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Before and After the Storm: Interactions between Tree-Fall Canopy Gaps, Plant Phenology, and Frugivorous Lemurs in Masoala National Park, Madagascar

by

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Abstract

Madagascar is one of Earth's top biodiversity hotspots, with 80% of life on the island considered endemic. Among the endemic species are lemurs, a diverse group of non-human primates. Unfortunately, Madagascar's diversity, including lemurs, is threatened by habitat degradation and loss. Despite intense anthropogenic pressure over the past 50 years, scientists have not detected any lemur extinctions during this period. Some researchers have proposed that lemurs' adaptations to natural disturbances have provided these taxa resiliency against anthropogenic disturbances. Certainly, Madagascar experiences an extreme disturbance regime: the island experiences an average of over three cyclones a year. These cyclones create numerous, small disturbances in the form of tree-fall canopy gaps. Consequently, lemurs have had to adapt to both large-scale and small-scale disturbances. While some research exists on the impact of cyclones on lemur behavior, ecology, and population dynamics, very little is known about how tree-fall canopy gap disturbances affect lemurs. This research was the first to address the role canopy gaps play in the behavioral ecology of lemurs.

Tree-fall canopy gaps are ubiquitous features within Masoala National Park (MNP), Madagascar, home of two closely related frugivorous lemur species: *Varecia rubra* and *Eulemur albifrons*. Research on other rain forest mammals suggests that canopy gaps may be ecologically important by contributing to high-density and high-quality food patches. Gaps can increase fruit, flower, and young leaf abundance, and increase protein content of young leaves.

V. rubra and *E. albifrons* evolved within the same disturbance regime at MNP yet differ in a variety of ways. *V. rubra* is larger (2.6 – 4.1 kg) and include a greater proportion of fruit in their diet than other lemur taxa. In contrast, the smaller (1.6 – 2.3) *E. albifrons* has greater dietary flexibility than *V. rubra*, with fruit making up a smaller proportion of the former's overall diet. *V. rubra* exhibits a highly dynamic fission-fusion social organization that is dictated by both seasonality and reproduction. They live in communities with 8 to 30 individuals and frequently form subgroups of two to five individuals. *E. albifrons* lives in small (seven to nine individuals), multi-male, multi-female groups that are cohesive year-round.

Some life history traits also differ strikingly. Female *V. rubra* give birth to litters of up to five offspring (commonly two or three) that develop rapidly with juveniles reaching two-thirds adult body weight by nine months. Females construct nests where infants are born and remain for the first couple of weeks of their lives. Infants are then carried orally and stashed while females forage. High-fat, high-energy milk provided on schedule allow nursing females to stash young for extended time periods. Adults of both sexes participate in extensive alloparenting. In contrast, female *E. albifrons* give birth to singletons (less commonly twins) and carry their offspring full-time, providing low-energy, low-fat milk on demand. In fact, females within the genus *Eulemur* produce some of the poorest quality milk of all primates.

Because *V. rubra* and *E. albifrons* have different life history traits, a comparison of their adaptations to the same disturbance regime should provide insight into the

interaction between life history strategy, natural disturbance, and ecological adaptations. The goal of my research was to determine the different behavioral responses of *V. rubra* and *E. albifrons* to tree-fall canopy gaps given their different ecological and life history characteristics. I asked whether *V. rubra* and *E. albifrons* use canopy gaps differently than closed canopy forest, and, if so, how. I hypothesized that canopy gaps would serve as food-rich sites for both species. I also predicted that *E. albifrons*, with its greater ecological and dietary flexibility, would be more closely associated with the tree-fall canopy gaps than *V. rubra*. Finally, I hypothesized that canopy gaps would provide high-quality food for both species.

My data provide evidence that *V. rubra* and *E. albifrons* tolerate the high rate of disturbance represented by tree-fall canopy gaps, at least during the hot, food-abundant seasons. Using generalized mixed effects models (GLMMs), I found that the difference to the nearest gap was significantly different for *E. albifrons*, *V. rubra*, and random transect trees. Compared to transect trees, *E. albifrons* were closer to canopy gaps than expected; *V. rubra* were farther from canopy gaps than expected during the early part of the hot, dry season and decreased the distance to the nearest gap throughout the hot, rainy season. These results applied to a period of high fruit availability in the hot seasons following Cyclone Enawo, 2017. During a period of low cyclone activity and corresponding low fruit availability, both *E. albifrons* and *V. rubra* maintained proximity near tree-fall gaps; only *E. albifrons*, however, was closer to gaps than random transect trees. Consequently, the two species do differ in their behavior response to canopy gaps as predicted.

The data also support the hypothesis that tree-fall canopy gaps serve as food-rich sites for frugivorous lemurs. GLMMs of tree and liana young leaves and fruit indicated that proximity to gaps was associated with increased fruit and young leaf abundance. Proximity to canopy gaps increased leaf and fruit abundance during the food-scarce, low cyclone activity period and the food-abundant, recent cyclone activity period, as predicted. Contrary to my hypothesis, however, proximity to tree-fall canopy gaps did not affect the nutritional content of young leaves or fruit. Energy and the percent of nitrogen, crude protein, non-structural carbohydrates, condensed tannins, and polyphenols of food samples were similar regardless of whether the samples were collected from gap edges or closed canopy.

The benefits and potential costs of association with tree-fall canopy gaps are affected by cyclones, food availability, and gap frequency. Whether or not lemurs associated with tree-fall gaps depended on food availability within the forest. In times when food was scarce, both species decreased their average distance from canopy gaps and spent more time traveling to do so. The value of canopy gaps also depended on their number and distribution; when common throughout the forest, the lemurs did not need to actively select gaps to be near and benefit from them. The interannual variation in tree-fall canopy gaps, plant phenology, and lemur food abundance in this study highlight the importance of long-term, multi-year studies for understanding complex relationships between disturbance and lemur ecology. Understanding these relationships is increasingly urgent as climate change is expected to significantly alter the intensity and frequency of tropical storms, the most common cause of canopy gaps.

Dedication

This dissertation is dedicated to Penelope, who started it all; Emilia, the mongoose lemur who enchanted me from the moment she was born; and my husband, John, whose unwavering support made it all possible.

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Chapter 1: Introduction

1.1 Madagascar and Disturbance

In many ways, Madagascar is an extraordinary place. Considered one of Earth's top biodiversity hotspots, roughly 80% of life on the island is endemic (Ganzhorn, Lowry II, Schatz, & Sommer, 2001; Myers, Mittermeier, Mittermeier, da Fonseca, & Kent, 2000). The island has diverse habitats, including mangroves, scrubland, seasonal dry forest, and humid evergreen forests (Figure 1.1; Du Puy & Moat, 2003). Amongst the endemic species are lemurs, a group of non-human primates ranging in size from the tiny mouse lemur (*Microcebus sp.*) to the nearly 10 kg indri (*Indri indri*) (Mittermeier *et al.*, 2006). Scientists continue to discover new species within Madagascar, including new additions to the more than 100 known lemur species (Platt, 2018).

In other ways, however, Madagascar is typical of many places in the tropics: declining populations of many plant and animal species are driven by habitat degradation and loss. The biodiversity of this island nation is increasingly threatened by anthropogenic pressures, including habitat conversion through strip mining, agriculture, and timber extraction (Ganzhorn *et al.*, 2001; Myers *et al.*, 2000). Figure 1.2 provides maps showing the alarming rate of deforestation in eastern Madagascar from 1950 to 1985 (Green & Sussman, 1990). More recent studies suggest that lemurs continue to face the loss of their forest homes - only 10-20% of Madagascar's forest remain (C. Schwitzer, Mittermeier, Johnson, *et al.*, 2014). At the same time, much of Madagascar's human population relies on natural forest products for fuel, food, medicine, and materials for transportation, housing, and furniture (Kremen *et al.*, 1999). 75% of the population live on less than $1.90 a day, and Madagascar has the fourth highest rate of child malnutrition in the world ("The World Bank in Madagascar," 2019). While access to forest products helps mitigate the impacts of poverty for humans, it greatly increases pressure on the lemurs who live within the forests (Borgerson, McKean, Sutherland, & Godfrey, 2016).

Despite intense anthropogenic pressure within the past 50 years, no lemur species have gone extinct during that time. Some researchers have proposed that lemurs' adaptations to natural disturbances has provided them with some resiliency to anthropogenic disturbances (Lehman, Rajaonson, & Day, 2006a). Disturbances events are ones that disrupt ecosystem, community, or population structure, alter resource availability, change the physical environment (or some combination of these) within a relatively discrete period of time (Turner, Dale, & Everham, 1997; White & Pickett, 1985). Disturbances can be anthropogenic, including clear-cut timber extraction, slash-and-burn agricultural practices, or the development of cities and towns, or natural, including fires, earthquakes, and volcanoes. For eastern Madagascar, natural disturbances include frequent and intense cyclones and the small, numerous tree-fall canopy gaps created by these storms. To understand their impacts, disturbances must be framed by the proper temporal and spatial scale. Some impacts are immediately visible while others can only be seen after generations (Clark, 1996). Because cyclones and tree-fall canopy gaps are not new to Madagascar, lemur populations have necessarily adapted to the impacts of these disturbances, allowing lemurs to persist. Such adaptations certainly vary by taxa, even amongst lemurs, and are not yet fully understood.

1.2 Disturbance Impacts

1.2.1 Disturbance and Extinction

Disturbance plays in important role in the lives of many currently threatened species, and predicting a population's response to current and future disturbance is increasingly more urgent in the face of climate change and other increasing anthropogenic threats (van Allen, Dunham, Asquith, & Rudolf, 2012). Some life history strategies buffer against disturbance better than others (Lytle, 2001; van Allen *et al.*, 2012). Therefore, comparing responses to disturbances of sympatric species with different life history traits can clarify the interactions among life history strategies, disturbance, behavioral adaptations, and long-term survival. Ultimately, such understanding can improve predictions of extinction threats and contribute to management plans to avert it.

Eastern Madagascar provides an opportunity for understanding behavioral responses to disturbance because it has frequent cyclones that affect lemur species that are closely related phylogenetically but have different life history strategies and behavioral adaptations. Red ruffed lemurs, *Varecia rubra,* and white-fronted brown lemurs, *Eulemur [fulvus] albifrons*, are members of the same family (Lemuridae) and live sympatrically in the forests on the Masoala Peninsula in northeastern Madagascar (Vasey, 1996). While they share some similarities in diet and behavior, they have different life history traits and ecological niches. Knowing how these two species respond behaviorally to disturbances within the constraints of their ecological adaptations, physiology and life history will allow conservation managers to make informed decisions about forest protection and use. Life history adaptations to natural habitat disturbance and forest re-growth were adumbrated for *V. rubra* (Vasey, 1996). In this genus birth rate and infant mortality vary widely from year to year, and its population growth potential was hypothesized to buffer them from local extinction when, for natural reasons (e.g., cyclones), birthrate is low and infant mortality is high (Vasey, 2003). Red ruffed lemurs are among the top 25 most critically endangered primates (Mittermeier *et al.*, 2009; C. Schwitzer, Mittermeier, Rylands, *et al.*, 2014), and white-fronted brown lemurs are threatened (IUCN, 2012). Both species are threatened by poaching and habitat degradation, fragmentation, and loss (IUCN, 2012; C. Schwitzer, Mittermeier, Johnson, *et al.*, 2014). In much of their geographic range these two species must cope with frequent natural disturbances associated with cyclones as well as intense anthropogenic disturbance (Ratsimbazafy, 2006). Without understanding the impacts of natural disturbance on these populations, it is likely that management efforts will underestimate measures needed to ensure continued survival of *V. rubra* and *E. albifrons.*

1.2.2 Life History and Disturbance

Disturbances play an important role in population dynamics and the evolution of life history traits for some species (Greenwood & Mcintosh, 2011). Mammalian population dynamics during periods of disturbance are influenced by interactions between life history traits and ecological factors (Gamelon *et al.*, 2014). While life history traits affect species sensitivity to disturbances, how this relationship is altered by other variables is only partially understood (Lytle, 2001; van Allen *et al.*, 2012). Natural disturbances vary in duration, size, frequency, and timing in relation to an organism's developmental and reproductive life stage. These variables interact to determine the nature, direction, and size of disturbance impacts on the selection for and flexibility of life history traits (Greenwood & Mcintosh, 2011; Lytle, 2001).

Predicting the evolutionary impact of disturbance on life history traits is challenging. Interaction of disturbance and life history is complicated by variation in the timing, predictability, frequency, and severity of the disturbance (Lytle, 2001). Some generalizations, however, are possible. Perhaps the most important one is that scale matters (Wiens, 1989); one should use a temporal scale relevant to an organism's lifespan and consider the physical scale of a disturbance relative to either the organism's home range or a species' geographic range (Lytle, 2001). Large-scale disturbances, like cyclones, potentially have greater impact on life history strategies than small-scale, frequent disturbances, like tree-fall canopy gaps (Lytle, 2001). Species with high reproductive rates, fast life history, and short life spans (r selected species) are resilient to disturbance (Williams, Shoo, Isaac, Hoffmann, & Langham, 2008). On the other hand, species with slow reproductive rates, slow life history, and long-life spans (K selected species) are more likely to respond strongly to disturbances than r selected species because longer-lived organisms have a greater probability of directly experiencing and surviving one or more large-scale disturbance (Lytle, 2001). Greater frequency of disturbances can increase selective pressure on life-history strategies compared to very rare disturbances (Lytle, 2001). Ecological plasticity can potentially minimize impacts of disturbances in the long term (Williams *et al.*, 2008) by enabling a species to respond to a range of disturbance regimes. However, outside of this range of disturbance, and in the absence of evolutionary change, an organism may become extinct and change the ecological community (Lytle, 2001). Life history strategies interact with disturbance regimes to determine species persistence over time, and changes in a disturbance regime may change population size, distribution, and persistence of a given species (Clark, 1996).

1.2.3 Disturbance in an Organism's Life

On the scale of an organism's lifespan, disturbance impacts range from catastrophic to minor. The former impacts are often associated with large-scale natural disasters, like landscape fires, cyclones, and multi-year droughts while the latter may be associated with temporary extreme temperatures, fallen trees, and storms. For the lemurs of eastern Madagascar, the disturbance regime includes catastrophic landscape-wide cyclones (Ganzhorn, 1995a) and localized canopy gaps created by a single fallen tree (Mogilewsky and Vasey, unpublished data). These disturbances are linked because most tree-fall gaps occur during or immediately following a tropical storm or cyclone (Birkinshaw & Randrianjanahary, 2007; Burslem, Whitmore, & Brown, 2000; Everham & Brokaw, 1996).

Many of the immediate effects of cyclones are striking and obvious, though less obvious effects are also important. Such storms cause defoliation, remove lianas, vines, and epiphytes, snap and uproot trees, accumulate large amounts of debris, cause landslides and debris flows, alter stream channels, and transform beaches (Lugo, 2008; Turton & Siegenthaler, 2004). Canopy defoliation is much greater than understory defoliation, although the extent of defoliation depends strongly on maximum daily wind speed (Lugo, 2008). High winds of cyclones can greatly alter tree communities through tree mortality and alterations in seedling recruitment rates and patterns. Cyclone-induced tree mortality in rain forests ranges from 1-23% and uprooting of trees ranges from 3-43% (Lugo, 2008). Characteristics of the tree, storm, and growing environment all contribute to likelihood of mortality. Some species of trees appear more vulnerable to uprooting and breaking, but in general, the probability of post-cyclone mortality is greatest for large (as defined by both height and girth) canopy trees, possibly because these trees tend to be more exposed to extreme winds compared to smaller understory trees (Lugo, 2008). Tree-falls, tree snaps, and uprooting transfers material to the forest floor. Together, a cyclone's impacts can significantly and sometimes permanently alter forest structure and function (Lugo, 2008).

Immediate effects and subsequent responses of animal populations to cyclone-induced changes depends on mobility, diet, forest strata preference, and scale (Lugo, 2008). Guild level patterns are often present, though they do not form absolute rules. For example, frugivores and nectivores experience greater population declines after hurricane passage than insectivores. Local, fine-scale changes in populations may or may not reflect changes at a broader, landscape scale (Lugo, 2008). Tropical storms can cause population decline of species at some sites more than others, resulting in heterogeneous responses within the same forest system. At landscape scales, interactions between environmental changes following cyclones and modified dispersal patterns alter species abundance distributions. As forests recover, however, environmental conditions can become more favorable for population growth (Willig *et al.*, 2007).

Populations of frugivores can be directly and indirectly impacted by cyclones. Populations may decline immediately following cyclone damage to a forest habitat, and recovery may depend on the rate of forest recovery and life history traits of the animal. Direct causes of population decline of frugivores include disruption in the timing and abundance of fruit availability, disruption of social groups due to high mortality, stochastic changes in age structure and sex ratio, decreased protection from predators, and reduced reproductive success, including high infant mortality (Johnson, Ingraldi, Ralainasolo, Andriamaharoa, & Ludovic, 2011). Population declines immediately following cyclones have been recorded for howler monkeys (*Aloutta pigra)* in Belize (Pavelka, McGoogan, & Steffens, 2007), black-and-white ruffed lemurs (*Varecia variegata)* in southeastern Madagascar (Ratsimbazafy, 2006), and red ruffed lemurs in northeastern Madagascar (Ratsisetraina, 2006). Data on potential long-term recovery of frugivores from cyclones is sparse, but for gray-headed lemurs at Manombo in southeast Madagascar, population size ten years after a cyclone was similar to before the cyclone (Johnson *et al.*, 2011). Frugivores may respond to cyclone-caused damage by altering activity budgets, diets, and microhabitat use (Johnson *et al.*, 2011; Ratsimbazafy, 2006). Flexible social organization and group structure may promote resilience to disturbance as well (Asensio, Korstjens, Schaffner, & Aureli, 2008).

1.3 Cyclones and Tree-fall Canopy Gaps

1.3.1 Canopy Gaps and Their Effects

Cyclones cause patchy destruction of the canopy, resulting in light gaps (Grove, Turton, & Siegenthaler, 2000). In many cases, these gaps are caused by the death of one or more trees, either through uprooting or snapping (Brokaw, 1982; Schliemann & Bockheim, 2011). In fact, "Tree-fall gaps are the most frequently occurring perturbation in tropical forests" (Beck *et al.*, 2004, p 27). Canopy gaps play an important role in tropical forest ecology and contribute to habitat heterogeneity (Burslem *et al.*, 2000; Burslem & Whitmore, 1999). Growth in tropical rainforests is characterized by a continuous process of canopy gap creation and subsequent growth and maturation of a large number of plant species; this process, called *gap dynamics*, is highly varied across space and time (Brokaw, 1985; A. G. Johns, 1997). Thus, a given stand of tropical rainforest will be a mosaic of gaps and all growth phases from seedling recruitment to mature trees (Whitmore, 1990). This mosaic creates great variation in light intensity, soil temperatures, humidity, and seedling and sapling communities (Chazdon & Fetcher, 1984; Whitmore, 1998; Whitmore & Brown, 1993). The duration of gaps and their impact varies but tends to range from four to six years (Everham & Brokaw, 1996; Fraver, Brokaw, & Smith, 1998).

Gap-generated diversity in local habitats directly contributes to the maintenance of species diversity (Barik, Pandey, Tripathi, & Rao, 1992; Beck *et al.*, 2004; Brokaw & Scheiner, 1989; Busing & Brokaw, 2002; Chapman *et al.*, 2010; Crome & Richards, 1988; Felton, Felton, Wood, & Lindenmayer, 2006; Gutiérrez, Armesto, & Aravena, 2004; Ostertag, 1998; Poulson & Platt, 1989; Svenning, 2000). Tree-fall canopy gaps alter forest species composition because some tree species are more prone to fall or snap than others (Bellingham, 2008; Burslem & Whitmore, 1999; Lugo, 2008; Metcalfe, Bradford, & Ford, 2008), and gap conditions favor seedling recruitment and seedling and juvenile growth of pioneer species (Brokaw, 1985; Brokaw & Scheiner, 1989; Busing & Brokaw, 2002). For fauna, the increased habitat heterogeneity created by gaps may allow more animal species to coexist through creation of specialized microhabitats which thereby allow niche partitioning (Beck *et al.*, 2004; Crome & Richards, 1988). For example, the bat community of a Queensland, Australia rain forest includes species that forage exclusively under closed canopy while others forage preferentially in canopy gaps (Crome & Richards, 1988). Use of canopy gaps impacted fitness differently for two terrestrial rodents within an Amazon rain forest; one species experience reduced infant survival within canopy gaps compared to the second species, suggesting that continued persistence of these two species may be maintained in part by differential responses to gap habitats (Beck *et al.*, 2004).

As with forest edge effects, impacts of canopy gaps on fauna are complex. Response to forest edges is highly variable across species, with evidence of edge-intolerant, edge-tolerant, and edge-neutral species in the same forest system (Chapman, Balcomb, Gillespie, Skorupa, & Struhsaker, 2000; Lehman *et al.*, 2006a; Lehman, Rajaonson, & Day, 2006b; Lenz, Jack, & Spironello, 2014). Similarly, some species may be gap-intolerant, gap-tolerant, or gap-neutral. For example, some bird species were more abundant in canopy gaps in Bent Wood Experimental Forest, North Carolina, but at least one bird species exhibited reduced abundance (Greenberg & Lanham, 2001). Likewise, hurricane created gaps in Appalachia were associated with an increase in reptile abundance while amphibian abundance was unaffected (Greenberg, 2001). Size, diet, social organization, group size, and life history strategies contribute to a species' response to forest edges (Brodie, Giordano, & Ambu, 2015; Chapman *et al.*, 2000; A. D. Johns & Skorupa, 1987; A. G. Johns & Johns, 1995; Lehman *et al.*, 2006a, 2006b; Sawyer, Fenosoa, Andrianarimisa, & Donati, 2017), and these same factors are likely to contribute to species' response to canopy gaps.

Studies on the interactions between canopy gaps and vertebrates suggest that canopy gaps can provide abundant, high-quality food resources. Plant productivity, including fruit production, is generally higher in gaps (Beck *et al.*, 2004; Denslow, Moermond, & Levey, 1986; Ganzhorn, 1995b) such that gaps may serve as important food patches for fauna (Alvarez-Buylla & Martínez-Ramos, 1990; Murray, 1987; Swaine, 1996). Gaps can alter plant phenology, including the timing and duration of fruit and flower production, seasonal variation, and abundance (Hemingway & Overdorff, 1999; Levey, 1988). The increased diversity in forest structure and composition created by a mosaic of canopy gaps may ensure year round food availability, particularly for frugivores (Balko & Underwood, 2005). Increased light intensity can also improve forage quality by enhancing primary productivity that increases protein content and improves protein to fiber ratios (Ganzhorn, 1995b). Gap microhabitats may also offer primates opportunities for behavioral thermoregulation because tree-fall gaps significantly increase light intensity to produce warmer and drier microclimates (Brown & Whitmore, 1992; Chazdon & Fetcher, 1984; Salvador-van Eysenrode, Bogaert, van Hecke, & Impens, 1998; Whitmore, 1978).

However, not all effects of tree-fall canopy gaps on fauna may be positive. Gaps can potentially increase travel time and distance by decreasing canopy density and eliminating travel routes. They may also increase predation risk by some types of predators as cover density is a factor in the probability of predator attack (Hill & Weingrill, 2007; Treves, 2002). For example, both vervets (*Chlorocebus pygerythrus*).and patas (*Erythrocebus patas*) monkeys increased vigilance behaviors (including scanning for predators and increased frequency of alarm calls) in microhabitats of tall trees that provided increased visibility of predators (Enstam, 2007). However, the relationship is not straightforward because while dense foliage may reduce visibility for predators it may also reduce the ability of primates to detect predators (Treves, 2002). Increased foliage at gap edges may reduce visibility to predators but may also increase obstructive cover - decreasing preys' ability to detect predators. Increased light and open edges may increase visibility of prey by predators but also increase visibility of predators by prey.

The climates of Madagascar have been described by various authors as less stable than other tropical regions, with the distribution of rainfall being particularly unpredictable (Dewar & Richard, 2007; Wright, 1999). Dewar & Richard (2007) found high precipitation variability in Madagascar - seasonally unpredictable in the west, interannually unpredictable in the east. An average of 3.5 cyclones per year pass over

Madagascar (Fitchett & Grab, 2014) and may have posed significant evolutionary selective pressures on a variety of Madagascar's plant and animal inhabitants (Dewar & Richard, 2007; Dunham, Erhart, & Wright, 2010; Ganzhorn, 1995a). Eastern Madagascar experiences 2.2 to 2.9 cyclones per year (de Gouvenain & Silander, 2003; Fitchett & Grab, 2014), creating ubiquitous tree-fall canopy gaps (Mogilewsky and Vasey, unpublished data). Ganzhorn (1995a) noted several characteristics of Madagascar's western dry deciduous forest that specify cyclones as an historic and current force in maintaining Madagascar's plant and animal diversity, including tree species with large seeds that require flooding for germination, tree species that require light gaps for successful recruitment, and tree species with seeds that require high wind speeds for dispersal. Dewar and Richard (2007) argue that Madagascar's disturbance regime is a strong force in the evolution of some of the island's animal communities. For example, Madagascar's hypervariable environment is viewed as a strong selective agent favoring the relatively low metabolic rates and strict breeding seasonality found in lemurs (Dewar & Richard, 2007; Pichon & Simmen, 2015; Wright, 1999). Across many lemur genera, weaning is timed with peak fruit availability, an adaptation hypothesized to reduce energy investment in offspring in a disturbance prone environment (Wright, 1999).

1.3.2 Lemur-Gap Interactions at Andranobe Forest

Frequent cyclones create ubiquitous, broadly distributed canopy gaps throughout Madagascar's eastern evergreen rain forests (Birkinshaw & Randrianjanahary, 2007). The southwest Indian Ocean tropical storm region, which includes Madagascar, had an annual average of 1.31 cyclones (of at least a category 1 on the Kaffir-Simpson Scale) between 1973 – 2000; only the northwest Pacific Ocean region experiences more frequent tropical storm activity (de Gouvenain & Silander, 2003). In fact, several authors have hypothesized that cyclone frequency is responsible for the relatively short stature and high tree density that characterizes eastern Madagascar's rainforests (De Gouvenain and Silander 2003). In addition to affecting tree stature and density, cyclones create canopy gaps by uprooting and/or breaking canopy trees. A 2014 pilot study conducted at Andranobe Forest, Masoala National Park (MNP), in northeastern Madagascar, mapped 30 tree-falls canopy gaps in 3.6 km of transects (Mogilewsky and Vasey, unpublished data). Canopy gaps were found at all topographic positions but were more frequent on ridge tops and convex upper slopes than at concave lower slopes and valley bottoms. Of these gaps, 73% were less than 50 m^2 and only one gap was greater than 200 m^2.

Tree-fall canopy gaps can directly alter microclimate by allowing more sunlight to reach the forest floor. For example, my comparison of temperature and light intensity of gaps to closed canopy forest at Andranobe Forest in 2015 showed that mean light intensity measured in lumens during the hot-dry season was significantly higher at gap edges than under closed canopy (32610 lm ± 14706 compared to 8454 lm ± 4329; one-tailed t test: $t = 3.5234$, $df = 4.688$, $p < 0.01$). Likewise, maximum light intensity was also significantly greater at gap edges than under closed canopy (258944 lm ± 31755 compared to 161477 lm ± 89069; one-tailed t test: $t = 2.541$, $df = 5.0007$, $p < 0.05$). Consequently, maximum temperature during the hot-dry season was significantly higher at gap edges than under closed canopy (42.6°C ±3.5 compared to 35.5°C ±3.4; one-tailed t test: $t = 3.2088$, $df = 8$, $p < 0.01$).

V. rubra population density is especially high at Andranobe Forest, and Vasey (1996, 1997b, 2003) hypothesized that *Varecia* populations may be larger in areas that experience intense natural disturbance. At the same time, *V. rubra* appear to be quite vulnerable to anthropogenic disturbance, especially when compared to sympatric *E. albifrons,* because of their reliance on trees of large girth for nesting and stashing young; these very trees are highly prized by loggers because of their size and hardwood characteristics (Vasey, Mogilewsky, & Schatz, 2018). Comparing *V. rubra* and *E. albifrons* provides a better understanding of the role of life history in adaptations to disturbance. This understanding is critical for predicting species' risk of extinction due to increased anthropogenic disturbance and climate change.

1.3.2.1 Contrasting Life History Strategies for Disturbance-Adapted Lemurs

Life history traits evolve in the context of interactions among climate (including seasonal variation), resource availability and distribution, predation pressures, and flexibility in life history trait expression (Greenwood & Mcintosh, 2011) and also constrain potential behavioral responses to disturbances. Compared across mammalian orders, lemur life history traits are not generally associated with resilience to environmental perturbations: they have low reproductive rates, slow life history, and long lifespans. However, compared with anthropoid primates (apes and monkeys), lemurs have relatively fast life history. Moreover, the timing of weaning with peak food abundance appears to be critical for infant survival in many lemur populations (Tecot, 2010; Wright, 1999; Wright, Razafindratsita, Pochron, & Jernvall, 2005), and Van Allen *et al.* (2012) found that those species with a single life stage that had a disproportionate impact on population growth were more vulnerable to increased environmental stochasticity. Nonetheless, the evolutionary radiation of lemur taxa on Madagascar and their survival for tens of millions of years suggests that these populations have successfully adapted to Madagascar's chaotic climate and natural disturbances (Dewar & Richard, 2007; Wright, 1999).

Red ruffed and white-fronted brown lemurs evolved within the same disturbance regime yet differ in a variety of ways. Red ruffed lemurs are larger (2.6 – 4.1 kg), and ruffed lemurs include a greater proportion of fruit in their diet than other lemur taxa (Martinez & Razafindratsima, 2014; Rigamonti, 1993; Vasey, 2003; Wright *et al.*, 2011). Wild populations are diurnal (Rigamonti, 1996; Vasey, 1996, 2003), but recent studies in captivity suggest that they may be cathemeral under some conditions (Bray, Samson, & Nunn, 2017; Rea, Figueiro, Jones, & Glander, 2014). Red ruffed lemurs exhibit a highly dynamic fission-fusion social organization that is dictated by both seasonality and reproduction (Baden, Webster, & Kamilar, 2016; Vasey, 2006).

The fission-fusion dynamics of ruffed lemurs show flexibility in size and composition with a strong seasonal component. At the broadest level, ruffed lemurs live in multimale/multifemale communal home ranges that they defend against non-community members. These communities range in size from 8 to around 30 individuals and are never seen all together (Morland, 1991; Vasey, 2006). The communities are composed of core groups. Core group size and composition vary, but most core groups include one adult male, one or two adult females, sub-adults and dependent offspring (Vasey, 2006). While individual ruffed lemurs frequently travel and forage alone, they also associate with different individuals throughout the day, forming subgroups of different sizes (two to five) and compositions. During the food-scarce cold season and gestation, these subgroups include only those individuals that share a core group. For the rest of the year, these subgroups may include individuals from multiple core groups within the community (Vasey, 2006). Overall, ruffed lemurs associate with members of their core group more frequently than with members of their community outside their core group.

In contrast, the smaller (1.6 – 2.3) white-fronted brown lemur (Junge *et al*., 2008; Vasey, 2002) is cathemeral and frugivorous like other members of the genus *Eulemur*. *E. albifrons* also has greater dietary flexibility than red ruffed lemurs with fruit making up a smaller proportion of the former's overall diet (Carl Toborowsky & Andriaharimalala, 2006; Vasey, 2000, 2002). White-fronted brown lemurs also live in small (seven to nine individuals), multi-male, multi-female groups that are cohesive year-round (Vasey, 2000, 2002), though groups may exhibit flexible fission-fusion organization under some ecological conditions such as degraded habitats (Donati, Kesch, *et al.*, 2011; Johnson *et al.*, 2011; Ca Toborowsky, 2008)

Some life history traits also differ strikingly. Female *V. rubra* give birth to litters of up to five offspring (commonly two or three) that develop rapidly with juveniles reaching two-thirds adult body weight by nine months (Periera, Klepper, & Simons, 1987; Vasey, 2007). Females construct nests where infants are born and remain for the first couple of weeks of their lives. Infants are then carried orally and stashed in the largest trees in the forest, with about 40 different trees used for each litter (Vasey *et al.*, 2018). High-fat, high-energy milk provided on schedule allow nursing females to stash young for extended time periods (Myher, Tilden, Kuksis, & Oftedal, 1994). Adults of both sexes participate in extensive alloparenting and take turns foraging and providing care to offspring (Baden, 2019; Baden, Wright, Louis, & Bradley, 2013; Tecot, Baden, Romine, & Kamilar, 2012; Vasey, 2006, 2007) and females sometimes even nurse unrelated infants (Baden, 2010; Baden *et al.*, 2013; Vasey, 2006, 2007). Nesting and stashing infants require less energy than continuously carrying offspring (Tecot *et al.*, 2012). Red ruffed lemurs do not always produce offspring every year and may not reproduce for several years following a cyclone or other significant disturbance (Martinez, 2010; Ratsimbazafy, 2006). Increasing investment in offspring during periods of food abundance to offset periods when conditions are unfavorable for reproduction allows an organism to adjust or accommodate changes in natural disturbance risk (Clark, 1996). Red ruffed lemurs may provide an example of this reproductive strategy as one way of coping with the unpredictability of cyclones. In contrast, female *E. fulvus* give birth to singletons (less commonly twins) and carry their offspring full-time, providing low-energy, low-fat milk on demand (Myher *et al.*, 1994; Tilden & Oftedal, 1995; Vasey, 2000). In fact, females within the genus *Eulemur* produce some of the poorest quality milk of all primates (Dewar & Richard, 2007; Tilden & Oftedal, 1995). Comparing adaptations to the same disturbance regime by these two species with very different life history traits should provide insight into the interaction between life history strategy, natural disturbance, and ecological adaptations.

1.3.2.2 Ecological Niche Partitioning for Disturbance-Adapted Lemur Populations

Red ruffed and white-fronted brown lemurs exhibit niche partitioning that reduces direct competition within the eastern rain forests they share on the Masoala Peninsula. Niche partitioning occurs via vertical stratification, and microhabitat and dietary differences (Vasey, 2000). As a large bodied frugivore, *V. rubra* are dependent on high quality plant foods that are temporally and spatially patchy (i.e., young leaves, flowers, and fruit, Vasey, 1997). Among lemurs, *Varecia* are the only obligate frugivore, spending 74 to 90% of feeding time eating fruit (Vasey, 2003). Vasey (2002) found that *V. rubra* used relatively large food patches, 87.8% of foraging time was spent eating fruit, and they preferred tree crowns 74% of the time. Red ruffed lemur diets vary little seasonally, except during the hot dry season and during lactation when females eat more young leaves and fewer flowers than males. Across three different populations of *Varecia* in northeastern Madagascar, all had similar ranging patterns, and concomitantly, a highly flexible fission-fusion social organization despite considerable variation in home range size, community size, and territorial behavior. Shifts in ranging patterns correspond with both seasonal food distribution and reproductive stages, particularly for female *V. rubra*. Vasey (2006) therefore posited that flexible social organization (i.e., fission-fusion) provides the means for maintaining ecological similarity, as most populations of *Varecia* are highly frugivorous, use the highest forest strata and the largest feeding trees, are active primarily by day, and are limited to eastern rain forests. Despite the ecological similarities across many study populations, *Varecia* do exhibit feeding flexibility that allows them to cope with disturbance (Ratsimbazafy, 2006). In the years following Cyclone Gretelle, *V. variegata* at Manombo (a fragmented forest in southeastern Madagascar) fed heavily on shrubs, despite being primarily a canopy dwelling primate in less disturbed forests. Similarly, *V. rubra* in the highly (anthropogenically) disturbed Ambatoladama forest corridor also fed heavily on a non-native shrub species (Martinez & Razafindratsima, 2014). Balko and Underwood (2005) also report flexibility in food species and strata height selected by *Varecia*. Their flexible social organization also allows *Varecia* to forage alone, decreasing intraspecific competition during periods of food scarcity (Balko & Underwood, 2005; Morland, 1991). During periods of low fruit availability in the cool-wet season, *Varecia* in Ranomafana National Park in southeast Madagascar spent more time alone and subgroups were smaller and less cohesive. Increased fruit availability, on the other hand, was correlated with larger, more cohesive subgroups. Despite this dietary flexibility and resilience to disturbance, it is important to note that Ratsimbazafy (2006) did not observe any successful reproduction in the five years following Cyclone Gretelle and that *Varecia* in the Ambatoladama forest corridor did not reproduce during Martinez's (2010) study either, though they may have in other years. It may be that such dietary resilience allows *Varecia* to survive until conditions can support reproduction.

In contrast to *Varecia*, *Eulemur* are more ecologically flexible, feeding on a wide assortment of foods while ranging widely through different forest strata and microhabitats (Johnson, 2006; Sussman, 2002; Tattersall & Sussman, 1998, 2016; Vasey, 2000). While *E. albifrons* are similar to *V. rubra* in some ways, Vasey (2002) found that they use smaller food patches, have a more varied diet (only 68.9% of their diet being fruit), include a greater variety of plants throughout the year (Vasey 2004), may include large amounts of nectar in their diet (Toborowsky & Andriaharimalala, 2006), and spent 78% of their time below 15m rather than in the forest canopy strata. Vasey (2002) also found that *E. albifrons* diet composition varied significantly from season to season. Females also rely more on flowers while males rely more on miscellaneous foods (mainly millipedes) during the hot dry season. More broadly, all *Eulemur* species studied to date complement the fruit in their diet with a wide range of foods including flowers, nectar, young leaves, and insects (Campera *et al.*, 2014; Donati, Bollen, Borgognini Tarli, & Ganzhorn, 2007; Overdorff, 1993; Simmen, Bayart, Marez, & Hladik, 2007; Sussman, 2002; Vasey, 2000). While relatively rare, some *Eulemur* species, including *E. mongoz* and *E. fulvus,* will supplement their diets with opportunistic inclusion of bird eggs and even small birds (personal observation). Dietary flexibility across *Eulemur* taxa may have contributed to their success across a wide range of habitats within Madagascar (Ossi & Kamilar, 2006). Fruit eaten by *E. fulvus* show great variation in pulp type, odor, fruit skin protection, total nitrogen content, tannin concentration, and fiber amounts, reflecting considerable flexibility even with the fruit component of their diet (Bollen *et al.*, 2005). Collared brown lemurs living in disturbed habitats show reduced consumption of ripe fruit and increased consumption of mature leaves than those living in primary forest (Donati, Ricci, Baldi, Morelli, & Borgognini Tarli, 2011), providing further evidence of dietary flexibility among lemurs within this genus.

During periods of fruit scarcity, *Eulemur* adopt a variety of behavioral shifts, including increased ranging, reduced cohesion (or fission) of large groups, increased time spent resting, and decreased daily travel (Sato *et al.*, 2016). In primates, these flexible behaviors are substitutes for dietary switching during periods when availability of preferred foods are low (Sato *et al.*, 2016). For example, increased home range size in response to food scarcity has been seen in different lemur populations/species across Madagascar. *E. macaco flavifrons* on the Sahamalaza Peninsula, northwest Madagascar (N. Schwitzer, Randriatahina, Kaumanns, Hoffmeister, & Schwitzer, 2007); *E. m. macaco* on the Nosy Faly Peninsula, northwest Madagascar (Simmen *et al.*, 2007); and *E. collaris* in Mandena, southeast Madagascar (Donati, Kesch, *et al.*, 2011) increased home range size in response to food scarcity. In contrast, some *Eulemur* species may adopt an energy preservation strategy in times of low fruit availability; Campera *et al.* (2014) found that *E. collaris* minimized daily distance traveled in degraded habitat, probably as an energy saving tactic (p 970), a finding consistent with studies of *E. collaris* by Donati *et al.* (2011) and *E. fulvus* by Sato (2012).

Despite this ecological, dietary, and behavioral flexibility, *Eulemur* species are still found at higher population densities in primary than in secondary forests; for example Wilson *et al.* (1989) found larger numbers of *E. coronatus* in primary forest; Overdorff (1992) found that both *E. rubriventer* and *E. rufus* preferred highest forest strata (rather than mid canopy levels), and Schwitzer *et al.* (2007) found greater densities of *E. m. flavifrons* in primary than secondary forest. *Eulemur* species may simply adjust group size and home range size to match habitat quality, including secondary forest (N. Schwitzer *et al.*, 2007) and edge habitats (Lehman *et al.*, 2006a, 2006b).

1.4 Research Objectives

The goal of my research is to determine the different behavioral responses of *V. rubra* and *E. albifrons* to tree-fall canopy gaps given their different ecological and life history characteristics. Specifically, I ask whether these lemurs interact with canopy gaps differently than they interact with closed canopy forest, and, if so, how. To address this question, I (1) characterize tree-fall canopy gaps within Andranobe Forest over time, (2) record tree and liana phenology for transect and lemur trees over time, and (3) compare lemur activity near canopy gaps to activity under closed canopy, with a focus on foraging behavior. I hypothesize that canopy gaps would serve as resource-rich sites for both species. Because *Eulemur* species in general exhibit considerable habitat and dietary flexibility (Ossi & Kamilar, 2006) and *E. albifrons* uses a greater variety of microhabitats than *V. rubra* at Andranobe (Vasey, 2000), I predict the tree-fall canopy sites will be most important for *E. albifrons*. I further hypothesize that lemur-gap associations will show seasonal and annual variation.

In Chapter 2 I provide my methodology in detail. In Chapter 3 I compare lemur-gap interactions before and after Cyclone Enawo. Prior to Cyclone Enawo, Andranobe Forest experienced a five-year period without any named storms passing over the Masoala Peninsula. I ask how the cyclone affected canopy gap number and size at Andranobe and how tree phenology responded six to nine months after the disturbance. I address how fruit abundance three years prior to Cyclone Enawo compared to fruit abundance seven months after the cyclone. I also compare *V. rubra* and *E. albifrons* activity budgets and mean distance to the nearest gap pre- and post-cyclone.

In Chapter 4 I compare plant productivity and fruit abundance between tree-fall canopy gap edges and closed canopy for the dry and rainy seasons. I show how the mean distance to the nearest gap of transect trees compares to the mean distance to the nearest gap of trees visited by *V. rubra* and *E. albifrons*. I also test whether V. *rubra* and *E. albifrons* are found at trees closer to the nearest gap than expected at random. I predict that plant productivity, as measured by the percent of young leaves and fruits in the canopy, will increase with proximity to the nearest tree-fall canopy gap edge. I also predict that *V. rubra* and *E. albifrons* will visit canopy gap edges to forage because of an increase in abundance of young leaves and fruit. Both species will be found in trees closer to gap edges than expected at random (as determined by transect trees). Based on their greater ecological flexibility, I predict that *E. albifrons* will be found closer to gaps compared to *V. rubra.* Flexibility in diet and strata use will allow *E. albifrons* to more easily take advantage of increased productivity in a greater number of tree and liana species. Moreover, because *V. rubra* tend to dominate canopy strata, the benefits of gap edges will be less pronounced when compared to those experienced by *E. albifrons*.

In Chapter 5 I test whether proximity to tree-fall canopy gaps correlates with higher concentrations of protein, higher quality, and lower polyphenols of potential lemur foods. I compare the nutritional quality of leaves and fruit from the edges of tree-fall canopy gaps to those from closed canopy. I predict that canopy gaps will be important sources of high-quality foods and that samples collected from gap edges will have higher protein and lower fiber content than samples collected under closed canopy. I also predict that tannin and polyphenol content will be lower in samples collected from gap edges compared to closed canopy.

1.5 Importance

1.5.1 Madagascar and Climate Change

This study is timely because within Madagascar and across the globe scientists are finding changes in disturbance regimes, phenology, and population dynamics that mirror findings expected under the most extreme climate change models. Madagascar is one of the highest global conservation priorities based on measures of endemism, species diversity, and rate of species loss (Goodman & Benstead, 2005). The vast majority of Madagascar's endemic species are found in forest or woodland, making the protection and conservation of these habitats critical (Harper, Steininger, Tucker, Juhn, & Hawkins, 2007). Yet loss of critical forest habitat greatly accelerated between 1950 and 1990 (Sussman, Green, & Sussman, 1994). As a consequence of deforestation, many forest dwelling species face a real risk of extinction within the next 10-30 years (Ganzhorn *et al.*, 2001). Masoala National Park (MNP) was established in response to the rapid loss of Madagascar's eastern rainforest in recent decades and protects 3000 km^2 of eastern humid evergreen rainforest, the largest intact, continuous expanse of such habitat in Madagascar (Kremen *et al.*, 1999). Results of surveys conducted as part of the park's establishment suggest a high level of β diversity (the ratio of local to regional biodiversity) and localized endemism (Kremen *et al.*, 1999). Despite the importance of natural disturbance regimes to Madagascar's eastern rainforests, canopy gap dynamics are poorly understood. At the same time, climate change is predicted to increase cyclone frequency and intensity (Ranson *et al.*, 2014; Ren, Liang, Wu, Dong, & Yang, 2011; Seo, 2014) and this intensification is likely to alter gap dynamics (Whitmore, 1998). Adapted to historically frequent and intense storms, the eastern evergreen rain forests of Madagascar can serve as model environments, helping us better understand and manage the effects of climate change-driven shifts in tropical storm regimes.

1.5.2 Predicting Future Extinction Vulnerability

Climate change has already shifted the timing of plant growth and reproduction (Denny *et al.*, 2014), which could have serious consequences for the long term survival of many lemur species (Wright, 1999; Wright, Greene, Rakotonirina, & Scirbona, 2008). Understanding the interaction between canopy gaps and plant phenology and lemur ecology, behavior, and reproduction is thus critical for understanding the potential effects of anthropogenic and natural disturbance on threatened lemur populations over time. Conservation managers can use the adaptations of *V. rubra* and *E. albifrons* to natural disturbances to model responses to novel disturbances, generating more accurate predictions of species' vulnerability to extinction – for these two lemur species and potentially other arboreal mammals. With anthropogenic disturbances threatening so many species, it is essential that conservation managers improve their tools for making such predictions (van Allen *et al.*, 2012).

1.5.3 Coping with Anthropogenic Change

Finally, the human population on the Masoala peninsula is expected to grow and increase demand for conversion of forest to agricultural land, and use of timber for fuel, house construction and canoe construction (Borgerson, 2015; Kremen *et al.*, 1999). The design of MNP attempted to balance conservation needs with the needs of local populations, but recent research suggests that the local population has borne a disproportionate amount of the conservation cost, leading to wildlife-human conflict that threatens the long-term success of the park (Keller, 2008). If the park is to be successful in protecting the rich biodiversity of Masoala Peninsula, the needs of the growing human population must be met in more sustainable ways. One approach is to practice reduced impact or selective logging in existing buffer zones. While reduced impact and selective logging still have significant negative effects on many forest species, in particular arboreal ripe fruit specialists like *V. rubra* (Peres, 1994), impact can be reduced if the selective logging process can mimic key characteristics of local gap dynamics. First the key characteristics of gap dynamics must be identified and quantified. Because canopy gaps naturally increase the amount of forest edge, the use of natural canopy gaps by these lemur species provides insight into their differing responses to anthropogenic forest edges. Management plans that do not account for disturbance, either natural or anthropogenic, are doomed to fail: population dynamics in stochastic environments deviate drastically from those predicted from traditional equilibrium models (Clark, 1996; Tuljapurkar, Horvitz, & Pascarella, 2003). Given the projected increase in both natural (Ranson *et al.*, 2014; Ren *et al.*, 2011) and anthropogenic (Ganzhorn *et al.*, 1997) disturbance in Madagascar, a better understanding of the interactions between disturbances and lemur behavior and ecology is essential to their future long-term survival.

1.6 Figures and Tables

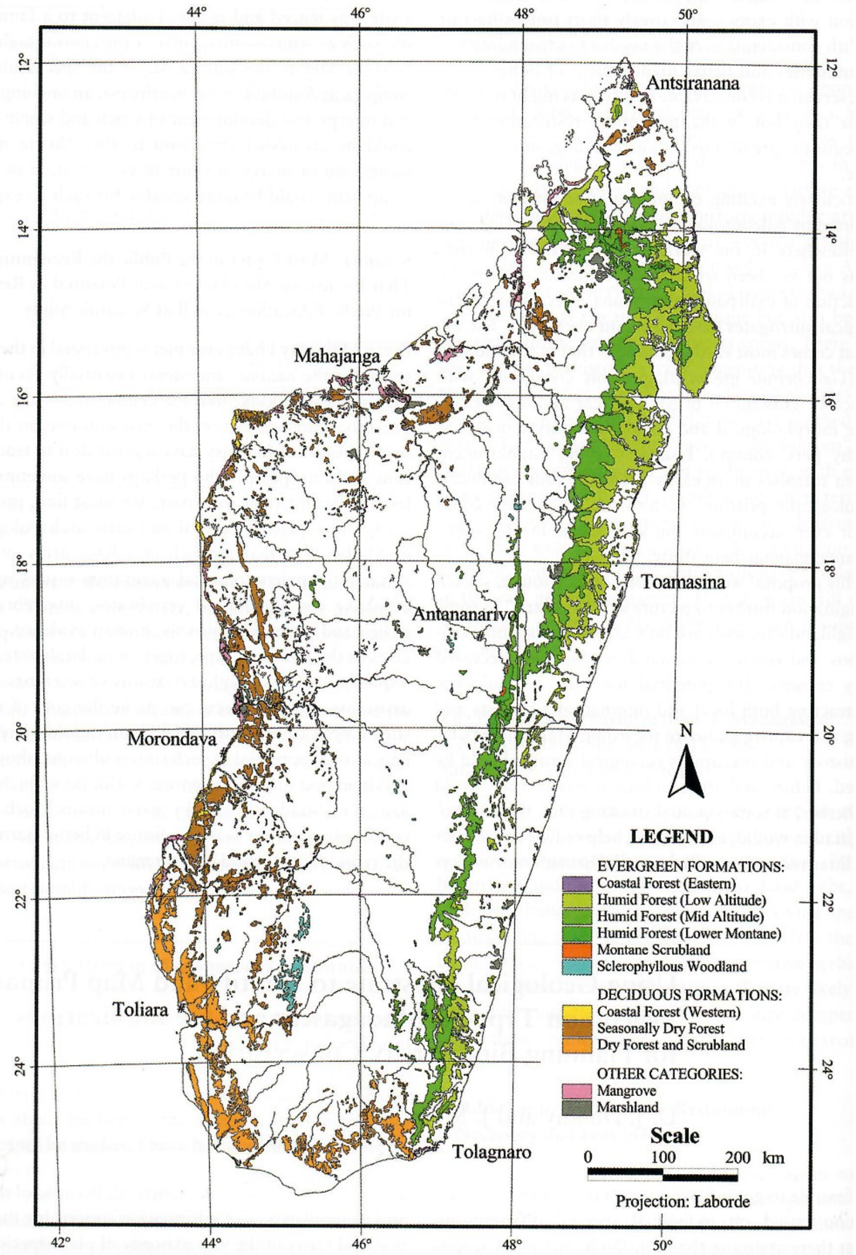

Figure 1.1. Types of primary vegetation in Madagascar. Figure from Du Puy & Moat, 2003.

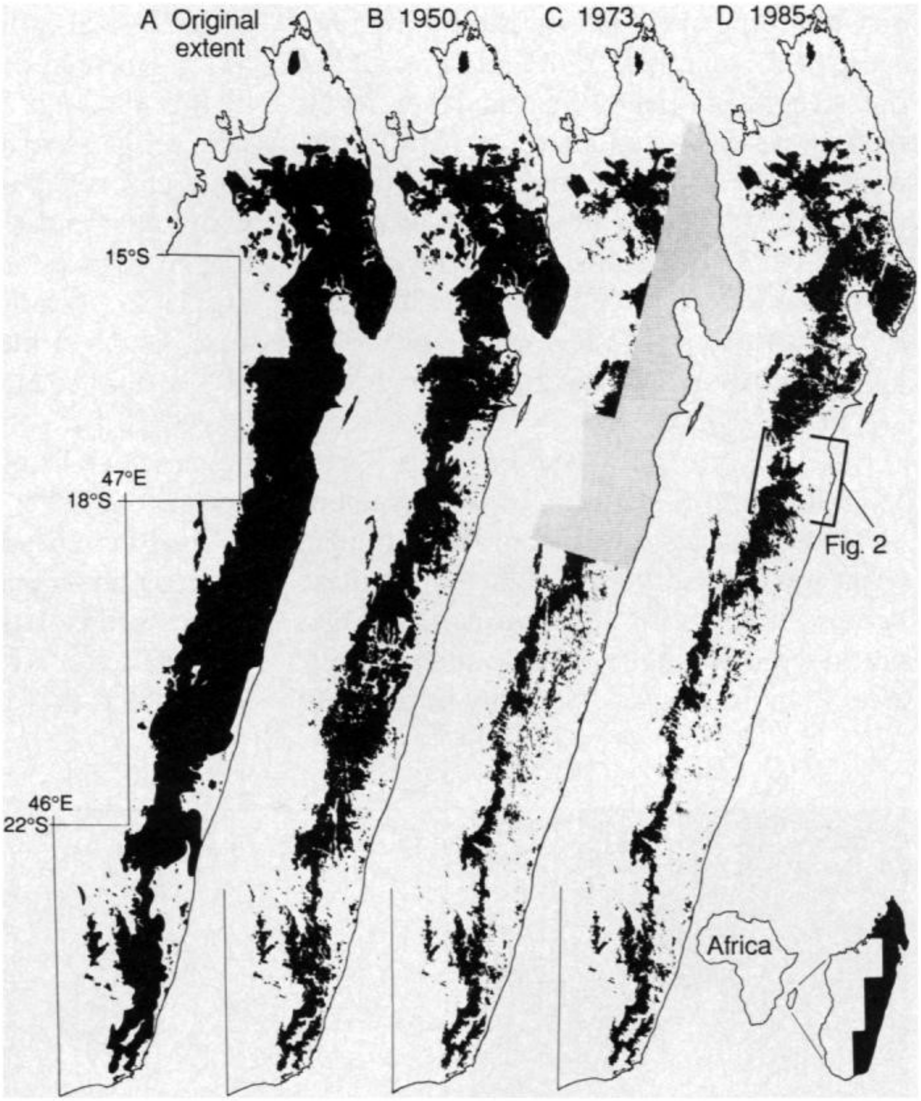

Figure 1.2. Deforestation in eastern Madagascar 1950 – 1985. Figure from Green & Sussman, 1990. Note that some satellite imagery was unavailable for 1973 map due to cloud cover.

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Chapter 2: Methods

2.1 Study Site

Field work was conducted at Andranobe Forest in Masoala National Park (MNP), Madagascar between 20 October to 18 December 2015 and 1 September 2017 to 22 February 2018. Andranobe Forest is a lowland, coastal, evergreen rain forest with a maximum elevation of 260 m above sea level. The 150 ha (1.5 km^2) area used for the study started 400 m from the Bay of Antongil and extended to 1700 m from the shore (Vasey, 2000) (Figure 2.1). MNP is designated as an IUCN category I protected area (Kremen *et al.*, 1999). Andranobe Forest is designated exclusively for research; tourists, locals, and others without an appropriate research permit are prohibited (Hatchwell, 1999). Locals have largely adhered to the use restrictions of the study site. Little evidence for large-scale illegal timber extraction or poaching existed within the study site during my research. Members of the research team frequently heard chainsaws operating on the western border of the park near the forest and fishing camp called Masiaposa throughout the 2017-2018 field season, but it was unclear whether the logging operation encroached on the MNP boundaries. The lemur populations within the forest were thus largely free of hunting pressure. Researchers have recovered shot gun shells from within Andranobe Forest (personal observation), suggesting that locals do at least occasionally hunt within the restricted area; it is uncertain what species are targeted by these hunters.

Andranobe Forest is topographically complex; the field site is divided by a prominent ridge and a path that was once used extensively by locals prior to the formation of the park and is now used primarily by researchers and park staff. Multiple small valleys flank each side of this main ridge; one of the western valleys leads eventually to the fishing camp of Masiaposa while the eastern valleys are part of the Andranobe River watershed. An extensive trail system throughout the field site was established to facilitate lemur observations (Vasey, 2006). This trail system was cleared and maintained during a series of studies from 2009 through 2018 (Figure 2.2). Trails are marked with highly visible survey flagging tape at 25 m intervals for easy navigation and accurate recording of locations.

Tropical rain forests are characterized by a difference of less than 5 °C between the warmest and coldest months of the year, and at least 100 mm of rainfall every month with only brief periods with less rainfall (Whitmore, 1990). At Andranobe Forest in 2015 and 2017 the temperature did not vary greatly between seasons or years, but rainfall did (Chapter 3). I monitored weather at Andranobe Forest for the 2015 and 2017-2018 field seasons by recording daily maximum and minimum temperatures with a Taylor Dual-Scale Maximum-Minimum Thermometer and by collecting daily rainfall with an All Weather Rain Gauge. Additionally, during the 2017-2018 field season, 50 HOBO Pendant dataloggers (Onset, Bourne, MA) were installed in selected transect trees at a height of 20 meters; these dataloggers collected temperature and light intensity data hourly. The 2015 field season coincided with the hot dry season, as defined by Vasey (2000). For the purpose of comparing seasonal differences in lemur-gap interactions, phenology, and lemur activity, I used a cluster analysis based on daily rain and temperature data collected throughout the 2017-2018 field season. The cluster analysis suggested two seasons, a dry season from September through November 2017 and a rainy season from December 2017 through February 2018 (Figure 2.3). Consequently, seasonal comparisons were restricted to just two seasons as defined by the cluster analysis: dry and rainy. The analysis was completed in R v. 3.2.3 with user interface RStudio v. 0.99.878. Results were identical regardless of whether k means or partitions around medoids (PAM) algorithms were used for the cluster analysis. These seasonal clusters differ slightly from those recorded in Vasey (2000), when the month of September was designated as a transitional month distinct from the hot dry season and December was included in the hot dry season because most rainfall in the month occurred at the very end.

Weather conditions at Andranobe Forest during the study period were similar to conditions recorded historically (Figure 2.4). From September 2017 through February 2018, the average monthly temperature maxima ranged from 23.8 °C to 27.7 °C, and average monthly minima ranged from 19.3 °C to 23.6 °C. During the same period, mean daily temperature was 24.6 °C. Historical climate data recorded at Andranobe Forest by a Peregrine Fund/MNP research assistant from 1991 through 1996 provide a basis for comparing climate data from this study (Thormstrom, unpublished data, printed with permission in Vasey, 1997). Mean temperatures from the study period were within the range recorded from 1991 through 1996. Mean monthly rainfall from September 2017 through February 2018 was 257.4 mm and ranged from 57.9 mm in September to 795.9 mm in January. September 2017 and February 2018 were drier, and January 2018 was wetter than historical rainfall for these months (Figure 2.4). For the study period, the dry season total rainfall was 293.1 mm; during the rainy season, it was 1251.5 mm. The dry season had a mean daily temperature of 23.5 °C, and the rainy season had a mean daily temperature of 25.8 °C (i.e., both were relatively hot, Figure 2.4).

The cyclone season in the Indian Ocean region is from November through May, though dates and duration vary slightly from year to year. From 2012 through 2015, no cyclones made direct contact with MNP. Consequently, the most recent cyclone pertinent to the 2015 field season was Cyclone Bingiza, which made landfall on the Masoala Peninsula in February 2011, had sustained winds of 155 km/h, and gusts of at least 185 km/h making it a Category 1 on the Saffir-Simpson Hurricane Wind Scale (SSHS) (Météo France, 2019). The next cyclone to make landfall in MNP was Cyclone Enawo in March 2017, a Category 3 on the SSHS with sustained winds of 205 km/h and peak gusts of 287 km/h (Météo France, 2019). Shortly after the conclusion of the 2017-2018 field season, Tropical Storm Eliakim impacted Andranobe Forest, making landfall in March 2018 with sustained winds of 110 km/h and gusts up to 151 km/h. Tropical storms in the Indian Ocean are not usually categorized according to the SSHS; Météo France lists Eliakim as a tropical storm rather than a cyclone, but using the SSHS, it was a Category 1 cyclone; SSHS categories are provided here to allow comparison between storms.

One of the many effects of cyclones are the creation of tree-fall canopy gaps when trees break or are uprooted by strong winds or flooding (Brokaw, 1982, 1985). In many cases, a domino effect from an initial tree fall creates large canopy gaps. The probability of multiple tree-falls increases when lianas connect tree canopies (Brokaw, 1985). Tree-fall canopy gaps are abundant throughout the Andranobe Forest. A pilot study conducted in October 2014 found 19 gaps per kilometer. Gaps ranged from 1 to 658 m^2 with a mean gap size of 63.5 m^2. The total area of canopy gaps along transects was 1967.1 m^2, and tree-fall gaps less than 100 m^2 were far more abundant than those greater than 100 m^2. Neither slope nor elevation were strong predictors of gap location or size; however, tree-fall gaps were far more likely to occur at ridgetop and convex upper slopes than at other topographic positions (unpublished data). Temporal proximity of cyclones appears to affect the number of tree-fall gaps and total gap area. Forty-four months had passed between Cyclone Bingiza and data collection in 2014. In contrast, my data collection for 2017 began only nine months after Cyclone Enawo made landfall on the Masoala Peninsula, and tree-fall gaps mapped along transects had increased from 19 per kilometer in 2014 to 45 in 2017 with a total area of 2891.7 m^2 (Chapter 3).

The high plant diversity of MNP (Consiglio *et al.*, 2006; Kremen *et al.*, 1999; Vasey, 2003) may be partially attributable to the high occurrence of cyclones and tree-fall gaps. Canopy gaps contribute to habitat heterogeneity and drive diversity in microclimate conditions, which in turn contributes to the maintenance of species biodiversity (Barik, Pandey, Tripathi, & Rao, 1992; Beck, Gaines, Hines, & Nichols, 2004; Brokaw & Scheiner, 1989; Busing & Brokaw, 2002; Chapman *et al.*, 2010; Crome & Richards, 1988; Felton, Felton, Wood, & Lindenmayer, 2006; Greenberg, 2001; Greenberg & Lanham, 2001; Gutiérrez, Armesto, & Aravena, 2004; Ostertag, 1998; Poulson & Platt, 1989; Svenning, 2000). From a survey of 1.6 km of transect trees with diameter at breast height (DBH) greater than 10 cm, 91 different vernacular species of trees were recorded at Andranobe in 2015. These trees had a mean height of 12.8 m (range = 3.6 m to 33.0 m; SE = 0.28 m, N = 303) and a mean DBH of 26.3 cm (range = 10 cm to 201 cm; SE = 3.4 cm, N = 303). To better characterize the structure of Andranobe Forest, 20 vertical line transects (Emlen, 1967) were completed during the 2017-2018 field season. Each vertical line transect (VLT) was 50 meters long. At the beginning of each VLT; I looked from the ground to the canopy and recorded the absence or presence of vegetation at 1 m height, 2 m height, 3 m height, etc. for each vertical meter up to and including canopy height. After recording vegetation absence/presence at all heights at the beginning of the VLT, I walked forward along the transect 1 m and repeated recording the presence or absence of vegetation at 1 m vertical increments. I repeated this for all 50 m of the transect. The structure of the forest was complex: multiple strata were present and contained dense vegetation, particularly in the understory (Figure 2.5).

In addition to the study species, *V. rubra* and *E. albifrons*, Andranobe Forest hosts a robust diversity of animals. Other lemurs observed at the field site during the study period include bamboo lemurs (*Hapalemur griseus)*, greater dwarf lemurs (*Cheirogaleus major),* Masoala sportive lemur (*Lepilemur scottorum*)*,* Moore's woolly lemur (*Avahi mooreorum*)*,* and brown mouse lemur (*Microcebus rufus*). Several predators were sighted regularly, including brown tailed mongoose (*Salanoia concolor*)*,* ring tailed mongoose [= ring tailed vontsira] (*Galidia elegans*), and striped civet (*Fossa fossana*)*;* two fossa

(*Cryptoprocta ferox*) and a Malagascar tree boa (*Sanzinia madagascariensis*) were also seen near camp during the study period. Birds of prey were also frequently seen, but none of the species were positively identified. Of the identified predators, *F. fossana, C. ferox,* and *S. madagascariensis* are known to consume lemurs. Many raptors in the region prey upon lemurs, particularly on smaller bodied lemurs like *E. albifrons*. Vasey (2000, 2007) noted that *S. concolor* and *G. elegans* will climb extensively in the canopy and could pose a predation threat to *V. rubra* infants unattended in nest and stash sites.

2.2 Study Populations

Andranobe Forest is home to *V. rubra* and *E. [fulvus] albifrons*. Red ruffed lemurs are sexually monomorphic with weight ranging between 2.6 – 4.1 kg (Vasey, 2003). Although long regarded as diurnal, recent studies in captivity have shown significant nocturnal activity, leading some authors to recommend investigating cathemerality in wild populations of *Varecia* (Bray, Samson, & Nunn, 2017; Rea, Figueiro, Jones, & Glander, 2014). Studies conducted on *V. rubra* at Andranobe since 2007 have habituated the population to human presence (Vasey, Mogilewsky, & Schatz, 2018). Preliminary results from an on-going, long-term demographic study on which I am collaborating indicate that Andranobe Forest is home to about 40 *V. rubra*; this population has remained relatively steady for the duration of the study (2007 to 2018) (Vasey and Borgerson, 2009; Vasey and Mogilewsky, unpublished data). This makes the population density at Andranobe higher than any other known population of *Varecia* in Madagascar (Vasey, 2003).

White-fronted brown lemurs are sexually dichromatic; males have white pelage around the face, on the forehead, and chin while females have brown pelage on and around the face. Both males and females weigh between 1.6 – 2.3 kg (Junge *et al.*, 2008). As is characteristic for *Eulemur* taxa*, E. albifrons* are cathemeral (Johnson, 2006; Tattersall, 2008). Based on a 2018 survey of lemurs at Andranobe, *E. albifrons* was the most frequently encountered of all lemur species and estimated to have significantly higher population density than *V. rubra* (Andriamahaihavana, unpublished data). During this study, I observed one community of *V. rubra* with an estimated size of 30 – 40 individuals and four to five groups of *E. albifrons* with an estimated combined total of 20 – 35 individuals. No individuals of either species were tagged for this study.

2.3 Study Design

2.3.1 Transects

My goal was to determine if the presence, location, and distribution of tree-fall canopy gaps influenced lemur behavior. Towards this end, I compared the characteristics of trees visited by the lemurs, hereafter referred to as lemur trees, to characteristics of trees sampled in transects, hereafter referred to as transect trees. Lemur trees, identified during focal animal sampling, were trees occupied by the focal animal on a time point. They were flagged and later re-visited for collection of ecological and phenological data.

Transects were used to select a random sample of control trees. At the beginning of the 2015 field season, 16 transects were established at five different topographic/aspect strata, dictated by the local geography: east valley, east mid-slope, ridgetop, west valley, and west mid-slope. Each transect was 100 m long x 2 m wide, and the starting location and compass direction of each transect was determined randomly within each stratum. This stratified random design allowed statistical analysis to account for known topographic influences on microclimate and phenology, and a power analysis of 2015 data confirmed that the transect tree sample size was adequate to detect medium to large effects. While botanical transects are often a kilometer long, the short length (100 m) of our transects ensured that an individual transect would not cross multiple topographic strata. In each transect, an aluminum forestry tag with a unique identification number was affixed to all trees with a diameter at breast height (DBH) of 10 cm or greater (= transect trees). Trees were included as transect trees if any part of the tree, including visible roots, intersected with any part of the 2 m wide transect line.

At the beginning of each field season, geographic, morphological, and phenological data were recorded for each transect tree (Table 2.1). I also measured the distance from each transect tree to the nearest canopy gap and the width and length of that gap (Figure 2.6). To measure length, I stood immediately under the leaves at the edge of the canopy gap (perpendicular to gap length and width) and used a Laser Technology, Inc. TruPulse 200 rangefinder to measure to the opposite side of the gap. I repeated this process to measure the width. The TruPulse 200 automatically calculates true horizontal distance (distance parallel to ground), eliminating the need to do calculations based on the true distance between the instrument and the target. Gaps were defined as "a hole in the forest extending through all levels down to an average height of two meters above ground" (Brokaw, 1982, p 159). Because vegetation within gaps grows relatively rapidly, this definition restricts the scope of this study to recent gaps made within three to five years. Most gaps older than five years would have regrowth in excess of two meters in height. Percentage of gap still open was estimated visually. Gap area was calculated using the formula for the area of an ellipse and the measured gap width and length, then multiplied by the percentage of the gap still open:

$$\text{Gap area } (m^2) = \pi * (1/2 * \text{ gap length}) * (1/2 \text{ gap width}) * \% \text{ of gap open}$$

The number of transects was reduced from 16 to 10 for the 2017-2018 field season to reduce the time required to collect phenology data. See Figure 2.7 for the locations and topographic positions of the ten transects used in both 2015 and 2017-2018 field seasons. The distance of each transect tree to the nearest gap was re-measured at the end of the 2017-2018 field season because gaps change over time, e.g. some decrease in size as edge vegetation grows towards the center of the gap.

All transect and lemur trees were mapped using a handheld Garmin GPSMAP 62st. GPS accuracy varied from ±2 m to ±10 m. GPS coordinates were not recorded when accuracy was not within 10 m. The Garmin was also used to record elevation. I used the. TruPulse 200 rangefinder collect gap measurements and tree height. During pilot studies in 2014 and 2015, team members successfully measured tree height and crown diameter with the rangefinder for all but one of 453 tagged trees (Mogilewsky and Vasey, unpublished data). The low canopy (≤ 35 m) of Andranobe Forest contributed greatly to this success. Visual height estimates were largely consistent with rangefinder measurements (Vasey *et al.*, 2018). In the rare occurrences when topography or adjacent trees prevented accurate measurement with the rangefinder, I visually estimated tree height. When possible, a botanical sample from each recognizably different type of tree and liana was collected using a Big Mouth Pruner (® Jameson) attached to fiberglass poles (® Jameson) collection poles. To ensure the collection of fertile samples (i.e., bearing the fruits or flowers necessary for species identification), collection took place throughout the project duration, timed with flowering and fruiting periods. A parabotanist from the Masoala National Park's guild of guides used the samples in conjunction with a site visit to assign scientific names to a subset of transect and lemur trees.

2.3.2 Behavioral Data Collection

To understand lemur behavior at tree-fall canopy gap edges, the research team recorded behavior on focal animals using instantaneous time point sampling (Altmann, 1974). During the month-long 2015 field season, 10-minute intervals were used for instantaneous time point sampling, and researchers observed *E. albifrons* for 42 hours and *V. rubra* for 150 hours. During the seven-month long 2017-2018 field season, five-minute intervals were used, and researchers observed *E. albifrons* for 280 hours and *V. rubra* for 308 hours. Only adult subjects were used for focal animal sampling. To the greatest extent possible, researchers divided observation time evenly between species and sex (Table 2.2 and Table 2.3). While sex identification was easy in the sexually dichromatic *E. albifrons,* detecting sex in monomorphic *V. rubra* was more difficult. During focal animal sampling in previous pilot projects, all team members were consistently able to use sex-specific scent marking behavior (primarily) and sex-specific vocalizations (secondarily) to record sex of *V. rubra* individuals. In the absence of such behaviors, individual *V. rubra* that could not be confidently identified by sex were recorded as unknown and discarded from analyses of sex differences. Observations were restricted to daylight hours, from 06:00 to 18:00. Future studies may incorporate nocturnal observations to better understand how cathemerality may impact gap use.

The field site was divided geographically based on previous studies of *V. rubra* ranging patterns (Vasey, 2006). For each observation session, a region was randomly selected, a species was chosen, and observers began searching for lemurs there. The first individual of that species seen became the focal animal. At the start of each session we recorded the sex of the focal animal (if obvious), and number, age category, and sex of all conspecifics present. If a focal animal was lost, observers attempted to locate a second focal animal either in the same group or within the same region and continued observations of the new focal animal.

At each instantaneous time point, we recorded the nearest trail point and the focal animal's activity. Activities were categorized as Rest, Travel, Social Interaction, Forage, and Other. Resting behaviors included sitting, laying, sleeping, and sitting in contact with other conspecifics but excluded grooming and maintenance behaviors (urinating, defecating, etc.). Locomotion was considered travel only when it was sustained for more than 30 seconds and involved movement from one tree to another. Within-tree locomotion was not recorded as travel. Social interaction included active socialization between two or more conspecifics, including allogrooming, mutual grooming, nursing, vocalizations, and play, but excluded passive social interactions like sitting or sleeping in contact. Foraging included actively searching for and assessing food, movement within a food tree, and the processing and ingestion of food. Finally, the “Other” category included self-maintenance behaviors like self-grooming, urination, defecation, and scent-marking, among others. To establish which trees *V. rubra* and *E. albifrons* used for daily activities, tree locations of individuals at each time point were flagged. The day following observation sessions, geographic, nearest gap, morphological, and phenological data were recorded for each lemur tree (Table 2.1) for later comparison of lemur and transect trees.

During the first two months of the 2017-2018 field season, the study subjects at Andranobe Forest were less habituated to human presence than during the remainder of that field season or in 2015. Groups of *E. albifrons* frequently ceased foraging and resting after spotting a researcher and instead exhibited increased vigilance and anti-predator behaviors like vocalizing, defecation, movement into higher strata and/or into liana tangles – sometimes even fleeing. Researchers no longer provoked a noticeable response for either species after about five to six weeks. As a result, observation hours for September and October 2017 are lower than for November 2017 – February 2018, especially for *E. albifrons*. Evening hours, 15:30 to 18:00, are under-represented as well; as researchers became fatigued over the course of the day, the likelihood of losing the target subject increased and the probability of finding another subject declined. This problem was exacerbated by poor lighting near dusk and team members' need to return to camp before dark.

2.3.3 Phenological Data Collection

Tree-fall canopy gaps potentially affect plant productivity and timing of phenology. To understand the interaction of canopy gaps, phenology, and lemur behavior, phenological data were collected from transect and lemur trees. Data were collected following best practices as described in Denny *et al.* (2014) for all transect and lemur trees with a DBH greater than 10 cm. For each tree and, in 2017-2018 only, for associated lianas, the percent of mature leaves, new leaves, buds, flowers, and fruits was visually estimated using binoculars and recorded as a continuous variable from 0 to 100%. Because observations were made from the forest floor, visual estimates of new leaves, buds, flowers, and fruits were necessarily based on the bottom and sides of tree crowns. The sampling method allowed detection and quantification of the high variation in phenological stages within tropical forest communities (Denny *et al.*, 2014). Transect trees were monitored every three weeks for the 2015 field season and biweekly during the 2017-2018 field season. Because only tree phenology was recorded in the 2015 field season, we successfully monitored 16 transects; the number of transects was reduced to ten for the 2017-2018 field season to allow phenology of all lianas at the canopy level to be recorded in addition to tree phenology. The transects allowed consistent monitoring of 303 trees and 261 lianas. To ensure that comparison of phenology data between transects was valid, all transects were completed within three days. This limited the number of transects that could be included as team members were only able to complete two to four transects a day, depending on the density of lianas in the transect trees. Lemur trees were monitored once, on the day following observation of the lemur in that location; the number of lemur trees and associated lianas monitored by lemur species and week (Table 2.4).

Interobserver reliability tests were used to ensure data quality between team members. However, weather conditions likely caused some variation in data quality; small fruits - particularly green fruits - buds, and new leaves were more difficult to detect during low light and heavy rain conditions. In a few extreme cases, heavy rainfall reduced visibility through binoculars to such an extent that phenology collection was deferred a day. In these cases, phenological data of some transects were not completed exactly two weeks apart during the 2017-2018 field season. Lemur trees were sampled multiple times if the tree was visited in multiple observation sessions. Such repetitions were noted and addressed appropriately in the analysis stage. Local guides provided the vernacular name for all trees and some lianas. A local parabotanist and professional MNP guide was hired in February to identify transect and lemur trees to family, genus, and, when possible, to species.

2.3.4 Microclimate Data Collection

Tree-fall canopy gaps alter microclimates by increasing light intensity in the immediate vicinity. Such alterations of microclimates offer lemurs at Andranobe Forest opportunities for behavioral thermoregulation. Thus, we installed HOBO Pendant dataloggers (Onset, Bourne, MA) to record temperature and light intensity in transect and lemur trees to test for microclimate variation related to canopy gaps. All data loggers were installed in the canopy between 15-20 m high using a slingshot/pulley system (Figure 2.8). To accomplish this, a lightweight throw line was tied to a 12 oz weight bag and launched over a branch of the appropriate height using a Big Shot Arborist Throwline Launcher (® Jameson). Once the line was successfully placed, the throw weight was replaced with a HOBO datalogger and both ends of the line were secured to form a loop. This loop allowed researchers to easily pull the datalogger up to the target height of 15-20 m and retrieve the datalogger. The throw line was securely tied to a nearby sapling or small tree to prevent accidental displacement. Data were downloaded from the data loggers in December 2017 and again in February 2018 and stored on an external hard drive. Forty data loggers were permanently installed in a randomly selected sub-sample of transect trees, 10 loggers in each topographical/aspect stratum. An additional 10 data loggers were installed for a randomly selected sub-sample of ten lemur trees the day after lemur observations took place and lemur tree locations had been established. These 10 data loggers were removed a week later to a new sub-sample of the most recently visited lemur trees. Moving data loggers each week allowed us to capture possible differences in microclimate preferences over time.

2.3.5 Nutritional Data

2.3.5.1. Sample Collection

To test for an effect of the distance to the nearest gap on nutrient availability, fruits and new leaves were sampled from tree-fall canopy gap edges and from closed canopy forest. Collection of botanical samples was authorized by Madagascar's Director of Protected Terrestrial Areas via research permits 189/17 and 006/18. Over a three-month period (December 2017 – February 2018), samples were collected from Andranobe Forest one to two days each month; collection was timed so that samples were quickly transported to Maroantsetra for drying in a small portable oven. Samples quickly molded or rotted if stored without drying. Drying samples in the field was not possible due to lack of power for an oven and lack of personnel needed to attend drying by fire. The research team only collected whole, ripe fruits and intact, young leaves known to be consumed by *V. rubra* or *E. albifrons*. When possible, team members used botanical collection poles with a maximum length of 4.8 m to gain access to samples from the canopy. However, in most cases, the height of the canopy and location of the fruit located therein exceeded the length of the collection poles, and most samples were collected opportunistically from the ground. A paired-sample method was used: for each tree of an operational taxonomic unit (OTU) (based on vernacular name) one L of material from each of two to three trees located at tree-fall gap edges and two to three trees located under closed canopy. However, in many cases, a particular tree of a given OTU would only be producing lemur-selected food at a gap edge or under closed canopy, but not in both locations (Table 2.5). This may reflect some microhabitat specialization by tree types but could be the result of sampling constraints. Such constraints included limited access to samples at canopy level, high predation rates of samples fallen to the ground, short collection period (only six days over three months) and the asynchronous phenology typical of trees in the tropics. In general, team members found that fruit, at least fruit accessible for collection, was not abundant under closed canopy. Sample details are provided in Table 2.5

2.3.5.2 Sample Preparation

In the laboratory, nutritional samples were processed to reflect those plant parts consumed by the lemurs. For example, for fruits where only flesh was eaten, seeds and skin were removed from the sample prior to drying. In many cases, the lemurs swallow pulpy flesh and seeds in their entirety, discarding tough skins. In such cases, fruit and seeds were dried, even though much of the seed passes through the gut undigested. A small, electric portable oven dried all samples at around 55°C to prevent mold and mildew. Drying time varied greatly by sample. Dried samples were wrapped in clean paper and sealed with silica desiccant in plastic storage bags. Despite these precautions, seven of the 63 samples developed fungal contamination prior to lab analysis and were discarded. In total 55 samples were analyzed for macronutrient content. Samples were shipped to the Department of Animal Biology, Universität Hamburg, Hamburg, Germany, and processed by university staff following methods published in Bollen *et al.*, 2004. Laboratory analysis provided the following data as a percent of dry ash for each sample: nitrogen, soluble proteins, neutral detergent fiber, acid detergent fiber, sugar, condensed tannins, polyphenols, fat, and ash. Crude protein was calculated by multiplying the percent of nitrogen by conversion factor 6.25 (Ortmann, Bradley, Stolter, & Ganzhorn, 2006). This conversion factor has been challenged in recent years, but as of yet no single alternative has been universally accepted in its place; it was used here to allow for comparison with a wide range of previous studies of primate diets (See Rothman *et al.*, 2012 for detailed discussion). The ratio of protein-to-fiber, a measure of dietary quality, was calculated using crude protein values and acid detergent fiber and used to compare with other published studies. Energy was calculated via the following equation:

$$ME = (9 \times L) + (4 \times SP) + (4 \times SC) + (3 \times [NDF \times 0.353])$$

where ME is the metabolizable energy per gram (in kcal g-1) of diet; L is the proportion of lipids; SP the proportion of soluble proteins; SC the proportion of structural carbohydrates, and [NDF x 0.353] is the fraction of neutral detergent fiber which are digested by ruffed lemurs (Campbell, Williams, & Eisemann, 2004). Total nonstructural carbohydrates (TNC) were used as a proxy for easily digestible carbohydrates and was calculated by the following equation:

$$TNC = 100\% - \text{Crude Protein} - NDF - \text{Lipid} - \text{Ash}.$$

2.3.6 Ethical Note

All research personnel and proposed methods abided by the International Primatological Society's Code of Best Practices for Field Primatology (Riley, Mackinnon, Fernandez-Duque, Setchell, & Garber, 2014); the protocol was approved by

Portland State University's Institutional Animal Care and Use Committee (PSU IACUC Protocol # 48). Madagascar's Director of Protected Terrestrial Areas authorized research permits 251/15, 189/17 and 006/18 for this project. Transport of botanical samples from Maroantsetra to Antananarivo was completed after receiving authorization to transport permit 182/18, issued by Madagascar's Director of Forests. The botanical samples were shipped to the Department of Animal Biology, Universität Hamburg, Hamburg, Germany, authorized by export permit 366N-EV12/MG18. The field research team included the primary investigator, Monica Mogilewsky; biology students from the Department of Animal Biology at the University of Antananarivo, Zo Fenosoa (2015) and Antonin Andriamahaihavana (2017-2018); and local forest guides, Alex, Be-Rozah, Geraldo, Jacquaria, Leon-Charles, and Nary. Data collection proceeded only after team members received training in field methods and passed inter-observer reliability tests administered by the primary investigator. The primary investigator administered inter-observer reliability tests for focal animal and phenological sampling every three months to detect and address drift in data collection methods.

2.4 Statistical Analysis

All statistical analyses were conducted using software R v.3.5.3 (R Core Team, 2012) and user interface RStudio v.1.1.463 (RStudio, 2012). Because gap effects extend beyond the immediate edge of the canopy gap, I used microclimate data as the basis for changing the continuous variable of distance from gap edges to discrete categories, either gap or closed canopy. Microclimate data were collected in October 2015 at 0, 5, 15, and

25 meters from a gap edge. Maximum light intensity leveled out between 15 and 25 m, but maximum temperature leveled out between 5 and 15 m. Mean light intensity and mean and minimum temperature did not vary by distance from the gap. Based on the combination of maximum light intensity and temperature gradients, I defined all trees located between zero to nine meters from a gap edge as being sufficiently influenced by gap effects to be gap trees; trees more than nine meters from the nearest gap edge were considered to be under closed canopy.

For the comparison of data from 2015 to data from the dry season, 2017, I used a Kruskal-Wallis one-way analysis of variance to test for significant differences between distance to the nearest gap for *V. rubra*, *E. albifrons*, and transect trees for each condition (pre- and post-cyclone). A post-hoc pairwise comparison was used to determine which groups had significant differences from one another using a Mann-Whitney U test (also known as a Wilcoxon rank sum test) and applying a Bonferroni correction for multiple pairwise comparisons. I used a chi square test of independence to assess whether post-cyclone activity budgets were significantly different from pre-cyclone activity budgets; activity budgets were calculated and analyzed separately for each species.

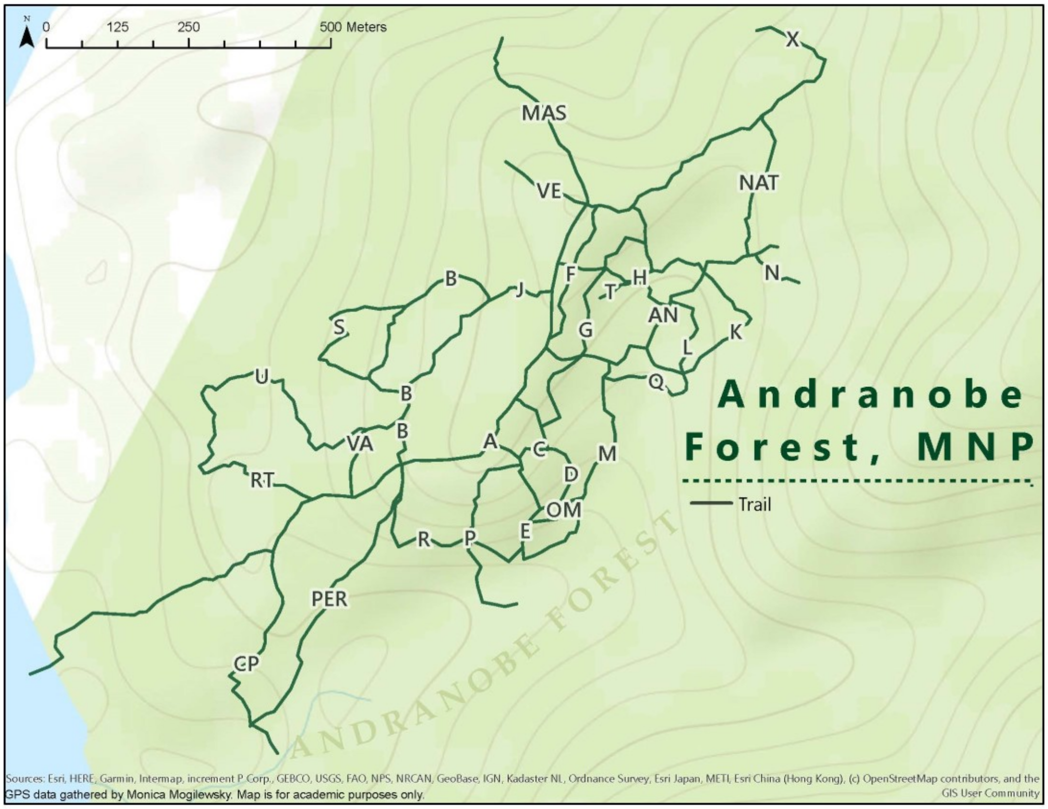
For analysis of 2017-2018 phenology data, I used non-metric multidimensional scaling (NMDS) to reduce the dimensionality of the tree data and better visualize the relationship between tree type, microclimate data, tree morphology, gap data, and tree phenology. NMDS attempts to place more similar objects together after reducing multivariate data to a small number of composite variables, preserving only rank ordering of the original distances (Kenkel & Orloci, 1986). Stress values are used to evaluate the fit of the data to the reduced dimensionality; a stress of 0.3 is considered arbitrary, 0.1 is considered a fair fit, and 0.05 is considered a good fit (Buttigieg & Ramette, 2014). Euclidean distances, 20 iterations (“runs”) and three axes were used for the NMDS. I z-transformed all variables prior to analysis. Data were then log transformed to dampen the impact of extreme values.

For analysis of 2017-2018 tree phenology variables and distance to the nearest gap, the glmer function of the lme4 package developed for R was used to fit general linear mixed-effects models (GLMMs) (Bates, Machler, Bolker, & Walker, 2015). For all GLMMs, the simplest model with the lowest AIC score was selected as the best model for each response variable. Continuous variables were scaled to standardize values with different units of measurement prior to fitting models. Standardized regression coefficients (β) were used to assess relative strength of the effect of each independent variable. The sign of β indicates the direction of the relationship: a positive β value indicates a direct relationship between the independent and response variables while a negative β value indicates an inverse relationship.

Prior to statistical analysis of nutrient content of lemur food items, log transformations were applied to nitrogen, crude protein, and soluble protein data, and to the calculated ME. I then used two sample t-tests to test for significant differences between canopy gap edges and closed canopy for percent nitrogen, percent crude protein, percent soluble protein, CP:ADF, ME, and TNC. I used two tailed t-tests to test for significant differences between canopy gap edges and closed canopy for condensed tannins and polyphenols.

2.5 Figures and Tables

Figure 2.1. Location of study site. All data were collected at Andranobe Forest, in Masoala National Park, northeast Madagascar.



Sources: Esri, HERE, Garmin, Intermap, increment P Corp., GEBCO, USGS, FAO, NPS, NRCAN, GeoBase, IGN, Kadaster NL, Ordnance Survey, Esri Japan, METI, Esri China (Hong Kong), (c) OpenStreetMap contributors, and the GIS User Community

GPS data gathered by Monica Mogilewsky. Map is for academic purposes only.

Figure 2.2. Trail system at study site. Trails used by researchers at Andranobe Forest during 2015 and 2017-2018 field seasons. Dark green lines indicate the trail system at the time of the study period and letters indicate the name of the trail. Trails were cleared of brush, flagged every 25 m, and maintained by the research team during the study period.

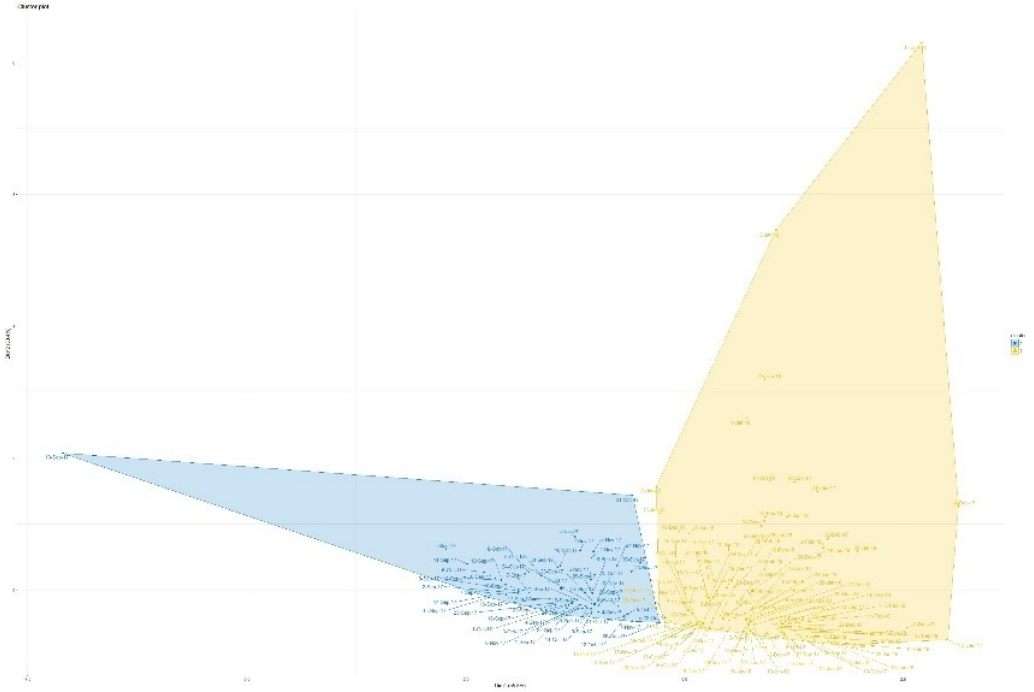


Figure 2.3. Cluster analysis for defining seasons. Daily rainfall, minimum and maximum temperatures from September 2017 through February 2018 were used in the cluster analysis, resulting in two clusters. The blue cluster (left cluster) included most of September, October, and November dates and was designated as the “dry season.” The yellow cluster (right cluster) included most of December, January, and February dates and was designated as the “rainy season.”

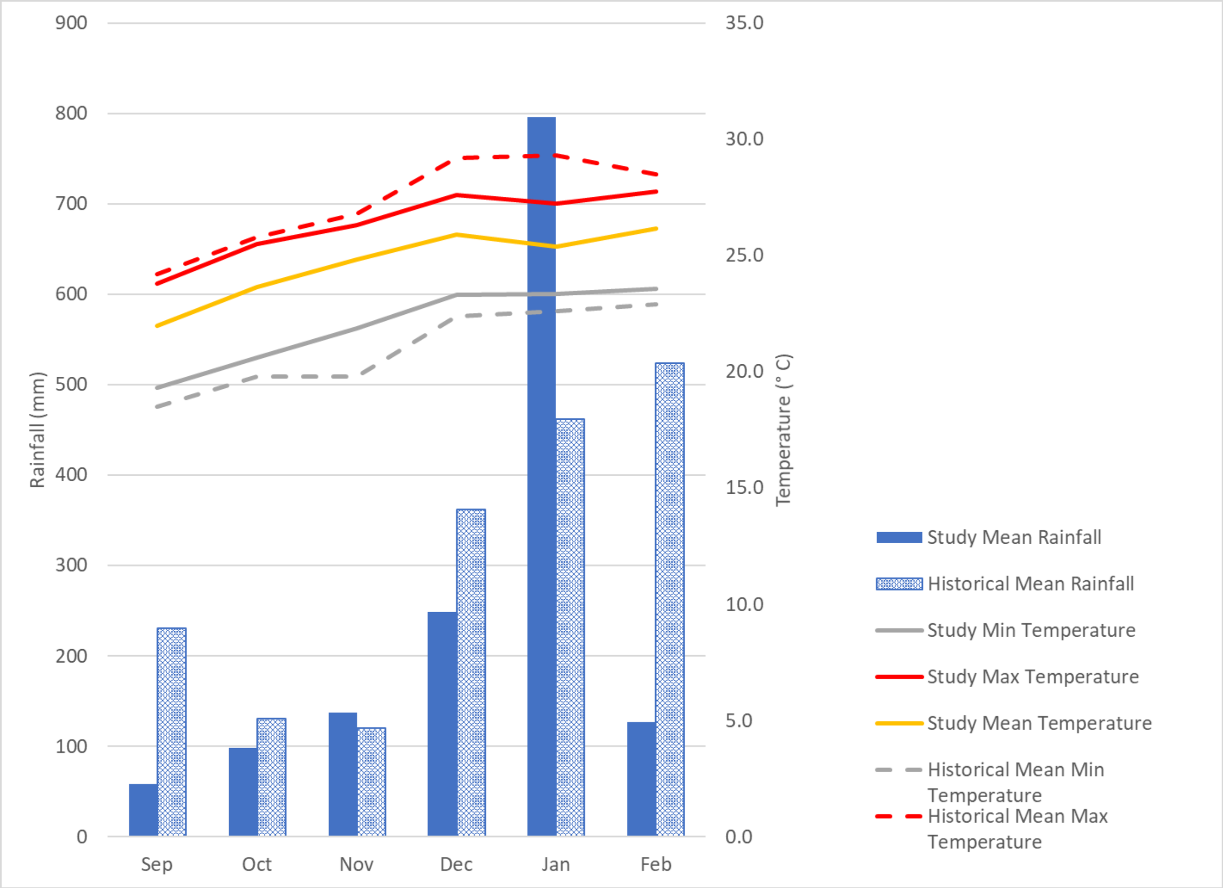


Figure 2.4. Weather at Andranobe Forest. Study data were collected from September 2017 through February 2018. Weather station was located at the campsite, approximately 0.5 km from the shore of the Bay of Antongil. Historical data were collected from November 1991 through December 1996 by Peregrine Fund staff (used by permission in Vasey, 1997).

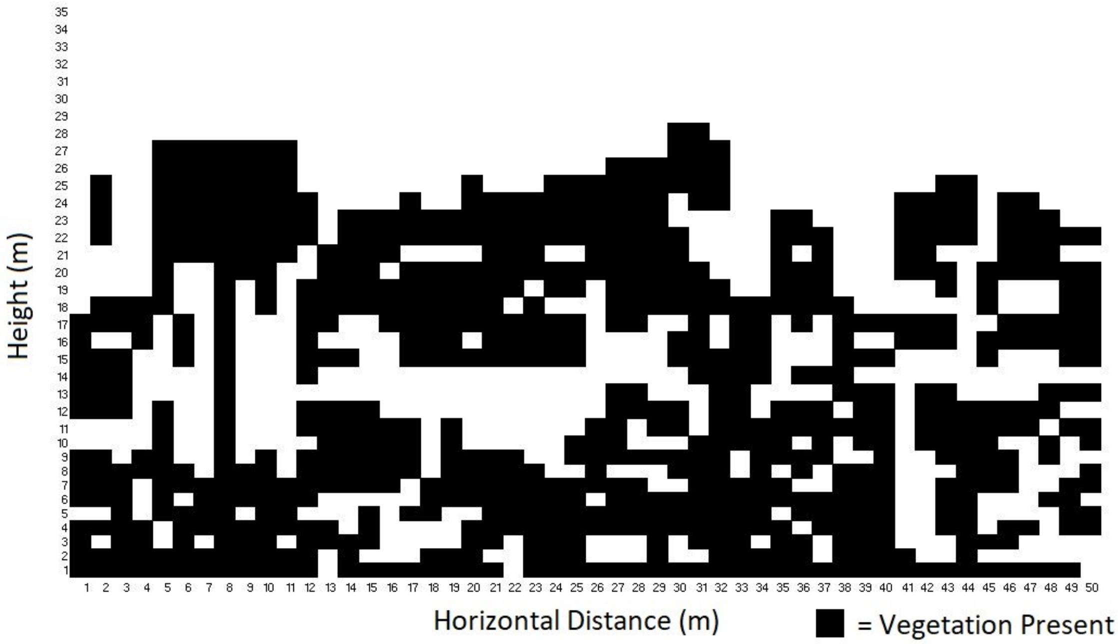


Figure 2.5. Diagram of representative vertical line transect (VLT). This VLT was located at Trail A1400, and is one of ten vertical line transects, each 50 meters long. Vegetation was recorded as present (black block) or absent (white block) at one-meter intervals vertically and horizontally.

Geographic
Location
Elevation
Topographic Level
Nearest Gap
Width
Length
Area
Tree Morphology (Trees with DBH ≥ 10cm)
Diameter at breast height (DBH)
Height
Vernacular
Samples for Identification
Phenology (Trees and Lianas)
Percent Mature Leaves
Percent New Leaves
Percent Buds
Percent Fruit
Percent Flower

Table 2.1. Data collected for transect and lemur trees. For transect trees, geographic and tree morphology were collected once, nearest gap data were collected in September 2017 and February 2018, and phenology data were collected bimonthly. For lemur trees, all data were collected within three days of being flagged during focal animal sampling.

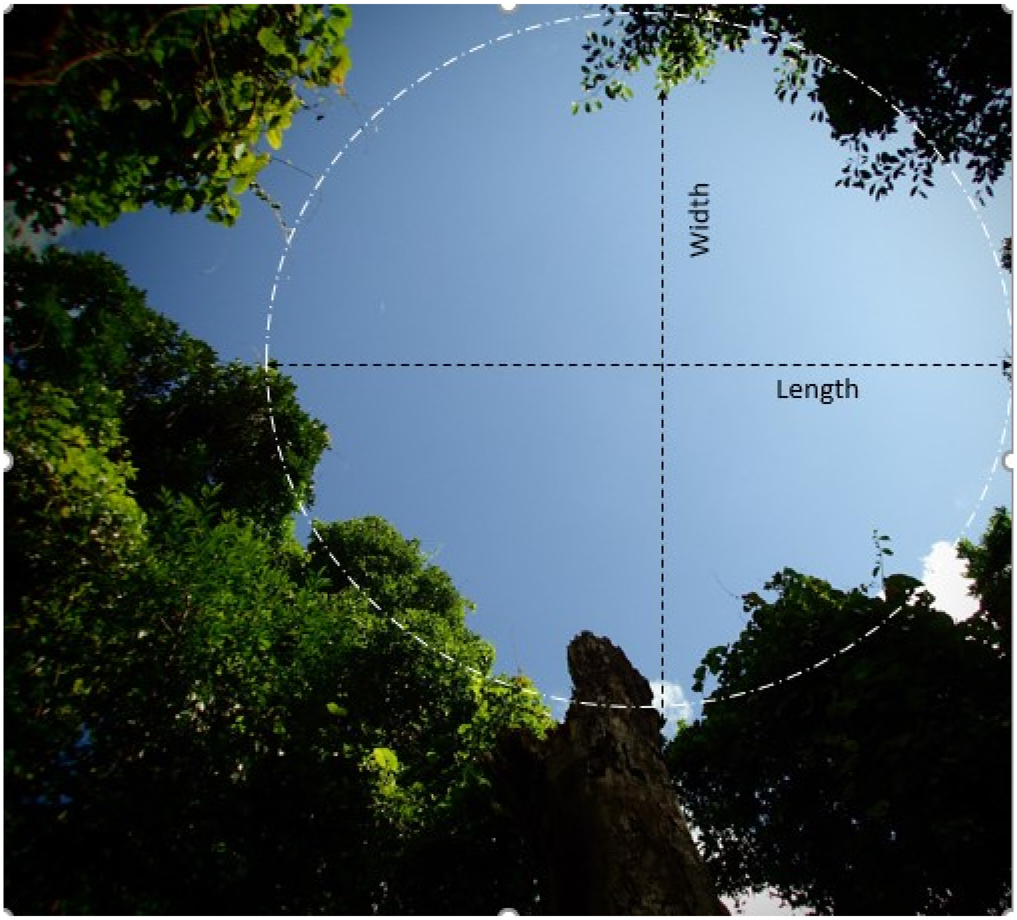
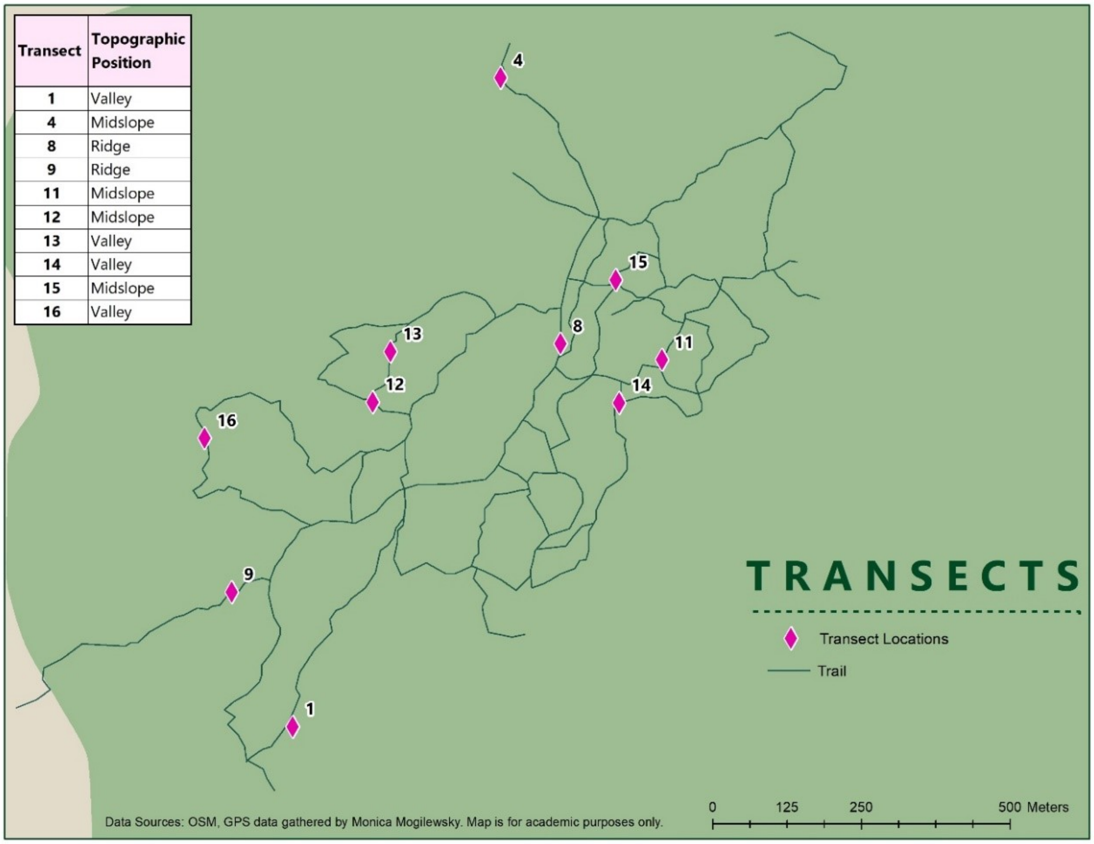


Figure 2.6. Diagram of tree-fall canopy gap measurements. Gaps were measured from canopy edge, not from tree trunks along the canopy edge.



Transect	Topographic Position
1	Valley
4	Midslope
8	Ridge
9	Ridge
11	Midslope
12	Midslope
13	Valley
14	Valley
15	Midslope
16	Valley

Data Sources: OSM, GPS data gathered by Monica Mogilewsky. Map is for academic purposes only.

Figure 2.7. Location of tree and gap transects. Transects were used for tree phenology during 2017-2018 field season. Transects were also used to map and measure gaps in September 2017 and February 2018. Transects eight and nine were located along a ridge that passes through the study site. Transects 4, 11, 12 and 15 were located mid-slope between the ridge and valley bottoms, and transects 1, 13, and 16 were located at valley bottoms. Each transect was 100 meters long.

	Male	**Female**	**Unknown/ Unrecorded**	**Total**
V. rubra	145	127	36	308
E. albifrons	150	129	1	280

Table 2.2. Hours of observation by sex in 2017-2018 field season. Sessions where the sex of the subject was not recorded or determined were excluded from all analysis of sex differences.

	Sept	**Oct**	**Nov**	**Dec**	**Jan**	**Feb**	**Total**
V. rubra	45	47	53	52	55	55	308
E. albifrons	18	24	56	66	64	52	280

Table 2.3. Hours of observation by month in 2017-2018 field season. The number of observation hours for *E. albifrons* increased over time as groups of this species became more habituated to the presence of researchers.

Month	**Week**	***E. albifrons***		***V. rubra***	
		Trees	Lianas	Trees	Lianas
Sept	0	10	13	5	6
Sept	1	7	24	16	22
Sept	2	5	16	47	78
Sept-Oct	3	14	21	19	23
Oct	4	14	29	0	0
Oct	5	7	14	9	8
Oct	6	38	82	18	43
Oct-Nov	7	12	28	38	56
Nov	8	40	81	6	7
Nov	9	5	13	27	47
Nov	10	60	94	40	56
Nov-Dec	11	82	183	39	46
Dec	12	58	126	38	72
Dec	13	14	32	20	20
Dec	14	47	71	17	29
Dec	15	8	11	65	105
Dec-Jan	16	46	97	19	26
Jan	17	75	0	60	106
Jan	18	16	27	47	45
Jan	19	32	45	25	23
Jan	20	49	55	0	0
Feb	21	45	61	66	95
Feb	22	56	80	21	29
Feb	23	30	41	36	33

Table 2.4. Weekly sample size for phenological data by lemur species and week. Phenological data was not collected from trees visited by *V. rubra* in weeks 4 and 20.

Figure 2.8. Installation of microclimate data loggers. Data logger (orange box) and rope enlarged to show detail.

Local name	**Latin identification (if known)**	**Collection Month**	**Plant parts analyzed in lab**	**# Samples**
Haramibe	*Canarium madagascariensis*	Feb	Fleshy fruit	2
Haramikonkona	*Lepidotrichilia sp.*	Dec	Fleshy fruit & seed	3
Haramitsitsika	*Canarium sp.*	Feb	Fleshy fruit & seed	2
Hazinina be	*Symphonia sp.*	Jan	Fleshy fruit	3
Hazinina madinky	*Symphonia sp.*	Jan	Fleshy fruit	7
Hazomamy	*Craterispermum sp.*	Dec	Young leaves	3
Mampay	*Cynometra sp.*	Dec	Young leaves	6
Mantabaratra		Jan	Fleshy fruit & seed	8
Nanto beravina	Family Sapotaceae	Dec	Fleshy fruit	2
Rotro	Family Myrtacaea	Feb	Fleshy fruit & seed	3
Tavolo		Dec	Fleshy fruit & seed	1
Trotrokintsina	*Dicoryphe sp.*	Jan	Fleshy fruit & seed	3
Vongo madinky		Jan	Fleshy fruit & seed	3
Vongo be		Jan	Fleshy fruit & seed	4
Total				50

Table 2.5. Collection details for nutritional samples. Samples were collected for three months, from trees of 16 different vernacular taxonomy, for a total of 55 samples. Table excludes those samples discarded prior to lab analysis due to fungal contamination. Most samples represent food items included in the diets of both *V. rubra* and *E. albifrons*. However, we only observed *V. rubra* consuming the seeds of Nanto madinky raviny and only *E. albifrons* consuming the fruit and seeds of Vongo be.

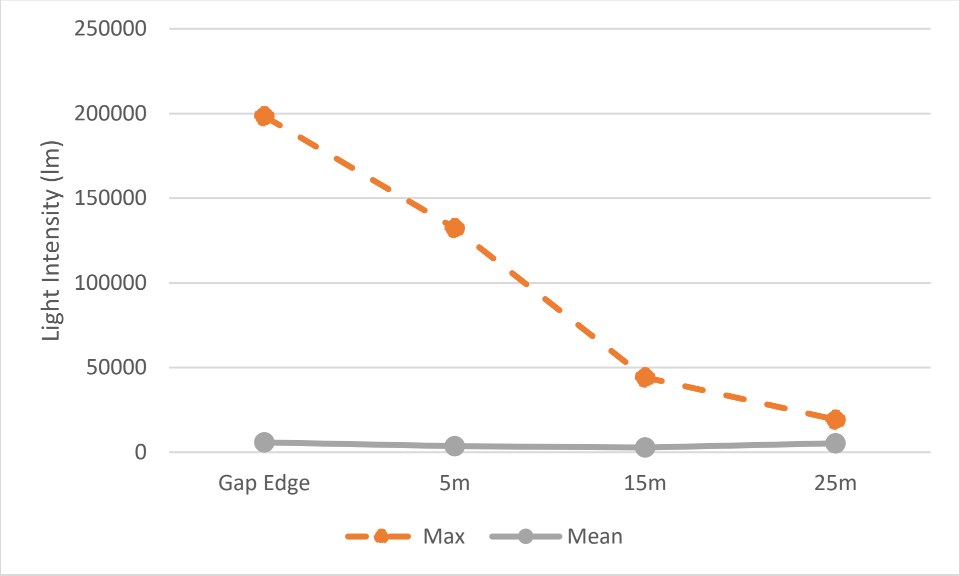


Figure 2.9. Light intensity gradient from gap edge. Data are averaged over 2 months. Distances were measured from a single canopy gap.

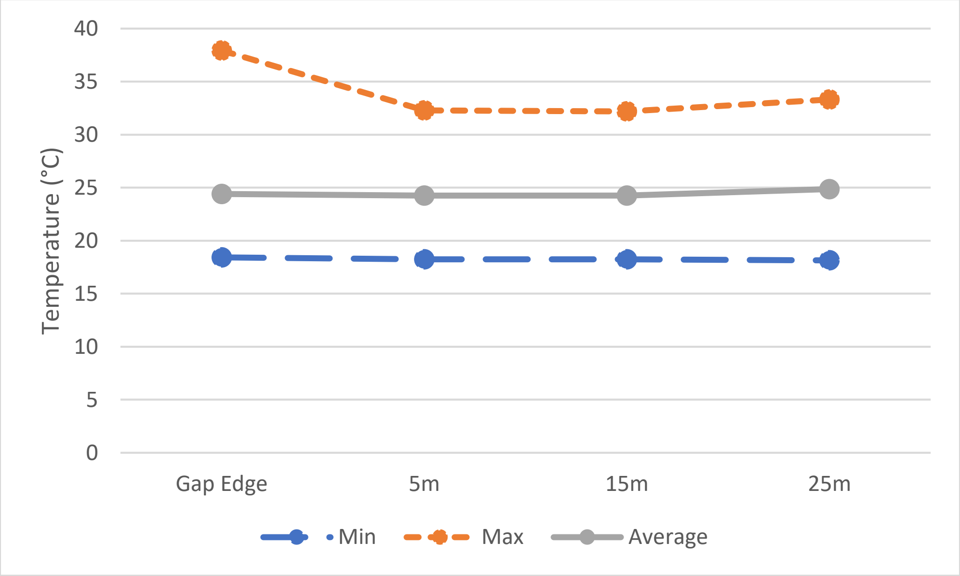


Figure 2.10. Temperature gradient from gap edge. Data are averaged over 2 months. Distances were measured from a single canopy gap.

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Chapter 3: Impact of Cyclones on Tree-Fall Canopy Gaps, Tree Phenology, and Lemur Behavior in Masoala National Park, Madagascar

3.1 Introduction

Organisms must adjust to environmental disturbances to survive and reproduce successfully. Thus, environmental disturbances have played, and continue to play, an important role in the evolution of behavior (Blumstein, 2006; Lytle, 2009). However, the exact nature and extent of these influences depend on many variables, e.g., the type, intensity, and frequency of the disturbance (Lytle, 2009; van Allen, Dunham, Asquith, & Rudolf, 2012). For the lemurs of eastern Madagascar, disturbances range from large catastrophic landscape-wide cyclones down to canopy gaps less than 100 m^2. created by a single fallen tree. These two disturbances are linked because most tree-fall canopy gaps, hereafter referred to canopy gaps, are created during or immediately following a tropical storm or cyclone (Everham and Brokaw, 1996; Burslem *et al.*, 2000; Birkinshaw and Randrianjanahary, 2007). Gaps are defined as “a canopy opening penetrating down to within 2 m of the ground” per Brokaw (1985a, p 682). The distribution and size of canopy gaps are affected by many factors, including the temporal proximity, average windspeed, amount of rainfall, and duration of the most recent tropical storms (Brokaw, 1985a, 1985b; Fraver, Brokaw, & Smith, 1998).

The impacts of cyclones on ecosystems are complex and not always immediately apparent. Certainly, cyclones can have profoundly deleterious effects on forest structure, phenology, and food availability, all of which result in decreased body weight, temporary cessation of reproductive activity, and poor health in the animal populations that live in impacted forests (Bellingham, 2008; Birkinshaw & Randrianjanahary, 2007; Lewis & Bannar-Martin, 2012; Ratsimbazafy, 2006). However in some ecosystems, cyclones may have beneficial outcomes in that they may facilitate successful plant dispersal and reproduction, create habitats that contribute to the maintenance of plant and animal diversity (Ganzhorn, 1995a), and increase forest structural heterogeneity (de Gouvenain & Silander, 2003; Franklin, Drake, McConkey, Tonga, & Smith, 2004). The tree-fall canopy gaps associated with cyclone activity generally exhibit higher plant productivity, including fruit production, than undisturbed, closed canopy forest (Beck, Gaines, Hines, & Nichols, 2004; Denslow, Moermond, & Levey, 1986). For example, some tree species in Ranomafana National Park (RNP) exhibited peak fruit production following moderate cyclones; the authors attribute this surge in productivity to rainfall (Balko & Underwood, 2005), but increased sunlight near canopy gaps may also have contributed. It is likely that the severity and frequency of the cyclone regime determine whether individuals and populations benefit or suffer, on balance, from these storms.

The evergreen tropical rain forests of eastern Madagascar experience frequent cyclones, averaging 2.2 named storm per year (de Gouvenain & Silander, 2003). Only the northwest Pacific basin has a higher annual rate of tropical storms, and lemur populations in Madagascan forests have adapted to these on-going disasters. Consequently, these forests provide excellent opportunities for exploring interactions between cyclone regimes, tree-fall canopy gaps, and frugivore behavior. Data collected before and after a cyclone may illuminate the impact of cyclones on patterns of canopy gap generation, food availability, and the adaptations of frugivores to these disturbances.

In this study I seek to document the effect of the temporal proximity of cyclones on tree-fall canopy gaps in a tropical evergreen rain forest of northeastern Madagascar. I will use these data to test the hypothesis that temporal proximity of cyclones affects the number and area of canopy gaps in a forest. I predict that the forest will have more canopy gaps and greater area within gaps during periods immediately following a cyclone in comparison to periods without cyclonic activity. I also seek to document the effects of canopy gap frequency and area on the food availability and activity budgets of frugivorous lemurs. If tree-fall canopy gaps serve as food-rich sites for frugivores, I predict an increase in the availability of food near such gaps. Specifically, I expect fruit and young leaves to be more abundant near canopy gaps than under closed canopy.

Frugivores can accommodate variation in fruit abundance caused by disturbance by altering activity budgets, foraging patterns, and perhaps even social structure (Houle, Chapman, & Vickery, 2007). Adjustments in foraging behavior are dependent on how much the disturbance alters food abundance and distribution, as well as the ecological and dietary flexibility of a given species. The most frugivorous lemurs found in the disturbance-prone forests of northeastern Madagascar are red ruffed lemurs (*Varecia rubra)* and white-fronted brown lemurs (*Eulemur [fulvus]albifrons)*. White-fronted brown lemurs are considered ecologically more flexible than red ruffed lemurs*;* while the latter are canopy-dwelling ripe-fruit specialists, the former use non-canopy strata extensively and incorporate more nonfruit food types in their diets (Vasey, 2000a). As a result of this ecological flexibility, *E. albifrons* may show a greater preference for canopy gaps as reflected in their proximity to canopy gap edges. I predict that *E. albifrons* and *V. rubra* will be found closer to gaps than expected at random and will spend more time traveling to do so. I expect that flexible use of microhabitats and strata by *E. albifrons* will result in this species being closer to tree-fall canopy gaps than *V. rubra*.

Madagascar because it ranks as one of the world's highest conservation priorities, based on measures of endemism, species diversity, and rate of loss (Brooks *et al.*, 2006, 2002; Ganzhorn *et al.*, 1997; Ganzhorn, Lowry II, Schatz, & Sommer, 2001; Irwin, Johnson, & Wright, 2005), making this a timely study. *V. rubra* were listed among the world's top 25 most critically endangered primates in 2009 and again in 2014 (Mittermeier *et al.*, 2009; Schwitzer *et al.*, 2014); *E. albifrons* is also listed as endangered by the IUCN (IUCN, 2012). Both species are apparently well-adapted to storm disturbances. In fact, *V. rubra* are found at high population densities in parts of this cyclone-prone region (Vasey, 1996, 2003). Lemurs frequently encounter tree-fall canopy gaps created by cyclonic disturbance and must adjust as gaps change in size, frequency and distribution over time. Adaptations to natural disturbances may mitigate the deleterious effects of anthropogenic disturbances for some populations (van Allen *et al.*, 2012). Consequently, data on lemur-canopy gap interactions are critical for managing populations within both intact forests and fragmented habitats.

3.2 Methods

3.2.1 Study Site

Data were collected from Andranobe Forest in the Masoala National Park (MNP), Madagascar, a World Heritage Site (Figure 3.1). Tree-fall canopy gaps are ubiquitous in Madagascar's eastern humid evergreen rainforests, including Andranobe Forest. Andranobe Forest is a lowland humid evergreen rain forest with a maximum elevation of 260 m above sea level; the 150 ha (1.5 km^2) study area is within 2 km of the Bay of Antongil (Vasey, 2000a). MNP is designated as an IUCN category I protected area (Kremen *et al.*, 1999). Andranobe Forest is designated exclusively for research; tourists, locals, and other persons without an appropriate permits are prohibited (Hatchwell, 1999). A pilot study conducted there in September 2014 recorded a gap frequency of 1 gap/50 meters of transect (unpublished data), and gaps were found at all topographic positions.

Seasons at Andranobe Forest are frequently described in terms of rainfall, with a single dry season and multiple rainy seasons differentiated by temperature trends (Vasey, 2000a). Total rainfall was 476.8 mm and 287.7 mm during the 2015 and 2017 dry seasons, respectively. The mean minimum and maximum temperatures for the dry season were similar between years: 21.7 °C and 26.4 °C in 2015 compared to 22.1 °C and 26.7 °C in 2017. During the 2017-2018 rainy season, total rainfall was 1251.5 mm, the mean minimum temperature was 23.4 °C and the mean maximum temperature was 27.5 °C. No data were collected during the rainy season in 2015. For these two study periods, at least, rainfall was more variable than temperature between years and seasons. High variation in rainfall has been recorded at other sites in Madagascar (Balko & Underwood, 2005; Dunham, Erhart, & Wright, 2010).

The study site experienced a relatively prolonged period without storm activity (Figure 3.2). No cyclones hit the Masoala Peninsula between 2012 and 2016. Although Tropical Storm Irina did impact this area in 2012, the most recent storm of cyclone-strength was Cyclone Bingiza, which made landfall on the Masoala Peninsula in February 2011, with sustained winds of 155 km/h and gusts of 185 km/h (Météo France, 2019). In March 2017, Cylcone Enawo, an intense tropical cyclone with sustained winds of 205 km/h and peak gusts at 287 km/h, passed within 75 km of the study site. Andranobe Forest did not have a weather station but based on reports from nearby towns, it likely experienced sustained winds of 154-177 km/hr and potentially as much as five meters of rain (Probst, Proietti, Annunziato, Paris, & Wania, 2017). Data for this study were collected 1) during a respite between storms, prior to Cyclone Enawo, from October 19 through December 19, 2015 and 2) after Cyclone Enawo from October 1 through December 31, 2017.

3.2.2 Study Populations

Andranobe Forest is home to red ruffed lemurs, and white-fronted brown lemurs. Both species are active during the day, although *E. albifrons* is generally considered cathemeral (Tattersall, 2008) while *V. rubra* has generally been regarded as diurnal (Vasey, 2003), although recent research has recorded cathemerality in captive *Varecia* (Bray, Samson, & Nunn, 2017; Rea, Figueiro, Jones, & Glander, 2014). *Varecia* are

Madagascar's only obligate frugivorous primates, with fruit making up to 90% of its diet in some populations (e.g., Vasey, 2003). Despite this dietary specialization, they can survive on leaves when fruits are unavailable, which occurs following intense cyclone damage. The shift to leaves may be a diet of last resort, because when not consuming their preferred diet of fruits, *Varecia* experience weight loss and cease reproduction (Ratsimbazafy, 2006). Vasey (2006) demonstrated that *Varecia* exhibit considerable variation in community size, group size, social structure, social organization and home range size and concluded that this behavioral and social flexibility may be an adaptation to maintaining a relatively narrow ecological niche (Vasey, 2000a). Similarly, researchers studying *Varecia* in southeastern Madagascar suggested that social flexibility appears to offset dietary specialization and relative sensitivity to disturbance (Baden, Webster, & Kamilar, 2016).

In contrast to *Varecia*, taxa in the brown lemur group (which includes *E. albifrons, E. albocollaris, E. cinereceps, E. collaris, E. fulvus, E. rufifrons, E. rufus,* and *E. sanfordi*, hereafter referred to as brown lemurs) are considered more ecologically flexible and more widely distributed. They occur across a broad range of forest strata, microhabitats, and feed on a wide assortment of foods (Johnson, 2002; Sussman, 2002; Tattersall & Sussman, 2016; Vasey, 2000a). *E. albifrons* exhibit dietary flexibility in at least two ways. Their diet includes leaves, insects, fungi, and sometimes even small animal prey, although fruit makes up the greatest proportion of the total diet (Sato, 2012). They also incorporate greater variety of plant parts throughout the year (Vasey, 2004).

For example, at Betampona Natural Reserve in eastern Madagascar, *E. albifrons* have been observed incorporating large amounts of nectar in their diet (Toborowsky and Andriaharimalala, 2006). *E. collaris* living in disturbed habitats show reduced consumption of ripe fruit and increased consumption of mature leaves than do conspecifics living in primary forest (Donati *et al.*, 2011), providing further evidence of dietary flexibility in brown lemurs.

3.2.3 Data Collection

I collected data from October 19 - December 19, 2015, hereafter referred to as "pre-cyclone", and from October 1, 2017 - December 31, 2017, hereafter referred to as "post-cyclone" (Figure 3.2; Chapter 2). Phenological data were collected for these two 45-day study periods in both years. In 2015, behavioral data collection spanned from November 15 – December 29, so analysis of behavioral data from 2017 is limited to the same date range, creating equal samples for analyses.

To document gap distribution and size, ten 100-m long transects were established (Schliemann & Bockheim, 2011), and situated equally along ridge tops, midslopes, and valley bottoms. To best detect and measure gaps, transects were five meters wide. For pre-cyclone data collection, 16 transects were sampled; only 10 of those 16 transects were used for post-cyclone data because of the increased time required to include crown-level lianas in the phenology data from 2017. All gaps greater than 1 m^2 that intersected the transects were mapped and measured for these variables: width, length, and percentage of the gap still open. Only those gaps created by a fallen tree were recorded as transect gaps; canopy gaps resulting from large branch falls or landslides were excluded to ensure consistent comparisons between transects and years. A handheld Garmin GPSMAP 62ST was used to record GPS coordinates for each gap and all trees. A Laser Technology, Inc. TruPulse 200 rangefinder was used to measure gap width and length, and tree height. The percentage of gap still open was approximated visually, comparable to methods for canopy cover (see Chapter 2). Gap area was calculated using the following formula:

$$\text{gap area} = (\pi * \frac{1}{2width} * \frac{1}{2length}) * \text{\% of gap free of vegetation}$$

To assess tree phenology and potential lemur food availability, the same transects (100 m long) were sampled at a two-meter width. All trees with trunks or visible roots intersecting the transects and with diameter at breast height (DBH) of 10 cm or greater were measured, tagged with a unique number, and identified with local vernacular taxonomy. Using these transect trees, phenological data were collected every three weeks in 2015 and every two weeks in 2017, using methods described in Denny *et al.*, 2014. For each tree, I scanned the crown to estimate the percent of young leaves, buds, flowers, and fruits, recording estimates as a continuous variable from 0 to 100%. Due to difficulty in discerning fine differences, the data were largely recorded in increments of 5%. Young leaves, buds, flowers, and fruits are potential food for *V. rubra* and *E. albifrons*. For analysis, a food index was created by summing the percent of new leaves, buds, fruits, and flowers. Finally, the nearest gap was located for each transect tree, and the distance to the gap, gap length, and width were measured using the TruPulse 200 rangefinder. The percentage of gap open or unfilled with vegetation was visually estimated. In many cases, the gap nearest the transect tree had already been measured as a transect gap.

To assess lemur-gap interactions, focal animal sampling of adult lemurs were conducted using 10-minute (2015) and five-minute (2017) instantaneous time point sampling to record the animal's activity (rest, travel, social interaction, forage/feed, other) (Altmann, 1974) during daylight hours. The location of the focal animal at each time point was marked with survey flagging tape and hereafter referred to as lemur trees. Only a single focal animal was followed at a time, and all subjects were adults. After three to four days of focal animal following, researchers returned to all flagged trees and recorded the distance to the nearest gap edge and the length and width of that gap. Distance to the nearest gap, gap area, morphology, and phenology from lemur trees were compared to those same data from transect trees. In cases where a flagged tree was on multiple gaps, i.e. distance to the nearest gap was zero for more than one gap, the length and width of all gaps were measured, and gap area was calculated as the sum of all gap areas. See Chapter 2 of this dissertation for further details.

Activity budgets for each species were calculated as percentage of time points for each activity category: rest, travel, social interaction, forage, other. For the pre-cyclone study period, white fronted brown lemurs were observed for 44 hours and red ruffed lemurs for 155 hours. For the post-cyclone period, white fronted brown lemurs were observed for 105 hours and red ruffed lemurs for 122 hours.

3.2.4 Data Analysis

All statistical analyses were conducted using software R v. 3.5.3 (R Core Team, 2012)and user interface RStudio v. 1.1.463 (RStudio, 2012). To compare gap number and gap area before and after Cyclone Enawo, I used one-tailed t tests for each variable. To compare food availability before Cyclone Enawo to food availability afterwards, a Wilcoxon test was used to test for significance. To address problems with unequal sample sizes, only a random subset of the data was analyzed (n = 300). I used the function "subsample" included in base R (R Core Team, 2012) to produce a random subset of my data. To test for the effect of distance to the nearest gap on food abundance, I ran an analysis of covariance (ANCOVA), with distance from the gap edge as covariate and pre- and post-cyclone as the fixed effect. Kruskal-Wallis one-way analysis of variance was used to test for significant differences between distance to the nearest gap for *V. rubra*, *E. albifrons*, and transect trees for each condition (pre- and post-cyclone). Canopy gap effects on microclimate approach zero around nine meters from the gap edge (Chapter 2). Consequently, samples were placed in one of two groups: closed canopy samples were those collected greater than nine meters from a canopy gap edge; canopy gap edge samples were those collected on a gap edge or within nine meters of a gap edge. For distance to the nearest gap data, sample sizes of transect trees and trees visited by each lemur species were not equal; data were first sub-sampled using the minimum group sample size (in this case, trees visited by *E. albifrons,* n = 95) and the "subsample" function in base R (R Core Team, 2012). A post-hoc pairwise comparison was used to determine which groups differed significantly using a Mann-Whitney U test (aka

Wilcoxon rank-sum test) and applying a Bonferroni correction for multiple pairwise comparisons. A chi square test of independence was used to assess whether post-cyclone activity budgets were significantly different from pre-cyclone activity budgets; activity budgets were calculated and analyzed separately for each species.

3.3 Results

3.3.1 Gap Distribution

There were more tree-fall canopy gaps post-Cyclone Enawo than pre-Cyclone Enawo. Pre-cyclone, 22 gaps were recorded along ten transects compared to 45 gaps recorded along the same transects post-cyclone (Figure 3.3). Total gap area increased by 67% from the pre-cyclone to post-cyclone period (Table 3.1). Neither mean nor median gap areas differed between years (Table 3.1), and thus the overall increase in gap area was due to the increase in number of gaps.

3.3.2 Food Availability Pre- and Post-Cyclone

Food availability was significantly greater six months after Cyclone Enawo than in the comparable period in 2015, prior to the cyclone (Wilcoxon test: $W = 59841$, $N = 300$, p-value < 0.001, Figure 3.4). Pre-cyclone, the mean percent of tree crowns with food was 4.7%, SD =12.0% compared to 6.8%, SD = 12.0% post-cyclone ($N = 300$). Young leaves, fruit, buds, and flowers were all considered potential lemur foods. Greater food availability post-cyclone was driven primarily by young leaves because fruit availability was consistently low both pre- and post-cyclone (Figure 3.5), though availability of both were significantly lower pre-cyclone than post-cyclone (young leaves: W = 59841, N= 300, $p < 0.001$; fruit: W = 47205, N = 300, $p < 0.05$).

3.3.3 Food Availability Near Canopy Gaps

In general, potential lemur food was found at greater distances from gap edges following Cyclone Enawo compared to before the cyclone. Pre-cyclone, most young leaves and fruit were found within 15 m of a gap edge; post-cyclone, young leaves and fruit were found at greater distances from a gap edge, with most food found within 25 m (Figure 3.6). While food availability was significantly greater post-cyclone than pre-cyclone (ANCOVA: N = 300, F = 66.3, df = 1, $p < 0.001$), distance to the nearest gap did not have a significant effect on food availability (ANCOVA: N = 300, F = 1.94, df = 1, p = 0.164). Before Cyclone Enawo, food availability near gap edges (mean = 5.2%, SD = 15.9%) was similar to food availability under closed canopy (mean = 4.3%, SD = 10.9). The same was true following Cyclone Enawo: food availability near gap edges (mean = 7.7%, SD = 14.4%) was similar to food availability under closed canopy (mean = 6.2%, SD = 8.2%).

3.3.4 Lemur Activity and Distance to the Nearest Gap

3.3.4.1 Pre- and Post-Cyclone Gap Proximity

There were significant differences in mean gap proximity for transect and lemur trees pre-cyclone compared to post-cyclone (Figure 3.7; Kruskal-Wallis: N= 95, χ^2 = 25.997, df = 5, $p < 0.001$). According to post-hoc pairwise comparisons, trees visited by *V. rubra* pre-cyclone were significantly closer to the nearest gap (mean = 2.2 m, SD = 3.4

m) than trees visited by *V. rubra* post-cyclone (mean = 5.1 m, SD = 5.8 m). Trees visited by *E. albifrons* pre-cyclone were a similar distance to the nearest gap (mean = 2.1 m, SD = 3.5 m) than trees visited by *E. albifrons* post-cyclone (mean = 3.9 m, SD = 5.3). Transect trees were also a similar distance from the nearest gap before (mean = 3.5 m, SD = 3.9 m) and after Cyclone Enawo (mean = 3.9 m, SD = 5.6 m).

3.3.4.2 Lemur and Transect Tree Comparison

Gap proximity for transect and lemur trees before and after Cyclone Enawo are presented in Figure 3.7. Pre-cyclone, trees visited by *E. albifrons* were significantly closer to the nearest gap than transect trees (mean = 2.1 m, SD = 3.5 m vs. 3.5 m, SD = 3.9 m). Post-cyclone, gap proximity for trees visited by *E. albifrons* was identical to the gap proximity of transect trees (mean = 3.9 m, SD = 5.3 m vs. 3.9 m, SD = 5.6 m). Pre-cyclone, trees visited by *V. rubra* were closer to the nearest gap than transect trees (mean = 2.2 m, SD = 3.4 m vs. 3.5 m, SD = 3.9 m), but post-cyclone, trees visited by *V. rubra* were farther from the nearest gap than transect trees (mean = 5.1 m, SD = 5.8 m vs. 3.9 m, SD = 5.6 m). However, these differences were not significant.

3.3.4.3 Pre- and Post-Cyclone Activity Budgets

Activity budgets for both lemurs differed significantly following Cyclone Enawo (Figure 3.8, χ^2 = 14,426, 4 d.f., N = 1453, p <0.001 for *E. albifrons* and χ^2 = 374, 4 d.f., N = 1327, p<0.001 for *V. rubra*). The most pronounced difference was that both *V. rubra* (33% to 13%) and *E. albifrons* (39% to 14%) traveled less (as measured by percent of timepoints spent traveling) following Cyclone Enawo (Figure 3.8). The reduction in travel coincided with a modest increase in foraging post-cyclone in *V. rubra* (19% to 22%) but substantial increase in *E. albifrons* (10% to 26%; Figure 3.8). Following the cyclone, *V. rubra* also increased the number of timepoints resting (44% to 54%) but *E. albifrons* resting time was unchanged (49% and 50%; Figure 3.8).

3.4 Discussion

As measured by both number and total area, Andranobe Forest had more tree-fall canopy gaps in October 2017, six months after a named storm, than it had in October 2015, four years after the impacts of two cyclones - Binzinga in 2011 and Irina in 2012 (Table 3.1). These results support the prediction that cyclones increase the number and total area of canopy gaps. By 2015, many canopy gaps created by Cyclone Binzinga had filled with vegetation, usually trees or lianas growing into the gap from the edges or secondary trees reaching towards the canopy. The increase in gap number and area following Cyclone Enawo likely resulted in increased light availability in strata below the canopy. Other researchers have found increased light in the understory and forest floor following cyclones, due in part to partial or complete stripping of leaves from trees (reviewed in Lugo, 2008). Canopy tree-fall gaps likely contribute to the increased sunlight that reaches below the canopy after a cyclone. It takes longer for these gaps to return to closed canopy compared to standing, living canopy trees that were temporarily denuded by storm winds. Thus, canopy gaps increase the duration of the increased light, and the subsequent increase in photosynthetic activity, forests experience after a cyclone. This impact is especially marked for lower strata at and near the gap edge.

This extended period of increased sunlight may partially explain the increase in productivity seen between the pre- and post-cyclone periods (Figure 3.4). Research on edge effects (Ganzhorn, 1995b; Lehman, Rajaonson, & Day, 2006b, 2006a), logging disturbance (Herrera, Wright, Lauterbur, Ratovonjanahary, & Taylor, 2011), canopy gaps (Beck *et al.*, 2004; Denslow *et al.*, 1986) and forest response to cyclones (Lugo, 2008) has found an increase in fruit and leaf production following these disturbances. It is plausible to attribute some of the difference in food availability post-cyclone to gaps; however, this study found no evidence for greater food availability near canopy tree-fall gaps. Most, tree-fall canopy gaps in this study were less than 200 m^2, much smaller than gaps included in other studies. The small size of the typical tree-fall canopy gap at Andranobe Forest may result in small or no change in microclimate conditions and, subsequently, plant productivity and phenology.

Plant phenology is driven by many environmental factors (Mendoza, Peres, & Morellato, 2017). Variation in fruit production and other phenological events within and among tree species is common in tropical trees (Chapman, Chapman, Zanne, Poulsen, & Clark, 2005; Couralet, van den Bulcke, Ngoma, van Acker, & Beeckman, 2013; Denny *et al.*, 2014; van Schaik, Terborgh, & Wright, 1993). For example, rainfall is often positively correlated with fruit availability (van Schaik *et al.*, 1993), although in this study, I found the opposite to be the case. Total rainfall for the 2015 field season was almost twice that of the same period in 2017, 476.8 mm versus 287.7 mm, respectively. Other potential contributors to differences in fruit availability include variation in masting by key food tree species. For example, during the 2015 field season, many of the *Canarium sp.* located on the northwest side of the study site did not fruit, but they did so during the 2017 field season. Certainly, plant phenology and subsequently food availability cannot be attributed to any one factor. However, the correlation between increased food availability following Cyclone Enawo combined with the relationship between proximity to gap edges and increased food production support the hypothesis that cyclone-created canopy gaps increase plant productivity and lemur food availability that canopy gaps created by the cyclone directly increased productivity. Additional observations of patterns across several years will help solidify data from my work.

Red ruffed and white fronted brown lemurs adjusted their activity following Cyclone Enawo in 2017 when compared to a period of relatively low disturbance, represented by data collected in 2015. As predicted, prior to Cyclone Enawo both species spent more time traveling (Figure 3.8) and maintained closer proximity to tree-fall canopy gaps (Figure 3.7) than following the cyclone. The trees visited by the lemurs during the pre-cyclone period were *closer* to tree-fall canopy gaps than expected despite fewer gaps and reduced gap area, though this was only statistically significant for *E. albifrons* (Figure 3.7). The difference in the lemurs' proximity to canopy gaps cannot be explained simply by changes in the distribution of the gaps themselves, as the distance to the nearest gap for transect trees did not change following Cyclone Enawo (Figure 3.7).

Prior to Cyclone Enawo, both *E. albifrons* and *V. rubra* were found closer to gaps than after Enawo. While both species exhibited similar habitat use with regard to canopy gaps within each study period, only *E. albifrons* maintained proximity to canopy gaps that was significantly less than the proximity of transect trees to canopy gaps and only prior to the cyclone. This supports the prediction that the ecological flexibility of *E. albifrons* allows this lemur to take greater adventure of tree-fall canopy gaps than *V. rubra*. However, this difference between species disappeared following Cyclone Enawo. The proximity to gaps by *V. rubra* was particularly surprising as this species is a canopy specialist (Vasey, 2000a). Canopy trees already benefit from increased sunlight compared to lower strata trees, and so it was unexpected that these canopy dwelling lemurs would distinguish canopy gaps from canopy tops. However, based on a comparison of trees visited by *V. rubra* and transect trees, *V. rubra* were significantly closer to canopy gaps than expected. As with *E. albifrons*, *V. rubra* increased the mean distance to the nearest gap following Cyclone Enawo. It may be that in periods with low cyclone activity, when canopy cover is denser, slowly diminishing canopy gaps provide a beneficial density of fruits, flowers, and young leaves. After cyclone activity, the entire canopy cover is less dense, and the benefits of canopy gaps may be less dramatic in comparison. During such conditions, the potential costs of proximity to canopy gaps, such as increased predation risk, may outweigh the benefits.

The positive relationship between proximity to gap edges and food availability both before and after Cyclone Enawo suggests that lemurs may perceive canopy gaps as food-rich sites. When food availability is relatively poor, as it was during the pre-cyclone study period compared to the post-cyclone study period, lemurs may choose to incur the cost of traveling to and remaining near canopy gaps for the benefit of more food. The food most strongly impacted by proximity to canopy gaps was young leaves, which are protein-rich and favored by lactating females of both species (Vasey, 2000a). In periods when storm activity has been low, tree-fall canopy gaps may be important locations for scarce young leaves and fruit. In contrast, after recent cyclone activity, lower leaf density, increased light through forest levels, and subsequent increase in tree production of leaves and fruit may decrease the value of tree-fall canopy gaps to lemurs.

To understand the complex relationship between cyclones, tree-fall canopy gaps, lemur diets and feeding behavior. more work is needed. For the purposes of this study, all trees visited by lemurs were treated equally. However, not all trees are equal contributors to the diets of *V. rubra* and *E. albifrons*. Previous work at Andranobe Forest despite *V. rubra* feeding on 132 different plant species, only seven to eight species made up 50% of their diet (Vasey, 2000b). Similarly, during this study *V. rubra* fed from over 50 different plant species, but 50% of their diet was from only 5 different tree species. It is uncertain if and how the relationship between tree-fall canopy gaps and the trees disproportionately represented in *V. rubra* and *E. albifrons* diets differs from the relationship between gaps and less represented tree species. In addition, all gaps created by tree-falls were included, regardless of size. It is likely that large gaps (> 200 m^2) have a greater effect on plant phenology compared to small gaps (< 50 m^2). Stronger relationships between canopy gaps, plant phenology, and lemur behavior may be more apparent if small gaps were removed from the analysis.

This study highlights some potentially important differences between the natural small-scale, local disturbances to which *V. rubra* and *E. albifrons* are adapted and the anthropogenic disturbances they are facing in much of their geographic range. Tree-fall gaps at Andranobe Forest are small and distributed throughout the forest. In contrast, results of a study conducted in northeastern MNP showed that anthropogenic disturbance within that part of the park is heavily concentrated near rivers and permanent villages (Allnutt, Asner, Golden, & Powell, 2013). In addition, tree-fall gaps created by storm winds tend to be, on average, smaller than gaps created by anthropogenic activities, even when gap formation was the result of low impact and selective logging that aim to balance resource extraction with the protection of species and ecosystem functions (Felton, Felton, Wood, & Lindenmayer, 2006). Extreme concentration of gaps and consistent creation of very large gaps from anthropogenic activity may alter habitats beyond the limits of lemurs' ability to adjust their behavior and diets, resulting in local extinctions. Despite this threat to long-term lemur survival, pressure on forests within Madagascar are only going to grow. In MNP in particular, anthropogenic disturbance, including selective logging and conversion of forest to agricultural land, has increased over time, particularly near the park boundaries (Allnutt *et al.*, 2013; Burivalova, Bauert, Hassold, Fatroandrianjafinonjasolomiovazo, & Koh, 2015; Zaehringer, Eckert, & Messerli, 2015). By comparing natural gaps to anthropogenically created gaps, conservation managers can identify potential adjustments to practices in community managed forests and forests in the MNP buffer zone that benefit lemur populations while still meeting human needs for timber and fuel. Improved practices in the few fragmented forests outside MNP may help reduce pressure on the park's trees and lemur populations.

3.5 Conclusions

Frugivorous lemurs may seek out tree-fall canopy gaps as sources of preferred foods like fruit and young leaves. The perceived value of such gaps may depend on the overall availability of food within the forest, which, in turn, may be impacted by cyclone activity. While tree-fall canopy gaps appear potentially to have increased production of young leaves and, to a lesser extent, fruit, the costs that lemurs may incur by visiting trees near tree-fall canopy gaps are not clear. In times when food is more abundant, both *V. rubra* and *E. albifrons* increase their average distance from canopy gaps. The costs of proximity to tree-fall gaps may outweigh the benefits during periods of abundance but not during periods of scarcity. Cyclones may in some ways benefit frugivores through the increased production of young leaves and fruit following the increased rainfall and sunlight (via reduced canopy cover) associated with these storms. Certainly, cyclones may have devastating consequences in the short-term, but over the longer term, they may provide benefits; an increase in productivity of surviving trees may be among them. Because cyclone intensity is predicted to increase as a result of climate change (Ranson *et al.*, 2014; Seo, 2014), understanding how populations and ecosystems adapt to such disturbances has become increasingly urgent. As lemurs face increased threats from anthropogenic sources, such as habitat destruction (Grinand *et al.*, 2013; Vieilledent *et al.*, 2018) and hunting (Borgerson, 2015; Gardner & Davies, 2014; Golden, 2009; Jenkins *et al.*, 2011), documenting their response to natural disturbances may provide insights into effective tools for conservation management.

3.6 Figures and Tables

Figure 3.1. Location of the study site. All data were collected at Andranobe Forest, Masoala National Park, Madagascar.

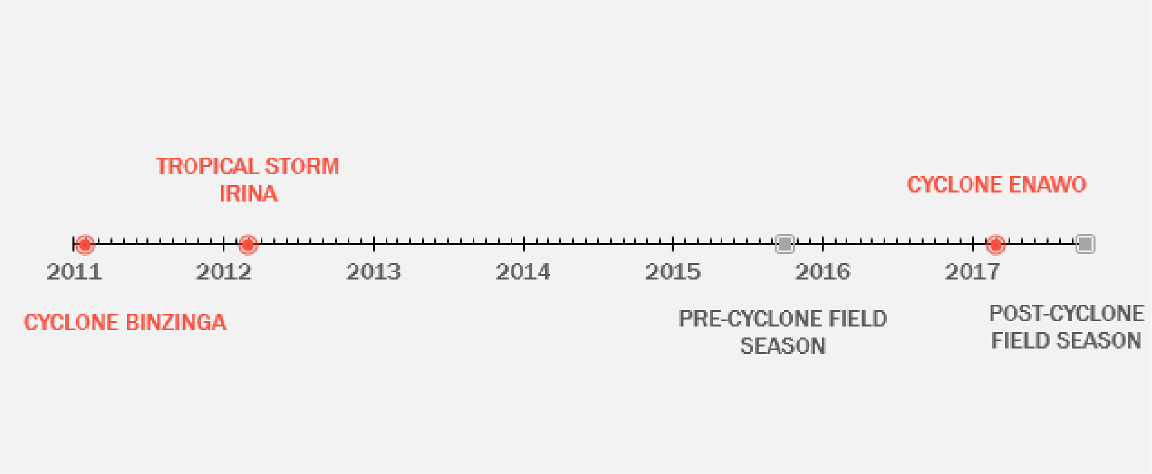
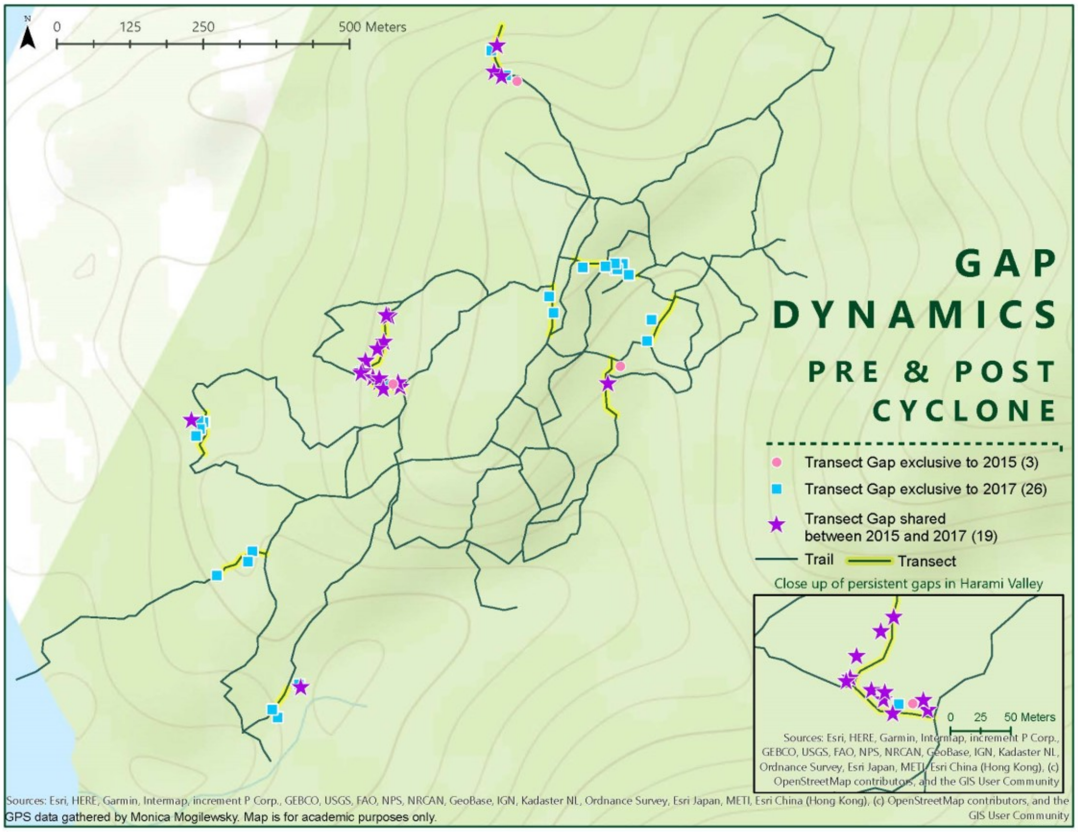


Figure 3.2. Timeline of major storm events and field seasons at Andranobe Forest, Madagascar. Storms are marked with red circles and field seasons are marked with grey squares. Pre-cyclone season refers to field data collected prior to Cyclone Enawo while post-cyclone season refers to field data collected following Cyclone Enawo.



Sources: Esri, HERE, Garmin, Intermap, increment P Corp., GEBCO, USGS, FAO, NPS, NRCAN, GeoBase, IGN, Kadaster NL, Ordnance Survey, Esri Japan, METI, Esri China (Hong Kong), (c) OpenStreetMap contributors, and the GIS User Community

Sources: Esri, HERE, Garmin, Intermap, increment P Corp., GEBCO, USGS, FAO, NPS, NRCAN, GeoBase, IGN, Kadaster NL, Ordnance Survey, Esri Japan, METI, Esri China (Hong Kong), (c) OpenStreetMap contributors, and the GIS User Community

GPS data gathered by Monica Mogilewsky. Map is for academic purposes only.

Figure 3.3. Gap dynamics at Andranobe Forest. Location of gaps mapped along ten transects pre-cyclone (2015) and post-cyclone (2017). Nineteen gaps mapped prior to Cyclone Enawo persisted through 2017 and were re-located and measured.

	Count	Mean Area	Median Area	Min Area	Max Area	Total Area (m^2)
Pre-cyclone	22	78.7	49.0	2.0	407.0	1731.1
Post-Cyclone	45	61.5	46.4	7.6	208.4	2891.7

Table 3.1. Tree-fall canopy gaps before and after Cyclone Enawo. Pre-cyclone data were collected in 2015, and post-cyclone data were collected 6 months after the cyclone in 2017. Pre-cyclone, 16 transects with a cumulative distance of 1.6 km were monitored for gaps but post-cyclone only ten transects with a cumulative distance of one kilometer were monitored for gaps. Results presented here are from the ten transects monitored both pre- and post-cyclone only. All areas were measure in square meters (m^2). There was no significant difference between mean gap area pre- and post-cyclone (t test: t = 1.3(df = 47), p = 0.20, N = 67). There were significantly more tree-fall gaps post-cyclone (mean = 1.6 per transect) than pre-cyclone (mean = 0.7 gaps/transect; t test: t = 2.5(df = 18) p < 0.02, N = 20).

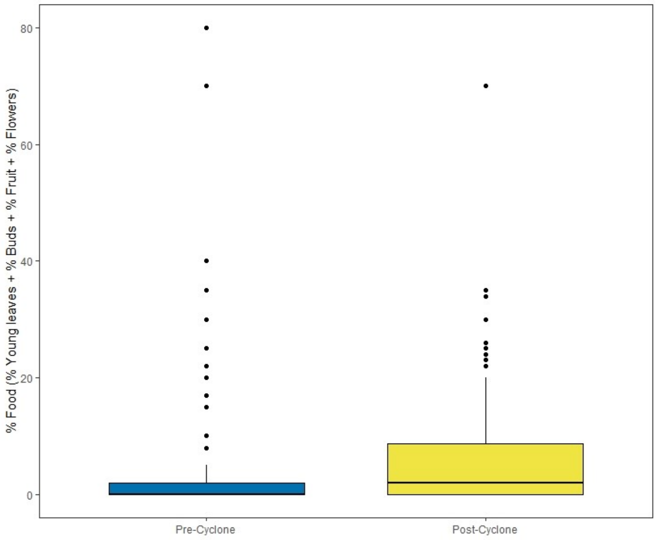


Figure 3.4. Food availability pre- and post-cyclone. Young leaves, buds, fruits, & flowers were all considered potential food. Data were collected from transect trees three times in each study period. Wilcoxon test: N = 300, W = 59841, p-value < 0.001.

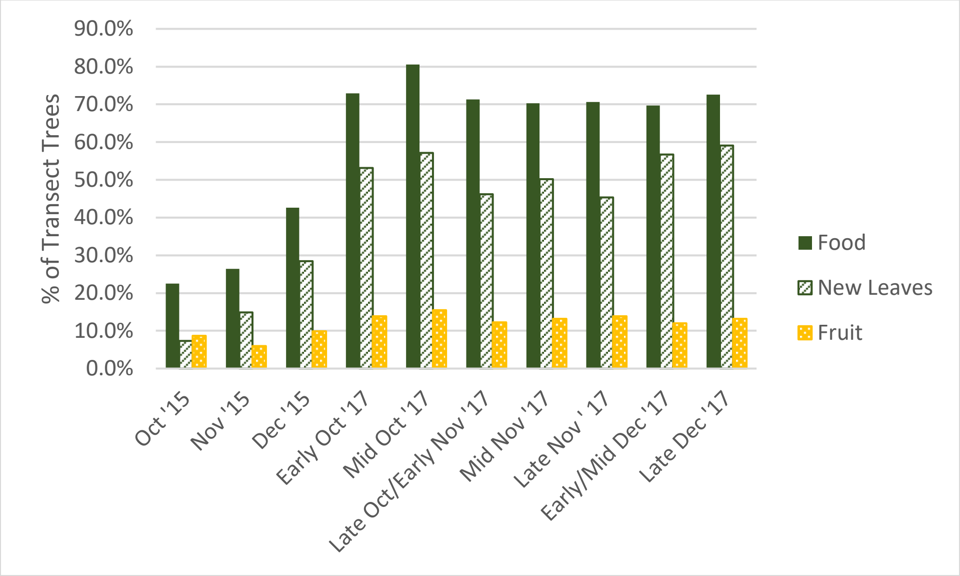


Figure 3.5. Availability of young leaves and fruit pre- and post-cyclone. Bars represent the percent of transect trees with food (solid green bar) for each month of the study. Young leaves, buds, fruit, & flowers were all included as potential lemur food. 2015 dates were prior to the cyclone; 2017 dates were after the cyclone. The percent of transect trees with young leaves (white with green lines) was smaller pre-cyclone than post-cyclone. The same was true for the percent of transect trees with fruit (yellow with white dots) but the difference between pre- and post-cyclone was smaller.

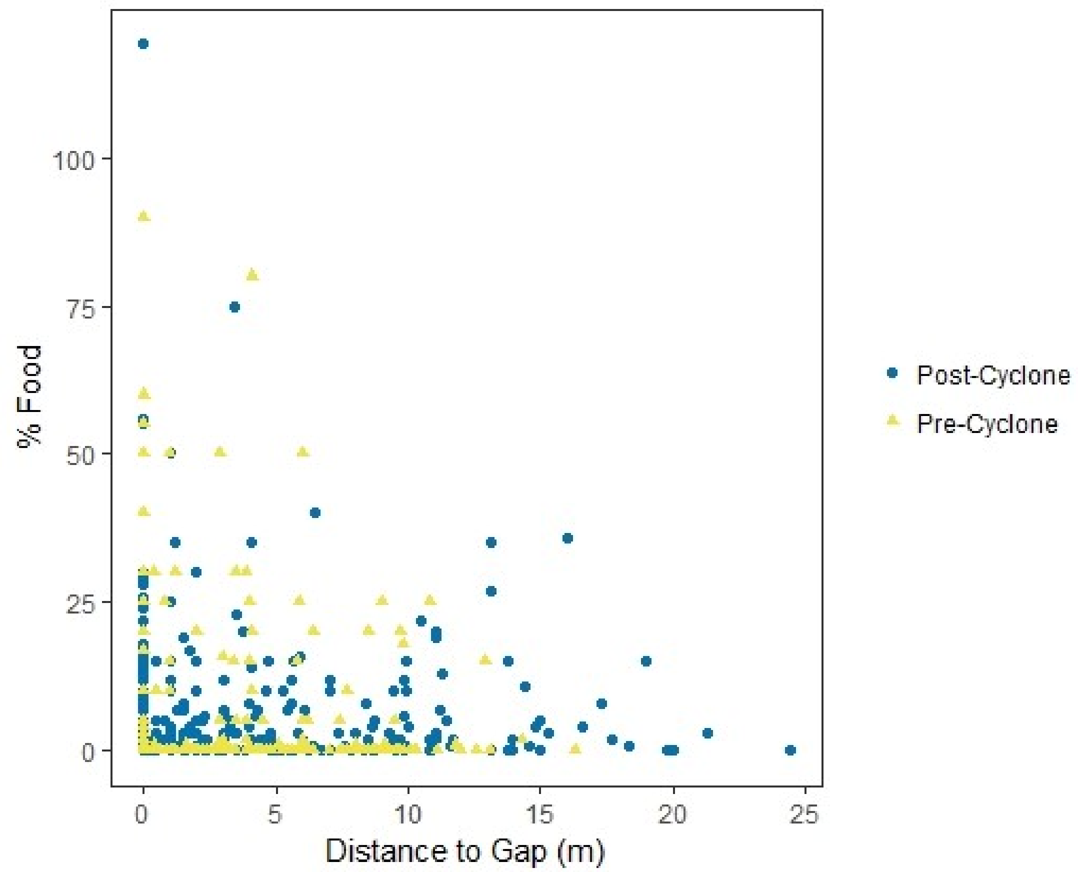


Figure 3.6. Food abundance and distance to gap pre-and post-cyclone. Points represent data collected from a single monitoring session of a single transect tree. N = 300 each, pre- and post-cyclone. Food includes young leaves, buds, fruits and flowers.

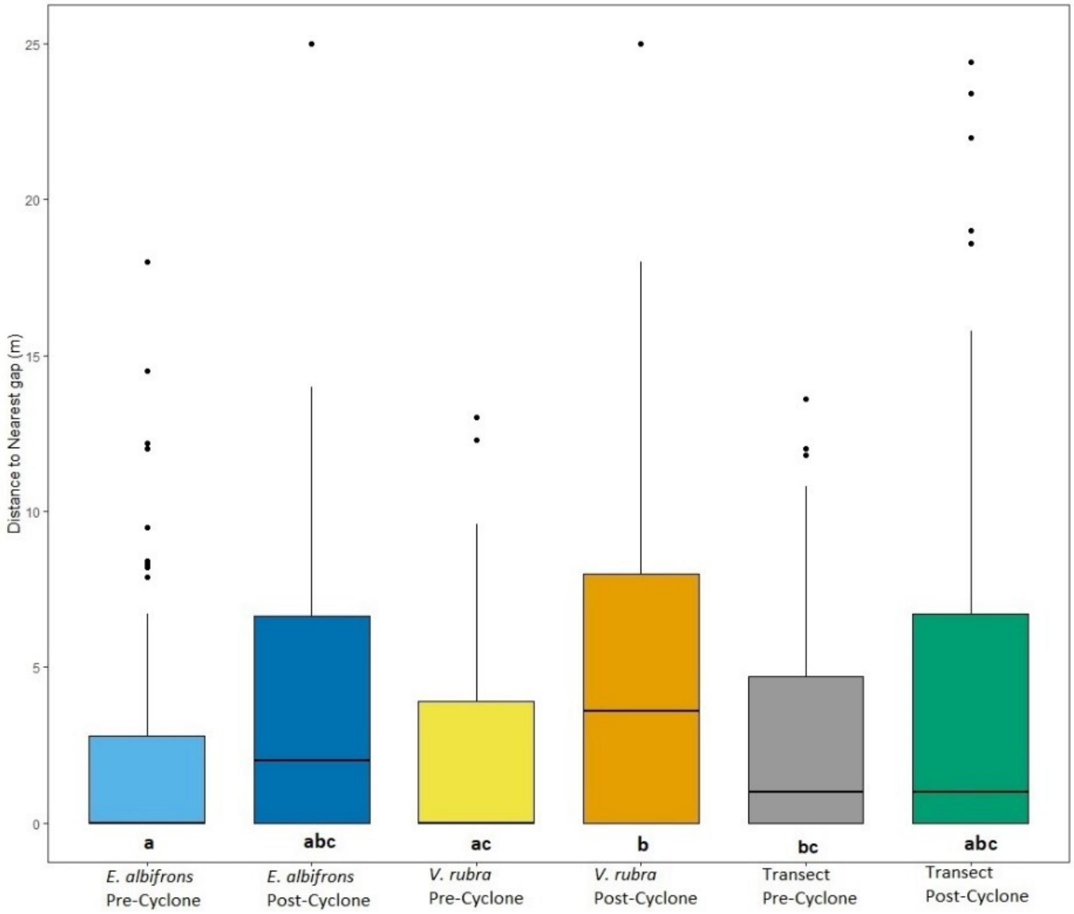


Figure 3.7. Distance to the nearest gap for transect and lemur trees before and after Cyclone Enawo. Groups are significantly different (Kruskal-Wallis: N= 95, $\chi2 = 25.997$, df = 5, p-value < 0.001). Groups that are similar are assigned the same letter (a, b, or c) while groups that are significantly different have different letters per the results of a post-hoc pairwise comparison using a Mann-Whitney U test (aka Wilcoxon rank-sum test) and applying a Bonferroni correction for multiple pairwise comparisons.

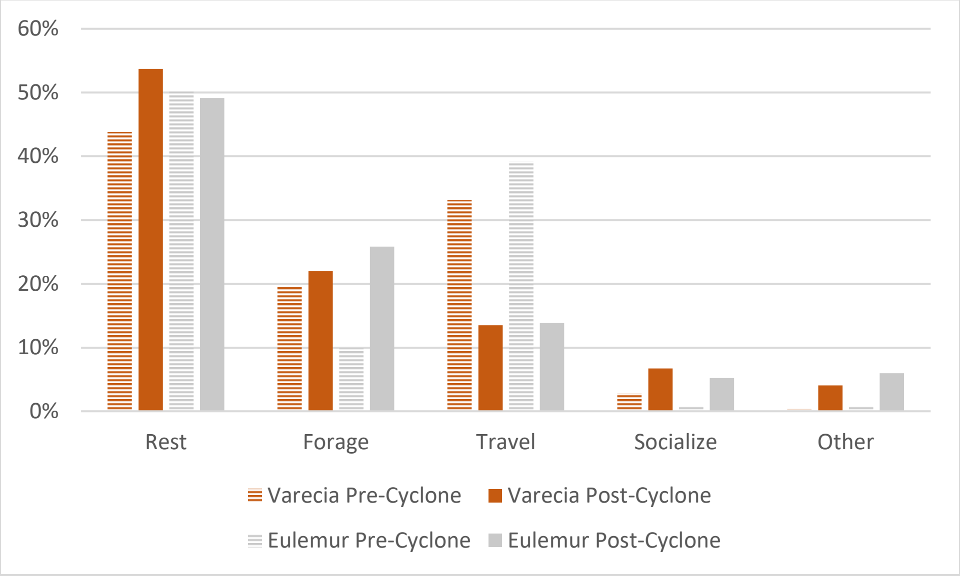


Figure 3.8. Activity budgets for *V. rubra* and *E. albifrons* pre- and post-cyclone. Activity budgets are based on percent of instantaneous timepoints during all-day follows of focal animals. Each lemur species was analyzed separately. Differences between years were significant for both species ($\chi2$ = 14,426, 4 d.f., N = 1453, p <0.001 for *E. albifrons* and $\chi2$ = 374, 4 d.f., N = 1327, p<0.001 for *V. rubra*)

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Chapter 4: Understanding the Relationship between Tree-fall Canopy Gaps, Food Availability, and Diet for *Varecia rubra* and *Eulemur albifrons* in Masaola National Park, Madagascar

4.1 Introduction

4.1.1 Disturbance Impacts on Food Availability

Tropical systems exhibit enormous diversity in plant phenology between individuals, species, and communities (Couralet, van den Bulcke, Ngoma, van Acker, & Beeckman, 2013; Lambert & Rothman, 2015; Mendoza, Peres, & Morellato, 2017; van Schaik, Terborgh, & Wright, 1993). For example, individual trees of the same species within a forest do not necessarily synchronize fruit production (Couralet *et al.*, 2013), and long-term studies have recorded both seasonal and interannual variation in timing and intensity of peak fruit and flower production (Brearley *et al.*, 2007; Heideman, 1989; Mohandass, Campbell, Chen, & Li, 2018; van Schaik *et al.*, 1993). While young leaf and flower production generally follow maximum solar radiation given sufficient water, fruit production patterns are less predictable (Lambert & Rothman, 2015). In Madagascar, plant phenology, and thus food availability, is especially impacted by the seasonality and unpredictability of the island's rainfall (Sato *et al.*, 2016). In eastern Madagascar, researchers have documented extensive spatial, seasonal, and annual variability in fruit availability (Balko & Underwood, 2005; Dewar & Richard, 2007; Ganzhorn, 1995; Johnson, 2002), and the evergreen rain forests of the east may have less abundant and more patchily distributed food resources than the dry, deciduous forests of western Madagascar (Bollen & Donati, 2005; Curtis & Zaramody, 1998; Wright, Razafindratsita, Pochron, & Jernvall, 2005). On a landscape scale, cyclones may be one of the drivers of the variation and unpredictability in food availability (Curtis, 2004); on an organismic scale, the tree-fall canopy gaps created by cyclones may be significant drivers of variation in food abundance.

Tree-fall canopy gaps, hereafter referred to as canopy gaps, may contribute to spatial and temporal patterns of fruit abundance. Fruit production often increases in response to disturbances (Levey, 1988; Lugo & Frangi, 1993; Restrepo & Gomez, 1999), and plant productivity, including fruit production, is generally higher in canopy gaps (Denslow *et al.*, 1986; Beck *et al.*, 2004). Increased seed predation (Alvarez-Buylla & Martínez-Ramos, 1990), herbivory (Swaine, 1996), and fruit removal (Murray, 1987) in gaps, compared to closed canopy, suggest that gaps serve as important sources of food for a variety of fauna quite likely as a result of increased sunlight in gaps. In a study of *Varecia* in southeast Madagascar, greater sun-exposure in the crowns of the trees following storm disturbance produced more fruit (Ratsimbazafy, 2006). After controlling for diameter at breast height (DBH) and taxonomy, leaf production of trees growing in full sun is roughly twice that of those growing in full shade; similarly, fruit density and production is greater near forest edges, though less evenly distributed (Ganzhorn, 1995).

4.1.2 Responses to Fluctuations in Food Availability

In areas with frequent disturbance and unpredictable food availability, flexibility is key for frugivores. This flexibility may be dietary, behavioral, or both. Examples of behavioral adaptations that allow lemurs to cope with fluctuations in food availability include cathemerality, as seen in many *Eulemur* species (Donati, Bollen, Borgognini Tarli, & Ganzhorn, 2007; Sato, 2012), and fission-fusion social organization, as seen in

Varecia (Holmes, Gordon, Louis, & Johnson, 2016; Vasey, 2006) and some *Eulemur* species as well (Johnson, 2006; Toborowsky, 2008). Some *Eulemur* species appear to reduce group size and cohesion in response to food scarcity and degraded habitats (Johnson, 2006; Lehman, Rajaonson, & Day, 2006; Schwitzer, Randriatahina, Kaumanns, Hoffmeister, & Schwitzer, 2007). The marked flexibility of the fission-fusion social organization seen in *Varecia* includes seasonal and annual variation in ranging patterns, subgroup size, and subgroup composition and has been proposed as a means of coping with the large variation fruit availability across seasons (Holmes *et al.*, 2016; Vasey, 2006). Individuals can also adjust their foraging patterns. For example, amongst *Eulemur* daily path length and home ranges may be increased in response to variation in fruit availability (Sato et al 2016). In periods of scarcity, *Eulemur* may respond by reducing energy expended by decreasing daily travel and increasing time spent resting (Sato *et al.* 2016). *Varecia* respond to disturbance-induced food scarcity by reducing travel and incorporating less-preferred foods into their diet (Ratsimbazafy 2006). During cold, food-scarce seasons, *V. rubra* also reduce travel (Vasey, 2005). In both cases, reducing travel likely reduces overall energy expenditure.

The evergreen tropical rain forests of eastern Madagascar experience particularly frequent cyclones compared to most of the planet, averaging more than three each year (de Gouvenain & Silander, 2003; Fitchett & Grab, 2014), and lemur populations in these forests have had to adapt to this disturbance regime that can lead to population declines. For example, a severe cyclone in 1984 may have reduced the population of *E. fulvus* on the island of Mayotte (Tarnaud & Simmen, 2002). Likewise, *Alouatta pigra* (howler monkeys) also experienced declines in southern Belize following Hurricane Iris in 2001 (Pavelka, McGoogan, & Steffens, 2007). Cyclones can also interrupt reproduction; successful reproduction of *Varecia* at several sites appeared to decline or temporarily cease following cyclones (Ratsimbazafy, 2006; Ratsisetraina, 2006, 2013; Vasey & Borgerson, 2009). In addition to cyclones in general, canopy tree-fall gaps that result from tropical storms can have detrimental impacts on forest animals. Gaps can potentially increase energy expenditure in primates by decreasing canopy density and reducing travel routes, subsequently increasing travel time, and by altering food abundance and distribution (Thompson, 2016). In addition, some gap edges may enhance predator detection of prey by increasing light and reducing canopy cover for prey (Treves, 2002). Consequently, canopy gaps may increase predation rates by some types of predators, as was the case for predation of infant *Oryzomys megacephalus* (large headed rice rats) by ants in the Amazon (Beck, Gaines, Hines, & Nichols, 2004).

By contrast, cyclones and canopy gaps can have positive impacts on forest fauna by increasing light availability, primary productivity, and increase the abundance and distribution of fruit and young leaves for folivorous/frugivorous species. A previous study found that food abundance, particularly the quantity of young leaves, increased with proximity to canopy gaps, with most food found within 15 m of a gap edge (see Chapter 3). The frugivorous lemurs found in these forests, *E. albifrons* and *V. rubra*, may take advantage of canopy gap edges for their denser food resources. *E. albifrons* exhibit considerable dietary variation in the proportion of non-fruit plant parts (Sato *et al.*, 2016) and in plant species (Simmen, Bayart, Marez, & Hladik, 2007). Other species within the brown lemur complex exhibit an ability to adjust to degraded habitats (Johnson, 2006; Lehman *et al.*, 2006; Schwitzer *et al.*, 2007). It is likely that *E. albifrons* can also adjust to disturbed habitats because of their ability to use multiple microhabitats (Vasey, 2002). Compared to *E. albifrons*, *V. rubra* are more restricted in their strata use and dietary composition (Vasey, 2002), though they broaden both in periods of extreme food scarcity (Ratsimbazafy, 2006). Despite these differences, both species traveled more and were closer to tree-fall canopy gaps than expected when food was relatively scarce (see Chapter 3). During periods of food scarcity, both lemur species may seek out canopy gaps as these gaps are correlated with higher availability of food, especially protein-rich young leaves. It remains to be seen whether the two species, with their differences in dietary and ecological flexibility, will still respond similarly to canopy gaps following a recent cyclone and subsequent wide-spread distribution of such gaps.

4.1.3 Research Objectives

My aim in this study is to assess the potential of canopy gaps to serve as food dense feeding sites during periods of relative abundance by comparing phenology near canopy gaps to phenology under closed canopy in a forest recovering from a recent (within the last 6 months) cyclone. Monitoring of lemur activity at the same site will allow me to determine whether lemurs take advantage of variation in abundance of potential food attributable to canopy gaps. If canopy gaps serve as important food patches for *V. rubra* and *E. albifrons,* I predict that gap edges will have more trees and lianas producing young leaves and fruits, which make up the greatest proportion of their diets, than closed canopy. Both frugivorous lemur species will be found closer to canopy gaps than expected. However, I predict also that *E. albifrons* will show a greater affinity for edges because their greater dietary flexibility that allows them to take advantage of increased productivity for a greater number of tree and liana species.

4.2 Methods

4.2.1 Study Site

Andranobe Forest in Masoala National Park (MNP), Madagascar served as the field site for this study. Andranobe Forest is a lowland coastal evergreen rain forest with a maximum elevation of 260 m above sea level; the study area used ranges from 400 m to 1700 m inland of the Bay of Antongil (Vasey, 2000) and is approximately 150 hectares (1.5 km2) (Figure 4.1). Masoala National Park is designated as an IUCN category I protected area (Kremen *et al.*, 1999). Andranobe Forest is designated exclusively for research; tourists, locals, and others without an appropriate research permit are prohibited (Hatchwell, 1999).

4.2.2 Data Collection

Data were collected from 1 September 2017 – 22 February 2018. To understand gap distribution and size, ten 5 m wide and 100 m long transects were measured, mapped, and located along ridge tops, mid slopes, and valley bottoms (Figure 4.2). A canopy gap was defined as any opening that started at the canopy and continued to within 2 meters of the ground (Brokaw, 1982). All gaps greater than 1 m^2 that intersected the transects were measured (width, length, and percentage of the gap still open) and mapped. A handheld

Garmin GPSMAP 62st was used to record GPS coordinates for each gap. A Laser Technology, Inc. TruPulse 200 rangefinder was used to measure gap width and length. Percentage of gap still open (no vegetation) was estimated visually while standing on the ground in the center of the gap and recorded as a continuous variable from 0 to 100%. Gap area was calculated using the formula for the area of an ellipse and the measured gap width and length, then multiplied by the percentage of the gap still open.

To assess tree phenology and lemur food availability at the field site, the research team used the same transect lengths but used a two-meter width. All trees with trunks or visible roots intersecting the transects and with diameter at breast height (DBH) of 10 cm or greater were measured, tagged with a unique number, and identified to local vernacular taxonomy. A handheld Garmin GPSMAP 62st was used to record GPS coordinates for each tree . GPS accuracy varied from ±2 m to ±10 m. GPS coordinates were not recorded when accuracy was not within 10 m. A Laser Technology, Inc. TruPulse 200 rangefinder was used to measure height. The TruPulse 200 automatically calculates vertical distance, eliminating the need to calculate it based on actual distance between the instrument and the target. DBH tape was used to measure DBH for all transect trees. Using these transect trees, phenological data were collected every two weeks using methods described in Denny *et al.*, 2014. Finally, for each transect tree, the nearest gap was located, and the distance to the gap, gap length, and width were measured using the TruPulse 200 rangefinder. The percentage of gap open or unfilled with vegetation was visually estimated. In many cases, the gap nearest the transect tree crossed the transect and had already been measured as a transect gap. For analysis, a food index was created by summing the percent of young leaves, buds, fruits, and flowers (% food available = % young leaves + % buds + % fruits + % flowers).

To assess lemur-gap interactions, all-day follows were conducted using five-minute instantaneous time point sampling to record the animal's activity (rest, travel, social interaction, forage/feed, other) (Altmann, 1974). The location of the focal animal at each time point was flagged using standard surveyor's flagging tape. Only adult *V. rubra* and *E. albifrons* were observed for this study, and observations were only conducted during daylight hours. After 3-4 days of focal animal follows, researchers returned to all flagged trees and recorded the distance to the nearest gap edge and the length and width of that gap. In cases where a flagged tree was on multiple gaps, i.e. distance to the nearest gap was zero for more than one gap, the length and width of all gaps were measured, and gap area was calculated as the sum of all gap areas. Trees flagged during focal animal follows will hereafter be referred to as lemur trees. In most cases, phenology data of lemur trees and associated lianas were also recorded. While the transects provided 303 trees for regular monitoring of phenology, the number of trees and lianas visited by lemurs varied by week. Thus, the number of lemur trees monitored for phenology also varied (Table 4.1).

To record microclimate data, we installed HOBO Pendant dataloggers (Onset, Bourne, MA) to record temperature and light intensity in transect and lemur trees to test for microclimate variation related to canopy gaps. All data loggers were installed in the canopy between 15-20 m high using a slingshot/pulley system (Chapter 2). To accomplish this, a lightweight throw line was tied to a 12 oz weight bag and launched over a branch of the appropriate height using a Big Shot Arborist Throwline Launcher (® Jameson). Once the line was successfully placed, the throw weight was replaced with a HOBO datalogger and both ends of the line were secured to form a loop. This loop allowed researchers to easily pull the datalogger up to the target height of 15-20 m and retrieve the datalogger. The throw line was securely tied to a nearby sapling or small tree to prevent accidental displacement. Data were downloaded from the data loggers in December 2017 and again in February 2018 and stored on an external hard drive. Forty data loggers were permanently installed in a randomly selected sub-sample of transect trees, 10 loggers in each topographical/aspect stratum.

4.2.3 Data Analysis

All statistical analyses were conducted using software R v. 3.5.3 (R Core Team, 2012) and user interface RStudio v. 1.1.463 (RStudio, 2012). Non-metric multidimensional scaling (NMDS) was used to reduce the dimensionality of the data to better visualize the relationship between tree type, microclimate data (mean, minimum and maximum temperature), tree morphology (height and DBH), gap data (distance to gap, gap area, gap length, and gap width), and tree phenology. NMDS attempts to place more similar objects together after reducing multivariate data to a small number of composite variables, preserving only rank ordering of the original distances (Kenkel & Orloci, 1986). Stress values are used to evaluate the fit of the data to the reduced dimensionality; a stress of 0.3 is considered arbitrary, 0.1 is considered a fair fit, and 0.05

is considered a good fit (Buttigieg & Ramette, 2014). Euclidean distances, 20 iterations ("runs"), and three axes were used for the NMDS (stress = 0.09). Data were first standardize to a mean of zero and standard deviation = 1.0 (i.e., Z-scores) to account for different units of measurement (e.g., meters for distance to the nearest gap, centimeters for DBH, % of crown for phenology data) and then log transformed to dampen the impact of extreme values. NMDS results were used to select those variables that were likely to have the greatest predictive power for use in GLMM models. Subsequently, for analysis of tree phenology variables, the glmer function of the lme4 package developed for R was used to fit general linear mixed-effects models (GLMMs) (Bates, Machler, Bolker, & Walker, 2015). The phenology response variables were percent of tree crowns with young leaves, percent of tree crowns with fruit, percent of liana volume with young leaves, and percent of liana volume with fruit. To compare canopy gap-lemur interactions qualitatively by lemur species, maps of gaps and trees visited by each lemur species were created in ArcMap 10.4.1 (ESRI, 2011). The kernel density tool was used to map gap density using one square meter output cell size and default search radius of 69.7 m. The default search radius minimizes the impacts of spatial outliers (ESRI, n.d.). To determine the influence of tree type on the distance to the nearest gap quantitatively, GLMMs for distance to the nearest gap were fitted using the glmer function of the lme4 packed developed for R. For all GLMMs, the simplest model with the lowest AIC score was selected as the best model for each response variable. Potential fixed effects included tree type (transect, *V. rubra*, or *E. albifrons*), tree DBH, tree height, gap area, distance to the nearest gap, sex (of lemur), and season. Random effects included week and individual tree identifier. Continuous variables were scaled to standardize values with different units of measurement prior to fitting models. Standardized regression coefficients (β) were used to assess relative strength of the effect of each independent variable. The sign of β indicates the direction of the relationship: a positive β value indicates a direct relationship between the independent and response variables while a negative β value indicates an inverse relationship.

4.3 Results

4.3.1 Canopy Gaps and Plant Productivity of Transect and Lemur Trees

4.3.1.1 Plant Productivity at Andranobe Forest

Plant productivity, as defined by the presence of young leaves, fruit, flowers, or buds, is expected to vary over time. Previous research at various sites in Madagascar found increases in the amount of fruit available as the dry season transitioned into the warm, rainy season (reviewed in Vasey, 2000, 2002). For this study period, there was a steady increase in food availability over time for transect trees (from 81% to 93%) but not for trees visited by lemur species (Figure 4.3). For trees visited by *E. albifrons*, the percent of trees with food ranged from 83% to 100% with no increase over time. Similarly, for trees visited by *V. rubra*, food availability ranged from 74% to 100% with no increase over time. For all tree types, food availability was calculated as the percent of trees with food in the crown and the lianas therein. Note that in many cases, a tree was visited by both lemur species and, thus, would contribute to calculations for each species. Lemurs also visited transect trees, so no category is entirely exclusive of the other. Young leaves became increasingly available in transect trees, starting around 71% and increasing to 87%, but varied widely from week to week in trees visited by either lemur species, ranging from 28% to 100% (Figure 4.4). Similarly, the availability of fruit in transect trees remained relatively steady, ranging from 8% to 21%, compared to the availability of fruit in trees visited by either lemur species, which varied from 6% to 70%; fruit availability increased relatively steadily over the study period for transect trees but varied from week to week for lemur trees (Figure 4.5). When averaged over the study period, lianas produced almost double the amount of young leaves than trees, regardless of tree type. The opposite was true for fruit: lianas produced about a quarter less fruit than trees regardless of tree type, and, in fact, lianas in transect trees produced almost no fruit at all (Figure 4.6).

Prior to testing for significant differences, phenology data were separated by season and tree type for data visualization and exploration. Using non-metric multidimensional scaling (NMDS), all phenological variables were collapsed into three dimensions using data from all trees visited by the lemurs during each season (stress = 0.09). NMDS 1 axis represented gap data; NMDS 2 axis represented microclimate conditions (Figure 4.7). For all potential lemur food – young leaves, buds, fruits, and flowers – on lianas and trees, distance to the nearest gap had a stronger effect on abundance than microclimate variables, as represented by the relative lengths of the associated vectors in the NMDS plots (Figure 4.7). Gap length, width, and area also have an impact on potential food abundance, but the impact is smaller than distance to the nearest gap. As the distance to the nearest gap decreased, food abundance in trees as well as abundance of food from lianas increased, regardless of season (Figure 4.8c and d). Distance to the nearest gap appeared to affect young tree leaves more in the rainy season (Figure 4.8a) and fruit in the dry season (Figure 4.8b). The relationship between the distance to the nearest gap and cumulative tree and liana fruit did not vary with season, however (Figure 4.8e). Decreasing the distance to the nearest gap increased tree and liana food abundance for both species (Figure 4.9a,c,d, and e) but had little effect on tree fruit for either species (Figure 4.9b).

4.3.1.2 Canopy Gaps and Tree Phenology

Trees visited by *E. albifrons* near gap edges (within nine meters) had more young leaves (mean = 5.2%, SD = 11.9%) than trees they visited under closed canopy (mean = 4.4%, SD = 8.2%), any of the trees visited by *V. rubra* (gap edges: mean = 4.3%, SD = 9.4%; closed canopy: mean = 4.1%, SD = 8.6%), or any transect trees (gap edge: mean = 4.3%, SD = 9.0%; closed canopy: mean = 4.2%, SD = 7.1%; Figure 4.10). Proximity to a tree-fall gap increased the percent of the crown containing fruit for transect trees and trees visited by *E. albifrons* (Transect gap edge: mean = 1.0%, SD = 5.6%; Transect closed canopy: mean = 0.4%, SD = 2.0%; *E. albifrons* gap edge: mean = 4.3%, SD = 9.9%; *E. albifrons* closed canopy: mean = 3.4%, SD = 7.5%; Figure 4.11). Trees near gap edges visited by *V. rubra* had slightly less fruit (mean = 4.3%, SD = 10.5%) than trees they visited under closed canopy (mean = 4.6%, SD = 12.6%; Figure 4.11).

Rather than directly testing for significant differences between means, GLMM models were used to test for significance of effects on the following response variables:

young tree leaves, tree fruit, young liana leaves, and liana fruit. Response variables were not correlated. I defined the best model as the simplest one with the lowest AIC score. The best models for young tree leaves and tree fruit were very similar. The two models showed that the same fixed effect variables were likely to influence the percent of young leaves or fruit in the tree crown: distance to the nearest gap, tree type (transect, visited by *E. albifrons*, visited by *V. rubra*), and tree DBH (Table 4.2). Of these, use by *V. rubra* was the strongest predictor ($p < 0.001$ for both models). Distance to the nearest gap had the least influence but was still significant ($p < 0.001$ for the model of young tree leaves; $p < 0.01$ for the model of tree fruit). Inclusion of season, gap area, tree height or interactions between variables did not improve the model for either young tree leaves or tree fruit. Individual tree and week were included as random effects to control for repeated monitoring of transects over time and inter-tree variation.

4.3.1.3 Canopy Gaps and Liana Phenology

Lianas in trees near gap edges had greater percent of young leaves than lianas in trees under closed canopy for all tree types (*E. albifrons* gap edge: mean = 11.7%, SD = 14.6%; *E. albifrons* closed canopy: mean = 7.8%, SD = 13.7%; *V. rubra* gap edge: mean = 8.1%, SD = 11.5%; *V. rubra* closed canopy: mean = 6.0%, SD = 9.7%; transect gap edge: mean = 9.2%, SD = 14.2%; transect closed canopy: mean = 7.0%, SD = 10.6%; Figure 4.12). Liana fruits were observed in very small quantities but followed the same pattern as young liana leaves with greater fruit abundance near gap edges than closed canopy for all tree types (*E. albifrons* gap edge: mean = 1.3%, SD = 7.4%; *E. albifrons* closed canopy: mean = 0.3%, SD = 1.4%; *V. rubra* gap edge: mean = 1.1%, SD = 5.0; *V.*

rubra closed canopy: mean = 0.7%, SD = 2.7%; transect gap edge: mean = 0.3%, SD = 2.6%; transect closed canopy: mean = 0.2%, SD = 1.1%).

The best GLMM models for young liana leaves and liana fruit included season, unlike the model of tree response variables. Individual tree and week were again included as random effects to control for lack of independence between samples caused by repeated monitoring. Distance to the nearest gap, tree type, tree DBH, and season were included as fixed effects in the final models for both liana response variables (Table 4.3). Season and tree type had the largest, statistically significant influence on young liana leaves and liana fruit ($p < 0.001$ for both predictors). Distance to the nearest gap had a slight but still statistically significant influence on the response variable ($p < 0.05$) while tree DBH improved the model but was not statistically significant ($p > 0.10$).

4.3.2 Lemur Activity and Distance to the Nearest Gap

4.3.2.1 Canopy Gaps and Lemur Tree Phenology

Most trees where lemurs were observed feeding were located within the area of gap influence (< 9 m from gap edge). See Table 4.4 for a complete list of the feeding trees identified by vernacular and, when possible, Latin names. During the dry season, 77% (249 of 322) of these feeding trees were near gap edges, and this increased to 83% (400 of 483) during the rainy season. To detect potential differences in the relationship between distance to the nearest gap and phenology of lemur trees only, a dataset with exclusively lemur trees was modeled for young tree leaves and tree fruit. Distance to the nearest gap, gap area, tree type, and tree DBH were included as fixed effects in the best model for young tree leaves of lemur trees (Table 4.5). Individual tree and observation session were included as random effects to control for lack of independence between trees visited by the same lemur within the same day and to quantify the influence of inter-tree variation. Tree DBH had the greatest influence on young tree leaf abundance (p <0.001), followed by tree type (p <0.001), and then distance to the nearest gap (p <0.001). Gap area improved the model but was not statistically significant (p >0.10). Distance to the nearest gap had a stronger influence on young leaf abundance of lemur trees alone than on transect and lemur trees combined. The best model of fruit abundance in lemur trees included session, individual trees, and week as random effects and distance to the nearest gap, gap area, and tree DBH as fixed effects. However, none of the fixed effects were statistically significant (Table 4.5). GLMM models of young liana leaves and liana fruit in lemur trees failed to converge using any of the variables measured during this study.

4.3.2.2 Tree Type and Distance to the Nearest Gap

Trees visited by *E. albifrons* more closely overlapped with gap density (Figure 4.13) than trees visited by *V. rubra* (Figure 4.14). GLMM models using data from all tree types were run to test for the influence of tree type on the distance to the nearest gap. Week was included as random effects to control for repeated monitoring of transects over time and repeat visits by lemurs to the same tree over time. The best model included only tree type (Table 4.6). Tree type had an influence on distance to the nearest gap, but this was only statistically significant for trees visited by *V. rubra* (p <0.01). Inclusion of season, sex, gap area, tree height, or interactions between variables did not improve the model. Trees visited by *V. rubra* averaged 4.9 m, SD = 6.5 m from canopy gaps, slightly farther than transect trees (4.3 m, SD = 5.1 m) and *E. albifrons* (4.0 m, SD = 5.3m). However, the mean distance to the nearest gap varied greatly from week to week (Figure 4.15).

4.4 Discussion

As predicted, I found a positive relationship between proximity to tree-fall canopy gaps and increased plant productivity that, ultimately, affected food abundance for frugivorous lemurs. Proximity to a tree-fall gap edge was associated with an increase in young leaves for trees and lianas. It was also associated with an increase in fruit for trees. However, proximity to the nearest gap was associated with a decrease in liana fruit. Overall, distance to the nearest gap was not the strongest predictor of potential lemur food abundance for any of the response variables measured. Many variables influence plant phenology in the tropics, including plant taxonomy, temperature, rainfall, solar radiation, photoperiod, climatic oscillations (like El Niño–Southern Oscillations), and predation pressures, among others (Mendoza *et al.*, 2017). Given such numerous and diverse drivers of food production in tropical forests, detecting the influence of small tree-fall canopy gaps is a matter of detecting a weak signal in a great deal of noise. My results suggest that canopy gaps play a significant role in variation of tree and liana phenology in the tropical rainforests of eastern Madagascar and consequently play a role in variation of lemur food abundance.

During the study period, lemurs did not appear to specifically select trees close to tree-fall gaps. Trees visited by *V. rubra* were only slightly farther from gaps than transect trees, and trees visited by *E. albifrons* were a similar distance from gaps as transect trees. Despite not differing from transect trees in mean distance to the nearest gap, trees visited by *E. albifrons* did tend to spatially correspond to areas of high gap density (Figure 4.13), unlike trees visited by *V. rubra* (Figure 4.14). However, the average distance varied greatly from week to week for both lemur species, most dramatically for *V. rubra* (Figure 4.15). Despite the similarity in food patch size during the hot-dry and hot- rainy seasons (Vasey, 2000), *V. rubra* appeared to decrease the distance from gaps over the course of the study from the dry to the rainy season, though this trend was not statistically significant. The influence of the distance to the nearest gap on young tree leaves was stronger for lemur trees than for transect trees.

I predicted that canopy gaps would be more important for *E. albifrons* than *V. rubra*. Both qualitatively (as visualized by the gap interactions map) and quantitatively (as quantified by the results of the GLMM), trees visited by *E. albifrons* were closer to canopy gaps than trees visited by *V. rubra*. However, the relationship between *V. rubra* and canopy gap appears to change over time, with distance to the nearest gap decreasing as potential energy requirements increase (due to lactation of rapidly growing young). These results do not support my prediction of greater reliance on these gaps by *E. albifrons* than by *V. rubra*. Instead, a more complex relationship is likely, and the importance of canopy gaps for both species is moderated by interactions between food availability at large, reproductive status, and protein needs.

The abundance of canopy gaps at Andranobe Forest may aid frugivorous lemurs in meeting protein needs. *E. albifrons* include a greater proportion of non-fruit items, particularly leaves, in their diet than *V. rubra* (Vasey, 2002). *Eulemur* tooth morphology is similar to that of folivorous lemurs (Sato *et al.*, 2016), and they are able to digest a greater proportion of fiber when compared to *Varecia* (Campbell, Williams, & Eisemann, 2004). This may allow them greater flexibility in diet composition, despite remaining highly frugivorous (Sato *et al.*, 2016). White-fronted brown lemurs regularly remained close to tree-fall gap edges, where abundance of young leaves was greatest, though the distribution of canopy gaps made it impossible to differentiate this from chance. However, *E. albifrons* maintain closer proximity to canopy gaps when storm disturbance is relatively low and gaps are slightly less abundant, suggesting that gaps may provide resources worthy of travel (Chapter 3).

The relationship between young leaf abundance in lianas and tree-fall canopy gaps during this study suggest canopy gaps may interact with lianas to make tree-fall gaps sites of abundant, protein-rich food. Globally, lianas greatly contribute to plant diversity and abundance in the tropics (Schnitzer & Bongers, 2002). Compared to trees, lianas have faster growth rates, longer production periods, and greater nutritional value (reviewed in Odell *et al.*, 2019). Vasey (2002) found that *V. rubra* and *E. albifrons* spent up to 10% of total feeding time consuming liana parts, and Ratsimbafazy (2006) found that 6% of *V. variegata* food sources came from lianas following Cyclone Gretelle. Lianas may be increasing in density over time, at least in Amazon forests (Phillips *et al.*, 2002), and lianas may benefit from rising carbon dioxide levels more than trees, though the greatest benefit occurs under low light conditions (Mayle, Beerling, Gosling, & Bush, 2004; Zotz, Cueni, & Körner, 2006). Moreover, lianas may increase the persistence of canopy tree-fall gaps by suppression regeneration and recruitment of tree species (Foster, Townsend, & Zganjar, 2008; Schnitzer, Dalling, & Carson, 2000). As climate change increases carbon dioxide levels and potentially increases the frequency and intensity of cyclones, the interaction between lianas and tree-fall gaps may become increasingly important for both *E. albifrons* and *V. rubra* as they respond to a shifting disturbance regime.

The stronger influence of distance to the nearest gap on young leaf abundance compared to fruit abundance suggests that tree-fall gaps may be important in balancing protein needs for lemurs, particularly *V. rubra*. While young leaves do not make up the bulk of *E. albifrons* or *V. rubra* diets in terms of quantity or calories, they are important seasonal sources of protein. It is notable that the distance to the nearest gap for *V. rubra* declined over the study period as the dry season gave way to the rainy season. Red ruffed lemurs give birth in mid-October (Vasey, 2000). Consequently, over the course of the study period, female *V. rubra* were likely to be nursing rapidly growing young, potentially multiple young. As the study progressed and the dry season shifted to the rainy season, the size and energy requirements of the nursing young increased, in turning increasing the energy and protein requirements of female *V. rubra*. Consequently, there is correspondence between foraging near gap edges, increased production of high protein plant parts near gap edges, and maximum energy/protein requirements for female *V. rubra*. While female *E. albifrons* are also lactating during the dry season, they have lower reproductive costs than female *V. rubra* because they give birth to fewer offspring (singletons or twins rather than litters of 3 or more) and produce less calorie dense milk (Myher, Tilden, Kuksis, & Oftedal, 1994; Tilden & Oftedal, 1995). Consequently, *E. albifrons* may receive fewer benefits from gap edges, though this may be counter-balanced by their dietary flexibility, as noted above. Differences between sexes were not detected during this study, but it is possible that such differences may be detectable when resources are scarce. To fully understand the relationship between foraging of frugivorous lemurs and tree-fall gaps, researchers need to greatly extend the study period or compare data from forests in different stages of cyclone recovery. This will provide more context for understanding the roles sex and reproductive stage may play in these relationships.

The preponderance of tree-fall gaps throughout Andranobe Forest during the study period may have increased the difficulty in detecting their role in plant phenology. All tree types tended to be close to tree-fall gaps, averaging four to five meters from the nearest gap. Most of the trees monitored were likely experiencing some level of canopy gap microclimate conditions because increased temperatures and light intensity extended up to nine meters beyond the gap edge. It was difficult to locate trees under closed canopy during the study period because the forest was recovering from a recent cyclone. Six months prior to the study, the eye of Cyclone Enawo had passed within 75 km of

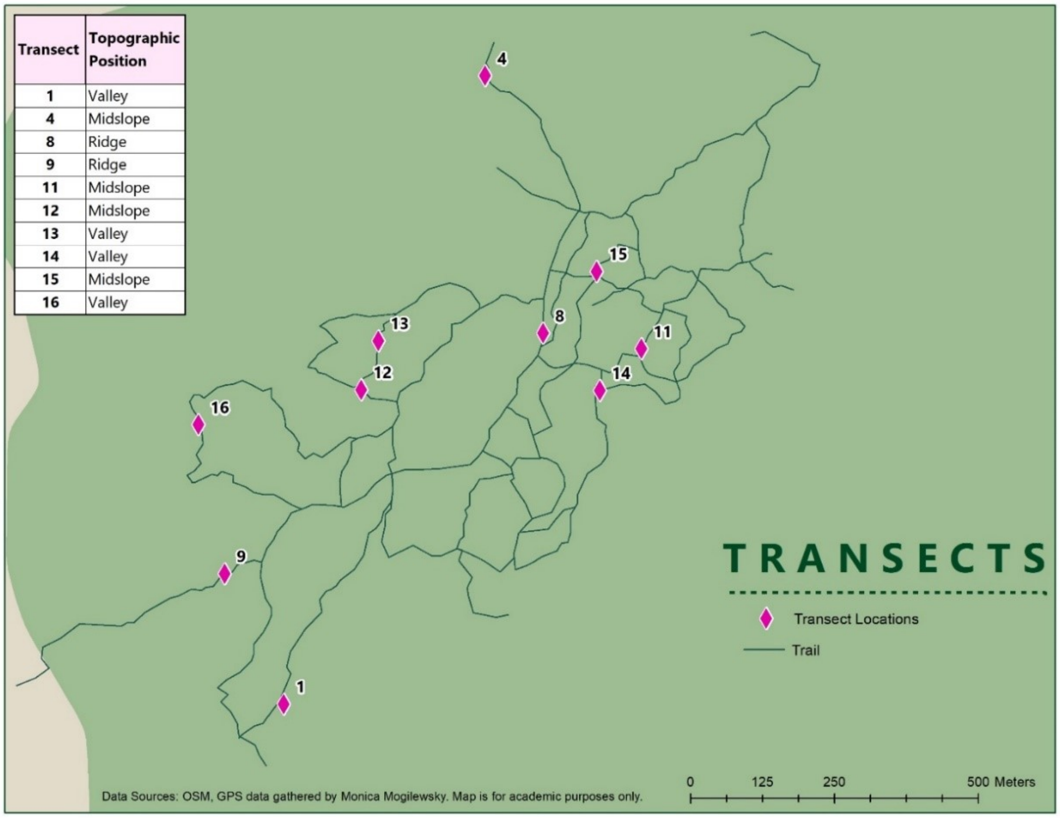
Andranobe Forest. The study site likely experienced sustained winds of 154-177 km/hr and potentially as much as five meters of rain (Probst, Proietti, Annunziato, Paris, & Wania, 2017). According to local field guides, Cyclone Enawo was responsible for the creation of many of the gaps mapped and measured for this study. Tree-fall canopy gaps greatly increased between 2015 and 2017 (see Chapter 3), and it seems likely that much of this increase can be attributed to Cyclone Enawo. Data from a period with little storm disturbance, collected in 2015, suggested that distance to the nearest gap had a stronger effect on food abundance during that period of relatively low disturbance. This period of low disturbance also coincided with a period of low food abundance. Mean percent tree crown with food was significantly less in October through December 2015, prior to the cyclone, compared to October through December 2017, after the cyclone (Chapter 3). It is possible that tree-fall canopy gaps exert greatest influence in periods with relatively little storm disturbance or during periods of food scarcity as opposed to periods of abundance. Perhaps these two factors are the same: the intermediate recovery period following cyclones may result in periods of food abundance. This study detected the influence of canopy gaps despite the reduction in overall canopy density caused by a recent cyclone, which reduced the contrast between canopy gaps and closed canopy in terms of light intensity and temperature.

4.5 Conclusion

Tree-fall canopy gaps appear to contribute to spatial variation in food abundance for frugivorous lemurs. These gaps are just one of many factors influencing plant phenology in Madagascar's evergreen rainforests and, while their influence may be small, it is nonetheless significant. The interannual variation in tree-fall canopy gaps, plant phenology, and lemur food abundance highlight the importance of long-term, multi-year studies for understanding complex relationships between disturbance and animal ecology, including lemurs. The effects of small-scale, frequent disturbance, like canopy gaps, on lemur ecology and behavior is likely to depend greatly on context, making it difficult to characterize the nature of those effects. Yet characterizing the impacts of such disturbances is necessary for understanding the ecology and population dynamics of the endangered *V. rubra* and *E. albifrons*. Conservation management plans that fail to account for fluctuations in ecology, behavior, and reproduction caused by disturbances will almost certainly under-estimate the measures needed to ensure continued survival of critically endangered species. Tropical storm intensity are projected to increase under many climate change models (Ranson *et al.*, 2014; Ren, Liang, Wu, Dong, & Yang, 2011; Seo, 2014), increasing the urgency of incorporating disturbance impacts into conservation decisions. With an average of 3.5 named storm systems making landfall in Madagascar each year (Fitchett & Grab, 2014), current conditions in Madagascar could serve as a model for future conditions of other tropical regions.

4.6 Figures and Tables

Figure 4.1. Location of Field Site in Masoala National Park, Madagascar.



Data Sources: OSM, GPS data gathered by Monica Mogilewsky. Map is for academic purposes only.

Figure 4.2. Location of transects. Transects were used for monitoring tree and liana phenology and measuring tree-fall canopy gap frequency and distribution.

Month	**Week**	***E. albifrons***		***V. rubra***	
		Trees	Lianas	Trees	Lianas
Sept	0	10	13	5	6
Sept	1	7	24	16	22
Sept	2	5	16	47	78
Sept-Oct	3	14	21	19	23
Oct	4	14	29	NA	NA
Oct	5	7	14	9	8
Oct	6	38	82	18	43
Oct-Nov	7	12	28	38	56
Nov	8	40	81	6	7
Nov	9	5	13	27	47
Nov	10	60	94	40	56
Nov-Dec	11	82	183	39	46
Dec	12	58	126	38	72
Dec	13	14	32	20	20
Dec	14	47	71	17	29
Dec	15	8	11	65	105
Dec-Jan	16	46	97	19	26
Jan	17	75	0	60	106
Jan	18	16	27	47	45
Jan	19	32	45	25	23
Jan	20	49	55	NA	NA
Feb	21	45	61	66	95
Feb	22	56	80	21	29
Feb	23	30	41	36	33
Mean		32	52	28	41

Table 4.1. Number of trees and liana visited by each lemur species. Totals are provided for each week and a weekly average provided. Phenological data from trees visited by *V. rubra* were not collected in weeks 4 and 20 due to field staff limitations.

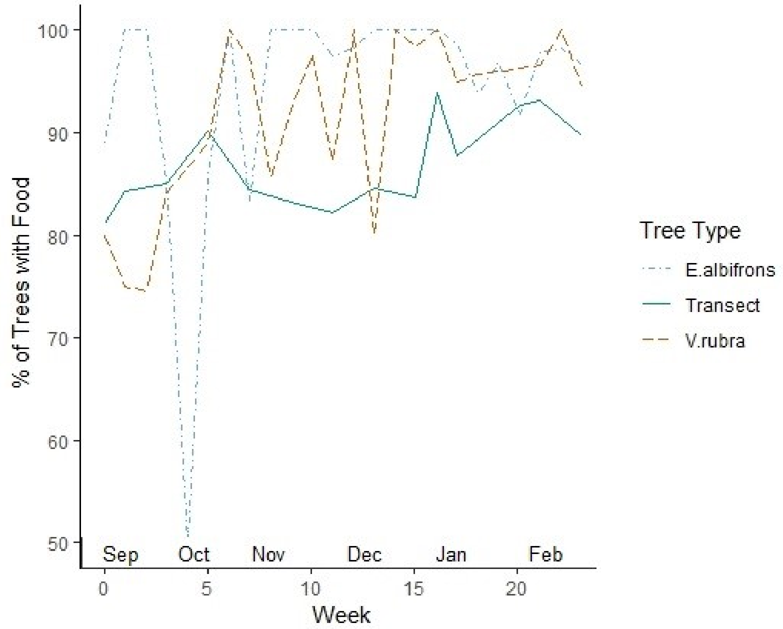


Figure 4.3. Changes in tree food availability over the study period. Young leaves, fruit, flowers, and buds of trees and crown lianas were all considered potential lemur food. The number of trees visited by each lemur species varied weekly from 5 to 89 for *E. albifrons* and from 5 to 66 for *V. rubra* (see Table 4.1); phenology data were collected and analyzed from 303 transect trees.

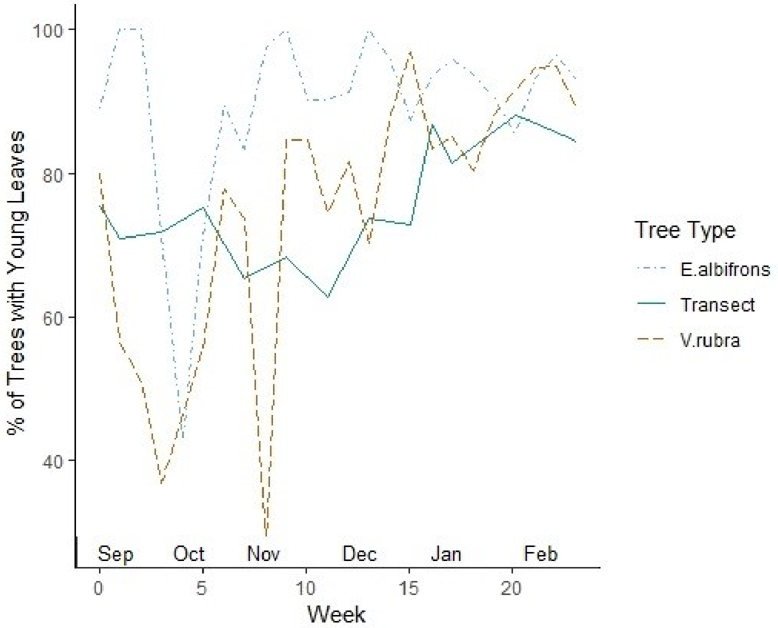


Figure 4.4. Changes in young tree leaf availability over the study period. The number of trees visited by each lemur species varied weekly from 5 to 89 for *E. albifrons* and from 5 to 66 for *V. rubra* (see Table 4.1); phenology data were collected and analyzed from 303 transect trees.

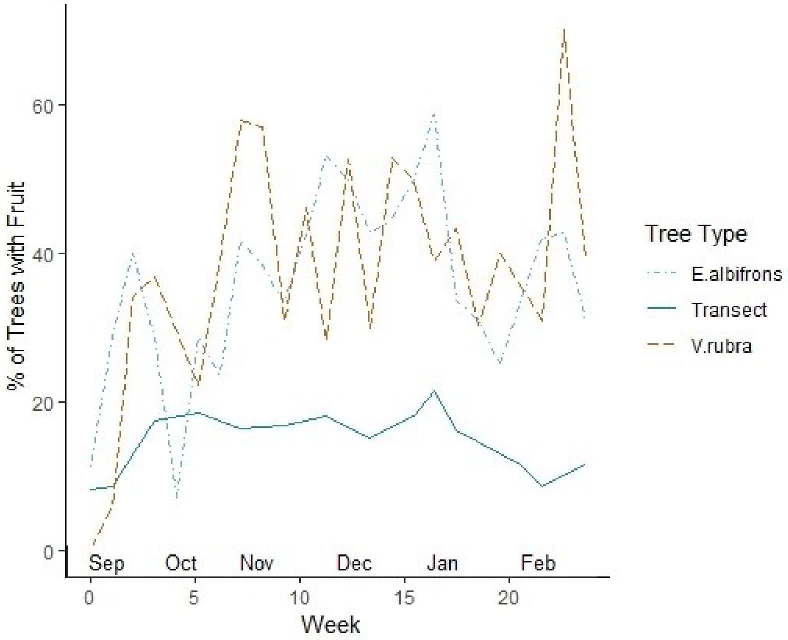


Figure 4.5. Changes in fruit availability over the study period. The number of trees visited by each lemur species varied weekly from 5 to 89 for *E. albifrons* and from 5 to 66 for *V. rubra* (see Table 4.1); phenology data were collected and analyzed from 303 transect trees.

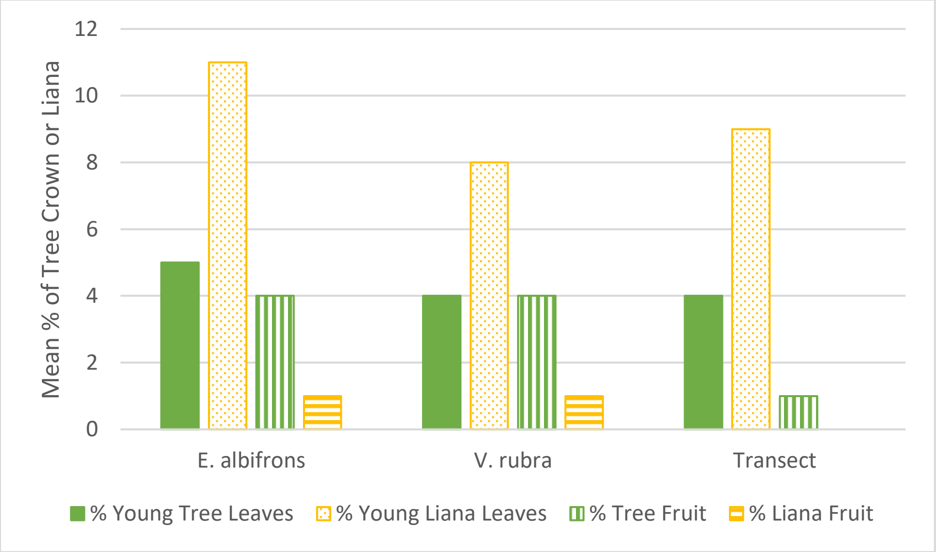


Figure 4.6. Comparison of tree and liana productivity. When the percent of young leaves or fruit was averaged over the study period, lianas produced more young leaves than trees but less fruit than trees, regardless of tree type.

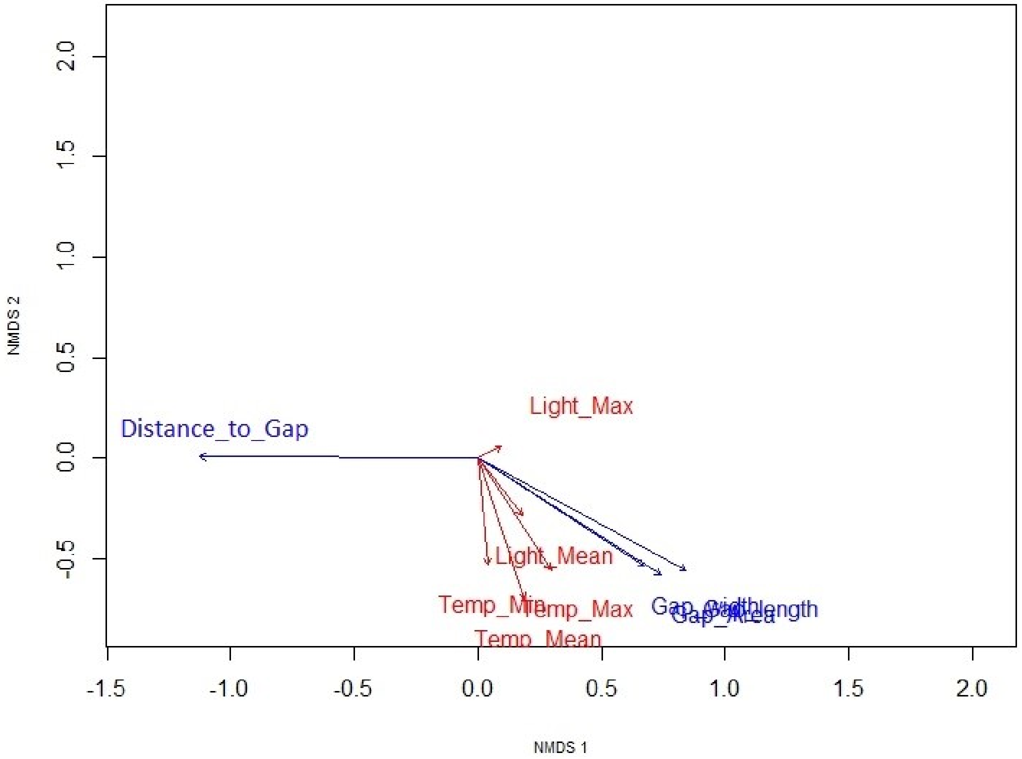


Figure 4.7. Fitting microclimate (red) and gap (blue) variables to the NMDS results. Data included lemur tree morphology and phenology. The vector indicates the relative strength (length) and direction of that variable's effect on the pattern of the trees on the NDMS axes.

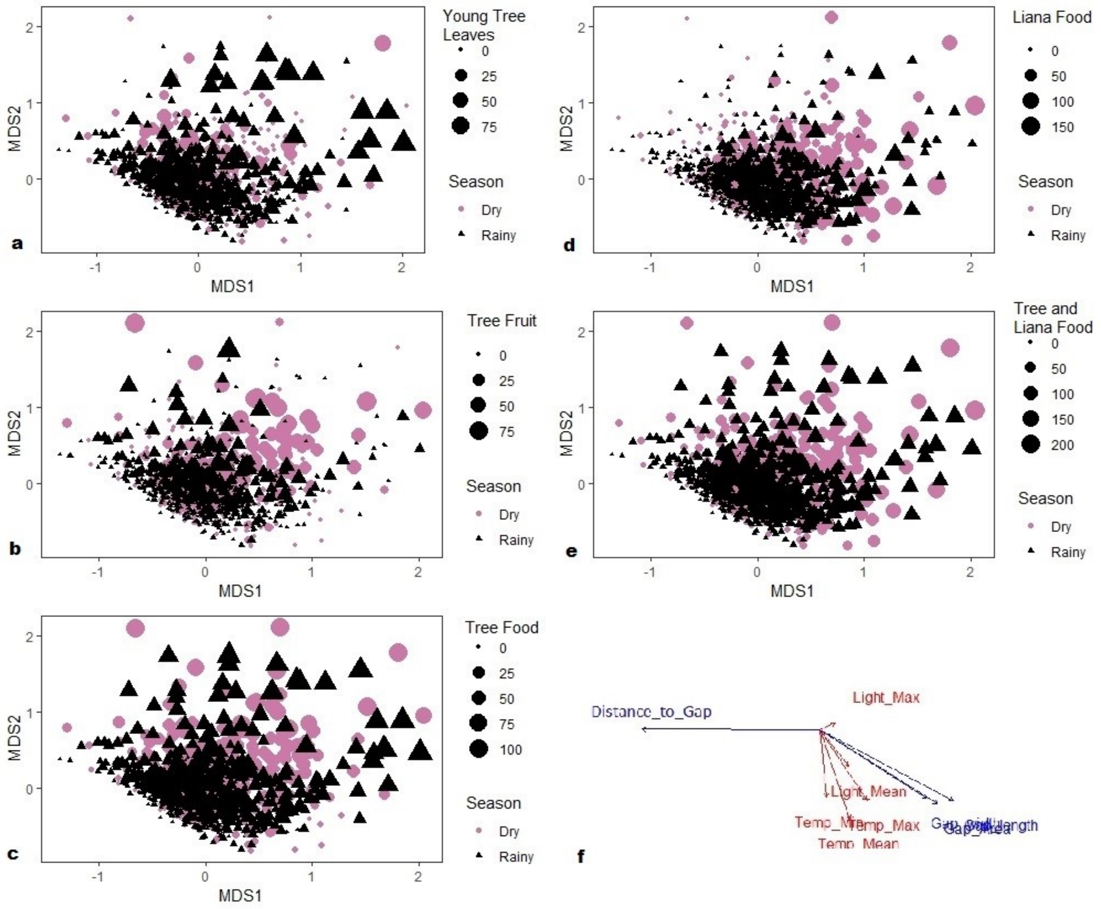


Figure 4.8. NMDS plot of food availability by season. Plots represent two of three axes. Shape size increases with increased abundance of featured phenophase. Trees from both seasons plotted similarly, suggesting that variables driving phenological patterns are similar between seasons.

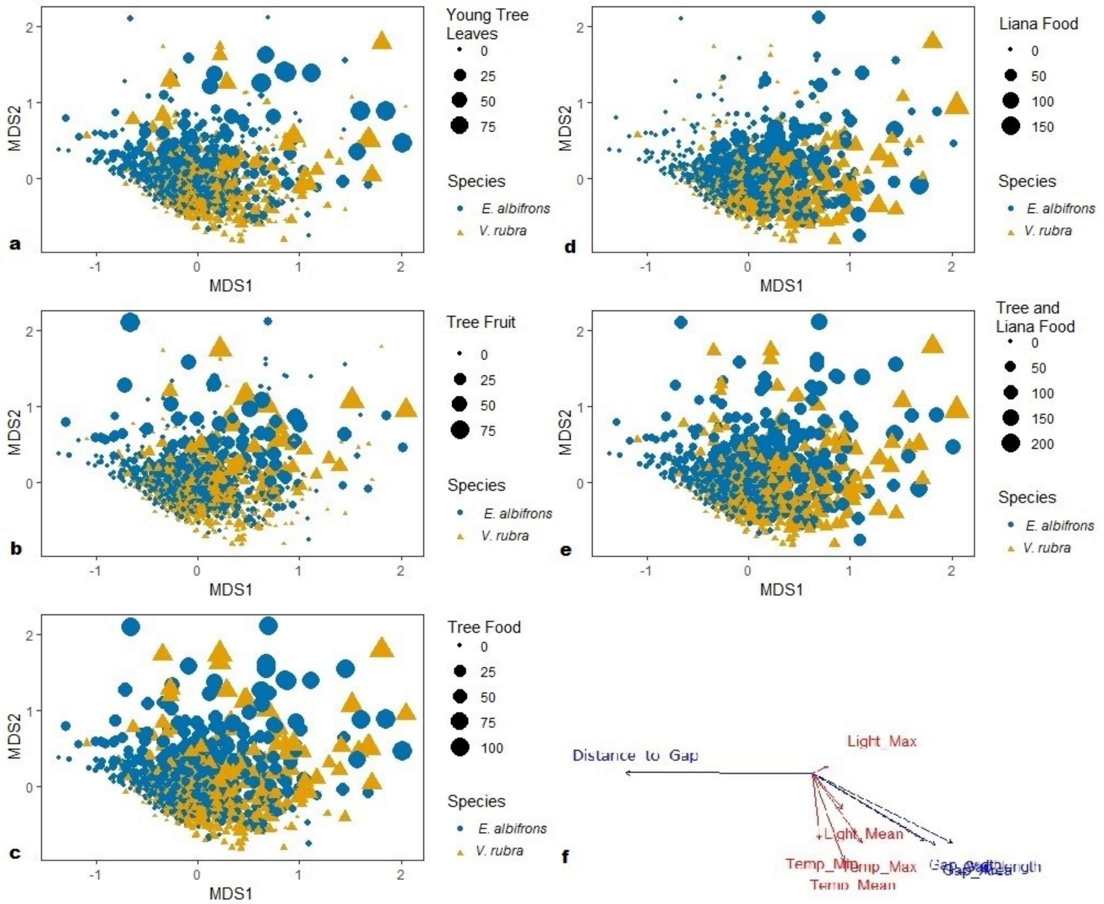


Figure 4.9. NMDS plot of food availability by species. Two of three NMDS axes are plotted. Shape size increases with increased abundance of featured phenophase. Trees visited by *E. albifrons* plotted similarly to those visited by *V. rubra*, suggesting that variables driving phenological patterns are similar between species.

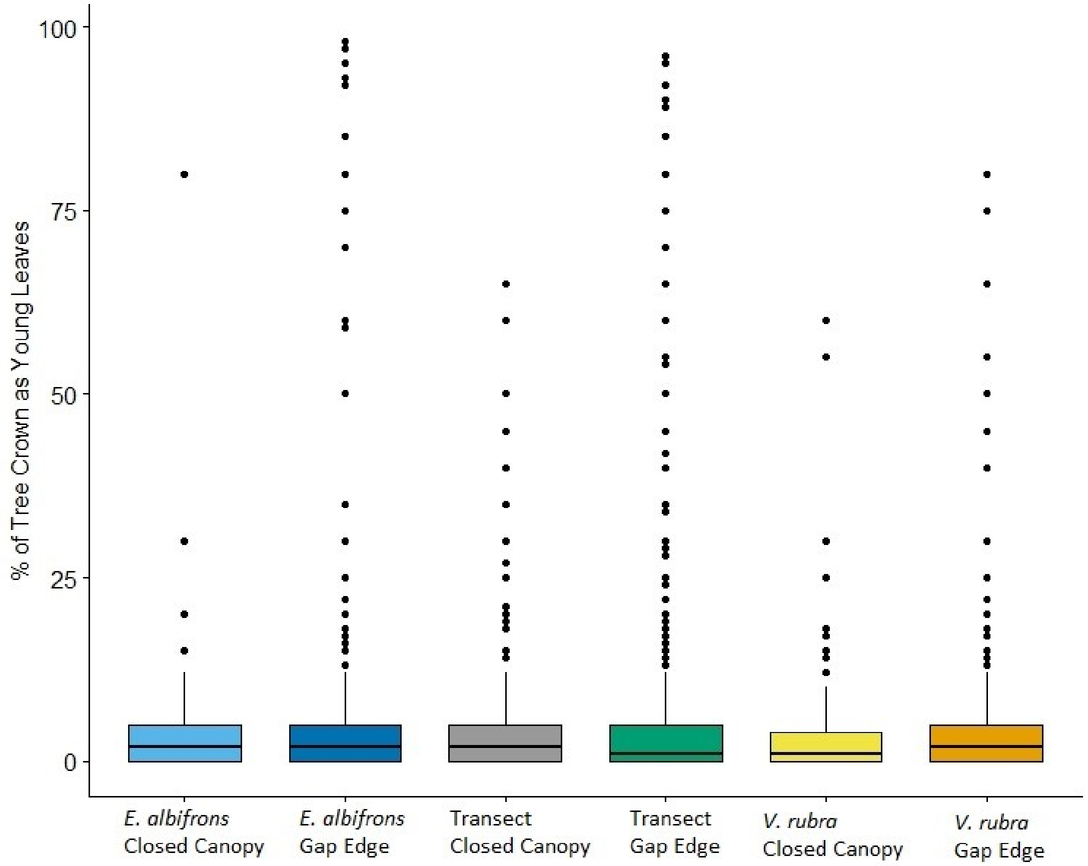


Figure 4.10. Young tree leaf abundance at canopy gaps compared to closed canopy. Boxplots show the median and quartiles for the percent of young tree leaves at gap edges and closed canopy for each tree type. Data collected from tree crowns only.

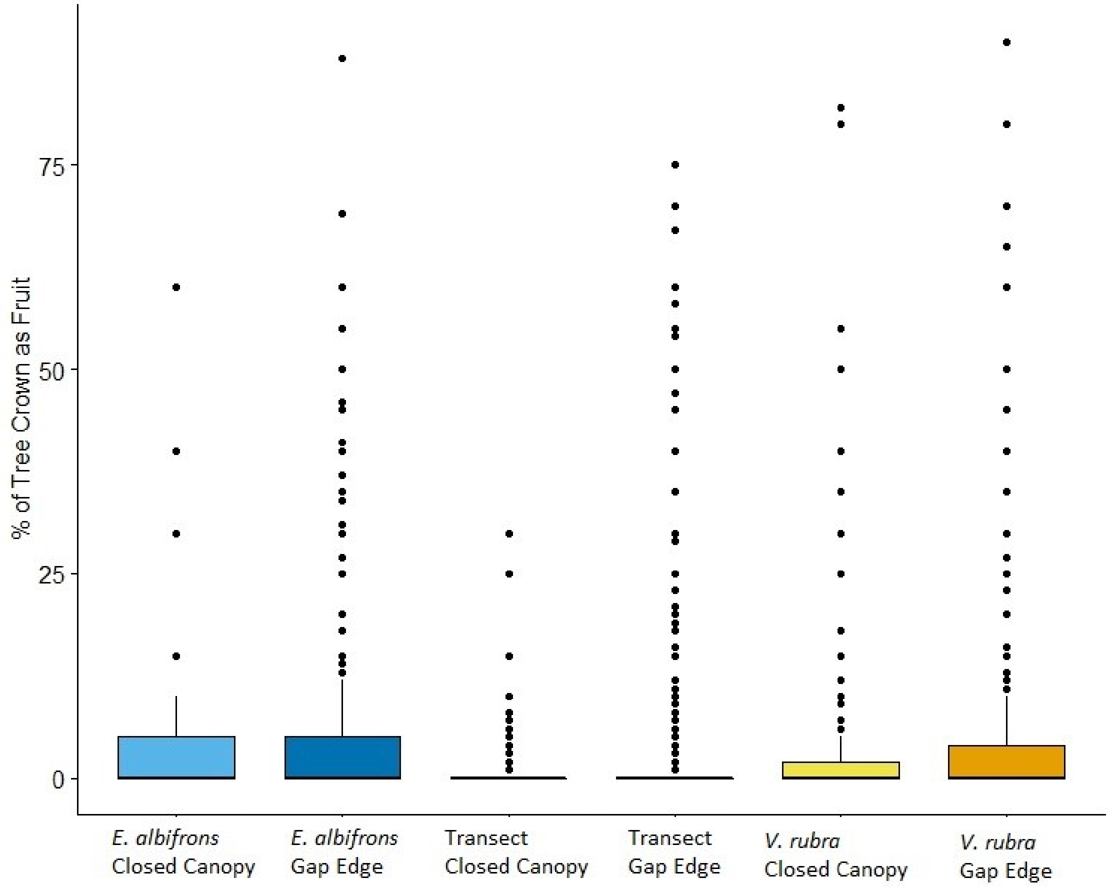


Figure 4.11. Tree fruit abundance at canopy gaps compared to closed canopy. Boxplots show the median and quartiles for the percent of tree fruit at gap edges and closed canopy for each tree type. Data collected from tree crowns only.

Food Type	Variable	β	SE	*t*	P
Young Tree Leaves	Fixed effects				
	Intercept (Tree Type, *E. albifrons)*	1.37	0.05	29.99	<0.001
	Distance to the Nearest Gap	**-0.13**	**0.01**	**-10.74**	**<0.001**
	Tree Type, Transect	**-0.31**	**0.05**	**-6.2**	**<0.001**
	Tree Type, *V. rubra*	**-2.09**	**0.04**	**-52.85**	**<0.001**
	Tree DBH	**0.68**	**0.03**	**26.02**	**<0.001**
	Random effect				
	Tree ID: Week	2.16	1.47		
	Week	0.00	0.05		
	Residual	1.09	1.04		
Tree Fruit	Fixed effects				
	Intercept	0.49	0.07	6.68	<0.001
	Distance to the Nearest Gap	**-0.05**	**0.02**	**-2.69**	**<0.01**
	Tree Type, Transect	**-0.09**	**0.03**	**-2.83**	**<0.01**
	Tree Type, *V. rubra*	**-0.45**	**0.02**	**-18.41**	**<0.001**
	Random effect				
	Tree ID: Week	1.82	1.35		
	Week	0.19	0.44		
	Residual	1.8	1.36		

Table 4.2. GLMM for tree productivity of transect and lemur trees. Results of GLMM for young tree leaves and tree fruit using data from all types of trees, transect trees and trees visited by both lemur species. Significant predictors in bold. A significant intercept indicates that the mean of the response variable is significantly different from 0. For tree type, the model sets the first group (trees visited by *E. albifrons*) as the intercept by default and then calculates β for the other tree types. β standardized regression coefficient; SE standard error; t t-value

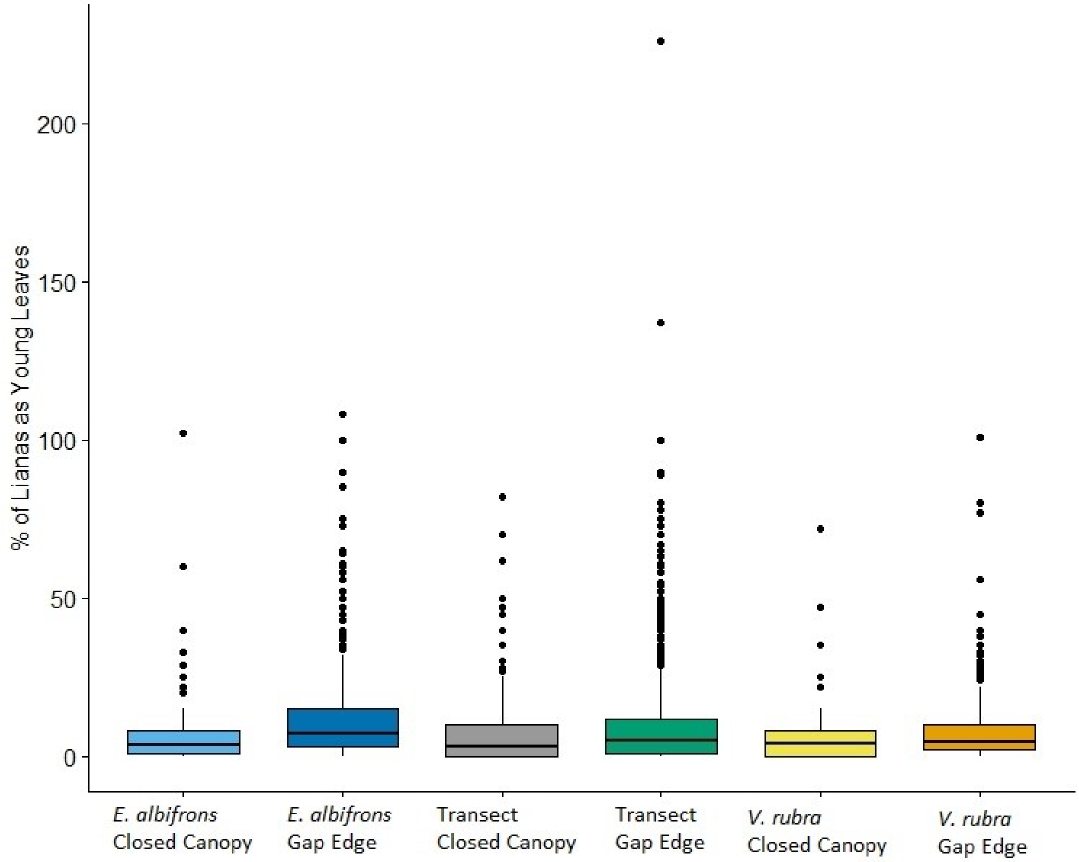


Figure 4.12. Young liana leaf abundance at canopy gaps compared to closed canopy. Boxplots compare the median and quartile for the percent of young liana leaves at gap edges and closed canopy for each tree type. Note that trees frequently had multiple lianas; percent of young leaves were summed across lianas, resulting in some values greater than 100. Data includes young leaves on lianas only; young tree leaves excluded.

Food Type	Variable	β	SE	*t*	P
Young Liana Leaves	Fixed effects				
	Intercept (Tree Type, *E. albifrons,* Dry Season)	2.76	0.17	16.35	<0.001
	Distance to the Nearest Gap	**-0.12**	**0.02**	**-6.41**	**<0.001**
	Tree Type, Transect	**-0.33**	**0.04**	**-7.62**	**<0.001**
	Tree Type, *V. rubra*	**-0.49**	**0.06**	**-8.55**	**<0.001**
	Tree DBH	**0.23**	**0.02**	**10.9**	**<0.001**
	Rainy Season	**-1.65**	**0.10**	**-16.72**	**<0.001**
	Random effect				
	Tree ID: Week	1.71	1.31		
	Week	0.78	0.88		
	Residual	1.38	1.18		
Liana Fruit	Fixed effects				
	Intercept (Tree Type, *E. albifrons,* Dry Season)	1.83	0.28	6.47	<0.001
	Distance to the Nearest Gap	**0.03**	**0.01**	**2.4**	**<0.05**
	Tree Type, Transect	**-1.552**	**0.03**	**-45.53**	**<0.001**
	Tree Type, *V. rubra*	**-0.76**	**0.05**	**-14.52**	**<0.001**
	Tree DBH	0.02	0.02	1.22	>0.10
	Rainy Season	**-2.60**	**0.15**	**-17.70**	**<0.001**
	Random effect				
	Tree ID: Week	0.46	0.68		
	Week	0.78	0.89		
	Residual	0.44	0.67		

Table 4.3. GLMM of liana productivity for transect and lemur trees. Results of GLMM for young liana leaves and liana fruit using data from all types of trees, transect trees and trees visited by both lemur species. Significant predictors in bold. A significant intercept indicates that the mean of the response variable is significantly different from 0. For tree type, the model sets the first group (trees visited by *E. albifrons*, dry season) as the intercept by default and then calculates β for the other tree types or season. β standardized regression coefficient; SE standard error; t t-value

Vernacular	**Family**	**Genus**	**Species**
Afonitsy	Tiliaceae	*Grewia sp.*	*E. albifrons*
Afotra	Tiliaceae	*Grewia sp.*	Both
Afotramena	Tiliaceae	*Grewia sp.*	*E. albifrons*
Antefanala			*E. albifrons*
Antevaratra	Lauraceae	*Belishmiedia sp*. or *Potameia micrantha*	Both
Antoravina	Bignoniaceae	*Phyllarthron antongiliense*	Both
Antsirina			*V. rubra*
Araka	Moraceae		Both
Arami	Anacardiaceae	*Micronychia tsiramiramy*	*E. albifrons*
Ary			*E. albifrons*
Asintoho			*E. albifrons*
Fandifihana			*E. albifrons*
Fotsidity	Moraceae or Apocynaceae	*Ficus politoria* or *Tabernaemontana eusepala*	*E. albifrons*
Harami midinky	Burseraceae	*Canarium sp.*	*E. albifrons*
Haramibe	Burseraceae	*Canarium madagascariense*	Both
Haramikonkona	Meliaceae	*Lepidotrichilia sp.*	Both
Haramitsitsika	Burseraceae	*Canarium sp.*	Both
Hazinimbalavo			V. rubra
Hazinina	Clusiaceae	*Symphonia sp., Mammea sp.,* or *Garcinia sp.*	Both
Hazinina - small fruit	Clusiaceae	*Symphonia sp*. or *Garcinia sp.*	*V. rubra*
Hazomafana	Ebenaceae	*Diospyros sp.*	*E. albifrons*
Hazomainty	Ebenaceae	*Diospyros sp.*	*E. albifrons*
Hazomalagny			*V. rubra*
Hazomamy	Rubiaceae	*Craterispermum sp.*	Both
Hazombato			*E. albifrons*
Hazotsiariana			Both
Hazavolo	Fabaceae	*Cynometra lyallii* or *Dalbergia baronii*	Both
Kafeala	Rubiaceae	*Coffea sp.*	Both
Lalogno			Both
Lombiry	Sphaerosepalaceae	*Rhopalocarpus sp*. or *Dialyceras parvifolium*	Both
Longotra			*V. rubra*

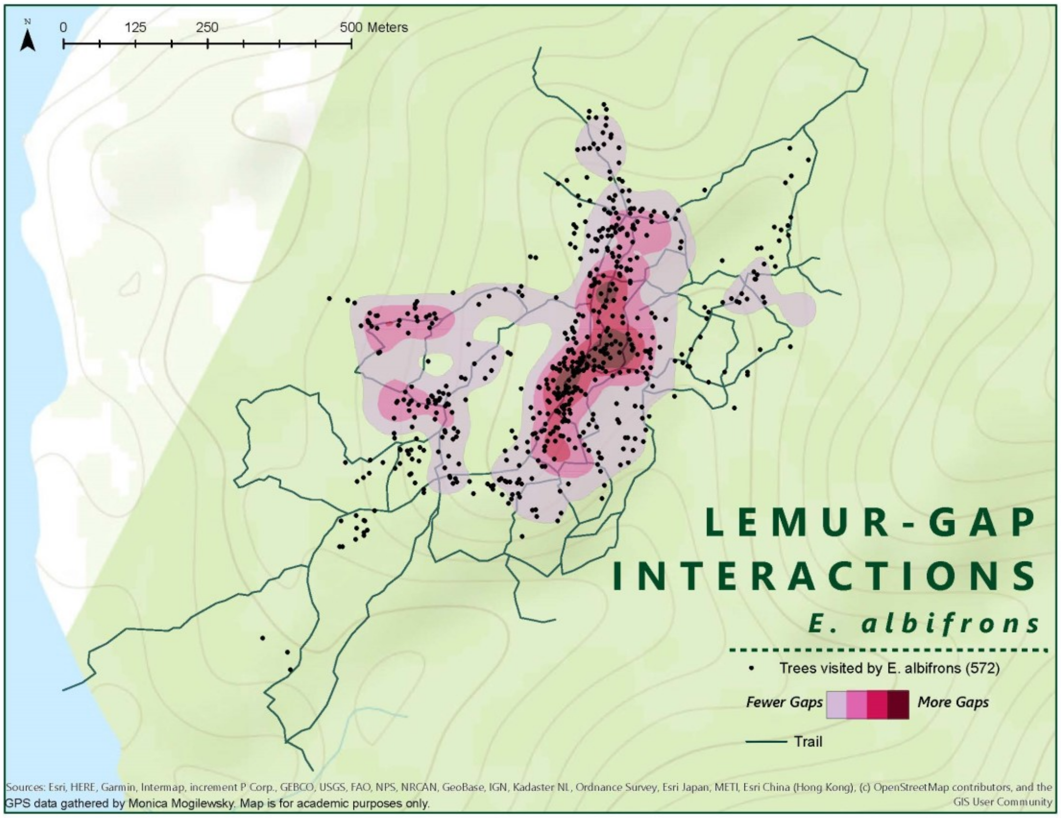
Vernacular	**Family**	**Genus**	**Species**
Mabavy			*E. albifrons*
Magna			*E. albifrons*
Mahintimpototra	Ebenaceae	*Diospyros sp.*	*E. albifrons*
Mampay	Fabaceae	*Cynometra sp.*	Both
Mandavoky			*E. albifrons*
Mantabaratra			Both
Mantadia	Sterculiaceae	*Nesogordonia sp.*	*V. rubra*
Mantalagny			Both
Meavongitra			*V. rubra*
Menavogny			Both
Mongy			*E. albifrons*
Moranga	Annonaceae	*Xylopia buxifolia*	*V. rubra*
Nandrovoky			*V. rubra*
Nanoka			*E. albifrons*
Nanto	Sapotaceae		Both
Nanto antodinga			Both
Nanto asaka			*E. albifrons*
Nanto be raviny	Sapotaceae	*Mimusops antongilensis*	Both
Nanto madinky raviny	Sapotaceae	*Capurodendron sp.*	*V. rubra*
Nanto mena			*V. rubra*
Ombivy	Meliaceae	*Lepidotrichilia sp.*	Both
Rahiny			Both
Rambo			*E. albifrons*
Rara	Myristicaceae	*Mauloutchia humblotii* or *Brochoneura sp.*	Both
Ravenala	Strelitziaceae	*Ravenala madagascariensis*	Both
Ravinavetro			Both
Rotro	Myrtaceae	*Eugenia sp.*	Both
Rotro be	Myrtaceae	*Eugenia sp*. or *Syzgium sp*.	Both
Sakaiala			*V. rubra*
Sodipaso			Both
Sombotrorana			Both
Sombotrorandahy			E. albifrons
Soretry			*E. albifrons*

Vernacular	**Family**	**Genus**	**Species**
Tafignonana			*E. albifrons*
Tamenaka			*V. rubra*
Tapiky			Both
tafonoνona	Ebenaceae	*Diospyros sp.*	*E. albifrons*
Tarantana			Both
Tavolo	Lauraceae, Sapotaceae, or Loganiaceae	*Cryptocarya sp.*, *Capurodendron sp.* or *Strychnos diplotricha*	Both
Tomenja			*E. albifrons*
Trotrokintsina			Both
Tsifo	Rubiaceae	*Canthium sp.*	Both
Tsinagvatra			*E. albifrons*
Tsivoagivoangy			E. albifrons
Vahintrafonaomby			V. rubra
Valotra			*E. albifrons*
Vapaka			*V. rubra*
Vasirindrina			*E. albifrons*
Vavohitra			Both
Vavositra			Both
Voaora	Moraceae	*Ficus tiliifolia*	*E. albifrons*
Voaraala			*V. rubra*
Vongo			Both
Vongo be			*E. albifrons*
Votro			Both
Wild ginger	Zingiberaceae	*Aframomum angustifolium*	*E. albifrons*
Zogna			*E. albifrons*

Table 4.4. Identification of lemur feeding trees. Vernacular provided by professional field guides. Latin names provided by MNP parabotanist or comparison to database of feeding trees from (Vasey, 1997). As plant samples were not identified by a professional botanist, scientific identification should be regarded as preliminary.

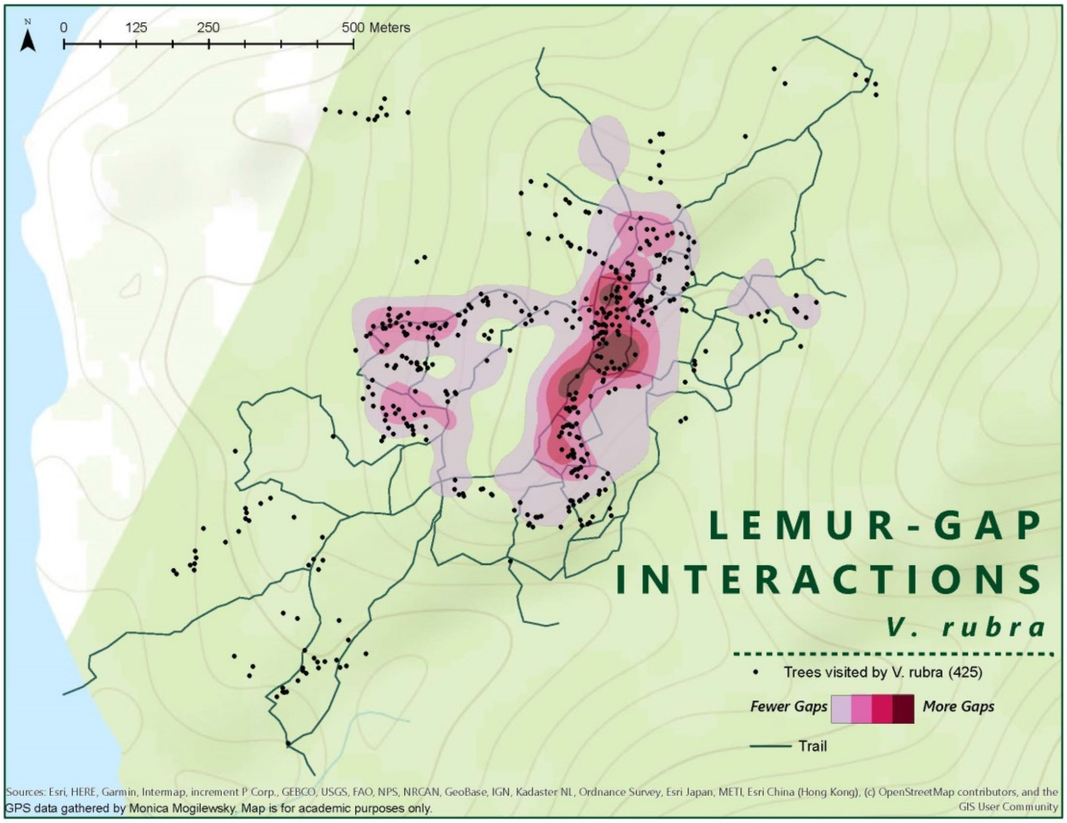
Food Type	Variable	β	SE	*t*	P
Young Tree Leaves	Fixed effects				
	Intercept (Tree Type, *E. albifrons*)	2.06	0.17	11.927	<0.001
	Distance to the Nearest Gap	**-0.68**	**0.06**	**-11.93**	**<0.001**
	Gap Area	-0.01	0.02	-0.39	0.70
	Tree DBH	**4.89**	**0.06**	**79.23**	**<0.001**
	Tree Type, *V. rubra*	**-1.24**	**0.19**	**-6.47**	**<0.001**
	Random effect				
	Session: Tree ID	2.51	1.59		
	Tree ID	9.88	3.14		
	Residual	0.30	0.55		
Tree Fruit	Fixed effects				
	Intercept	0.38	0.04	10.31	<0.001
	Distance to the Nearest Gap	-0.06	0.04	-1.46	0.14
	Gap Area	0.02	0.04	0.43	0.67
	Tree DBH	0.02	0.04	0.48	0.63
	Random effect				
	Session:Tree ID: Week	0.71	0.84		
	Tree ID: Week	0.67	0.82		
	Week	0.00	0.00		
	Residual	0.72	0.85		

Table 4.5. GLMM of tree productivity for lemur trees. Results of GLMM for young tree leaves and tree fruit using data from **lemur trees only**. Significant predictors are in bold. A significant intercept indicates that the mean of the response variable is significantly different from 0. For tree type, the model sets the first group (trees visited by *E. albifrons*) as the intercept by default and then calculates β for the other trees visited by *V. rubra*. β standardized regression coefficient; SE standard error; t t-value



Sources: Esri, HERE, Garmin, Intermap, increment P Corp., GEBCO, USGS, FAO, NPS, NRCAN, GeoBase, IGN, Kadaster NL, Ordnance Survey, Esri Japan, METI, Esri China (Hong Kong), (c) OpenStreetMap contributors, and the GIS User Community
GPS data gathered by Monica Mogilewsky. Map is for academic purposes only.

Figure 4.13. Gap interactions of *E. albifrons*. Map shows all trees visited by *E. albifrons* (572) during observation sessions for the duration of the study and all canopy gaps associated with those trees. Lemurs frequently visited multiple trees near a given gap.



Sources: Esri, HERE, Garmin, Intermap, increment P Corp., GEBCO, USGS, FAO, NPS, NRCAN, GeoBase, IGN, Kadaster NL, Ordnance Survey, Esri Japan, METI, Esri China (Hong Kong), (c) OpenStreetMap contributors, and the GIS User Community

GPS data gathered by Monica Mogilewsky. Map is for academic purposes only.

Figure 4.14. Gap interactions of *V. rubra*. Map shows all trees visited by *V. rubra* (425) during observation sessions for the duration of the study and all canopy gaps associated with those trees. Lemurs frequently visited multiple trees near a given gap.

Variable	β	SE	*t*	P
Fix Effects				
Intercept (*E. albifrons*)	0.17	0.01	28.36	<0.001
Transect Tree	-0.01	0.01	1.7	<0.1
V. rubra	**-0.02**	**0.01**	**-2.5**	**<0.01**
Random Effect				
Week	0.00	0.02		
Residual	0.71	0.85		

Table 4.6. GLMM of distance to the nearest gap. Results of GLMM for distance to the nearest gap using data from all types of trees, transect trees and trees visited by both lemur species. Significant predictors in bold. A significant intercept indicates that the mean of the response variable is significantly different from 0. For tree type, the model sets the first group (trees visited by *E. albifrons*) as the intercept by default and then calculates β for the other tree types.

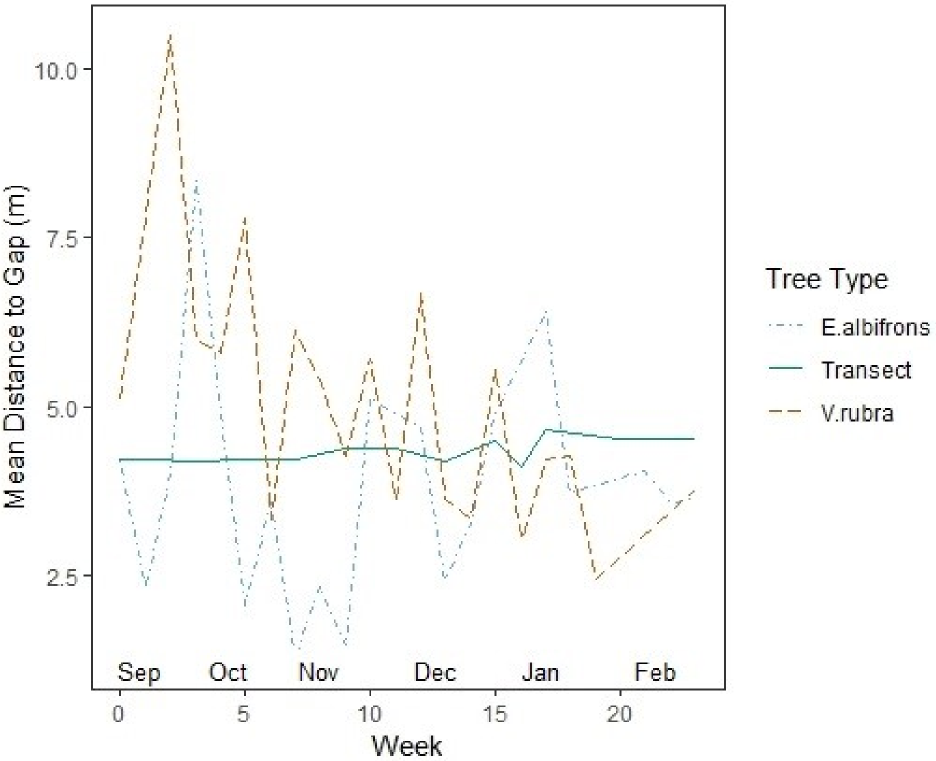


Figure 4.15. Distance to the nearest gap over time. The study period began with week 0 at the beginning of September 2017 and ended at week 23 near the end of February 2018.

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Chapter 5: The Effect of Tree-fall Canopy Gaps on Nutritional Content and Quality of Potential Food for Frugivorous Lemurs in Masoala National Park, Madagascar

5.1 Introduction

5.1.1 Nutritional Content of Plant Parts Consumed by Primates

Nutritional needs vary depending on body size, metabolic requirements, lifestyle, and digestive system. Strategies to meet these needs can incorporate energy maximization, protein maximization, avoidance of plant secondary metabolites, regulation of fiber intake, and nutrient balancing (Felton *et al.*, 2009a). Primates are no exception. No single food type can meet all nutrient and energy needs for primates, and in that absence animals must consume a variety of foods that result in a balance of nutrients (Lambert and Rothman, 2015). Fruits are usually high in easily digested sugars, moderate in fiber, and low in protein, although some fruits do have exceptionally high lipid levels, typically low in lipids (Lambert and Rothman, 2015). Ripe fruit tends to be higher in sugar, lower in fiber, and lower in secondary plant compounds than unripe fruit (Houle *et al.*, 2014). Young leaves, by contrast, have moderate levels of both sugar and fiber concentration but are high in nitrogen and protein; mature leaves tend to have higher fiber content and greater concentration of secondary plant compounds than young leaves and fruit (Lambert and Rothman, 2015). Flowers and mature leaves may have similar nitrogen and protein levels (Oftedal *et al.*, 1991).

The presence of plant secondary compounds complicates the assessment of nutritional content and value of plant parts because these chemicals can make plants unpalatable, toxic, interfere with digestibility, or reduce availability of macronutrients (Glander, 1982). Condensed tannins, a plant secondary compound frequently included in studies on herbivore diets, reduce available protein by binding to peptides, rendering them indigestible (McManus *et al.*, 1981). The concentration of these compounds may play a role in foraging and diet for many primates (Glander, 1982; Ganzhorn, 1989; Chapman and Chapman, 2002). Moreover, increased consumption of condensed tannins can reduce reproductive success in some mammals (Abriel *et al.*, 2009). Some polyphenols, however, improve digestibility of proteins (Waterman, 1984) and not all primates avoid plant parts with high concentrations of polyphenols (Milton, 1979; Remis *et al.*, 2001; Gould *et al.*, 2009). Even among lemurs, selection against condensed tannins and polyphenols is inconsistent, with *Lemur catta* in the spiny forests of Berenty appearing tolerant of high concentrations (Gould *et al.*, 2009) and *Propithecus verreauxi* in the dry forests of Kirindy avoiding high concentrations of these secondary plant compounds (Norscia *et al.*, 2006). Given that there are thousands of different plant secondary compounds and many ways in which they can interact with macronutrients, it is impossible to make broad generalizations about how concentrations of these chemicals in plant parts affect consumption by primates. Add to this, the laboratory analysis of such compounds varies in methodology and results, making inter-study comparisons more difficult (Rothman *et al.*, 2009).

Locating and identifying high nutritional quality foods must be done without expending excessive energy or exposing oneself to risks of predation or costs associated with interspecific and intraspecific competition, and exposure to plant toxins (Houle *et al.*, 2007; Lambert and Rothman, 2015). Contributing to the challenge of meeting nutritional needs is the often large distance between individual trees of the same species within tropical forests and seasonal variation in productivity (Milton, 1993; Houle *et al.*, 2007). Interannual variation in productivity (Chapman *et al.*, 2005) and seasonal variation in quality (Worman and Chapman, 2005) also poses challenges for primates trying to meet nutritional needs.

Primates may prioritize meeting daily protein needs while foraging, rather than maximizing calories or consumption of any one macronutrient. Felton *et al.* (2009) found that for wild spider monkeys (*Ateles chamek*) the daily intake of available protein was highly regulated, while carbohydrate and fat intake varied widely from day to day. This pattern held true across seasons, fruit availability, relative incorporation of folivory, and consumption of dietary tannins (Felton *et al.*, 2009b). A meta-analysis by Ganzhorn *et al.* (2017) added nuance to this protein-balancing theory: folivorous primates select leaves high in protein in environments or times when protein concentration is low. In other words, selection for leaves that are high in protein is necessary only when protein concentrations in the environment are low; when protein concentrations are adequate, food selection is based on other criteria like availability or avoidance or minimization of secondary plant compounds (Ganzhorn *et al.*, 2017).

5.1.2 Protein Challenges for Madagascar’s Frugivores

It may be especially difficult for frugivorous primates to meet protein needs because while high in easily digested carbohydrates, protein content of fruits is too low to meet most primate's needs. Consequently, frugivores must supplement their diet with other sources of protein - leaves, insects, or other animal matter (Milton, 1993). In addition, fruit production is much more spatially and temporally variable than young leaf and flower production. Given enough water, young leaf and flower production is more predictable, following maximum exposure to solar radiation (Lambert and Rothman, 2015). Tropical trees often do not produce fruit crops every year, and interannual crop size varies even in years when fruit is produced (Fleming *et al.*, 1987; Balko and Underwood, 2005; Worman and Chapman, 2005). As a result, strict frugivory in vertebrates is rare, and frugivorous primates must supplement their diet with other sources of protein (Hawes and Peres, 2014; Donati *et al.*, 2017). It may be that careful selection for high protein content of supplemental young leaves is especially important for frugivores. The challenges of frugivory are particularly striking in Madagascar. Based on protein needs, primates should prefer foods with nitrogen contents above 1.1%, yet many of the fruits found in lemur diets have nitrogen concentrations below this threshold (Ganzhorn *et al.*, 2009). Low nitrogen levels of Madagascan fruit may help explain the small number of frugivorous primates there compared to the New World. In fact, most lemurs are primarily folivores; *Varecia* and *Eulemur* are the only genera of lemurs considered frugivorous (Donati *et al.*, 2017), if one defines frugivores as those animals that include fleshy fruits as 50% or more of their diet (Terborgh, 1986).

While folivorous primates have some morphological adaptations to gain some nutritional value from fiber, with colobines as the most striking and extreme example, most primates depend on behavioral adaptations for balancing nutritional needs and fiber intake (Milton, 1993). A common behavioral strategy is choosing only the highest quality plant foods. Procurement of these rare and patchily distributed high-quality food items requires behaviors that minimize or mitigate the cost of searching for and obtaining them. Selective pressure for adaptations that ensure intake of limiting nutrients will only be strong for those nutrients that are not abundant in the environment (Oftedal *et al.*, 1991) like plant-based protein in Madagascar (Ganzhorn *et al.*, 2009; Donati *et al.*, 2017). Based on guidelines established by the National Research Council, non-human primates need a diet containing 1.02 – 1.28% nitrogen (NRC, 2003). Oftedal *et al.* (1991) recommended 1.1 - 1.8% nitrogen to offset the impact of condensed tannins on protein availability. The average concentration of nitrogen in primate diets (2.05 ± 0.57 in Neotropics; 1.74 ± 0.73 in Madagascar) easily meet either requirement (Ganzhorn *et al.*, 2009). Given this, folivorous primates may not need to be highly selective for leaves of high nitrogen and protein content (Donati *et al.*, 2017). Because nitrogen and protein content in fruit is lower than in leaves, frugivores, on the other hand, may experience greater pressure for increased selectivity of plant parts to meet their protein needs.

5.1.3 Variation in Nutrient Content, Protein Concentration, and Food Quality

Nutrient content and quality vary not just by plant part but also by the age of the plant part, and plant nutrition varies widely over many spatial and temporal scales

(Fleming *et al.*, 1987; Chapman *et al.*, 2003; Lambert and Rothman, 2015). Factors that may cause variation in nutritional content across plant samples of the same species include, location, plant age, fruit ripeness, environmental temperatures, precipitation, and light intensity (Chapman *et al.*, 2003; Houle *et al.*, 2007). Light intensity and subsequently photosynthetic activity are strong drivers of fruit production (Houle *et al.*, 2007) and nutritional quality (Ganzhorn, 1995). For example, near the canopy, where light intensity is greatest, fruit production and caloric content tends to be greater than in shaded, interior locations (Houle *et al.*, 2007). Increased sun exposure at forest edges increases extractable protein content while fiber content remains constant, thus improving forage quality, and tree-fall canopy gaps may affect fruit production and nutritional quality similarly (Ganzhorn, 1995). Tree-fall gaps, however, are significantly smaller than forest edges created by even low-intensity logging (Asner *et al.*, 2004) and are not accompanied by the damage of heavy machinery and road creation (Johns, 1997). It is thus far unknown then whether tree-fall gaps result in improved quality of leaves and fruit. Trees and lianas at canopy gaps do increase productivity in response to increased light intensity (Denslow *et al.*, 1990; Beck *et al.*, 2004), similar to increased productivity seen at forest edges (Ganzhorn, 1995). Additionally, these gaps provide habitat conditions preferred by early successional tree specialists, whose leaves tend to be higher quality than late successional trees (Ganzhorn, 1995; Chapman *et al.*, 2002; Eppley *et al.*, 2016). As it remains unknown if the increase in light intensity created by small canopy gaps is sufficient to impact macronutrient content, I sought to examine the nutritional quality of foods selected by two frugivorous lemurs, *V. rubra* and *E. albifrons*.

5.1.4 Study Goals and Hypotheses

My goal is to compare the nutritional quality of young leaves and fruit from the edges of tree-fall canopy gaps to those from closed canopy for feeding trees of two frugivorous lemurs, *Varecia rubra* and *Eulemur albifrons*, in an evergreen tropical rainforest of eastern Madagascar. I used data gathered here to test if canopy gaps were important sources of high-quality foods in areas of frequent disturbance. I predicted that samples collected from gap edges would have higher protein and lower fiber content than samples collected under closed canopy. I predicted that tannin and polyphenol content would differ between gap edges and closed canopy. Because leaves generally have higher protein concentrations than fruit (Lambert and Rothman, 2015), I further predicted that differences in protein content between samples from gap edges and those from closed canopy should be greater for leaves than for fruit. Because fruits provide the bulk of calories for frugivores (Milton, 1993), I predicted that fruits collected from near canopy gaps would have higher energy content than fruits collected under closed canopy.

5.2 Methods

5.2.1 Study Site

Andranobe Forest is a lowland humid evergreen rain forest with a maximum elevation of 260 m above sea level; the 150 hectares (1.5 km^2) area used for the study ranged from 400 m to 1700 m inland of the Bay of Antongil (Vasey, 2000). Masoala

National Park (MNP) is designated as an IUCN category I protected area (Kremen *et al.*, 1999). It is home to two day-active, frugivorous lemurs, *V. rubra* and *E. albifrons.* Andranobe Forest is designated exclusively for research. During the period of this study there was little evidence for large-scale illegal timber extraction or poaching within the study site. Eastern Madagascar experiences 2.2 to 3.5 cyclones per year (de Gouvenain and Silander, 2003; Fitchett and Grab, 2014), that create numerous tree-fall canopy gaps that are well-distributed throughout Andranobe Forest (Mogilewsky and Vasey, 2015).

5.2.2 Sample Collection

To test the effect of the distance to the nearest gap on nutrient availability, fruits and young leaves from trees fed on by *V. rubra* and *E. albifrons* were sampled from tree-fall canopy gap edges and from closed canopy forest. I collected samples from the study site one to two days each month over a three-month period between December 2017 and February 2018. The research team conducted focal animal sampling during daylight hours on a single adult lemur using instantaneous time point sampling at 5 min intervals (Altmann, 1974). Researchers observed *E. albifrons* for 280 hours and *V. rubra* for 308 hours. To the greatest extent possible, researchers divided observation time evenly between sexes. Fruit and young leaves from a subset of flagged feeding trees identified during focal animals sampling were collected (see Chapters 2 and 4, this dissertation, for detailed methods of focal animal sampling and feeding tree identification). Due to the height of the canopy, we collected most samples from the ground. Collection was timed so that samples could be quickly transported to the closest town with reliable electricity, Maroantsetra, for drying in a small portable oven. The research team only collected whole, ripe fruits and intact, young leaves known to be consumed by *V. rubra* or *E. albifrons*.

5.2.3 Ethical Note

Collection of botanical samples was authorized by Madagascar's Director of Protected Terrestrial Areas via research permits 189/17 and 006/18. Transport from Maroantsetra to Antananarivo was completed after receiving authorization to transport permit 182/18, issued by Madagascar's Director of Forests. Samples were shipped to the Department of Animal Biology, Universität Hamburg, Hamburg, Germany, authorized by export permit 366N-EV12/MG18.

5.2.4 Sample Preparation

Nutritional samples of plants were limited to those parts consumed by the lemurs. For example, for fruits where only flesh was eaten, seeds and skin were removed from the sample prior to drying. In many cases, the lemurs swallow pulpy flesh and seeds in their entirety, discarding tough skins. In such cases, fruit and seeds were dried, even though much of the seed passes through the gut undigested. A small, electric portable oven set at 55°C dried all. Samples were dried to prevent the growth of mold and mildew between collection and laboratory analysis. Drying time varied greatly by sample. Dried samples were wrapped in clean paper and sealed with silica desiccant in plastic storage bags. In total, 55 samples were analyzed for macronutrient content. Samples were further dried and analyzed at the Universität Hamburg lab following methods published in

Bollen *et al.*, 2004. Laboratory analysis provided the following data for each sample, calculated as the percent of total dry matter: nitrogen, soluble protein, neutral detergent fiber (NDF), acid detergent fiber (ADF), sugar, condensed tannins, polyphenols, fat, and ash. Crude protein (CP) was calculated by multiplying the percent nitrogen by conversion factor 6.25 (Ortmann *et al.*, 2006). This conversion factor has been challenged in recent years, but no single alternative has been universally accepted in its place. I therefore used it to allow for comparison with a wide range of previous studies of primate diets (See Rothman *et al.*, 2012 for detailed discussion). The ratio of protein-to-fiber, a measure of dietary quality, was calculated using crude protein values and acid detergent fiber (CP:ADF) and was calculated to compare with other study results. Energy content (ME; kcal/g of food) was calculated as:

$$ME = (9 \text{ x } L) + (4 \text{ x } SP) + (4 \text{ x } SC) + (3 \text{ x } [NDF \text{ x } 0.353])$$

where L is the proportion of lipids; SP the proportion of soluble proteins; SC the proportion of structural carbohydrates, and [NDF x 0.353] is the fraction of neutral detergent fiber (NDF) that are digested by *Varecia. variegata*, another species of ruffed lemur (Campbell *et al.*, 2004). The fraction of NDF digested by *E. albifrons* is unknown but was found to be 0.415 for *E. fulvus*, another member of the brown lemur complex (Campbell *et al.*, 2004). For purposes of this study, the lower value was used so the ME would represent a minimum value. Total nonstructural carbohydrates (TNC) were used as a proxy for easily digestible carbohydrates and was calculated as:

$$TNC = 100\% - \text{Crude Protein} - NDF - \text{Lipid} - \text{Ash}.$$

5.2.5 Statistical Analysis

All statistical analyses were conducted using R Version 3.6.1 (R Core Team, 2012) and RStudio Version 1.1.463 (RStudio, 2012). Leaf samples were analyzed separately from fruit samples. Sample details are provided in Table 5.1. Linear models were used to test for the significance of the distance to the nearest gap on nitrogen, crude protein, soluble protein, CP:ADF, condensed tannin, polyphenol, TNC, and ME content of leaves and fruit.

5.3 Results

Protein content of young leaves from lemur feeding trees was not affected by distance to the nearest gap, regardless of whether measured as percent nitrogen, crude protein, or soluble protein (Figure 5.1). Quality of young leaves as measured by CP:ADF was also unaffected by the distance to the nearest gap (Figure 5.1). Distance to the nearest gap did not significantly affect condensed tannins, polyphenol, TNC, or ME of young leaves, either (Figure 5.2). Distance to the nearest gap had no significant effect on nutritional content of fruits; none of the measures of protein had a significant relationship with distance to the nearest gap (Figure 5.3), nor did measures of quality, like CP:ADF, TNC, ME, condensed tannins or polyphenols (Figure 5.3 and Figure 5.4). The results of linear models for nutritional content of young leaves and fruit as predicted by distance to the nearest gap are recorded in Table 5.2.

5.4 Discussion

Contrary to my predictions, distance from the nearest tree-fall canopy gap edge did not affect nitrogen, crude protein, or soluble protein of young leaves or fruit. Nor did distance to the nearest gap affect food quality as measured by CP:ADF, ME, TNC, condensed tannins, or polyphenols. Previous work suggests that young leaves and fruit may be more abundant near tree-fall canopy gap edges (Chapter 4). Based on results presented here, while canopy gaps do not increase protein content or improve quality of lemur foods, proximity to gaps do not decrease protein content or decrease quality, either. Thus, lemurs optimizing food intake by feeding near gaps are unlikely to incur costs in terms of reduced food quality. Lemurs may be able to meet protein needs while reducing foraging effort and energy expended by targeting high density of young leaves near canopy gaps.

Unlike young leaves, fruit are unlikely to be primary sources of protein, instead providing the bulk of calories for frugivores (Milton, 1993). Compared with young leaves, fruit had low protein concentration, regardless of how protein was measured. In contrast, fruits had much higher ME than young leaves. It then makes sense to frame fruit quality in terms of high ME and low condensed tannins and polyphenols, so that ME is maximized while risks associated with potential toxins and protein-binding compounds are reduced. However, contrary to predictions, fruit had similar ME content whether collected from closed canopy or from gap edges. This contrasts with studies finding increased calorie content of fruits exposed to greater solar radiation in the upper canopy (Houle *et al.*, 2014). This may reflect a difference between canopy gap edges and canopy microclimates. The increase in solar radiation from small tree-fall canopy gaps may insufficient to impact fruit quality.

Results regarding protein and secondary plant compounds were also contrary to expectations. Distance to the nearest gap had no effect on any measure of protein: % nitrogen, crude protein, or soluble protein. Condensed tannins and polyphenols bind to protein, effectively reducing protein availability (DeGabriel *et al.*, 2008). Primates frequently select against these phytochemicals when foraging (Glander, 1982), though variation in the laboratory analysis of condensed tannins has resulted in uncertainty regarding the role of condensed tannins in primate diets (Rothman *et al.*, 2009). If frugivorous lemurs select against condensed tannins and polyphenols, then the lower energy content of fruits at gap edges may be an acceptable tradeoff for avoiding fruits with especially high concentrations of these secondary plant compounds. Lemurs may not have difficulty meeting calorie needs if they have access to large quantities of fruit, and fruits appear to be more abundant near gap edges compared to closed canopy (Chapter 4). Paired with the rapid gut transit time of *V. rubra* and *E. albifrons* (Campbell *et al.*, 2004), calorie content of fruit may not be important when fruit is abundant.

Results from this study suggest that the potential for locating high-protein, high-quality food near canopy gaps is equivalent to the potential for these foods under closed canopy. While the average quality of young leaves near canopy gaps may not be remarkable, lemurs may benefit from careful selection of young leaves of higher quality near gaps, since young leaves are more abundant near gaps than under closed canopy.

Controlled experiments have demonstrated that frugivorous lemurs use sensory cues, particularly olfactory cues, to select particular items amongst high-quality food (Rushmore *et al.*, 2012), so such selectivity within their forest environments is expected. However, the results of this study were not statistically significant and this, along with restrictions on sampling intensity, prevent definitive conclusions. In general, team members found that fruit accessible for collection were not abundant under closed canopy. This is reflected in the trees where lemurs were observed foraging: the majority of the lemurs' feeding trees were located within the area of gap influence (< 9 m). During the dry season (September 2017 through November 2017), 77% (249 of 322) of the lemurs' feeding trees were near gaps, and this increased to 83% (400 of 483) during the rainy season (December 2017 through February 2018). More research is needed to determine if the scarcity of fruit under closed canopy was typical, but phenology data collected from this site in 2015 and in 2017 support the importance of canopy gaps for lemur food availability (Chapters 3 and 4). The results of this study suggest that food quality is relatively unaffected by canopy gaps with important implications for the foraging adaptations of the lemurs living in the disturbance-prone, evergreen rainforests of eastern Madagascar.

Food quality is a critical factor in survival and reproductive success, and access to high- quality foods during lactation and weaning is especially important for primates with small body size because their energy stores are limited by their size (Oftedal *et al.*, 1991; Tarnaud, 2006; Ganzhorn *et al.*, 2009). Female red ruffed lemurs (Vasey, 2002), white-fronted lemurs (Vasey, 2000), red-fronted lemurs (Overdorff, 1993), and golden-crowned sifaka (Meyers and Wright, 1993) increased consumption of high protein food during gestation, lactation, or both. This was also the case for ring-tailed lemur populations in gallery forest (Sauther, 1994) but not ring-tailed lemur populations in dry spiny forest (Gould *et al.*, 2011). However, the results of these studies should be viewed with some caution as, with the exception of Gould *et al.* (2011), protein intake was not measured directly; instead, the amount of time spent feeding on young leaves was used as a proxy for measuring quantity of the food and macronutrients associated with that food. Some studies suggest that foraging effort is a poor predictor of nutrient intake (Rothman *et al.*, 2012). Increasing consumption of a required nutrient will have the greatest impact on survival, reproduction, and fitness when that nutrient is relatively rare (Oftedal 1991). Thus, because Madagascar's eastern evergreen rainforest's are particularly low in protein (Ganzhorn *et al.*, 2009), one would expect selection for high-protein foods to have significant impact on lemur fitness. Selection for high-protein, high-quality foods is not limited to adult female primates; a review by Righini (2017) also found that juveniles of many primate species carefully select foods to meet higher energy and macronutrient needs. Selectivity among primates is driven by developmental stage, reproductive stage, site-specific characteristics, and the degree of variation in available food resources (Righini, 2017).

Previous research suggests that lactating females of both species are likely to select young leaves, assumed to be high in protein (Vasey, 2000, 2002; Tarnaud, 2006).

The importance of canopy gaps as high-quality food resources may be different for *E. albifrons* than *V. rubra* because the latter have much higher reproductive costs than the former. Red ruffed lemurs give birth to up to five rapidly growing infants, feeding them with high-fat, high calorie milk on schedule. White-fronted brown lemurs give birth to singletons or twins, nursing them on demand with some of the lowest quality milk of any primate (Myher *et al.*, 1994; Vasey, 2000; Tarnaud, 2006). However, the larger-bodied *V. rubra* dominate the forest canopy (Vasey, 2000), potentially monopolizing the higher quality food that grows in response to canopy-level light intensity (Houle *et al.*, 2007, 2014). White-fronted brown lemurs, frequently excluded from the canopy by red ruffed lemurs (Vasey, 2000), may thus find that tree-fall canopy gaps offer an alternative source of high-quality foods. The number and distribution of canopy gaps (See Chapter 3 and 4, this dissertation) makes the monopoly of these sites nearly impossible, and it is likely that they are frequently accessed by multiple species and groups. Both *E. albifrons* and *V. rubra* were found closer to canopy gaps than expected during a period of relatively low disturbance when potential food was scarce, though data were insufficient to test for sex differences (Chapter 3, this dissertation). Female *V. rubra* were observed feeding from trees closer to gaps than expected when lactating after a recent cyclone, when potential food and canopy gaps were abundant. Female *E. albifrons* were observed feeding from trees closer to canopy gaps than expected when gestating but not during lactation (Chapter 4, this dissertation). Because canopy gaps increase quantity and quality of potential foods, more research is needed to understand the relative importance of each for lemur-gap interactions, particularly for females.

5.5 Conclusion

Tree-fall canopy gaps do not appear to have a strong effect on the quality of young leaves and fruit in terms of protein concentrations, plant secondary compounds, or metabolizable energy. However, young leaves and fruits were more likely to be located near canopy gaps. Thus, lemurs looking for high-quality food or looking to reduce risk of protein binding secondary plant compounds may be more successful when foraging near canopy gaps than when foraging under closed canopy. Due to the low levels of nitrogen in eastern Madagascar's rainforests (Ganzhorn *et al.*, 2009), the canopy gaps created by frequent cyclone disturbance may, in effect, help frugivorous lemurs meet protein requirements. Selecting food items with high protein content (or a high protein to fiber ratio) may be most important for gestating and/or lactating females and developing infants (Felton *et al.*, 2009a). Both reproductive costs and interspecific niche partitioning may dictate the value of such gaps, though additional research is needed to understand the relative importance of each. Moreover, we must learn more about how canopy gaps influence predation pressure and perceived predation risk for day-active lemurs before we can understand the true costs and benefits of canopy gaps to lemurs. As members of the most endangered mammalian taxa (Schwitzer *et al.*, 2014), it is increasingly critical that conservation management plans ensure *V. rubra* and *E. albifrons* are able to meet energy and macronutrient needs within the context of their current and predicted disturbance regimes. Understanding the role of canopy gaps is essential for understanding how *V. rubra* and *E. albifrons* adapt to the unpredictability in fruit availability and meet their protein needs in a low-protein environment. Only then will conservation managers understand the potential for these lemurs to further adapt to increasing environmental and anthropogenic pressures (Allnutt *et al.*, 2008; Schwitzer *et al.*, 2014)

5.6 Figures and Tables

Local name	**Latin identification (if known)**	**Collection Month**	**Plant parts analyzed in lab**	**# Samples**
Haramibe	*Canarium madagascariensis*	Feb	Fleshy fruit	2
Haramikonkona	*Lepidotrichilia sp.*	Dec	Fleshy fruit & seed	3
Haramitsitsika	*Canarium sp.*	Feb	Fleshy fruit & seed	2
Hazinina be	*Symphonia sp.*	Jan	Fleshy fruit	3
Hazinina madinky	*Symphonia sp.*	Jan	Fleshy fruit	7
Hazomamy	*Craterispermum sp.*	Dec	Young leaves	3
Mampay	*Cynometra sp.*	Dec	Young leaves	6
Mantabaratra		Jan	Fleshy fruit & seed	8
Nanto beravina	Family Sapotaceae	Dec	Fleshy fruit	2
Rotro	Family Myrtacaea	Feb	Fleshy fruit & seed	3
Tavolo		Dec	Fleshy fruit & seed	1
Trotrokintsina	*Dicoryphe sp.*	Jan	Fleshy fruit & seed	3
Vongo madinky		Jan	Fleshy fruit & seed	3
Vongo be		Jan	Fleshy fruit & seed	4
			Young leaves	9
			Fruit	41
			Total	50

Table 5.1. Collection details for nutritional samples used for statistical analysis. Samples were collected during the austral summer. Samples represent a random sub-sample for each condition (gap and closed canopy) of each food type (fleshy fruit, young leaves, and fleshy fruit with seed).

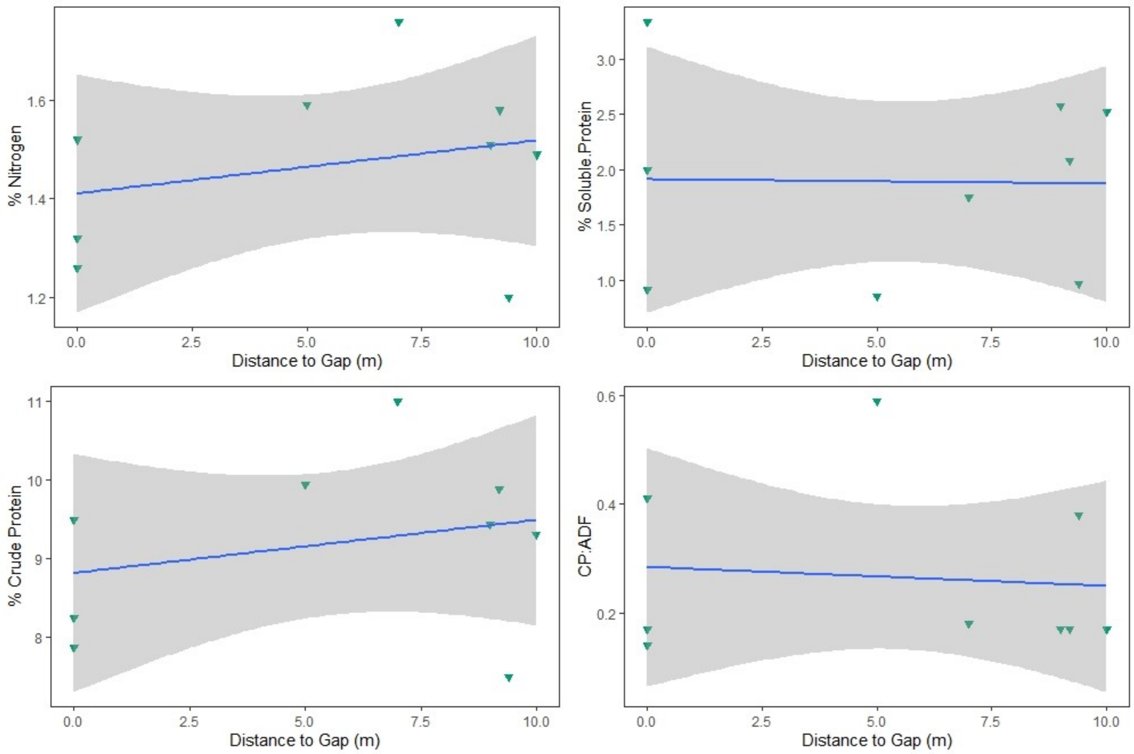

Figure 5.1. Protein content of young leaves. Regression line is blue and confidence interval is indicated with grey shading. There was no relationship between distance to the nearest gap and any protein-related measures of food quality. We did not find samples > 10 m from a tree-fall canopy gap edge.

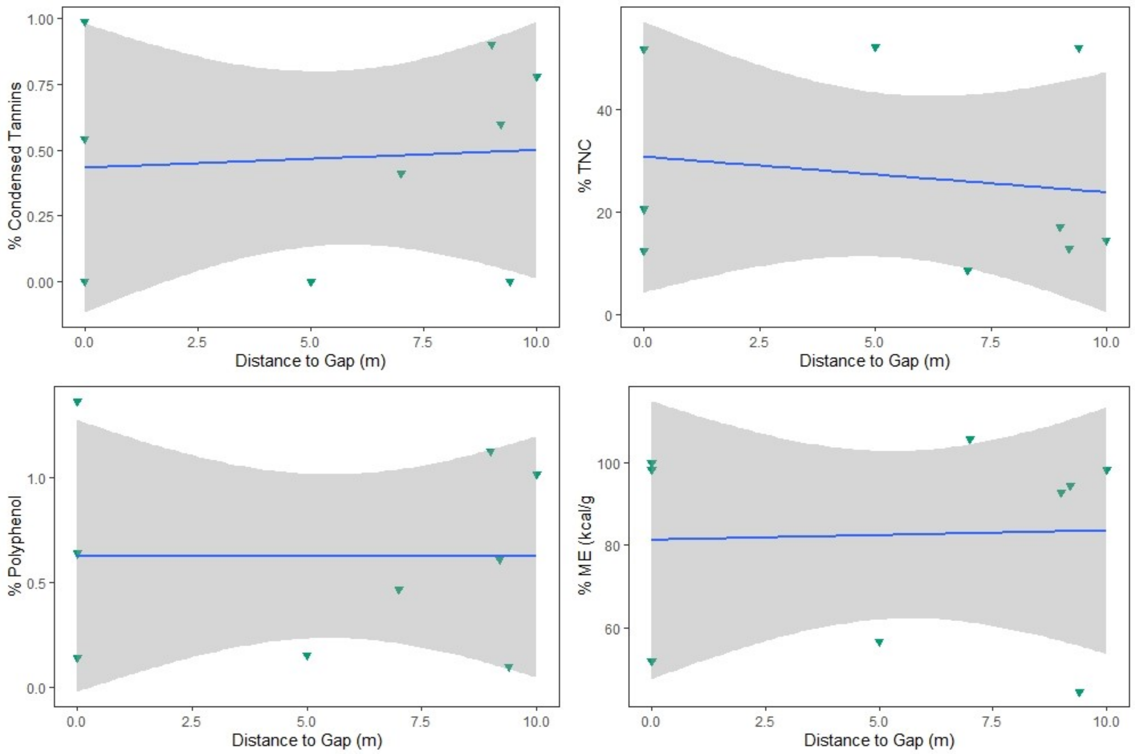

Figure 5.2. Non-protein nutritional content of young leaves. Regression line is blue and confidence interval is indicated with grey shading. There was no relationship between distance to the nearest gap and secondary plant compounds, nor was there a relationship between distance to the nearest gap and energy content. We did not find samples > 10 m from a tree-fall canopy gap edge.

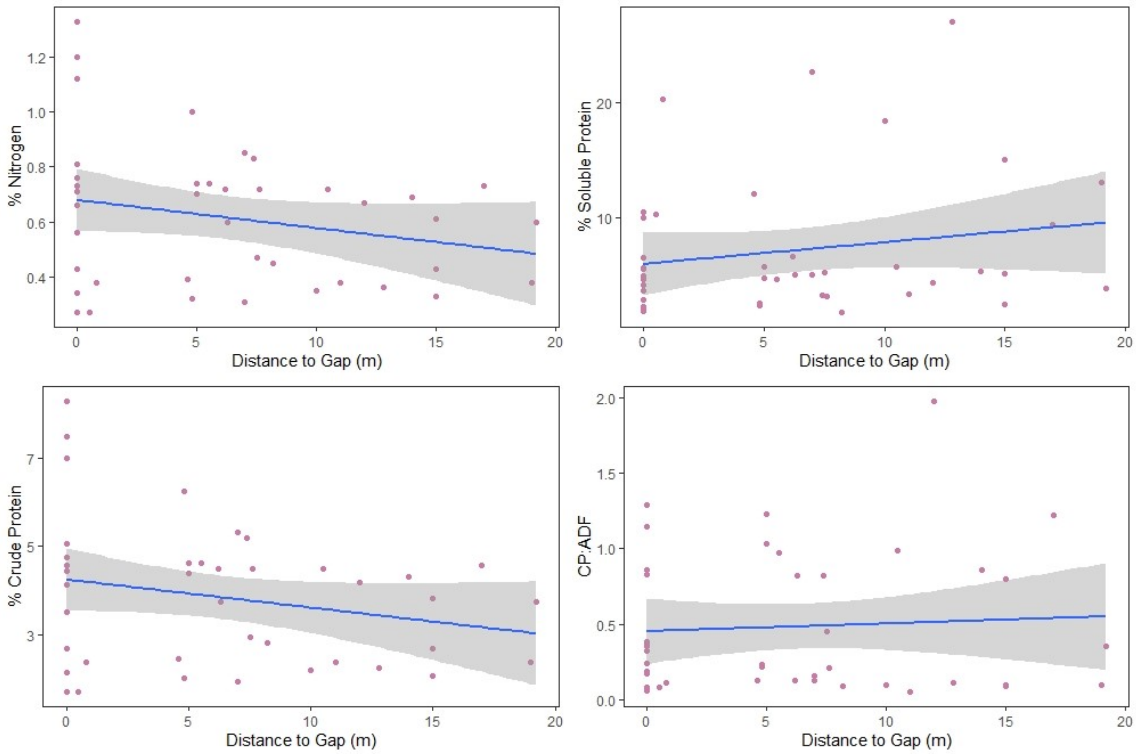

Figure 5.3. Protein content of fruit. Regression line is blue and confidence interval is indicated with grey shading. There was no relationship between distance to the nearest gap and any protein-related measures of food quality.

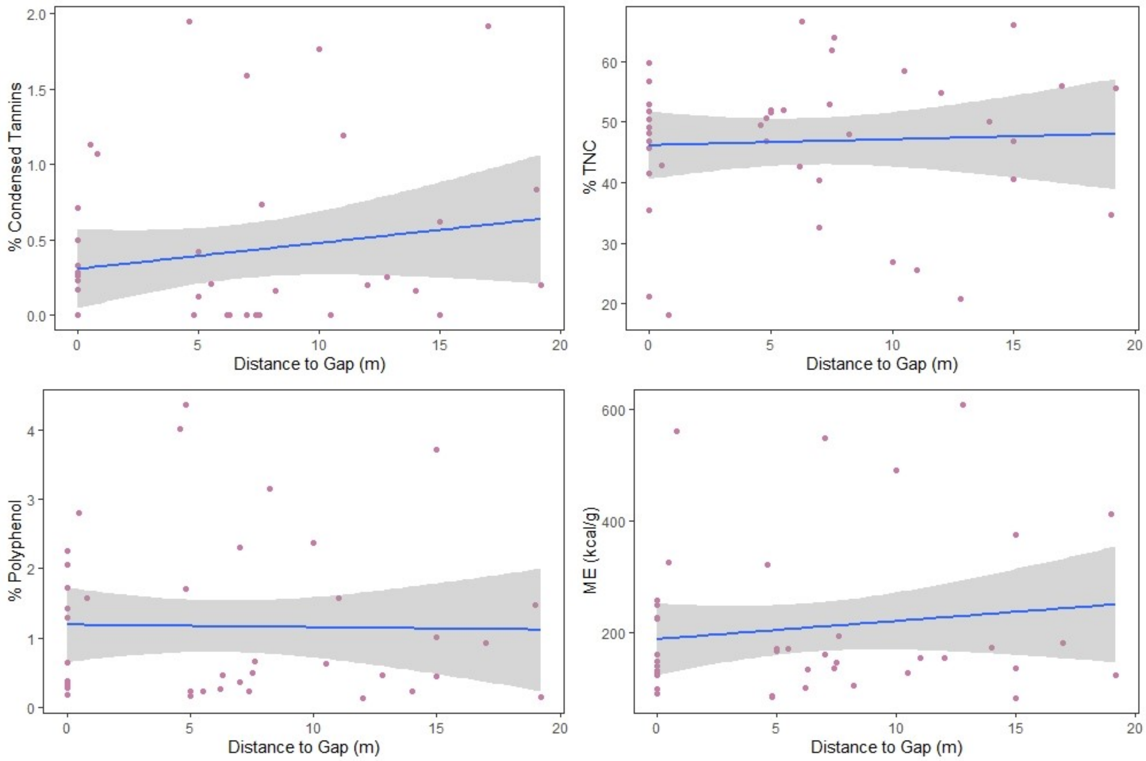

Figure 5.4. Non-protein nutritional content of fruit. Regression line is blue and confidence interval is indicated with grey shading. There was no relationship between distance to the nearest gap and secondary plant compounds, nor was there a relationship between distance to the nearest gap and energy content.

	F	**P value**	**Adjusted R^2**
Young Leaves			
Nitrogen	0.53	0.49	-0.06
Crude Protein	0.53	0.49	-0.06
Soluble Protein	0.00	0.96	-0.14
CP:ADF	0.07	0.80	-0.13
Cond. Tannins	0.04	0.85	-0.14
Polyphenols	0.00	0.99	-0.14
TNC	0.18	0.68	-0.11
ME	0.01	0.92	-0.14
Fruit			
Nitrogen	2.43	0.13	0.03
Crude Protein	2.43	0.13	0.03
Soluble Protein	1.46	0.24	0.01
CP:ADF	0.17	0.68	-0.02
Cond. Tannins	1.34	0.25	0.00
Polyphenols	0.01	0.90	-0.03
TNC	0.09	0.76	-0.02
ME	0.80	0.36	-0.00

Table 5.2. Results of linear regression for distance to the nearest gap and nutritional content. Young leaves and fruit analyzed separately. Degrees of freedom for leaves = (1, 7) and for fruit = (1, 39). Due to the likely bias of R^2 values when sample sizes are small, adjusted R^2 values are provided.

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Chapter 6: Conclusions

6.1 General Conclusions

6.1.1. Summary of Results

With this study I addressed the questions of if and how tree-fall canopy gaps affected plant food abundance and quality at Andranobe Forest, MNP and if and how *Varecia rubra* and *Eulemur albifrons* responded to these gaps and any associated differences in food abundance and quality. I found that tree-fall canopy gaps impacted patterns of tree and liana phenology. Data collected during a period lacking recent cyclone activity showed that trees and lianas produced more young leaves and fruit in proximity to canopy gap edges when compared to closed canopy forest. After Cyclone Enawo, distance to the nearest gap was still a significant predictor of young leaf abundance for trees and lianas. The increase in young leaves in trees and lianas near gap edges was small, however, and only detected in transect trees and trees visited by *E. albifrons*, not trees visited by *V. rubra*. Furthermore, proximity to the nearest gap increased fruit abundance for transect trees and trees visited by *E. albifrons* post-cyclone. However, trees visited by *V. rubra* had lower fruit abundance if located near a canopy gap compared with trees under closed canopy. Liana fruit, on the other hand, increased near canopy gaps for transect trees and trees visited by both lemur species following Cyclone Enawo.

Tree-fall canopy gaps do not appear to have a strong effect on the quality of young leaves and fruit in terms of either protein concentrations, plant secondary compounds, or metabolizable energy. However, young leaves and fruit were more abundant near gap edges than under closed canopy forest. Thus, lemurs looking for high-quality food or looking to reduce risk of protein binding secondary plant compounds may be more successful when foraging near canopy gaps than when foraging under closed canopy because they have more options.

The behavioral response of lemurs to canopy gaps varied by species and by year. Data from a period with no recent cyclone activity indicated that *V. rubra* and *E. albifrons* may spend more time travelling and visit trees closer to canopy gap edges when gaps and food availability in the forest are low. After Cyclone Enawo, the availability of young leaves and fruits at Andranobe Forest increased. More trees had young leaves and fruits and the average percent of crowns as young leaves and fruit increased. While proximity to canopy gaps still correlated with an increase in young leaves in tree crowns, no significant differences were seen in the distance to the nearest gap for transect trees and trees visited by lemurs. During this post-cyclone period, trees visited by *E. albifrons* were about the same distance from the nearest gap as transect trees, and trees visited by *V. rubra* were slightly farther from the nearest gap than transect trees.

6.1.2 Summary of Conclusions

My data provide evidence that *V. rubra* and *E. albifrons* can and do tolerate the high rate of disturbance represented by tree-fall canopy gaps, at least during the hot, food abundant seasons. The data presented in this dissertation provide evidence supporting the hypothesis that tree-fall canopy gaps increase plant productivity and subsequently increase potential food availability for frugivorous lemurs at Andranobe Forest. These gaps are just one of many factors influencing plant phenology in Madagascar's evergreen rainforests and, while their influence may be small, it is nonetheless significant. By foraging near canopy gaps during periods with low cyclone activity, lemurs may have access to a higher density of young leaves and fruit. The relationship between tree-fall canopy gaps, plant productivity, food availability, and lemur foraging likely varies considerably depending on ecological conditions. Andranobe Forest had many more tree-fall canopy gaps after Cyclone Enawo than before the storm. The increase in canopy gaps correlated with an increase in young leaves and fruit, suggesting that cyclones can result in increased food availability for lemurs as the forest recovers. Whether or not lemurs perceive the value of tree-fall gaps may depend on the overall availability of food within the forest, which, in turn, may be impacted by cyclone activity. Perception of value of canopy gaps may also depend on the number and distribution of these gaps: when common, the lemurs need not actively select gaps to be near and benefit from them. In times when food is scarce, both species decrease their average distance from canopy gaps and appear to spend more time traveling to do so. During periods when food is scarce, lemurs may take advantage of the positive relationship between proximity to canopy gaps and plant productivity to improve foraging. In contrast, during times when food is more abundant, both *V. rubra* and *E. albifrons* increase their average distance from these canopy gaps. The costs of foraging near tree-fall gaps may outweigh the benefits during periods of abundance but not during periods of scarcity. The interannual variation in tree-fall canopy gaps, plant phenology, and lemur food abundance highlight the importance of long-term, multi-year studies for understanding complex relationships between disturbance and lemur ecology.

The data presented here compliment and expand findings on the interactions between anthropogenic forest edges and primates. While few primates can survive after conversion of forest to an alternate habitat via clear-cutting or slash-and-burn agriculture, the responses of primates to edges created during selective logging, reduced impact logging, and small-scale resource extraction have been more varied (Johns & Skorupa, 1987). Primates are sometimes tolerant of forest edges and, in some cases, even favor such edges (Ingraldi, 2010; Johns & Skorupa, 1987; Lehman, Rajaonson, & Day, 2006a, 2006c; Lenz, Jack, & Spironello, 2014). Smaller-bodied folivores, in particular, appear to respond positively to increased forest edges in the absence of hunting pressure, though this generalization should not be taken as an absolute rule (Johns & Skorupa, 1987; Lehman *et al.*, 2006c; Lehman, Rajaonson, & Day, 2006b). Forest edges often have increased production of young leaves and fruit (Ganzhorn, 1995; Lehman *et al.*, 2006c, 2006a). In addition, protein content of leaves of all ages appear to increase near forest edges (Ganzhorn, 1995). Together, the increased availability and quality of leaves may at least partially explain favorable responses to edges by folivorous primates. My data suggest that under certain circumstances, the benefits of increased productivity at tree-fall canopy gaps may extend to frugivores. This appears to be the case even though natural tree-fall canopy gaps tend to be much smaller than most anthropogenic gaps. For example, one of the largest gaps at Andranobe Forest was over 200 m^2 and was a clearing cut to install a *laly* prior to the forest's designation as a protected area in 1998. A *laly* is a kind of snare; the hunter clears part of the forest to force lemurs to move across specified bridges made of saplings, often towards a favored fruit tree, leading them into a snare (Golden, 2009). Most of the tree-fall canopy gaps at Andranobe, in contrast to the *laly* gap, were less than 50 m^2 (Mogilewsky & Vasey, 2015). Tree-fall canopy gaps increased abundance of young leaves and fruit of trees and canopy-level lianas in two different field seasons. When food was scarce, both *V. rubra* and *E. albifrons* were found closer to gap edges than expected at random. Results on nutritional quality suggest that tree-fall canopy gaps do not impact protein content of young leaves or sugar content of fruit.

6.2 Importance of Research

6.2.1 Climate Change

Climate change is likely to affect cyclone frequency and intensity (as measured by maximum sustained windspeed), and most models suggest that intensity is likely to increase while changes in frequency remain less certain (Elsner, Kossin, & Jagger, 2008; Ranson *et al.*, 2014; Seo, 2014). The greatest increase in intensity is expected in the North Atlantic, and Northern and Southern Indian basins (Elsner *et al.*, 2008). Changes in cyclone intensity will alter gap dynamics, as stronger cyclones result in greater tree mortality, increasing the number and size of canopy gaps (Lugo, 2008). Data presented here suggest that the number of canopy gaps and food availability may affect the response of lemurs to those gaps by altering the balance of costs and benefits. Larger gaps may, like larger forest edges, more dramatically increase protein content of leaves, increasing the benefit of canopy gaps for lemurs, particularly lactating females and juveniles. At the same time, larger gaps may increase predation risks by increasing visibility of prey and reducing escape routes. Understanding canopy gap-lemur interactions under current climate conditions (the focus of this dissertation) is an essential first step in making accurate predictions for how these interactions will change under various climate change models.

For most species, the environment is not conducive for growth or successful reproduction year-round. Instead, these activities must take place when conditions are favorable, in a window of time. "Ultimately, the activity that is the most demanding for an organism should take place at the time of optimal conditions" (Visser and Both 2005, p 2561). For most species, optimal conditions mean a period of above average or peak food abundance (Visser & Both, 2005). For lemurs, this activity is lactation, and it coincides with peak fruit production for almost all lemur taxa (Wright, 1999). Change in the timing of plant life stages – i.e., change in phenology - is one of the most well-documented effects of global climate change (Forrest & Miller-Rushing, 2010; Parmesan, 2006; Parmesan & Yohe, 2003). However, climate change may alter the timing of development, reproduction, and dormancy of organisms within the same ecosystem differently - resulting in a mismatch of previously coordinated events (Bradshaw & Holzapfel, 2007; Forrest & Miller-Rushing, 2010; Stenseth *et al.*, 2002; Visser & Both, 2005). In fact, Visser & Both (2005) reviewed cases of changes in phenology over the past decade and found that in most cases the changes resulted in mismatches with organisms upon which the species depend. Depending on species, some advanced and others delayed their responses to the species upon which they depended. In addition to altering the timing of phenological events, climate change will likely alter rainfall patterns. For tropical systems, changes in rainfall patterns are likely to impact plant phenology more than changes in temperature (Cleland, Chuine, Menzel, Mooney, & Schwartz, 2007). If changes in phenology result in a mismatch of peak fruit production and weaning in lemurs, this could have grave consequences for the long-term survival of many lemur species. Yet climate change does not necessarily mean negative impacts on primate populations. At Kibale National Park, Chapman et al (2005) found that annual rainfall increased between 1903 and 2003, with a corresponding decrease in the frequency of drought years. They also found that the average monthly minimum temperature decreased during that same period. They also detected a (non-statistically significant) warming trend in average monthly maximum temperatures. These climatic changes coincided with an increase in fruit availability, a decrease in the frequency of fruit scarcity, and a decrease in the duration of periods of fruit scarcity (Chapman, Chapman, Zanne, Poulsen, & Clark, 2005). Since tree-fall gaps play an important role in variation of food availability, future management plans should consider the interaction between gaps, phenology, and climate change to increase the likelihood of long-term survival of lemurs and other primates in cyclone-prone regions.

6.2.2 Extinction Vulnerability of Lemurs

As members of the most endangered mammalian taxa (Schwitzer *et al.*, 2014), it is increasingly critical that conservation management plans ensure *V. rubra* and *E. albifrons* can meet energy and macronutrient needs while confronted with their current and predicted disturbance regimes. Understanding the role of canopy gaps is essential for understanding how *V. rubra* and *E. albifrons* adjust to the unpredictability in fruit availability and meet their protein needs in a low-protein environment. Lehman *et al.* (2006b) noted that no lemur species have gone extinct in the past 50 years, despite extraordinary habitat loss and fragmentation. Their research on edge effects on lemurs in southeast Madagascar surprisingly found that several species responded either neutrally or positively to edge effects, suggesting that adaptations to natural disturbance have provided lemurs with some resilience to anthropogenic disturbance (Lehman *et al.*, 2006a, 2006c). The authors conclude that ". . . there may be a threshold of habitat disturbance and possibly edge effects for lemurs. Determining what this edge threshold is may hold important answers for questions about extirpation and extinction patterns in lemurs" (Lehman *et al.*, 2006b, p 239). Understanding lemur-gap interactions is part of determining this threshold for *V. rubra* and *E. albifrons.*

Moreover, conservation management plans that account for disturbance are more likely to prevent extinction of populations over the long-term because they more accurately predict population changes, particularly growth rates, over time (Clark, 1996; Tuljapurkar *et al.*, 2003). Because *V. rubra* and *E. albifrons* have different reproductive and foraging strategies, a comparison of their canopy gap use can illuminate interactions between life history and behavioral adaptations to frequent disturbance. Thus, data on canopy gap-lemur interactions are critical, not only for managing populations within the rare remaining intact forests of Madagascar, but perhaps even more so for managing populations coping with increased fragmentation and associated edge effects. Given the current increase in anthropogenic disturbance (Allnutt, Asner, Golden, & Powell, 2013; Brooks *et al.*, 2006; Ganzhorn *et al.*, 1997; Herrera, 2017; Waeber, Wilmé, Mercier, Camara, & Lowry II, 2016) and the projected increase in natural disturbance (Elsner *et al.*, 2008; Ranson *et al.*, 2014) in Madagascar, a better understanding of the interactions between disturbances and lemur behavior and ecology is essential to their long-term survival.

6.2.3 Canopy Contributions

To date most research on the role of tree-fall canopy gaps in forest ecology have been from a terrestrial, rather than arboreal, perspective. This is due, in part, to the relatively young age (about 60 years) of canopy research (Lowman, Schowalter, & Fanklin, 2012). This study is one of the first to examine effects of canopy gaps on phenology and arboreal mammal at the canopy level. Tree-fall gaps create sunlight and weather conditions similar to those found in the canopy so it was uncertain whether arboreal animals would distinguish gaps from the canopy more generally. This dissertation partially addressed that uncertainty. During a period of food scarcity and low cyclone activity, *E. albifrons* was closer to gap edges than expected at random while *V.*

rubra and transect trees were at similar distance to the nearest gap (Chapter 3). During a period of food abundance following recent cyclone activity, *V. rubra* was found farther from gap edges than expected at random while *E. albifrons* and transect trees were a similar distance to the nearest gap (Chapter 4). Variation between years and over seasons leaves more questions, particularly how these arboreal primates might associate with tree-fall gaps during the cold, food scarce season. An additional component of the canopy level approach of this research was the unusual but informative inclusion of liana phenology. It was challenging to distinguish lianas from the tree crown and difficult of quantifying fruit and young leave abundance of lianas. However, abundance of liana fruits increased as distance to the nearest gap increased; the inverse was true for tree fruits, which decreased in abundance as distance to the nearest gap increased. Lianas are important components of *V. rubra* (Ratsimbazafy, 2006; Vasey, 2002) and *E. albifrons* diets (Vasey, 2002) and are likely to increase in importance as carbon dioxide levels increase (Mayle, Beerling, Gosling, & Bush, 2004). This study highlights the importance of distinguishing between lianas and trees when studying phenology as well as the feasibility of repeated monitoring of lianas in the canopy.

6.3 Future Directions

6.3.1 Food Scarcity

Data for this study were collected during the hot seasons of northeast Madagascar; September roughly marks the transition from austral winter to summer and precipitation is less heavy from October through early December. Precipitation and temperature increase from January through March. These changes correspond with peak in fruit availability (Vasey, 2000). No data were collected during the cold season, when fruit availability declines such that it becomes quite scarce in August and early September. However, August marks a peak in flower availability and a rise in young leaf abundance (Vasey, 2000). While food availability did not increase in proximity to gap edges during the pre-cyclone period, food may have been available sooner near gaps compared to closed canopy. Phenology data were not collected during the transition between winter and summer, as food scarcity first gave way to increased availability. I predict that lemur feeding trees near gap edges will produce fruit earlier in the transition between seasons compared to trees under closed canopy. The early arrival of food, combined with potential thermoregulatory benefits (see 6.3.2 below), may increase the benefits of tree-fall canopy gaps for the smaller-bodied *E. albifrons*, who are known for huddling and seeking shelter from the elements in liana tangles. The finding that *E. albifrons* fed in trees closer to gaps than expected at random when food was scarce during the pre-cyclone period provides some support for this hypothesis (Chapter 3). Moreover, *E. albifrons* do not have infants to protect from predators during the cold season, potentially reducing predation risks associated with gaps (see 6.3.3 below). While *V. rubra* could potentially benefit from an early arrival of fruits near gap edges, they have greater access to the canopy, which presumably would also have early arrival of fruits compared to understory. *V. rubra* can also use canopy access to warm themselves. Finally, *V. rubra* decreased their mean distance to gap edges over the study period, keeping the greatest distance from canopy gaps during the transition from the cold season to the hot season.

Because of these factors, I predict that *V. rubra,* in contrast to *E. albifrons,* will not be found closer to canopy gaps than expected at random during the cold season.

6.3.2 The Role of Canopy Gaps in Behavioral Thermoregulation

In addition to altering food availability and resource distribution, canopy gap microhabitats may offer opportunities for behavioral thermoregulation for primates and other arboreal animals. Tree-fall gaps significantly alter light intensity and microclimate conditions, particularly temperature and humidity (Brown & Whitmore, 1992; Chazdon & Fetcher, 1984; Salvador-van Eysenrode, Bogaert, van Hecke, & Impens, 1998; Whitmore, 1978). Such microclimate changes can last for months or years (Turton & Siegenthaler, 2004). In a pilot study conducted at Andranobe Forest, MNP, temperature and light intensity differed significantly between gap edges and areas under closed canopy (Chapter 1, this dissertation). These findings were consistent with other studies conducted throughout temperate and tropical forests (Baraloto & Couteron, 2010; Bellingham, 2008; Bellingham, Tanner, Rich, & Goodland, 1996; Everham & Brokaw, 1996; Ewel, Zheng, Pinzon, & Bourgeois, 1998; Turton & Siegenthaler, 2004). Similarly, forest edges are associated with elevated temperatures and light levels (Lehman *et al.*, 2006c). Like forest edges, tree-fall gaps create microclimates that may be optimal for behavioral thermoregulation during colder seasons and, conversely, suboptimal during warmer seasons. I collected temperature and humidity data from closed canopy forest and gap edges during this study for future analysis.

Behavioral thermoregulation may be especially important for lemurs (Tecot, Baden, Romine, & Kamilar, 2012), given the relatively low metabolic rates for their size (Young, Richard, & Aiello, 1990). Many primate taxa, including *Varecia* and *Eulemur*, use behavioral processes, such as huddling, resting, postural changes, and microhabitat selection, to reduce the physiological costs of regulating body temperature (Table 6.1). For example, ruffed lemurs at Nosy Mangabe, MNP, increased resting during the cool-wet season compared to other, warmer seasons; they also used upright and prone positions more often, and huddled positions less often, in the warm-wet season than in the cool-wet season (Morland, 1993). Brown lemurs also frequently exhibit huddling behavior (Donati, Ricci, Baldi, Morelli, & Borgognini Tarli, 2011; Ostner, 2002; Vasey, 2004). Both species may seek out microhabitats for behavioral thermoregulation (Vasey, 2000, 2002, 2004). Seasonal changes in microhabitat use by *V. rubra* at Andranobe Forest, MNP, was attributed to a combination of predator avoidance and behavioral thermoregulation (Vasey, 2002). During the hot-dry season, *V. rubra* regularly descend into the lower canopy to rest, drink, and travel (Vasey, 2002, 2004), while during the cool seasons, they use the upper canopy to sun themselves (Vasey, 2004). *E. albifrons* tend to use dense liana tangles at multiple strata, though typically not in the uppermost canopy. Liana tangles presumably buffer both heat and cold; they are cooler than more open forest during the hot-dry season and offer some protection from wind and rain during transitional and cool-wet seasons (Vasey, 2004). Future research is needed to answer if and how *V. rubra* and *E. albifrons* may use tree-fall canopy gaps for behavioral thermoregulation.

6.3.3 Predation Risk at Canopy Gaps

In addition to altering food resources and microclimate, canopy gaps may affect actual predation rates and preys' perception of risk. Many ecological factors contribute to primates' perception of risk (Hill & Weingrill, 2007). These factors include exposure to predators, visibility due to cover and light, unfamiliar habitat, accessibility and availability of refuges, and habitat structure (Enstam, 2007; Hill & Weingrill, 2007; Treves, 2002). Some microhabitats have greater visual exposure to predators than others; for example, upper and lower edges of food patches, upper canopy, and ground may increase visibility (Overdorff, Strait, & Seltzer, 2002). Cover density affects the probability of predator attack (Hill & Weingrill, 2007; Treves, 2002). For instance, both *Chlorocebus pygerythrus* and *Erythrocebus patas* increased vigilance behaviors in microhabitats, such as tall trees, that provided increased visibility of predators (Enstam, 2007). However, the relationship between cover and perceived predation risk is not straightforward; dense foliage may reduce predator detection by prey while simultaneously offering more cover from potential predators (Treves, 2002). Moreover, a microhabitat's impact on perceived predation risk depends in part on the type of predator. Canopy foraging and location at terminal branches may increase exposure to aerial predators but reduce exposure to terrestrial predators (Treves, 2002).

As well as ecological factors, social factors impact perceptions of predation risk. For example, several studies found that large groups are better at detecting potential predators than small groups (Sauther, 2002). Foraging strategies reflect compromises among predation risk, environmental factors, and group size. After controlling for body size, lemurs living in larger groups foraged in habitats with greater predation risk than lemurs living in smaller groups (between species, Overdorff *et al.*, 2002; within species, Sauther, 2002). Larger groups of *Lemur catta* were more likely to forage on the ground and spent more time in upper and lower strata than small groups (Sauther, 2002). *Propithecus diadema edwardsi* and *E. fulvus rufus,* lemurs that typically live in larger groups, foraged in a greater range of food sources, canopy levels, and food patch sizes than *E. rubriventer,* which typically live in smaller groups (Overdorff *et al.*, 2002).

Ruffed lemurs likely experience differences in predation risk compared to brown lemurs. Predation rates of these taxa at MNP are unknown, but data from Ranamafana National Park in southeast Madagascar suggest that *Eulemur* taxa experience greater predation pressure than *Varecia* (Karpanty, 2006; Karpanty & Wright, 2007). One possible reason for this is simply body size: adult *V. rubra* are about 30% larger than adult *E. albifrons* (Vasey, 1997). *E. albifrons* may mitigate some of this increased predation pressure through use of increased cover, like liana tangles, and larger social groups. Furthermore *E. albifrons* live in multi-male-multi-female groups of 7-9 individuals that are cohesive year-round (Vasey, 1997). In contrast, *V. rubra* are most frequently found in smaller subgroups of 2-5 individuals or even solitary, given their fission-fusion social organization (Vasey, 2006). Though adult *E. albifrons* may be more vulnerable to predators than adult *Varecia,* the opposite is likely true for offspring. Ruffed lemurs nest and stash their young (Vasey, 1997, 2003, 2007); brown lemur infants, in contrast, cling to their mother until they are large enough to travel on their own (Vasey, 2000). Clinging infants may be less vulnerable to predation than stashed infants.

These ecological, social, and life history factors may interact with canopy gap edges to impact predator risk perception for *V. rubra* and *E. albifrons*. Greater light availability, increased range of visibility, and fewer escape routes likely contribute to an increase in predation risk at canopy gap edges. While one would not expect this increase in predation risk to eliminate the use of canopy gap edges for foraging or thermoregulation, predation risk may contribute to the costs of canopy gap use. Increased predation risk near canopy gap edges is one potential explanation for the lack of preference for gaps during periods of food abundance. When food is scarce, the benefits of food abundance associated with gap edges may outweigh the cost of increased predation. The balance of cost-benefits may very well vary by species, age, sex, and reproductive stage. Additional research is needed to better define the costs as well as the benefits of tree-fall canopy gaps for lemurs under current and future conditions.

6.4 Tables

Behavior	Select Citations
Resting	Campos and Fedigan 2009; Gestich, Caselli, and Setz 2014; Bicca-Marques and Calegaro-Marques 1998; Hill 2006; Donati *et al.* 2011; Sato 2012; Kosheleff and Anderson 2009; Morland 1993
Huddling	Wada, Tokida, and Ogawa 2007; Donati *et al.* 2011; Hanya, Kiyono, and Hayaishi 2007; Ostner 2002
Postural Changes	Morland 1993; Gestich, Caselli, and Setz 2014; Bicca-Marques and Calegaro-Marques 1998; Campos and Fedigan 2009
Microhabitat Selection	Kosheleff and Anderson 2009; Hanya, Kiyono, and Hayaishi 2007; Hill 2006; Bicca-Marques and Calegaro-Marques 1998; Gestich, Caselli, and Setz 2014

Table 6.1. Behavioral thermoregulation in primates.

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