADP	ADP B	SR	No Fire	No Hunt	0	0.52	3918
ANK E	NOS D	NP	Fire	Hunt	0.28	0	3167
ANK E	SBO A	NP	Fire	Hunt	0.09	0	3167

ANK E	NOS C	NP	Fire	Hunt	0.09	0	3167
ANK W	ANI A	NP	No Fire	No Hunt	0.13	0	200
ANK W	DRV C	NP	No Fire	No Hunt	0	0	200
ANK W	DRV D	NP	No Fire	No Hunt	0	0	200
ANT	ANT A	Cat 5	No Fire	Hunt	0.08	0.12	2185
ANT	ANT B	Cat 5	No Fire	Hunt	0	0.12	2185
MAD	MAD A	Cat 5	No Fire	No Hunt	0	0.49	4000
MAD	MAD B	Cat 5	No Fire	No Hunt	0.02	0.49	4000
MAD	MAD C	Cat 5	Fire	No Hunt	0.06	0.49	4000
MAH L	MAH A	Cat 5	No Fire	No Hunt	0.02	0.83	3500
MAH S	MAH B	Cat 5	Fire	No Hunt	0.04	0.83	11919
MAH S	MAH C	Cat 5	No Fire	No Hunt	0.04	0.83	11919

Table 3.7. Model averaging results for determinants of *P. perrieri* population density excluding all structural variables quantifying habitat differences.

Parameter	Estimate*	Unconditional SE	Confidence Interval	Relative Importance
Intercept	0.359	0.451	(-0.526, 1.244)	
Substrate	3.329	0.958	(1.452, 5.206)	1.00
Fire	1.079	0.485	(0.128, 2.02)	0.84
Disturbance	1.277	0.450	(0.396, 2.158)	0.86

Table 3.8. Model averaging results for determinants of *P. perrieri* population density with variables quantifying the spatial attributes of fragments and substrate type removed to reduce multi-collinearity.

Parameter	Estimate*	Unconditional SE	Confidence Interval	Relative Importance
Intercept	0.3532	0.2475	(-0.132, 0.838)	
Fire	-1.23	0.368	(-1.95, -0.509)	1.00
Disturbance	0.927	0.132	(0.668, 1.19)	1.00
Tree DBH	-2.66	0.677	(-3.988, -1.335)	1.00
Top Ten Foods	1.247	0.368	(0.949, 1.545)	1.00
Crown Diameter	-0.567	0.294	(-1.14, 0.008)	0.45
Tree Height	-0.331	0.219	(-0.759, 0.098)	0.18

Table 3.9. Model averaging results for determinants of *E. coronatus* population density with patch area, patch shape, and substrate type removed to reduce multicollinearity.

Parameter	Estimate*	Unconditional SE	Confidence Interval	Relative Importance
Intercept	3.553	0.112	(3.332, 3.773)	
PI (250m)	-0.997	0.285	(-1.555, -0.439)	1.00
E. sanfordi Density	0.502	0.248	(0.016, 0.988)	0.61
Tree Height	0.380	0.234	(-0.079, 0.839)	0.43
Large Tree Density	0.211	0.227	(-0.235, 0.657)	0.21
Avg. Tree DBH	-0.036	0.318	(-0.660, 0.588)	0.16

Table 3.10. Model averaging results for determinants of *E. sanfordi* population density with patch area, patch shape, and substrate type removed to reduce multicollinearity.

Parameter	Estimate*	Unconditional SE	Confidence Interval	Relative Importance
lntercept	2.188	0.200	(1.79, 2.580)	
E. coronatus Density	1.936	0.550	(0.858, 3.014)	1.00
Large Tree Density	1.175	0.550	(0.381, 1.969)	0.94
PI (250m)	-1.487	0.551	(-2.568, -0.406)	0.86
Avg. Tree Height	-0.742	0.497	(-1.715, 0.232)	0.36
Avg. Tree DBH	0.471	0.401	(-0.323, 1.264)	0.25

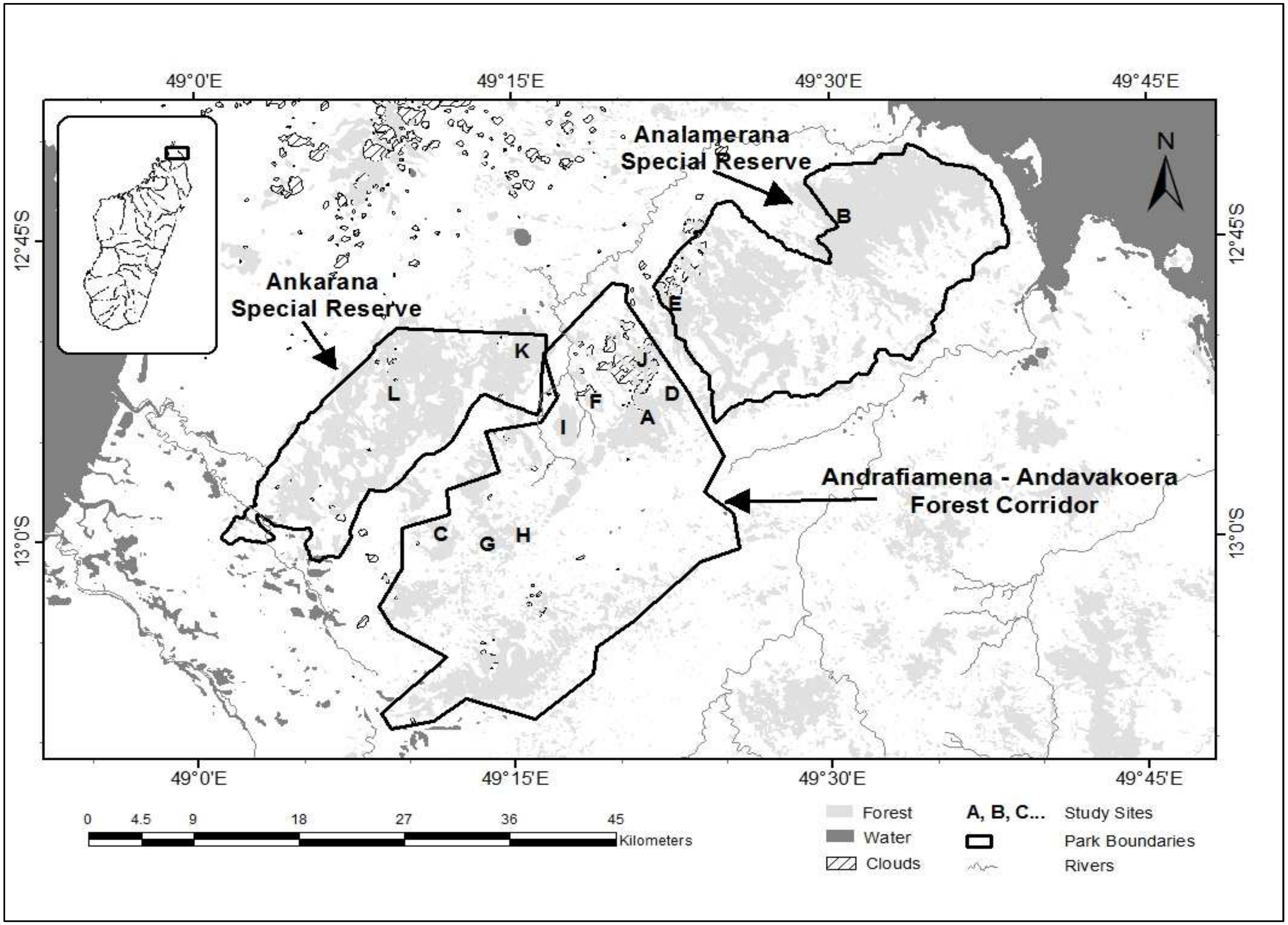

Figure 3.1. A map of the study region with protected area boundaries indicated. See Table 3.1. for all site names.

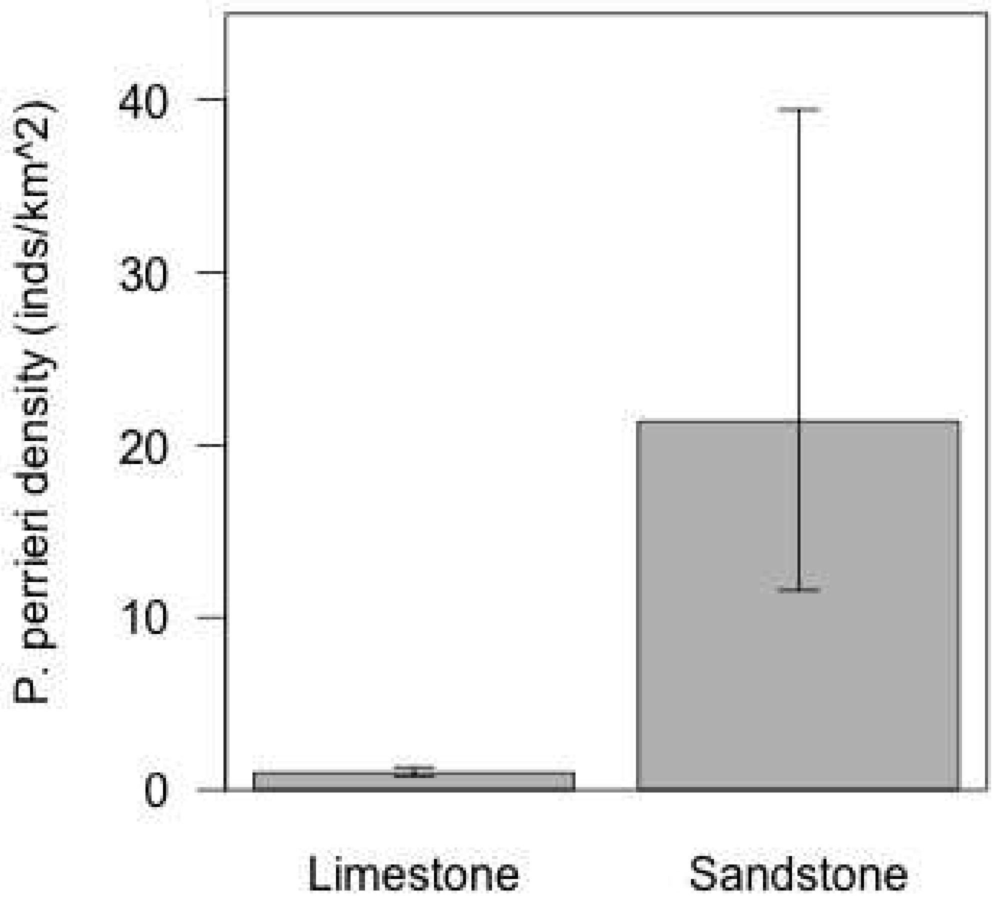

Figure 3.2. *Propithecus* densities depicted as a function of substrate type

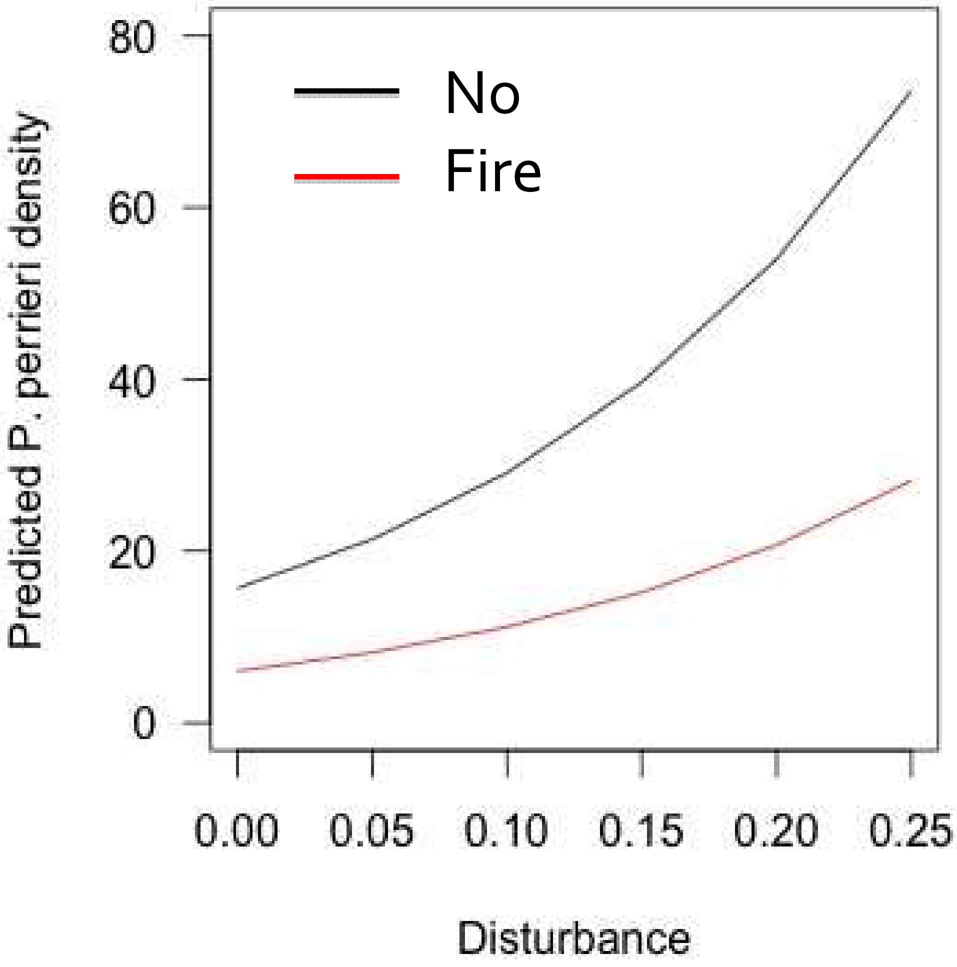

Figure 3.3. Predicted trajectories for *Propithecus* densities using model averaged parameters for disturbance and presence/absence of fire from the confirmatory stage of analysis.

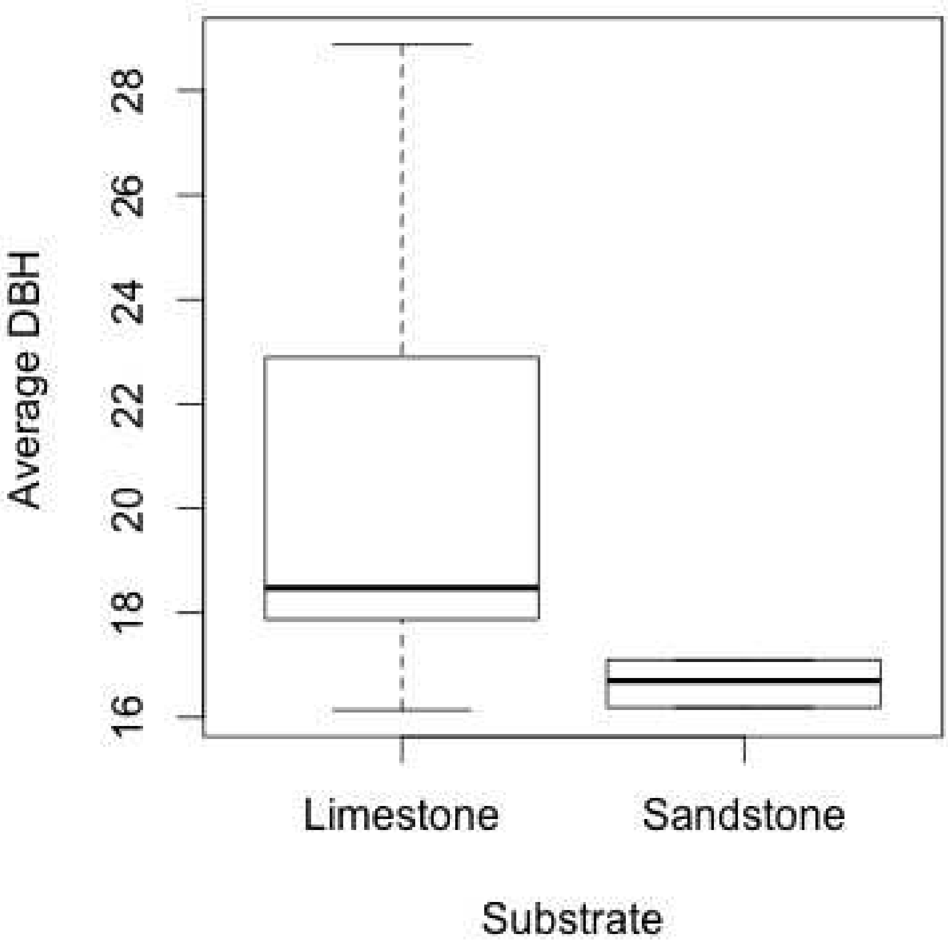

Figure 3.4. Average diameter at breast height (DBH) of trees in 500 m and 1000 m^2 botanical plots in all eleven study fragments from the Diana region, northern Madagascar

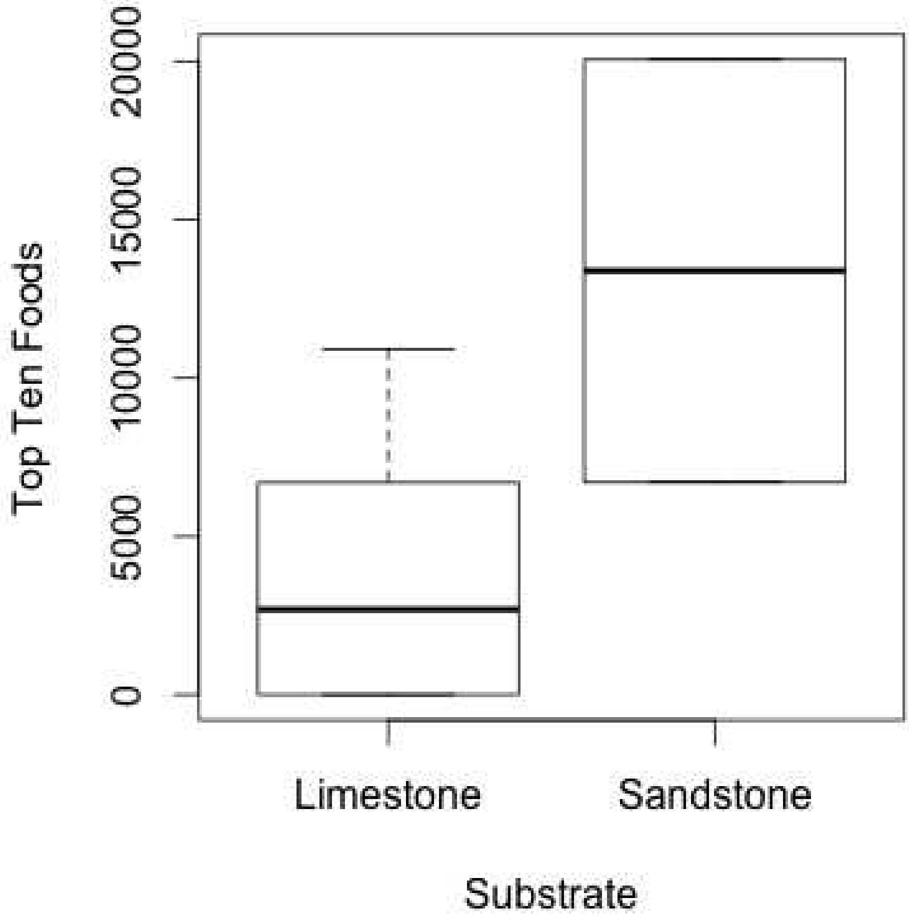

Figure 3.5 Top ten dry season *Propithecus* food species abundance plotted as a function of substrate type

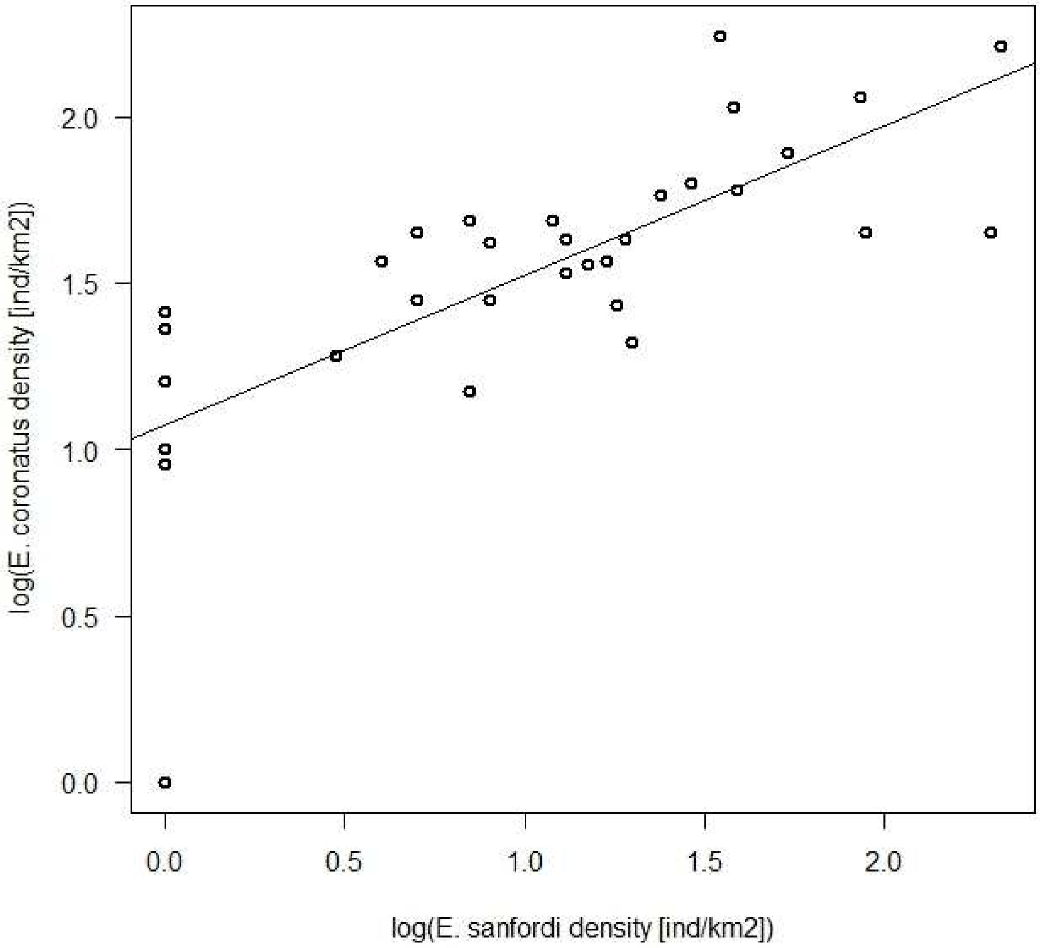

Figure 3.6. Densities of sympatric *Eulemur* species modeled as linear relationship. Densities have been log transformed to ease interpretation.

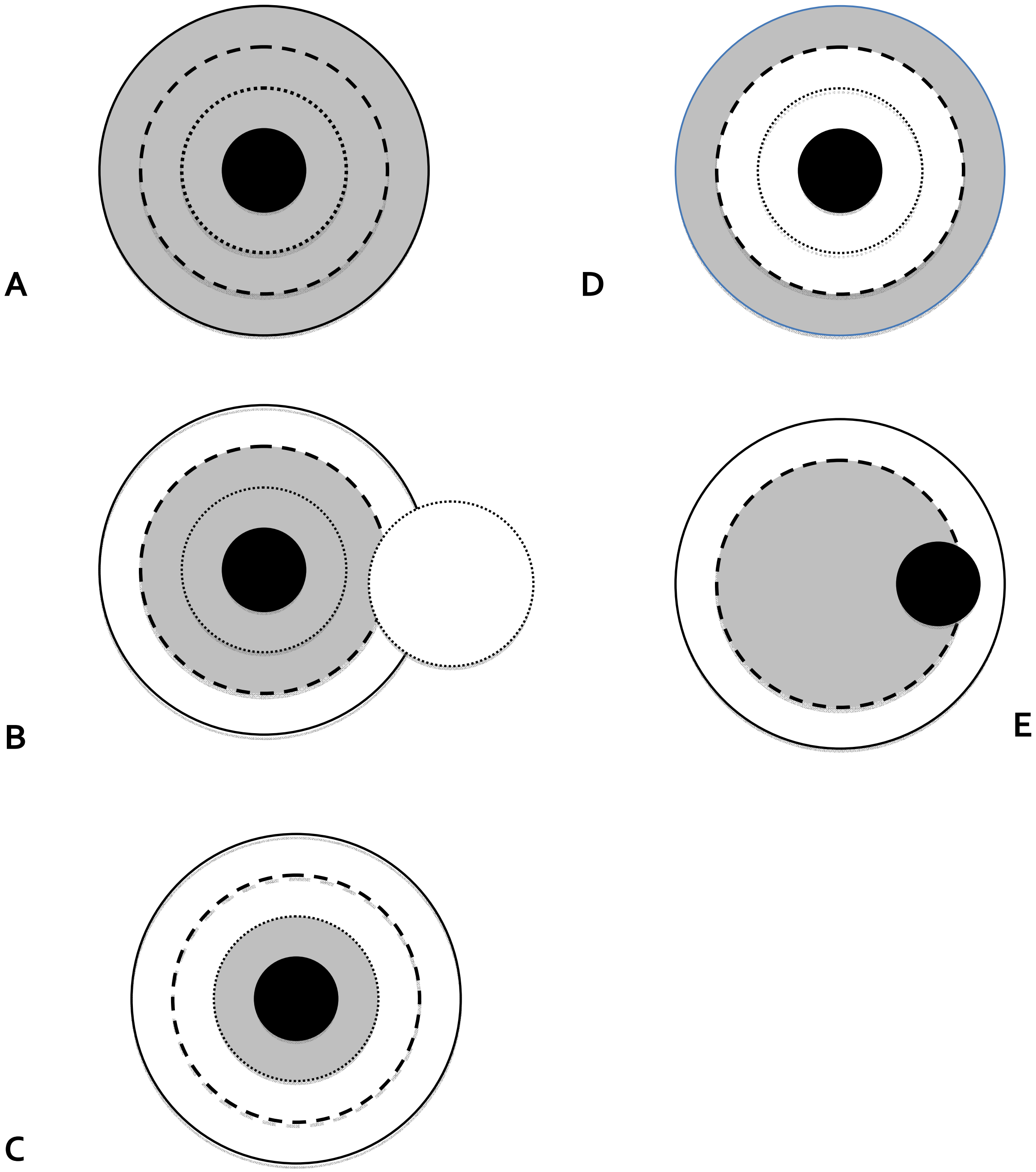

Figure 3.7. Simplified illustration of the differences in the total area considered in the calculation of the original proximity indices and their restructured analogues. Measures included the original variables, (A) PI (1 km), (B) PI (0.5 km), (C) PI (0.25 km) and linear combinations of these variables used to allow for broader comparison and to reduce multi-collinearity, (D) PI (0.5 km LIN) and (E) PI (0.25 km LIN). The black area represents the focal patch while the boundary enclosed within the finely dotted line indicates a search radius of 0.25 km, the heavy dotted line a search radius of 0.5 km, and the solid outermost line a search radius of 1 km. The gray shaded areas highlight the area being considered in the calculation of that particular index.

References

Arroyo-Rodríguez V, Dias P (2010) Effects of habitat fragmentation and disturbance on howler monkeys: a review. American Journal of Primatology 72:1-16

Arroyo-Rodríguez V, Mandujano S (2006) Forest Fragmentation Modifies Habitat Quality for Alouatta palliata. International Journal of Primatology 27:1079-1096

Arroyo-Rodríguez V, Mandujano S (2009) Conceptualization and Measurement of Habitat Fragmentation from the Primates' Perspective. International Journal of Primatology 30:497–514

Balko E, Underwood H (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

Banks MA, Ellis ER, Antonio, Wright PC (2007) Global population size of a critically endangered lemur, Perrier's sifaka. Animal Conservation 10:254–262

Bartón K (2012) MuMIn: multi-model inference. In: R package version

Beaudrot L, Marshall A (2011) Primate communities are structured more by dispersal limitation than by niches. The Journal of Animal Ecology 80:332-341

Bohlman SA (2010) Landscape patterns and environmental controls of deciduousness in forests of central Panama. Global Ecology and Biogeography 19:376-385

Bolker B, Brooks M, Clark C, Geange S, Poulsen J, Stevens MH, White J-S (2009) Generalized linear mixed models: a practical guide for ecology and evolution. Trends in ecology & evolution 24:127-135

Bourlière F (1985) Primate communities: Their structure and role in tropical ecosystems. International Journal of Primatology 6:1-26

Buchanan-Smith H (1999) Tamarin polyspecific associations: Forest utilization and stability of mixed-species groups. Primates 40:233-247

Buckland ST, Anderson DR, Burnham KP, Laake JL, Borchers DL, Thomas L (2001) Introduction to Distance Sampling. Oxford University Press, Oxford, UK

Buřivalová Z (2011) Remote Sensing of Vegetation in Conservation: A Case Study from the Dry and Transitional Forests of Andrafiamena, Northern Madagascar. In: Université de Geneve and Conservatoire et Jardin Botanique de la Ville de Geneve. Université de Geneve, Geneva, Switzerland, pp 89

Burnham K, Anderson D (2002) Model selection and multi-model inference: a practical information-theoretic approach. Springer-Verlag, New York, NY

Cardiff S, Befourouack J (2003) The Reserve Spéciale d'Ankarana. In: Goodman SM, Benstead JP (eds) The Natural History of Madagascar. University of Chicago Press, Chicago, IL, pp 1501-1507

Chapman C, Chapman L (1999) Implications of small scale variation in ecological conditions for the diet and density of red colobus monkeys. Primates 40:215-231

Chapman C, Chapman L, Naughton-Treves L, Lawes M, McDowell L (2004) Predicting folivorous primate abundance: validation of a nutritional model. American Journal of Primatology 62:55-69

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

Chatterjee S, Hadi AS (2013) Regression analysis by example. John Wiley & Sons, Inc., Hoboken, NJ

Cochrane M (2003) Fire science for rainforests. Nature 421:913-919

Cochrane MA, Alencar A, Schulze MD, Souza Jr. CM, Nepstad DC, Lefebvre P, Davidson EA (1999) Positive feedbacks in the fire dynamic of closed canopy tropical forests. Science 284:1832-1835

Cristóbal-Azkarate J, Veà J, 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

Dehgan A (2003) The Behavior of Extinction: Predicting the Incidence and Local Extinction of Lemurs in Fragmented Habitats of Southeastern Madagascar. In. University of Chicago, Chicago, IL, pp 248

Du Puy DJ, Moat J (2003) Using Geological Substrate to Identify and Map Primary Vegetation Types in Madagascar and the Implications for Planning Biodiversity Conservation. In: Goodman SM, Benstead JP (eds) The Natural History of Madagascar. University of Chicago Press, Chicago, IL, pp 51-66

Fleagle JG, Janson CH, Reed KE (1999) Primate communities. Cambridge University Press, Cambridge, UK

Fleagle JG, Reed KE (1999) Phylogenetic and temporal perspectives on primate ecology. In: Fleagle JG, Janson CH, Reed KE (eds) Primate Communities. Cambridge University Press, Cambridge, UK, pp 92-115

Forman RTT, Godron M (1981) Patches and structural components for a landscape ecology. BioScience 10:733-740

Fowler SV, Chapman P, Checkley D, Hurd S, McHale M, Ramangason GS, Randriamasy JE, Stewart P, Walters R, Wilson JM (1989) Survey and management proposals for a tropical deciduous forest reserve at Ankarana in northern Madagascar. Biological Conservation 47:297-313

Fox BJ (1987) Species assembly and the evolution of community structure. Evolutionary Ecology 1:201-213

Freed BZ (2006) Polyspecific Associations of Crowned Lemurs and Sanford's Lemurs in Madagascar. In: Gould L, Sauther M (eds) Lemurs. Springer Science, New York, NY, pp 111-131

Freed BZ (1996) Co-occurrence among crowned lemurs (*Lemur coronatus*) and Sanford's lemurs (*Lemur fulvus sanfordi*) of Madagascar. In: Department of Anthropology. Washington University, pp 450

Ganzhorn JU (1992) Leaf chemistry and the biomass of folivorous primates in tropical forests. Oecologia 91:540-547

Ganzhorn JU (1993) Flexibility and constraints of *Lepilemur* ecology. In: Kappeler P, Ganzhorn J (eds) Lemur social systems and their ecological basis. Springer, Gôttingen, pp 153-166

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

Ganzhorn JU (1997) Test of Fox's assembly rule for functional groups in lemur communities in Madagascar. Journal of Zoology 241:533-542

Ganzhorn JU (1998) Nested Patterns of Species Composition and Their Implications for Lemur Biogeography in Madagascar. Folia Primatologica 69:332–341

Ganzhorn JU (1999) Body mass, competition and the structure of primate communities. In: Fleagle JG, Janson CH, Reed KE (eds) Primate communities. Cambridge University Press, Cambridge, UK, pp 141-157

Ganzhorn JU (2002) Distribution of a folivorous lemur in relation to seasonally varying food resources: integrating quantitative and qualitative aspects of food characteristics. Oecologia 131:427–435

Ganzhorn JU, Malcomber S, Andrianantoanina O, Goodman SM (1997) Habitat Characteristics and Lemur Species Richness in Madagascar. Biotropica 29:331-343

Ganzhorn JU, Wright PC, Ratsimbazafy J (1999) Primate communities: Madagascar. In: Fleagle J, Janson C, Reed K (eds) Primate Communities. Cambridge University Press, Cambridge, UK, pp 75-89

García G, Goodman SM (2003) Hunting of protected animals in the Parc National d'Ankarafantsika, north-western Madagascar. Oryx 37:115-118

Gautier L, Goodman SM (2003) Introduction to the Flora of Madagascar. In: Goodman SM, Benstead JP (eds) The Natural History of Madagascar. The University of Chicago Press, Chicago, IL, pp 229-249

Gautier-Hion A, Brugière D (2005) Significance of Riparian Forests for the Conservation of Central African Primates. International Journal of Primatology 26:515-523

Glander KE, Tapia RJ, Fachin TA (1984) The impact of cropping on wild populations of *Saguinus mystax* and *Saguinus fuscicollis* in Peru. American Journal of Primatology 7:89-97

Godfrey LR, Irwin MT (2007) The evolution of extinction risk: past and present anthropogenic impacts on the primate communities of Madagascar. Folia Primatologica 78:405-419

Golden CD (2009) Bushmeat hunting and use in the Makira Forest, north-eastern Madagascar: a conservation and livelihoods issue. Oryx 43:386–392

Goodman SM, Ganzhorn JU (2004a) Biogeography of lemurs in the humid forests of Madagascar: the role of elevational distribution and rivers. Journal of Biogeography 31:47-55

Goodman SM, Ganzhorn JU (2004b) Elevational Ranges of Lemurs in the Humid Forests of Madagascar. International Journal of Primatology 25:331-350

Grueber CE, Nakagawa S, Laws RJ, Jamieson IG (2011) Multimodel inference in ecology and evolution: challenges and solutions. Journal of Evolutionary Biology 24:699-711

Gustafson EJ, Parker GR (1994) Using an index of habitat patch proximity for landscape design. Landscape and Urban Planning 29:117-130

Hamilton W (1971) Geometry for the selfish herd. Journal of Theoretical Biology 31:295-311

Hanski I (1999) Habitat connectivity, habitat continuity, and metapopulations in dynamic landscapes. Oikos 87:209-219

Haugaasen T, Peres CA (2009) Interspecific primate associations in Amazonian flooded and unflooded forests. Primates 50:239-251

Hawkins AFA, Chapman P, Ganzhorn JU, Bloxam QMC, Barlow SC, Tonge SJ (1990) Vertebrate Conservation in Ankarana special reserve, Northern Madagascar. Biological Conservation 54:83-110

Heymann EW, Buchanan-Smith HM (2007) The behavioural ecology of mixed-species troops of callitrichine primates. Biological Reviews 75:169-190

Humbert H, Cours-Darne G (1965) Carte Internationale de Tapis Vegetale: Madagascar, 1:1,000,000. Travaux de la Section Scientifique et Technique de l'Institut Français de Pondichéry (hors serie), Toulouse, France

Irwin MT, Wright PC, Birkinshaw C, Fisher BL, Gardner CJ, Glos J, Goodman SM, Loiselle P, Rabeson P, Raharison J-L (2010) Patterns of species change in anthropogenically disturbed forests of Madagascar. Biological Conservation 143:2351–2362

Janson C, Chapman C (1999) Resources and primate community structure. In: Primate communities. Cambridge University Press, Cambridge, UK, pp 237-267

Johnson SE (2006) Evolutionary Divergence in the Brown Lemur Species Complex. In: Gould L, Sauther ML (eds) Lemurs Ecology and Adaptation. Springer, New York, NY., pp 450

Jury MR (2003) The Climate of Madagascar. In: Goodman SM, Benstead JP (eds) The Natural History of Madagascar. University of Chicago Press, Chicago, IL, pp 75-85

Kamilar JM (2009) Environmental and geographic correlates of the taxonomic structure of primate communities. American Journal of Physical Anthropology 139:382-393

Kamilar JM, Muldoon KM (2010) The climatic niche diversity of malagasy primates: a phylogenetic perspective. PloS ONE 5:e11073

Kamilar JM, Guidi LM (2010) The phylogenetic structure of primate communities: variation within and across continents. Journal of Biogeography 37:801-813

Koenig A, Borries C, Chalise MK, Winkler P (1997) Ecology, nutrition, and timing of reproductive events in an Asian primate, the Hanuman langur (*Presbytis entellus*). Journal of Zoology 243:215-235

Laurance WF, Delamônica P, Laurance SG, Vasconcelos HL, Lovejoy TE (2000) Rainforest fragmentation kills big trees. Nature 404:836

Laurance WF, Lovejoy TE, Vasconcelos HL, Bruna EM, Didham RK, Stouffer PC, Gascon C, Bierregaard RO, Laurance SG, Sampaio E (2002) Ecosystem Decay of Amazonian Forest Fragments: a 22-Year Investigation. Conservation Biology 16:605-613

Lees A, Peres C (2008) Conservation value of remnant riparian forest corridors of varying quality for amazonian birds and mammals. Conservation Biology 22:439-449

Lehman S (2007) Spatial variations in *Eulemur fulvus rufus* and *Lepilemur mustelinus* densities in Madagascar. Folia Primatologica 78:46-55

Lehman S, Mayor M (2004) Dietary patterns in Perrier's sifakas (*Propithecus diadema perrieri*): a preliminary study. American Journal of Primatology 62:115-122

Lehman S, Rajaonson A, Day S (2006) Lemur responses to edge effects in the Vohibola III classified forest, Madagascar. American Journal of Primatology 68:293-299

Letsara R (2007) Inventaire rapide de la flore et de la vegetation du corridor forestier d'Andrafiamena. In: Conservation International Rapid Assessment Program Report, Alexandria, VA

MacArthur RH, Diamond JM, Karr JR (1972) Density compensation in island faunas. Ecology 53:330-342

Markolf M, Kappeler P (2013) Phylogeographic analysis of the true lemurs (genus *Eulemur*) underlines the role of river catchments for the evolution of micro-endemism in Madagascar. Frontiers in Zoology 10:70

Marques T, Thomas L, Fancy S, Buckland S (2007) Improving estimates of bird density using multiple-covariate distance sampling. The Auk 124:1229-1243

Marshall A, Boyko C, Feilen K, Boyko R, Leighton M (2009) Defining fallback foods and assessing their importance in primate ecology and evolution. American Journal of Physical Anthropology 140:603-614

Marshall A, J. , Wrangham R, W. (2007) Evolutionary Consequences of Fallback Foods. International Journal of Primatology 28:1219–1235

McGarigal K, Marks B (1995) Spatial pattern analysis program for quantifying landscape structure. In: Gen. Tech. Rep. PNW-GTR-351. US Pacific Northwest Research Station, Portland, OR

McGill B, Enquist B, Weiher E, Westoby M (2006) Rebuilding community ecology from functional traits. Trends in Ecology & Evolution 21:178-185

Meyers DM (1993) The effects of resource seasonality on behavior and reproduction in the golden-crowned sifaka (*Propithecus tattersalli*, Simons, 1988) in three Malagasy forests. In: Department of Biological Anthropology and Anatomy. Duke University, Durham, NC, pp 230

Milton K (1979) Factors influencing leaf choice by howler monkeys: a test of some hypotheses of food selection by generalist herbivores. American Naturalist 114:362-378

Muldoon KM, Goodman SM (2010) Ecological biogeography of Malagasy non-volant mammals: community structure is correlated with habitat. Journal of Biogeography 37:1144-1159

Noë R, Bshary R (1997) The formation of red colobus-diana monkey associations under predation pressure from chimpanzees. R. Soc. Lond. B 264:253-259

Norconk MA (1990) Mechanisms promoting stability in mixed *Saguinus mystax* and *S. fuscicollis* troops. American Journal of Primatology 21:159-170

Norconk MA, Grafton BW, Marsh L (2003) Changes in forest composition and potential feeding tree availability on a small land-bridge island in Lago Guri, Venezuela. Primates in Fragments: Ecology and conservation:211-227

Oates J, Whitesides G, Davies A, Waterman P (1990) Determinants of variation in tropical forest primate biomass: new evidence from West Africa. Ecology 71:328-343

Overdorff D, Johnson SE (2003) *Eulemur*, true lemurs. In: Goodman SM, Benstead JP (eds) The Natural History of Madagascar. Chicago University Press, Chicago, IL, pp 1320-1324

Peres C (1997) Effects of habitat quality and hunting pressure on arboreal folivore densities in neotropical forests: a case study of howler monkeys (*Alouatta* spp.). Folia Primatologica 68:199-222

Peres C (1999) Effects of subsistence hunting and forest types on the structure of Amazonian primate communities. In: Fleagle J, Janson C, Reed K (eds) Primate Communities. Cambridge University Press, Cambridge, UK

Peres C, Barlow J, Haugaasen T (2003) Vertebrate responses to surface wildfires in a central Amazonian forest. Oryx 37:97–109

Peres CA, Dolman PM (2000) Density compensation in neotropical primate communities: evidence from 56 hunted and nonhunted Amazonian forests of varying productivity. Oecologia 122:175–189

Porter L (2001) Benefits of polyspecific associations for the Goeldi's monkey (*Callimico goeldii*). American Journal of Primatology 54:143-158

Porter L, Garber P (2007) Niche expansion of a cryptic primate, *Callimico goeldii,* while in mixed species troops. American Journal of Primatology 69:1340-1353

Potts K, Chapman C, Lwanga J (2009) Floristic heterogeneity between forested sites in Kibale National Park, Uganda: insights into the fine-scale determinants of density in a large-bodied frugivorous primate. The Journal of Animal Ecology 78:1269-1277

Powzyk JA, Mowry CB (2003) Dietary and Feeding Differences Between Sympatric *Propithecus diadema diadema* and *Indri indri*. International Journal of Primatology 24:1143-1162

R Core Development Team (2013) R: Language and Environment for Statistical Computing. In. R Foundation for Statistical Computing, Vienna, Austria

Reed K, Fleagle J (1995) Geographic and climatic control of primate diversity. Proceedings of the National Academy of Sciences of the United States of America 92:7874-7876

Root RB (1973) Organization of a plant-arthropod association in simple and diverse habitats: the fauna of collards (*Brassica oleracea*). Ecological Monographs 43:95-124

Stensland E, Angerbjorn A, Berggren P (2003) Mixed species groups in mammals. Mammal Review 33:205–223

Stevenson P (2001) The relationship between fruit production and primate abundance in Neotropical communities. Biological Journal of the Linnean Society 72:161-178

Symonds MRE, Moussalli A (2010) A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. Behavioral Ecology and Sociobiology 65:13–21

Terborgh J (1984) Five New World primates: a study in comparative ecology. Princeton University Press. Princeton, NJ. pp.280

Terranova CJ, Coffman BS (1997) Body weights of wild and captive lemurs. Zoo Biology 16:17-30

Thomas L, Buckland S, Rexstad E, Laake J, Strindberg S, Hedley S, Bishop J, Marques T, Burnham K (2010) Distance software: design and analysis of distance sampling surveys for estimating population size. The Journal of Applied Ecology 47:5-14

Tischendorf L, Bender DJ, Fahrig L (2003) Evaluation of patch isolation metrics in mosaic landscapes for specialist vs. generalist dispersers. Landscape Ecology 18:41-50

van Schaik C, Madden R, Ganzhorn J (2005) Seasonality and primate communities. In: Brockman D, van Schaik C (eds) Seasonality in Primates: Studies of Living and Extinct Human and Non-Human Primates. Cambridge University Press, Cambridge, UK, pp 445-463

Waterman PG, Ross JAM, Bennett EL, Davies AG (1988) A comparison of the floristics and leaf chemistry of the tree flora in two Malaysian rain forests and the influence of leaf chemistry on populations of colobine monkeys in the Old World. Biological Journal of the Linnean Society 34:1-32

White FJ, Overdorff DJ, Balko EA, Wright PC (1995) Distribution of Ruffed Lemurs (*Varecia variegata*) in Ranomafana National Park, Madagascar. Folia Primatologica 64:124-131

Wiens JA, Moss MR (2005) Issues and Perspectives in Landscape Ecology: Cambridge Studies in Landscape Ecology. Cambridge University Press, New York, NY. pp.390

Wilmé L, Goodman SM, Ganzhorn JU (2006) Biogeographic evolution of Madagascar's microendemic biota. Science 312:1063-1065

Wright P, Volonlontiana R, Razafindratsita V, Pochron S, Jernvall J (2005) The Key to Madagascar Frugivores. In: Dew JL, Boubli JP (eds) Tropical Fruits and Frugivores: The Search for Strong Interactors. Springer, Dordrecht, Netherlands, pp 121-138

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

CHAPTER FOUR:

Primate Species Richness and Occupancy Patterns in Forest Fragments of the Diana Region, Antsiranana Province, Northern Madagascar

Abstract

Studies in ecology that examine processes operating at large spatial scales such as habitat loss and fragmentation need to conduct analyses at appropriate scales to assess the role of these factors in determining population structure, abundance and health. In this study I evaluate patterns of occupancy across a fragmented landscape for diurnal members of extreme northern Madagascar's primate community. I use two species attributes (i.e. diet and dispersal capability) to derive a suite of predictions relative to patterns of occupancy in dry deciduous (n = 24) and semi-evergreen forest (n = 21) fragments of variable spatial characteristics, disturbance intensity and habitat characteristics. I test several hypotheses pertaining to the occurrence of individual primate species and species richness patterns using generalized linear mixed models and model averaging techniques. During five years of study field teams collected a minimum of two full days of presence absence records for all 45 fragments. The results indicate that species richness patterns for this system are not well explained using the spatial characteristics of fragments, habitat type or disturbance intensity as explanatory variables. There was also substantial variation that went unexplained for the species, *Eulemur coronatus* and *Hapalemur occidentalis*. Alternatively, modeling occupancy patterns for *Propithecus perrieri* revealed that disturbance, habitat type, isolation and fragment shape are all important predictors of occurrence. In models for *Eulemur sanfordi*, fragment area predicted occupancy perfectly above a threshold size of $2km^2$. The paucity of effects in general is attributed to the energy frugality hypothesis of Wright (1999), whereby as a radiation lemurs combine a unique suite of traits aimed at coping with harsh and unpredictable conditions. In contrast, the importance of multiple effects in modeling *Propithecus* occupancy are probably the result of its folivorous diet, behavioral strategies for dispersing between fragments and somewhat aggravated relationship with human populations.

Introduction

The extensive role that habitat loss and fragmentation currently play in shaping patterns of primate species distributions is widely recognized (Ganzhorn et al. 2000b; Chapman and Peres 2001) yet syntheses of primate research on these topics identify few consistent, non-random components to the processes involved. These discrepancies might simply be attributed to methodological differences among studies and variation in the capacity of research to separate the various human and natural factors that are most relevant to particular study systems (Fahrig 2003; Arroyo-Rodríguez and Mandujano 2009). In particular, a number of studies with primates focus on the role of factors operating at a local scale through the study of a few primate groups that occur in either "continuous" or "fragmented" habitats (Tutin 1999; Irwin 2007a; Donati et al. 2011). While such studies provide valuable insights into the responses of individual species to fragmentation, inquiry at broader scales of the landscape are also required to uncover long-term trends in the population structure, abundance and health of fragmented primate populations (Arroyo-Rodríguez and Mandujano 2009).

This discrepancy in approach is particularly stark among Malagasy primates where few studies have investigated the population levels of primate populations in multiple habitat fragments where a gradient of pressure can be discerned and used to better characterize the landscape (but for a few recent exceptions see Ganzhorn et al. 2003, Quémére et al. 2010a, 2010b and Craul et al. 2009). Indeed with the growth of statistical techniques that can accommodate spatial data that are inherently spatially autocorrelated (Fortin and Dale 2005), as well as capture generalized patterns that are more characteristic of ecological datasets (Bolker et al. 2009), there has been a surge in research that has taken on this perspective in other areas (see Arroyo-Rodriguez and Dias 2010 for review of literature with *Alouatta*, Isabirye-Basuta and Lwanga 2008 for a summary of the literature with African primates). In this chapter I attempt to narrow the gap in the literature for Malagasy primates by using patterns of primate occupancy in the extreme north of the country to evaluate various hypotheses regarding species distribution patterns. I assess the efficacy of prevailing theory in characterizing the role of spatial configuration and other patch-level attributes in driving species composition in habitat fragments within this study system.

Not unlike many of the regions that continue to support wild primate populations, the biodiversity of Madagascar is widely influenced by habitat loss and fragmentation, and the state of the country's wildlife provides one of the most extreme examples regarding the extent of these threats globally (Ganzhorn et al. 2001; Harper et al. 2007). In particular, the dry forests of the west and extreme northern coasts in Madagascar represent the country's most fragmented form of native vegetation and continue to experience the highest rates of deforestation nationally (i.e. 1.9%; Harper et al. 2007). Accordingly it is very timely that the effects of habitat loss and fragmentation on wildlife in Madagascar's dry forests be enumerated so that appropriate responses from conservation agencies can be designed and implemented. Furthermore, the contention that the effects of fragmentation become most important for wildlife species at threshold values of remaining habitat within the larger landscape (Fahrig 2003; Lehman et al. 2006a; Arroyo-Rodríguez et al. 2008) suggests that Madagascar's dry forests provide a suitable backdrop to frame questions aimed at finding a biological basis for many of the processes involved.

Studies aimed at assessing how wildlife are influenced by habitat change can be used to address a variety of questions in ecological theory, including patterns of response in particular taxonomic (Colin et al. 2007; Arroyo-Rodríguez and Dias 2010) and functional groups (Lehman et al. 2006a), as well as evaluating the determinants of primate community structure (Estrada and Coates-Estrada 1996; Ganzhorn et al. 2000b). The theoretical basis for many of these inquiries has traditionally been rooted in Island Biogeography Theory (IBT; MacArthur and Wilson 1967), yet the rapidly growing number of empirical studies in fragmented habitats has helped to draw attention to the broad range of factors generally ignored by IBT (Laurance 2008). In addition to acknowledging the importance of considering the role of fragment area and isolation in driving primate distribution patterns, recent studies have also highlighted strong influences arising from variable permeability in matrix habitats (Asensio et al. 2009), differences in dispersal ability (Irwin 2006), and synergism with other anthropogenic factors (Peres 2001; Irwin et al. 2009).

Hypotheses Tested: Diurnal Primate Species Richness

To address the potential for prevailing fragmentation theory to provide insights into primate community structure and individual species occupancy patterns I outlined the following predictions for the diurnal primates of the Diana region, Antsiranana Province in the extreme north of Madagascar. The region supports four diurnal primate species including two frugivorous species, *Eulemur coronatus* (average body mass: 1.18 kg; Terranova and Coffman 1997) and *Eulemur sanfordi* (average body mass: 1.85 kg; Terranova and Coffman 1997), one bamboo specialist, *Hapalemur occidentalis* (average body mass: 1.03 kg; Louis Jr. unpubl. data) and one folivore-frugivore, *Propithecus perrieri* (average body mass: 4.48 kg; Ranaivoarisoa et al. 2006, Lehman et al. 2007 and Louis Jr. and Banks unpubl. data). Following Island Biogeography Theory (IBT; MacArthur and Wilson 1967), **I expect that larger patches will support more diverse communities of primates.** Indeed there has been strong support for classic species-area relationships with primates elsewhere (Reed and Fleagle 1995; Harcourt and Doherty 2005) including in other parts of Madagascar (Dehgan 2003; Ganzhorn et al. 2003). **As forest area decreases the capacity of the habitat to support species that occur at low densities (i.e. typically the largest species) is reduced and accordingly I predicted that smaller forests would contain lower primate species richness than large forests.**

IBT also provides the context for similar predictions regarding species richness and the degree of isolation across habitat patches. In particular, more isolated habitats are less likely to be colonized by dispersing primates given the impending risks from terrestrial predators (Pavelka et al. 2003; Pozo-Montuy and Serio-Silva 2007) and the general reluctance of largely arboreal species to come to the ground (Arroyo-Rodríguez and Mandujano 2009). **I predicted a negative relationship between species richness and fragment isolation for subpopulations of primates found in forest fragments.**

Patterns of primate abundance are widely expected to track food resource patterns, namely those related to food quality and availability (Ganzhorn et al. 1997; Reed 1999; Irwin et al. 2010). Similarly and given the interrelationship between occupancy and abundance (Prugh et al. 2008; Zuckerberg et al. 2009), it might be expected that food resources exert selective pressures on primates and their ability to colonize certain habitats. Edge effects result in reduced tree biomass through heightened tree mortality (Laurance et al. 2000), as well as alterations to plant species composition and vegetation structure (Godfrey and Irwin 2007), all factors that may translate into reduced food quantity and quality for primates (Arroyo-Rodríguez and Mandujano 2006). Furthermore and although some primates have been shown to be tolerant to habitat edges, others have not (Lehman et al. 2006c), suggesting that primate species richness will be lower in more irregularly shaped fragments that possess greater proportions of edge. **As such I predicted that primate species richness will decrease with increasing shape complexity (i.e. relative proportion of edge) in forest fragments.**

Other factors frequently share strong relationships with food resources in forest fragments including the degree of anthropogenic disturbance (Smith et al. 1997; Chiarello and de Melo 2001) and the type of vegetation that best characterizes the fragment (Ganzhorn et al. 2000a; Ganzhorn et al. 2000b; Palacios and Peres 2005). In Madagascar, comparisons of primate species richness in different forest types have often highlighted differences between the evergreen forests of the east coast and the seasonal, deciduous forests of the west and extreme north (Ganzhorn et al. 1999). Differences in habitat diversity, such as a through a greater breadth of tree species and the presence of a year-round supply of fleshy fruit have been used to explain higher primate species richness in wet rather than dry forests (Ganzhorn et al. 1999). Although tree species composition differs starkly in the dry deciduous and semi-evergreen, transitional forests that occur within a few kilometers of one another in the Diana region of northern Madagascar, levels of tree species diversity have been found to be comparable (Buřivalová 2011). Despite this similarity, two predominant geological formations characterize these two forest types and highlight strong differences in deciduousness across the mixture of evergreen and dry, xerophytic forests that occur in in northern Madagascar (Fowler et al. 1989; Hawkins et al. 1990). Previous research among the primate communities of Amazonia and Madagascar uncovered a tendency for evergreen forests to support higher numbers of primate species than do more deciduous forests (Peres 1997; Ganzhorn et al. 1999). Ganzhorn et al. (1999) suggested that higher tree species diversity may be responsible for a greater breadth of microhabitats in evergreen forests, and therefore provides a greater niche space for potentially competing lemur species. Despite the similarities in tree species diversity across the habitats sampling during this study, taller trees on average and hence greater forest structural complexity in semi-evergreen forests might be expected to have a similar effect on primate species richness as would high tree species diversity (Ganzhorn et al. 1997). **Accordingly, I predicted that primate species richness will be higher in semi-evergreen rather than dry deciduous forests, reflecting a negative relationship between primates species richness and the degree of deciduousness of the habitat.**

Smith et al. (1997) found that lemur diversity in western dry forest fragments was strongly influenced by habitat clearing and human disturbance within 8 km of human settlements. The study revealed that the presence of villages was also a strong predictor of the occurrence of secondary habitats and the incidence of hunting. Slash and burn agriculture, root harvesting and the raising of domestic animals were positively correlated with the proximity to villages and help to explain the prevalence of secondary habitats in such areas. Highly modified habitats may prove unfavorable to some lemurs and accordingly they may be restricted to more pristine vegetation (e.g. Wright et al. 2008, Balko and Underwood 2005). All of the pressures mentioned in the Smith et al. (1997) study are know to occur in northern Madagascar (Banks et al. 2007; Ranaivoarisoa et al. 2013). **Using the nearest Euclidean distance to villages as a proxy for the occurrence of secondary and highly modified habitats, hunting and grazing, I predicted that the number of primate species will decline with increasing proximity to human settlements.**

Hypotheses Tested: Individual Primate Species Occurrence

In addition to predicting patterns of primate species richness, prevailing fragmentation theory also provides a number of explicit expectations regarding the occurrence of individual primate species. Although phylogenetic divisions have often been used to illustrate patterns of niche space within single primate communities (e.g. Fleagle and Reed 1999), trophic and other functional categories may be particularly useful for characterizing primate community structure in Madagascar (Ganzhorn et al. 1999). Using this framework it is possible to derive several predictions regarding the direction of effect for lemurs from different trophic guilds and their expected presence/absence reponse in forest fragments of variable size, shape, isolation, disturbance history and forest type.

Kirika et al. (2008) found that frugivores were more depauperate in small forest fragments than in the main forest block in Kakamega Forest, western Kenya. Similarly, Worman and Chapman (2006) found a lower biomass of frugivorous primate food trees and food categories in forest fragments peripheral to Kibale National Park. This latter result helped to explain the absence of frugivorous primates in the fragments. Alternatively, folivorous primates generally have lower area requirements than do frugivores and may be less affected by differences in fragment size (Chiarello and Melo 2001, Norscia 2008). **Accordingly, I predicted that the occurrence of frugivores will be positively associated with fragment area while the one diurnal folivore-frugivore, *Propithecus perrieri* should not be affected by fragment size relative to its probability of occurrence. *Hapalemur* are widely classified as folivores owing to their heavy reliance on foliage (Ganzhorn 1997) and as such *Hapalemur occidentalis* is not predicted to experience an area effect on its pattern of fragment occupancy.** This prediction is further supported in light of generally small home range requirements (Tan 1999) as well as patterns of habitat use that reflect ecological plasticity in *Hapalemur* (Grassi 2006).

Fragment isolation may affect individual primate species quite differently and in their comprehensive list of guidelines for the study of fragmented primate populations Arroyo-Rodriguez and Mandujano (2009) recommend that knowledge of species-specific dispersal capabilities should be considered when predicting individual patterns of response to varying degrees of habitat isolation. In the Diana region, only *P. perrieri* is known to occasionally come to the ground to reach isolated *Scerlocaryan sp.* and *Mangifera indica* trees for food or to reach neighboring patches of forest (Lehman and Mayor 2004, Banks pers. obs.). **As such it was predicted that the three dispersal limited species, including the two *Eulemur spp.* and *H. occidentalis* occupancy would be negatively associated with increasing forest isolation. On the other hand, *Propithecus*, is known to cross open areas of up to 600m within the study region (Mayor and Lehman 1999) and I predict that this species will be more tolerant of isolated habitats and therefore no relationship with forest isolation is expected.**

Complex fragment shapes are more vulnerable to edge effects and notably among those that negatively impact primates, the loss of large trees (Laurance et al. 2002; Lehman 2007). In particular, this relationship may reduce food availability for frugivorous primates that rely on rare fruit trees (Worman and Chapman 2006). Alternatively, folivores-frugivores and folivorous primates would be expected to experience more of a neutral response to complex forest shapes given the contention that leaf availability should not change along forest edges (Lehman 2007) and edges may even contain leaves with higher protein concentrations (Waterman et al. 1988; Ganzhorn 1995; Lehman 2007). In support of this contention, at Vohibola III Classified Forest, in southeastern Madagascar, Lehman (2007) found that the heavily folivorous *Lepilemur mustelinus* showed a tolerance for edge habitats and was generally as ubiquitous along forest edges as within the interior. Furthermore as a species that relies heavily on bamboo and grasses (Bambuseae and Poaceae), *Hapalemur* readily accepts edge habitats where bamboo often appears as an early successional species (Arrigo-Nelson and Wright 2004). **Accordingly I predict a negative relationship between frugivore occupancy and fragment shape complexity whereas no relationship is expected for the folivore specialist *Hapalemur* or folivore-frugivores within this study system.**

Folivores tend to show greater tolerance for disturbed forests because of the increases in leaf quality that are typically coincident with the light to moderate disturbances (Ganzhorn 1995) that predominate in close proximity to isolated human subsistence populations (Peres and Lake 2003). Frugivores to the contrary are predicted to be more sensitive to disturbances as a result of their generally large home range requirements and preference for rare fruit trees (Balko and Underwood 2005; Wright et al. 2005; Wright et al. 2011). **Given comparable availability of food for folivores in disturbed and more pristine forests I predicted that folivore occupancy would be unrelated to patterns of habitat disturbance throughout forest fragments. Similarly for the trophic specialist *Hapalemur* that often exploits the secondary, successional bamboos (e.g. *Valiha perrieri*) that frequently colonize areas of disturbance following selective logging and fires (Binggeli 2003; Dransfield 2003), no relationship was predicted between these two variables. Based on the vulnerabilities of frugivorous primates to human disturbance that have previously been described for Malagasy lemurs, I predicted reduced frugivore occurrence with increasing disturbance across the sample of forest fragments sampled here.**

Finally, van Schaik and others (2005) contend that the level of deciduousness of a habitat provides a proxy measure of leaf quality. The result is supported by comparative studies of leaf quality in deciduous and more evergreen forests where leaves in more deciduous habitats have been found to have higher metabolic rates and therefore higher protein contents than in more evergreen habitats (Janzen 1975; Coley and Barone 1996). This trend is presumed to exert a strong influence on the upper limit in population size for folivores because leaf quality has been shown to be a strong determinant of folivore biomass (Oates et al. 1990; Ganzhorn 1995; Janson and Chapman 1999). A similar relationship might be expected with respect to patterns of folivore occupancy in semi-evergreen transitional, versus dry deciduous forest fragments that predominate in the Diana region. **Folivore-frugivores should show a preference for higher quality foods found in the deciduous forests on limestone and a positive relationship between patch deciduousness and patterns of occupancy was predicted for this dietary guild.** Alternatively, primate frugivores are expected to be more sensitive to the length to the interval between the periods of peak flush and fruit production (van Schaik et al. 2005). This variable corresponds to the extent of resource scarcity experienced in a particular area. Flush is a common fallback for frugivores and a larger interval between peak flush and fruit production should increase the chances that fruigivores do not lose opportunities to capitalize on peak flush availability during corresponding periods of low fruit availability. Although this measure of seasonality may limit frugivore density it should not necessarily have an equivalent effect on frugivore incidence (van Schaik et al. 2005). Furthermore all fragments in the Diana region fall within a maximum of a few kilometers of one another and actual seasonal differences in rainfall and cloud cover are not expected to differ dramatically across forest fragments in the landscape being considered here (Meyers 1993; Meyers and Wright 1993). Despite these potential differences canceling one another out, ultimately higher quality flush should be attractive to both folivorous primates as well as frugivores relying on foliage during periods of low fruit availability. In fact several lemur species, including both folivorous and frugivorous taxa respond to periods of fruit scarcity by eating more leaves (Richard and Dewar 1991; Wright 1999). **Accordingly I predicted a positive relationship between frugivore occupancy and patch seasonality or deciduousness.**

Methods

Study Sites

Field teams and I collected data on lemur occupancy in 45 forest fragments falling within the Diana Region of the Antsiranana Province, northern Madagascar from 29 April 2007 to 14 July 2012 (Figure 4.1; for site names please see Table 4.1). Study sites were situated in one of three different protected areas, although one of these areas was only recently elevated to “provisional” protected status as of October of 2008 (France diplomatie 2011; cited in Buřivalová 2011). This is the IUCN Category V landscape/seascape, the Andrafiamena – Andavakoera forest corridor (hereafter Andrafiamena; approximate geographic center: S12°58'53.07", E 49°18'5.39"). The protected landscape/seascape category was designated in the interest of integrating management initiatives for conservation with traditional practices such as farming and hunting. Here nature conservation is typically overseen by an entity that also provides infrastructure to support various subsistence activities as well as activities for economic development. This entity, the NGO Fanamby also facilitates the execution of management objectives outlined by surrounding communities. Twenty-two of the total 45 sites were located within the boundaries of Andrafiamena. The majority of the remaining sites (n = 21) occurred within the Analamerana Special Reserve (hereafter Analamerana; S12°46'34.30", E 49°29'6.34), but we also included the two largest forest fragments that comprise the Ankarana National Park (hereafter Ankarana; S 12°53'34.25", E 49° 8'12.05").

I used two Landsat 7 scenes (170/69, 158/69) and recent satellite imagery, including ICONOS Spot imagery readily available using the standard Google Earth© software package to identify 45 forest fragments using a randomly stratified selection procedure for the study of primate occupancy. The location of all fragments is depicted in Figure 4.1 and summary statistics on the spatial and other attributes of all fragments is provided in Table 4.1. Forest patches ranged in size from .03 to 124 km^2 with nearly half represented by sandstone (n = 21) and limestone (n = 24) substrates. We decided only to consider forests falling within the relatively narrow band of geological formations that are strongly characteristic of the region and could be clearly identified in Du Puy and Moat (1996), namely Mesozoic limestones and sedimentary sandstones (Figure 4.2). The forest types associated with the two substrates are primarily dry deciduous forests on limestone and semi-evergreen or transitional forests on sandstone. Forests patch are situated within a landscape covering approximately 450 km^2 (Banks, unpubl. data).

Forests on the exposed limestone outcrops that characterize the protected areas of Analamerana and parts of Ankarana have a shallow, alkaline soil layer, are more water deprived and support a more xeric and deciduous vegetation (Fowler et al. 1989). Trees in the driest areas are characterized by strong resilience to water scarcity (e.g. *Adenia*, *Aloe* and *Euphorbia* on xerophytic thicket, *Adasonia*, *Hildegardia*, *Commiphora* and *Pachypodium* in dry deciduous forests). When controlling for differences in topography, species typical of the limestone forest include *Diospyros spp*., *Xylopia bemarivensis*, *Norhonia spp*., *Coffea spp*., *Commiphora sp*., *Cynometra sp*., *Hildegardia sp.* and closely related members of the Sapotaceae family such as *Mimusops* and *Faucherea sp*. Alternatively, in the semi-evergreen forests that occur on sandstone, trees are less water deprived and many more cogeners from humid eastern rainforests are present. In these forests, the representative tree species include *Sarcolaena condonochlamys*, *Schizolaena viscosa*, *Sapotaceae sp*., *Diospyros spp*., *Uapaca spp*., *Pandanus sp*. *Grewia spp*. and *Bathiorhamus cryptophorus* and *Dypsis madagascariensis* (Banks unpubl. data). Structurally the two forest types have also been found to differ relative to the homogeneity of the canopy, the above ground biomass and tree size diversity. Furthermore, a mere 4% overlap in tree species has been found between the two habitat types (Buřivalová 2011). Roughly 50% of trees on limestone substrate were deciduous while the majority of trees on sandstone substrate were evergreen (> 80%; Banks pers. obs).

Forests were surrounded primarily by a matrix of grasslands dominated by the following grasses (i.e. Poaceae), *Aristida rufescens*, *Hyparrhenia sp.*, *Trachypogon spicatus* (Letsara 2007). Cultivated lands are also intermixed with the savanna matrix, frequently at the foothills of the region's mountains. These include dry rice paddies, crops of cassava, small produce gardens, and plantations of *Eucalyptus sp*. Although, *P. perrieri*, one of the primate species studied here, is known to cross open areas of savanna to reach isolated food trees (e.g. *Mangifera indica*, *Scelerocaryan sp*.) these feeding bouts are abbreviated events and always followed by a return to the closed canopy of forested habitat. So isolated trees do not form a continuous canopy nor are they used as sleep sites or breeding grounds and as such I did not include them in area calculations as extensions of the habitat or as separate sites. None of the other three diurnal primates observed during the nine-year study period were ever found to come to the ground to cross open areas. Thin bands of riparian forests dissect more open areas along major watercourses. These habitats are typically only a few tens of meters in width and generally were not detecting using Landsat 7 (30m resolution) imagery for the landscape analysis. This potential source of connectivity between fragments could therefore not be considered here.

Primate Occupancy Surveys

Occupancy surveys were performed in all forest fragments by walking slowly along existing trails or those left by cattle (*Bos indicus*) and bush pigs (*Potamochoerus larvatus*). Observers relied largely on stealth to detect primates (Ross and Reeve 2003) since some hunting is known to occur throughout the study region (Banks et al. 2007). Only visual contact with at least one individual of a particular species would be recorded as present for that forest fragment. When primates were encountered we noted the time of contact, species identity, group composition, group spread (i.e. average distance of all conspecifics from the imagined group center), activity and response to observer presence. We restricted our surveys to morning (6 – 11:30) and afternoon (14:00 -17:30) hours and attempted to sample forests exhaustively by working in multiple teams across the entire surface area of the fragment. Forest fragments were visited a minimum of two full days and attempts were made to sample fragments during both dry and wet periods. We approximated species richness by simply recording the total number of primate species observed within each study fragment.

Spatial Attributes of Forest Fragments

I derived a supervised classification of all forest and non-forest classes using Landsat 7 imagery downloaded from the Global Land Cover Facility (University of Maryland) website and ERDAS Imagine 8.6© software. All spatial layers including the resultant vegetation extents were georeferenced in ESRI © ArcMap 10 with the aid of topographic maps prepared by the Foiben-Taosarintanin'i Madigasikara (FTM; Malagasy Geographical Institute). I calculated patch areas, shape indices and proximity indices using the Patch Analyst (Elkie et al. 1999) and FragStats (McGarigal and Marks 1995) software extensions to the ESRI ArcGIS package. A description of the various spatial indices is provided in Table 4.2 and a simplified illustration of the total area considered in the calculation of proximity indices is provided in Figure 4.3. It is important to make the distinction here that an area- as opposed to distance-based metric was used. The proximity index of Gustafson and Parker (1994) considers both the amount of available habitat and the distances of neighboring fragments within a predefined search radius. Search radii were chosen based on knowledge of individual species-specific dispersal capacities and the results of exploratory analyses (see "Statistical Tests" below). In the case of the latter scenario, linear combinations of the original proximity indices were used to reduce multicollinearity and to allow comparison at different spatial extents.

Disturbance and Fragment Geometry

Following Smith et al. (1997) I used the nearest Euclidean distance to large villages as a proxy for human disturbances. The authors uncovered a strong relationship between the nearest village distance and the extent of forest clearing and secondary habitats present at sites in the dry deciduous forests of western Madagascar. Furthermore the measure also provided a good approximation of the influence of domesticated animals in the area including dogs (*Canis lupis familiaris*) that pose an imminent threat to primates attempting to cross matrix habitat to reach neighboring forest. I considered only villages with ≥ 10 households as recorded during recent human census efforts initiated by

ONG Fanamby, Anjahankely throughout the study region (Ranirison and Rabarivelo unpub. data).

I also imported the simplified geology classification for Madagascar (Du Puy and Moat 1996) as a shapefile layer in ArcMap 10 (Figure 4.2) to identify forests on limestone and sandstone substrates. Field observations were used to ground truth these determinations, as differences in the two classes were conspicuous throughout the study region (Buřivalová 2011). To facilitate comparisons we attempted to consider only forest fragments where one of the two substrate classes was present. In the rare cases where forests contained a mixed geology of both substrate types we classified the site by the more predominant (i.e. ≥ 75% surface area) substrate.

Statistical Tests

I used generalized linear mixed models (GLMM) and an information-theoretic (IT; Burnham and Anderson 2002) model averaging approach to identify the factors with the greatest relative importance (Grueber et al. 2011) in predicting overall primate species richness and the occupancy of individual primate species within forest patches. The use of information theory and model averaging provides a parsimonious approach to model selection uncertainty by calculating a weighted average of parameter estimates. Covariates that provide limited information regarding the variance in the response variable are given lower weights. To assess differences in the information provided by competing models, Akaike's Information Criterion (AIC; Akaike 1973) and more specifically its correction for small sample size (i.e. AIC_c) was used (Grueber et al. 2011).

To reduce the number of explanatory variables and avoid such pitfalls as Freedman's paradox (Freedman 1983) during the averaging of parameter effects, I initiated an "all subset" approach (Symonds and Moussalli 2010) to the analysis. Since generating a predictive model using a model averaging approach was the ultimate aim of the analysis, considering all potential covariate effects was necessary. The procedure consisted of first specifying a saturated global model (i.e. all explanatory variables are considered after correcting for multicollinearity; see below) and subsequently deriving a full submodel set (i.e. all possible combinations of the explanatory variables are modeled). The global model is standardized to allow for a comparison of parameter estimates on the same scale (Grueber et al. 2011). A full submodel set was generated using the *dredge* function from the *MuMIn* package (Bartón 2012), an accompaniment package to the R statistical software environment (R Core Development Team 2013). A 95% confidence set of models is then derived through evaluation of individual model Akaike weights. Akaike weights are calculated based on the difference in AIC values between a competing model and the model with the lowest AIC value. Model averaging was performed for the 95% confidence set of models using the *model.avg* function in the *MuMIn* package. Akaike weights were not only used to determine which models provided the best fits to the data but were also used to determine the relative support of one variable over another by summing weights for all models that included that variable (Zuur et al. 2009). A variable with a relative importance of 1 therefore appears in all of the models included in the 95% confidence set. Variables with a relative importance of ≥

0.5 were retained for a hypothesis testing stage of the analysis. In cases where none of the explanatory variables achieved a relative importance of 0.5 or greater, the hypothesis testing stage of the analysis was abandoned and the results were deemed inconclusive.

The hypothesis testing stage of the analysis considered a reduced subset of explanatory variables, but aside from this difference the procedure was analogous to the exploratory analyses described above. The results of model averaging were then used to compare the magnitude and direction of effect for the different explanatory variables isolated within the 95% confidence set for this stage.

A mixed modeling approach was selected to control for data that are inherently spatially autocorrelated (Zuur et al. 2009). In all models site identity was introduced as a random effect. Additionally, a generalized approximating equation with a binomial response and logit link function was fit to the presence absence data as opposed to using data transformations or non-parametric tests that require more restrictive assumptions regarding the underlying distributions of the data. Explanatory variables included fragment area, shape and isolation (i.e. as measured by the proximity index at various spatial extents). Models were parameterized using both overall primate species richness and individual primate species occupancy as response variables.

To reduce collinearity we first evaluated variance inflation factors (VIF) within a matrix containing all explanatory variables considered for that particular model. In exploratory analyses we attempted to keep the VIFs well below the cutoff of 10 where multicollinearity is no longer considered to pose major problems (Chatterjee and Hadi 2013). At the hypothesis testing stage of modeling a more stringent cutoff of 2.5 was adopted (Zuur et al. 2009). In the case of spatial extent variables, namely the proximity index used to approximate fragment isolation, linear combinations of the orginal variables were calculated to enable broader comparisons and reduce multicollinearity (Chatterjee and Hadi 2013). This approach is particularly well suited to spatial data where the smallest extents are nested within larger ones. To address this problem the areas for the variables measured at the two smallest extents (i.e. 0.25 and 0.5 km) are recalculated as the difference between the original variable and the variable within which they are nested (please see Table 4.2 and Figure 4.3; Zuur et al. 2009).

Results

Over the five years that we gathered data on primate species richness and primate occupancy in the Diana Region of northern Madagascar we accumulated presence/absence records for 45 forest fragments that varied in their spatial characteristics, disturbance pressure and geology (Table 4.1). After reducing the number of explanatory variables I found that attempts to model species richness patterns as a function of the spatial attributes of forest fragments, human disturbances and substrate (i.e. habitat) type, revealed that only the shape index was represented in just over half (i.e. RI = 0.55) of the models in a 95% confidence set (Table 4.3). Notably through an examination of the confidence intervals for this parameter estimate, neither a positive nor negative direction to the effect could definitively be assigned with the data on hand. The nature of influence for the remaining explanatory variables is similarly ambiguous and neither the available habitat within a 1 or 0.5 km radius exhibits a clear direction of effect on species richness patterns (Table 4.3). Additionally, the null model performed second best in the 95% confidence set of models and was 1.19 times less likely than the "best" model to capture species richness patterns.

Along with species richness patterns, neither the occupancy of *E. coronatus* or *H. occidentalis* could be effectively modeled using the spatial attributes, habitat type or the intensity of disturbance among forest fragments. In fact the null model was consistently the best model for characterizing the data and through an evaluation of evidence ratios the "next best" competing models in the 95% confidence set were several times less likely than the null to be the best model (range = 2.2 - 2.9). Furthermore, even after simplifying models following the "all subset" stage of the analysis, the standard errors associated with several parameter estimates were several times larger than the estimates themselves, indicating convergence problems.

Occupancy in the medium-sized folivore, *E. sanfordi* was positively associated with the area of the forest fragment (Table 4.4). The size of the effect of area on *E. sanfordi* occupancy (i.e. Estimate = 81.36) was several orders of magnitude higher than that of the only other explanatory variable retained for the hypothesis testing stage of the analysis, substrate type (i.e. Estimate = -1.3; Table 4.4). Nonetheless the only model in the 95% confidence set during this stage of the analysis contained both variables. This model provided a perfect fit to the data above a threshold fragment size (i.e. 2 km^2), an example of the Hauck-Donner effect (Figure 4.5; Hauck and Donner 1977). The negative relationship with substrate indicates that limestone forests are more likely to be occupied by this species than are sandstone forests (Table 4.4).

Propithecus occupancy patterns are potentially influenced by a number of factors including, in order of decreasing relative importance, the distance from villages, substrate type, available habitat within a 0.5 km radius, shape complexity and available habitat within a 1 km radius (Table 4.5). Nevertheless, confidence intervals for all parameter estimates failed to exhibit a clear direction of effect although for variables with the highest RIs, (i.e. distance from villages, substrate type, PI at 0.5km, and shape complexity; Table 4.5) these intervals were more tightly packed around the value of zero. If these values for the parameter estimates are taken at face value, distance from villages has the greatest effect on *Propithecus* occupancy and shape complexity the next largest effect (Estimates: 2.2 and 1.6 respectively, Table 4.5). The effects of substrate type and the PI at 0.5 km are not negligible however and if the models in the 95% confidence set are directly compared, the best model contains all four explanatory variables. There was considerable uncertainty even with the best fitting model however, and it was only 1.3 times more likely than the next best model to provide an optimal fit with the data on hand. Finally, the effect of the PI at 1 km is particularly unclear with a confidence interval of -1.2 – 3.2, and modest representation in the 95% confidence set (i.e. RI = 0.3; Table 4.5.).

Discussion

Why doesn't diurnal species composition vary as a function of habitat fragmentation in the Diana region?

One explanation for the absence of any strong relationships with primate species richness patterns and the variables used to quantify fragmentation in this study may be that lemurs have adapted to be tolerant of dramatic landscape changes (Lehman et al. 2006a; Johnson et al. 2011). Indeed there has been support in several lineages of Malagasy primates for the "Energy Frugality Hypothesis" of Wright (1999) positing that many of the unique biological traits among lemurs have been derived as the result of coping with a harsh and unpredictable environment (Godfrey et al. 2004; Irwin 2006; Dewar and Richard 2007; Johnson et al. 2011; Dewar and Richard 2012). There is evidence from a number of studies of Madagascar's prehistory (see Burney 1999 for a comprehensive review) that argue for the role of late Pleistocene/Holocene climatic viccisitudes in triggering vegetational shifts and influencing the structure of extant primate (Godfrey and Irwin 2007) and other faunal communities (Burney et al. 2003; Burney et al. 2004; Virah-Sawmy et al. 2010; Rakotoarisoa et al. 2013). The negative impact of Madagascar's unpredictable climate on the availability of resources for lemurs has been widely documented (Ganzhorn et al. 1999; Ratsimbazafy 2002; Wright et al. 2005; Johnson et al. 2011). While humans may have a history of contact with lemurs that doubles the figures that have previously been suggested (Dewar et al. 2013), this time frame is insufficient to accommodate evolutionary change in taxa with generation times as long as the relatively long-lived Malagasy primates. The hypothesis that there was pronounced dessication and concomitant environmental change throughout the Holocene (Virah-Sawmy et al. 2010), lends more tenable support to the idea that habitat and climate change have long influenced the natural ecology and resilience of lemurs to habitat disturbance and fragmentation. An alternative explanation for the lack of strong effects in modeling primate richness patterns may relate to the low degrees of freedom for this analysis. Future occupancy studies in this region should attempt to consider nocturnal lemurs as these taxa are more speciose and may represent a substantial portion of the total primate community biomass (Ratelolahy 2007).

As a further example of resilience to habitat change Lehman et al. (2006a) found little evidence for intolerance of edge habitats in his study of the lemur community in southeastern Madagascar. Even *Eulemur rubriventer*, a frugivorous species that was expected to be edge-intolerant was found to range widely into edge habitats during the study. The authors argued that seasonal variation in fruit availability during the period at which they sampled lemur populations might have led to this species' penetration of edge habitats in an effort to use locally abundant leaves as fallback. Evidence has been presented elsewhere for augmented leaf quality and abundance in the gaps left from selective logging, along edges (Ganzhorn 1995) and in forest fragments (Chapman et al. 2004) as a result of increased exposure to sunlight, which in turn stimulates growth and greater plant investment in protein contents in such areas. Northern Malagasy primate communities have been characterized as representing an unfavorable state owing to the unequal representation of different dietary guilds within extant lemur communities (Ganzhorn 1997). Recent Holocene lemur extirpations in the north provide an alternative mechanism for the patterns of community structure here and may also be responsible for the absence of more fragmentation sensitive species.

As with elsewhere in Madagascar, in the Diana region lemurs are likely to use leaves and other foods that predominate along edges as fallback during period of resource scarcity that is associated with the onset of the dry season (Wright et al. 2005). Irwin (2007) found that *Propithecus diadema* in the humid forests of Tsinjoarivo often fallback on mistletoes (*Bakerella sp.*) during the dry season and in forest fragments where fruit trees are scarce and mistletoes form more of a mainstay in the diet of *Propithecus* groups. Many *Eulemur* species have been argued to be habitat generalists (Overdorff and Johnson 2003; Johnson 2006) and this paradigm should apply for the two sympatric *Eulemur* that were studied here. Both are cathemeral, known to have a diverse diet and can exist in a wide variety of habitat types (Freed 1996). Furthermore, Freed (2006) observed that both species would feed in *Lantana camara* and *Bombax* sp. treelets along the edges of rice fields. Similar plants were found in degraded areas during this study and particularly those recently influenced by fire (Banks, pers. obs.). The dietary specialization and habitat preferences of *Hapalemur* limit opportunities to reliably sample this species using line transect surveys but the species' (Chapter 2) lack of response to the effects of fragmentation in this study may also be a result of its preference for grasses and bamboos (Poaceae and Bambuseae; Mutschler and Tan 2003). Furthermore, the successional nature of most *Bambusoidea* species has been documented for the Region Diana and variable patterns of habitat degradation and landslides were cited as explanations for the scattered and disturbance associated distribution of bamboo habitats here (Buřivalová 2011).

The additional lack of clear results with two of the four species studied here (i.e. *E. coronatus* and *H. occidentalis*) may be a reflection of the ambiguity encountered in attempting to model species richness patterns. Difficulty with modeling occupancy patterns in these two species may be an artifact of the sampling regime adopted here as a number of workers have outlined the caveats associated with the role of imperfect detection as a source of bias in occupancy surveys (MacKenzie et al. 2002; Keane et al. 2012). Nevertheless, the decision was taken not to systematically evaluate the probability of detecting each species because detection probability was perceived to be high and efforts were made to control for sources of bias that were documented during a parallel study of primate detectability using the largely analogous technique of line transects (Chapter 2). Although these sources of bias have been shown to confound inference regarding primate population levels in other areas, the primary sources of bias in detecting primates in the Diana region were found to be controlled by working with experienced observers, sampling in both seasons and sampling all habitat types within a particular forest fragment, namely secondary and more pristine habitats (Chapter 1). All of these allowances were made for the occupancy surveys presented here.

Hapalemur did nonetheless provide a special case of imperfect detection (Chapter 2) and few inferences could be drawn from the limited number of records available from sampling the species using line transects in eleven forest fragments over a period of nine years. Imperfect detectability is well known for *Hapalemur* elsewhere (Arrigo-Nelson and Wright 2004) as well as for other specialist primate taxa (i.e. *Daubentonia*; Sterling 2003) in Madagascar. Although bamboo forests were occasionally accessible to observers during surveys this habitat type remains notoriously difficult to sample. Exceptions would need to be made if reliably sampling this taxon were to be targeted as a more explicit goal of the research. As such it is necessary to acknowledge that the most likely explanation for the absence of any effect of fragmentation on the occurrence of

Hapalemur is rooted in imperfect detection and sampling biases that disfavor detection of this species.

Yet another potential source of bias in predicting primate species richness may have been an underrepresentation of smaller sites. DeGamma-Blanchet and Fedigan (2006) used a similar argument to explain the lack of relationship between fragment area and howler (*Alouatta*) monkey occupancy in six forest fragments in Costa Rica. However, sites in this study were selected using a random, stratified design and different fragment sizes were sampled at a frequency proportional to their representation in the landscape. Furthermore, the possibility that the landscape was under-sampled as a product of selecting too few study fragments is unlikely given that Ganzhorn et al. (2003) found strong evidence for species-area relationships in other parts of Madagascar using an average sample of n = 10 forest fragments whereas the sample used here reached n = 45 fragments.

Which species have occupancy patterns that can be explained using the dataset from the Diana Region?

Although there was limited evidence for the role of spatial attributes of fragments, proximity to large villages and habitat type in driving occupancy patterns for *Eulemur coronatus* and *Hapalemur occidentalis,* some patterns did emerge for the other two diurnal primates sampled here. In particular, *Eulemur sanfordi* and *Propithecus perrieri* show signs of responding to fragmented habitats in the case of the former and in demonstrating preferences for particular habitat types and disturbance intensities in the case of the latter species. These findings offer support for the possibility that habitat quality and the influences from human populations are variable across the landscape.

In *E. sanfordi* the strong relationship shared with fragment area provided a perfect fit to the data as an example of a Hauck-Donner effect (Hauck and Donner 1977). The fact that this species is ubiquitous in forest fragments above a threshold size (i.e. 200ha) is probably related to its frugivorous diet and reliance on rare fruit trees (Lehman 2007), which are more likely to absent in smaller fragments (Arroyo-Rodríguez and Mandujano 2009). The effect was several orders of magnitude higher than that of any other variable, even when considering analogous models for the other primates, a pattern which suggests that this species is the most vulnerable member of the diurnal primate community to habitat fragmentation.

While *E. sanfordi* provided an example of an explanatory variable with a very large magnitude of effect, *P. perrieri* was the only species that responded to multiple factors when attempting to explain primate incidence using this dataset. The result is extremely important because it highlights differences in how different primates perceive the same habitats in a variable and fragmented landscape. In the case of *Propithecus*, strong support has already been shown for its preference for sandstone forests (Chapter 2). Densities can be up to three orders of magnitude higher on sandstone vs limestone substrates (0.01 ind/ha vs 0.32 ind/ha). This result contrasts with predictions from the seasonality hypothesis of van Schaik et al. (2005) where more deciduous formations are expected to provide higher quality leaves for herbivores. Sandstone forests are considered to be a semi-evergreen formation plants are expected to invest more energy towards the production of plant chemical defenses aimed at limiting predation from herbivores (van Schaik et al. 2005). Nevertheless, sandstone forests support higher abundances of trees from the top ten *Propithecus* food species (Chapter 3, see Figure 4.5) and this result may help to explain preferences for this habitat type. Unfortunately it is currently not possible to answer the question of whether or not *Propithecus* foods are of higher quality in limestone forests and this determination awaits chemical analyses of the nutritional characteristics of *Propithecus* foods in both habitats (Rothman et al. 2011). Nevertheless, results from this study draw attention to the possibility that the reverse might actually be true or that *Propithecus* don't discriminate between different forests on the basis of food quality.

In addition to the relationship with habitat type, *Propithecus* also showed a preference for forest fragments that are both isolated from large human settlements as well as from other forests. The former result was unexpected given evidence presented elsewhere in support of *Propithecus* tolerance for disturbed habitats (e.g. Lehman et al. 2006c, Irwin 2008). However, in Smith and other's (1997) study of primate occupancy patterns in the dry forests of western Madagascar, the authors demonstrated that the nearest distance to a large village was not only a good proxy for the frequency of human disturbances, but also shared a positive relationship with the intensity of hunting pressure at sites. Although *Propithecus* are protected by an ethnic taboo that forbids hunting of this species throughout the Diana region, this taboo appears to be eroding in many places (Banks et al. 2007). Snares as well as the remains of slingshots were found along fragment edges and within forest interiors at some sites during this study. Although *Propithecus* are not effectively hunted with snare traps, projectile weapons such as slingshots may pose a considerable threat to the species (Golden 2009). Golden (2009) has also shown how hunting wild lemurs may be more prevalent in isolated communities than was once thought. Furthermore and despite widespread reverence for this species, encounters with *Propithecus* can be tense, and large groups frequently approach observers while assuming aggressive postures (Chapter 1, Banks et al. 2007). These encounters can evoke fear and defensive behaviors in humans, factors that may contribute to the avoidance of heavily human dominated habitats by *Propithecus*.

The finding that *Propithecus* are tolerant of isolated forest fragments differs from the neutral response that was predicted but is not inconsistent with the species' willingness to disperse across open areas. The negative relationship with available habitat that was recorded indicates that this species is capable of thriving in isolated habitats likely as a function of flexibility in its capacity for dispersal. Additionally it may help to further explain the above result that habitats close to human settlements are avoided by *Propithecus*. Isolated fragments are not only isolated from neighboring forest but also from human settlements. In addition to an increased potential for hunting this pattern might also relate to higher densities of domestic dogs (*Canis lupus familiarus*) in close proximity to villages. Indeed Smith et al. (1997) found that the number of encounters with domestic animals and their signs increased at greater proximities to villages. Dogs are known to attack *Propithecus* that have come to ground to cross open areas (Banks pers.obs) and this threat is also well known for *Alouatta spp.* in fragmented landscapes (Arroyo-Rodríguez and Dias 2010). Mayor and Lehman (1999) observed a group of *P. perrieri* cross open areas of up to 600 m to reach neighboring forest as well as to visit isolated *Sclerocaryan sp.* and *Mangifera indica* trees for food. This tendency to come to the ground appears likely to facilitate movement to neighboring forest patches for dispersal as well as to supplement limited dry season food resources (Dunning et al. 1992), thereby increasing the species' chances at survival. However this behavior also exposes *P. perrieri* to the risk of predation by domestic dogs (Estrada and Coates-Estrada 1996; Estrada et al. 2002; Anzures-Dadda and Manson 2007), a factor that helps to further explain its preference for habitats well removed from human settlements.

In summary, the strong positive association that exists between *Propithecus* occupancy and substrate type, as well as the species' tendency to avoid heavily human dominated habitats were the most useful factors in characterizing *Propithecus* distribution in dry deciduous and semi-evergreen forest fragments than are the spatial attributes of the fragments themselves. Alternatively, modeling the role of differences in fragment area alone provided a perfect fit to the data for *E. sanfordi*. There was no effect of fragmentation, habitat type or proximity to human settlements in modeling occupancy patterns in *E. coronatus* despite predictions that the species' frugivorous diet and limited dispersal capability would predispose it to follow closely the tenants of IBT. Sampling limitations and the crypticity of *H. occidentalis* made our results inconclusive regarding the nature of its distribution across fragmented landscapes.

Tables and Figures

Table 4.1. Site attributes for 45 forest fragments occurring within the Region Diana, northern Madagascar. Abbreviations are as follows: SI: shape index, PI (1 km): proximity index within a search radius of 1 km, VlgDis: Euclidean distance to nearest village with ≥ 10 households. Occupancy for EC = Eulemur coronatus, ES = *Eulemur sanfordi*, PP = *Propithecus perrieri*, and HO = *Hapalemur occidentalis* coded as 1: present, or 0: absent. Tot. Spp = Total species number recorded. Subst: Substrate type, either SAN = sandstone or LIM = Limestone.

SITE	SITE NO.	Latitude	Longitude	Area (km^2)	SI	PI (1 km)	VlgDis	EC	ES	PP	HO	Tot. Spp.	Subst
Mosoromikoty Hely	23	12°53'13.18"S	49°23'3.71"E	0.03	1.24	3060.51	10.88	0	0	1	0	1	SAN
Mahanoro Hely	25	12°59'31.67"S	49°15'26.32"E	0.04	1.24	33.74	1.63	0	0	0	0	0	SAN
Andasibe East 2	32	12°48'36.08"S	49°34'49.03"E	0.07	1.21	2833.5	3.62	0	0	0	0	0	SAN
Lakandrary Sud	27	12°59'9.89"S	49°14'48.94"E	0.08	1.65	113.66	2.55	1	0	0	0	1	LIM
Ambariosikerera	26	12°59'42.00"S	49°15'45.10"E	0.10	1.37	635.34	1.13	1	1	1	0	3	SAN
Ankijiabe Est	12	12°59'54.17"S	49°13'17.77"E	0.13	1.19	3185.02	4.85	1	1	0	0	2	LIM
Analandrafia	6	12°55'34.97"S	49°19'38.65"E	0.14	1.51	487.16	2.96	0	0	1	0	1	SAN
Tsaratafiana	21	12°49'9.69"S	49°33'30.46"E	0.22	1.53	3829.75	4.15	1	0	0	0	1	LIM
Anahidrano	46	12°49'38.92"S	49°21'15.15"E	0.25	1.31	185.91	3.73	1	1	0	0	2	LIM
Andohan'Ambatabe	8	12°44'57.60"S	49°35'16.08"E	0.26	1.60	3831.23	6.83	1	1	1	0	3	LIM
Antobiratsy	14	12°48'50.48"S	49°32'50.01"E	0.27	2.26	589.31	7.05	1	1	1	0	3	LIM
Magnembaheba	24	12°52'29.90"S	49°23'50.10"E	0.30	1.23	1574.17	9.52	0	0	1	0	0	SAN
Antsahaben'Andampy Lh	17	12°50'24.33"S	49°31'5.90"E	0.33	1.5	26.32	2.93	1	0	1	0	2	SAN
Ankatokabe	11	12°49'45.17"S	49°21'40.77"E	0.40	2	608.43	3.59	1	0	1	0	2	LIM
Antsakaitany	18	12°59'16.02"S	49°14'16.13"E	0.43	1.31	327.3	2.53	1	0	0	0	1	LIM
Andaranomamy	13	12°48'2.22"S	49°30'0.76"E	0.49	2.2	3456.98	0.82	1	0	1	0	2	LIM

Ampamoambahy Est	43	12°50'47.69"S	49°21'36.16"E	0.54	1.31	500.25	4.37	1	0	1	0	1	LIM
Ambatalagny	1	12°52'9.50"S	49°22'6.10"E	0.57	2.52	1272.73	5.59	1	1	1	0	3	LIM
Andranomantsiny	10	12°44'53.90"S	49°25'26.45"E	0.68	2.02	2049.3	1.62	1	0	1	0	2	LIM
Bentso	28	12°54'46.95"S	49°22'20.57"E	0.81	1.77	867.15	8.82	1	1	1	0	3	SAN
Mahanoro Sud	20	13° 0'44.70"S	49°14'49.77"E	0.94	3.34	107.8	4.41	1	0	1	0	2	SAN
Antsafirabe	15	12°52'9.72"S	49°18'12.44"E	0.99	1.99	3.17	1.6	1	1	0	0	2	LIM
Analamay	5	12°52'9.66"S	49°27'39.43"E	1.08	2.31	614.47	4.82	1	0	1	0	1	SAN
Antsosoboka	19	12°51'14.50"S	49°29'17.23"E	1.09	1.96	72.71	5.84	1	0	1	0	1	SAN
Benivao	31	12°44'20.91"S	49°23'35.46"E	1.10	2.51	12576.53	2.1	1	0	1	0	2	LIM
Andavakoera	7	12°52'21.58"S	49°30'30.71"E	1.19	2.56	8.48	3.29	1	0	0	0	1	SAN
Madiromasina	44	12°53'24.27"S	49°18'44.90"E	1.28	2.84	103.05	1.31	1	1	1	1	4	LIM
Anaborano	4	12°47'59.32"S	49°21'5.20"E	1.51	2.04	596.13	0.81	1	1	0	0	2	LIM
Beangivy	30	12°55'56.60"S	49°18'48.70"E	1.60	2.35	1065.14	1.92	1	1	1	0	3	SAN
Antsahaben'Andampy Jj	16	12°50'14.53"S	49°29'32.41"E	1.72	2.02	43.65	5.16	1	1	1	0	3	SAN
Ambohibe Est	3	13° 2'29.60"S	49°11'48.64"E	2.0	4.92	362.01	7	0	0	1	0	1	SAN
Antazaolava	45	12°50'31.60"S	49°34'0.83"E	2.1	4.46	25.46	0.53	1	1	1	0	3	SAN
Mahanoro Grès	36	13° 0'1.20"S	49°15'2.54"E	2.61	3.44	333.55	2.44	1	1	1	0	3	SAN
Bekafaiky	29	12°56'39.68"S	49°18'14.21"E	4.03	3.75	46.62	2	1	1	1	0	3	SAN
Mahanoro Calcaire	35	13° 0'12.48"S	49°14'17.29"E	4.58	3.8	373.94	3.8	1	1	1	0	3	LIM
Andampibe	39	12°53'9.60"S	49°22'11.90"E	4.62	2.4	3359.36	8.75	1	1	1	1	4	SAN
Grotte	40	12°51'1.42"S	49°21'5.04"E	5.2	3.19	5078.8	4.78	1	1	1	1	4	LIM
Antsahabe	37	12°54'23.83"S	49°17'20.48"E	5.38	2.05	8.55	1.04	1	1	0	1	3	LIM

Ampondrabe	34	13° 0'22.85"S	49°11'43.58"E	5.97	4.43	67.84	2.59	1	1	1	0	3	LIM	
Ambohibe	2	13° 2'37.59"S	49°10'13.28"E	10.39	1.13	70.71	2.74	0	1	1	0	2	SAN	
Ambatovazaha	38	12°55'9.19"S	49°21'30.27"E	17.71	4.27	1861.77	0.72	1	1	1	1	4	SAN	
Ankarana Est	47	12°51'4.23"S	49°14'54.64"E	25.64	6.49	195.48	1.69	1	1	0	0	2	LIM	
Analamerana Ouest	41	12°48'45.76"S	49°22'53.05"E	90.87	9.17	3087.13	2.98	1	1	1	0	3	LIM	
Ankarana Ouest	33	12°55'49.27"S	49° 6'56.51"E	121.84	7.61	153.64	0	1	1	0	0	2	LIM	
Analamerana Est	42	12°45'2.82"S	49°30'10.72"E	124.0	6.15	2001.89	0.04	1	1	1	1	3	LIM	

Table 4.2. Description of the explanatory variables used to model species richness and occupancy patterns.

Variable Name	Description
Fragment Spatial Attributes	
Area	Fragment surface area (km2)
Shape Index (SI)	Fragment perimeter (m) divided by the square root of fragment area (km2), adjusted by a constant to simulate a square or circular standard. The value of the index increases as shapes become more irregular.
Proximity Index (PI)	Sum of fragment area (km2) divided by the nearest edge-to-edge distance squared between the focal fragment and adjacent fragments of the same vegetation class as long as their edges are within a predifined search radius (e.g. 250, 500 and 1000 m) of the focal fragment. The value of the index increases as greater proportions of habitat at closer proximities fall within the search radius of the focal fragment.
PI (1 km)	The original variable for the proximity index calculated by considering all available forested habitat within a search radius of 1000 m.
PI (0.5 km)	The original variable for the proximity index calculated by considering all available forested habitat within a search radius of 500 m.
PI (0.25 km)	The original variable for the proximity index calculated by considering all available forested habitat within a search radius of 250 m.
PI (0.5 km LIN)	A linear combination of the original proximity indices, PI (1 km) and PI (0.5 km), calculated as: PI (0.5 km LIN) = PI (1 km) – PI (0.5 km). Effectively the area of forested habitat between the 1000 and 500 m bands only is considered in the calculation.
PI (0.25 km LIN)	A linear combination of the original proximity indices, PI (0.5 km) and PI (0.25 km), calculated as: PI (0.25 km LIN) = PI (0.5 km) – PI (0.25 km). Effectively the area of forested habitat between the 500 and 250 m bands only is considered in the calculation.

Table 4.3. Model averaging results for determinants of primate species richness in 45 forest fragments in northern Madagascar, Diana Region.

Parameter	Estimate	Unconditional SE	Confidence Interval	Relative Importance
Intercept	0.76	0.10	(0.56 – 0.96)	
Shape Index (SI)	0.32	0.18	(-0.04 – 0.68)	0.55
Proximity Index, PI (1 km)	0.07	0.2	(-0.31 – 0.45)	0.25
PI (0.5 km LIN)*	-0.18	0.24	(-0.65 – 0.28)	0.18

* Indicates the linearly combined version of the proximity index at a search radius of 0.5 km.

Table 4.4. Parameter estimates for the best fitting GLMM of *E. sanfordi* occurrence, standardized and modeled as a function of fragment area and substrate type. The binomial variable, substrate type was coded as 0 = limestone and 1 = sandstone.

Parameter	Estimate	Unconditional SE
Intercept	12.8	5.68
Area	81.36	35.40
Substrate	-1.3	0.87

Table 4.5. Model averaging results for determinants of *P. perrieri* occupancy in 45 forest fragments in northern Madagascar, Diana Region.

Parameter	Estimate	Unconditional SE	Confidence Interval	Relative Importance
Intercept	1.22	0.47	(0.3 – 2.14)	
Village Distance	2.17	1.3	(-0.37 – 4.73)	0.73
Substrate	1.44	0.86	(-0.24 – 3.12)	0.61
Proximity Index; PI (0.5 km LIN)*	-1.35	0.87	(-3.05 – 0.36)	0.58
Shape Index	1.62	1.06	(-0.47 – 3.72)	0.55
PI (1 km)	0.99	1.11	(-1.19 -3.17)	0.3

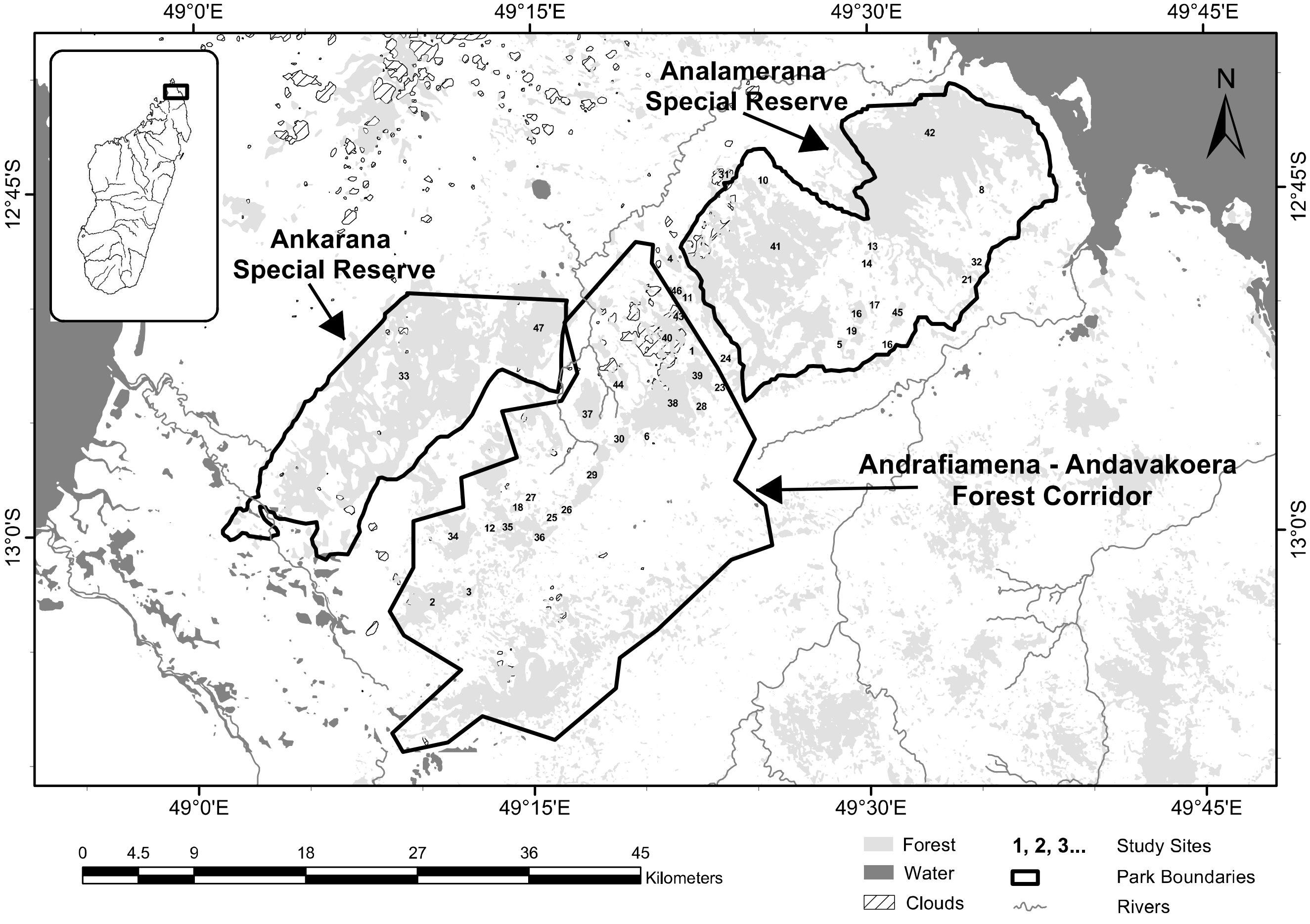

Figure 4.1. Map of all study sites visited during occupancy surveys for primates during the period from April 2007 to July 2012. Numbers correspond to site numbers as presented in Table 4.1.

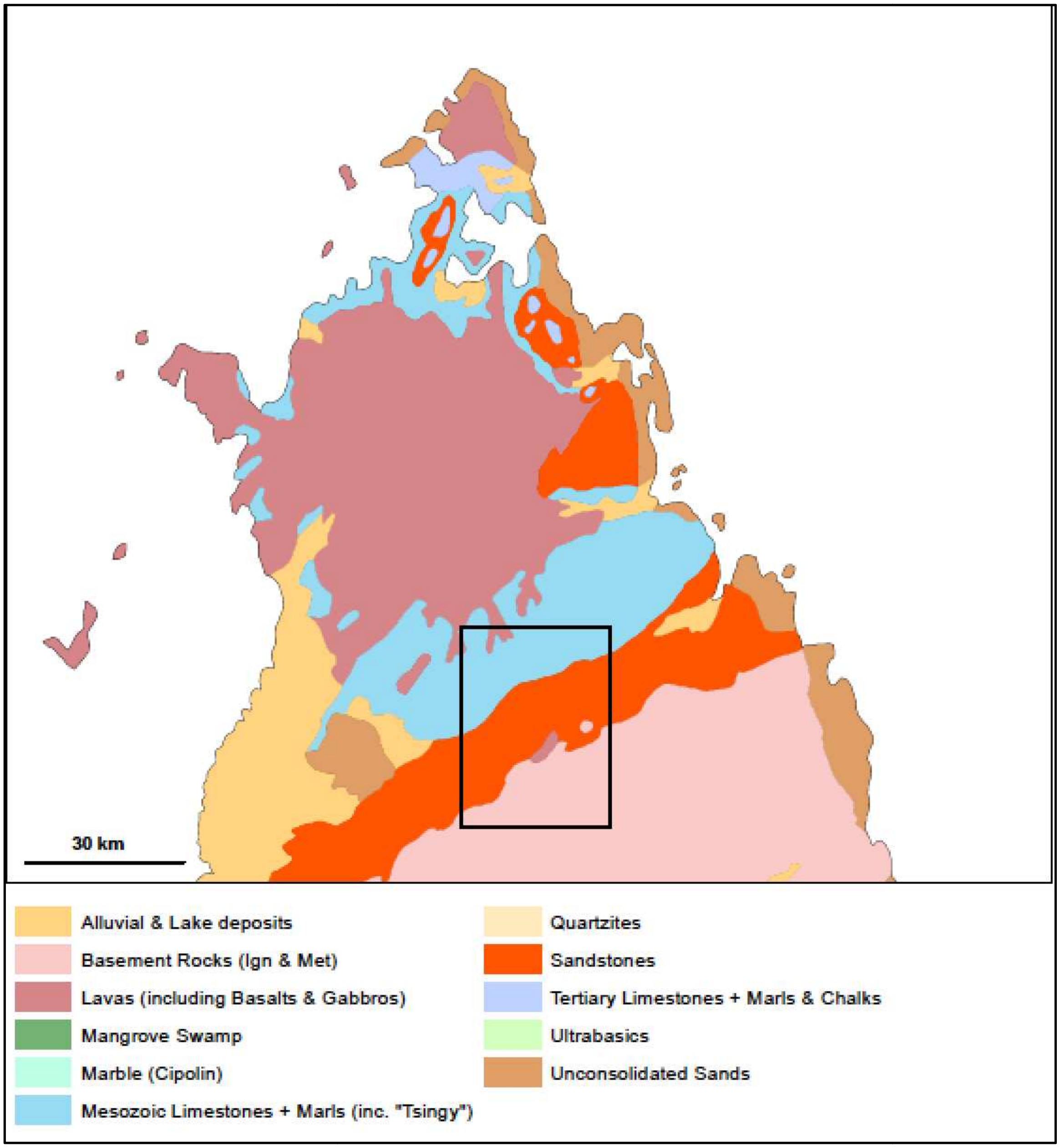

Figure 4.2. Simplified geological classes for the Diana region of northern Madagascar as presented in Du Puy and Moat (1996). An approximate outline of the geographic center of the study region is provided in the black square. Figure is adapted from Buřivalová (2011)

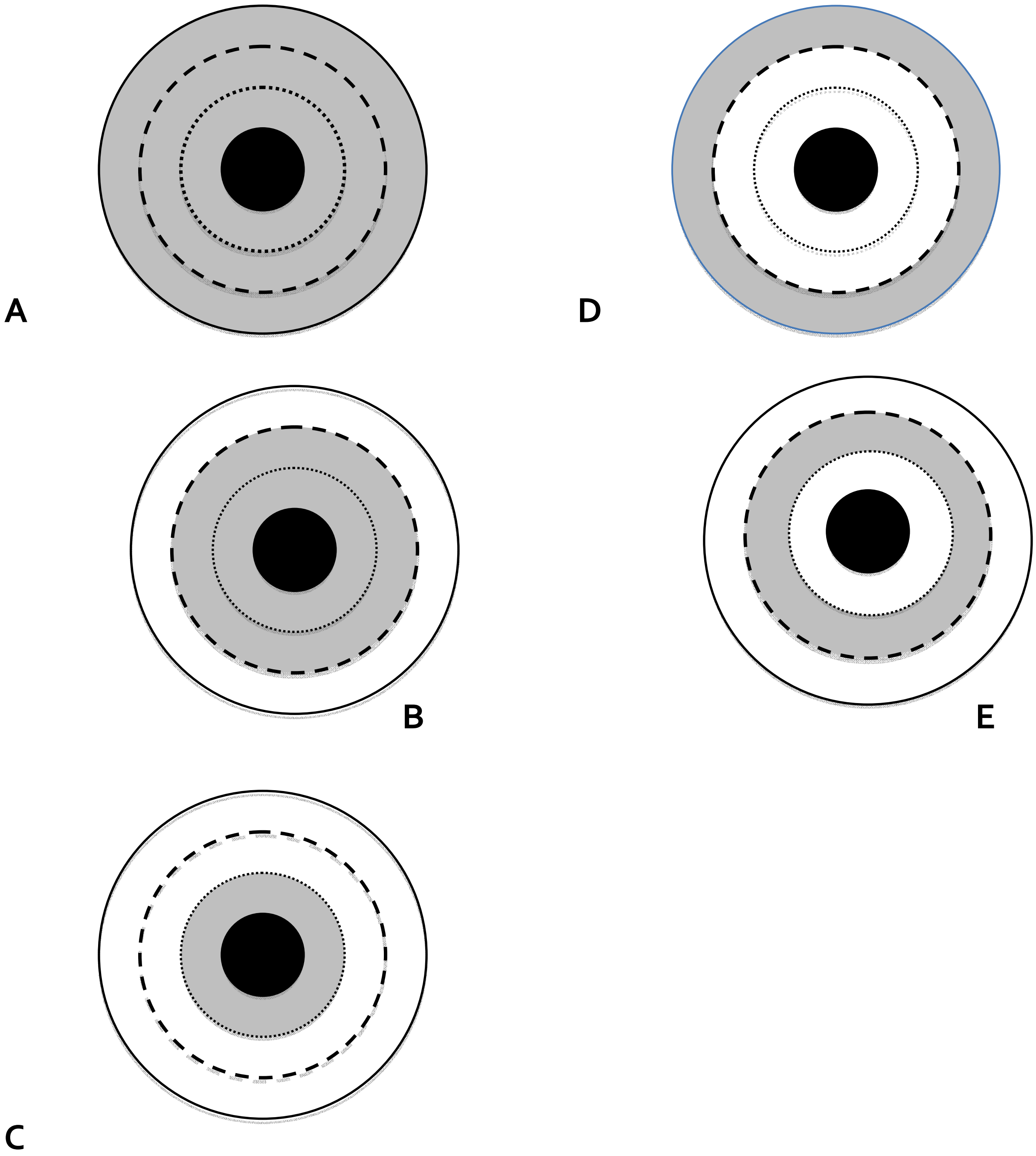

Figure 4.3. Simplified illustration of the differences in the total area considered in the calculation of the original proximity indices and their restructured analogues. Measures included the original variables, (A) PI (1 km), (B) PI (0.5 km), (C) PI (0.25 km) and linear combinations of these variables used to allow for broader comparison and to reduce multi-collinearity, (D) PI (0.5 km LIN) and (E) PI (0.25 km LIN). The black area represents the focal patch while the boundary enclosed within the finely dotted line indicates a search radius of 0.25 km, the heavy dotted line a search radius of 0.5 km, and the solid outermost line a search radius of 1 km. The gray shaded areas highlight the area being considered in the calculation of that particular index.

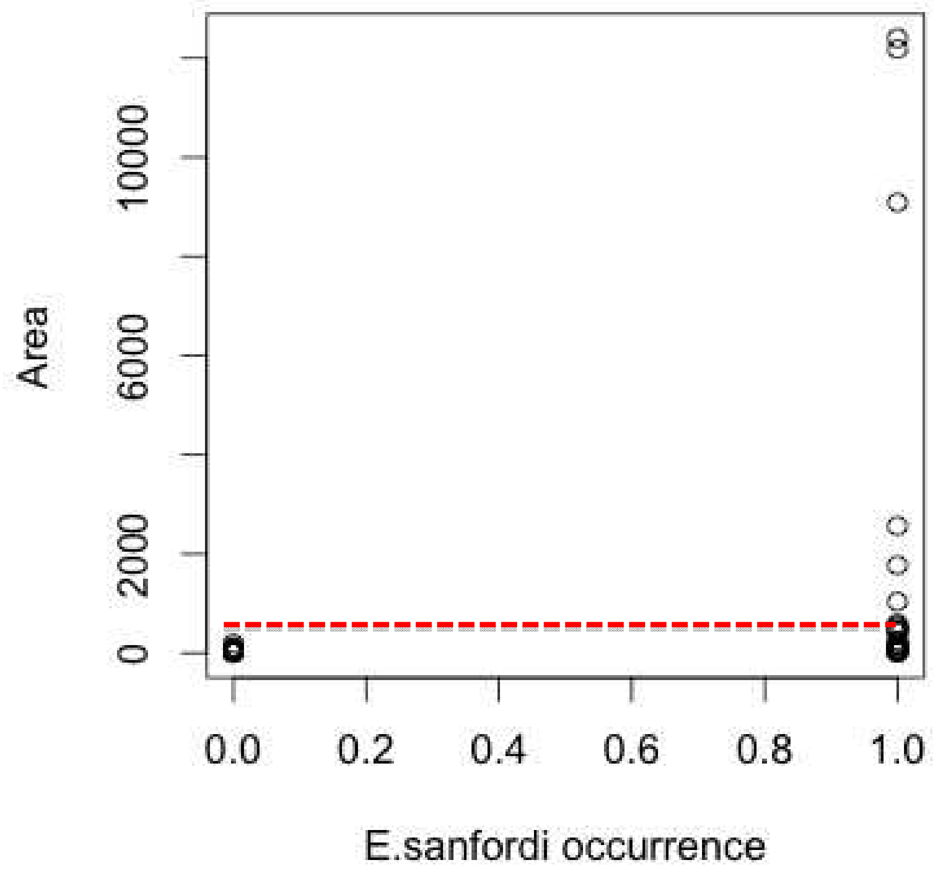

Figure 4.4. *Eulemur sanfordi* occurrence plotted as a function of fragment area. Area are presented in hectares to ease interpretation. The red dotted line describes the boundary of the Hauck-Donner (Hauck and Donner 1977) threshold that characterizes the relationship, estimated at 200 ha or 2 km^2.

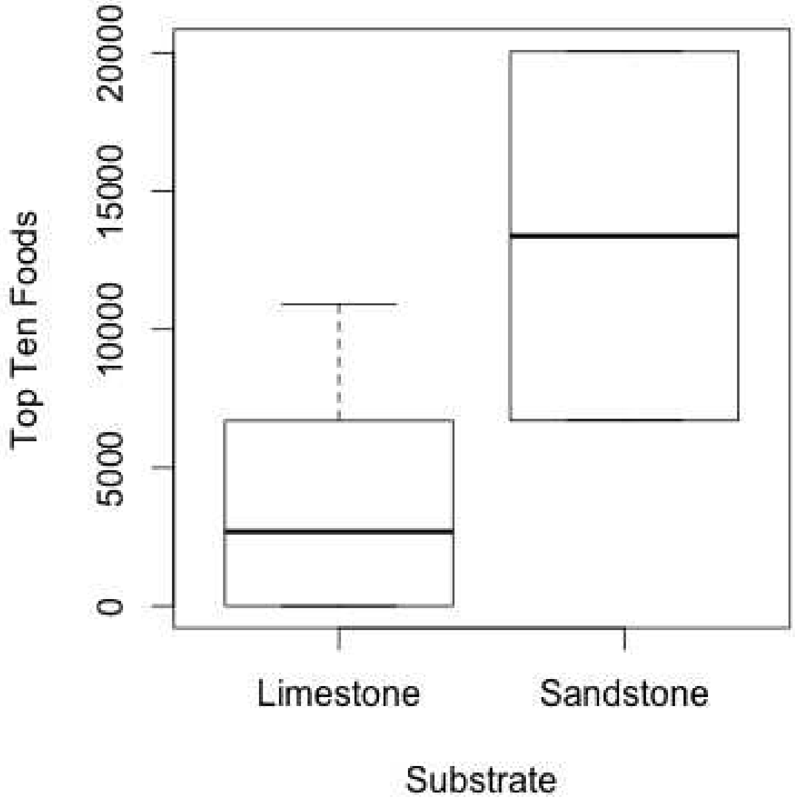

Figure 4.5. Top ten dry season *Propithecus* food species abundance plotted as a function of substrate type.

References

Akaike H (1973) Information theory and an extension of the maximum likelihood principle. Akademinai Kiado:267-281

Anzures-Dadda A, Manson RH (2007) Patch- and landscape-scale effects on howler monkey distribution and abundance in rainforest fragments. Animal Conservation 10:69–76

Arrigo-Nelson S, Wright P (2004) Survey results from Ranomafana National Park: new evidence for the effects of habitat preference and disturbance on the distribution of Hapalemur. Folia Primatologica 75:331-334

Arroyo-Rodríguez V, Dias P (2010) Effects of habitat fragmentation and disturbance on howler monkeys: a review. American Journal of Primatology 72:1-16

Arroyo-Rodríguez V, Mandujano S (2006) Forest Fragmentation Modifies Habitat Quality for *Alouatta palliata*. International Journal of Primatology 27

Arroyo-Rodríguez V, Mandujano S (2009) Conceptualization and Measurement of Habitat Fragmentation from the Primates' Perspective. International Journal of Primatology 30:497–514

Arroyo-Rodríguez V, Mandujano S, Benítez-Malvido J (2008) Landscape attributes affecting patch occupancy by howler monkeys (Alouatta palliata mexicana) at Los Tuxtlas, Mexico. American Journal of Primatology 70:69-77

Asensio N, Arroyo-Rodríguez V, Dunn JD, Cristóbal-Azkarate J (2009) Conservation Value of Landscape Supplementation for Howler Monkeys Living in Forest Patches. Biotropica 41:768-773

Balko E, Underwood H (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

Banks MA, Ellis ER, Antonio, Wright PC (2007) Global population size of a critically endangered lemur, Perrier's sifaka. Animal Conservation 10:254–262

Bartón K (2012) MuMIn: multi-model inference. In: R package version

Binggeli P (2003) Introduced and Invasive Plants. In: Goodman SM, Benstead JP (eds) The Natural History of Madagascar. The University of Chicago Press, Chicago, IL, pp 257-268

Bolker B, Brooks M, Clark C, Geange S, Poulsen J, Stevens MH, White J-S (2009) Generalized linear mixed models: a practical guide for ecology and evolution. Trends in Ecology & Evolution 24:127-135

Buřivalová Z (2011) Remote Sensing of Vegetation in Conservation: A Case Study from the Dry and Transitional Forests of Andrafiamena, Northern Madagascar. In: Université de Geneve and Conservatoire et Jardin Botanique de la Ville de Geneve. Université de Geneve, Geneva, Switzerland, pp 89

Burney D, Burney L, Godfrey L, Jungers W, Goodman S, Wright H, Jull A (2004) A chronology for late prehistoric Madagascar. Journal of Human Evolution 47:25-63

Burney D, Robinson G, Burney L (2003) Sporormiella and the late Holocene extinctions in Madagascar. Proceedings of the National Academy of Sciences of the United States of America 100:10800-10805

Burney DA (1999) Rates, patterns, and processes of landscape transformation and extinction in Madagascar. Extinctions in near time: causes, contexts, and consequences:145-164

Burnham K, Anderson D (2002) Model selection and multi-model inference: a practical information-theoretic approach. Springer-Verlag, New York, NY. pp.488

Chapman C, Chapman L, Naughton-Treves L, Lawes M, McDowell L (2004) Predicting folivorous primate abundance: validation of a nutritional model. American Journal of Primatology 62:55-69

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

Chatterjee S, Hadi AS (2013) Regression analysis by example. John Wiley & Sons, Inc., Hoboken, NJ. pp.308

Chiarello AG, de Melo FR (2001) Primate population densities and sizes in Atlantic forest remnants of northern Espirito Santo, Brazil. International Journal of Primatology 22:379-396

Coley P, Barone J (1996) Herbivory and plant defenses in tropical forests. Annual Review of Ecology and Systematics 27:305-335

Colin AC, Lisa N-T, Michael JL, Michael DW, Thomas RG (2007) Population Declines of Colobus in Western Uganda and Conservation Value of Forest Fragments. International Journal of Primatology 28:513–528

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

De-Gama Blanchet HN, Fedigan LM (2006) The effects of forest fragment age, isolation, size, habitat type, and water availability on monkey density in a tropical dry forest. In: Estrada A, Garber PA, Pavelka MSM, Leandra L (eds) New Perspectives in the Study of Mesoamerican Primates: Distribution, Ecology, Behavior and Conservation. Springer, New York, NY., pp 165-188

Dehgan A (2003) The Behavior of Extinction: Predicting the Incidence and Local Extinction of Lemurs in Fragmented Habitats of Southeastern Madagascar. In. University of Chicago, Chicago, IL, pp 248

Dewar R, Radimilahy C, Wright H, Jacobs Z, Kelly G, Berna F (2013) Stone tools and foraging in northern Madagascar challenge Holocene extinction models. Proceedings of the National Academy of Sciences of the United States of America 110:12583-12588

Dewar R, Richard A (2007) Evolution in the hypervariable environment of Madagascar. Proceedings of the National Academy of Sciences of the United States of America 104:13723-13727

Dewar R, Richard A (2012) Madagascar: A History of Arrivals, What Happened, and Will Happen Next*. Annual Review of Anthropology 41:495-517

Donati G, Kesch K, Ndremifidy K, Schmidt S, Ramanamanjato J-B, Borgognini-Tarli S, Ganzhorn J (2011) Better few than hungry: flexible feeding ecology of collared lemurs *Eulemur collaris* in littoral forest fragments. PloS one 6:e19807

Dransfield S (2003) Poaceae, Bambuseae, Bamboos. In: Goodman SM, Benstead JP (eds) The Natural History of Madagascar. The University of Chicago Press, Chicago, IL, pp 467-471

Du Puy DJ, Moat J (1996) A refined classification of the primary vegetation of Madagascar based on the underlying geology: using GIS to map its distribution and to assess its conservation status. In: Lourenço WR (ed) Proceedings of the International Symposium on the Biogeography de Madagascar. Editions de l'ORSTROM, Paris, Paris, France, pp 205-218 + 3 maps

Dunning JB, Danielson BJ, Pulliam HR (1992) Ecological Processes That Affect Populations in Complex Landscapes. Oikos 65:169-175

Elkie PC, Rempel RS, Carr A (1999) Patch analyst user's manual: a tool for quantifying landscape structure. In. Ontario Ministry of Natural Resources, Boreal Science, Northwest Science & Technology, Ontario, Canada

Estrada A, Coates-Estrada R (1996) Tropical rain forest fragmentation and wild populations of primates at Los Tuxtlas, Mexico. International Journal of Primatology 17:759-783

Estrada A, Mendoza A, Castellanos L, Pacheco R, Van Belle S, García Y, Muñoz D (2002) Population of the black howler monkey (*Alouatta pigra*) in a fragmented landscape in Palenque, Chiapas, Mexico. American Journal of Primatology 58:45-55

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

Fleagle JG, Reed KE (1999) Phylogenetic and temporal perspectives on primate ecology. Primate Communities, Cambridge University Press, Cambridge pp.92-115

Fortin M-J, Dale MRT (2005) Spatial Analysis: A Guide for Ecologists. Cambridge University Press, Cambridge, UK

Fowler SV, Chapman P, Checkley D, Hurd S, McHale M, Ramangason GS, Randriamasy JE, Stewart P, Walters R, Wilson JM (1989) Survey and management proposals for a tropical deciduous forest reserve at Ankarana in Northern Madagascar. Biological Conservation 47:297-313

Freedman DA (1983) A note on screening regression equations. American Statastician 37:152-155

Ganzhorn JU, Goodman SM, Dehgan A (2003) Effects of Forest Fragmentation on Small Mammals and Lemurs. In: Goodman S, Benstead J (eds) The Natural History of Madagascar. University of Chicago Press, Chicago, pp 1228-1234

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

Ganzhorn JU (1997) Test of Fox's assembly rule for functional groups in lemur communities in Madagascar. Journal of Zoology 241:533-542

Ganzhorn JU, Goodman SM, Ramanamanjato J-B, Rakotondravony D, Rakotosamimanana B, Vallan D (2000a) Vertebrate species in fragmented littoral forests of Madagascar. In: Lourenço WR, Goodman SM (eds) Diversité et Endémisme à Madagascar. Mémoires de la Société de Biogéographie, Paris, pp 155–164.

Ganzhorn JU, Goodman SM, Ramanamanjato J-B, Ralison J, Rakotondravony D, Rakotosamimanana B (2000b) Effects of fragmentation and assessing minimum viable populations of lemurs in Madagascar. In: Rheinwald G (ed) Isolated Vertebrate Communities in the Tropics. 4th Int. Symp., Bonn, Germany, pp 265–272

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

Ganzhorn JU, Malcomber S, Andrianantoanina O, Goodman SM (1997) Habitat Characteristics and Lemur Species Richness in Madagascar. Biotropica 29:331-343

Ganzhorn JU, Wright PC, Ratsimbazafy J (1999) Primate communities: Madagascar. In: Fleagle J, Janson C, Reed K (eds) Primate Communities. Cambridge University Press, Cambridge, UK, pp 75-89

Godfrey LR, Irwin MT (2007) The evolution of extinction risk: past and present anthropogenic impacts on the primate communities of Madagascar. Folia Primatologica 78:405-419

Godfrey LR, Samonds KE, Jungers WL, Sutherland MR, Irwin MT (2004) Ontogenetic correlates of diet in Malagasy lemurs. American Journal of Physical Anthropology 123:250-276

Golden CD (2009) Bushmeat hunting and use in the Makira Forest, north-eastern Madagascar: a conservation and livelihoods issue. Oryx 43:386-392

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

Grueber CE, Nakagawa S, Laws RJ, Jamieson IG (2011) Multimodel inference in ecology and evolution: challenges and solutions. Journal of Evolutionary Biology 24:699-711

Harcourt AH, Doherty DA (2005) Species-area relationships of primates in tropical forest fragments: a global analysis. Journal of Applied Ecology 42:630-637

Harper GJ, Steininger MK, Tucker CJ, Juhn D, Hawkins F (2007) Fifty years of deforestation and forest fragmentation in Madagascar. Environmental Conservation 34

Hauck W, Donner A (1977) Wald's test as applied to hypotheses in logit analysis. Journal of the American Statistical Association 72:851-853

Hawkins AFA, Chapman P, Ganzhorn JU, Bloxam QMC, Barlow SC, Tonge SJ (1990) Vertebrate Conservation in Ankarana special reserve, Northern Madagascar. Biological Conservation 54:83-110

Irwin MT, Wright PC, Birkinshaw C, Fisher BL, Gardner CJ, Glos J, Goodman SM, Loiselle P, Rabeson P, Raharison J-L (2010) Patterns of species change in anthropogenically disturbed forests of Madagascar. Biological Conservation 143:2351-2362.

Irwin MT (2006) Ecologicallty Enigmatic Lemurs: The Sifakas of the Eastern Forests. In: Gould L, Sauther ML (eds) Lemurs: Ecology and Adaptation. Springer, New York, NY., pp 305-326

Irwin MT (2007a) Feeding Ecology of *Propithecus diadema* in Forest Fragments and Continuous Forest. International Journal of Primatology 29:95-115

Irwin MT (2008) Diademed Sifaka (*Propithecus diadema*) Ranging and Habitat Use in Continuous and Fragmented Forest: Higher Density but Lower Viability in Fragments? Biotropica 40:231–240

Irwin MT, Raharison JL, Wright PC (2009) Spatial and temporal variability in predation on rainforest primates: do forest fragmentation and predation act synergistically? Animal Conservation 12:220–230

Isabirye-Basuta GM, Lwanga J, S. (2008) Primate Populations and Their Interactions with Changing Habitats. International Journal of Primatology 29:35–48

Janson C, Chapman C (1999) Resources and primate community structure. In: Primate communities. Cambridge University Press, Cambridge, UK, pp 237-267

Janzen DH (1975) Ecology of Plants in the Tropics. Edward Arnold., London

Johnson SE (2006) Evolutionary Divergence in the Brown Lemur Species Complex. In: Gould L, Sauther ML (eds) Lemurs Ecology and Adaptation. Springer, New York, NY., pp 450

Johnson SE, Ingraldi C, Ralainasolo FB, Andriamaharoa HE, Ludovic R, Birkinshaw CR, Wright PC, Ratsimbazafy JH (2011) Gray-headed Lemur (*Eulemur cinereiceps*) Abundance and Forest Structure Dynamics at Manombo, Madagascar. Biotropica 43:371–379

Keane A, Hobinjatovo T, Razafimanahaka HJ, Jenkins RKB, Jones JPG, Res A, Michael S (2012) The potential of occupancy modelling as a tool for monitoring wild primate populations. Animal Conservation 15:457–465

Kirika JM, Bleher B, Böhning-Gaese K, Chira R, Farwig N (2008) Fragmentation and local disturbance of forests reduce frugivore diversity and fruit removal in *Ficus thonningii* trees. Basic and Applied Ecology 9:663-672

Laurance WF, Delamônica P, Laurance SG, Vasconcelos HL, Lovejoy TE (2000) Rainforest fragmentation kills big trees. Nature Vol. 404:836

Laurance WF, Lovejoy TE, Vasconcelos HL, Bruna EM, Didham RK, Stouffer PC, Gascon C, Bierregaard RO, Laurance SG, Sampaio E (2002) Ecosystem Decay of Amazonian Forest Fragments: a 22-Year Investigation. Conservation Biology 16:605-618

Laurance WF (2008) Theory meets reality: How habitat fragmentation research has transcended island biogeographic theory. Biological Conservation 141:1731-1744

Lehman S (2007) Spatial variations in *Eulemur fulvus rufus* and *Lepilemur mustelinus* densities in Madagascar. Folia Primatologica 78:46-55

Lehman S, Mayor M (2004) Dietary patterns in Perrier's sifakas (*Propithecus diadema perrieri*): a preliminary study. American Journal of Primatology 62:115-122

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

Lehman S, Rajaonson A, Day S (2006b) Lemur responses to edge effects in the Vohibola III classified forest, Madagascar. American Journal of Primatology 68:293-299

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

Letsara R (2007) Inventaire rapide de la flore et de la vegetation du corridor forestier d'Andrafiamena. In: Conservation International Rapid Assessment Program Report, Alexandria, VA

MacArthur RH, Wilson EO (1967) The Theory of Island Biogeography. Princeton University Press pp.203

MacKenzie DI, Nichols JD, Lachman GB, Droege S, Royle JA, Langtimm CA (2002) Estimating Site Occupancy Rates When Detection Probabilities Are Less Than One. Ecology 83:2248–2255

Mayor M, Lehman SM (1999) Conservation of Perrier's sifakas. Lemur News 4:21-23

McGarigal K, Marks B (1995) Spatial pattern analysis program for quantifying landscape structure. In: Gen. Tech. Rep. PNW-GTR-351. US Pacific Northwest Research Station, Portland, OR

Meyers DM (1993) The effects of resource seasonality on behavior and reproduction in the golden-crowned sifaka (*Propithecus tattersalli*, Simons, 1988) in three Malagasy forests. Duke University

Meyers DM, Wright PC (1993) Resource tracking: food availability and *Propithecus* seasonal reproduction. Lemur social systems and their ecological basis. New York: Plenum Press. p:179-192

Mutschler T, Tan CL (2003) *Hapalemur*, Bamboo or Gentle Lemurs. In: Goodman SM, Benstead JP (eds) The Natural History of Madagascar. The University of Chicago Press, Chicago, IL, pp 1324-1329

Oates J, Whitesides G, Davies A, Waterman P (1990) Determinants of variation in tropical forest primate biomass: new evidence from West Africa. Ecology 71:328-343

Overdorff D, Johnson SE (2003) *Eulemur*, true lemurs. In: Goodman SM, Benstead JP (eds) The Natural History of Madagascar. Chicago University Press, Chicago, IL, pp 1320-1324

Palacios E, Peres CA (2005) Primate population densities in three nutrient-poor amazonian terra firme forests of south-eastern Colombia. Folia Primatologica 76:135-145

Pavelka MSM, Brusselers OT, Nowak D, Behie AM (2003) Population reduction and social disorganization in *Alouatta pigra* following a hurricane. International Journal of Primatology 24:1037-1055

Peres CA (2001) Synergistic Effects of Subsistence Hunting and Habitat Fragmentation on Amazonian Forest Vertebrates. Conservation Biology 15:1490-1505

Peres CA (1997) Primate community structure at twenty western Amazonian flooded and unflooded forests. Journal of Tropical Ecology 13:381-405

Peres CA, Lake IR (2003) Extent of Nontimber Resource Extraction in Tropical Forests: Accessibility to Game Vertebrates by Hunters in the Amazon Basin. Conservation Biology 17: 521–535

Pozo-Montuy G, Serio-Silva J (2007) Movement and resource use by a group of *Alouatta pigra* in a forest fragment in Balancán, México. Primates 48:102-107

Prugh L, Hodges K, Sinclair A, Brashares J (2008) Effect of habitat area and isolation on fragmented animal populations. Proceedings of the National Academy of Sciences of the United States of America 105:20770-20775

Quéméré E, Champeau J, Besolo A, Rasolondraibe E, Rabarivola C, Crouau-Roy B, Chikhi L (2010a) Spatial variation in density and total size estimates in fragmented primate populations: the golden-crowned sifaka (*Propithecus tattersalli*). American Journal of Primatology 72:72-80

Quéméré E, Crouau-Roy B, Rabarivola C, Louis E, Chikhi L (2010b) Landscape genetics of an endangered lemur (*Propithecus tattersalli*) within its entire fragmented range. Molecular Ecology 19:1606-1621

R Core Development Team (2013) R: Language and Environment for Statistical Computing. In. R Foundation for Statistical Computing, Vienna, Austria

Rakotoarisoa JE, Raheriarisena M, Goodman S (2013) Late Quaternary climatic vegetational shifts in an ecological transition zone of northern Madagascar: insights from genetic analyses of two endemic rodent species. Journal of Evolutionary Biology 26:1019-1034

Ranaivoarisoa JF, Ramanamahefa R, Louis Jr. EE, Brenneman RA (2006) Range extension of Perrier's Sifaka, *Propithecus perrieri*, in the Andrafiamena Classified Forest. Lemur News 11:21

Ranaivoarisoa JF, Zaonarivelo J, Lei R, Johnson SE, Wyman TM, Mittermeier RA, Louis Jr. EE (2013) Rapid Survey and Assessment of the Northern Sportive Lemur, *Lepilemur septentrionalis*, in Northern Madagascar. Primate Conservation Early Online Edition

Ratelolahy FJ (2007) Rapport d'inventaire biologique rapide dans la forêt d'Andrafiamena. In: Conservation International Rapid Assessment Program Report, Alexandria, VA

Ratsimbazafy J (2002) How do black and white ruffed lemurs still survive in a highly disturbed habitat. Lemur News 7:7-10

Reed KE, Fleagle JG (1995) Geographic and climatic control of primate diversity. Proceedings of the National Academy of Sciences of the United States of America 92:7874-7876

Reed KE (1999) Population density of primates in communities: differences in community structure. In: Fleagle JG, Janson CH, Reed KE (eds) Primate Communities. Cambridge University Press, Cambridge, UK, pp 116-140

Richard AF, Dewar RE (1991) Lemur ecology. Annual Review of Ecology and Systematics 22:145-175

Ross C, Reeve N (2003) Survey and census methods: population distribution and density. In: Setchell JM, Curtis DJ (eds) Field and Laboratory Methods in Primatology. Cambridge University Press, Cambridge, UK, pp 90-109

Rothman JM, Chapman CA, Soest PJ (2011) Methods in Primate Nutritional Ecology: A User's Guide. International Journal of Primatology 33:542–566

Smith AP, Horning N, Moore D (1997) Regional Biodiversity Planning and Lemur Conservation with GIS in Western Madagascar. Conservation Biology 11:498–512

Sterling E (2003) *Daubentonia madagascariensis*, Aye-Aye, *Aye-aye*. In: Goodman SM, Benstead JP (eds) The Natural History of Madagascar. The University of Chicago Press, Chicago, IL, pp 1348-1351

Symonds MRE, Moussalli A (2010) A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. Behavioral Ecology and Sociobiology 65:13–21

Tan CL (1999) Group composition, home range size, and diet of three sympatric bamboo lemur species (genus Hapalemur) in Ranomafana National Park, Madagascar. International Journal of Primatology 20:547-566

Terranova CJ, Coffman BS (1997) Body weights of wild and captive lemurs. Zoo Biology 16:17-30

Tutin C (1999) Fragmented living: Behavioural ecology of primates in a forest fragment in the Lopé Reserve, Gabon. Primates 40:249-265

van Schaik CP, Madden R, Ganzhorn JU (2005) Seasonality and primate communities. In: Brockman D, van Schaik C (eds) Seasonality in Primates: Studies of Living and

Extinct Human and Non-Human Primates. Cambridge University Press, Cambridge, UK, pp 445-463

Virah-Sawmy MJ, Willis K, Gillson L (2010) Evidence for drought and forest declines during the recent megafaunal extinctions in Madagascar. Journal of Biogeography 37:506–519

Waterman PG, Ross JAM, Bennett EL, Davies AG (1988) A comparison of the floristics and leaf chemistry of the tree flora in two Malaysian rain forests and the influence of leaf chemistry on populations of colobine monkeys in the Old World. Biological Journal of the Linnean Society 34:1-32

Worman COD, Chapman CA (2006) Densities of Two Frugivorous Primates with Respect to Forest and Fragment Tree Species Composition and Fruit Availability. International Journal of Primatology 27:203-225

Wright P, Johnson S, Irwin M, Jacobs R, Schlichting P, Lehman SM, Louis Jr. EE, Arrigo-Nelson SJ, Raharison JL, Radoniana R, Rafalirarison, Razafindratsita V, Ratsimbazafy J, Ratelolahy FJ, Dolch R, Tan C (2008) The crisis of the critically endangered greater bamboo lemur (Prolemur simus). Primate Conservation 23:5-17

Wright P, Tecot S, Erhart E, Baden A, King S, Grassi C (2011) Frugivory in four sympatric lemurs: implications for the future of Madagascar's forests. American Journal of Primatology 73:585-602

Wright P, Volonlontiana R, Razafindratsita V, Pochron S, Jernvall J (2005) The Key to Madagascar Frugivores. In: Dew JL, Boubli JP (eds) Tropical Fruits and Frugivores: The Search for Strong Interactors. Springer, Dordrecht, Netherlands, pp 121-138

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

Zuckerberg B, Porter W, Corwin K (2009) The consistency and stability of abundance-occupancy relationships in large-scale population dynamics. The Journal of Animal Ecology 78:172-181

Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009) Mixed effects models and extensions in ecology with R. Springer, New York, NY.

CHAPTER FIVE:

Synthesizing Results from Studies of Primate Abundance and Distribution and Formulating Recommendations for Conservation Management and Future Research

In this chapter I revisit the key results of chapters two, three and four and place them in the broader context of recommendations for wildlife management and safeguarding northern Madagascar's highly threatened primate fauna from extinction. As mentioned previously, recent assessments of the levels of endangerment among the Malagasy primates indicates that over 90% of this lineage are classified as threatened, endangered or critically endangered by the IUCN (Schwitzer et al. 2013). It is important that comprehensive plans for conservation management are urgently provided as a means for mitigating the enormous degree of threat faced by the country's primate fauna. To outline recommendations for these taxa I return to the following questions in sequence: 1) which of the factors known to influence detectability in line transect surveys are a consistent source of bias in estimating lemur densities and how can this information be used to improve future surveys with primates, 2) how important are human factors in determining the abundance, occupancy and species richness patterns among primates occurring in the fragmented forests of northern Madagascar and can the results be used to help predict future impacts from human-nonhuman primate interactions on the survival prospects for these lemurs, 3) were major differences in the factors determining abundance distinguishable when contrasted with those driving primate occupancy and did the use of presence absence data serve as a useful surrogate for primate abundance in this study and 4) what possible directions for future research should be prioritized in the interest of filling the gaps from this study and contributing further towards the development of clear recommendations for the management of northern Madagascar's primate fauna?

Integrating the concept of imperfect detection in recce and line transect surveys with primates

To address the first of the dissertation's broader questions in an attempt to better conceptualize the study's results relative to common sources of bias in line transect surveys with primates it is important to acknowledge that many improvements in the accuracy of results from line transects for primates appear to be rooted in the design of the survey itself. While it is widely understood among primatologists that several of the strict assumptions of line transect theory are difficult to uphold with primates given the complexity of their 3-dimensional environment and variable behavioral tendencies (Plumptre and Cox 2006; Hassel-Finnegan et al. 2008), line transect methodology has the potential to provide a quantitatively rigorous approach to obtaining reliable estimates of population abundance for primates. Accordingly researchers using these methods should attempt to meet as many of the basic assumptions of the theory as available resources and time will allow. Still given the idiosyncrasies of primate ecology and behavior there will always be exceptions and it is important to determine under what circumstances some of these assumptions can be relaxed.

Systematic sampling designs based on a grid of survey lines are strongly recommended by the engineers of line transect sampling methods (Buckland et al. 2010; Thomas et al. 2010), but the regulations of protected areas where primate studies typically take place generally preclude use of this sampling procedure. Alternatively, random stratified sampling schemes have been suggested to ensure that estimates of primate densities can be reliably converted to estimates of population density (Plumptre and Cox 2006). Indeed recent extensions to the popular software package, Distance © include the use of geographic information systems (GIS) to design the placement of transects based on the distribution of representative vegetation types, topography and altitudinal gradients (Thomas et al. 2010). In addition to relying on these sources of information in advance of the survey, researchers should seek additional insights from reconnaissance surveys to ensure the proportional representation of the various human factors that shape the existing landscape. These data are critical for developing informed management plans and present opportunities to address a variety of questions in ecology and in documenting patterns of change in wildlife (Chapman and Peres 2001). Nonetheless, activities such as hunting, charcoal production, selective logging, and domestic animal ranging are cryptic and unlikely to be detected using GIS and other remote sensing analyses.

Although the majority of evidence from this study suggests that non-random sampling procedures based on the presence of existing trails at sites (i.e. recce surveys) may capture much of the same detection process as on line transects prepared using compass bearings, a weak effect of survey route type on the distribution of sighting distances with *Propithecus* (Table 2.6) suggests that this factor continues to warrant some attention in future surveys with lemurs. Although accounting for this variation did not result in more precise density estimates for this species (Table 2.7), the influence may have been greater if a larger proportion of recce trails (i.e. ≥ 38%) were employed or if there was greater effort along recce trails (i.e. ≥ 36%). The lack of clear direction of effect makes it difficult to speculate about the ultimate source of this variation. Estimates of primate densities based exclusively on results from recce surveys nonetheless have the potential to introduce bias into estimates of primate density that, if left uncontrolled could lead to erroneous biological inference. If researchers are unable to randomly establish line transects using compass bearings for comparison with recce trails, as is often the case with protected areas in Madagascar (e.g. Marojejy National Park, Ankarana National Park; Patel, pers.comm., Banks pers.obs.), efforts could be made to borrow results from previous surveys from different times and places with the same and/or related species that might provide baseline information regarding the detection process for the species of interest (MacKenzie et al. 2005). Attempts to borrow information from related species should be approached with greater caution however as this as well as other studies (Nijman 2001; Lynne et al. 2011; Nijman and Nekaris 2012) show that behavioral differences can lead to variable detectability across primate species.

The only sampling effect with both a strong and clear direction of effect on the distribution of sighting distances involved differences in the levels of observer experience.

In particular sighting distances recorded by more experienced observers had more of a uniform distribution than did those of less experienced ones (Figure 2.2B). Notably however, this effect was only seen in the case of one species, *E. coronatus*. Ultimately the magnitude of effect had a limited impact on the precision of density estimates in this study, likely because untrained observers contribute a very small number of records to the total number of observations (i.e. less than 3%). Furthermore, training observers to use a laser rangefinder and precision compass may have presented an improvement over previous studies (e.g. Mitani et al. 2000; Rovero et al. 2006). In areas where density estimates are designed to inform the management of primate populations, efforts to procure financial support to maintain teams of wildlife experts over the long-term should be prioritized. As Mitani and others (2000) contend, monitoring threatened species over long time frames inevitably leads to some turnover in wildlife personnel, but therein also lies one of the main advantages of a community based monitoring schemes. Community based monitoring programs employ individuals that are more likely to be available to participate in long-term studies than are researchers or students from outside of the country hosting the research. Furthermore, turnover in personnel can more easily be balanced by passing on skillsets to the emerging generation of locally based wildlife experts. As an enterprise these endeavors with local communities develop a resource base for future work that builds professional expertise, provides an alternative source of income, and safeguards local, natural resources. Finding long-term support for field teams is an on-going challenge for work with highly threatened species and establishing trust through commitments to sites is a major factor in determining the success of management efforts (Richard and Ratsirarson 2013).

Contrary to predictions, only limited evidence was found for the role of sampling effects in determining the detectability of primates in this study. By using standardized guidelines for the study's design (Peres 1999) including a random stratified sampling scheme, the extended training of observers, and the use of precision instruments in recording measurements many of the pitfalls highlighted were avoided or at least, controlled during the study. Nonetheless, other sources of variation influenced detection and there was broad variability in the sources of bias that influenced the detectability of different species. Although controlling for covariates to detectability did not result in major improvements in the precision of density estimates for any lemurs the results highlight the potential for very different sources of bias to influence the results of line transect surveys. Ultimately these findings support recent calls for researchers to integrate the concept of imperfect detection into density estimates by evaluating the role of multiple covariates in driving the detection process (Rovero et al. 2006; Marques et al. 2007). Researchers should look to previous studies for guidelines in isolating covariates for evaluation that are relevant to the particular study system of interest. Given its prevalence in the literature on primates and the prominence of an observer effect in this study, future studies with primates should always screen data for the effect of observer differences in determining primate detectability.

As in previous abundance studies with primates (Mitani et al. 2000; Lehman 2006; Rovero et al. 2006), seasonal differences appear to also represent a consistent source of bias. In fact, seasonality influenced density estimates for four out of the five primates sampled in Lehman's (2006) study of lemur abundance in southeastern

Madagascar. Seasonal differences were also important in estimating the abundance of *E. coronatus* in this study. Future research with lemurs should be careful to address this common source of bias as part of interpreting the results from surveys along recce trails and line transects. Additionally, the role of disturbance along survey routes has frequently received attention in previous research (Skorupa 1987; Mitani et al. 2000; Lehman 2006) and represents an additional source of variation in estimating the density of *E. coronatus*. Finally, differences in behavioral response to the presence of human observers across the primates sampled in this study led to missed sightings with *E. coronatus* and a disproportionate number of sightings close to the survey line with large groups of the species, *P. perrieri*. The results reinforce the importance of, in the absence of quantitative information on the factors that covary with sighting distances of the target species, pay special attention to the influence of seasonality, habitat disturbance and behavioral differences in driving the detectability of primates during surveys.

Human factors determining primate abundance and occupancy

The role of humans in influencing basic ecological patterns continues to attract attention as a major topic in contemporary studies of wildlife populations (Woodroffe et al. 2005; Milner-Gulland and Rowcliffe 2007; Marsh and Chapman 2013). Distinguishing the role played by human factors from those reflective of the underlying ecology of systems is an important goal for conservation management (Lehman 2006) and in ensuring that appropriate biological inference is drawn in studies of the adaptive significance of traits and other trends in evolutionary biology (Struhsaker 1999). A second major question for this dissertation addresses the need to find characteristic patterns of population response to human factors across different primate species, ecological guilds and other categories used to distinguish between the members of primate communities. Although researchers have previously demonstrated considerable utility in deriving predictions for the responses of particular lemur species to human activities as a function of their dietary habitats (Lehman et al. 2006; Irwin et al. 2010; Herrera et al. 2011), the results from this study were not entirely consistent with the expectations for primates. In particular, by assessing variability in abundance and patch occupancy frugivores were generally found to be resilient to human activities whereas more folivorous lemurs were more vulnerable to these factors.

The finding that abundance and occupancy in the folivore-frugivore, *P. perrieri* were negatively influenced by large-scale fire and the proximity of large villages respectively, is cause for concern given the grave conservation status currently assigned to this species (Banks et al. 2007; Mittermeier et al. 2010; Schwitzer et al. 2013). More striking yet also more encouraging for future conservation efforts is the possibility that frugivorous lemurs are coping well with the impacts from human activities in the Diana region as suggested through the near absence of any negative population responses to variables used to quantify human pressure in this study. Only the occupancy of *E. sanfordi* was negatively affected by the smaller size of forest fragments and as a result the relative absence of large trees. Notably, neither *Propithecus* nor *E. coronatus* populations were reduced in abundance or found to be absent in smaller fragments, so park officials should attempt to mitigate threats to all forests, regardless of size.

The lack of a role for large-scale fires in influencing the populations of either *Eulemur* species is particularly unexpected, given the impacts predicted for large fruit trees, and existing fruit crops in habitats heavily influenced by fire (Peres et al. 2003). Fires appear to play an enormous role in shaping forests in the Diana region and based on analyses of patterns of forest loss over an eight-year period, in the subset of forest fragments used to study primate abundance patterns an average loss of 41% in forest cover was recorded (Table 2.1). Indeed recent estimates of emissions from the 1997-1998 El Niño event suggest that fire activity was higher on average in Madagascar's dry central and western (including the north) regions (van der Werf et al. 2004 cited in Kull and Laris 2009) than elsewhere in Madagascar. Cardiff and Befourouack (2003) also present data from Eaux et Forêts indicating that about 85 ha burned within Ankarana and another 197 ha in the peripheral zone during the year 2000. Although incentives for the use of fire in Madagascar are diverse (Kull 2000) much of the blame for current trends falls on increases in the urban demand for charcoal, the annual burning of grasses to promote pasture and in more isolated instances, the slash-and-burn agriculture of immigrant populations and the maintenance of agricultural fields (Banks pers.obs.). The growing prevalence of fires in northern Madagascar presents a bleak outlook for conservation efforts in this region given that surface fires have been shown to dramatically reduce seed availability and the potential for the re-colonization of habitat by forest-dwelling plant species (reviewed in Cochrane 2003). Habitat degradation of this sort is considered to pose the most serious threat to Madagascar's primate fauna (Mittermeier et al. 2010) so the unexpected results with the study's two frugivores warrants further investigation to better explain the anamoly of their relative success in such heavily human modified habitats.

Despite the relative lack of support for the role of human effects in modeling diurnal lemur abundance and occupancy, models for all species, with the exception of the elusive *H. occidentalis*, responded in some way to the natural characteristics of the environment. Not only were the population levels of all species influenced by the natural ecology of the study region but the variables with the greatest magnitude of effect in the models for *Propithecus* were also reflective of natural heterogeneity in site characteristics. The result highlights the importance of focusing on the natural ecology of the region as a basis for formulating plans for the management of the region's remaining primate populations. The fact that *Propithecus* densities attain levels an order of magnitude greater on sandstone substrates than in forests on limestone is quite arguably the single most important finding for the future conservation of this species. Ironically, data on forest loss indicates average losses of a remarkable 64% forest cover in sandstone forests during the period from 1994-2002 compared to a 31% loss of cover on average in forests on limestone (Table 2.1). Incidentally, the most critical habitats for this species are also the most threatened and rises in the incidence of fire may be responsible for these trends. Indeed forest fragments that had experienced a large-scale (≥ 0.005 km^2) fire during the nine years of study presented here were associated with reduced *Propithecus* abundance (Table 2.6, Figure 2.7). Future management initiatives have integrated fire fighting and fire prevention as part of a mandatory training module for park rangers at Analamerana, Ankarana and Andrafiamena but more staff are needed to cover these vast areas at the height of the fire-prone season.

Propithecus occupancy was also negatively affected by increasing proximity to large villages and I argue that the tendency of this species to cross open areas to access isolated food trees and reach neighboring forest fragments makes individuals susceptible to predation by domestic dogs (*Canis lupus familiaris*) in more heavily populated areas. This suggestion is supported by evidence from the Atlantic forest remnants of south-eastern Brazil where camera-trap records with dogs reached their highest frequencies in close proximity to human settlements (Srbek-Araujo and Chiarello 2008). In these areas, records with domestic dogs comprised the majority of sightings over that of any other carnivore. Predation of a *Propithecus* individual by dogs was observed on at least one occasion within a few 100 meters of the village of Anjahankely during the study period and there were several reports of similar incidents throughout the wider region. More data on the level of interaction between humans and *Propithecus* are needed to better categorize the full nature and degree of threat posed to lemur populations situated in close proximity to villages. Surprisingly, the intensity of hunting pressure as measured using indirect evidence of hunting presence (i.e. snares, sling remains, animal carcasses etc.) did not limit *Propithecus* abundance. However it may be that this index does not accurately quantify the influence of hunting pressures on primates in this region and despite taboos protecting *Propithecus* (Banks et al. 2007), more information is needed to better assess the risks that human hunting poses to *Propithecus* populations. Outreach should be extended to the inhabitants of large villages situated in the matrix between forest fragments to encourage responsible dog ownership, to strongly condemn hunting practices that target lemur populations and to provide communities with clear guidelines for enforcement in cases of non-compliance. The local Eaux et Forêt office in Anivorano-Nord should be considered a critical ally towards meeting these goals and along with the local gendarmerie, represent the primary means for ensuring the enforcement of protected area regulations.

Primate abundance versus primate occupancy patterns in assessing conservation status

As an alternative means for the assessment of conservation status, a number of scientists have recently suggested the use of data on occupancy or the proportion of area occupied by a species (MacKenzie et al. 2002) as opposed to more intensive data on population densities (MacKenzie et al. 2006; Baker et al. 2011; Keane et al. 2012). The limitations of methods aimed at estimating population densities with primates have been described at length elsewhere (Plumptre and Cox 2006; Hassel-Finnegan et al. 2008; Marshall et al. 2008), but in general, occupancy surveys are proposed to offer some advantages over the former methods, given their relative simplicity, and that they minimize the need for expert knowledge and specialty equipment (Baker et al. 2011). Furthermore, there are circumstances in which the data gathered during repeat occupancy surveys can be used to derive reliable estimates of density (He and Gaston 2000). This capacity originates from the positive relationship that exists between occupancy and abundance (Gaston et al. 2000). Accordingly occupancy surveys present an opportunity to gather information regarding primate population status in cases where the opportunity to estimate abundance is not an alternative. Despite these advantages, absolute changes in the size of a population, which may represent a more comprehensive measure of population status aren’t captured using data on occupancy (MacKenzie and Nichols 2004), so it is important to assess the information that is potentially lost by investing in occupancy as opposed to abundance surveys with primates. This dissertation presents a rare opportunity to investigate these differences since information has been presented on both the abundance (Chapter Three) and occupancy (Chapter Four) of primates within the same landscape.

In the studies of the primate community of the Diana region presented here, there was fairly strong conformity between the results characterizing population status based on abundance patterns and those reflective of differences in occupancy across the landscape. However, an inability to accumulate more than two repeat occupancy records for the 45 forest fragments included in the occupancy sample limits the potential to make strong inferences regarding the role of imperfect detection, to model the determinants of occupancy across all primate species, and to describe patterns of species richness across sites. Given the lack of a clear response relative to patterns of occupancy in the species *E. coronatus* and *H. occidentalis* it is difficult to contrast the results using these two complementary approaches for these species. Behavioral tendencies, including dietary and habitat preferences for *Hapalemur* (Mutschler and Tan 2003; Grassi 2006; Tan 2006) presented obstacles for both methods in achieving an adequate number of records and in achieving constant detectability. Additionally, attempts to model population density in *E. coronatus* only generated responses that followed a clear direction of effect for two of the explanatory variables included in the full model set. This lack of response in general may help to explain limitations in drawing comparisons between the two methods for these species.

E. sanfordi was found to be reach higher densities in forest fragments with the largest trees (Table 3.10). This result is consistent with findings from parallel studies of occupancy with this species and specifically the positive relationship between *E. sanfordi* occupancy and fragment area. Smaller fragments have been shown to support fewer large trees and one of the most widespread effects of increasing fragmentation on forested habitats involves the loss of large trees (Laurance et al. 2000). As mentioned previously the result is not surprising when considering the highly frugivorous diet of *E. sanfordi* and its lack of reliance on secondary dietary items (Freed 1996). Elevated *E. sanfordi* densities in more isolated forest fragments (Table 3.10.) were not reflected through attempts to model occupancy as a function of proximity to available habitat. This discrepancy between the two approaches appears to highlight limitations in the resolution of occupancy studies. Occupancy is scored as a presence absence variable and one limitation of this method is that it does not typically enable analysts to address quantitative differences or changes in abundance across different habitat patches. Although some researchers have used occupancy records from repeat surveys to estimate primate abundance (Baker et al. 2011), no data have been presented that allow for an assessment of the method’s accuracy with primates.

While occupancy methods may suffer from limitations in measuring changes in abundance, more intensive studies of population density are likely to be similarly limited in assessing changes in the range or geographic extent of target species. Although area effects were detected in the occupancy models with *E. sanfordi*, a similar effect was not detected using data on densities in forest fragments. This finding is probably an artifact of the scale at which patterns of abundance were considered in this study and specifically the omission of smaller sized fragments (i.e. ≤ 100 ha). Line-transect methods may be too cumbersome for smaller sized fragments and many researchers suggest conducting complete counts instead (Chapman pers.comm). This approach is analogous to the methods described for using occupancy surveys to estimate population abundance (Mackenzie and Royle 2005). In any case the discrepancies that arise from choosing to use either method provide some support for the use of both methods to ensure that all population-level effects are considered by studying population status at multiple scales.

The success of *E. sanfordi* in isolated habitats that are potentially closed to dispersal points to an additional aspect of their population ecology that would otherwise be overlooked by focusing exclusively on presence absence patterns across the landscape. The disparity in results from using one approach in favor of the other is does not result in stark differences in the recommendations aimed at improving survival prospects for this species in the immediate future however. The potential for habitat crowding in isolated forest fragments may instead have implications for the longevity of these populations since they may be more likely experience genetic drift as a function of inbreeding and reduced genetic diversity in smaller fragments (Schad et al. 2004; Bergl et al. 2008). Individuals that are tightly packed in high-density habitats are more likely to transmit disease, suffer from physiological stress and losses of genetic diversity (Arroyo-Rodríguez and Dias 2010). Whether investing disproportionately in the more isolated forest fragments that support higher densities of *E. sanfordi* represents a viable management strategy should await data on potential differences in biomedical health between isolated and more connected habitats and the potential fitness consequences of living at high local population densities (Irwin et al. 2010).

The findings with *P. perrieri* showed a high level of conformity when the results from abundance and occupancy studies are compared. In particular, elevated *Propithecus* densities in more disturbed habitats (Table 3.?, Figure 3.?) are consistent with the positive relationship existing between *Propithecus* occupancy and more complex fragment shapes (Table 4.?). Fragments characterized by complex shapes are likely to be strongly influenced by edge effects and experience many of the changes in forest structure and composition as habitats affected by low to moderate disturbances (e.g. low intensity selective logging, extraction of small plants, domestic animal browsing/foraging, etc.). Although the presence of *Propithecus* in fragments is negatively associated with the proxy I used for human disturbances in formulating the models that determine occupancy, the disparity between the two results likely represents a difference in the scale at which disturbance was measured. As a proxy variable, distance to villages has been shown to associate with factors such as hunting, stock grazing and harvesting (Smith et al. 1997). These factors represent higher intensities of pressure than do small-scale extractive activities along the routes used to survey primates. It would be interesting to assess if the proximity to villages serves as a better proxy for high rather than low to moderate disturbances in this study. Hunting pressure was considered in modeling abundance for all species, but did not elicit a response from any of the lemurs studied here. Alternatively, *Propithecus* populations did respond negatively to the recent presence of large-scale fire in forest fragments and I argue that fires represent a form of heavy disturbance on lemur habitats in the Diana region. Fires remove large trees, cause reductions in the rate of flowering and fruiting and can cause death through the direct burning of individuals attracted to forest edges where fires occur (e.g. *Propithecus*). Future occupancy work may benefit from testing this hypothesis by assessing whether proximity to villages is associated with large-scale fires.

Finally, the finding that *Propithecus* densities are elevated on sandstone substrates is reinforced by the results that demonstrate greater occupancy in sandstone forest fragments. The magnitude of effect from this variable however was strongest and most important in modeling *Propithecus* abundance. Although occupancy studies did capture some element of this important relationship the results were not nearly as stark as in the parallel study of *Propithecus* abundance. Alternatively, proximity to large villages was the most important variable in modeling *Propithecus* occupancy (Table 4.?). Exclusively using data on occupancy might cause analysts to overlook the full importance of sandstone habitats in supporting a large proportion of the remaining *Propithecus* population in the Diana region. Given the threats currently facing sandstone forests and limitations in the resources available for conservation in the region it is important to distinguish between these two results. While the results from modeling abundance patterns argue quite firmly for the prioritization of improving protection for sandstone forests, the results of the occupancy study risk distorting this interpretation by emphasizing other factors (e.g. minimizing human-nonhuman primate interactions).

Directions for future research and recommendations for conservation management

To better understand the patterns that have emerged from this study and to outline strategies for safeguarding existing primate diversity in the Diana region the following recommendations for future studies of this system are proposed. Firstly, the relative lack of response to the explanatory variables used to model abundance and occupancy in the *Eulemur* species studied here suggests that important factors determining the population status of these species were likely missing from the models. One explanation for this result may be that the use of ecological guilds for these primates represents an ineffective approach for distinguishing between the different members of primate communities. Recent work on the nutritional characteristics of primate diets has illuminated stark differences in the nutrients prioritized among closely related taxa and even in separate populations of the same species (Rothman et al. 2011). Behavioral studies with the two *Eulemur* species that incorporate the nutritional analysis of foods could provide important insights into the nutrients being prioritized by these species in high- and low-density habitats. The results have implications for testing new hypotheses regarding the determinants of abundance and occupancy for these two species as well as in finding alternative mechanisms for patterns of niche separation among primates (Rothman pers.comm.). For example, understanding the nutrients and plant secondary metabolite concentrations that are being prioritized by the two species should provide a means by which to test the hypothesis that polyspecific associations provide a better explanation for the observed correlation between the abundances of these two lemurs than does environmental filtering. In addition to the inferences regarding nutritional ecology, the behavioral study of groups that actively range into edge habitats may also help to clarify the capacity for dispersal in these species.

Studies of primate nutrition are not only likely to provide new insights into the factors that determine *Eulemur* abundance in the Diana region but should also assist with finding better explanations for the current results with *Propithecus*. As a primarily folivorous species, *Propithecus* were predicted to reach higher abundances in dry deciduous rather than semi-evergreen forests as a function of proposed differences in leaf quality (Coley and Barone 1996). To the contrary, *Propithecus* densities in semi-evergreen forests on sandstone were up to an order of magnitude higher than in more deciduous habitats (Figure 3.?). By evaluating the nutritional characteristics of *Propithecus* foods in both habitats through on-going behavioral studies researchers will be able to directly test the hypothesis that dry deciduous forests provide better quality leaves for folivores than do more evergreen habitats. A better understanding of the nutritional characteristics of *Propithecus* diets in high- and low-density habitats should facilitate novel assessments of habitat quality at large spatial scales since new technologies in infrared reflectance spectroscopy permit the mapping of nutrient concentrations using remote sensing techniques (Ganzhorn et al. 1997; Kay et al. 1997; DeGabriel et al. 2013). These and other alternatives for assigning value to particular forests may offer conservation managers clearer strategies for how to invest limited resources into the protection of nature.

In addition to nutrition, experts of the mechanisms responsible for structuring primate communities advocate for the inclusion of additional environmental variables, including rainfall (Kay et al. 1997, Ganzhorn et al. 1997), soil nutrient status (Peres 1997), and elevation (Steven and Jorg 2004; Wilmé et al. 2006) in modeling correlates to primate community biomass (Fleagle et al. 1999). Furthermore, recent meta-analyses argue for the importance of environmental factors in the structuring of modern primate communities (Kamilar 2009; Muldoon and Goodman 2010). Peres (1997) for example, found that differences in soil fertility, specifically the concentrations of nutrients linked to tropical forest productivity provided the best explanation for variability in habitat and primate community structure and biomass across several sites of the Amazon basin. Forests on limestone substrates in northern Madagascar are often distinguished from more evergreen formations by a shallow, alkaline soil layer (Fowler et al. 1989; Hawkins et al. 1990) but a more comprehensive evaluation of soil nutrient status is unavailable at present. Whether differences in soil fertility provide a better framework for comparing sandstone and limestone forests in the context of habitat quality for primates, and specifically *Propithecus* requires further investigation. Additionally, by integrating new environmental variables as part of the modeling process that was adopted here, complementary data on behavior could help researchers to return to the question of whether or not the frequency of polyspecific associations is accurately predicted by plant productivity (Lehman 2000; Freed 2006). Finally, given previous success with finding meaningful correlates to patterns of community structure using abiotic environmental variables as predictors (Muldoon and Goodman 2010) suggests that these new data might also enable a more meaningful reevaluation of the factors underpinning differences in primate species richness.

As well as improving the analyses presented here by including new explanatory variables that capture nutritional and abiotic differences across habitats, future research should also attempt to include data on the abundance of nocturnal primates in addition to implementing methods aimed at improving the detectability of *H. occidentalis*. Low degrees of freedom in the analyses relating primate occupancy to species richness patterns may explain the absence of any consistent predictor variables in these analyses. Furthermore, preliminary investigations of nocturnal primate abundance suggest that these species represent a substantial proportion of the total primate community biomass (Ratelolahy 2007, Banks unpubl. data). Only with data on these additional members of the primate community at these sites can hypotheses that relate to the structuring of primate communities be comprehensively addressed.

Finally, the finding that the abundance of both *Eulemur* species is positively associated with the degree of isolation of the forest fragment was unexpected and has implications for the crowding of habitats. A major goal for future work aimed at understanding this pattern should improve the spatial resolution of landscape analyses so that riparian forests are also considered as potential corridors for transfer between fragments and as available habitat for the two *Eulemur* species. The degree to which *Propithecus* are able to exploit these narrow habitats has yet to be determined, but preliminary evidence demonstrates the regular presence of both *Eulemur* species in these habitats.

These suggestions for future directions in research would be incomplete without complementary suggestions for the management of the remaining forests in the region. Based on the findings presented in this dissertation, I have outlined the following recommendations:

1. **Greatly enhance the protection of sandstone forests regardless of size, throughout the region, and particularly against the threat of fire (see below).** Despite near equal numerical representation in the sample used to investigate primate occupancy patterns here, sandstone forests represent only 11.8% of the total surface area studied. Not only is this forest type restricted in distribution but also it is the most threatened by habitat loss (64 and 31% loss in sandstone and limestone forests respectively). Substrate type was the single most important determinant of *Propithecus* abundance and despite differences in the amount of surface area covered in each habitat, sandstone forests still account for nearly 40% of the total 2133 “known” individuals sampled in this study. *Propithecus* densities were not found to be diminished in smaller forests so sandstone forest fragments of all sizes should be integrated into conservation plans, particularly those connected to other forests within one half kilometer of forest edges. *Propithecus* populations exhibited a weak negative response to forests that were more isolated in a band at between 0.5 and 1 kilometer from forest edges (Table 4.5).
2. **Improve the protection of forests against large-scale surface fires by reducing forest flammability and preventing combustion of flammable forests (Barlow and Peres 2004)**. Reducing forest flammability primarily involves effective enforcement campaigns aimed at regulating selective logging and other human activities that reduce canopy openness and augment understorey fuel loads. Preventing fires from reaching forests relies on the use of firebreaks and local outreach aimed at encouraging fire-sensitive forms of agriculture and land use. In addition to the suggestions for future research with the primate community presented above, increasing research into the potential management strategies that

may enhance ecosystem recovery processes should also be prioritized (Cochrane 2003).

3. **With the exception of sandstone forests, prioritize the protection of forest fragments > 2 km^2 in size.** Small forests have a large proportion of edge and may be more susceptible to fire (Barlow and Peres 2004), predation (Irwin et al. 2009) and hunting (Peres 2001). Additionally, *E. sanfordi* occupancy patterns show a very strong effect of forest area on the probability of incidence in a particular fragment with a clearly defined threshold of 2 km^2. Smaller forests should not be ignored, as they support populations of other primates. However, with limited resources available for conservation efforts, fragments > 2 km^2 may represent the safest investment for safeguarding the greatest assemblages of primate faunal diversity.
4. **Advocate for on-going research presence in the study region.** This study initiated a training program in primate population sampling techniques for five teams (total = 24 individuals) of remotely stationed wildlife experts and in behavioral sampling techniques for one of these teams (4 individuals). Community-based conservation programs have gained widespread support across the conservation community but require stable investments, long-term commitments and the existence of mutual benefits for all stakeholders (Richard and Ratsirarson 2013). Maintaining research presence in the study region will reinforce the importance and value of investing in a local intellectual resource base for conservation. In addition to working at the community level, improving collaborative agreements and involvement at the regional level including with universities, state and externally funded organizations should further improve conservation efforts.

References

Arroyo-Rodríguez V, Dias P (2010) Effects of habitat fragmentation and disturbance on howler monkeys: a review. American Journal of Primatology 72:1-16

Baker LR, Arnold TW, Olubode OS, Garshelis DL (2011) Considerations for using occupancy surveys to monitor forest primates: a case study with Sclater's monkey (*Cercopithecus sclateri*). Population Ecology 53:549-561

Banks MA, Ellis ER, Antonio, Wright PC (2007) Global population size of a critically endangered lemur, Perrier's sifaka. Animal Conservation 10:254-262

Barlow J, Peres C (2004) Ecological responses to el Niño-induced surface fires in central Brazilian Amazonia: management implications for flammable tropical forests. Philosophical Transactions of the Royal Society of London. Series B, Biological sciences 359:367-380

Bergl R, Bradley B, Nsubuga A, Vigilant L (2008) Effects of habitat fragmentation, population size and demographic history on genetic diversity: the Cross River gorilla in a comparative context. American Journal of Primatology 70:848-859

Buckland ST, Plumptre AJ, Thomas L, Rexstad EA (2010) Design and Analysis of Line Transect Surveys for Primates. International Journal of Primatology 31:833-847

Cardiff S, Befourouack J (2003) The Reserve Spéciale d'Ankarana. In: Goodman SM, Benstead JP (eds) The Natural History of Madagascar. University of Chicago Press, Chicago, IL, pp 1501-1507

Chapman CA, Peres CA (2001) Primate conservation in the new millennium: The role of scientists. Evolutionary Anthropology 10:16–33

Cochrane M (2003) Fire science for rainforests. Nature 421:913-919

Coley P, Barone J (1996) Herbivory and plant defenses in tropical forests. Annual Review of Ecology and Systematics 27:305-335

DeGabriel JL, Moore BD, Felton AM, Ganzhorn JU, Stolter C, Wallis IR, Johnson CN, Foley WJ (2013) Translating nutritional ecology from the laboratory to the field: milestones in linking plant chemistry to population regulation in mammalian browsers. Oikos 000:1-11

Fleagle JG, C. J, K.E. R (1999) Concluding remarks. In: Fleagle JG, Janson C, Reed KE (eds) Primate Communities. Cambridge University Press, Cambridge, UK, pp 310-314

Fowler SV, Chapman P, Checkley D, Hurd S, McHale M, Ramangason GS, Randriamasy JE, Stewart P, Walters R, Wilson JM (1989) Survey and management proposals for a tropical deciduous forest reserve at Ankarana in northern Madagascar. Biological Conservation 47:297-313

Freed BZ (2006) Polyspecific Associations of Crowned Lemurs and Sanford's Lemurs in Madagascar. In: Gould L, Sauther M (eds) Lemurs. Springer Science, New York, NY, pp 111-131

Freed BZ (1996) Co-occurrence among crowned lemurs (*Lemur coronatus*) and Sanford's lemurs (*Lemur fulvus sanfordi*) of Madagascar. In: Department of Anthropology. Washington University, pp 450

Ganzhorn JU, Malcomber S, Andrianantoanina O, Goodman SM (1997) Habitat Characteristics and Lemur Species Richness in Madagascar. Biotropica 29:331-343

Gaston KJ, Blackburn TM, Greenwood JJD, Gregory RD, Quinn RM, Lawton JH (2000) Abundance-occupancy relationships. Journal of Applied Ecology 37:39-59

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

Goodman SM, Ganzhorn JU (2004) Biogeography of lemurs in the humid forests of Madagascar: the role of elevational distribution and rivers. Journal of Biogeography 31:47-55

Hassel-Finnegan HM, Borries C, Larney E, Umponjan M, Koenig A (2008) How Reliable are Density Estimates for Diurnal Primates? International Journal of Primatology 29:1175-1187

Hawkins AFA, Chapman P, Ganzhorn JU, Bloxam QMC, Barlow SC, Tonge SJ (1990) Vertebrate Conservation in Ankarana special reserve, Northern Madagascar. Biological Conservation 54:83-110

He F, Gaston KJ (2000) Occupancy-abundance relationships and sampling scales. Ecography 23:503-511

Herrera JP, Wright PC, Lauterbur E, Ratovonjanahary L, Taylor LL (2011) The Effects of Habitat Disturbance on Lemurs at Ranomafana National Park, Madagascar. International Journal of Primatology 32:1091-1108

Irwin MT, Wright PC, Birkinshaw C, Fisher BL, Gardner CJ, Glos J, Goodman SM, Loiselle P, Rabeson P, Raharison J-L (2010) Patterns of species change in anthropogenically disturbed forests of Madagascar. Biological Conservation 143:2351–2362

Irwin MT, Raharison JL, Wright PC (2009) Spatial and temporal variability in predation on rainforest primates: do forest fragmentation and predation act synergistically? Animal Conservation 12:220-230

Kamilar JM (2009) Environmental and geographic correlates of the taxonomic structure of primate communities. American Journal of Physical Anthropology 139:382-393

Kay RP, Madden RM, Van Schaik CP, Higdon D (1997) Primate species richness is determined by plant productivity: implications for conservation. Proceedings of the National Academy of Sciences of the United States of America 94:13023-13027

Keane A, Hobinjatovo T, Razafimanahaka HJ, Jenkins RKB, Jones JPG, Res A, Michael S (2012) The potential of occupancy modelling as a tool for monitoring wild primate populations. Animal Conservation 15:457-465

Kull C (2000) Deforestation, erosion, and fire: degradation myths in the environmental history of Madagascar. Environment and History Vol. 6 423-450

Kull C, Laris P (2009) Fire ecology and fire politics in Mali and Madagascar. In: Tropical Fire Ecology: Climate Change, Land Use and Ecosystem Dynamics. Praxis Publishing, Chichester, UK, pp 645

Laurance WF, Delamônica P, Laurance SG, Vasconcelos H, Lovejoy TE (2000) Rainforest fragmentation kills big trees. Nature Vol. 404:836

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

Lehman SM (2000) Primate community structure in Guyana: a biogeographic analysis. International Journal of Primatology 21:333-351

Lehman SM (2006) Effects of Transect Selection and Seasonality on Lemur Density Estimates in Southeastern Madagascar. International Journal of Primatology 27

Lynne RB, Todd WA, Oluseun SO, David LG (2011) Considerations for using occupancy surveys to monitor forest primates: a case study with Sclater's monkey (*Cercopithecus sclateri*). Population Ecology 53:549-561

MacKenzie D, Nichols J (2004) Occupancy as a surrogate for abundance estimation. Animal Biodiversity and Conservation 27:461-467

MacKenzie DI, Nichols JD, Royle JA, Pollock KH, Bailey LI, Hines JE (2006) Occupancy Estimation and Modeling: Inferring Patterns and Dynamics of Species Occurrence. Elsevier Academic Press, Burlington, MA.

MacKenzie DI, Nichols JD, Sutton N, Kawanishi K, Bailey L (2005) Improving inferences in population studies of rare species that are detected imperfectly. Ecology 86:1101-1113

Mackenzie DI, Royle JA (2005) Designing occupancy studies: general advice and allocating survey effort. Journal of Applied Ecology 42:1105-1114

Marques TA, Thomas L, Fancy SG, Buckland ST (2007) Improving estimates of bird density using multiple-covariate distance sampling. The Auk 124:1229-1243

Marsh LK, Chapman CA (2013) Primates in Fragments: Complexity and Resistance. Springer, New York

Marshall A, Lovett J, White P (2008) Selection of line-transect methods for estimating the density of group-living animals: lessons from the primates. American Journal of Primatology 70:452-462

Milner-Gulland E, Rowcliffe J (2007) Conservation and Sustainable Use: A Handbook of Techniques. Oxford University Press, Oxford, UK.

Mitani JC, Struhsaker TT, Lwanga JS (2000) Primate community dynamics in old growth forest over 23.5 years at Ngogo, Kibale National Park, Uganda: implications for conservation and census methods. International Journal of Primatology 21:269-286

Mittermeier RA, Louis Jr. EE, Richardson M, Schwitzer C, Langrand O, Rylands AB, Hawkins F, Rajaobelina S, Ratsimbazafy J, Rasoloarison R, Roos C, Kappeler PM, MacKinnon J (2010) Lemurs of Madagascar. Panamericana Formas e Impresos S.A., Bogotá, Columbia

Muldoon KM, Goodman SM (2010) Ecological biogeography of Malagasy non-volant mammals: community structure is correlated with habitat. Journal of Biogeography 37:1144-1159

Mutschler T, Tan CL (2003) *Hapalemur*, Bamboo or Gentle Lemurs. In: Goodman SM, Benstead JP (eds) The Natural History of Madagascar. The University of Chicago Press, Chicago, IL, pp 1324-1329

Nijman V (2001) Effects of behavioural changes due to habitat disturbance on density estimation of rain forest vertebrates, as illustrated by gibbons (primates: Hylobatidae). In: Hillegers PJM, de Iongh HH (eds) The Balance between Biodiversity Conservation and Sustainable Use of Tropical Rain Forests: Workshop Proceedings Tropenbos, Wageningen, Netherlands, pp 217-225

Nijman V, Nekaris K (2012) Loud calls, startle behaviour, social organisation and predator avoidance in arboreal langurs (Cercopithecidae: *Presbytis*). Folia primatologica 83:274-287

Peres CA (1997) Effects of habitat quality and hunting pressure on arboreal folivore densities in neotropical forests: a case study of howler monkeys (*Alouatta* spp.). Folia Primatologica 68:199-222

Peres CA (1999) General guidelines for standardizing line-transect surveys of tropical forest primates. Neotropical Primates 7:11-16

Peres CA, Barlow J, Haugaasen T (2003) Vertebrate responses to surface wildfires in a central Amazonian forest. Oryx 37:97-109

Peres CA (2001) Synergistic Effects of Subsistence Hunting and Habitat Fragmentation on Amazonian Forest Vertebrates. Conservation Biology 15:1490-1505

Plumptre A, Cox D (2006) Counting primates for conservation: primate surveys in Uganda. Primates 47:65-73

Ratelolahy FJ (2007) Rapport d'inventaire biologique rapide dans la forêt d'Andrafiamena. In: Conservation International Rapid Assessment Program Report, Alexandria, VA

Richard AF, Ratsirarson J (2013) Partnership in practice: making conservation work at Bezà Mahafaly, southwest Madagascar. Madagascar Conservation & Development 8:12-20

Rothman J, Raubenheimer D, Chapman C (2011) Nutritional geometry: gorillas prioritize non-protein energy while consuming surplus protein. Biology letters 7:847-849

Rovero F, Struhsaker TT, Marshall AR, Rinne TA, Pedersen UB, Butynski TM, Ehardt CL, Mtui AS (2006) Abundance of Diurnal Primates in Mwanihana Forest, Udzungwa Mountains, Tanzania: A Multi-Observer Comparison of Line-Transect Data. International Journal of Primatology 27:675-697

Schad J, Sommer S, Ganzhorn JU (2004) MHC Variability of a Small Lemur in the Littoral Forest Fragments of Southeastern Madagascar. Conservation Genetics 5:299-309

Schwitzer C, Mittermeier RA, Davies N, Johnson S, Ratsimbazafy J, Razafindramanana J, Louis Jr. EE, Rajaobelina S (2013) Lemurs of Madagascar: A Strategy for Their Conservation 2013–2016. SSC Primate Specialist Group, Bristol Conservation and Science Foundation, and Conservation International, Bristol, UK

Skorupa JP (1987) Do line-transect surveys systematically underestimate primate densities in logged forests? American Journal of Primatology 13:1-9

Smith AP, Horning N, Moore D (1997) Regional Biodiversity Planning and Lemur Conservation with GIS in Western Madagascar. Conservation Biology 11:498–512

Srbek-Araujo A, Chiarello A (2008) Domestic dogs in Atlantic forest preserves of south-eastern Brazil: a camera-trapping study on patterns of entrance and site occupancy rates. Brazilian Journal of Biology 68:771-779

Struhsaker T (1999) Primate communities in Africa: The consequence of long-term evolution or the artifact of recent hunting? In: Fleagle J, Janson, C, Reed, KE (ed) Primate Communities. Cambridge University Press, Cambridge, UK, pp 289-294

Tan CL (2006) Behavior and Ecology of Gentle Lemurs (Genus *Hapalemur*). In: Gould L, Sauther ML (eds) Lemurs: Ecology and Adaptation. Springer, New York, NY., pp 369-382

Thomas L, Buckland S, Rexstad E, Laake J, Strindberg S, Hedley S, Bishop J, Marques T, Burnham K (2010) Distance software: design and analysis of distance sampling surveys for estimating population size. The Journal of Applied Ecology 47:5-14

van der Werf G, Randerson J, Collatz G, Giglio L, Kasibhatla P, Arellano A, Olsen S, Kasischke E (2004) Continental-scale partitioning of fire emissions during the 1997 to 2001 El Niño/La Niña period. Science 303:73-76

Wilmé L, Goodman SM, Ganzhorn JU (2006) Biogeographic evolution of Madagascar's microendemic biota. Science 312:1063-1065

Woodroffe R, Thirgood S, Rabinowitz A (2005) People and wildlife, conflict or co-existence? Cambridge University Press, New York, NY.

Bibliography

Akaike H (1973) Information theory and an extension of the maximum likelihood principle. Akademinai Kiado:267-281

Alldredge MW, Pollock KH, Simons TR, Johnson D (2006) Estimating detection probabilities from multiple-observer point counts. The Auk 123:1172-1182

Anderson D, Burnham K (2002) Avoiding pitfalls when using information-theoretic methods. The Journal of Wildlife Management 66:912-918

Anderson DR, Burnham KP, Lubow BC, Thomas L, Corn PS, Medica PA, Marlow RW (2001) Field trials of line transect methods applied to estimation of desert tortoise abundance. The Journal of Wildlife Management 65:583-597

Anderson DR, Link WA, Johnson DH, Burnham KP (2001) Suggestions for Presenting the Results of Data Analyses. The Journal of Wildlife Management 65:373-378

Anderson J, Cowlishaw G, Rowcliffe JM (2007) Effects of Forest Fragmentation on the Abundance of (*Colobus angolensis palliatus*) in Kenya's Coastal Forests. International Journal of Primatology 28:637-655

Andren H (1994) Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. Oikos 71:355-366

Anzures-Dadda A, Manson RH (2007) Patch- and landscape-scale effects on howler monkey distribution and abundance in rainforest fragments. Animal Conservation 10:69-76

Arrigo-Nelson S, Wright P (2004) Survey results from Ranomafana National Park: new evidence for the effects of habitat preference and disturbance on the distribution of *Hapalemur*. Folia Primatologica 75:331-334

Arroyo-Rodríguez V, Dias P (2010) Effects of habitat fragmentation and disturbance on howler monkeys: a review. American Journal of Primatology 72:1-16

Arroyo- Rodríguez V, Mandujano S (2006) Forest Fragmentation Modifies Habitat Quality for *Alouatta palliata*. International Journal of Primatology 27:1079-1096

Arroyo- Rodríguez V, Mandujano S (2009) Conceptualization and Measurement of Habitat Fragmentation from the Primates' Perspective. International Journal of Primatology 30:497-514

Arroyo- Rodríguez V, Mandujano S, Benítez-Malvido J (2008) Landscape attributes affecting patch occupancy by howler monkeys (*Alouatta palliata mexicana*) at Los Tuxtlas, Mexico. American Journal of Primatology 70:69-77

Arroyo- Rodríguez V, Mandujano S, Benítez-Malvido J, Cuende-Fanton C (2007) The Influence of Large Tree Density on Howler Monkey (*Alouatta palliata mexicana*) Presence in Very Small Rain Forest Fragments. Biotropica 39:760-766

Asensio N, Arroyo- Rodríguez V, Dunn JD, Cristóbal-Azkarate J (2009) Conservation Value of Landscape Supplementation for Howler Monkeys Living in Forest Patches. Biotropica 41:768-773

Aureli F, Schaffner CM, Boesch C, Bearder SK, Call J, Chapman CA, Connor R, Di Fiore A, Dunbar RIM, Henzi SP (2008) Fission Fusion Dynamics. Current Anthropology 49:627-654

Baker LR, Arnold TW, Olubode OS, Garshelis DL (2011) Considerations for using occupancy surveys to monitor forest primates: a case study with Sclater's monkey (*Cercopithecus sclateri*). Population Ecology 53:549-561

Balko E, Underwood H (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

Banks MA, Ellis ER, Antonio, Wright PC (2007) Global population size of a critically endangered lemur, Perrier's sifaka. Animal Conservation 10:254-262

Barlow J, Peres C (2004) Ecological responses to el Niño-induced surface fires in central Brazilian Amazonia: management implications for flammable tropical forests. Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences 359:367-380

Bartón K (2012) MuMIn: multi-model inference. In: R package version

Bates D, Maechler M (2010) lme4: Linear mixed-effects models using S4 classes. R package. In, Version 0.999375-34 edn

Beaudrot L, Marshall A (2011) Primate communities are structured more by dispersal limitation than by niches. The Journal of Animal Ecology 80:332-341

Bergl R, Bradley B, Nsubuga A, Vigilant L (2008) Effects of habitat fragmentation, population size and demographic history on genetic diversity: the Cross River gorilla in a comparative context. American Journal of Primatology 70:848-859

Binggeli P (2003) Introduced and Invasive Plants. In: Goodman SM, Benstead JP (eds) The Natural History of Madagascar. The University of Chicago Press, Chicago, IL, pp 257-268

Bohlman SA (2010) Landscape patterns and environmental controls of deciduousness in forests of central Panama. Global Ecology and Biogeography 19:376-385

Bolker B, Brooks M, Clark C, Geange S, Poulsen J, Stevens MH, White J-S (2009) Generalized linear mixed models: a practical guide for ecology and evolution. Trends in Ecology & Evolution 24:127-135

Bond WJ, Silander Jr. JA, Ranaivonasy J, Ratsirarson J (2008) The antiquity of Madagascar's grasslands and the rise of C 4 grassy biomes. Journal of Biogeography 35:1743-1758

Borries C, Larney E, Kreetiyutanont K, Koenig A (2002) The diurnal primate community in a dry evergreen forest in Phu Khieo Wildlife Sanctuary, Northeast Thailand. Natural History Bulletin Siam Society 50:75-88

Bourliére F (1985) Primate communities: Their structure and role in tropical ecosystems. International Journal of Primatology 6:1-26

Boyce MS (1992) Population viability analysis. Annual Review of Ecology and Systematics 23:481-506

Brenneman RA, Johnson SE, Bailey CA, Ingraldi C, Delmore KE, Wyman TM, Andriamaharoa HE, Ralainasolo FB, Ratsimbazafy JH, Louis EE (2011) Population genetics and abundance of the Endangered grey-headed lemur *Eulemur cinereiceps* in south-east Madagascar: assessing risks for fragmented and continuous populations. Oryx 46:298-307

Brockelman W, Ali R (1987) Methods of surveying and sampling forest primate populations. In: Marsh CW, Mittermeier RA (eds) Primate conservation in the tropical rain forest. Alan R. Liss, Inc., New York, NY, pp 23-62

Brown J, Kodric-Brown A (1977) Turnover rates in insular biogeography: Effect of immigration on extinction. Ecology 58:445-449

Brown K, Gurevitch J (2004) Long-term impacts of logging on forest diversity in Madagascar. Proceedings of the National Academy of Sciences of the United States of America 101:6045-6049

Buchanan-Smith H (1999) Tamarin polyspecific associations: Forest utilization and stability of mixed-species groups. Primates 40:233-247

Buckland ST, Borchers DL, Johnston A, Henrys PA, Marques TA (2007) Line transect methods for plant surveys. Biometrics 63:989-998

Buckland ST, Anderson DR, Burnham KP, Laake JL, Borchers DL, Thomas L (2001) Introduction to Distance Sampling. Oxford University Press, Oxford, UK

Buckland ST, Anderson DR, Burnham KP, Laake JL, Borchers DL, Thomas L (2004) Advanced distance sampling. Oxford University Press, Oxford, UK

Buckland ST, Plumptre AJ, Thomas L, Rexstad EA (2010) Design and Analysis of Line Transect Surveys for Primates. International Journal of Primatology 31:833-847

Buckland ST, Plumptre AJ, Thomas L, Rexstad EA (2010) Line Transect Sampling of Primates: Can Animal-to-Observer Distance Methods Work? International Journal of Primatology 31:485-499

Buřivalová Z (2011) Remote Sensing of Vegetation in Conservation: A Case Study from the Dry and Transitional Forests of Andrafiamena, Northern Madagascar. In: Université de Geneve and Conservatoire et Jardin Botanique de la Ville de Geneve. Université de Geneve, Geneva, Switzerland, pp 89

Burney DA (1996) Climate Change and Fire Ecology as Factors in the Quaternary Biogeography of Madagascar. In: Lourenço W (ed) Biogéographie de Madagascar. ORSTROM, Paris, pp 49-58

Burney DA (2003) Madagascar's prehistoric ecosystems. In: Goodman SM, Benstead JP (eds) The Natural History of Madagascar. Univ. Chicago Press, Chicago, pp 47-51

Burney DA, Burney LP, Godfrey LR, Jungers WL, Goodman SM, Wright HT, Jull AJ (2004) A chronology for late prehistoric Madagascar. Journal of Human Evolution 47:25-63

Burney DA, James HF, Grady FV, Rafamantanantsoa J-G, Ramilisonina, Wright HT, Cowart JB (1997) Environmental change, extinction and human activity: evidence from caves in NW Madagascar. Journal of Biogeography 24:755-767

Burney DA, Robinson GS, Burney LP (2003) Sporormiella and the late Holocene extinctions in Madagascar. Proceedings of the National Academy of Sciences of the United States of America 100:10800-10805

Burney DA (1999) Rates, patterns, and processes of landscape transformation and extinction in Madagascar. In: Extinctions in near time: causes, contexts, and consequences, pp 145-164

Burney DA (1999) Rates, patterns, and processes of landscape transformation and extinction in Madagascar. Extinctions in near time: causes, contexts, and consequences:145-164

Burnham KP, Anderson DR (2002) Model selection and multi-model inference: a practical information-theoretic approach. Springer-Verlag, New York, NY

Burnham KP, Anderson DR, Huyvaert KP (2010) AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. Behavioral Ecology and Sociobiology 65:23-35

Cardiff S, Befourouack J (2003) The Reserve Spéciale d'Ankarana. In: Goodman SM, Benstead JP (eds) The Natural History of Madagascar. University of Chicago Press, Chicago, IL, pp 1501-1507

Chapman CA, Bonnell TR, Gogarten JF, Lambert JE, Omeja PA, Twinomugisha D, Wasserman MD, Rothman JM (2012) Are Primates Ecosystem Engineers? International Journal of Primatology 34:1-14

Chapman CA, Chapman LJ (1999) Implications of small scale variation in ecological conditions for the diet and density of red colobus monkeys. Primates 40:215-231

Chapman CA, Chapman LJ, Jacob AL, Rothman JM, Omeja P, Reyna-Hurtado R, Hartter J, Lawes MJ (2010) Tropical tree community shifts: Implications for wildlife conservation. Biological Conservation 143:366-374

Chapman CA, Chapman LJ, Naughton-Treves L, Lawes MJ, McDowell LR (2004) Predicting folivorous primate abundance: validation of a nutritional model. American Journal of Primatology 62:55-69

Chapman CA, Lawes MJ (2003) Primate survival in community-owned forest fragments: Are metapopulation models useful amidst intensive use. In: Marsh LK (ed) Primates in Fragments: Ecology and Conservation. Springer, New York, pp 63-77

Chapman CA, Struhsaker TT, Skorupa JP, Snaith TV, Rothman JM (2010) Understanding long-term primate community dynamics: implications of forest change. Ecological Applications 20:179-191

Chapman CA, Balcomb SR, Gillespie TR, Skorupa JP, Struhsaker TT (2000) Long-Term Effects of Logging on African Primate Communities: a 28-Year Comparison From Kibale National Park, Uganda. Conservation Biology 14:207-217

Chapman CA, Chapman LJ (1999) Implications of small scale variation in ecological conditions for the diet and density of red colobus monkeys. Primates 40:215-231

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, Bjorndal KA, Onderdonk DA (2002) Application of protein-to-fiber ratios to predict colobine abundance on different spatial scales. International Journal of Primatology 23:283-310

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

Chatterjee S, Hadi AS (2013) Regression analysis by example. John Wiley & Sons, Inc., Hoboken, NJ

Chiarello AG, de Melo FR (2001) Primate population densities and sizes in Atlantic forest remnants of northern Espirito Santo, Brazil. International Journal of Primatology 22:379-396

Clifford MH, Chih-Ling T (1990) The Impact of Model Selection on Inference in Linear Regression. The American Statistician 44:214-217

Cochrane M (2003) Fire science for rainforests. Nature 421:913-919

Cochrane MA, Alencar A, Schulze MD, Souza Jr. CM, Nepstad DC, Lefebvre P, Davidson EA (1999) Positive feedbacks in the fire dynamic of closed canopy tropical forests. Science 284:1832-1835

Coley P, Barone J (1996) Herbivory and plant defenses in tropical forests. Annual Review of Ecology and Systematics 27:305-335

Colin AC, Lisa N-T, Michael JL, Michael DW, Thomas RG (2007) Population Declines of Colobus in Western Uganda and Conservation Value of Forest Fragments. International Journal of Primatology 28:513-528

Colquhoun IC (1993) The socioecology of *Eulemur macaco*: A preliminary report. In: Kappeler PM, Ganzhorn JU (eds) Lemur social systems and their ecological basis. Plenum Press, New York, pp 11-23

Colquhoun IC (2007) Anti-Predator Strategies of Cathemeral Primates: Dealing with Predators of the Day and the Night. In: Gursky SL, Nekaris K (eds) Primate Anti-predator Strategies. Springer, New York, NY pp.146-172

Cowlishaw G, Dunbar RIM (2000) Primate Conservation Biology. University of Chicago Press: 498 pp.

Cowlishaw G, Pettifor R, Isaac N (2009) High variability in patterns of population decline: the importance of local processes in species extinctions. Proc. R. Soc. Lond. B 276:63-69

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

Crowley BE (2010) A refined chronology of prehistoric Madagascar and the demise of the megafauna. Quaternary Science Reviews 29:2591-2603

Davies A (1994) Colobine populations. In: Davies A, Oates J (eds) Colobine Monkeys: Their Ecology, Behaviour and Evolution. Cambridge University Press, Cambridge, UK, pp. 285-310

De-Gama Blanchet HN, Fedigan LM (2005) The effects of forest fragment age, isolation, size, habitat type, and water availability on monkey density in a tropical dry forest. In: Estrada A, Garber PA, Pavelka MSM, Leucke L (eds) New Perspectives in the Study of Mesoamerican Primates: Distribution, Ecology, Behavior and Conservation. Springer, New York, NY pp. 165-188

Defler TR, Pintor D (1985) Censusing primates by transect in a forest of known primate density. International Journal of Primatology 6:243-259

DeGabriel JL, Moore BD, Felton AM, Ganzhorn JU, Stolter C, Wallis IR, Johnson CN, Foley WJ (2013) Translating nutritional ecology from the laboratory to the field: milestones in linking plant chemistry to population regulation in mammalian browsers. Oikos 000:1-11

Dehgan A (2003) The Behavior of Extinction: Predicting the Incidence and Local Extinction of Lemurs in Fragmented Habitats of Southeastern Madagascar. In. University of Chicago, Chicago, IL, pp 248

Dewar R, Radimilahy C, Wright H, Jacobs Z, Kelly G, Berna F (2013) Stone tools and foraging in northern Madagascar challenge Holocene extinction models. Proceedings of the National Academy of Sciences of the United States of America 110:12583-12588

Dewar R, Richard A (2007) Evolution in the hypervariable environment of Madagascar. Proceedings of the National Academy of Sciences of the United States of America 104:13723-13727

Dewar R, Richard A (2012) Madagascar: A History of Arrivals, What Happened, and Will Happen Next*. Annual Review of Anthropology 41:495-517

Dochtermann NA, Jenkins SH (2010) Developing multiple hypotheses in behavioral ecology. Behavioral Ecology and Sociobiology 65:37-45

Donati G, Kesch K, Ndremifidy K, Schmidt S, Ramanamanjato J-B, Borgognini-Tarli S, Ganzhorn J (2011) Better few than hungry: flexible feeding ecology of collared lemurs *Eulemur collaris* in littoral forest fragments. PloS one 6:e19807

Dransfield S (2003) Poaceae, Bambuseae, Bamboos. In: Goodman SM, Benstead JP (eds) The Natural History of Madagascar. The University of Chicago Press, Chicago, IL, pp 467-471

Du Puy DJ, Moat J (1996) A refined classification of the primary vegetation of Madagascar based on the underlying geology: using GIS to map its distribution and to assess its conservation status. In: Lourenço WR (ed) Proceedings of the International Symposium on the Biogeography de Madagascar. Editions de l'ORSTROM, Paris, Paris, France, pp 205-218 + 3 maps

Du Puy DJ, Moat J (2003) Using Geological Substrate to Identify and Map Primary Vegetation Types in Madagascar and the Implications for Planning Biodiversity Conservation. In: Goodman SM, Benstead JP (eds) The Natural History of Madagascar. University of Chicago Press, Chicago, IL, pp 51-66

Dunning JB, Danielson BJ, Pulliam HR (1992) Ecological Processes That Affect Populations in Complex Landscapes. Oikos 65:169-175

Elkie PC, Rempel RS, Carr A (1999) Patch analyst user's manual: a tool for quantifying landscape structure. In. Ontario Ministry of Natural Resources, Boreal Science, Northwest Science & Technology, Ontario, Canada

Emmons L (1984) Geographic variation in densities and diversities of non-flying mammals in Amazonia. Biotropica 16:210-222

Erkert HG, Kappeler PM (2004) Arrived in the light: diel and seasonal activity patterns in wild Verreaux's sifakas (*Propithecus v. verreauxi*; Primates: Indriidae). Behavioral Ecology and Sociobiology 57:174-186

Estrada A, Coates-Estrada R (1996) Tropical rain forest fragmentation and wild populations of primates at Los Tuxtlas, Mexico. International Journal of Primatology 17:759-783

Estrada A, Mendoza A, Castellanos L, Pacheco R, Van Belle S, Garc√≠a Y, Mu√±oz D (2002) Population of the black howler monkey (*Alouatta pigra*) in a fragmented landscape in Palenque, Chiapas, Mexico. American Journal of Primatology 58:45-55

Ewers R, Didham R (2006) Confounding factors in the detection of species responses to habitat fragmentation. Biological Reviews of the Cambridge Philosophical Society 81:117-142

Fahrig L (2002) Effects of Habitat Fragmentation on the Extinction Threshold: A Synthesis. Ecological Applications 12:346-353

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

Fashing P, Cords M (2000) Diurnal primate densities and biomass in the Kakamega Forest: an evaluation of census methods and a comparison with other forests. American Journal of Primatology 50:139-152

Fashing PJ, Dierenfeld ES, Mowry CB (2007) Influence of Plant and Soil Chemistry on Food Selection, Ranging Patterns, and Biomass of *Colobus guereza* in Kakamega Forest, Kenya. International Journal of Primatology 28:673-703

Felton AM, Felton A, Lindenmayer DB, Foley WJ (2009) Nutritional goals of wild primates. Functional Ecology 23:70-78

Fleagle J, Janson C, Reed K (1999) Primate communities. Cambridge University Press, Cambridge, UK.

Fleagle JG, Janson D, Reed, KE (1999) Concluding remarks. In: Fleagle JG, Janson C, Reed KE (eds) Primate Communities. Cambridge University Press, Cambridge, UK, pp 310-314

Fleagle JG, Reed KE (1999) Phylogenetic and temporal perspectives on primate ecology. In: Fleagle JG, Janson C, Reed KE (eds) Primate Communities. Cambridge University Press, Cambridge, UK, pp 92-115

Forman RTT, Godron M (1981) Patches and structural components for a landscape ecology. BioScience 10:733-740

Fortin M-J, Dale MRT (2005) Spatial Analysis: A Guide for Ecologists. Cambridge University Press, Cambridge, UK

Fowler SV, Chapman P, Checkley D, Hurd S, McHale M, Ramangason GS, Randriamasy JE, Stewart P, Walters R, Wilson JM (1989) Survey and management proposals for a tropical deciduous forest reserve at Ankarana in Northern Madagascar. Biological Conservation 47:297-313

Fox BJ (1987) Species assembly and the evolution of community structure. Evolutionary Ecology 1:201-213

Freed BZ (2006) Polyspecific Associations of Crowned Lemurs and Sanford's Lemurs in Madagascar. In: Gould L, Sauther M (eds) Lemurs. Springer Science, New York, NY, pp 111-131

Freed BZ (1996) Co-occurrence among crowned lemurs (Lemur coronatus) and Sanford's lemurs (Lemur fulvus sanfordi) of Madagascar. In: Department of Anthropology. Washington University, pp 450

Freedman DA (1983) A note on screening regression equations. American Statastician 37:152-155

Ganzhorn JU, Goodman SM, Dehgan A (2003) Effects of Forest Fragmentation on Small Mammals and Lemurs. In: Goodman S, Benstead J (eds) The Natural History of Madagascar. University of Chicago Press, Chicago, pp 1228-1234

Ganzhorn JU (1992) Leaf chemistry and the biomass of folivorous primates in tropical forests. Oecologia 91:540-547

Ganzhorn JU (1993) Flexibility and constraints of Lepilemur ecology. In: Kappeler PM, Ganzhorn JU (eds) Lemur social systems and their ecological basis. Springer, Göttingen, pp 153-166

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

Ganzhorn JU (1997) Test of Fox's assembly rule for functional groups in lemur communities in Madagascar. Journal of Zoology 241:533-542

Ganzhorn JU (1998) Nested Patterns of Species Composition and Their Implications for Lemur Biogeography in Madagascar. Folia Primatologica 69:332-341

Ganzhorn JU (1999) Body mass, competition and the structure of communities. In: Fleagle JG, Janson CH, Reed KE (eds) Primate Communities. Cambridge University Press, Cambridge, UK, pp 141-157

Ganzhorn JU (1999) Body mass, competition and the structure of primate communities. In: Fleagle JG, Janson CH, Reed KE (eds) Primate communities. Cambridge University Press, Cambridge, UK, pp 141-157

Ganzhorn JU (2000a) Vertebrate species in fragmented littoral forests of Madagascar. In: Lourenço W, Goodman S (eds) Diversité et Endémisme à Madagascar. Mémoires de la Societé de Biogéographie, Paris, pp 155-164

Ganzhorn JU, Goodman SM, Ramanamanjato J-B, Ralison J, Rakotondravony D, Rakotosamimanana B (2000b) Effects of fragmentation and assessing minimum viable populations of lemurs in Madagascar. In: Rheinwald G (ed) Isolated Vertebrate Communities in the Tropics. 4th Int. Symp., Bonn, Germany, pp 265-272

Ganzhorn JU (2002) Distribution of a folivorous lemur in relation to seasonally varying food resources: integrating quantitative and qualitative aspects of food characteristics. Oecologia 131:427-435

Ganzhorn JU (2003) Effects of introduced *Rattus rattus* on endemic small mammals in dry deciduous forest fragments of western Madagascar. Animal Conservation 6:147-157

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

Ganzhorn JU, Malcomber S, Andrianantoanina O, Goodman SM (1997) Habitat Characteristics and Lemur Species Richness in Madagascar. Biotropica 29:331-343
Ganzhorn JU, Wright PC, Ratsimbazafy J (1999) Primate communities: Madagascar. In: Fleagle J, Janson C, Reed K (eds) Primate Communities. Cambridge University Press, Cambridge, UK, pp 75-89

García G, Goodman SM (2003) Hunting of protected animals in the Parc National d'Ankarafantsika, north-western Madagascar. Oryx 37:115-118

Gaston KJ, Blackburn TM, Greenwood JJD, Gregory RD, Quinn RM, Lawton JH (2000) Abundance-occupancy relationships. Journal of Applied Ecology 37:39-59

Gause G (1934) The struggle for existence. Williams and Wilkins, Baltimore

Gautier L, Goodman SM (2003) Introduction to the Flora of Madagascar. In: Goodman SM, Benstead JP (eds) The Natural History of Madagascar. The University of Chicago Press, Chicago, IL, pp 229-249

Gautier-Hion A, Brugiére D (2005) Significance of Riparian Forests for the Conservation of Central African Primates. International Journal of Primatology 26:515-523

Gautier-Hion A, Michaloud G (1989) Are figs always keystone resources for tropical frugiviorous vertebrates? A test in Gabon. Ecology 70:1826-1833

Gelman A (2008) Scaling regression inputs by dividing by two standard deviations. Statistics in medicine 27:2865-2873

Gilbert KA (2003) Primates and fragmentation of the Amazon forest. In: Marsh LK (ed) Primates in Fragments: Ecology and conservation. Springer, New York, NY, pp 145-157

Gillespie TR, Chapman CA (2006) Prediction of parasite infection dynamics in primate metapopulations based on attributes of forest fragmentation. Conservation Biology 20:441-448

Glander KE, Tapia RJ, Fachin TA (1984) The impact of cropping on wild populations of *Saguinus mystax* and *Saguinus fuscicollis* in Peru. American Journal of Primatology 7:89-97

Godfrey LR, Irwin MT (2007) The evolution of extinction risk: past and present anthropogenic impacts on the primate communities of Madagascar. Folia Primatologica 78:405-419

Godfrey LR, Samonds KE, Jungers WL, Sutherland MR, Irwin MT (2004) Ontogenetic correlates of diet in Malagasy lemurs. American Journal of Physical Anthropology 123:250-276

Gogarten JF, Guzman M, Chapman CA, Jacob AL, Omeja PA, Rothman JM (2012) What is the predictive power of the colobine protein-to-fiber model and its conservation value? Tropical Conservation Science 5:381-393

Golden CD (2009) Bushmeat hunting and use in the Makira Forest, north-eastern Madagascar: a conservation and livelihoods issue. Oryx 43:386-392

Goodman SM, Ganzhorn JU (2004a) Elevational Ranges of Lemurs in the Humid Forests of Madagascar. International Journal of Primatology 25:331-350

Goodman SM, Ganzhorn JU (2004b) Biogeography of lemurs in the humid forests of Madagascar: the role of elevational distribution and rivers. Journal of Biogeography 31:47-55

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

Green G, Sussman R (1990) Deforestation history of the eastern rain forests of madagascar from satellite images. Science 248:212-215

Grueber C, Nakagawa S, Laws R, Jamieson I (2011) Multimodel inference in ecology and evolution: challenges and solutions. Journal of Evolutionary Biology 24:699-711

Gustafson EJ, Parker GR (1994) Using an index of habitat patch proximity for landscape design. Landscape and Urban Planning 29:117-130

Hamilton W (1971) Geometry for the selfish herd. Journal of Theoretical Biology 31:295-311

Hanski I (1999) Habitat connectivity, habitat continuity, and metapopulations in dynamic landscapes. Oikos 87:209-219

Hanya G, Yoshihiro S, Zamma K, Kubo R, Takahata Y (2003) New method to census primate groups: estimating group density of Japanese macaques by point census. American Journal of Primatology 60:43-56

Harcourt AH, Doherty DA (2005) Species-area relationships of primates in tropical forest fragments: a global analysis. Journal of Applied Ecology 42:630-637

Harper GJ, Steininger MK, Tucker CJ, Juhn D, Hawkins F (2007) Fifty years of deforestation and forest fragmentation in Madagascar. Environmental Conservation 34:325-333

Hassel-Finnegan HM, Borries C, Larney E, Umponjan M, Koenig A (2008) How Reliable are Density Estimates for Diurnal Primates? International Journal of Primatology 29:1175-1187

Hauck W, Donner A (1977) Wald's test as applied to hypotheses in logit analysis. Journal of the American Statistical Association 72:851-853

Haugaasen T, Peres C (2009) Interspecific primate associations in Amazonian flooded and unflooded forests. Primates 50:239-251

Hawkins AFA, Chapman P, Ganzhorn JU, Bloxam QMC, Barlow SC, Tonge SJ (1990) Vertebrate Conservation in Ankarana special reserve, Northern Madagascar. Biological Conservation 54:83-110

He F, Gaston KJ (2000) Occupancy-abundance relationships and sampling scales. Ecography 23:503-511

Hemingway CA, Bynum N (2005) The influence of seasonality on primate diet and ranging. In: Brockman DK, van Schaik CP (eds) Seasonality in primates: Studies of living and extinct human and non-human primates. Cambridge University Press, Cambridge, UK, pp 57-105

Herrera JP, Wright PC, Lauterbur E, Ratovonjanahary L, Taylor LL (2011) The Effects of Habitat Disturbance on Lemurs at Ranomafana National Park, Madagascar. International Journal of Primatology 32:1091-1108

Heymann EW, Buchanan-Smith HM (2000) The behavioural ecology of mixed-species troops of callitrichine primates. Biological Reviews of the Cambridge Philosophical Society 75:169-190

Hilário R, Rodrigues F, Chiarello A, Mourthé I (2012) Can roads be used as transects for primate population surveys? Folia Primatologica 83:47-55

Holger S (2010) Simple means to improve the interpretability of regression coefficients. Methods in Ecology and Evolution 1:103-113

Humbert H (1927) La destruction d'une flore insulaire par le feu: principaux aspects de la vegetation à Madagascar, documents photographiques et notices. Memoires de l'Academic Malagache Fascicule V

Humbert H, Cours-Darne G (1965) Carte Internationale de Tapis Vegetale: Madagascar, 1:1,000,000. Travaux de la Section Scientifique et Technique de l'Institut Français de Pondichéry (hors serie), Toulouse, France

Irwin MT, Junge RE, Raharison J-L, Samonds KE (2010) Variation in physiological health of diademed sifakas across intact and fragmented forest at Tsinjoarivo, Eastern Madagascar. American Journal of Primatology 72:1013-1025

Irwin MT, Wright PC, Birkinshaw C, Fisher BL, Gardner CJ, Glos J, Goodman SM, Loiselle P, Rabeson P, Raharison J-L (2010) Patterns of species change in anthropogenically disturbed forests of Madagascar. Biological Conservation 143:2351-2362

Irwin MT (2006) Ecological impacts of forest fragmentation on diademed sifakas (*Propithecus diadema*) at Tsinjoarivo, eastern Madagascar: Implications for conservation in fragmented landscapes. In: Department of Anthropology. Stony Brook University, ProQuest, pp 433

Irwin MT (2006) Ecologicallty Enigmatic Lemurs: The Sifakas of the Eastern Forests. In: Gould L, Sauther ML (eds) Lemurs: Ecology and Adaptation. Springer, New York, NY pp 305-326

Irwin MT (2007) Living in forest fragments reduces group cohesion in diademed sifakas (*Propithecus diadema*) in eastern Madagascar by reducing food patch size. American Journal of Primatology 69:434-447

Irwin MT (2007) Feeding Ecology of *Propithecus diadema* in Forest Fragments and Continuous Forest. International Journal of Primatology 29:95-115

Irwin MT (2008) Diademed Sifaka (*Propithecus diadema*) Ranging and Habitat Use in Continuous and Fragmented Forest: Higher Density but Lower Viability in Fragments? Biotropica 40:231-240

Irwin MT, Raharison JL, Wright PC (2009) Spatial and temporal variability in predation on rainforest primates: do forest fragmentation and predation act synergistically? Animal Conservation 12:220-230

Isabirye-Basuta GM, Lwanga J, S. (2008) Primate Populations and Their Interactions with Changing Habitats. International Journal of Primatology 29:35-48

Janson C, Chapman C (1999) Resources and primate community structure. In: Primate communities. Cambridge University Press, Cambridge, UK, pp 237-267

Janzen DH (1975) Ecology of Plants in the Tropics. Edward Arnold, London.

Jernvall J, Wright PC (1998) Diversity components of impending primate extinctions. Proceedings of the National Academy of Sciences of the United States of America 95:11279-11283

Johns AD, Skorupa JP (1987) Responses of rain-forest primates to habitat disturbance: a review. International Journal of Primatology 8:157-191

Johns AD (1985) Differential detectability of primates between primary and selectively logged habitats and implications for population surveys. American Journal of Primatology 8:31-36

Johnson SE, Overdorff D (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 (2006) Evolutionary Divergence in the Brown Lemur Species Complex. In: Gould L, Sauther ML (eds) Lemurs Ecology and Adaptation. Springer, New York, NY., pp 450

Johnson SE, Ingraldi C, Ralainasolo FB, Andriamaharoa HE, Ludovic R, Birkinshaw CR, Wright PC, Ratsimbazafy JH (2011) Gray-headed Lemur (*Eulemur cinereiceps*) Abundance and Forest Structure Dynamics at Manombo, Madagascar. Biotropica 43:371-379

Jungers WL, Godfrey LR, Simons EL, Chatrath PS (1995) Subfossil Indri indri from the Ankarana Massif of northern Madagascar. American Journal of Physical Anthropology 97:357-366

Jury MR (2003) The Climate of Madagascar. In: Goodman SM, Benstead JP (eds) The Natural History of Madagascar. University of Chicago Press, Chicago, IL, pp 75-85

Kamilar JM (2009) Environmental and geographic correlates of the taxonomic structure of primate communities. American Journal of Physical Anthropology 139:382-393

Kamilar JM, Muldoon KM (2010) The climatic niche diversity of malagasy primates: a phylogenetic perspective. PloS ONE 5:e11073

Kamilar JM, Guidi LM (2010) The phylogenetic structure of primate communities: variation within and across continents. Journal of Biogeography 37:801-813

Kappeler PM, Erkert HG (2003) On the move around the clock: correlates and determinants of cathemeral activity in wild redfronted lemurs (*Eulemur fulvus rufus*). Behavioral Ecology and Sociobiology 54:359-369

Karpanty S, Wright PC (2007) Predation on lemurs in the rainforest of Madagascar by multiple predator species: observations and experiments. In: Gursky SL (ed) Primate anti-predator strategies. Springer, New York, NY pp 77-99

Kay RF, Madden RH, Van Schaik C, Higdon D (1997) Primate species richness is determined by plant productivity: implications for conservation. Proceedings of the National Academy of Sciences of the United States of America 94:13023-13027

Keane A, Hobinjatovo T, Razafimanahaka HJ, Jenkins RKB, Jones JPG, Res A, Michael S (2012) The potential of occupancy modelling as a tool for monitoring wild primate populations. Animal Conservation 15:457-465

Kirika JM, Bleher Böhning-Gaese K, Chira R, Farwig N (2008) Fragmentation and local disturbance of forests reduce frugivore diversity and fruit removal in *Ficus thonningii* trees. Basic and Applied Ecology 9:663-672

Koenig A, Borries C, Chalise MK, Winkler P (1997) Ecology, nutrition, and timing of reproductive events in an Asian primate, the Hanuman langur (*Presbytis entellus*). Journal of Zoology 243:215-235

Kull CA (2000) Deforestation, erosion, and fire: degradation myths in the environmental history of Madagascar. Environment and History Vol. 6:423-450

Kull CA, Laris P (2009) Fire ecology and fire politics in Mali and Madagascar. In: Tropical Fire Ecology: Climate Change, Land Use and Ecosystem Dynamics. Praxis Publishing, Chichester, UK, pp 171-226

Kullback S, Leibler RA (1951) On information and sufficiency. The Annals of Mathematical Statistics 22:79-86

Laurance WF, Delamônica P, Laurance SG, Vasconcelos HL, Lovejoy TE (2000) Rainforest fragmentation kills big trees. Nature Vol. 404:836

Laurance WF, Ferreira L, Rankin-de J (1998) Rain forest fragmentation and the dynamics of Amazonian tree communities. Ecology 79:2032-2040

Laurance WF, Lovejoy TE, Vasconcelos HL, Bruna EM, Didham RK, Stouffer PC, Gascon C, Bierregaard RO, Laurance SG, Sampaio E (2002) Ecosystem Decay of Amazonian Forest Fragments: a 22-Year Investigation. Conservation Biology 16:605-618

Laurance W, Nascimento H, Laurance S, Andrade A, Fearnside P, Ribeiro J, Capretz R (2006) Rain forest fragmentation and the proliferation of successional trees. Ecology 87:469-482

Laurance W, Useche D, Rendeiro J, Kalka M, Bradshaw C, Sloan S, Laurance S, Campbell M, Abernethy K, Alvarez P, Arroyo-Rodriguez V, Ashton P, Benítez-Malvido J, Blom A, Bobo K, Cannon C, Cao M, Carroll R, Chapman C, Coates R, Cords M, Danielsen F, De Dijn B, Dinerstein E, Donnelly M, Edwards D, Edwards F, Farwig N, Fashing P, Forget P-M, Foster M, Gale G, Harris D, Harrison R, Hart J, Karpanty S, Kress W, Krishnaswamy J, Logsdon W, Lovett J, Magnusson W, Maisels F, Marshall A, McClearn D, Mudappa D, Nielsen M, Pearson R, Pitman N, van der Ploeg J, Plumptre A, Poulsen J, Quesada M, Rainey H, Robinson D, Roetgers C, Rovero F, Scatena F, Schulze C, Sheil D, Struhsaker T, Terborgh J, Thomas D, Timm R, Urbina-Cardona J, Vasudevan K, Wright S, Arias-G J, Arroyo L, Ashton M, Auzel P, Babaasa D, Babweteera F, Baker P, Banki O, Bass M, Bila-Isia I, Blake S, Brockelman W, Brokaw N, Brühl C, Bunyavejchewin S, Chao J-T, Chave J, Chellam R, Clark C, Clavijo J, Congdon R, Corlett R, Dattaraja H, Dave C, Davies G, Beisiegel B, da Silva R, Di Fiore A, Diesmos A, Dirzo R, Doran-Sheehy D, Eaton M, Emmons L, Estrada A (2012) Averting biodiversity collapse in tropical forest protected areas. Nature 489:290-294

Laurance WF (2008) Theory meets reality: How habitat fragmentation research has transcended island biogeographic theory. Biological Conservation 141:1731-1744

Laurance WF, Lovejoy TE, Vasconcelos HL, Bruna EM, Didham RK, Stouffer PC, Gascon C, Bierregaard RO, Laurance SG, Sampaio E (2002) Ecosystem Decay of Amazonian Forest Fragments: a 22-Year Investigation. Conservation Biology 16:605-613

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

Lawes MJ, Mealin P, Piper S (2000) Patch Occupancy and Potential Metapopulation Dynamics of Three Forest Mammals in Fragmented Afromontane Forest in South Africa. Conservation Biology 14:1088-1098

Lee PC (1987) Nutrition, fertility and maternal investment in primates. Journal of Zoology 213:409-422

Lees A, Peres CA (2008) Conservation value of remnant riparian forest corridors of varying quality for amazonian birds and mammals. Conservation Biology 22:439-449

Lehman SM (2006) Effects of Transect Selection and Seasonality on Lemur Density Estimates in Southeastern Madagascar. International Journal of Primatology 27:1041-1057

Lehman SM (2007) Spatial variations in *Eulemur fulvus rufus* and *Lepilemur mustelinus* densities in Madagascar. Folia Primatologica 78:46-55

Lehman SM, Mayor MM (2004) Dietary patterns in Perrier's sifakas (*Propithecus diadema perrieri*): a preliminary study. American Journal of Primatology 62:115-122

Lehman SM, Rajaonson A, Day S (2006) 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 (2006) Lemur responses to edge effects in the Vohibola III classified forest, Madagascar. American Journal of Primatology 68:293-299

Lehman SM (2000) Primate community structure in Guyana: a biogeographic analysis. International Journal of Primatology 21:333-351

Lehman SM (2007) Ecological and Phylogenetic Correlates to Body Size in the Indriidae. International Journal of Primatology 28:183-210

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

Lehman SM, Ratsimbazafy J, Rajaonson A, Day S (2005) Decline of *Propithecus diadema edwardsi* and *Varecia variegata variegata* (Primates: Lemuridae) in south-east Madagascar. Oryx 40:108-111

Letsara R (2007) Inventaire rapide de la flore et de la vegetation du corridor forestier d’Andrafiamena. In: Conservation International Rapid Assessment Program Report, Alexandria, VA

Lowry PP, Schatz GE, Phillipson PP (1997) The classification of natural and anthropogenic vegetation in Madagascar. In: Goodman S, Patterson BD (eds) Natural Change and Human Impact in Madagascar. Smithsonian Institution Press, Washington, DC, pp 93-123

Lynne RB, Todd WA, Oluseun SO, David LG (2011) Considerations for using occupancy surveys to monitor forest primates: a case study with Sclater’s monkey (Cercopithecus sclateri). Population Ecology 53:549-561

MacArthur RH, Diamond JM, Karr JR (1972) Density compensation in island faunas. Ecology 53:330-342

MacArthur RH, Wilson EO (1967) The Theory of Island Biogeography. Princeton University Press pp.203

MacKenzie D, Nichols J (2004) Occupancy as a surrogate for abundance estimation. Animal Biodiversity and Conservation 27:461-467

MacKenzie DI, Nichols JD, Lachman GB, Droege S, Royle JA, Langtimm CA (2002) Estimating Site Occupancy Rates When Detection Probabilities Are Less Than One. Ecology 83:2248-2255

MacKenzie DI, Nichols JD, Royle JA, Pollock KH, Bailey LI, Hines JE (2006) Occupancy Estimation and Modeling: Inferring Patterns and Dynamics of Species Occurrence. Elsevier Academic Press, Burlington, MA.

MacKenzie DI, Nichols JD, Sutton N, Kawanishi K, Bailey L (2005) Improving inferences in population studies of rare species that are detected imperfectly. Ecology 86:1101-1113

Mackenzie DI, Royle JA (2005) Designing occupancy studies: general advice and allocating survey effort. Journal of Applied Ecology 42:1105-1114

Markolf M, Kappeler P (2013) Phylogeographic analysis of the true lemurs (genus *Eulemur*) underlines the role of river catchments for the evolution of micro-endemism in Madagascar. Frontiers in Zoology 10:70

Marques FFC, Buckland S (2004) Covariate models for the detection function. In: Buckland ST, Anderson DR, Burnham KP, Laake JL, Borchers DL, Thomas L (eds) Advanced Distance Sampling. Oxford University Press, Oxford, UK, pp 31-47

Marques TA, Thomas L, Fancy SG, Buckland ST (2007) Improving estimates of bird density using multiple-covariate distance sampling. The Auk 124:1229-1243

Marques TA, Buckland ST, Bispo R, Howland B (2012) Accounting for animal density gradients using independent information in distance sampling surveys. Statistical Methods & Applications 22:67-80

Marsh LK (2003) Primates in Fragments: Ecology in Conservation. Kluwer Academic/Plenum Publishers New York

Marsh LK, Chapman CA (2013) Primates in Fragments: Complexity and Resistance. Springer, New York

Marshall AJ, Boyko CM, Feilen KL, Boyko RH, Leighton M (2009) Defining fallback foods and assessing their importance in primate ecology and evolution. American Journal of Physical Anthropology 140:603-614

Marshall AJ, Lovett JC, White PC (2008) Selection of line-transect methods for estimating the density of group-living animals: lessons from the primates. American Journal of Primatology 70:452-462

Marshall AJ, Wrangham RW (2007) Evolutionary Consequences of Fallback Foods. International Journal of Primatology 28:1219-1235

Mayor MM, Lehman SM (1999) Conservation of Perrier's sifakas. Lemur News 4:21-23

McGarigal K, Marks BJ (1995) Spatial pattern analysis program for quantifying landscape structure. In: Gen. Tech. Rep. PNW-GTR-351. US Pacific Northwest Research Station, Portland, OR

McGill BJ, Enquist BJ, Weiher E, Westoby M (2006) Rebuilding community ecology from functional traits. Trends in Ecology & Evolution 21:178-185

Medley K (1993) Primate Conservation along the Tana River, Kenya: An Examination of the Forest Habitat. Conservation Biology 7:109-121

Meyers D, Ratsirarson J (1989) Distribution and conservation of two endangered sifakas in northern Madagascar. Primate Conservation 10:81-86

Meyers DM (1993) The effects of resource seasonality on behavior and reproduction in the golden-crowned sifaka (*Propithecus tattersalli*, Simons, 1988) in three Malagasy forests. In: Department of Biological Anthropology and Anatomy. Duke University, Durham, NC, pp 230

Meyers DM, Wright PC (1993) Resource tracking: food availability and Propithecus seasonal reproduction. In: Lemur social systems and their ecological basis. Plenum Press, New York, NY pp. 179-192

Milner-Gulland E, Rowcliffe J (2007) Conservation and sustainable use: a handbook of techniques. Oxford University Press, Oxford, UK

Milton K (1979) Factors influencing leaf choice by howler monkeys: a test of some hypotheses of food selection by generalist herbivores. American Naturalist 114:362-378

Milton K (1998) Physiological ecology of howlers (*Alouatta*): energetic and digestive considerations and comparison with the Colobinae. International Journal of Primatology 19:513-548

Mitani JC, Struhsaker TT, Lwanga JS (2000) Primate community dynamics in old growth forest over 23.5 years at Ngogo, Kibale National Park, Uganda: implications for conservation and census methods. International Journal of Primatology 21:269-286

Mittermeier RA, Louis EE, Richardson M, Schwitzer C, Langrand O, Rylands AB, Hawkins F, Rajaobelina S, Ratsimbazafy J, Rasoloarison R, Roos C, Kappeler PM, MacKinnon J (2010) Lemurs of Madagascar. Conservation International, Arlington, VA.
Mittermeier RA, Louis Jr. EE, Richardson M, Schwitzer C, Langrand O, Rylands AB, Hawkins F, Rajaobelina S, Ratsimbazafy J, Rasoloarison R, Roos C, Kappeler PM, MacKinnon J (2010) Lemurs of Madagascar. Panamericana Formas e Impresos S.A., Bogotá, Columbia

Muldoon KM (2010) Paleoenvironment of Ankilitelo Cave (late Holocene, southwestern Madagascar): implications for the extinction of giant lemurs. Journal of Human Evolution 58:338-352

Muldoon KM, Goodman SM (2010) Ecological biogeography of Malagasy non-volant mammals: community structure is correlated with habitat. Journal of Biogeography 37:1144-1159

Müller P, Velo A, Raheliarisoa E-O, Zaramody A, Curtis DJ (2000) Surveys of sympatric lemurs at Anjamena, north-west Madagascar. African Journal of Ecology 38:248-257

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

Mutschler T (2003) Alaotran gentle lemur: Some aspects of its behavioral ecology. Evolutionary Anthropology 11:101-104

Mutschler T, Tan CL (2003) *Hapalemur*, Bamboo or Gentle Lemurs. In: Goodman SM, Benstead JP (eds) The Natural History of Madagascar. The University of Chicago Press, Chicago, IL, pp 1324-1329

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

Nijman V (2001) Effects of behavioural changes due to habitat disturbance on density estimation of rain forest vertebrates, as illustrated by gibbons (primates: Hylobatidae). In: Hillegers PJM, de Iongh HH (eds) The Balance between Biodiversity Conservation and Sustainable Use of Tropical Rain Forests: Workshop Proceedings Tropenbos, Wageningen, Netherlands, pp 217-225

Nijman V, Nekaris KA (2012) Loud calls, startle behaviour, social organisation and predator avoidance in arboreal langurs (Cercopithecidae: *Presbytis*). Folia Primatologica 83:274-287

Noë R, Bshary R (1997) The formation of red colobus-diana monkey associations under predation pressure from chimpanzees. R. Soc. Lond. B 264:253-259

Norconk MA (1990) Mechanisms promoting stability in mixed *Saguinus mystax* and *S. fuscicollis* troops. American Journal of Primatology 21:159-170

Norconk MA, Grafton BW, Marsh L (2003) Changes in forest composition and potential feeding tree availability on a small land-bridge island in Lago Guri, Venezuela. In Marsh LK (ed) Primates in Fragments: Ecology and conservation, pp.211-227

NRC (1981) Techniques for the study of primate population ecology. National Academy Press, Washington, DC

Oates J (1978) Water-plant and soil consumption by guereza monkeys (*Colobus guereza*): a relationship with minerals and toxins in the diet? Biotropica 10:241-253

Oates J, Whitesides G, Davies A, Waterman P (1990) Determinants of variation in tropical forest primate biomass: new evidence from West Africa. Ecology 71:328-343

Ogutu JO, Bhola N, Piepho HP, Reid R (2006) Efficiency of strip- and line-transect surveys of African savanna mammals. Journal of Zoology 269:149-160

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

Otto MC, Pollock KH (1990) Size bias in line transect sampling: a field test. Biometrics 46:239-245

Overdorff D, Johnson SE (2003) *Eulemur*, true lemurs. In: Goodman SM, Benstead JP (eds) The Natural History of Madagascar. Chicago University Press, Chicago, IL, pp 1320-1324

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

Palacios E, Peres C (2005) Primate population densities in three nutrient-poor amazonian terra firme forests of south-eastern Colombia. Folia Primatologica 76:135-145

Pareliussen I, Olsson EGA, Armbruster WS (2006) Factors Limiting the Survival of Native Tree Seedlings Used in Conservation Efforts at the Edges of Forest Fragments in Upland Madagascar. Restoration Ecology 14:196-203

Pavelka MSM, Brusselers OT, Nowak D, Behie AM (2003) Population reduction and social disorganization in *Alouatta pigra* following a hurricane. International Journal of Primatology 24:1037-1055

Peres CA (1997) Effects of habitat quality and hunting pressure on arboreal folivore densities in neotropical forests: a case study of howler monkeys (Alouatta spp.). Folia Primatologica 68:199-222

Peres CA (1999) Effects of subsistence hunting and forest types on the structure of Amazonian primate communities. In: Fleagle JG, Janson CH, Reed KE (eds) Primate Communities. Cambridge University Press, Cambridge, UK, pp 268-284

Peres C (1999) General guidelines for standardizing line-transect surveys of tropical forest primates. Neotropical Primates 7:11-16

Peres CA (2001) Synergistic Effects of Subsistence Hunting and Habitat Fragmentation on Amazonian Forest Vertebrates. Conservation Biology 15:1490-1505

Peres CA, Barlow J, Haugaasen T (2003) Vertebrate responses to surface wildfires in a central Amazonian forest. Oryx 37:97-109

Peres CA (1997) Primate community structure at twenty western Amazonian flooded and unflooded forests. Journal of Tropical Ecology 13:381-405

Peres CA (2001) Synergistic Effects of Subsistence Hunting and Habitat Fragmentation on Amazonian Forest Vertebrates. Conservation Biology 15:1490-1505

Peres CA, Dolman PM (2000) Density compensation in neotropical primate communities: evidence from 56 hunted and nonhunted Amazonian forests of varying productivity. Oecologia 122:175-189

Peres CA, Lake IR (2003) Extent of Nontimber Resource Extraction in Tropical Forests: Accessibility to Game Vertebrates by Hunters in the Amazon Basin. Conservation Biology 17:521-535

Perez VR, Godfrey LR, Nowak-Kemp M, Burney DA, Ratsimbazafy J, Vasey N (2005) Evidence of early butchery of giant lemurs in Madagascar. Journal of Human Evolution 49:722-742

Perrier de la Báthie H (1921) La Végétation Malagache. In: Annals du Musée Colonial de Marseille, pp 1-266

Petrovan S, Ward A, Wheeler P (2011) Detectability counts when assessing populations for biodiversity targets. PloS one 6:e240206

Plumptre A, Cox D (2006) Counting primates for conservation: primate surveys in Uganda. Primates 47:65-73

Plumptre AJ (2000) Monitoring mammal populations with line transect techniques in African forests. Journal of Applied Ecology 37:356-368

Porter L (2001) Benefits of polyspecific associations for the Goeldi's monkey (*Callimico goeldii*). American Journal of Primatology 54:143-158

Porter L, Garber P (2007) Niche expansion of a cryptic primate, *Callimico goeldii*, while in mixed species troops. American Journal of Primatology 69:1340-1353

Potts K, Chapman C, Lwanga J (2009) Floristic heterogeneity between forested sites in Kibale National Park, Uganda: insights into the fine-scale determinants of density in a large-bodied frugivorous primate. The Journal of Animal Ecology 78:1269-1277

Powzyk J, Mowry C (2003) Dietary and Feeding Differences Between Sympatric *Propithecus diadema diadema* and *Indri indri*. International Journal of Primatology 24:1143-1162

Pozo-Montuy G, Serio-Silva J (2007) Movement and resource use by a group of *Alouatta pigra* in a forest fragment in Balancán, México. Primates 48:102-107

Prugh L, Hodges K, Sinclair A, Brashares J (2008) Effect of habitat area and isolation on fragmented animal populations. Proceedings of the National Academy of Sciences of the United States of America 105:20770-20775

Purvis A, Cardillo M, Grenyer R, Collen B (2005) Correlates of extinction risk: phylogeny, biology, threat and scale. In: Purvis A, Gittleman JL, T. B (eds) Phylogeny and Conservation pp 295-316

Purvis A, Gittleman J, Cowlishaw G, Mace G (2000) Predicting extinction risk in declining species. Proc. R. Soc. Lond. B 267:1947-1952

Quéméré E, Amelot X, Pierson J, Crouau-Roy B, Chikhi L (2012) Genetic data suggest a natural prehuman origin of open habitats in northern Madagascar and question the deforestation narrative in this region. Proceedings of the National Academy of Sciences of the United States of America 109:13028-13033

Quéméré E, Champeau J, Besolo A, Rasolondraibe E, Rabarivola C, Crouau-Roy B, Chikhi L (2010) Spatial variation in density and total size estimates in fragmented primate populations: the golden-crowned sifaka (Propithecus tattersalli). American Journal of Primatology 72:72-80

Quéméré E, Crouau-Roy B, Rabarivola C, Louis E, Chikhi L (2010) Landscape genetics of an endangered lemur (*Propithecus tattersalli*) within its entire fragmented range. Molecular Ecology 19:1606-1621

R Core Development Team (2013) R: Language and Environment for Statistical Computing. In. R Foundation for Statistical Computing, Vienna, Austria

Raherilalao MJ (2007) Les oiseax de la forêt séche, semi-caducifoliée d’Ampatsona, Andrafiamena. In: Conservation International Rapid Assessment Program Report, Alexandria, VA

Rakotoarisoa JE, Raheriarisena M, Goodman S (2013) Late Quaternary climatic vegetational shifts in an ecological transition zone of northern Madagascar: insights from genetic analyses of two endemic rodent species. Journal of Evolutionary Biology 26:1019-1034

Ranaivoarisoa JF, Ramanamahefa R, Louis Jr. EE, Brenneman RA (2006) Range extension of Perrier's Sifaka, *Propithecus perrieri*, in the Andrafiamena Classified Forest. Lemur News 11:21

Ranaivoarisoa JF, Zaonarivelo J, Lei R, Johnson SE, Wyman TM, Mittermeier RA, Louis Jr. EE (2013) Rapid Survey and Assessment of the Northern Sportive Lemur, *Lepilemur septentrionalis*, in Northern Madagascar. Primate Conservation Early Online Edition

Ransom JI (2012) Detection probability in aerial surveys of feral horses. The Journal of Wildlife Management 76:299-307

Ratelolahy FJ (2007) Rapport d’inventaire biologique rapide dans la forêt d’Andrafiamena. In: Conservation International Rapid Assessment Program Report, Alexandria, VA

Ratsimbazafy J (2002) How do black and white ruffed lemurs still survive in a highly disturbed habitat. Lemur News 7:7-10

Ratsirarson J, Ranaivonasy J (2002) Ecologie des Lémuriens dans la forêt littorale de Tampolo. Lemur News 7:26-30

Razafimaharatra B (2007) Reptiles et amphibiens de la forêt d’Andrafiamena. In: Conservation International Rapid Assessment Program Report, Alexandria, VA

Reed K, Fleagle J (1995) Geographic and climatic control of primate diversity. Proceedings of the National Academy of Sciences of the United States of America 92:7874-7876

Reed KE (1999) Population density of primates in communities: differences in community structure. In: Fleagle JG, Janson C, Reed KE (eds) Primate Communities. Cambridge University Press, Cambridge, UK, pp 116-140

Rhodes JR, McAlpine CA, Zuur AF, Smith GM, Ieno EN (2009) GLMM Applied on the Spatial Distribution of Koalas in a Fragmented Landscape. In: Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (eds) Mixed Effects Models and Extensions with R. Springer, New York, NY, pp.469-492

Richard AF, Dewar RE (1991) Lemur ecology. Annual Review of Ecology and Systematics 22:145-175

Richard AF, Ratsirarson J (2013) Partnership in practice: making conservation work at Bezá Mahafaly, southwest Madagascar. Madagascar Conservation & Development 8:12-20

Rode KD (2003) Mineral resource availability and consumption by colobus in Kibale National Park, Uganda. International Journal of Primatology 24:541-573

Root RB (1973) Organization of a plant-arthropod association in simple and diverse habitats: the fauna of collards (*Brassica oleracea*). Ecological Monographs 43:95-124

Ross C, Reeve N (2003) Survey and census methods: population distribution and density. In: Setchell JM, Curtis DJ (eds) Field and Laboratory Methods in Primatology. Cambridge University Press, Cambridge, UK, pp 90-109

Rothman J, Raubenheimer D, Chapman C (2011) Nutritional geometry: gorillas prioritize non-protein energy while consuming surplus protein. Biology letters 7:847-849

Rothman J, Van Soest P, Pell A (2006) Decaying wood is a sodium source for mountain gorillas. Biology Letters 2:321-324

Rothman JM, Chapman CA, Soest PJ (2011) Methods in Primate Nutritional Ecology: A User’s Guide. International Journal of Primatology 33:542-566

Rovero F, Struhsaker T (2007) Vegetative predictors of primate abundance: utility and limitations of a fine-scale analysis. American Journal of Primatology 69:1242-1256

Rovero F, Struhsaker TT, Marshall AR, Rinne TA, Pedersen UB, Butynski TM, Ehardt CL, Mtui AS (2006) Abundance of Diurnal Primates in Mwanihana Forest, Udzungwa Mountains, Tanzania: A Multi-Observer Comparison of Line-Transect Data. International Journal of Primatology 27:675-697

Rylands A, Keuroghlian A (1988) Primate populations in continuous forest and forest fragments in central Amazonia. Acta Amazonica 18:291-307

Salmona J, Rasolondraibe E, Jan F, Besolo A (2013) Conservation Status and Abundance of the Crowned Sifaka (*Propithecus coronatus*). Primate Conservation Published electronically prior to print

Savage A, Thomas L, Leighty K, Soto L, Medina F (2010) Novel survey method finds dramatic decline of wild cotton-top tamarin population. Nature communications 1:30

Schad J, Sommer S, Ganzhorn JU (2004) MHC Variability of a Small Lemur in the Littoral Forest Fragments of Southeastern Madagascar. Conservation Genetics 5:299-309

Schipper J, Chanson J, Chiozza F, Cox N, Hoffmann M, Katariya V, Lamoreux J, Rodrigues A, Stuart S, Temple H, Baillie J, Boitani L, Lacher T, Mittermeier R, Smith A, Absolon D, Aguiar J, Amori G, Bakkour N, Baldi R, Berridge R, Bielby J, Black P, Blanc J, Brooks T, Burton J, Butynski T, Catullo G, Chapman R, Cokeliss Z, Collen B, Conroy J, Cooke J, da Fonseca G, Derocher A, Dublin H, Duckworth J, Emmons L, Emslie R, Festa-Bianchet M, Foster M, Foster S, Garshelis D, Gates C, Gimenez-Dixon M, Gonzalez S, Gonzalez-Maya J, Good T, Hammerson G, Hammond P, Happold D, Happold M, Hare J, Harris R, Hawkins C, Haywood M, Heaney L, Hedges S, Helgen K, Hilton-Taylor C, Hussain S, Ishii N, Jefferson T, Jenkins R, Johnston C, Keith M, Kingdon J, Knox D, Kovacs K, Langhammer P, Leus K, Lewison R, Lichtenstein G, Lowry L, Macavoy Z, Mace G, Mallon D, Masi M, McKnight M, Medell√≠n R, Medici P, Mills G, Moehlman P, Molur S, Mora A, Nowell K, Oates J, Olech W, Oliver W, Oprea M, Patterson B, Perrin W, Polidoro B, Pollock C, Powel A, Protas Y, Racey P, Ragle J, Ramani P, Rathbun G (2008) The status of the world's land and marine mammals: diversity, threat, and knowledge. Science 322:225-230

Schmidt B (2003) Count data, detection probabilities, and the demography, dynamics, distribution, and decline of amphibians. Comptes rendus biologies 326 Suppl 1:24

Scholz F, Kappeler PM (2004) Effects of Seasonal Water Scarcity on the Ranging Behavior of *Eulemur fulvus rufus*. International Journal of Primatology 25:599-613

Schwarzkopf L, Rylands AB (1989) Primate species richness in relation to habitat structure in Amazonian rainforest fragments. Biological Conservation 48:1-12

Schwitzer C, Mittermeier RA, Davies N, Johnson S, Ratsimbazafy J, Razafindramanana J, Louis Jr. EE, Rajaobelina S (2013) Lemurs of Madagascar: A Strategy for Their Conservation 2013‚Äì2016. SSC Primate Specialist Group, Bristol Conservation and Science Foundation, and Conservation International, Bristol, UK

Setchell JM, Curtis DJ (2011) Field and laboratory methods in primatology: a practical guide. Cambridge University Press

Silanikove N, Perevolotsky A, Provenza FD (2001) Use of tannin-binding chemicals to assay for tannins and their negative postingestive effects in ruminants. Animal Feed Science and Technology 91:69-81

Simberloff D (1988) The contribution of population and community biology to conservation science. Annual Review of Ecology and Systematics 19:473-511
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

Skorupa JP (1987) Do line-transect surveys systematically underestimate primate densities in logged forests? American Journal of Primatology 13:1-9

Smith AP, Horning N, Moore D (1997) Regional Biodiversity Planning and Lemur Conservation with GIS in Western Madagascar. Conservation Biology 11:498-512

Soulé ME (1987) Viable populations for conservation. In Soule ME, Wilcox BA (1980) Conservation biology. An evolutionary-ecological perspective. Sinauer Associates, Inc., The University of California

Srbek-Araujo A, Chiarello A (2008) Domestic dogs in Atlantic forest preserves of south-eastern Brazil: a camera-trapping study on patterns of entrance and site occupancy rates. Brazilian Journal of Biology 68:771-779

Stensland E, Angerbjorn A, Berggren P (2003) Mixed species groups in mammals. Mammal Review 33:205-223

Stephens PA, Zaumyslova OY, Miquelle DG, Myslenkov AI, Hayward GD (2006) Estimating population density from indirect sign: track counts and the Formozov-Malyshev-Pereleshin formula. Animal Conservation 9:339-348

Sterling E (2003) *Daubentonia madagascariensis*, Aye-Aye, Aye-aye. In: Goodman SM, Benstead JP (eds) The Natural History of Madagascar. The University of Chicago Press, Chicago, IL, pp 1348-1351

Stevenson P (2001) The relationship between fruit production and primate abundance in Neotropical communities. Biological Journal of the Linnean Society 72:161-178

Strier K, Boubli J, Possamai C, Mendes S (2006) Population demography of Northern muriquis (*Brachyteles hypoxanthus*) at the Estação Biológica de Caratinga/Reserva particular do Patrimônio Natural-Felìciano Miguel Abdala, Minas Gerais, Brazil. American Journal of Physical Anthropology 130:227-237

Strier K, Ives A (2012) Unexpected demography in the recovery of an endangered primate population. PLoS ONE 7: e44407:1-11

Struhsaker TT (1999) Primate communities in Africa: The consequence of long-term evolution or the artifact of recent hunting? In: Fleagle JG, Janson CH, Reed KE (ed) Primate Communities. Cambridge University Press, Cambridge, UK, pp 289-294

Struhsaker TT (1997) Ecology of an African Rain Forest: Logging in Kibale and the Conflict between Conservation and Exploitation. University Presses of Florida, Gainesville, Florida

Symonds MRE, Moussalli A (2010) A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. Behavioral Ecology and Sociobiology 65:13-21

Tan C (2000) Behavior and ecology of three sympatric bamboo lemur species (Genus: *Hapalemur*) in Ranomafana National Park, Madagascar. . In: Anthropology. The State University of New York at Stony Brook, Stony Brook, NY.

Tan CL (1999) Group composition, home range size, and diet of three sympatric bamboo lemur species (genus *Hapalemur*) in Ranomafana National Park, Madagascar. International Journal of Primatology 20:547-566

Tan CL (2006) Behavior and Ecology of Gentle Lemurs (Genus *Hapalemur*). In: Gould L, Sauther ML (eds) Lemurs: Ecology and Adaptation. Springer, New York, NY pp.369-382

Terborgh J (1983) Five New World primates: a study in comparative ecology. Princeton University Press, Princeton, NJ

Terborgh J (1986) Keystone plant resources in the tropical forest. In: Conservation Biology: The Science of Scarcity and Diversity. Sinauer Associates, Sunderland, Massachusetts, pp 330-344

Terborgh J, Estes JA (2010) Trophic cascades: predators, prey, and the changing dynamics of nature. Island Press, Washington, DC

Terborgh J, Van Schaik CP (1987) Convergence vs. nonconvergence in primate communities. In: Gee P, Giller P (eds) Organisation of Communities. Blackwell Publishing, Oxford, UK pp.205-226

Terranova CJ, Coffman BS (1997) Body weights of wild and captive lemurs. Zoo Biology 16:17-30

Thomas L, Buckland S, Rexstad E, Laake J, Strindberg S, Hedley S, Bishop J, Marques T, Burnham K (2010) Distance software: design and analysis of distance sampling surveys for estimating population size. The Journal of Applied Ecology 47:5-14

Tilman D (1982) Resource Competition and Community Structure. Princeton University Press, Princeton, NJ

Tischendorf L, Bender DJ, Fahrig L (2003) Evaluation of patch isolation metrics in mosaic landscapes for specialist vs. generalist dispersers. Landscape Ecology 18:41-50

Treves A, Palmqvist P (2007) Reconstructing hominin interactions with mammalian carnivores (6.0¬1.8 Ma). In: Gursky SL, Nekaris K (eds) Primate anti-predator strategies. Springer, New York, NY pp. 355-381

Trombulak SC, Frissell CA (2000) Review of Ecological Effects of Roads on Terrestrial and Aquatic Communities. Conservation Biology 14:18-30

Tutin C (1999) Fragmented living: Behavioural ecology of primates in a forest fragment in the Lopé Reserve, Gabon. Primates 40:249-265

Tutin C, Ham R, White L, Harrison M (1997) The primate community of the Lopé Reserve, Gabon: diets, responses to fruit scarcity, and effects on biomass. American Journal of Primatology 42:1-24

Tutin C, White L (1999) The recent evolutionary past of primate communities: Likely environmental impacts during the past three millennia. In: Fleagle J, Janson C, Reed K (eds) Primate Communities. Cambridge University Press, Cambridge, UK, pp. 220-236

Umapathy G, Kumar A (2000) The occurrence of arboreal mammals in the rain forest fragments in the Anamalai Hills, south India. Biological Conservation 92:311-319

Umapathy G, Kumar A (2000) The demography of the lion-tailed macaque (*Macaca silenus*) in rain forest fragments in the Anamalai Hills, South India. Primates 41:119-126

van der Werf G, Randerson J, Collatz G, Giglio L, Kasibhatla P, Arellano A, Olsen S, Kasischke E (2004) Continental-scale partitioning of fire emissions during the 1997 to 2001 El Niño/La Niña period. Science 303:73-76

van Schaik CP, Madden RM, Ganzhorn JU (2005) Seasonality and primate communities. In: Brockman DK, van Schaik CP (eds) Seasonality in Primates: Studies of Living and Extinct Human and Non-Human Primates. Cambridge University Press, Cambridge, UK, pp. 445-463

Vasey N (2000) Niche separation in Varecia variegata rubra and Eulemur fulvus albifrons: I. Interspecific patterns. American Journal of Physical Anthropology 112:411-431

Virah-Sawmy M (2009) Ecosystem management in Madagascar during global change. Conservation Letters 2:153-170

Virah-Sawmy M, J. Willis K, Gillson L (2010) Evidence for drought and forest declines during the recent megafaunal extinctions in Madagascar. Journal of Biogeography 37:506-519

Vogel E, Haag L, Mitra-Setia T, van Schaik C, Dominy N (2009) Foraging and ranging behavior during a fallback episode: *Hylobates albibarbis* and *Pongo pygmaeus wurmbii* compared. American Journal of Physical Anthropology 140:716-726

Wallis I, Edwards M, Windley H, Krockenberger A, Felton A, Quenzer M, Ganzhorn J, Foley W (2012) Food for folivores: nutritional explanations linking diets to population density. Oecologia 169:281-291

Walsh PD, White LJT (1999) What It Will Take to Monitor Forest Elephant Populations. Conservation Biology 13:1194-1202

Waltert M, Abegg C, Ziegler T, Hadi S, Priata D, Hodges K (2008) Abundance and community structure of Mentawai primates in the Peleonan forest, north Siberut, Indonesia. Oryx 42:375-379

Wasserman MD, Chapman CA (2003) Determinants of colobine monkey abundance: the importance of food energy, protein and fibre content. Journal of Animal Ecology 72:650-659

Waterman PG, Ross JAM, Bennett EL, Davies AG (1988) A comparison of the floristics and leaf chemistry of the tree flora in two Malaysian rain forests and the influence of leaf chemistry on populations of colobine monkeys in the Old World. Biological Journal of the Linnean Society 34:1-32

White FJ, Overdorff DJ, Balko EA, Wright PC (1995) Distribution of Ruffed Lemurs (*Varecia variegata*) in Ranomafana National Park, Madagascar. Folia Primatologica 64:124-131

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

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

Wiens JA, Moss MR (2005) Issues and perspectives in landscape ecology: Cambridge Studies in Landscape Ecology. Cambridge University Press, New York, NY.

Williams BK, Nichols JD, Conroy MJ (2002) Analysis and management of animal populations: modeling, estimation, and decision making. Academic Press, San Diego, CA

Williams R, Thomas L (2009) Cost-effective abundance estimation of rare animals: Testing performance of small-boat surveys for killer whales in British Columbia. Biological Conservation 142:1542-1547

Wilmé L, Goodman S, Ganzhorn J (2006) Biogeographic evolution of Madagascar's microendemic biota. Science 312:1063-1065

Woodroffe R, Thirgood S, Rabinowitz A (2005) People and wildlife, conflict or co-existence?:Cambridge University Press, New York, NY.

Worman COD, Chapman CA (2006) Densities of Two Frugivorous Primates with Respect to Forest and Fragment Tree Species Composition and Fruit Availability. International Journal of Primatology 27:203-225

Wright PC (1999) Lemur traits and Madagascar ecology: coping with an island environment. American Journal of Physical Anthropology 42:31-72

Wright PC (2007) Considering climate change effects in lemur ecology and conservation. In: Gould L, Sauther ML (eds) Lemurs: Ecology and Adaptation. Springer, New York, NY, pp 385-401

Wright PC, Andriamihaja B, King S, Guerriero J, Hubbard J (in press) Lemurs and tourism in Ranomafana National Park, Madagascar: economic boom and other consequences. In: Russon A, Wallis J (eds) Primate-focused tourism. Cambridge University Press, Cambridge, UK

Wright PC, Johnson SE, Irwin MT, Jacobs R, Schlichting P, Lehman SM, Louis Jr. EE, Arrigo-Nelson SJ, Raharison JL, Radoniana R, Rafalirarison, Razafindratsita V, Ratsimbazafy J, Ratelolahy FJ, Dolch R, Tan C (2008) The crisis of the critically endangered greater bamboo lemur (Prolemur simus). Primate Conservation 23:5-17

Wright PC, Tecot SR, Erhart EM, Baden AL, King SJ, Grassi C (2011) Frugivory in four sympatric lemurs: implications for the future of Madagascar's forests. American Journal of Primatology 73:585-602

Wright P, Volonlontiana R, Razafindratsita V, Pochron S, Jernvall J (2005) The Key to Madagascar Frugivores. In: Dew JL, Boubli JP (eds) Tropical Fruits and Frugivores: The Search for Strong Interactors. Springer, Dordrecht, Netherlands, pp.121-138

Wright PC (1998) Impact of predation risk on the behaviour of *Propithecus diadema edwardsi* in the rain forest of Madagascar. Behaviour 135:483-512

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

Wright PC, Razafindratsita VR, Pochron ST, Jernvall J (2005) The key to Madagascar frugivores. In: Dew JL, Boubli JP (eds) Tropical fruits and frugivores: The search for strong interactors. Springer, Dordrecht, Netherlands, pp 121-138

Young A, Clarke G (2000) Genetics, demography and viability of fragmented populations. Cambridge University Press, Cambridge, UK

Zuckerberg B, Porter W, Corwin K (2009) The consistency and stability of abundance-occupancy relationships in large-scale population dynamics. The Journal of Animal Ecology 78:172-181

Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009) Mixed effects models and extensions in ecology with R. Springer, New York, NY.