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Coexistence of Confamilial, Folivorous Indriids, Propithecus diadema and Indri indri, at Betampona Strict Nature Reserve, Madagascar

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Coexistence of Confamilial, Folivorous Indriids, *Propithecus diadema* and *Indri indri,* at Betampona Strict Nature Reserve, Madagascar

by

Lana Kerker Oliver

A dissertation presented to
The Graduate School
of Washington University in
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Dedicated to Robert W. Sussman and Joseph F. Skomal.

ABSTRACT OF THE DISSERTATION

Coexistence of Confamilial, Folivorous Indriids, *Propithecus diadema* and *Indri indri*, at Betampona Strict Nature Reserve, Madagascar

by

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Doctor of Philosophy in Anthropology

Washington University in St. Louis, 2017

Professor Crickette Sanz, Chair

Abstract

In this dissertation, I examine how two confamilial and ecologically similar indriids, indri (*Indri indri*), and diademed sifakas (*Propithecus diadema*) maintain coexistence in Betampona Nature Reserve (BNR), an eastern lowland rainforest in Madagascar. These two species occur sympatrically throughout much of their species ranges and are similarly-sized folivorous primates. As anatomic folivores, they present an opportunity to investigate how niche differentiation and resource partitioning allow two sympatric primate species with similar feeding patterns to coexist. I examined coexistence strategies and the general behavioral ecology of each species by examining their activity patterns, dietary profiles, home range use, and daily path lengths throughout an annual cycle. I also compared results from my study site to results from other long-term studies.

I collected data on six indri groups and three diademed sifaka groups from April 2013 until May 2014. All indications from this study and other reports indicate that both species are diurnal. Both species spent the majority of their daily active period resting followed by feeding. I found a significantly positive relationship between the time spent active and daily maximum temperature. Diademed sifakas had a significantly shorter daily active period on days with higher rainfall but I did not find the same correlation for indri. I found species-specific difference in the time spent, and activities performed in different levels of the forest. While both species spent the majority of their time in the continuous canopy, diademed sifakas traveled to the ground and occupied the under-canopy layer more than indri.

Both indri and diademed sifakas consumed young leaves more than any other plant part but dietary overlap was low. Indri primarily fed from only trees whereas diademed sifakas fed from significantly more non-trees (epiphytes, lianas, and ferns), particularly when resource availability was low. I also found significant differences in the forest level occupied while feeding. While both species primarily fed in the continuous canopy level, diademed sifakas fed on the ground and in the under-canopy layer more than indri. Indri fed in the emergent canopy layer more than diademed sifakas.

Diademed sifakas had larger home ranges and significantly longer daily path lengths than indri. Both species exhibited clear preferences for some areas of their home ranges over others. Neither species used their home ranges homogenously. This was the first study to examine home range overlap using Kernel Density Estimations (KDE). Using this method, I found that, interspecifically, indri and diademed sifaka home range overlap to be low. Low spatio-temporal overlap was also evident in that interspecific encounters were rare. For both species, daily path length was shortest in the cold, rainy season, and longest in the warm, rainy season. Diademed sifakas, however, decreased their daily path length significantly in the cold, rainy season. Indri decreased their daily path length during this time but not significantly.

In summary, I found that indri and diademed sifakas employ coexistence strategies in their activities, dietary profiles, home range use, and daily path lengths. For both species, activity, feeding, and ranging patterns fluctuated throughout the year. General activity, diet, and home range use patterns were consistent with other sites. Throughout primate taxa, sympatric folivorous primates exhibit several non-mutually exclusive strategies through a combination of differing activity patterns, dietary profiles, forest strata occupation, and ranging patterns. The indri and diademed sifakas at BNR exhibited a combination of coexistence strategies primarily via differing dietary profiles and low spatio-temporal overlap.

Chapter 1: Introduction

1.1 Overview

The extant lemurs of Madagascar are a taxonomically diverse group of primates with over 100 recognized species (Mittermeier et al. 2010). The prevailing theory to explain this species diversity was that lemurs were the result of an adaptive radiation (Martin 1972). By definition, an adaptive radiation is a period characterized by high rates of speciation generally due to the availability of new ecological niches. The rate of speciation then decreases as ecological availability decreases. In light of new evidence, lemur evolution did was not the result of an adaptive radiation (Herrera 2017). Instead, a founder population of lemurs arrived on Madagascar and experienced rapid phenotypic evolution into large groups and the rapid increase in extant species occurred more recently (Herrera 2017; Herrera and Davalos 2016). There are currently five families of lemurs, Cheirogaleidae, Lemuridae, Lepilemuridae, Daubentoniidae, and Indriidae and three families of extinct "subfossil" lemurs, Archaeolemuridae, Megaladapidae, and Paleopropithecidae (Tattersall 2006). Indri (*Indri indri*) (Gmelin 1788) and diademed sifakas (*Propithecus diadema*) (Bennett 1831) are two ecologically and phylogenetically similar lemur species from the family Indriidae. The two genera are estimated to have diverged approximately 30 million years ago (mya) (Horvath and Willard 2007; Roos et al. 2004). They are sympatric throughout much of their species ranges. Both are considered anatomical folivores and, due to these morphological and ecological similarities, present an opportunity to investigate how niche differentiation and resource partitioning allow two sympatric primate species with similar feeding patterns to coexist. This understanding of relationship of habitat preferences, differences in resource use, and morphological adaptations associated with these differences can also help illustrate coexistence patterns of, not only extant primates, but extinct populations as well.

Primatology is finally entering an era in which between-site comparisons for a growing number of primate species can now yield important insights on the behavioral and ecological variability within species along with species differences in the presence or absence of potential resource competitors. We know that human and non-human primate species did not evolve in a vacuum but, rather, in dynamic, changing environments, many times in sympatry with other potential competitors. With a growing number of studies of sympatric primates, we can address broader anthropological questions regarding human and non-human primate evolution. Between-site comparisons, such as those included in this dissertation, of the same species now allow us to examine behavioral and ecological variability within species. This current study, along with other research on sympatric primates are now able to contribute valuable insights into the factors that contributed to their evolution in the same environment can now be used to determine how the presence of one species impacts the evolution of another species.

In this dissertation, I address how and why indri and diademed sifakas are able to coexist sympatrically when they share so many dietary, ecological, and anatomical characteristics. My overall objective is to expand our knowledge of the species-specific ecological niches and evolutionary mechanisms that facilitate the coexistence of sympatric indri and diademed sifaka through documentation of their behavioral ecology. The data which I collected on indri and diademed sifakas at Betampona Nature Reserve (BNR), an eastern lowland rainforest in Madagascar, from April 2013 through March 2014 represents the most comprehensive comparative study of these species conducted to date. My aim in applying the same survey methods to both species within the same study period was to provide a comparative perspective on group size, demography, diet, ranging patterns and activity patterns of these two indriids without the confounds of different study periods or ecological settings. In this dissertation, I will: 1) present species-specific activity patterns and their seasonal fluctuations; 2) discuss species-level variation in dietary preferences and how these change throughout the year; 3) quantify the effects of resource distribution and availability on each species' ranging behavior through spatial analysis; and 4) synthesize these findings to advance our understanding of niche differentiation within sympatric primates. I also assess the behavioral and ecological variation in indri and diademed sifakas by comparing results from BNR to long-term studies conducted at other sites.

In this chapter, I present brief overviews of the following topics:

1) Coexistence strategies of sympatric species;
2) Co-occurrence of sympatric folivorous primates;
3) Primate community structure and seasonality in Madagascar;
4) Behavior, ecology, and morphology of indri and diademed sifakas;
5) Specific research questions and hypotheses of this dissertation;
6) Outline of the chapters in this dissertation.

1.1.1 Coexistence

Understanding how differing activity, dietary, and habitat preferences lead to the successful coexistence of sympatric species is a key question in many disciplines, including behavioral ecology, community ecology, and primatology. Two concepts are central to this understanding: ecological niches and resource competition. An ecological niche is defined, in a general sense, as the biotic and abiotic environmental variables required for the growth, development and reproduction of a species (Schoener 1974). It is important to note the difference between a habitat and a niche. Habitat refers to a physical space, whereas a niche describes that pattern by which an animal uses the habitat (Krebs and Davies 1978). An ecological niche is characterized as a multidimensional (or n-dimensional) hypervolume in which the *n* dimensions are the environmental variables necessary for the species' survival (Hutchinson 1957; Tokeshi 1999).

Resource competition is explained by the principle of competitive exclusion, which posits that two or more sympatric species are unable to coexist if they exploit the same density dependent and limited resource (Gause 1934). Through the mechanism of niche differentiation (also referred to as resource partitioning), sympatric species are able to coexist by exploiting distinct niches in which limited resources are either 1) differentially used by each species, or 2) when the use of limited resources do not extensively overlap.

The most well-known example of competitive exclusion was demonstrated in laboratory experiments by Gause (1934) using two closely related protozoan species, *Paramecuim aurelia* and *P. caudatum.* In identical conditions but in separate cultures, both species' populations grew until they reached an equilibrium. This demonstrates that they were able to survive and thrive in the same environments. When the same volumes of both species were placed in a culture together, the population of *P. aurelia* increased more quickly and consumed more of the limited food resource than did *P. caudatum.* Although initially the population of *P. caudatum* grew faster with *P. aurelia* than it did alone, the population began to gradually decline after the fourth day of coexistence. Accompanying this decline was the increase in the population of *P. aurelia* until it plateaued around day seven (Gause 1934). While neither species engaged in direct physical or chemical attacks against each other, *P. aurelia* consumed more of the limited food resources available than *P. caudatum*. After an average of 16 days, *P. aurelia* was the only species in the culture, which clearly demonstrated its competitive advantage (Gause 1934).

These findings formed the basis for the principle of competitive exclusion by illustrating that two species with completely overlapping ecological niches could not coexist in an environment with limited resources (Gause 1934). In a further experiment, Gause (1934) found that *P. caudatum* could coexist with *P. bursaria* because, while the exploited the same food resources, they did not overlap in the space they occupied in the culture. As such, these species were able to reach an equilibrium of coexistence. These experiments illustrate that niche overlap can occur without competitive exclusion when coexisting species either 1) utilize overlapping resources that are abundant or 2) utilize limited resources in different ways through resource partitioning.

The competitive exclusion principle demonstrated in Gause's (1934) first experiment is rarely observed in nature (Hardin 1960). This is because, if two species completely overlap in their use of limited resources, it is predicted that one species will possess a competitive advantage which will lead to increased reproductive success and eventual exclusion of the other species from the environment (Grinnell 1904; Hardin 1960). Instead, the more common observation in nature is of ecological communities operating at an equilibrium of coexistence like that observed in Gause's experiments with both species of *Paramecuim* (Gause 1934). By partitioning limited resources, species avoid competition by exploiting different ecological niches in a spatially and temporally heterogeneous environment (Tokeshi 1999). Resource partitioning among sympatric species is the result of species interactions and adaptations over evolutionary time to avoid competition by reducing extensive overlap for limited resources (Schoener 1986). In a general sense, resources are partitioned to reduce overlap between sympatric species in three main categories: habitat, food type and time (Chase and Liebold 2003; Pianka 2000; Schoener 1986).

Most primate communities exhibit a combination of resource partitioning mechanisms. In a meta-analysis of interspecific competition and niche separation in primates, Schreier *et. al.* (2009) reported that, out of 673 primate species-pairs in 43 sites, only 45 species-pairs were potential competitors. The most common methods of niche separation were differentiation of diet, distinction in use of forest strata, and segregation in use of different forest types (Schreier et al. 2009). Further, niche separation strategies of primate species varied geographically. In African and Asian primate communities, niche separation was obtained most often by the use of different forest strata, and by dietary differentiation (Schreier et al. 2009). These two types of niche separation were also the most commonly observed strategies among Central and South American primate communities, but dietary differentiation was more frequently observed than differences in forest strata use (Schreier et al. 2009). A greater diversity of niche separation strategies have been documented in Madagascar where lemurs used differences in height, diet, forest type, activity patterns and ranging patterns to distinguish species-specific ecological niches and maintain coexistence (Schreier et al. 2009; Sussman 2002).

1.1.2 Primate Diets and Sympatric Folivorous Primates

Most primates can be designated as being primarily folivorous or frugivorous (Kay 1975). The broad dietary classifications are based on the type of food that comprises most of a primate species' diet, but actual primate diets are more nuanced and may vary based on resource availability, seasonality, and presence of competitors among other factors (Li et al. 2010; Schreier et al. 2009). Frugivores often eat both the pulp and seeds of fruit (Janson and Chapman 1999), whereas folivores tend to be highly selective in not only the species but even the part of the plant they consume (Clutton-Brock 1977). The general characterization of dietary patterns is useful in extrapolating information regarding other aspects of a primate behavioral ecology and social structure. For example, folivores commonly have shorter daily path lengths on average and rest more frequently than frugivores (Hladik 1977; Oates 1987). It has been hypothesized that these behavioral differences in ranging and activity budget are due to differences in food resource distribution in that leaves are more abundant and evenly distributed throughout the environment than fruits (Clutton-Brock and Harvey 1977; Milton 1980; Milton and May 1976). Folivore behavior can also shift with preferences for particular plant species or as they pursue specific plant parts such as young leaves, mature leaves and petioles which may not be uniformly available in time or space (Clutton-Brock and Harvey 1977; van Schaik et al. 2005). Additionally, differences in nutritional quality coupled with the presence or absence of secondary compounds can influence plant part/species preferences (Committee on Animal Nutrition et al. 2003; Lambert 1998). Fruits, while patchily distributed compared to leaves, are more energy rich and easier to digest (Chivers and Hladik 1980; Lambert 1998). This is due to their high concentration of sugars and carbohydrates and low concentration of fiber relative to leaves (Milton 1981).

There are two primary ways in which primates digest the cellulose found in plants and extract vital minerals from plant resources: forestomach fermentation and caceo-colic fermentation (Lambert 1998). Forestomach or “foregut” fermenters have specialized sacculated stomachs resembling that of ruminant ungulates and only occurs in the primate subfamily, Colobinae (Lambert 1998). Caeco-colic fermenters are more widespread taxonomically and geographically in primates and include prosimian, platyrrhine, and catarrhine species (Lambert 1998). This digestive strategy and accompanying morphological suite of characteristics has evolved at least four times in primates (Lambert 1998). Fermentation occurs either in the enlarged caecum or colon where plant material is exposed to digestive enzymes and microbes for an extended period (Bauchop 1978; Lambert 1998). In several primate communities, two or more folivorous primates may exist in sympatry, which provides an opportunity to examine the relationship between primate species' digestive morphology, degree of folivory, and patterns of activity both within and between species.

While much of the literature on sympatric primates has focused on interspecific competition for resources, some of the more intriguing questions are those that seek to discover how species that have existed in sympatry over evolutionary time and seem to do so without engaging in competition for resources. Uncovering coexistence strategies can be best achieved by examining sympatric species from a holistic perspective. This includes gaining a deeper understanding of the ecological requirements, morphological specializations, and behavioral patterns of each species throughout their species range, and, if possible, in areas where they exist in sympatry and where they are allopatric.

Sympatric folivorous primates are found in many environments throughout the world and use a variety of strategies to maintain coexistence. Generally, one species will consume more leaves and expend less energy throughout the day while the diet of the other species contains more non-leaf items such as fruits, seeds and flowers (Clutton-Brock and Harvey 1977). Primates that consume more fruits, seeds and flowers tend to exhibit more travel and increased energy expenditure compared to species that rely more heavily on leaves, which correlates with fruits being easier to digest and more energy dense than leaves (Lambert 1998). One of the sympatric folivores is essentially an "energy minimizer" (Milton 1998) while the other can be characterized as an "energy maximizer" (Terborgh 1983).

Along with divergences in dietary profiles and activity patterns, sympatric folivores may also differ in their locomotor behavior and preferences for particular vertical stratigraphic levels in the forest. The more folivorous primate species will generally spend more time in the continuous canopy, whereas the more frugivorous primate will utilize all stratigraphic levels (Fleagle 1977; Fleagle 1978). An individual that remains in the continuous canopy can move throughout the forest by leaping between adjacent tree canopies, but an animal in the middle or understory levels must either ascend to the continuous canopy or descend to the ground to travel between trees which is less energy efficient (Fleagle 1977; Fleagle 1978). Such differences in use of different vertical strata have been reported in sympatric Asian colobines including *Presbytis senex* and *Presbytis entellus* (Hladik 1977)*; Presbytis melalophos* and *Trachypithecus obscurus* (Fleagle 1977; Fleagle 1978); *Trachypithecus leucocephalus* and *T. francoisi* (Xiong et al. 2009), African colobines (e.g. *Colobus guereza* and *Procolobus tephrosceles*) (Oates 1987; Struhsaker and Leland 1979)), Neotropical primates (*Alouatta guarbia* and *A. caraya*) (Agostini et al. 2010a)), and among lemurs in Madagascar (*Indri indri* and *Hapalemur griseus* (Ganzhorn 1988); *Indri indri* and *Propithecus diadema* (Blanchard 2007; Powzyk 1997)). Within the following sections, I will describe some examples of coexistence strategies among sympatric folivorous primates.

In a study of two folivorous congeneric leaf monkeys, *Presbytis senex* and *Presbytis entellus*, Hladik (1977) reported that *P. senex* lived in smaller groups, traveled less, and fed on considerably fewer tree species than *P. entellus*. While both species were classified as folivores, *P. entellus* consumed more fruit than *P. senex* (Hladik 1977). They overlapped in their exploitation of some tree species, but varied in type of food consumed and the proportion that each tree species contributed to their overall diet (Hladik 1977). Similar suites of niche separating behaviors including differences in diet, locomotion, and activity patterns have also been reported for other sympatric Asian colobines (see Curtin and Chivers 1978; Curtin 1976; Davies et al. 1988; Fleagle 1977; Hadi et al. 2011; Vandercone et al. 2012; Xiong et al. 2009).

Sympatric African colobines also exhibit distinct differences in diet and activity patterns. In a study of five sympatric monkey species in the Kibale forest of Uganda, Struhsaker and Leland (1979) found that the red colobus monkey (*Procolobus tephrosceles)* diets more closely aligned with three sympatric omnivorous primates (*Cercocebus albigena, Cercopithecus ascanius* and *Cercopithecus mitis*) than the sympatric black and white colobus monkey (*Colobus guereza)*. They also reported that the degree of a species' folivory was positively correlated with the amount of time spent resting (Struhsaker and Leland 1979). When black-and-white colobus monkeys coexist with red colobus, the overall dietary and behavioral patterns reported have been consistent with patterns of other sympatric folivores. Black-and-white colobus monkeys relied more heavily on leaves (>79%), spent less time feeding, had lower overall dietary diversity, and spent more time in the continuous canopy relative to sympatric red colobus (Oates 1987; Struhsaker and Leland 1979; Tombak et al. 2012).

Similar patterns of niche separation which effectively reduce or eliminate interspecific competition have also been reported among coexisting Neotropical primates. Fewer folivorous primate species exist in the Neotropics relative to Africa, Asia, and Madagascar which limits the potential for the study of their coexistence strategies. The largest Neotropical primates, wooly monkeys (*Brachyteles*) and howler monkeys (*Alouatta*) are classified as folivores (Heymann 2001; Milton 1980; Strier 1992). Howler monkeys are highly folivorous energy minimizing primates (Milton 1980). They generally have a parapatric distribution throughout their range, but are found in sympatry within some areas and occasionally occur syntopically (co-occurring in the same habitat at the same time) (Cortes-Ortiz et al. 2003). In a study of syntopic black and gold howler monkeys (*Alouatta caraya*) and brown howlers (*A. guariba clamitans*), these species showed considerable dietary overlap (45.64% +/- 2.97%) (Agostini et al. 2010b). The two species exhibited different ranging patterns in times of resource scarcity where black and gold howlers increased both the speed and distance of their daily travel patterns (Agostini et al. 2010a). Brown howlers did not adjust their travel speed or distance during this time (Agostini et al. 2010a; Agostini et al. 2012). Both species had larger home ranges and lower population densities where they are sympatric than where they exist allopatrically (Agostini et al. 2010b). While these species only overlap in small areas of their species' ranges, they exhibit some exhibited some flexibility in their habitat use patterns to facilitate coexistence (Agostini et al. 2010b). In summary, when folivorous primates coexist throughout the world, they exhibit some degree of niche separation through a combination of dietary differences, differences in activity budget, vertical stratification preferences, and varied ranging patterns (Schreier et al. 2009).

1.1.3 Seasonality in Primates

Nearly all primates live in the tropics and are subject to seasonal shifts in climatic variables (temperature and rainfall) and fluctuations in resource availability (van Schaik and Brockman 2005). Rather than migrate to new environments during seasonal fluctuations, most primates respond to these changes by either increasing or decreasing the length of their daily active period and/or the amount of time spent engaging in each behavior throughout the day (van Schaik and Brockman 2005). Many primate species adjust their active period in response to food resource availability and abundance throughout the year (Hemingway and Bynum 2005). Other responses to food scarcity include feeding on lower quality foods or decreasing their daily ranges/movements (Milton 1980; Milton 1998). Alternatively, a primate species may increase their daily movement patterns to exploit high quality but patchily distributed foods (Terborgh

1983). Another strategy to cope with fluctuating resources involves the ability to flexibly alter group size and composition, so that groups can fission into smaller subgroups when resources are scarce (Plavcan et al. 2005). During times of food scarcity, sympatric species generally show less resource overlap and greater niche partitioning presumably as a means to reduce interspecific competition (Ganzhorn et al. 1999; Gautier-Hion et al. 1983; Terborgh 1983; Waser 1987).

1.1.4 Malagasy Primate Communities and Seasonality

Madagascar has been referred to as an “evolutionary laboratory” for the study of primate diversity due to the fact that a single colonization event occurred approximately 62 mya (Yoder and Yang 2004). The diversity of lemur species and length of isolation from other primate taxa on Madagascar allows for an excellent opportunity to examine how coexistence is maintained among closely related primate species across a gradient of habitat types. Madagascar is ecologically diverse with dry, deciduous and spiny forests in the south and west and rainforests in the east (Du Puy and Moat 1996). Biologically, eastern rainforests have a higher abundance of plant and animal species than the more arid environments in the south and west (Ganzhorn et al. 1999).

Primate habitats in Madagascar experience seasonal changes in temperature and rainfall, as well as seasonal resource fluctuations (Wright 1999). Lemurs have responded to this harsh seasonality in a number of ways. Their reproduction is strictly seasonal across all taxa (Wright 1999). In the eastern rain forests which experience dramatic fluctuations in temperature, rainfall, and resource availability, infant weaning occurs during times of higher resource availability (Wright 1999). Diet quality can impact reproductive fitness. For example, females with higher quality diets produce more offspring throughout their lifetime and infants experience lower mortality rates when compared to females with low quality diets (Brockman and van Schaik 2005). Female dominance is common in lemurs and females have priority of access to resources (Pollock 1979; Powzyk 1997) which may offset some of the impacts of fluctuating diet quality.

Sympatric lemurs exhibit a variety of responses to resource scarcity. While some species adjust their diets to reduce overlap during certain seasons, others form polyspecific associations to feed and forage together (Freed 2006). Other closely related, sympatric lemurs rarely temporally overlap (Powzyk 1997; Sussman 1977; Sussman 1979). Additionally, species exhibit varying degrees of behavioral variation throughout their species ranges (Richard 1978).

1.1.5 Subfossil Lemurs

Since the arrival of humans on Madagascar, several lemur species have gone extinct, most likely due to anthropogenic effects (Burney et al. 2004). To-date, at least seventeen species of "subfossil" extinct lemurs have been discovered from five separate families. Three families have no extant species (Paleopropithecidae, Megaladapidae, and Archaeolemuridae). Two families, Daubentoniidae and Lemuridae have extant species. All of these lemurs were larger in size than extant species ranging in weight from approximately the size of current indriids (e.g. *Mesopropithecus*: 11-13 kg) to sizes close to, or potentially even larger than an adult male gorilla (e.g. *Archaeoindri*: ~160 kg) (Godfrey and Jungers 2003; Godfrey et al. 2006; Jungers et al. 1995).

The family Paleopropithecidae is most closely related to the extant indriids and includes four genera: *Babakotia, Paleopropithecus, Archaeoindris,* and *Mesopropithecus* (Godfrey and Jungers 2003). This family is commonly called the "sloth lemurs" due to their similarities to arboreal, slow-moving, folivorous sloths (Godfrey et al. 2006). Members of the

Paleopropithecidae exhibited an enormous amount of morphological diversity weighing from under 10 kg to over 200 kg (Godfrey and Jungers 2003). Due to poor preservation conditions, no subfossil primates have been recovered from the eastern rainforest areas of Madagascar but *Archaeoindri, Paleopropithecus,* and *Mesopropithecus* have been found in the central highlands of the country and may have inhabited the eastern rainforests (Godfrey and Jungers 2003). Morphological analyses indicate that members of this family were diurnal and primarily folivorous (Godfrey and Jungers 2003). While it is not possible to fully state the degree of habitat overlap or potential resource competition between these extinct lemur species with extant lemurs, it is highly likely that members of the family Paleopropithecidae shared their habitat with the closely related Indriidae.

1.1.6 Indriids

The taxonomic family Indriidae (indriids) consists of three genera: *Indri* (Day et al.), *Propithecus* (sifakas) and *Avahi* (woolly lemurs). Indriids are medium to large bodied lemurs including the two largest extant lemur species, the indri *(I. indri*) and the diademed sifaka (*P. diadema*) which are the focus of this dissertation (Mittermeier et al. 2010). *Indri* and *Propithecus* are considered diurnal whereas *Avahi* are nocturnal (Mittermeier et al. 2010). Sexual dimorphism is low among indriids although females may be slightly larger than males (van Schaik and Kappeler 1993). All indriids are arboreal and exhibit vertical clinging and leaping to propel themselves between vertical substrates.

The genus *Propithecus* consists of nine species: *P. verreauxi*, *P. coquereli, P. tattersalli, P. coronatus, P. deckenii, P. edwardsi, P. candidus, P. perrieri,* and *P. diadema*. *Propithecus verreauxi* and *P. coquereli* are the smallest species in the genera (3-4 kg) and inhabit the dry forests in the south and west of Madagascar. All other *Propithecus* species are found in

Madagascar's eastern rainforests which are larger than the southern and western forests (5-7 kg) (Richard 2003). Their vernacular name is "sifaka" is an onomatopoeia of the dry forest *Propithecus* species' alarm call (Richard 2003). Locally, though, the Malagasy people commonly refer to the eastern sifakas as "simpona" (Powzyk 1997).

The diademed sifaka (*P. diadema*) is the largest of the genus *Propithecus* inhabiting the northeastern rainforests of Madagascar from the Antainambalana River in the north to as far south as the Onive River (Irwin 2006) (Figure 1-1, Figure 1-2). This species inhabits primary, secondary, and fragmented forest habitats (Irwin 2006; Powzyk 1997). They are distinguished by white or light colored hair around the face with darker hair on the top of the head giving them a "crowned" or "diadem" appearance. Diademed sifakas are categorized as folivores or folivore/frugivores (Irwin 2008). Groups are multi-male/multi-female and vary in size from 2 to 7 individuals (Blanchard 2007; Irwin 2006; Powzyk 1997, current study Chapter 2). In concordance with other lemur species, they exhibit strict reproductive seasonality where infants are born between May and August and are weaned at six to nine months of age (Richard 2003).

Figure 1-1. Adult male diademed sifaka at Betampona Nature reserve, Madagascar. (Photo by Lana Kerker Oliver)

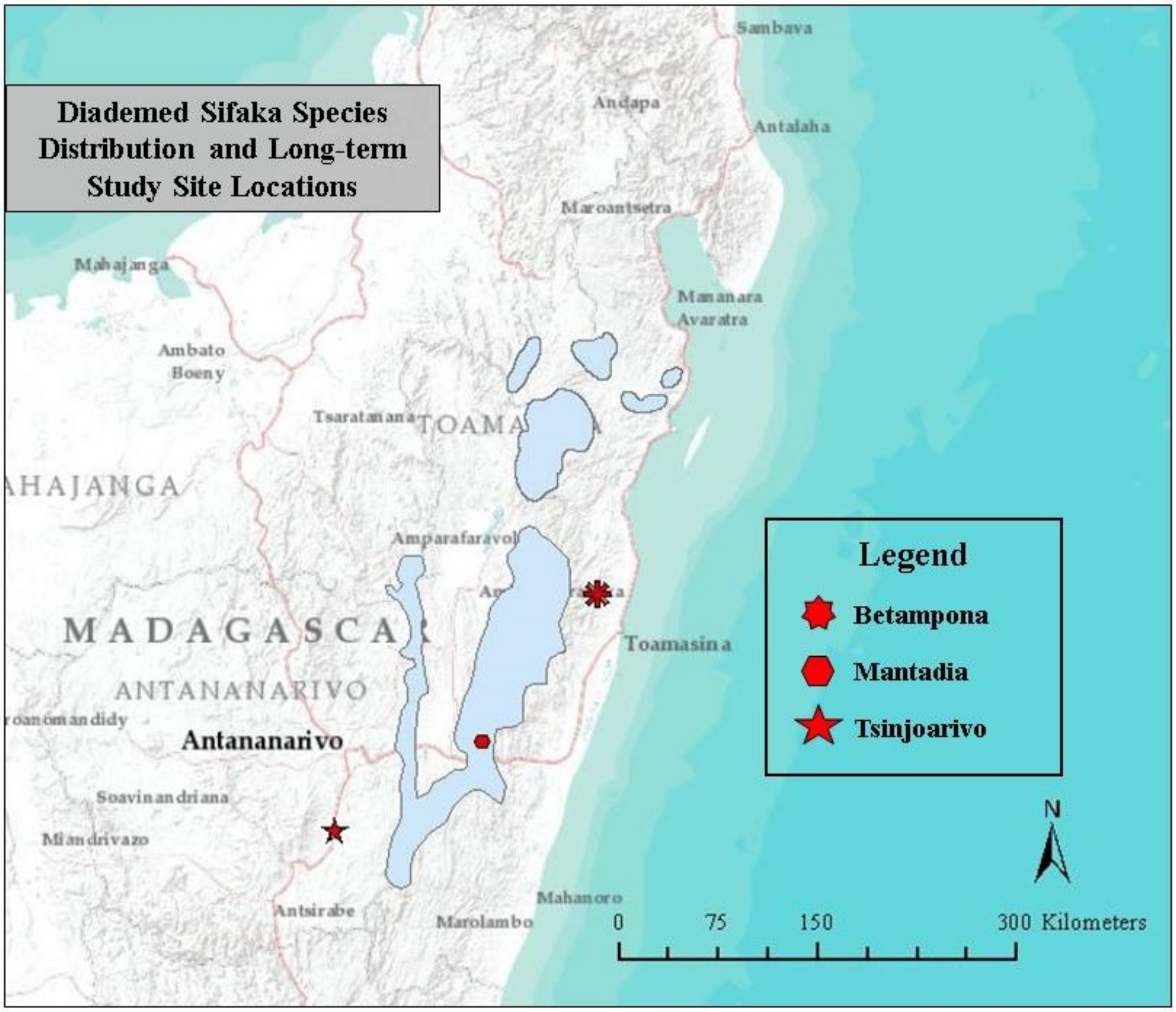

Figure 1-2. Diademed sifaka species distribution and long-term study sites. Species distribution is indicated by the blue polygon and long-term research sites are indicated with red symbols. Diademed sifaka species distribution shapefile downloaded from IUCN.org (2014). Note that the species ranges are generalizations and some study-sites are located outside the IUCN species range. This is intended to provide the viewer with a general sense of the location of this species.

The monotypic genus *Indri* (*I. indri*) is the largest extant lemur species weighing approximately 6.5 to 8.8 kg (Powzyk and Mowry 2007). The local Malagasy term for indri is “Babakoto” or “Endrina”. Indris are easily recognized by their large body size, black and white pelage, and rudimentary tail. This species also has an unmistakable long call that consists of a duet between the adult group members that can be heard up to 3 km away and is used to mark territorial boundaries between groups (Pollock 1977). Their pelage color varies throughout their species range with individuals in southern populations having more white hair on their arms, legs, and head while northern populations tend to be darker overall (Thalmann et al. 1993; Zaonarivelo et al. 2007). Despite this phenotypic difference, neither morphometric (Zaonarivelo et al. 2007) nor genetic (Brenneman et al. 2016) analyses have found evidence to support that distinct indri subspecies exist.

I. indri is diurnal and inhabits the eastern rainforests of Madagascar (Figure 1-3, Figure 1-4) (Powzyk and Thalmann 2003). Historically the species range included areas further to the North and West, but they are currently found from the Bemarivo River which is the northern extent of their range to the Mongoro River in the South (Goodman and Ganzhorn 2004; Powzyk and Thalmann 2003). Today, the indri species distribution only overlaps with *P. diadema* but subfossil indri remains have been found in areas that overlap with *P. perrieri* in the northeastern forests of Madagascar (Jungers et al. 1995).

Indri are the most folivorous of all indriids and, as such, have the highest degree of morphological specialization for the consumption and digestion of leaves (Powzyk and Mowry 2003). They have also been reported to consume fruits, seeds, plant galls, bark, and soil (Powzyk and Mowry 2007). Group sizes range from 2 to 5 individuals (Blanchard 2007; Pollock 1975; Powzyk 1997). They live in pair-bonded groups consisting of an adult male and an female with their related offspring (Powzyk and Thalmann 2003). While some researchers refer to their mating system as monogamous, an instance of extra-pair copulation has been documented (Bonadonna et al. 2014). Female dominance has been reported for indri whereby females have priority-of-access to food resources and may displace males for preferred feeding spots (Pollock

1979). Mating and weaning of infants occurs congruently with diademed sifakas (Powzyk and Thalmann 2003).

Figure 1-3. Adult male indri at Betampona Nature Reserve, Madagascar. (Photo by Lana Kerker Oliver)

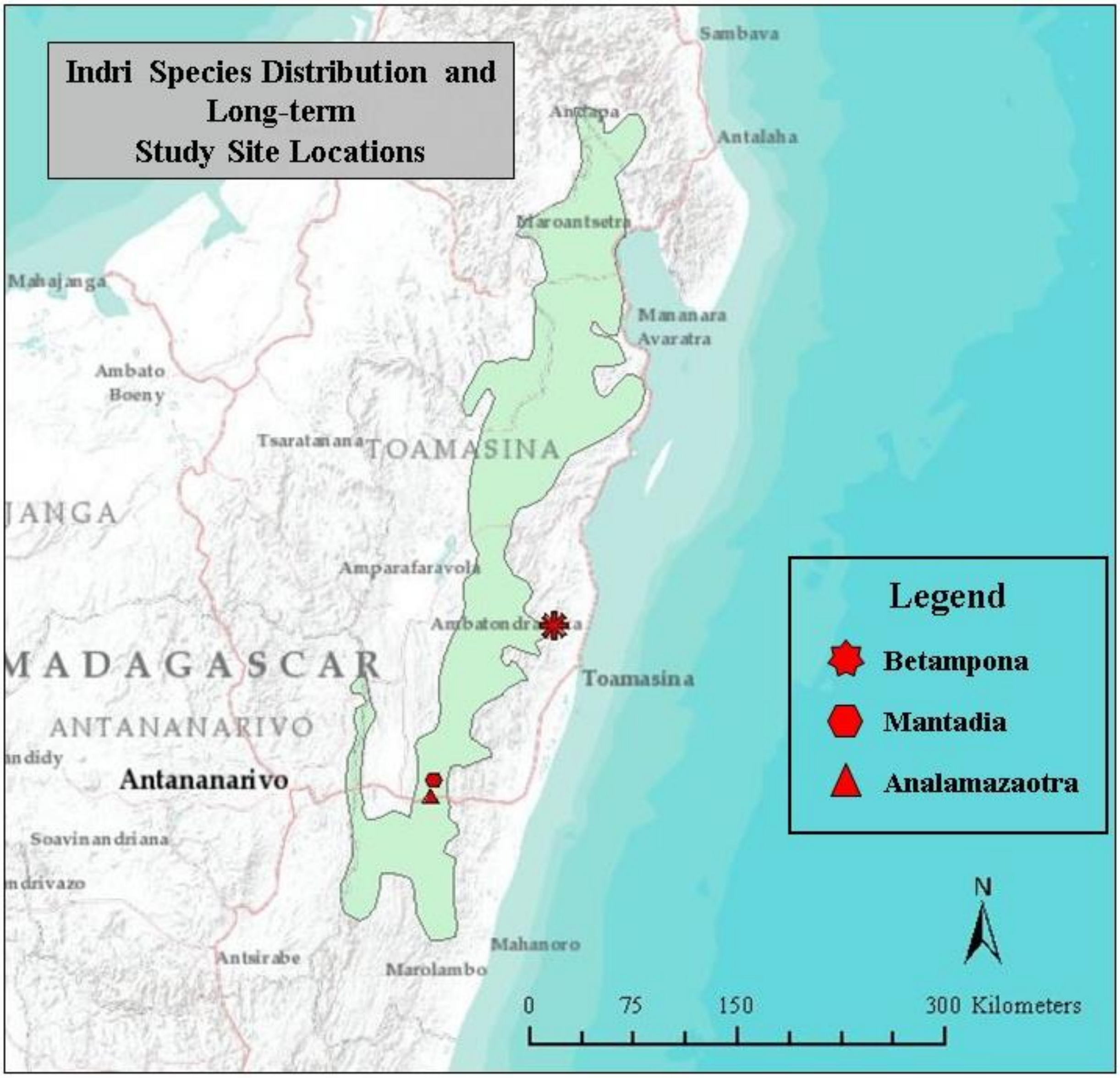

Figure 1-4. Indri species distribution and long-term study sites. Species distribution indicated by green polygon and long-term study sites indicated with red symbols. Species distribution shapefile downloaded from IUCN.org (2014).

Morphology

Indri and diademed sifakas exhibit differences in their cranial morphology. Diademed sifakas have a shorter rostrum and a more robust mandible relative to indri (Figure 1-5, Figure 1-6) (Hill 1953; Viguier and Tort 2000). In fact, diademed sifakas have the most robust mandible of all indriids whereas the indri mandible is the most gracile (Viguier and Tort 2000). Both lemur species have the dental formula: 2.1.2.3/2.0.2.3 (Hill 1953; Kay and Hylander 1978). Their dentition differs from other lemurs in that the indriid toothcomb consists of four instead of six teeth and they possess one less premolar in each jaw quadrant (Hill 1953; Kay and Hylander 1978). The molars for both species are indicative of a folivorous diet with high crowns and surfaces designed to crush and shear leafy material (Kay and Hylander 1978). Relative to diademed sifakas, indri have slightly more specialized dentition for folivory in that they have a longer crista obliqua on their lower second molar (Kay 1975). This increase in the shearing edge has been associated with an advantage for efficiently slicing leaves (Kay 1975; Yamashita 1998). Kay and Hylander (1978) likened the manner in which the upper and lower molar surfaces come together to a pair of scissors.

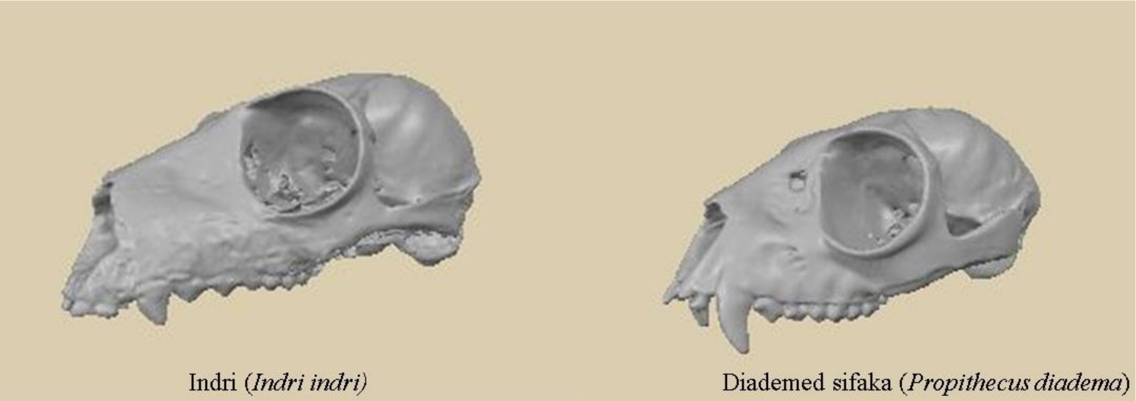

Figure 1-5. Comparison of indri and diademed sifaka skull morphology. (Indri: USNM 06197); (Diademed sifaka: USNM 64437)

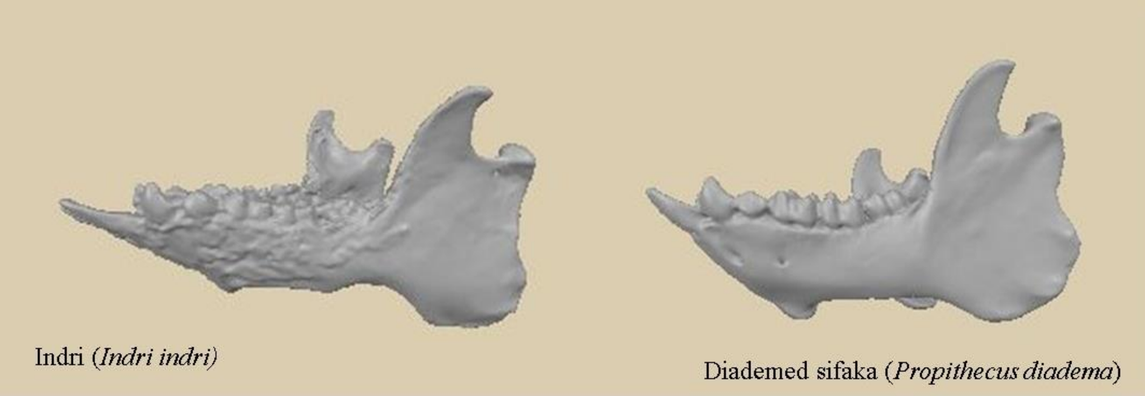

Figure 1-6. Indri and diademed sifaka mandibles. (Indri: USNM 06197); (Diademed sifaka: USNM 64437)

Both indri and diademed sifakas possess many morphological adaptations for folivory, including specialized gut morphology. While both species have enlarged caecums relative to other lemurs, the indri caecum is longer (three times its body length) than two congeneric sifakas, *Propithecus tattersalli* and *P. coquereli* (less than one body length) (Campbell et al. 2000; Hill 1953). It is in the caecum where fermentative bacteria assist in the digestion of plant material (Bauchop 1978; Lambert 1998). Alternately, diademed sifakas have a longer small intestine (nine times body length) relative to indri (seven times body length) (Hill 1953). Sugars, carbohydrates, and fats are absorbed in the small intestine (Campbell et al. 2000; Hladik 1978). While both species are predominantly folivorous, these differences in the length of the caecum relative to the small intestine support the notion that indri are more specialized folivores than diademed sifakas that rely on leaves in combination with more easily digestible foods such as fruits and seeds (Hladik 1978; Lambert 1998; Powzyk and Mowry 2003).

As an adaptation to vertical clinging and leaping locomotion, indriids have the longest legs relative to their arms of all lemurs. They have an average intermembral index (ratio of forelimb length to hindlimb length) of 62 (Ankiel-Simons 2007). This limb ratio combined with their trunk morphology requires indriids to naturally assume an orthograde posture. Consistent with other indriids, indri and diademed sifakas long fingers and toes that allow them to maintain a powerful grasp on vertical substrates.

As with other lemurs, indriids are seasonal breeders, however, breeding and birthing seasons differ between species. A single infant is born from May to July for *Indri*, June to July for *Propithecus* and September to October for *Avahi* (Pollock 1975; Powzyk 1997). Female indriids are dominant over males, and adult females have priority of access to food resources over males and younger group members. Seasonal breeding and female dominance in lemurs are hypothesized to be a response to the combination of Madagascar's harsh, highly seasonal environments and the high energetic cost of reproduction for females (Gould et al. 2011).

Previous Long-term Studies

Diademed sifakas have been the subject of three long-term studies at two different sites (Table 1-1, Figure 1-2). Powzyk (1997) conducted the first long-term research on diademed sifakas at Mantadia, a large (~10,000 ha) continuous forest with little anthropogenic disturbance, with a focus on dietary and behavioral differences between sifakas and indri. The second study occurred near the southern extent of their species range at Tsinjoarivo where they are allopatric with indri (Irwin 2006). At Tsinjoarivo, Irwin (2006) followed four groups, two were in continuous forest and two were in patchy forest fragments. Finally, Blanchard (2007) followed one group of diademed sifakas at Mantadia (see above for site description) for nine months with a focus on activity and locomotion.

Table 1-1. Previous long-term studies of diademed sifakas.

Study Site	**# of Study Groups**	**Average Group Size**	**Study Duration (months)**	**Source**
Mantadia	1	7	9	Blanchard 2007
Mantadia	2	4.5	12	Powzyk 1997
Tsinjoarivo	4	5	12	Irwin 2006

Prior to my dissertation research, indri were the subject of four long-term studies at three sites throughout their species range (Table 1-2, Figure 1-4). The earliest study of indri was conducted at near the southern extent of their species' range at Analamazaotra, a small (~800 ha) forest patch that has been subjected to selective logging and can be considered to have the highest degree of anthropogenic disturbance of the three indri study sites (Junge et al. 2011; Pollock 1977). Analamazaotra is surrounded by *Eucalyptus* plantations and the two indri study groups were separated by a road (Junge et al. 2011; Pollock 1977). At Mantadia which is located 20 km north of Analamazaotra, Powzyk (1997) studied two groups of indri in a large (~10,000 ha) montane rain forest which is pristine and undisturbed by humans (Powzyk 1997; Powzyk and Mowry 2003). At Betampona where my research was conducted, three groups of indri were the subject of a 12-month study on their diet, feeding ecology, and population density (Britt et al. 2002). Finally, Blanchard (2007) contributed to the existing body of literature with a nine-month (February to October) study of one group of indri at Mantadia with a focus on activity and locomotion.

Table 1-2. Previous long-term indri studies with study site and sampling effort.

Study Site	**# of groups**	**Group Size**	**Duration (months)**	**Source**
Betampona	3	3	12	Glessner and Britt 2005, Britt *et. al.* 2002
Mantadia	1	3	9	Blanchard 2007
Mantadia	2	2	12	Powzyk 1997
Analamazaotra	2	3.75	12	Pollock 1977

Conservation

Both indri and diademed sifakas are classified as critically endangered with decreasing populations (Andriaholinirina et al. 2014a; Andriaholinirina et al. 2014b). The massive-scale deforestation of Madagascar's eastern rainforests in the last 60 years have caused severe habitat loss and fragmentation for both species (Andriaholinirina et al. 2014a; Andriaholinirina et al. 2014b; Green and Sussman 1990; Harper et al. 2007). This fragmentation has caused populations to become genetically isolated as gene flow is restricted or impossible between forest fragments (Nunziata et al. 2016). Hunting has seriously impacted many populations of diademed sifakas throughout their species range (Andriaholinirina et al. 2014b; Jenkins et al. 2011). Diademed sifakas are not only hunted for bushmeat, but also for their colorful pelage (Andriaholinirina et al. 2014b). Until recently, indri were somewhat protected from hunting by a local taboo or "*fady*" against eating them (Thalmann et al. 1993). In some areas, only the consumption of indri is taboo (Jenkins et al. 2011). In these areas, indri are still hunted and the bushmeat is sold (Jenkins et al. 2011). In recent years, however, a decrease in belief in these *fadys* among Malagasy people coupled with an increase in immigrants who do not have these taboos has caused an unsustainable increase in indri hunting (Golden and Comaroff 2015; Jenkins et al. 2011). Captive populations do not exist for either species, which emphasizes the importance of *in-situ* conservation efforts to 1) increase suitable habitat, 2) maintain genetic diversity in isolated populations, and 3) decrease hunting pressure to ensure the survival of these species (Andriaholinirina et al. 2014a; Andriaholinirina et al. 2014b).

1.2 Research Questions and Hypotheses

When primates with similar dietary patterns coexist, they avoid resource competition via niche partitioning. The most common niche partitioning mechanisms are 1) dietary divergence, 2) lack of spatial overlap, 3) use of different levels in the forest (Schreier et al. 2009). I undertook this research project to describe how the morphological characteristics of indri and diademed sifakas relate to niche differentiation via differential activity patterns, dietary profiles, and home range use. Cranial and digestive morphology can be used to predict the dietary profiles of primate species (Milton 1981). Diets, in turn, reflect the amount of energy available for daily activities where folivorous primate species rest more and travel less because their food is more evenly distributed throughout their environment relative to frugivorous primates (Clutton-Brock and Harvey 1977; Houle 1997). Additionally, animals that are more folivorous tend to be less flexible in their use of stratigraphic levels in the forest (Porter 2001; Singh et al. 2011). More folivorous primates tend to spend most of their time in the continuous canopy because that is where the majority of young leaves are located whereas more frugivorous primates use all levels more uniformly and travel to the ground more often to feed from food items such as fallen fruits (Porter 2001; Singh et al. 2011). Indri morphology indicates that they are more specialized folivores than diademed sifakas (Hill 1953; Kay and Hylander 1978; Powzyk 1997; Viguier and Tort 2000). I hypothesize that, if primate-wide trends regarding the relationship between morphology, diet, activity, home range size, and daily path length remain consistent for indri and diademed sifakas, then niche differentiation strategies can be predicted from their differences in morphology.

1.2.1 Activity Budget

Q1.1: What are the differences in the activity patterns between groups of indri and diademed sifakas?

H$_{1.1}$: The amount of leafy material in an animal's diet has been correlated with more time resting throughout the day relative to animals that consume a higher proportion of fruits and seeds. If indri are more folivorous than diademed sifakas then they should spend more time resting throughout the day and have shorter, overall, daily active periods.

Q$_{1.2}$: What, if any, differences in activity occur for indri and diademed sifakas in relation to seasonal changes in temperature and rainfall?

H$_{1.2}$: The eastern rainforest of Madagascar experiences seasonal differences in temperature, rainfall, and resource availability (Wright 1999). If variation in temperature and rainfall exist, then the length of the individuals' daily active period will be positively correlated with daily maximum temperature and negatively correlated with daily amount of rainfall.

Q$_{1.3}$: What is the degree of intraspecific variation in activity patterns between the groups of indri? Between groups of diademed sifakas?

H$_{1.3}$: Previous reports have suggested minimal intraspecific variation in activity budgets for indri and diademed sifaka groups at the same study site (Irwin 2006; Pollock 1975; Powzyk 1997). Therefore, the null hypothesis is that there will not be intraspecific differences in activity budgets between groups of indri and diademed sifakas at BNR. However, some inter-site differences have been reported for diademed sifakas which has been attributed to levels of anthropogenic disturbance (Irwin 2006).

Q$_{1.4}$: Do males and females exhibit sex-specific differences the amount of time spent feeding?

$H_{1.4}$: Sex differences in time spent feeding have been reported at other sites whereby females fed more than males (Irwin 2006; Powzyk 1997). If females incur more energetic costs due to reproduction than males, then they will spend more time feeding than males.

$Q_{1.5}$: How do the activity budgets of indri and diademed sifakas compare to those reported from other sites?

$H_{1.5}$: If species-specific activity patterns are consistent between sites, then activity patterns of indri and diademed sifakas at BNR will not differ statistically from previously reported activity patterns from Mantadia and Analamazaotra for indri and from Mantadia and the continuous forest at Tsinjoarivo for sifakas.

1.2.2 Feeding Ecology

$Q_{2.1}$: How do the dietary profiles of indri and diademed sifakas differ in proportions of plant parts consumed?

$H_{2.1}$: An animal that is more hyper-specialized, morphologically, for breaking down leaf particles would be more constrained toward a more folivorous diet (Milton 1980). Previous studies have shown that diademed sifaka diets contain a higher proportion of fruits, seeds, and flowers relative to indri. Indri and diademed sifaka diets at BNR will show similar dietary profiles to past research.

$Q_{2.2}$: Do indri and diademed sifakas differ in the types of plants in their diets?

$H_{2.2}$: If diademed sifakas consume a higher proportion of fruits, flowers, and seeds relative to indri, they will also feed from a wider variety of plant types (trees, lianas, epiphytes, and ferns).

$Q_{2.3}$: Do indri and diademed sifakas feed from a similar number of plant species?

$H_{2.3}$: If diademed sifakas had a higher proportion of fruits, seeds, and flowers in their diet relative to indri, they will also feed from a greater number of plant species.

$Q_{2.4}$: How do the dietary profiles of indri and diademed sifakas change relative to resource availability?

$H_{2.5}$: Food availability has been reported to fluctuate throughout the year in eastern Madagascar (Wright 1999). If this seasonal trend in resource availability occurs at BNR, then indri and diademed sifakas will exhibit temporal variation in relation to the abundance of that resource.

$Q_{2.6}$: Do indri and diademed sifakas feed in different stratigraphic levels in the forest?

$H_{2.6}$: Animals that are more folivorous tend to be less flexible in their use of the different levels in the forest due to the energy required to travel vertically through the environment and because their primary food source, leaves, are located in the continuous canopy. Vertical stratification differences is also a niche separation mechanism (Blanchard 2007; Buzzard 2006; Singh et al. 2011). Previous research has shown that indri and diademed sifakas have species-specific differences in home range size, with indri home ranges being smaller than those of diademed sifakas.

1.2.3 Home Range Use and Daily Path Length

$Q_{3.2}$: What is the degree of interspecific and intraspecific home range overlap?

$H_{3.2}$: Territorial primates do not overlap with conspecifics in the parts of their home ranges that are actively defended (Krebs and Davies 1978) Indri and diademed sifakas are reported to be territorial primates (Blanchard 2007; Pollock 1975; Powzyk 1997). If these species are territorial, then home ranges will not overlap intraspecifically but will overlap interspecifically.

Q$_{3.3}$: What is the degree of intraspecific home range overlap between groups of indri and diademed sifakas?

H$_{3.3}$: Indri and diademed sifakas have been characterized as sympatric confamilial primates that maintain coexistence through niche separation (Powzyk 1997; Powzyk and Mowry 2003). If differentiation of habitat preferences is one of their strategies to maintain coexistence, then they will overlap less in core areas than less intensively used areas of their home ranges.

Q$_{3.4}$: Do indri and diademed sifakas differ in their daily path length?

H$_{3.4}$: Based on the knowledge that indri are more folivorous than diademed sifakas and, as such, do not need to travel as far to reach patchily distributed food sources, indri DPL will be shorter than that of diademed sifakas.

Q$_{3.5}$: Do indri and diademed sifaka daily path lengths change relative to seasonal fluctuations in temperature and rainfall?

H$_{3.5}$: Indri and diademed sifakas decrease their daily active period in cold, rainy months. DPL will also decrease during this time.

1.3 Outline of the Dissertation

In Chapter Two, I provide a detailed description of Betampona Nature Reserve including the natural history of the reserve, climate, floral and faunal biodiversity, and previous research as relevant to this study. I discuss the demographic composition of each study group, and describe the materials and methods utilized for this project. This includes equipment used, data collection schedules, data collection protocols, methodological and logistical limitations, a description of analyses conducted and details of how they relate to the overall research objectives.

In Chapter Three, I describe the general activity budget for indri and diademed sifakas. Specifically, I address how activity patterns vary interspecifically and throughout the year. I also include an analysis of vertical forest stratification between species for each activity. Coexistence strategies as they relate to differences in activity patterns are discussed.

Chapter Four is an analysis of the feeding ecology of indri and diademed sifakas and how their feeding patterns and species consumed change seasonally. I measure the degree of resource overlap between the two species. Important and frequently used resources are identified for each species. The most frequently consumed tree species at Betampona Nature Reserve are then compared with data from other sites to assess the ecological plasticity of these indriids and to identify important food sources for each species.

The focus of Chapter Five is a spatio-temporal analysis of indri and diademed home range use, which begins with an overview of home range use in primates and folivorous primates. I then discuss how DPL and home range use fluctuates seasonally in folivorous primates. I examine variation in DPL both within and between species, as well as discuss how it changes based on temperature and rainfall variables. Overall home range size is compared among groups of the same species and between these indriid species. The distribution of food sources is compared between species to identify core areas of preferred habitat. I also assess whether DPL and home range size fluctuate based on temperature, rainfall and type of resources consumed at BNR. Finally, these variables are compared to other sites to facilitate a discussion of behavioral plasticity in these species.

Chapter Six is a synthesis of the findings of my research and their importance. Results are discussed in the context of the main research hypotheses and predictions of this dissertation, and extended to advancing broader discussions of the evolutionary mechanisms that enable folivorous primates maintain coexistence where they are sympatric. Finally, recommendations for future research directions are made.

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Chapter 2: Study Site and Subjects

2.2 Site Description and History

Betampona Natural Reserve (BNR) (17◦15′-17◦55′S and 49◦12′-49◦15′E) is one of the last remaining tracts of primary eastern lowland rainforest in Madagascar (Green and Sussman 1990; Harper et al. 2007). It is located 40 km north-west of Madagascar’s second largest city and largest seaport, Toamasina (Figure 2-1). The ethnic identity of the Malagasy people in this area of Madagascar is Betsimisaraka. First established in 1927, BNR was designated as the first strict nature reserve in Madagascar in 1966 and is the second oldest protected area in Africa (Andriamampianina 1972). The reserve is managed by Madagascar National Parks (MNP), the government agency that oversees all protected areas in the country. It is classified as a Strict Nature Reserve which restricts entrance to the forest to those with scientific purposes accompanied by research permits from MNP. The Madagascar Fauna and Flora Group (MFG), an international consortium of zoos and botanical gardens, serves as a research partner with MNP and has been an active conservation presence in the reserve for over 25 years (Freeman et al. 2014).

The eastern lowland rainforests of Madagascar, BNR included, are characterized by low nutrients and high sand content in the soil (Grubb 2003). As a result, the trees are small both in height and girth when compared to montane forests (Grubb 2003). These forests have a notably high abundance of the following tree families: palm (Arecaceae), pandan (Pandanaceae), bamboo (Graminaceae) and tree-ferns (Cyatheaceae) (Armstrong et al. 2011).

The BNR encompasses 2228 ha (22.28 km^2) and is comprised of 50% primary rainforest (Britt et al. 1999). The forest canopy is broken with an average height of 20 to 25 m with emergent trees that are >30 m (Britt et al. 1999). The terrain is steep with slopes that vary from 0° to 55° and the mean elevation is 270 m and ranges from 92 to 571 m (Figure 2-2) (Ghulam 2014).

The most abundant tree families are Euphorbiaceae, Lauraceae, Rubiaceae, Arecaceae, Clusiaceae, and Moraceae, respectively (Armstrong et al. 2011). Invasive plants including guava (*Psidium cattleianum*), Molucca raspberry (*Rubus molluccanus*), and Madagascar cardamom (*Aframomum angustifloium*) are also present in and around the reserve (Ghulam 2014; Welch and Katz 1992). A survey of these three species from 2005-2012 revealed that they are spreading within the reserve at the expense of primary forests (Ghulam 2014). During this time period, Molucca raspberry increased 188.4% (27.6 ha to 79.6 ha) followed by guava with a 42.7% increase (126.8 ha to 181 ha) (Ghulam 2014). The presence of Madagascar cardamom increased in the forest by 39.2% (101.7 ha to 142 ha) (Ghulam 2014). Current efforts from MNP and MFG are underway to reduce the spread of these plants and to reforest affected areas (Freeman et al. 2014). The MFG is in the process of testing several methods of invasive plant removal along with the cost and efficacy of each removal method. They have supported both Malagasy master's and Ph.D. students who have conducted these experiments in the reserve and are currently formulating management plans related to this issue (Freeman et al. 2014).

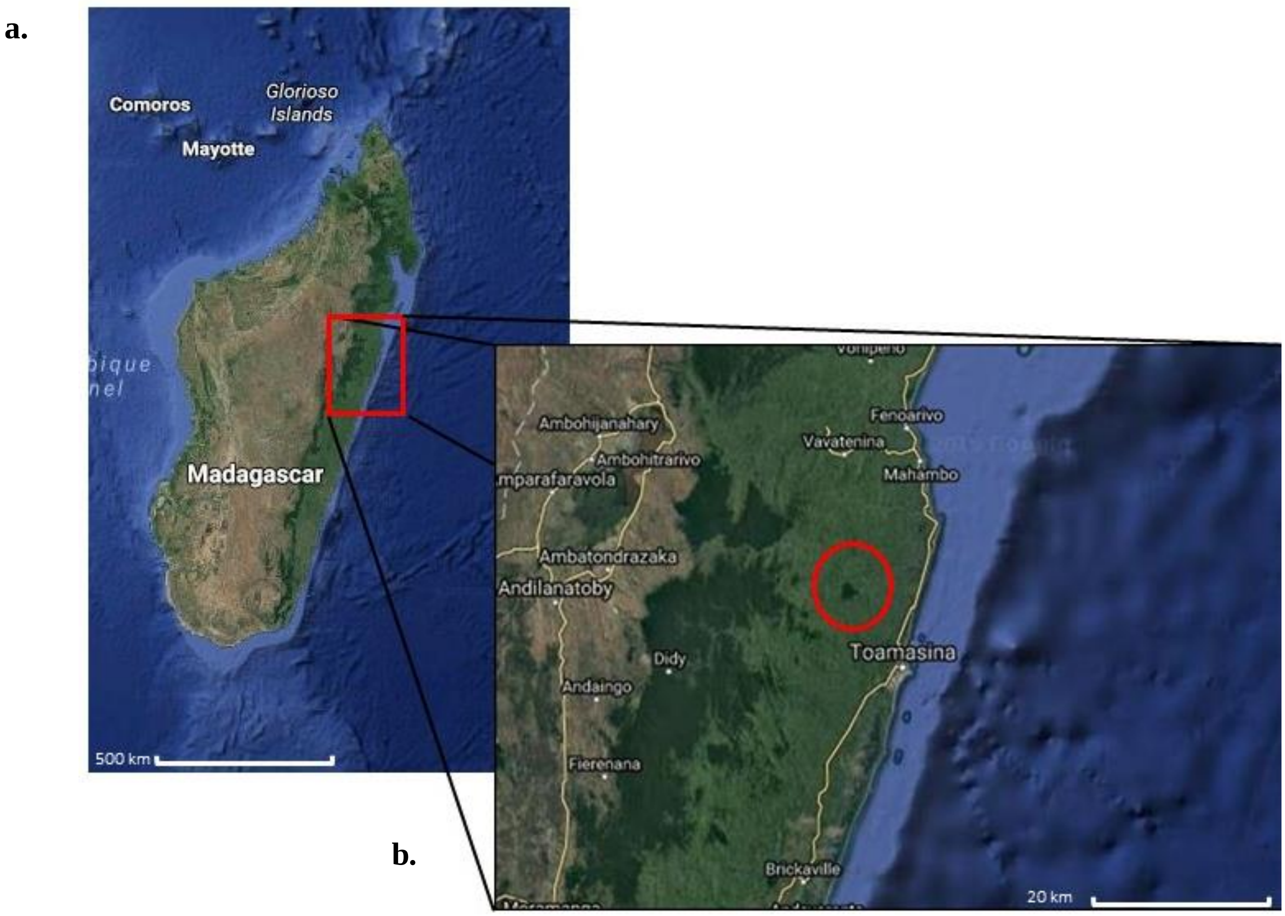

Figure 2-1. **a.** Map of Madagascar with study site and surrounding areas indicated in the red box. **b.** Location of Betampona Nature Reserve in red circle.

Figure 2-2. View of BNR boundary and adjacent farmland. Note that this represents one view of the reserve to depict the slope of the terrain and contrast between the forest cover within and outside the reserve boundary. This does not depict the entire reserve.

BNR is an isolated forest island surrounded completely by farmland and villages. The MFG has a research station, Rendrirendry, near the boundary of the reserve in the south (Figure 2-3). Until approximately 60 years ago, BNR was contiguous with two smaller forest patches, Antanamalaza (231 ha) and Sahivo (225 ha) but these forests no longer exist or have been greatly diminished in size (Britt et al. 1999). Currently, the closest forests to the reserve are the Parc National de Zahamena and the Reserve Speciale de Mangerivola which are 20 and 30 kilometers away, respectively (Britt et al. 1999). Slash-and-burn agriculture or “tavy” is practiced annually in the areas surrounding the reserve which maintains its isolation from other forest patches. In an effort to maintain the reserve boundaries, the MFG has worked with local villagers to create, maintain, and reforest a 100 m Zone of Protection (ZOP) around the entire reserve. Currently there are four campsites in the interior of the reserve that are used occasionally by research teams but the establishment of new campsites along with the cutting of new trails is prohibited by MNP without proper justification and permits. Additional anthropogenic disturbances include the presence of bush pigs (*Potamochoerus larvatus*), domestic dogs (*Canis familiaris*), and cats (*Felis sp.*) but a lack of larger mammals, such as zebu, within the reserve (Oliver, pers obs).

Many of the Malagasy people living in villages surrounding the reserve live far below the poverty line (Golden et al. 2014). In a survey of 298 households in villages around BNR, Golden et al. (2014) reported 8% of the households had no cash income in the year preceding the study. Agriculture primarily centers around rice cultivation but coffee, corn, bananas, and cloves are also common cash crops (Golden et al. 2014). Despite active patrols in and around the reserve by MFG and MNP agents, local villagers have reported to occasionally enter the reserve for the collection of firewood, building materials, medicinal plants, and hunting bushmeat (Golden et al. 2014). The most commonly sold species hunted in the reserve were bush pigs, hedgehog tenrecs (*Setifer setosus*) and common tenrecs (*Tenrec ecaudatus*) (Golden et al. 2014). Some poaching of lemurs also occurs in and around BNR. Golden et al. (2014) reported that five wild animals were consumed per household on average annually and approximately 20% of households surveyed had consumed a lemur within the year preceding the survey. The presence of the MFG field agents at the Rendrirendry research station has had a significant positive conservation impact, as evidenced by reduced rates of plant and animal harvesting from this area (Golden et al. 2014).

As previously mentioned, the MFG is an active conservation presence in and around BNR. MFG field conservation agents work with local Malagasy communities to raise awareness of the biodiversity in the reserve and importance of protecting the plants and animals within BNR (Freeman 2009; Freeman et al. 2014). They also provide education regarding sustainable farming practices in an effort to reduce the slash-and-burn agriculture that occurs in this area

(Freeman et al. 2014). Additionally, the MFG has a strong commitment to capacity building and, as such, the field agents are from the surrounding villages. This combination of the MFG's presence in and around the reserve and conservation education programs undoubtable helps to protect and preserve the biodiversity at BNR. While it is clear that residents living near BNR occasionally access the reserve and exploit its resources, the active conservation presence of the MFG and MNP are a positive presence in the area and are integral to the conservation of biodiversity in this reserve.

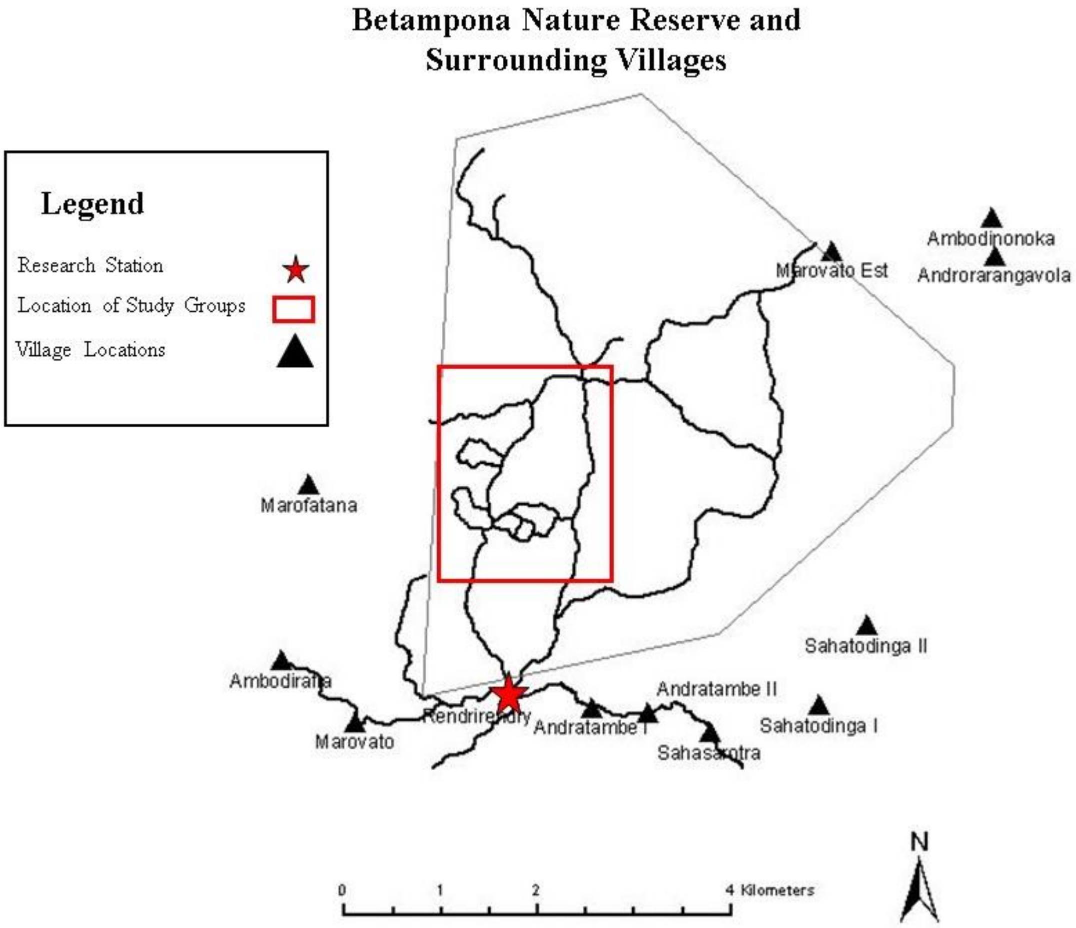

Figure 2-3. Map of BNR with surrounding villages and the trail system.

2.3 Biodiversity at BNR

Despite the small size of BNR relative to other protected areas in Madagascar, faunal biodiversity is high. Recent biodiversity surveys have confirmed the presence of 69 reptile, 79 amphibian, 89 bird, and 11 lemur species in the reserve (Freeman et al. 2014). Potential lemur predators include the fossa (*Cryptoprocta ferox*), barn owls (*Tyto alba*), and boa constrictor (*Acrantophis madagascarensis*) (Goodman 2003).

Three diurnal lemur species occur in BNR: *Propithecus diadema* (diademed sifaka), *Indri* (Day et al.), and *Varecia variegata* (black and white ruffed lemur) (Britt et al. 2003; Mittermeier et al. 2010; Welch and Katz 1992). Two lemur species that exist at BNR have been reported to exhibit a combination of diurnal, cathemeral, and crepuscular activity patterns at other sites; *Eulemur albifrons* (white fronted brown lemur) and *Hapalemur griseus* (bamboo lemur) (Mittermeier et al. 2010; Tan 1999). There are also six nocturnal primate species: *Microcebus simmonsi* (mouse lemur), *Cheirogaleus major* (fat tailed dwarf lemur), *Phaner furcifer* (fork-marked lemur), *Lepilemur mustelinus* (sportive lemur), *Avahi laniger* (woolly lemur) and *Daubentonia madagascariensis* (aye-aye) (Britt et al. 2003; Mittermeier et al. 2008; Mittermeier et al. 2010; Welch and Katz 1992).

All primates in the reserve are arboreal and, with the recent separation from other forests mentioned earlier, they are isolated. A species-wide survey of indri genetic diversity found that the indri at Betampona are, in fact, genetically isolated, and highlighted the threat of loss of genetic diversity without conservation intervention (Nunziata et al. 2016). The black and white ruffed lemur population has benefited from a successful reintroduction program here and this may be a consideration for future lemur conservation initiatives (Britt et al. 2003; Britt et al. 2004; Nunziata et al. 2016). In a comparison of anthropogenic effects on indri health between BNR and Analamazaotra, a site characterized by high levels of tourism and fragmented forest habitats, indri at BNR had fewer parasites and were, overall, characterized as healthier relative to Analamazaotra (Junge et al. 2011). While this is promising for the outlook of indri and other primates at BNR, the loss of genetic diversity is concerning (Nunziata et al. 2016). Population viability surveys are necessary for the lemurs in this reserve to adequately determine conservation priorities and adequate interventions. The MFG is working with MNP and several researchers to accomplish this goal (Freeman pers. comm.).

2.4 Temperature and Rainfall

I calculated average monthly rainfall (in mm), maximum, and minimum temperature (ºC) from a data set from 2002-2014 supplied by the MFG. I also calculated these monthly averages for the specific period of data collection for the current study (April 2013 – March 2014). Monthly values were based on daily rainfall and temperature measurements collected by MFG agents and shared with myself and other researchers. Rainfall occurs in all months of the year at the BNR, but October and November were the driest months, and January through March were the wettest. On average, rainfall occurs over 300 days per year (Ghulam 2014). Average rainfall from 2002 to 2014 was 3279 mm (SD: 6.336) (Figure 2-4). The average yearly maximum temperature in the same period was 29.75 °C (SD: 3.175) and the average yearly minimum temperature was 20.58 °C (SD: 3.436) (Figure 2-5; Figure 2-6). Temperatures begin to decrease in April and May and are lowest from June to August. The warmest months are October through March. When the 2002-2014 data set was compared to data collected during the study period, rainfall was slightly less than average from May through December and average maximum temperature was higher from November through January in the study period.

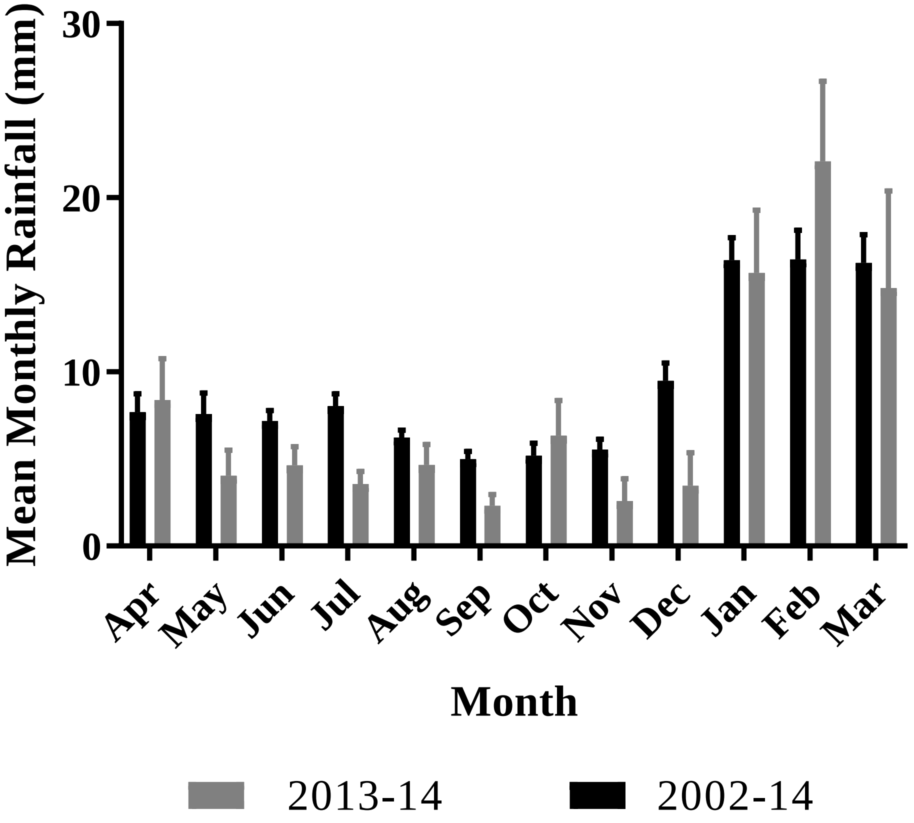

Figure 2-4. Comparison of rainfall by month at BNR from 2002-2014 and for study period only with monthly mean and std. error represented. Raw data provided by the MFG.

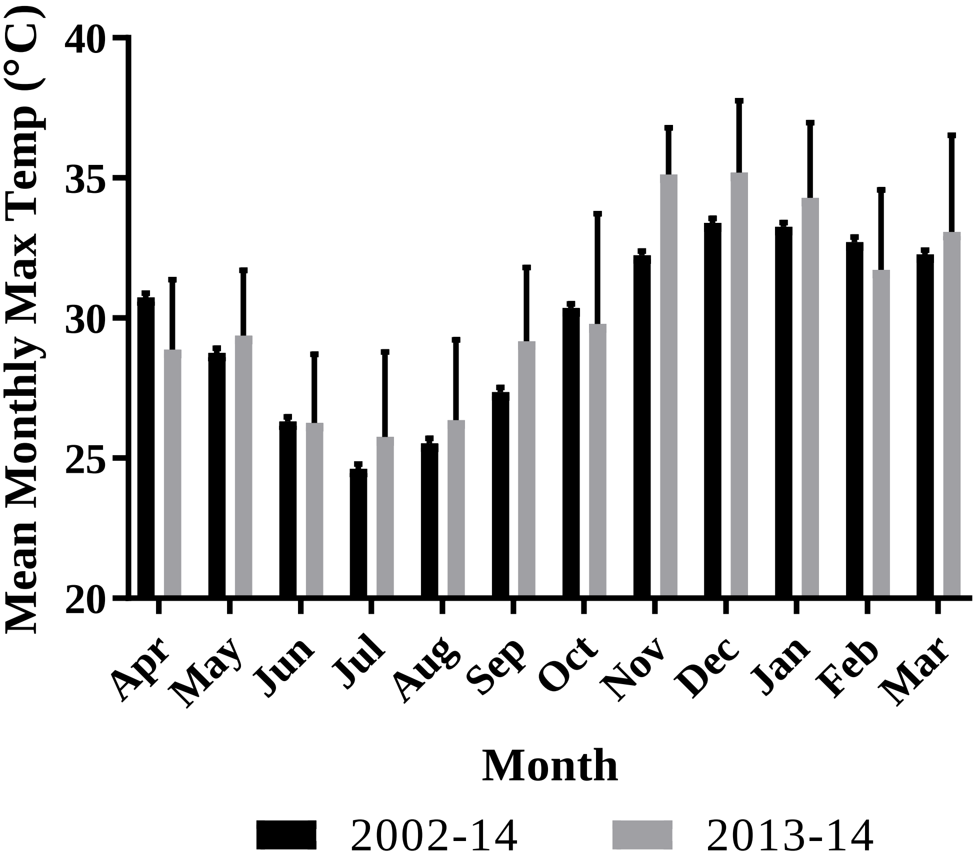

Figure 2-5. Comparison of average monthly maximum temperature at BNR from 2002-2014 and for the study period with monthly mean and std. error represented. Raw data provided by the MFG.

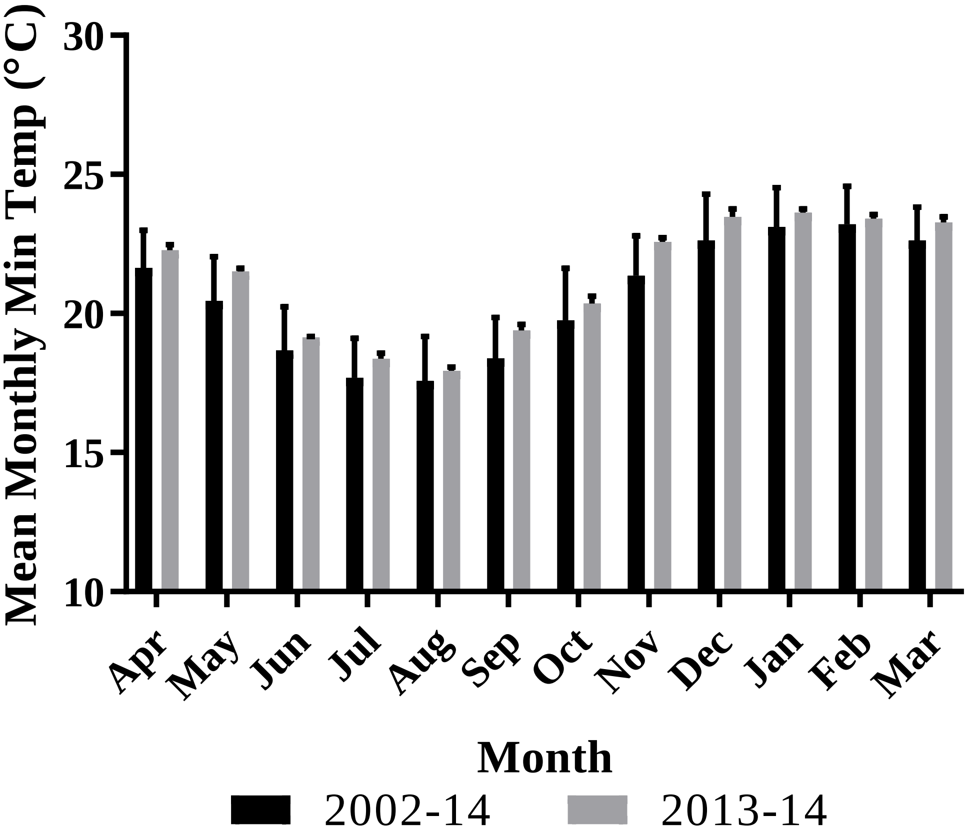

Figure 2-6. Comparison of average monthly minimum temperature at BNR from 2002-2014 and for the study period only with monthly means and std. error represented. Raw data provided by MFG.

2.5 Data Collection Methods

2.5.1 Darting, Biomedical Assessments, and Radio Collaring

In November 2011, a team of veterinarians, led by Sharon Deem DVM, and MFG conservation agents performed biomedical assessments on fifteen indri and four diademed sifakas within the BNR. A second biomedical assessment mission was conducted in July 2013, led by Fidisoa Rasambanarivo DVM, in which one indri and two diademed sifakas were captured for health assessments. The data collected are part of a larger prosimian biomedical assessment research project with the aim of facilitating collaboration between veterinarians and field biologists in conservation projects at several locations throughout Madagascar (Rasambanarivo pers. comm.). Protocols were approved by the Institutional Animal Care and Use Committee of the Saint Louis Zoo and complied with Malagasy research requirements. This protocol also complies with the American Society of Primatologists principles for the ethical treatment of primates. Individuals were anesthetized using tiletamine and zolazepam (Fort Dodge Animal Health, Overland Park, KS 66210, USA; 10-15 mg/kg, i.m.) by dart (Type «P» Disposable Dart, Pneu-Dart, Williamsport, PA 17701, USA). While under the anesthetic, rectal temperature, heart rate and respiratory rate were monitored. Blood, hair, feces, and ectoparasite samples were collected. An electrolyte solution equal to the amount of blood collected was subcutaneously administered. Each individual was also weighed, measured, sexed and an estimated age was recorded. Age estimates only categorized animals into the following classes: infant, juvenile, subadult, young adult, adult and were based on size and weight. One individual from each group was affixed with a radio collar (Advanced Telemetry Systems, Isanti, MI) and medallion for positive identification. No animals were injured during the darting and capture procedures.

Overall, individuals appeared healthy and weights were in the normal range for their species, sex, and age (Deem and Rasambanarivo, pers. comm.). Some diademed sifakas had ticks in their nostrils but these have been found in this population previously and behavioral observations do not indicate that these impact the activity of individuals with these ticks when compared to individuals without and there is no indication that these ticks carry disease (Oliver pers. obs.). Females of both species were slightly heavier than males and indri were heavier than diademed sifakas (morphometric data courtesy of MFG) (Figure 2-7; Table 2-1).

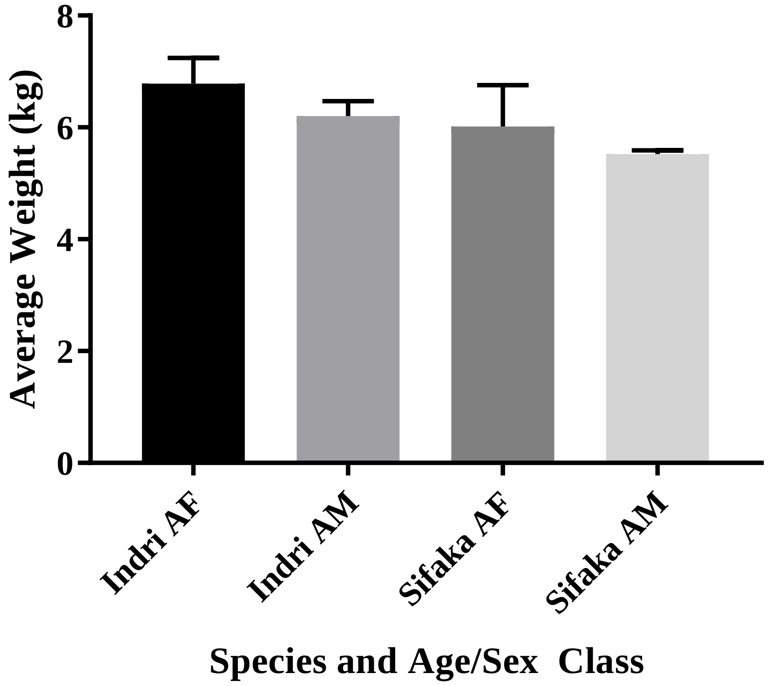

Figure 2-7. Average weights for indri and diademed sifaka males and females at BNR with mean and SD.

Table 2-1. Weights for indri and diademed sifakas at BNR with range, SD, and sample size

	Indri		Diademed Sifaka	
Weight (kg)	**AF**	**AM**	**AF**	**AM**
Mean	6.78	6.2	6.02	5.53
SD	0.46	0.27	0.74	0.07
Range	5.8-7.5	5.9-6.8	5.2-6.7	5.45-5.6
N	19	12	3	4

2.5.2 Data Collection Protocols

Data were collected by myself, a Malagasy research counterpart and two MFG trained guides from April 2013 through March 2014. For clarity, the term “we” refers to the team and “I” indicates actions taken by myself only. In February and March 2013, we habituated the six indri and one diademed sifaka study group. Two additional diademed sifaka study groups were added in August 2013. I chose a "breadth" rather than "depth" approach for this research whereby I followed many groups for approximately two days each month instead of following a small number of groups for many days each month. The "depth" approach was taken by previous researchers. By adding the "breadth" approach, it 1) increases the sample size of groups and individuals that have been studied for each species, and 2) yields insights into the amount of between group variation (or lack thereof) at BNR. Animals were considered habituated when the presence of humans did not visibly impact their behavior. We maintained a minimum distance of 10 m from all animals to reduce the chance of disease transmission and to minimize the impact of our presence on the actions of any animal behaviors. On occasions when an animal moved within 10 meters of an observer, we remained still and avoided eye contact with the animal until it moved away. We also practiced data collection protocols during this time to obtain inter-observer reliability. Inter-observer reliability was reached when >95% of observations of behavior, height, and forest level were identical between observers.

For 12 months, we conducted all-day follows on each group for two full days each month. Due to the steep terrain of the forest, we stayed on main trails until it was light enough to safely leave the trail each morning. We made every attempt to return to the main trails by dusk for personal safety while navigating the steep terrain. Groups were generally found within an hour of leaving the main trail. The radio collar signals began to fade in February and March 2014 which made locating groups more difficult. We recorded the time, GPS location, and group composition once the radio collared animal was located. At that time, we also began recording a track log to record our position every minute using a Garmin GPSmap 60csx, and began collecting behavioral data. We recorded group scans at 15-minute intervals, which included general behavior pattern of each animal (Table 2-2), the identity of the nearest neighbor, and the distance to that individual. Distance categories were recorded as follows: in contact, in proximity <1m, 1-5m, 5-10m, >10m, and not visible (Altmann 1974). Initially, we attempted to determine group spread and group cohesion patterns but were unable to reliably view all group members at each scan interval. Many times, one or more group individuals were out of sight but it was unclear if they were present but not visible or if they had moved away from the group. Due to this inconsistency in reliable data collection because of visibility issues, group cohesion was not included in data analyses.

We also conducted 10-minute continuous focal follows on indri and 5-minute continuous focal follows on diademed sifakas (Altmann 1974). While I had initially attempted 10-minute continuous focal follows for diademed sifakas, this did not prove feasible or safe within the rugged terrain so the focal duration was adjusted to 5-minutes. To account for this difference in data collection protocol between species, only the first five minutes of each indri focal animal session are used for analysis when behavioral comparisons are made between species. Before each focal session began, I recorded the group ID, focal ID, time of day, weather conditions, nearest neighbor ID, distance to the nearest neighbor, and activity of the nearest neighbor. Focal animals were randomly selected but were not resampled until three times the length of the sample period had passed (30 minutes for indri and 15 minutes for diademed sifakas). If a focal animal was out of sight for more than 20% of the sample period, the session was stopped and a new focal animal was selected. During each focal session, the animal’s behavior, height in the canopy (in meters) and forest strata was continuously recorded for 5 or 10 minute bouts depending on the species observed. General behavior recorded during focal observations included rest, feed, move, social, other, and not visible (Table 2-2). Duration of behaviors were recorded using a Timex Ironman ® digital watch with a countdown timer.

Table 2-2. Behavioral ethogram used in this study of indri and diademed sifakas.

Behavior	**Definition**
Rest (R)	Individual is inactive. May include sleep
Feed/Forage (F)	Masticating and ingesting or searching for food material
Move (M)	Animal locomotes either within or between trees.
Social (S)	Behaviors that involve more than one individual Includes resting in proximity or in contact
Other (O)	Any behavior not described above
Not Visible (NV)	Animal cannot be seen

The focal animal's height in the forest was measured by using both absolute and relative measurements. Absolute measurements of height in the forest were recorded in meters above the ground. Relative measures were recorded by dividing the forest into five stratigraphic levels: 1 = ground, 2 = underbrush, 3 = under canopy 4 = continuous canopy, and 5 = emergent canopy (Richards 1966). Both measures were used because a wide range of absolute measurements could account for different forest levels. For example, an animal could be nine meters from the ground and could occupy either level three (under canopy) or four (continuous canopy) depending on the forest structure in that specific area. Relative measurements were used for most analyses unless otherwise specified.

We recorded all occurrences of group feeding and collected the following for each feeding tree or liana: GPS point, time, individuals feeding, plant part (or other food type) consumed (young leaf, mature leaf, fruit, seed, flower, earth, other and unknown), diameter at breast height (DBH), tree height and phenological stage for each plant part. Phenology was measured on a scale of 0 to 4. A score of zero indicated that the plant part was not visible while a score of four indicated that the plant part was at its greatest possible abundance (Chapman and Wrangham 1994). Tree height was measured using a Nikon Forestry 550 hypsometer and range finder when possible and was otherwise approximated. When known, we recorded the vernacular and/or scientific name of the plants; otherwise, we collected samples and photographs of unknown food sources and consulted a local botanical expert for positive plant identification. Each tree was marked to determine if animals revisited specific trees repeatedly during date collection.

2.5.3 Description of Focal Groups

A total of three diademed sifaka (Table 2-3) and six indri groups (

Table 2-4) were followed for two full days each month. Groups were named per their geographic location in the reserve: I refer to groups by name throughout the remainder of the dissertation. Group locations are depicted in Chapter 5. During the period of data collection, females in three out of the six indri groups had infants (SE, CE, and NW) and two groups contained one juvenile each (CW and NW). Only one of the three diademed sifaka groups had a juvenile (Central) no females gave birth during the study period.

Table 2-3. Demographics of three diademed sifaka study groups.

Group Name	**Adult Male**	**Adult Female**	**Subadult**	**Juvenile**	**Infant**	**Total**
South	1	1				2
Central	2	1	1*			4
North	2	1	1	1**		4

* last seen in September 2013, ** found deceased in August 2013 and not included in this study

Table 2-4. Demographics of six indri study groups

Group Name	Adult Male	Adult Female	Subadult	Juvenile	Infant	Total
Southeast (SE)	1	1			1	3*
Southwest (SW)	1	1				2
Central East (CE)	1	1			1	3*
Central West (CW)	1	1		1		
Northeast (NE)	1	3	1	1	1	7**
Northwest (NE)	1	1	1		1	4*

* all infants were born in late June 2013

** see description of social structure for a detailed explanation of the demography of this group

2.5.4 Social Structure of Study Groups

Previous studies of indri have reported stable grouping patterns with an adult male, adult female, and their presumably related offspring (Blanchard 2007; Pollock 1975; Powzyk 1997). Only five indri groups have been the subject of long-term studies to-date (see Chapter 1). Some researchers refer to indri as “monogamous” but the term “pair bond” is more appropriate as one anecdotal occurrence of an extra-pair copulation has been reported (Bonadonna et al. 2014). In this instance, an adult female traveled to a neighboring group’s territory, copulated with the neighboring male, and returned to her original group (Bonadonna et al. 2014). This occurred during the mating season at a site called Maromizaha, near Toamasina (Bonadonna et al. 2014). The grouping pattern of the groups in the Bonadonna et al. (2014) study did not change. Instead, an extra-pair copulation occurred then each group returned to their original demographic composition.

In my current study, indri group composition remained mostly stable with the exception of the NE group (see group demography table). The male indri in this group was observed with three separate females at different times. Adult females did not overlap spatially or temporally and the male was, at times, observed to wake up with one female then travel to another part of his territory and spend days with another female. He also long-called with all three females. One female (AF1) was with a subadult and a juvenile from February 2013 through July 2013. They were not seen after July 2013. The second adult female (AF2) was not observed with offspring or with any other individuals. The NE adult male was seen with a third adult female (AF3) and her dependent infant on only one occasion. The adult male had a radio collar which enabled us to reliably find him. All adult females had individually identifiable collars but two were not radio collars and the third was a radio collar from a previous research project that was no longer functional. Due to these constraints, we were unable to follow adult females when they were not with the radio collared adult male. This is the first occurrence of this novel indri grouping pattern and requires further investigation.

Diademed sifakas have been reported in groups from 2-7 with a variety of adult males and adult females in each group (Blanchard 2007; Irwin 2006; Powzyk 1997; Current Study). I observed the smallest diademed sifaka stable group reported to-date that consisted of only one adult male and one adult female. Adult group composition remained mostly stable throughout the study period. The Central group contained an individual classified as a “young adult” by the veterinarians due to the smaller size and lower weight at the time of capture. This individual disappeared from the group in September 2013 and may have dispersed. No remains were found but predation cannot be ruled out as a cause for disappearance. The North group had a juvenile at the time of darting and habituation (July 2013). MFG agents found the headless body of this individual in a tree in August 2013 in an apparent predation event (MFG agents pers. comm..).

In conclusion, the social structure of indri and diademed sifakas at BNR has both consistencies and inconsistencies with reports from other sites. Further studies on these and other groups at this site are necessary to determine the underlying causes for these extraordinary grouping patterns.

2.5.5 Contact and Observation Hours

We conducted 59 all-day follows on the three diademed sifaka groups and 150 all-day follows on the six indri groups from April 2013 through March 2014. A total of 1897 hours of scan observations were recorded during these follows, comprised of 595 hours of scan data on diademed sifakas and 1301 hours of scan data on indri (Table 2-5). We measured and cataloged 3138 food sources, 1994 for indri and 1144 for diademed sifakas. A total of 561 hours of continuous focal animal data were also recorded for indri and 159 hours for diademed sifakas. Specific data sets and methods of data analysis will be discussed in subsequent chapters.

Table 2-5. Total hours of scan data and days followed by group and species

Species	**Group ID**	**Total Hours Observed**	**Total # Follow Days**
Propithecus diadema	Central	279	23
	South	131	15
	North	196	21
Indri indri	SE	214	24
	SW	220	24
	CE	213	26
	CW	227	26
	NE	230	27
	NW	199	23

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Chapter 3: Activity Patterns of Indri and Diademed Sifakas at Betampona Nature Reserve, Madagascar

3.1 Introduction

An animal’s activity budget can be defined as the allocation of an individual’s daily active period to a set of mutually exclusive behaviors. Daily activities are influenced by a variety of factors including an animal’s diet, food availability, habitat quality, climatic conditions, and overall physiology (Agostini et al. 2012; Dunbar et al. 2009; Milton 1980). The amount of time an individual can devote to any one behavior in a day is inherently linked to the need to find food, mating opportunities, and sleeping sites (Dunbar et al. 2009; Hladik 1977). The amount of energy available to an animal for each behavior is, in turn, a direct result of food quality, availability, and overall metabolic intake (Dunbar et al. 2009). Seasonal changes in temperature, rainfall, and reproductive status can also alter the amount of time devoted to specific behaviors throughout the day (van Schaik and Brockman 2005).

Diet and activity budgets are inherently connected, as an animal’s energy expenditure is constricted by its energy intake (Clutton-Brock and Harvey 1977; Lambert 1998). Folivorous primates tend to spend more time resting and less time traveling and engaging in social behaviors than frugivores, insectivores, and gummivores as more energy is required to extract nutrients from leaves than other food types (Clutton-Brock and Harvey 1977; Milton 1981). Generally, folivores are considered “energy minimizers” in that they rest more and move less than species that consume more easily digestible foods such as fruits and seeds (Milton 1980). The degree of folivory in a primate species’ diet positively correlates with the amount of time spent resting relative to other behaviors such that primates with the highest proportion of leaves in their diet tend to rest more than those species that consume lower proportions of leaves (Hladik 1977; Oates 1987). For example, howler monkeys are highly folivorous and often spend the majority of their daily active period resting (e.g. Agostini et al. 2012; Milton 1998; Richard 1970).

When folivorous diurnal primates exist in sympatry, they reduce intraspecific competition by partitioning resources and/or by displaying different activity patterns (e.g. Agostini et al. 2010; Blanchard 2007; Hadi et al. 2011; Hladik 1977; Powzyk and Mowry 2003; Vandercone et al. 2012; Yeager and Kool 2000) . In these cases, two general and related patterns have emerged: 1) one species will consume a higher proportion of leaves whereas the other species, will consume a higher proportion of fruits and seeds relative to each other, and 2) the species that consumes more leaves will spend a larger portion of the daily active period resting relative to the species that consumes more fruits and seeds (see Chapter 1 for a more detailed discussion of this topic). Sympatric, closely related primates may also express differences in the amount of time or activities performed in different stratigraphic levels of the forest (Freed 1996; Gautier-Hion et al. 1983; Sussman 1977; Sussman 1979).

Nearly all primates live in the tropics and are subject to seasonal fluctuations in temperature, rainfall, and resource availability (van Schaik and Brockman 2005). Most primates do not migrate to new environments during seasonal fluctuations, individuals often respond to these changes by altering their rates of activity throughout the day (van Schaik and Brockman 2005). Additionally, primate species adjust their active period in concordance with food resource availability and abundance throughout the year (Hemingway and Bynum 2005). Madagascar experiences particularly harsh seasonal changes in both resource availability and climatic variables (Wright 1999). Lemurs respond to these changes by seasonally restricting reproduction, shifting their dietary profiles, and adjusting time devoted to feeding, locomotion, and resting throughout the year. Lemur reproduction is strictly seasonal across all taxa (Wright 1999). Particularly in the eastern rain forests, infant weaning occurs during times of higher resource availability (Wright 1999). Female dominance is common in lemurs and females have priority of access to resources presumably to offset the energetic cost of reproduction (Pollock 1979; Powzyk 1997). Lemurs also decrease their basal metabolic rate and decrease activity when resources are scarce and as a response to cold temperatures (Schmid and Ganzhorn 1996; Wright 1999). This varies interspecifically, but has been documented in both folivorous and frugivorous lemurs (Wright 1999).

Male and female primates are subject to different energetic constraints as the female energetic investment in reproduction and lactation is far greater than that for males (Oftedal 1991). Reproductive females can either decrease energy expenditure by shortening their daily travel, spending more time feeding, increasing food quality, or employing any combination of these strategies to offset reproductive energetic costs (Gittleman and Thompson 1988; Meyers and Wright 1993). Regarding indriids, specifically, Hemingway (1999) found no male/female differences in time spent resting and feeding in Milne-Edwards sifakas (*Propithecus edwardsi*) at Ranomafana. However, these sifakas did show differences in time spent feeding on different plant parts, while time spent engaging in resting and feeding was similar between sexes, they differed in specific dietary choices (Hemingway 1999). For diademed sifakas, Irwin (2006) found a significant difference in the amount of time spent feeding between males and females. Powzyk (1997) found the same trend, but the sex difference was less pronounced and was not statistically significant. Powzyk (1997) did report a significant difference in time spent feeding between males and females for indri.

While both indri and diademed sifakas are predominantly folivorous, the diet of indri contains a higher proportion of leaves relative to diademed sifakas (Blanchard 2007; Britt et al. 2002; Powzyk 1997; Powzyk and Mowry 2003). As with other primates, the more folivorous indri has been reported to spend more time resting than diademed sifakas (Blanchard 2007; Powzyk 1997). Seasonal differences in activity budget have been reported at Mantadia where these two species are sympatric (Blanchard 2007; Powzyk 1997). Irwin (2006) also found seasonal differences in activity budgets for diademed sifakas where they are allopatric with indri at Tsinjoarivo. Significantly positive relationships have been reported between daily active period and maximum temperature for both species, whereas negative relationships have been reported between daily active period and rainfall (Blanchard 2007; Irwin 2006; Pollock 1975; Powzyk 1997). Additionally, Irwin (2006) examined differences between diademed sifakas living in areas of low versus high levels of anthropogenic disturbance. Diademed sifakas in the continuous forest spent more time resting and traveling and less time feeding than their counterparts in fragmented forest patches (Irwin 2006). In summary, indri and diademed sifakas differ in their activity budgets relative to each other, both species experience seasonal fluctuation in activity patterns, and habitat quality was found to impact activity patterns in diademed sifakas (Blanchard 2007; Irwin 2006; Pollock 1975; Powzyk 1997).

In this chapter, I describe the general activity budgets for indri and diademed sifakas at BNR with a focus on species-specific differences in activity patterns. I discuss inter- and intraspecific variation in activity patterns, seasonal changes in rates of activity, forest levels as it relates to activity, as well as sex in activity budgets. I then compare my results from BNR to other sites to examine between-site variability in rates of activities for these two indriids.

3.2 Hypotheses and Predictions

When primates with similar dietary patterns coexist, they avoid resource competition via niche partitioning. Cranial and digestive morphology can be used to predict the dietary profiles of primate species which, in turn, are intrinsically linked to an animal's activity patterns (Milton 1981). A primate-wide trend in in activity patterns is that, as folivory increases, the amount of time resting increases while energy-expensive activities like traveling and locomotion decrease. This is due to the more evenly distributed leaves in an environment relative to patchily distributed fruits and seeds combined with notion that leaves yield less readily accessible energy from sugars and carbohydrates than fruits and seeds (Clutton-Brock and Harvey 1977; Houle 1997). Additionally, animals that are more folivorous tend to be less flexible in their use of stratigraphic levels in the forest (Porter 2001; Singh et al. 2011). More folivorous primates tend to spend most of their time in the continuous canopy because that is where the majority of young leaves are located whereas more frugivorous primates use all levels more uniformly and travel to the ground more often to feed from food items such as fallen fruits (Porter 2001; Singh et al. 2011). Indri morphology indicates that they are more specialized folivores than diademed sifakas (Hill 1953; Kay and Hylander 1978; Powzyk 1997; Viguier and Tort 2000). I hypothesize that, if primate-wide trends regarding the relationship between morphology, diet, activity, remain consistent for indri and diademed sifakas, then niche differentiation strategies can be predicted from their differences in morphology. Based on the current body of literature, indri and diademed sifaka dietary profiles differ interspecifically and also fluctuate throughout the year (Blanchard 2007; Irwin 2006; Pollock 1975; Pollock 1977; Powzyk 1997). I have formulated the following hypotheses and predictions based on primate-wide trends for coexistence strategies of sympatric folivores as well as the current body of literature for indri and diademed sifaka behavioral ecology, specifically.

$H_{1.1}$: Previous researchers reported that diademed sifakas consume more seeds, fruits, and flowers than indri (Blanchard 2007; Powzyk 1997; Powzyk and Mowry 2003). Indri, in turn, are more folivorous than diademed sifakas.

$P_{1.1}$: Indri will spend more time resting than diademed sifakas.

$P_{1.2}$: Diademed sifakas will spend more time feeding than indri.

$P_{1.3}$: Diademed sifakas will spend more time engaging in locomotor behaviors than indri.

$H_{2.1}$: The eastern rainforest of Madagascar experience seasonal differences in temperature, rainfall, and resource availability (Wright 1999). If variation in temperature and rainfall exist, then the length of the individuals' daily active period will be positively correlated with daily maximum temperature and negatively correlated with daily amount of rainfall.

$P_{2.1}$: Diademed sifakas will have a longer daily active period than indri.

$P_{2.2}$: Daily active period will be positively correlated with temperature.

$P_{2.3}$: Daily active period will be negatively correlated with rainfall.

$H_{3.1}$: Previous reports have suggested minimal intraspecific variation in activity budgets for indri and diademed sifaka groups at the same study site (Irwin 2006; Pollock 1975; Powzyk 1997). Therefore, the null hypothesis is that there will not be intraspecific differences in activity budgets between groups of indri and diademed sifakas at BNR. However, some inter-site differences have been reported for diademed sifakas which has been attributed to levels of anthropogenic disturbance (Irwin 2006).

$P_{3.1}$: No statistically significant differences will be found in the amount of time engaging in each activity pattern between groups of the same species.

$H_{4.1}$: Differences in the use of different forest levels have been reported at Mantadia for indri and diademed sifakas (Blanchard 2007; Powzyk 1997). If this pattern is consistent between sites, then indri and diademed sifakas will partition their environment by expressing differences in the amount of time and activities performed in each forest level.

$P_{4.1}$: Indri will spend more time in the continuous canopy than diademed sifakas.

$P_{4.2}$: Diademed sifakas will spend more time in lower levels of the forest than indri

$H_{5.1}$: Sex differences in time spent feeding have been reported at other sites whereby females fed more than males (Irwin 2006; Powzyk 1997). If females incur more energetic costs due to reproduction than males, then they will spend more time feeding than males.

$P_{5.1}$: Females will spend more time feeding and less time resting than males for both lemur species.

$H_{6.1}$: If species-specific activity patterns are consistent with general primate-wide trends regarding the interaction of morphology, diet, and activity, the activity patterns of indri and diademed sifakas at BNR will not differ statistically from previously reported activity patterns from Mantadia and Analamazaotra for indri and from Mantadia and the continuous forest at Tsinjoarivo for sifakas.

$P_{6.1}$: Activity patterns of indri and diademed sifakas at BNR will correspond with those reported at other sites.

3.4 Methods

3.4.1 Data Collection

A detailed description of the study site, demographic information about the study groups, and operational definitions of general activity patterns can be found in Chapter 2. To determine activity budgets of indri and diademed sifakas at BNR, we (myself, a Malagasy research counterpart, and two trained guides) conducted group scans at 15-minute intervals on all visible individuals in a daily focal group from April 2013 through March 2014 (Altmann 1974). We noted the time, weather, individual identification, and behavior of each visible group member at each scan interval. Activities analyzed in this study were rest, feed, and locomotion as these were the most commonly observed behaviors. All other behaviors were categorized as “other”. I used the groups can data to calculate overall percent of time engaged in each behavior for each species for the entire study period. I also calculated monthly average amount of time engaged in each activity by species, by group, and by sex. Finally, I determined the average amount of time spent engaging in each activity during each hour of the day. Only activities from all-day follows were analyzed to determine activity budgets, as incomplete days would bias the results if certain times of day were overrepresented and other times underrepresented. All-day follows are defined here as a day where the focal group was located before 7:30 am or was located at their sleeping site and followed until 16:30 or to their sleeping site. The continuous focal animal data set was used to determine differences in the amount of time spent engaging in activities in the different forest levels. Finally, daily temperature minimum, maximum, and rainfall measures were collected by MFG field agents and provided for use in this dissertation with permission from the MFG (see Chapter 2).

3.4.2 Data Analysis

Data sets were tested for normality before analysis. When the assumptions for normality were met, parametric statistics were used. When these assumptions were violated, the non-parametric counterpart was used. To determine overall activity patterns for each lemur species, I calculated the overall mean percent of scans for each behavior (resting, feeding, locomotion, and "other" behaviors) for the entire study period as well as monthly means per activity for all individuals. The annual and monthly mean, range, and standard deviation were compared between species using a chi-square test to determine overall differences for the amount of time spent resting, feeding, and locomoting.

I calculated each group's daily active period by recording the time of the first group movement from their sleeping spot and the time that the group arrived in their evening sleeping spot. However, it was not possible to follow groups from sleeping site to sleeping site in some instances. This was particularly problematic during the hot, dry months and for diademed sifakas throughout the year. I included days in which we found the group before 7:00 and either 1) followed them to their sleeping site or 2) followed the group past 16:00. Between group differences were assessed using a Chi-Square test. Differences were considered significant when $p \leq 0.05$. I then examined relationships between the daily active period and the recorded maximum temperature, minimum temperature, and amount of rainfall (mm) for that specific day using a linear regression (indri, $N = 85$ days; diademed sifakas, $N = 33$ days). Vertical stratification preferences were assessed by first dividing the forest into five stratigraphic levels: (1 = ground, 2 = underbrush, 3 = below canopy , 4 = continuous canopy, and 5 = emergent canopy) then determining the amount of time each species spent engaged in each activity pattern in each level (Richards 1966).

3.5 Results

3.5.1 Sampling Effort

Calculation of indri activity budget includes a total of 1301 hours from 150 days of group scan data and 595 hours from 59 days for diademed sifakas, along with 246 and 159 hours of 5-minute continuous focal animal data for indri and diademed sifakas respectively.

3.5.2 Overall Activity Patterns

Indri and diademed sifakas spent the majority of their daily active period resting followed by feeding (Table 3-1). Although both species spent a similar amount of time resting, feeding, and engaging in "other" behaviors, there was a larger range of variation for each behavior in diademed sifakas than indri (Figure 3-1; Figure 3-2). The percentage of time spent in each activity category did not statistically differ among indri study groups (Chi-square, $\chi^2 = 3.124$, df = 15, n.s.) (Figure 3-3). Similarly, no statistically significant differences were detected among groups of diademed sifakas ($\chi^2 = 5.013$, df = 6, n.s.) (Figure 3-4).

Table 3-1. Activity budgets of indri and diademed sifakas at BNR. Values reported are proportion of general activity patterns.

		Rest	**Feed**	**Locomotion**	**Other**
Diademed sifaka	Mean	60.36	29.99	5.44	4.21
	SD	5.24	5.63	2.12	1.12
	Range	53.23 - 69.19	22.37 - 39.54	2.65 - 9.48	2.52 - 6.49
Indri	Mean	60.37	31.03	2.67	5.93
	SD	3.35	4.35	0.70	1.34
	Range	56.44 - 66.87	23.66 - 37.23	1.92 - 4.19	3.23 - 8.32

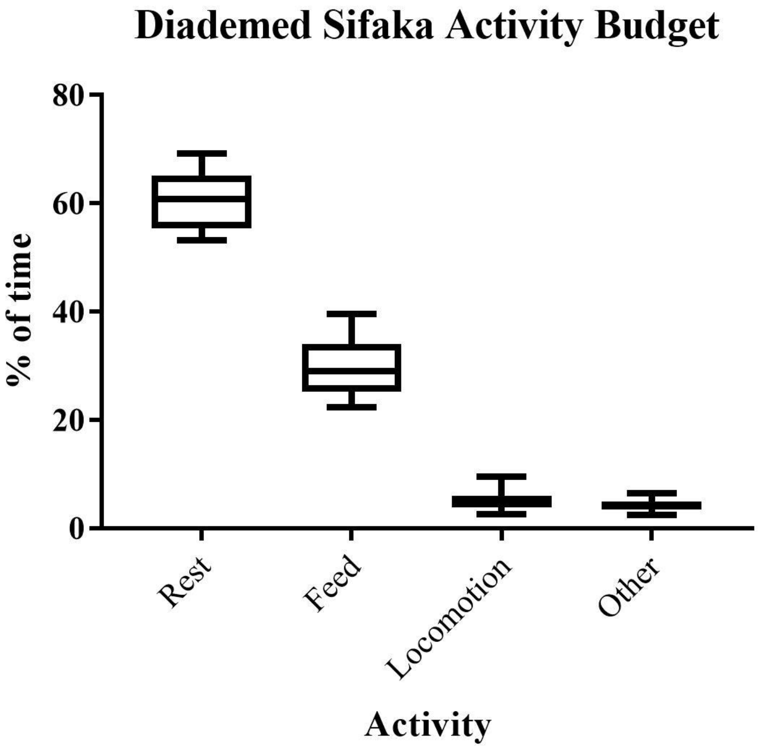

Figure 3-1. Diademed sifaka activity budget with median and range. Activity means represented here depict the species averages from all study groups and all full-follow days.

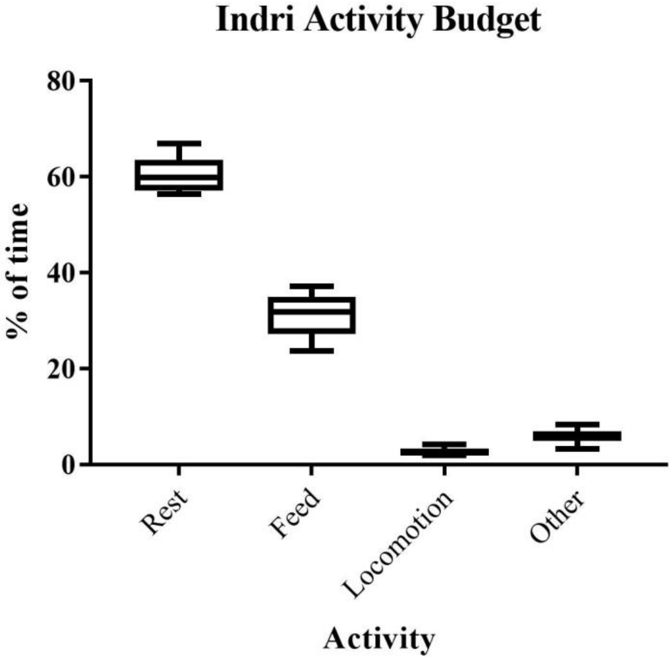

Figure 3-2. Indri activity budget with median and range. Activity means represented here depict the species averages from all study groups and all full-follow days.

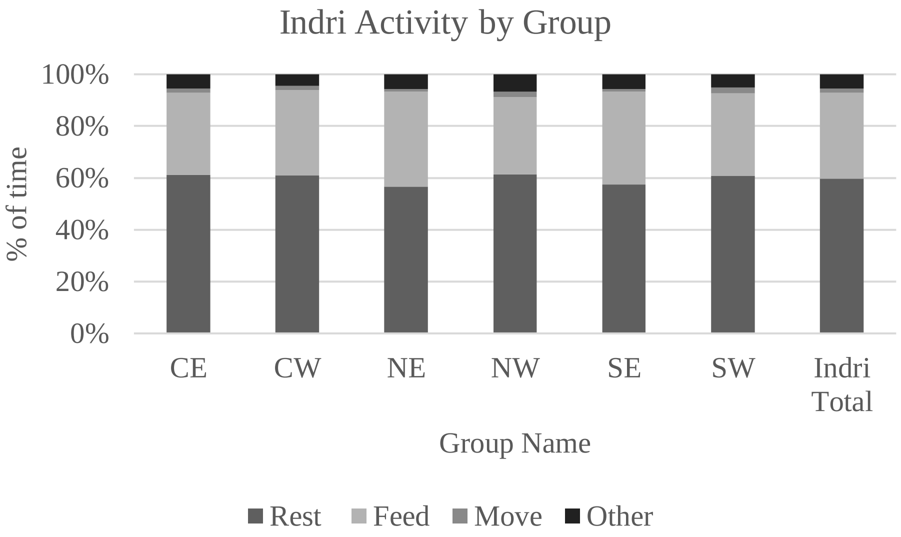

Figure 3-3**.** Indri activity budget by group and with all groups combined. No statistically significant differences were detected among indri groups ($\chi^2 = 3.124$, df = 15, n.s.).

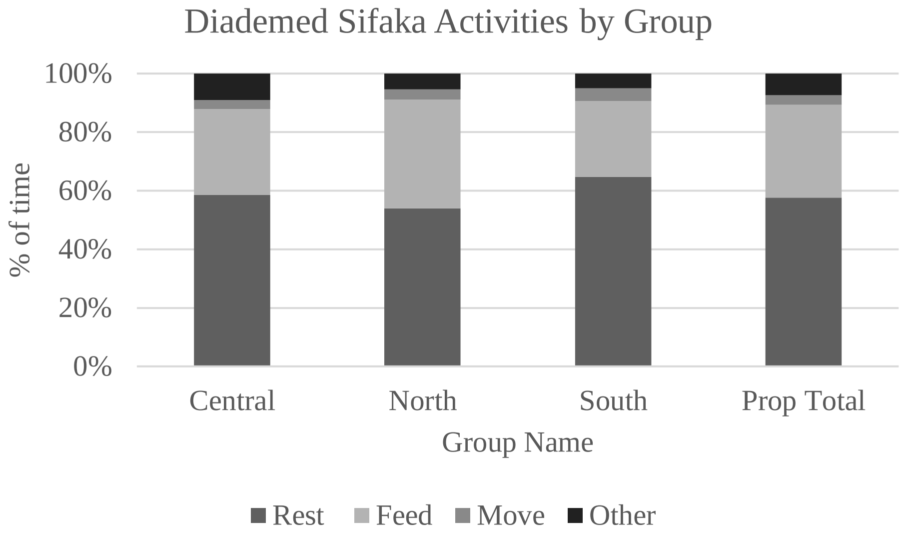

Figure 3-4. Diademed sifaka activity budget by group and with all groups combined. No statistically significant differences were detected among groups ($\chi^2 = 5.013$, df = 6, n.s.).

Although both species exhibited some monthly variation in time spent resting (Figure 3-5) and feeding (Figure 3-6), I found no significant differences in the monthly mean rates of these behaviors (t test, resting: $t = 0.9997$, p= 0.997, df = 11, n.s.; feeding: $t = 0.4925$, p = 0.632, df = 11, n.s.). The monthly average amount of time engaging in locomotion was higher for diademed sifakas than indri in all months but August (Figure 3-7). The average amount of time engaged in locomotor behaviors for the entire study period was significantly higher for diademed sifakas when compared to indri ($t = 4.635$, p = 0.0007, df = 11). Within species, I detected a significantly negative relationship between resting and feeding for indri ($r = -0.9441$, p = <0.0001) and for diademed sifakas ($r = -0.9204$, p = < 0.0001) such that when the frequency of one behavior increased, the other behavior decreased and vice versa.

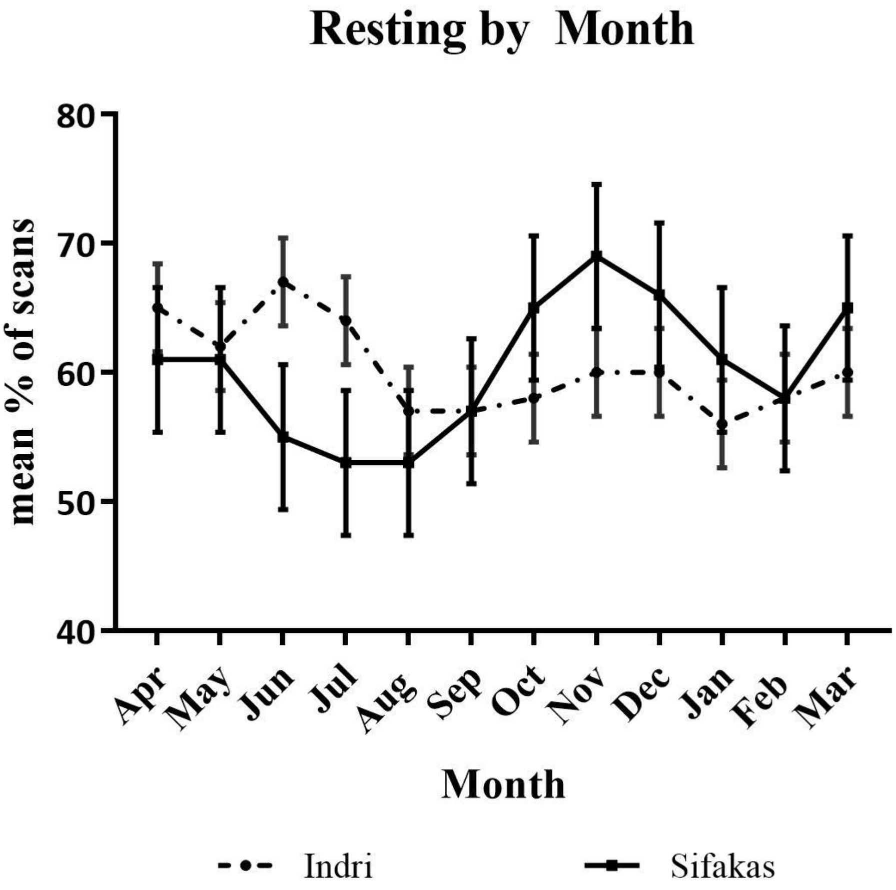

Figure 3-5. Mean monthly percent of time spent resting for indri and diademed sifakas.

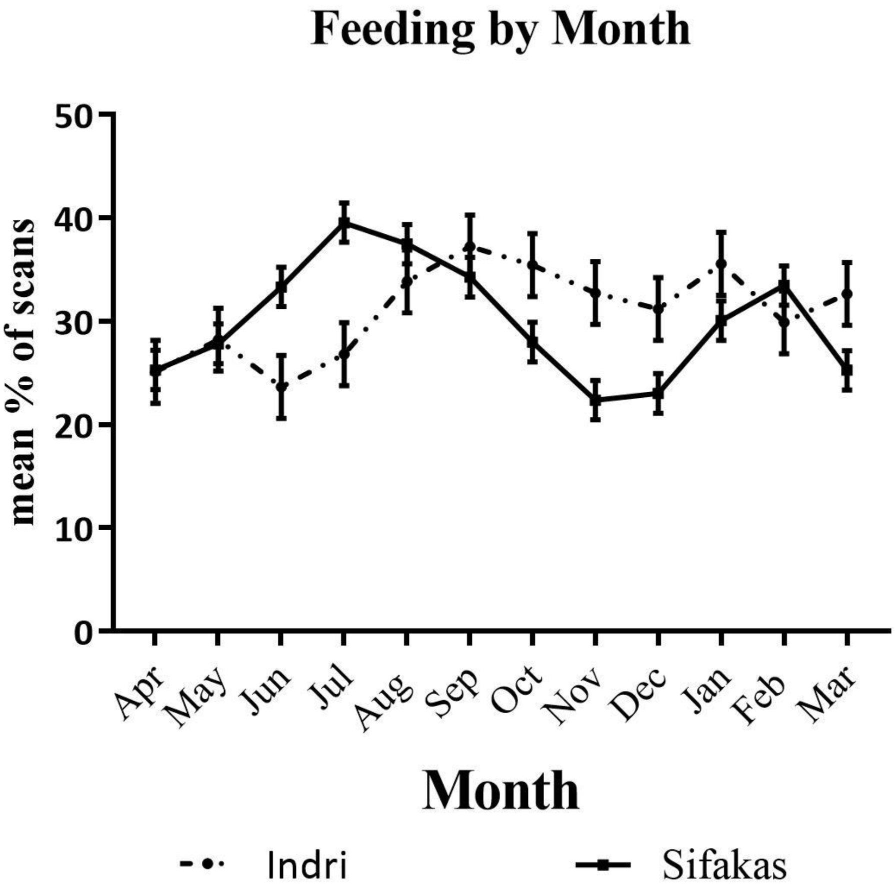

Figure 3-6. Mean monthly percent of time spent feeding for indri and diademed sifakas.

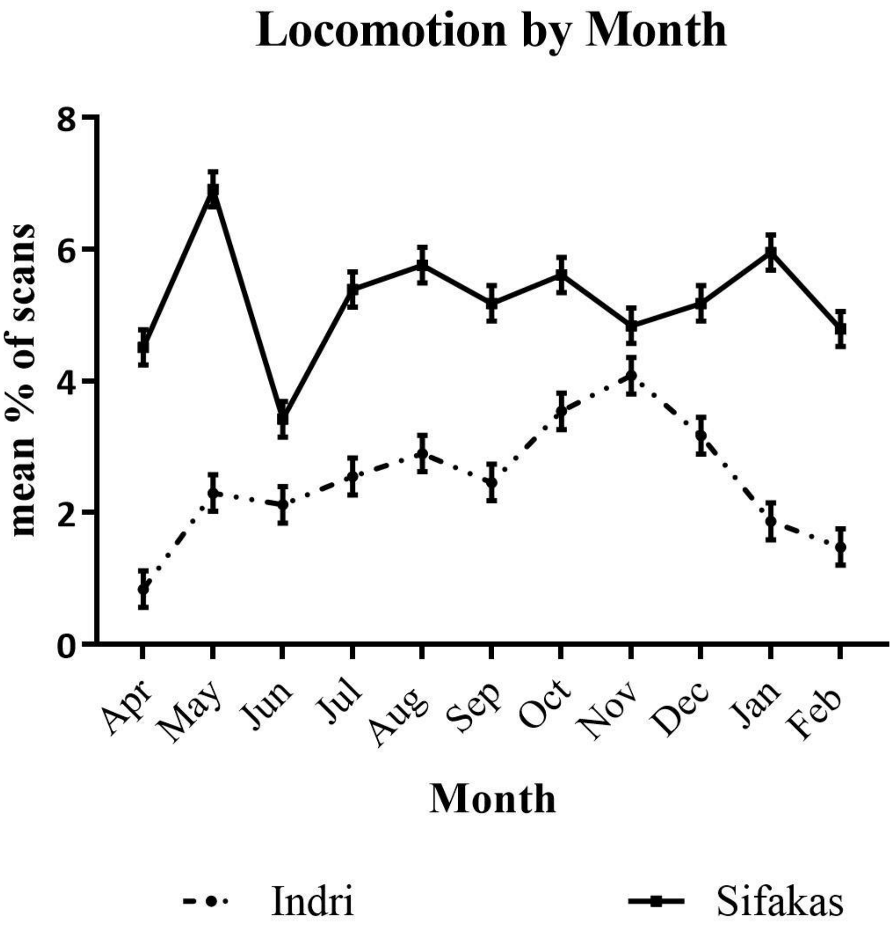

Figure 3-7. Mean monthly percent of time locomoting for indri and diademed sifakas.

3.5.3 Hourly Differences in Activity Patterns

Species differed in how their activities varied throughout the day. Diademed sifakas rested less frequently in the morning (6:00 to 10:00) and late afternoon (15:00 to 16:00) hours than indri, but rested more frequently mid-afternoon (10:00 to 14:00) than indri (Figure 3-8). Both species showed a steep increase in resting in the late afternoon. I found a similar pattern in feeding behavior where diademed sifakas fed more in the morning and late afternoon than indri (Figure 3-9). Indri fed more frequently in the late morning and mid-afternoon periods. Both species showed a late afternoon decline in feeding behavior. As expected, diademed sifakas showed a higher frequency of locomotion in each hour of the day relative to indri (Figure 3-10). Finally, locomotion decreased in frequency earlier in the day (after 13:00) for indri than for diademed sifakas.

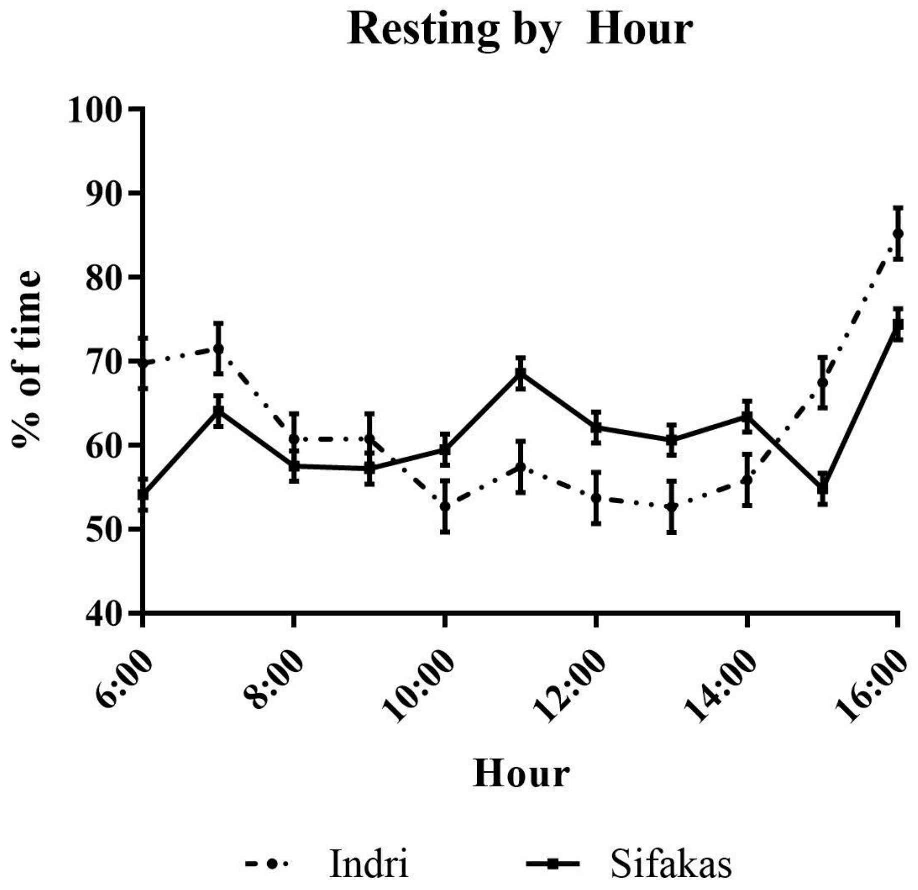

Figure 3-8. Mean hourly percent of scans for resting for indri and diademed sifakas

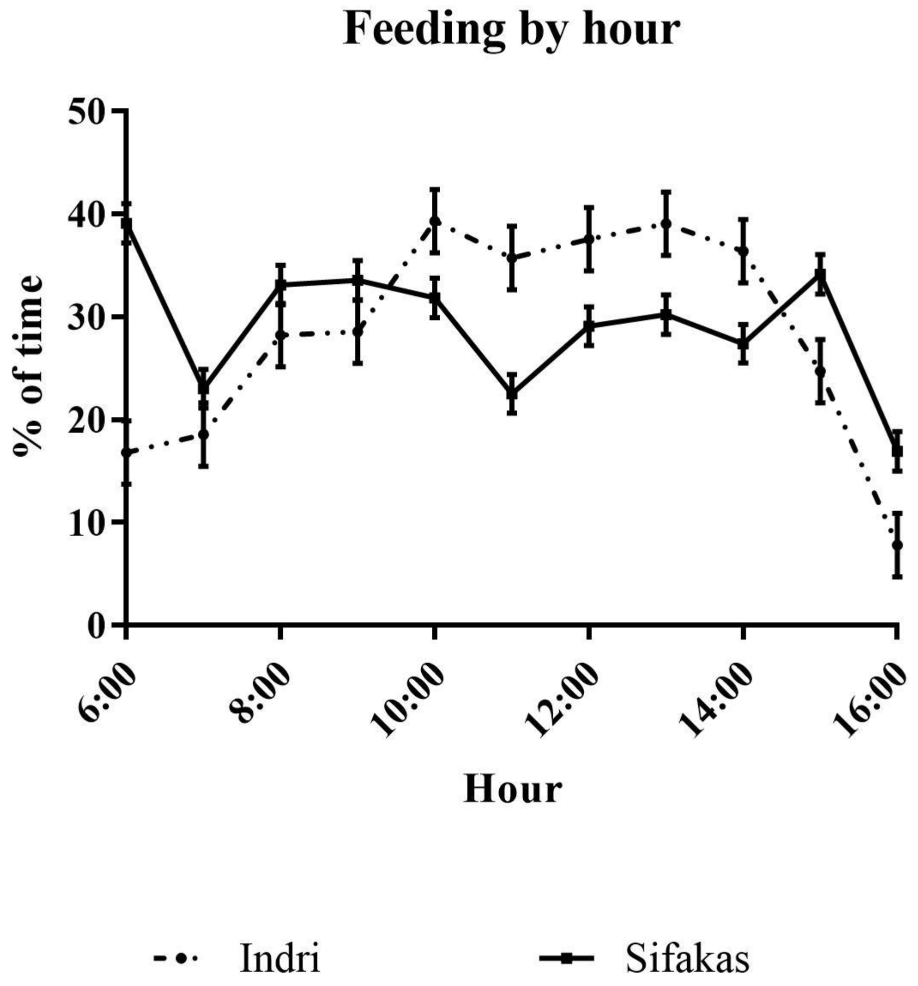

Figure 3-9. Mean hourly percent of scans for feeding for indri and diademed sifakas

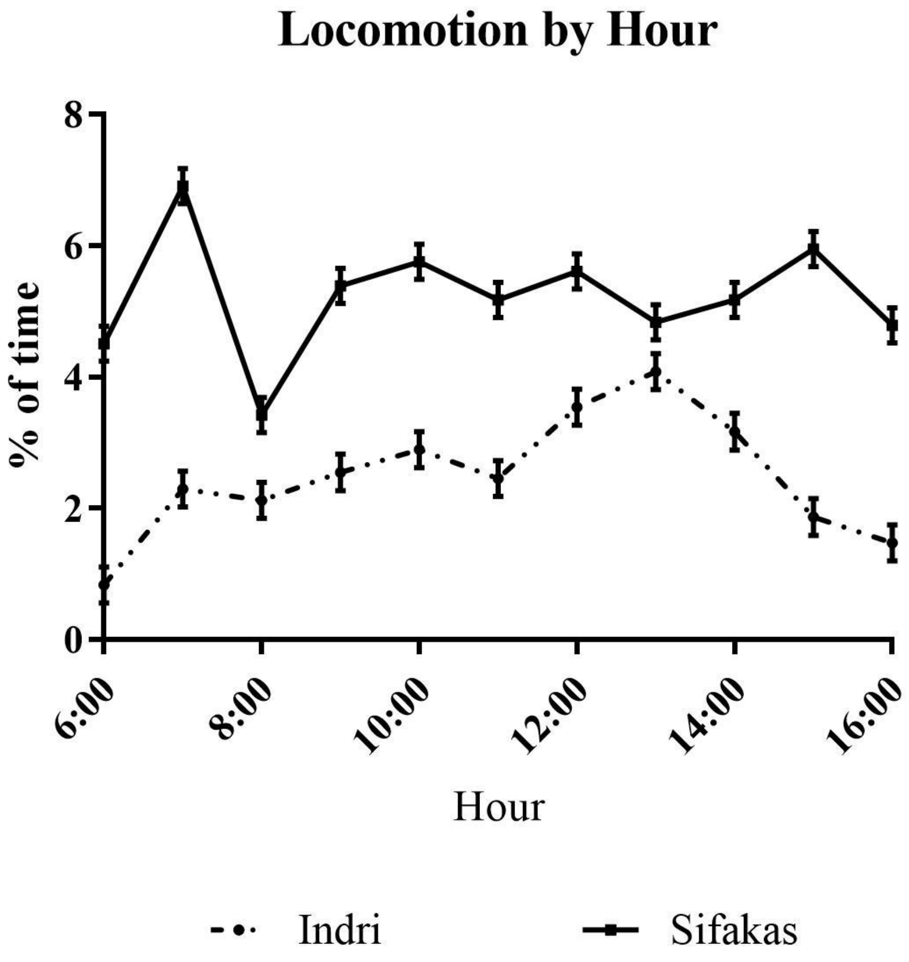

Figure 3-10. Mean hourly percent of scans for locomotion for indri and diademed sifakas.

3.5.6 Seasonal Fluctuations and Daily Active Period

Activity patterns varied throughout the year for both species. The shortest daily active period recorded for diademed sifakas was in June 2013 when they left their previous night's sleeping site at 08:00 and ended their day at the next sleeping site at 15:30 (7h 30min). The longest recorded active period was in October 2013. We located the focal group at 06:15, after they had already left the previous night's sleeping site and they entered their sleeping spot at 16:48 (minimum 10h 33min). On the two occasions that we followed a diademed sifaka group to their sleeping spot in the evening and found them still sleeping in the morning, they were in the same spot and did not appear to have moved during the night.

The shortest recorded active period for indri occurred in June 2013 and lasted 4h 15min (first movement recorded at 10:30 and entered sleeping site at 14:45). The longest active period occurred in December and was more than 10 hours in length. We were unable to follow the group to their sleeping site, but they first moved at 06:23 and were still active when we left them at 16:30. We did not observe indri to move before first light on any day. In all cases when we left an indri group in their sleeping spot and followed the same group the next day, individuals were predictably found in the same location on the same branch and did not appear to have moved.

3.5.7 Daily Active Period and Climatic Variables

I detected significant relationships between the length of the daily active period and the climatic variables of daily maximum temperature and rainfall. Diademed sifakas had longer daily active periods as the daily maximum temperature increased ($r^2 = 0.3566$, $F = 17.18$, $p = 0.0002$) (Figure 3-11) whereas active periods decreased on days with higher rainfall ($r^2 = 0.2004$, $F = 7.77$, $p = 0.009$) (Figure 3-12). Indri also had longer daily active periods as daily maximum temperatures increased ($r^2 = 0.478$, $F = 75.99$, $p < 0.0001$) (Figure 3-13) but no significant relationship was found between active periods and daily rainfall ($r^2 = 0.00052$, $F = 0.0434$, n.s.) (Figure 3-14).

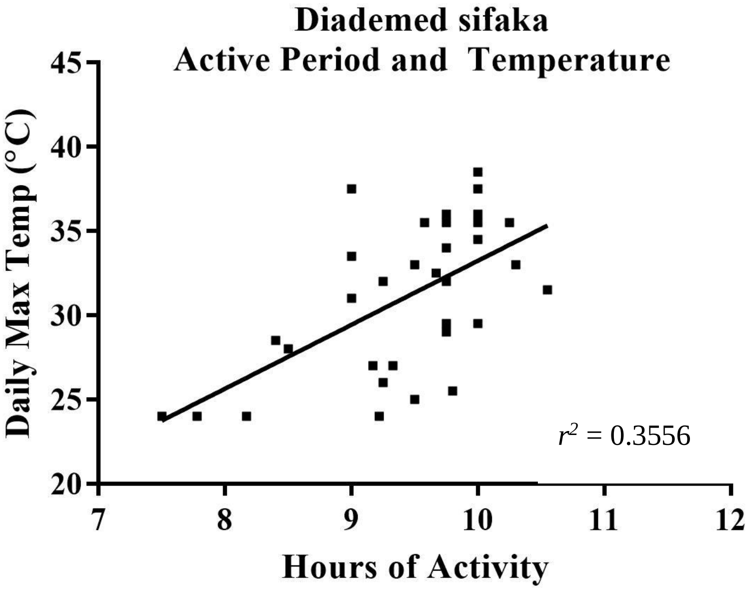

Figure 3-11. Linear regression of length of daily active period and daily maximum temperature for diademed sifakas (slope = 3.79 +/- 0.92).

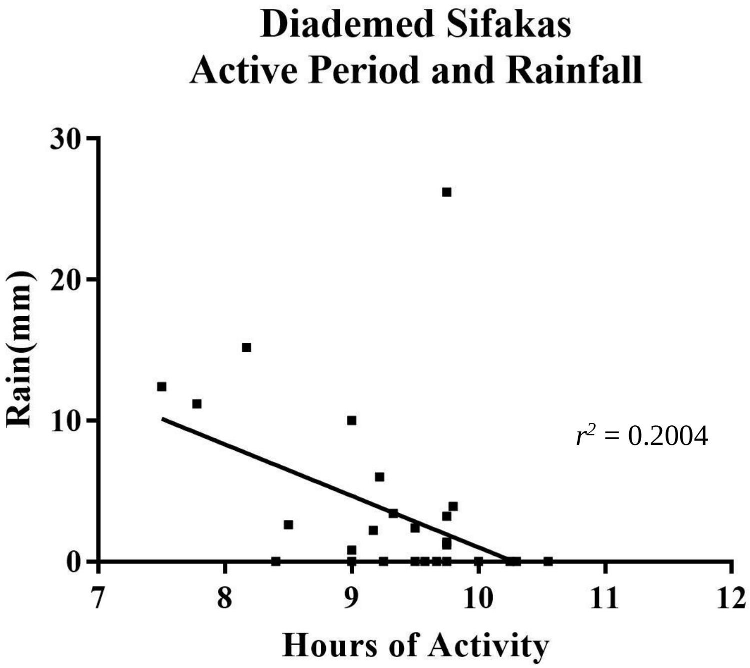

Figure 3-12**.** Linear regression of length of daily active period and daily amount of rainfall for diademed sifakas (slope = -.05 +/- 0.02).

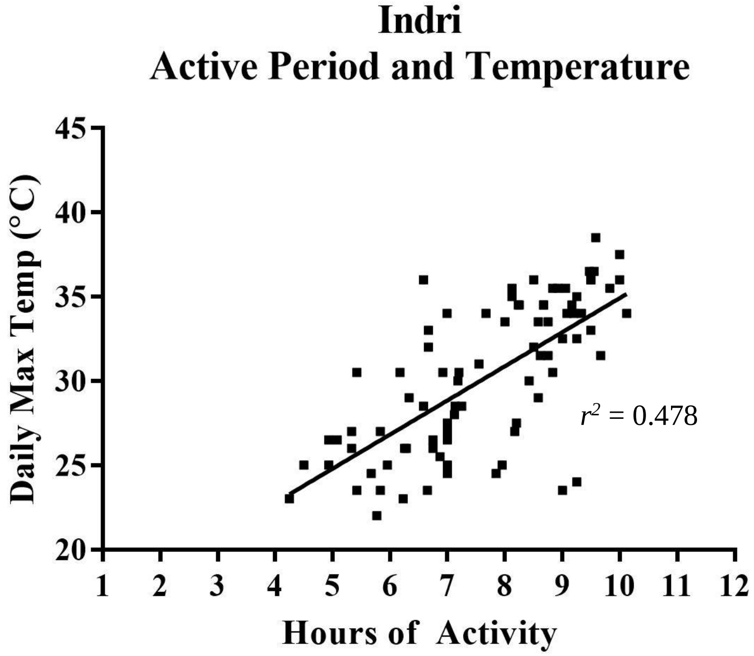

Figure 3-13. Linear regression of length of daily active period and daily maximum temperature for indri (slope = 2.02 +/- 0.23).

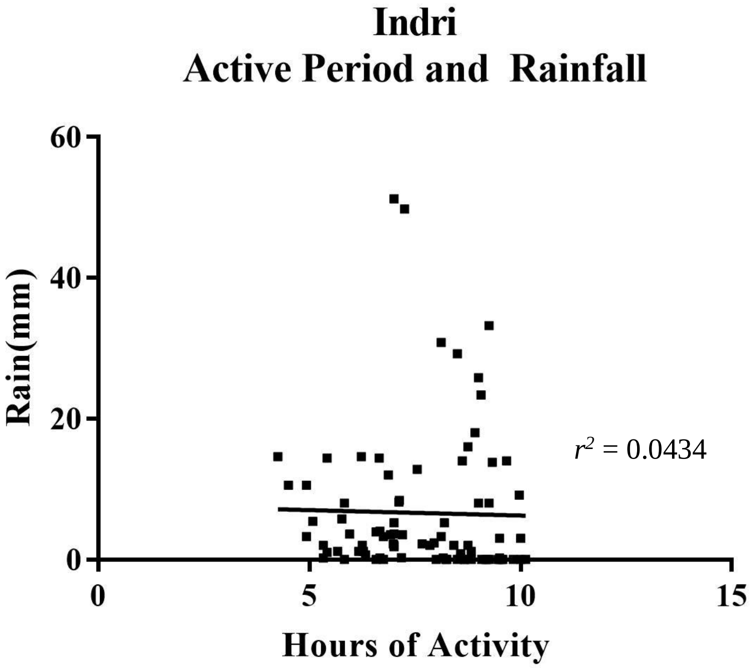

Figure 3-14. Linear regression of length of daily active period and daily amount of rainfall for indri (slope = -.003 +/- 0.02).

3.5.8 Vertical Stratification of Activity Patterns

Indri and diademed sifakas exhibited species-specific preferences for different vertical strata levels within the same habitats. Diademed sifakas used different canopy levels more frequently than indri that spent the majority of their time in the continuous canopy (Level 4) (Table 3-2). While both species spent the majority of time in the understory and continuous canopy, diademed sifakas utilized the ground and under canopy more often than indri. Indri spent the majority of their time in the continuous canopy, but also used the understory and emergent canopy. The two species also differed in their activities in each layer, particularly Levels 1 and Level 2. Indri only descended to the ground to feed, whereas diademed sifakas fed, sat, and played on the ground (Figure 3-15). We recorded no observations of indri in the underbrush layer (Level 2). They briefly moved between levels 1 and 3 through level 2 but these events were rare and were not captured during behavioral collection bouts.

Table 3-2. Percent of total time spent in different forest levels at BNR.

Forest Strata	Indri	Diademed Sifakas
Level 1	0.005%	2.08%
Level 2	0.00%	1.68%
Level 3	16.83%	34.70%
Level 4	71.10%	59.49%
Level 5	12.06%	2.05%

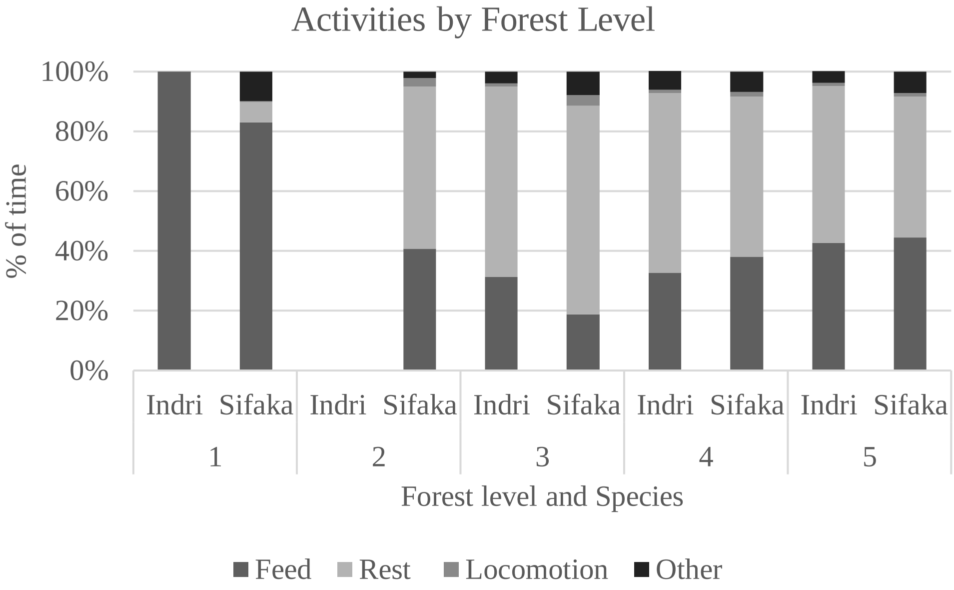

Figure 3-15**.** Comparison of activities in each forest level for indri and diademed sifakas at BNR.

3.5.9 Sex Differences in Activity Patterns

Indri males rested significantly more and fed significantly less than females when monthly means were compared (rest: t = 3.684, p = 0.0036, df = 11; feeding: t = 6.726, p < 0.0001, df = 11) (Table 3-3). I found no sex-specific significant differences for diademed sifaka resting or feeding (rest: t = 1.505, p = 0.1608, df = 11, n.s.; feed: t = 0.6863, p = 0.5068, df = 11, n.s.) but the overall trend was that females rested more and fed less than males (Table 3-4).

Table 3-3. Percent of time engaged in each behavior for indri adult females, adult males, and for all adults.

		Adult Female	Adult Male	All Adults
Rest	Mean:	58.26	61.85	60.06
	SD:	4.31	3.2	3.34
	Range:	52.75 - 67.68	56.41 - 67.36	56.72 - 66.75
Feed	Mean:	33.57	28.83	31.23
	SD:	4.35	3.86	3.94
	Range:	25.61 - 37.95	23.27 - 35.33	24.44 - 36.64
Locomotion	Mean:	2.4	2.84	2.59
	SD:	0.98	0.78	0.65
	Range:	1.1 - 4.18	1.35 - 4.18	1.84 - 3.76
Other	Mean:	9.15	6.39	7.8
	SD:	3.42	1.72	2.28
	Range:	6.52 - 19.79	3.29 - 9.09	4.98 - 14.06

Table 3-4. Percent time engaged in each behavior for diademed sifaka adult females, adult males, and for all adults

		Adult Female	Adult Male	All Adults
Rest	Mean:	63.13	60.07	61.6
	SD:	5.1	8.07	5.76
	Range:	54.93 - 71.11	41.51 - 71.93	48.22 - 70.79
Feed	Mean:	27.7	29.39	28.55
	SD:	4.51	9.06	5.74
	Range:	21.11 - 34.31	17.78 - 49.06	21.6 - 41.3
Locomotion	Mean:	5.52	6.3	5.91
	SD:	2.06	3.18	1.88
	Range:	1.59 - 7.83	2.56 - 13.33	3.22 - 9.77
Other	Mean:	3.65	4.24	3.94
	SD:	2.14	1.87	1.11
	Range:	0 - 7.69	1.54 - 7.65	1.65 - 5.71

3.5.10 Between-Site Comparisons

Overall, activity patterns correspond with previous studies at other sites. Indri and diademed sifakas spent the majority of their daily active period resting followed by feeding and locomoting (Blanchard 2007; Britt et al. 2002; Irwin 2006; Pollock 1977; Powzyk 1997). Powzyk (1997) reported that indri spent significantly more time resting and less time feeding than diademed sifakas.

Irwin (2006) reported the shortest active periods for diademed sifakas in June and July (~7h total active time) and the longest active periods from September through November (~11h total active time). While we were rarely able to leave a diademed sifaka group at their sleeping site and consistently find them before they moved the next morning at BNR, reports from Mantadia and Tsinjoarivo support the notion that diademed sifakas are a diurnal species (Blanchard 2007; Irwin 2006; Powzyk 1997).

For indri at Mantadia, Powzyk (1997) reported that the longest daily active period was in December 1994 (11h 6min) and the shortest day was in July 1994 (4h 6min). At Analamazaotra, indri have been reported to rest for up to 18 hours and day lengths ranged from 5 to 11 hours (Pollock 1975). Irwin (2006) and Powzyk (1997) reported similar patterns for diademed sifakas in relation to their daily active period and maximum temperature and rainfall. Powzyk (1997) found the same patterns for the daily active period of indri as it relates to maximum temperature and rainfall. Pollock (1975) reported a significant negative correlation between rainfall and daily active period in January and April, and a negative trend which was not statistically significant for the remaining months of the year. My findings at BNR were consistent with reports from Powzyk (1997) that, when an indri group was left at their sleeping site in the evening and found the next day, they had not moved during the night. To summarize, all of my observations at

BNR support the notion that indri and diademed sifakas are diurnal which is consistent with previous reports (Blanchard 2007; Irwin 2006; Pollock 1975; Powzyk 1997).

Irwin (2006) and Powzyk (1997) reported that female diademed sifakas spent significantly more time feeding than males. At BNR, males spent slightly more time feeding overall (1.69%) but also had a wider range of variation when compared to females.

3.6 Discussion

As predicted, indri and diademed sifakas exhibit interspecific differences in 1) overall activity patterns, 2) variation in activities throughout the day, and 3) their vertical use of the forest as it relates to different activity patterns. Diademed sifakas spent more time engaged in locomotion than indri, had a longer daily active period, and spent more time in lower forest levels than indri. They also moved more in all hours of the day, with the exception of between 10:00 and 14:00 when indri fed more and rested less than sifakas. These activity differences correspond with a primate-wide relationship between activity and diet whereby activity decreases as folivory increases (Clutton-Brock and Harvey 1977). Additionally, in an analysis of 22 primate species, Powzyk (1997) found a strong correlation between time spent resting and percent of leaves in a primate species' diet. These activity differences and dietary differences (discussed in Chapter 4) are strategies used by these two confamilial indriids to maintain coexistence at BNR and other sites where they are sympatric.

3.6.1 General Activity Patterns

Results from this study confirm indri and diademed sifakas activity patterns as reported from other sites in which resting was the most commonly observed behavior for both species followed by feeding. Locomotion and "other" behaviors accounted for a relatively small proportion of scans. Although predictions related to species-specific differences in amount of time spent resting and feeding were not supported, diademed sifakas did engage in locomotion significantly more often than indri as predicted.

Powzyk (1997) reported that indri spent significantly more time resting and feeding than diademed sifakas at Mantadia, and that diademed sifakas spent significantly more time traveling than indri. The discrepancy in resting and feeding between the current study and reports from Powzyk (1997) may be linked to the length of all-day follows between the two studies. At BNR, the terrain is steep and uneven. Due to safety concerns, we did not travel off trails in most areas before sunrise and after sunset. This impacted our ability to follow groups from sleeping site to sleeping site when they were active far from trails or in steep areas early in the morning and in the late afternoon and was particularly problematic when following diademed sifakas as their daily active period often continued longer than we were able to safely follow them. Intraspecific comparisons of the hourly rates of resting, feeding, and locomotion throughout the day illustrate the pattern that diademed sifakas rested less frequently but fed and moved more often than indri in the earliest and latest hours of the day. However, indri engaged in locomotion more often than diademed sifakas during August. After further investigation, it is likely that this can be attributed to temperature and rainfall on the days each species was followed during that month. Average temperature was lower and rainfall was higher on days when diademed sifaka were followed (diademed sifakas, temp: 24ºC, rainfall: 10.6 mm/day) than on indri follow days (indri, temp: 25ºC, rainfall: 7.1 mm/day). In Chapter 5, I present daily path length (DPL) as another measure of indri and diademed sifaka travel patterns to further understand the difference in energy expenditure between these two species.

Activity rates in the three diademed sifaka groups represented in this study were compared with the activity rates from both continuous and fragmented habitats at Tsinjoarivo. All three groups at BNR resided primarily in the primary forest, but entered secondary and disturbed forest on occasion. While diademed sifakas were observed near the forest edge, none were observed to leave the boundary of BNR. Rates of resting, feeding, and locomotion were more similar to the activities of the continuous forest groups at Tsinjoarivo (Irwin 2006). This followed my expectations, as all the home ranges of the BNR study groups were within the boundaries of the reserve in continuous forest. Irwin (2006) also reported that the diademed sifakas at Tsinjoarivo (54.48%) rested more than those at Mantadia (43.65%), and that the diademed sifakas at Tsinjoarivo consumed a higher proportion of foliage (53.1%) than the same lemur species at Mantadia (42.1%) (Irwin 2006; Powzyk 1997; Powzyk and Mowry 2003). Diademed sifakas at BNR consumed more foliage and spent more time resting that at Mantadia and Tsinjoarivo, which is congruent with the expected relationship between activity and amount of dietary foliage. A similar pattern occurred for indri in which indri at BNR spent more time resting and consumed more foliage than at Mantadia (Powzyk 1997; Powzyk and Mowry 2003). This demonstrates that each species exhibits some degree of behavioral and dietary flexibility between sites.

3.5.2 Daily Active Period, Temperature, and Rainfall

Increase in daily active period coincident with rising temperatures has been previously reported for indri (Blanchard 2007; Powzyk 1997) and diademed sifakas (Irwin 2006; Powzyk 1997). I confirmed this pattern for both species at BNR. Indri exhibited less variation in their DAP relative to rainfall than diademed sifakas overall. On one full-follow day, diademed sifakas appeared to have a long DAP on a day with heavy rainfall. When this day was examined more closely, rainfall only occurred rarely during the period of data collection. Rainfall measures were collected every 24 hour so this outlying data point is the result of heavy rainfall in the absence of researchers.

The patterns found in the current study were consistent with the activity patterns found in lemurs whereby they decrease their activity during cold and rainy months to conserve energy (Schmid and Kappeler 1998; Wright 1999). So, while this does not necessarily represent a coexistence strategy, it does demonstrate an intraspecific strategy for coping with seasonality at BNR and throughout their species' ranges.

3.5.3 Intraspecific Comparisons Between Males and Females

Female dominance is common in lemurs in general and has been found in indri and diademed sifakas, specifically (Pollock 1975; Pollock 1979; Powzyk 1997). One explanation for female dominance is that females require priority of access to food sources to increase reproductive success in Madagascar's highly seasonal environment (Hemingway 1999; Hemingway and Bynum 2005; Wright 1999). At BNR, indri females fed more and rested less than males, but this pattern was not found for diademed sifakas. During the period of data collection, females in three out of the six indri groups had infants and two groups contained one juvenile each. Only one of the three diademed sifaka groups had a juvenile and no females gave birth during the study period. One explanation for the sex differences in indri but lack thereof in diademed sifakas found in this study may be due to the lack of energetic demands from reproduction for diademed sifakas. Additional longitudinal data on indri and diademed sifakas are needed to better understand sex differences in the activity patterns of these sympatric indriids in order to determine the degree to which reproductive energetic costs impact lemur activity budgets.

3.6 Conclusions and Future Directions

Summary of main findings:

- Resting and feeding were the most common activities for both species;
- Diademed sifakas spent more time engaging in locomotion than indri;
- Diademed sifakas had longer daily active periods than indri;
- Intraspecifically, group behaviors did not significantly differ;
- Both species increased their daily active period as temperature increased;
- Indri spent more time in the continuous and emergent canopy levels of the forest than diademed sifakas;
- Diademed sifakas used a greater range of forest strata than indri. They spent >50% of their time in the continuous canopy level, but also spent more time than indri in the lower levels of the forest. They also used the ground level for both feeding and playing whereas indri only came to the ground rarely to feed.

There are a few potential weaknesses in my study which should be addressed in future investigations of indri and diademed sifakas. For example, it was necessary to combine travel and move into a single "locomotion" category during this study because visibility was difficult-to-impossible when animals moved over long distances. When a group traveled quickly, it was rarely possible to maintain visual contact for more than a few seconds. This is primarily due to the steep terrain and high tree stem density at BNR and other areas of eastern lowland rainforest in Madagascar relative to other types of rainforest (Armstrong et al. 2011). The behavior "travel" changed to "not visible" as soon as we lost visual contact. Another challenge occurred when diademed sifakas fed in trees with lianas or in an area with many lianas, and moved in and out of visual contact with observers. We only recorded behaviors when animals were visible enough to confidently assess behaviors, and defaulted to recording “not visible” when visibility was impaired. Another improvement to the study design would be to conduct all-day follows for sifakas. We were unable to follow them from sleeping site to sleeping site so had to create an arbitrary cutoff regarding what constitutes a full day. More widespread use of GPS collars would be particularly useful for studying diademed sifakas, as we were rarely able to follow them from sleeping site to sleeping site. GPS collars would also facilitate tracking of indriid activity patterns at night so that one could definitively address whether or not these species exhibit any degree of cathemerality.

In order to more fully understand the activity budgets of indri and diademed sifakas at BNR, further longitudinal data collection is necessary. Since no diademed sifaka infants were born during the study, we lack an understanding of the energetic requirements of females and if females with dependent infants adjust their activities relative to females without infants or adult males. A long-term study of these groups and others in the reserve will also enhance our understanding of inter-annual variation in activity cycles and how that variation relates to factors including presence or absence of infants, fluctuations in resource availability, and differences in temperature and rainfall from year to year.

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Chapter 4: Dietary diversity and feeding patterns of *Indri indri* and *Propithecus diadema* in Betampona Nature Reserve, Madagascar

4.1 Introduction

In this chapter, I present a comparative analysis of the feeding behavior of two confamilial species of lemur – indri (*Indri indri)* and diademed sifaka (*Propithecus diadema*). The objectives of this chapter are to 1) describe the overall feeding patterns of each species, 2) quantify the degree of resource overlap between species, 3) identify seasonal differences in feeding preferences, and 4) discuss species-specific foraging preferences such as time of day, and forest level during feeding. Comparisons are made with previous published reports of indri and diademed sifaka feeding behavior.

All primates must make choices regarding the foods they consume. Each choice has costs and benefits related to resource availability/abundance and the nutritional benefit gained from these resources. For example, plants that provide a substantial nutritional and energetic contribution to an animal may also contain secondary toxins that require specific adaptations to neutralize (Lambert 1998; Lambert and Rothman 2015). Another consideration is where to forage as primates foraging on fallen fruit on the ground may be at greater risk of predation (Lambert and Rothman 2015). Primates may also face dietary constraints due to seasonal variation in food availability and competition from other animals (Lambert and Rothman 2015; Wright 1999).

Different plant parts provide varying amounts of fiber, fat, protein, sugar, and plant secondary metabolites. Generally, leaves are higher in protein and fiber whereas reproductive plant parts (fruits and seeds) tend to contain less protein and fiber but more fat and sugar (Lambert and Rothman 2015). Flowers tend to have moderate levels of fiber and sugar with protein levels close to that of leaves (Lambert and Rothman 2015; Oftedal 1991) These are, however, generalizations and both inter- and intraspecific variability in nutritional content has been reported (Chapman et al. 2003; Lambert and Rothman 2015). Nutritional content of specific food items is discussed later in this chapter.

Food selection and nutritional intake impact nearly all aspects of primate behavior including activity patterns, daily path length, home range size, territoriality, and sociality (Chapman and Pavelka 2005; Milton 1980; Oates 1987; Powzyk 1997; Sussman 1977). Fruits and seeds contain more easily digestible carbohydrates and sugars, which coincides with observations that frugivorous primates have longer day ranges and home range sizes (Clutton-Brock and Harvey 1977). In contrast, leaves require more energy to digest. This pattern is supported by observations that, the higher proportion of leaves in a primate species' diet, the shorter the species' daily path length and home range size (Clutton-Brock and Harvey 1977).

Sympatric, folivorous primates are found in many environments throughout the world and use a variety of strategies to maintain coexistence. The three main coexistence strategies for ecologically similar species are 1) divergence in dietary preferences, 2) differential habitat use, and 3) temporal avoidance (Chase and Liebold 2003; Pianka 2000; Schoener 1986). Sympatric primates generally coexist using a combination of these non-mutually exclusive strategies. One common coexistence strategy for sympatric folivorous primates, as it relates to dietary profiles is that one species will often consume more leaves and expend less energy throughout the day while the diet of the other species will include more non-leaf items such as fruits, seeds and flowers (Clutton-Brock and Harvey 1977). Primate that consume more fruits, seeds and flowers travel more and expend more energy, as those food types are easier to digest and more energy dense than leaves (Lambert 1998). Essentially one species (in this study, indri)is more of an "energy minimizer" (Milton 1998) while the other is an "energy maximizer" (diademed sifakas) (Terborgh 1983). Dietary overlap can, and often does, occur between sympatric folivores as long as that resource is not limited in supply and necessary for the survival of both species (Schoener 1974; Schoener 1986; Tokeshi 1999).

As outlined in Chapter 1, indri and diademed sifakas are anatomical folivores. Each species has specialized morphology that correlates with their specific dietary preferences. Indri have morphological features that indicate an increased specialization for a folivorous diet relative to diademed sifakas (Chapter 1). Previous research on these two-species described their diets as primarily folivorous, but indri have been reported utilize fewer plant species than diademed sifakas (Blanchard 2007; Britt et al. 2002; Irwin 2008; Powzyk 1997; Powzyk and Mowry 2003). Additionally, diademed sifakas are reported to consume a higher proportion of fruits, flowers, and seeds whereas indri specialized in the consumption of young leaves (Blanchard 2007; Powzyk 1997; Powzyk and Mowry 2003). This difference in the proportion of plant parts along with the greater dietary diversity of diademed sifakas relative to indri is considered a coexistence strategy as it reduces competition for food resources (Powzyk 1997; Powzyk and Mowry 2003). In this chapter, I aim to describe how factors related to the dietary profiles of these confamilial allow for coexistence while minimizing resource competition.

4.2 Hypotheses and Predictions

When primates with similar dietary patterns coexist, they avoid resource competition via niche partitioning. One of the most common niche partitioning strategies in sympatric primates is differing dietary profiles, particularly when two primate species consume the same type of resource (i.e. fruits, leaves, seeds, etc) (Schreier et al. 2009). Cranial and digestive morphology can be used to predict the dietary profiles of primate species (Milton 1981). Primates that are more folivorous tend to have less catholic diets than those species that consume a higher proportion of fruits and seeds in that more folivorous primates tend to feed from fewer plant species and feed primarily from trees rather than from lianas and epiphytes (Milton 1980; Milton 1981). More folivorous primates also tend to spend most of their time in the continuous canopy because that is where the majority of young leaves are located whereas more frugivorous primates use all levels more uniformly and travel to the ground more often to feed from food items such as fallen fruits (Porter 2001; Singh et al. 2011). Indri morphology indicates that they are more specialized folivores than diademed sifakas (Hill 1953; Kay and Hylander 1978; Powzyk 1997; Viguier and Tort 2000). I hypothesize that, if primate-wide trends regarding the relationship between morphology and diet are consistent for indri and diademed sifakas, then niche differentiation strategies as they relate to diet can be predicted from their differences in morphology. I have formulated the following predictions regarding the dietary profiles for these two species at BNR based on the primate-wide trends outlined above and on the patterns observed at other sites for these species.

H_1: While the morphology of both diademed sifakas and indri indicates that they are both folivorous, indri are more highly specialized, morphologically for a diet high in leaves. Animals with morphology specialized for the digestion of leafy material tend to consume fewer overall plant species than those animals that consume a higher proportion of fruits of seeds.

P$_{1.1}$: Leaves will comprise a significantly higher proportion of the diet of indri than that of diademed sifakas whereas the diademed sifaka diet will include higher proportions of fruits, seeds, and flowers.

P$_{1.2}$: Diademed sifakas will exploit non-tree food sources such as lianas, epiphytes, and ferns more often than indri.

P$_{2.3}$: Diademed sifakas will consume a greater overall number of plant species than indri.

H$_{2}$: Among most sympatric, folivorous primates, dietary overlap is most common in consumption of leaves. Indri and diademed sifakas will overlap in the consumption of leaves more often than fruits, flowers, and seeds.

P$_{2.1}$: Resource overlap whereby indri and diademed sifakas consume the same plant part from the same plant species will occur more often in young leaves than fruits, flowers, and seeds.

P$_{22}$: Overlapping resources will be abundant in the forest.

H$_{3}$: Food availability has been reported to fluctuate throughout the year in eastern Madagascar (Wright 1999). If this seasonal trend in resource availability occurs at BNR, then indri and diademed sifakas will exhibit temporal variation in relation to the abundance of that resource.

P$_{3.1}$: Indri and diademed sifakas will demonstrate differences in plant parts consumed throughout the year relative to the abundance of those parts in the forest.

H_4: Indri and diademed sifakas express different preferences regarding their use of forest stratigraphic levels (Chapter 3). If they express differences in vertical stratification while feeding, they will also express differences on the types of plant parts consumed while in these different forest levels.

> **$P_{4.1}$:** Diademed sifakas will feed in all stratigraphic levels of the forest, whereas indri will primarily feed in the low canopy and continuous canopy levels.

4.3 Methods

We recorded all occurrences of feeding by any visible individual in the group during all-day follows. The following variables were noted at when a new feeding tree, liana, fern, or other food source was observed: time of day, GPS coordinates, common name (and scientific name if known), plant part consumed, individuals feeding, diameter at breast height (DBH), and tree height in meters. If a tree was fed from multiple times throughout the study, we recorded all the aforementioned variables except DBH and tree height. The DBH and height of non-trees (e.g. lianas, ferns, hemi parasitic plants, and epiphytes) was not recorded. We also noted the phenological status (young leaves, mature leaves, flowers, and fruits) of the food source when possible on a scale of 0 (absence) to 4 (maximum amount of food item) (Chapman et al. 1994). Plant parts were divided into the following categories: young leaves, mature leaves, leaf petioles, fruits, flowers, and seeds (Table 4-1). The categories of flower buds and flowers were combined, as some flowers were so small that we could not reliably distinguish between the two categories. In these cases, samples were unable to be obtained. Non-vegetative food items were classified as soil and bark (Table 4-1).

Table 4-1. Definitions of plant parts and non-vegetative food items consumed by indri and diademed sifakas at BNR

Plant Part	Definition
Young Leaves	New leaves or leaf buds. Generally more pliable than the mature leaves of the same species
Mature Leaves	Mid to old leaves. Generally darker and more rigid when compared to young leaves of the same species
Fruit	Outer layer and fleshy pulp is consumed
Flower	Both flower buds and open flowers
Seed	Seed only consumed. Fruit flesh recorded separately
Petiole	Stalk of the leaf
Bark	Outermost layer of the tree trunk and branches
Soil	Consumption of earth

Trees were identified based on extensive inventories of the tree species present as well as with the help of experienced guides and two local botanical experts (Armstrong 2009; Armstrong et al. 2011). Lianas were identified by common name when possible, but many remained unidentified. One hemi parasitic plant, *Bakarella clavata*, was identifiable but all other epiphytes, hemi parasitic plants, and ferns were identified to local name, when possible. Due to the difficulty in identifying epiphytes from hemi parasites in this forest, I lumped these two categories into the term “epiphyte”.

Armstrong et. al. (2011) inventoried tree species in Betampona by surveying 100 ten-meter circular plots in randomly chosen locations throughout the reserve and catalogued all trees > 5cm DBH. They then calculated indices of abundance (A_i), frequency (F_i), dominance (D_i), and importance value (IVI_i) for each tree species using the following formulas (from Armstrong et. al. 2011).

$$A_i = \frac{stem\ count\ of\ species\ i}{stem\ count\ of\ all\ species}$$

$$F_i = \frac{occurrence\ of\ species\ i\ in\ plots}{occurrence\ of\ all\ species\ in\ plots}$$

$$D_i = \frac{basal\ area\ of\ species\ in\ (\frac{m^2}{ha})}{total\ basal\ area\ of\ species\ in\ (\frac{m^2}{ha})}$$

$$IVI_i = (A_i \text{ x } 100) + (F_i \text{ x } 100) + (D_i \text{ x } 100)$$

I calculated dietary niche breadth both monthly and for the entire study period for indri and diademed sifakas using Levin's Measure B (Krebs 1999) using the following formula:

$$B = \frac{1}{\sum p_i^2}$$

where p_i is the proportion of species i in the diet. This was then standardized on a 0 to 1 scale using the formula

$$B_A = \frac{B - 1}{n - 1}$$

where B_A is the standardized niche breadth, and n is the total number of food species consumed. Dietary overlap was defined as any instance when both indri and diademed sifakas fed from the same plant part from the same plant species. This overlap was calculated both annually and monthly using Pianka's (1986) measure of overlap:

$$O_{jk} = \frac{\sum p_{ij}\, p_{ik}}{\sqrt{\sum p_{ij}^2\, p_{ik}^2}}$$

where O_{jk} is the measure of overlap between species *j* and species *k*, p_{ij} is the proportion that resource *i* is of the total resources used by species *j*, and p_{ik} is the proportion that resource *i* is of the total resources used by species *k*. Pianka's measure ranges from 0 (no resource overlap) to 1 (complete resource overlap) (Pianka 1986).

I collected phenological data each month from March through November 2013 (N = 540 trees, 35 genera, 42 species). I used the 9-month phenological data set to determine the availability of fruits, flowers, and young leaves for specific indri and diademed sifaka feeding trees when possible. Both data sets yielded the same phenological patterns (i.e. fruit, flower, and young leaf availability increased or decreased in the same months).

Due to the lack of phenological data from December 2013 to March 2014, I calculated overall resource availability by using phenological data collected at BNR by Sarah Federman over a two-year period (September 2013 to September 2015) (N = 899 trees, 23 genera, 27 species) (Federman, unpub. data), who granted permission for use of this data set. Phenological status was recorded on a scale from 0 (absence of the resource) to 4 (full abundance of the resource type) for young leaf, fruit, and flower availability for both data sets (Chapman and Wrangham 1994).

I used the focal animal sampling data set (Chapter 2) to examine differences in feeding in each forest level. Vertical stratification preferences were determined by calculating the percent of feeding time spent in each level (1 = ground, 2 = underbrush, 3 = below continuous canopy, 4 = continuous canopy, 5 = emergent canopy) ((Richards 1966). I then calculated the proportion of time that indri and diademed sifakas spent feeding on each plant part in each vertical stratification level and compared this between lemur species.

Data Analysis

Data were tested for normality before each analysis to determine the appropriate use of parametric versus non-parametric statistical tests. I used a chi-square test to examine between-species differences in the proportions of plant part consumed and for the type of food source (tree, liana, epiphyte, fern, soil). When the chi-square test showed a significant between-species difference in the proportion of plant parts or plant types in the diets of indri and diademed sifakas, I used the z test for proportions to determine exactly which differences conferred statistical significance. Temporal patterns of resource use relative to the abundance of that food type were examined using Spearman's rank-order correlation coefficient (r_s) between food type consumed and the availability of that food type each month. Differences were considered statistically significant for all analyses when $p \leq 0.05$.

4.4 Results

We conducted 150 indri and 59 diademed sifaka all-day follows and a total of 1301 contact hours with indri and 605 contact hours with diademed sifaka. During this time, we observed 3067 feeding occurrences (indri: N = 1954 and diademed sifaka N = 1113). This includes feeding on vegetative items (young leaves, mature leaves, leaf petioles, fruits, and flowers) as well as non-vegetative items (bark and earth). Each feeding instance was treated as an independent event. Identification was not possible in all instances. Lianas were the most commonly unidentified plant type (N = 120 feeding instances). We also recorded 37 instances of feeding on unidentified trees. A full list of identified plant species consumed, plant parts consumed, and number of feeding instances is provided in Appendix 1.

4.4.1 General Feeding Behaviors

Both lemur species consumed varying amounts of young leaves, mature leaves, fruits, flowers, seeds, petioles, bark, and soil each month. Neither species drank water during our observations. Both species plucked flowers directly from branches by using their mouths. Indri used their mouths to pick the leaf or flower with their teeth then ate the item from the base to the tip, between their canines and premolars (Figure 4-1). Diademed sifakas primarily consumed leaves from the tip to near the base. Like indri, they almost exclusively used their mouths for this. When necessary, both species used their hands to pull distant branches closer toward themselves to collect food items with their mouths.

These lemur species exhibited similar food processing behavior when consuming fruits and seeds. They used their mouths to acquire fruit. Small fruits were consumed whole. They held larger fruits in their hands while using their incisors or premolars to penetrate the exocarp and peel it away. Then either the fruit flesh, seed or both were consumed. As seed predators, most seeds were masticated before they were swallowed.

Other items that comprised a small proportion of both species' diets included leaf petioles, bark, and soil. Both indri and diademed sifakas consumed leaf petioles meaning that they only ate the leaf stem and let the remaining leaf fall to the ground. They also consumed bark from tree trunks by first biting into the bark then peeling it off in strips and eating it. Trees from which bark was consumed were small to medium in diameter and individuals would consume bark from the entire circumference of the tree. We also observed geophagy for both species. In these instances, animals traveled to the ground or sat on the roots of a fallen tree. In all observations, the soil consumed was either from around the roots of a fallen tree or from freshly exposed soil after a small landslide. They did not dig into the leaf litter to consume soil. No observations were made of feeding on mushrooms, insects, or other animals. Occasionally an individual would swat at a biting fly or other insect but we did not observe consumption of these insects although it is possible that they occasionally do consume these insects.

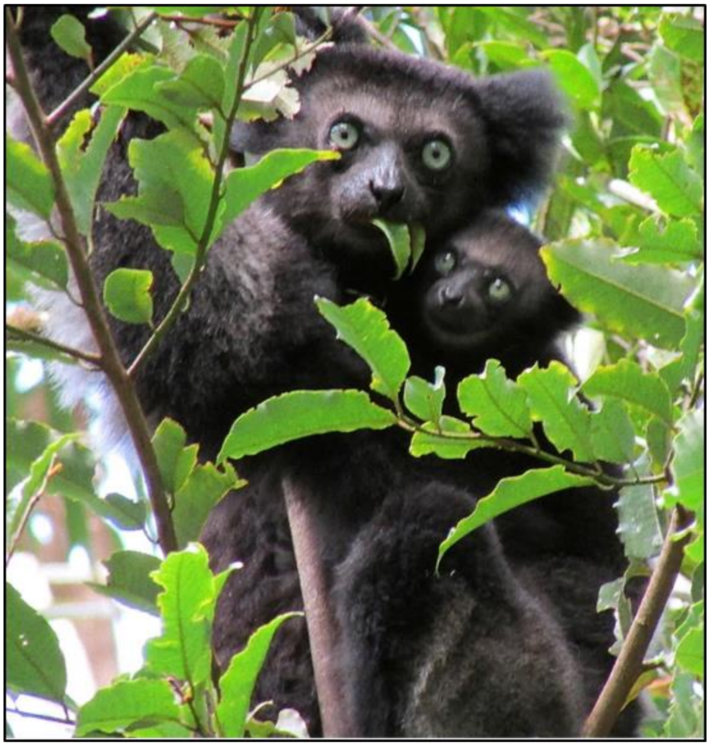

Figure 4-1. Adult female indri feeding on a young leaf from base to top at BNR (Photo by Lana Kerker Oliver).

4.4.2 Dietary Profiles of Indri and Diademed Sifakas

Young leaves comprised the highest proportion of both indri and diademed sifaka diets. However, leaves comprised a statistically higher proportion of the indri diet when compared to diademed sifakas ($z = 7.268$, $p \leq 0.001$) (Table 4-2). Bark also comprised a significantly higher proportion of the indri diet than that of diademed sifakas ($z = 3.9937$, $p \leq 0.001$) (Table 4-2).

Conversely, diademed sifakas consumed a significantly higher proportion of fruits and seeds relative to indri (fruit: z = -9.8491, $p \leq 0.001$; seed: z = -5.0282, $p \leq 0.001$) (Table 4-2). No statistically significant differences were found for the consumption of soil, flowers, mature leaves, or petioles (Table 4-2).

Table 4-2**.** Percent of feeding occurrences by lemur species and resource type

	Bark**	**Soil**	**Flower**	**Fruit****	**Seed****	**Mature Leaf**	**Young Leaf****	**Petiole**
Indri	**1.78**	1.12	7.44	3.36	3.31	2.29	**79.26**	1.12
Diademed Sifaka	0.18	1.43	6.61	**12.60**	**7.33**	3.40	67.47	0.45

** indicates a significant between-species difference where $p < 0.001$.

While both species fed primarily from trees, diademed sifakas fed from a wider variety of plant types than indri. The diademed sifaka diet contained significantly higher proportions of epiphytes, ferns, and lianas relative to indri (epiphytes: z = -6.7813, $p < 0.001$; ferns: z = -2.6517, p < 0.00l; lianas z = -17.9926, $p < 0.001$ respectively) (Table 4-3). The combination of epiphytes, ferns, and lianas comprised 19.1% of the diademed sifakas diet and only 0.06% of the indri diet (Table 4-3). The proportion of trees in the indri diet (98.3%) was significantly higher that of diademed sifakas (79.4%) (z = 17.9926, $p < 0.001$). No significant differences were found in the proportion of soil in the diet of either species (z = -0.7503, $p > 0.05$, n.s.).

Tree versus non-tree feeding varied throughout the year. Indri fed nearly exclusively from trees but fed on an epiphyte once in February 2014, and from lianas in June to July and from October to December (

Figure 4-2). Diademed sifakas exhibited much more variation in the types of plants consumed. They primarily fed from trees, but were observed to increase their frequency of feeding from epiphytes and lianas from May through August (Figure 4-3).

Table 4-3. Proportion of different resource types consumed by indri and diademed sifakas.

Resource Category	**Indri**	**Diademed sifaka**
Soil	1.1%	1.4%
Epiphyte**	0.1%	**2.5%**
Fern**	0.0%	**0.4%**
Liana**	0.5%	**16.3%**
Tree**	**98.3%**	79.4%

** indicates a significant between-species difference where p <0.001

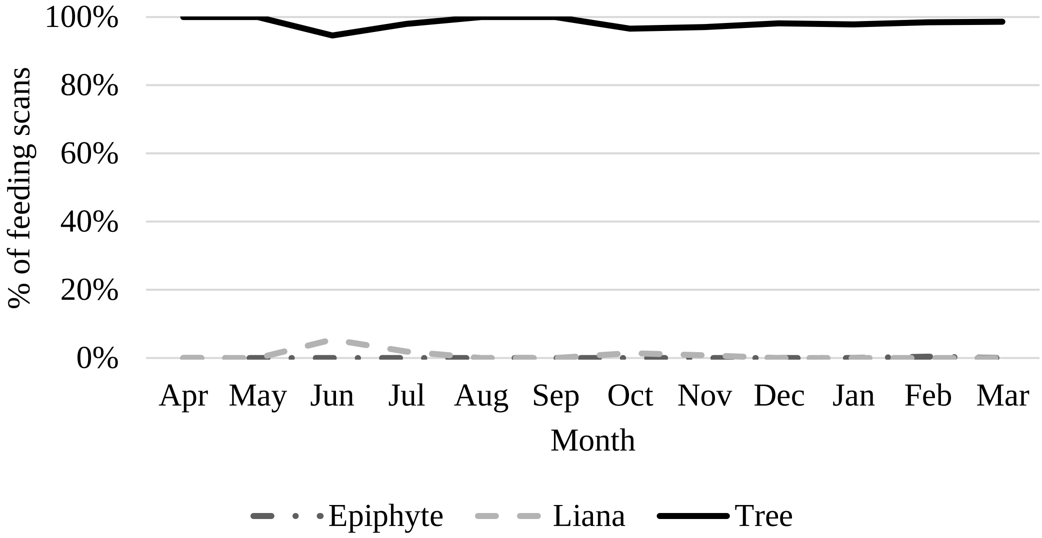

Figure 4-2. Indri feeding from different plant types throughout the year.

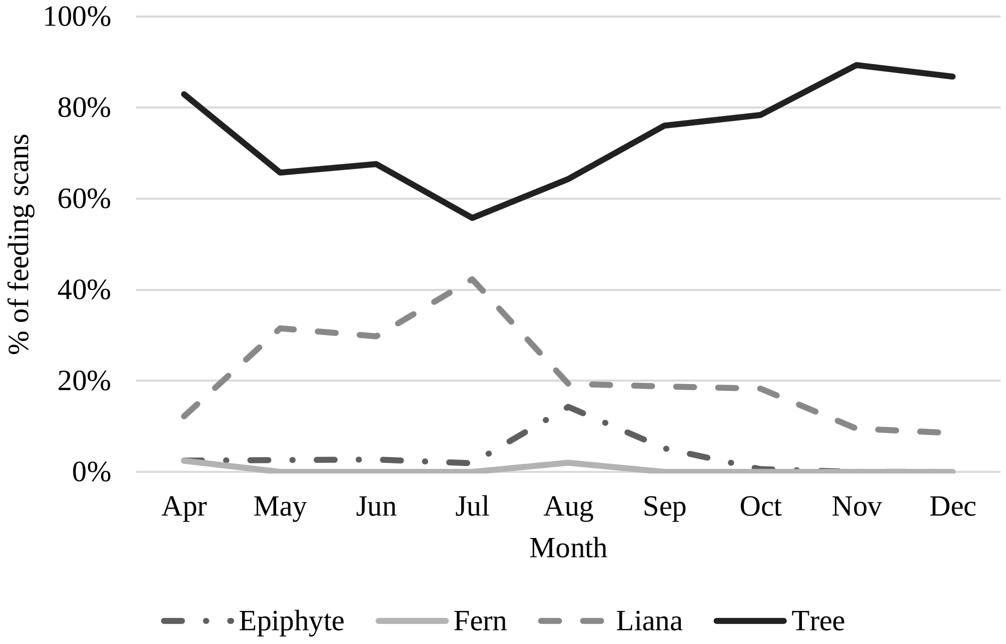

Figure 4-3. Diademed sifaka feeding from different plant types throughout the year.

Diademed sifakas consumed a larger number of plant species (N = min 127 species) than indri (N = min 67 species). These numbers are underestimations of actual dietary diversity as they exclude some unidentified lianas, ferns, and trees. Unidentified feeding occurrences for diademed sifakas included 114 instances of feeding on lianas, 20 feeding events from trees, and four ferns. For indri, we recorded 17 instances of feeding from unidentified trees and six unidentified lianas.

The top 10 food sources for indri comprised 60.8% of the overall indri feeding (Table 4-4) whereas the top 10 food sources for diademed sifakas comprised 47.7% of feeding records (Table 4-5). Only two plant species, *Symphonia pauciflora* and *S. louveli*, are in the top ten preferred food sources for both indri and diademed sifakas.

Diademed sifakas exhibited greater diversity in the number of plant families in their diet (N = 24) than indri (N = 17). The top ten plant families comprised 62.2% of diademed sifakas feeding occurrences and 94.5% of indri feeding occurrences. They overlapped in eight out of the top 10 plant families consumed, but consumed these plants in differing quantities (Table 4-6). We did not observe indri feeding from the plant family Apocynaceae but it comprised 7.74% of diademed sifaka feeding records primarily from the genus *Petchia*. Indri fed primarily from the families Lauraceae, Clusiaceae and Myristicaeeae. Clusiaceae was the most common plant family consumed for diademed sifakas followed by Moraceae (Table 4-6).

Table 4-4. Top ten indri preferred plant species. Names in bold indicates a top 10 food source for both indri and diademed sifakas.

Species	**Family**	**% of feeding records**
Cryptocarya sp2	Lauraceae	8.7%
Cryptocarya sp1	Lauraceae	6.7%
Ocotea racemosa	Lauraceae	6.4%
Symphonia pauciflora	Clusiaceae	6.1%
Mauloutchia humblotii	Myristicaceae	5.7%
Haematodendron glabrum	Myristicaceae	5.6%
Aspidostemon spp	Lauraceae	5.5%
Symphonia louveli	Clusiaceae	5.5%
Bronchoneura sp1	Myristicaceae	5.4%
Uapaca louveli	Euphorbiaceae	5.3%
	Total	**60.8%**

Table 4-5. Top ten diademed sifaka preferred plant species. Names in bold indicates a top 10 food source for both indri and diademed sifakas.

Species	**Family**	**% of feeding records**
Symphonia pauciflora	Clusiaceae	8.3%
Rheedia sp.	Clusiaceae	7.2%
Sorendea madagascariensis	Anacardiaceae	6.6%
Petchia sp1	Apocynaceae	5.1%
Cynometra spp	Fabaceae	4.0%
Symphonia louveli	Clusiaceae	4.0%
Syzygium sp3	Myrtaceae	4.0%

Mammea bongo	Clusiaceae	3.0%
Treculia sp	Moraceae	2.9%
Trophis spp	Moraceae	2.6%
	Total	**47.7%**

Table 4-6. Preferred plant families for indri and diademed sifakas. Percentages in bold indicate top 10 plant families for each lemur species

	Indri	**Diademed sifaka**
Plant Family	**% of feeding records**	
Anacardiaceae	**0.69%**	**8.22%**
Apocynaceae	0.00%	**7.74%**
Annonaceae	**1.06%**	0.85%
Araliaceae	**0.48%**	**3.02%**
Clusiaceae	**21.84%**	**23.70%**
Euphorbiaceae	**7.88%**	2.30%
Fabaceae	**1.59%**	**6.05%**
Lauraceae	**42.62%**	**8.95%**
Moraceae	**4.49%**	**13.66%**
Myristicaceae	**17.72%**	**3.02%**
Myrtaceae	**0.53%**	**5.44%**
Sapindaceae	0.26%	**4.84%**
Total	**99.15%**	**87.79%**

4.4.3 Monthly Dietary Profiles and Dietary Overlap

Dietary overlap was said to occur when the diet of both lemur species included the same plant part from the same plant species. Most overlap occurred in the consumption of young leaves although some overlap occurred in species of mature leaves, fruits, seeds, bark, and petioles (Table 4-7).

Table 4-7. Number of plant species consumed for each lemur species. Numbers in the overlap row indicate the number of overlapping plant species for each plant part.

	Young leaves	Mature Leaves	Fruit	Seed	Bark	Petiole	Flower
Indri	49	20	20	15	10	11	23
Diademed sifaka	65	13	32	24	1	2	21
# of Overlapping Species	38	5	5	4	1	1	2

Bark

Bark consumption rose from June to September for indri and was only observed in July for diademed sifakas (Figure 4-4). Indri consumed bark more often (N = 34 occurrences and 10 plant species) than diademed sifakas (N = 2 instances and 1 plant species). The species consumed by diademed sifakas, *Ocotea sp2*, was also eaten by indri on two occasions. This species comprised 100% of the diademed sifakas bark consumption and 5.89% of occurrences of indri bark feeding.

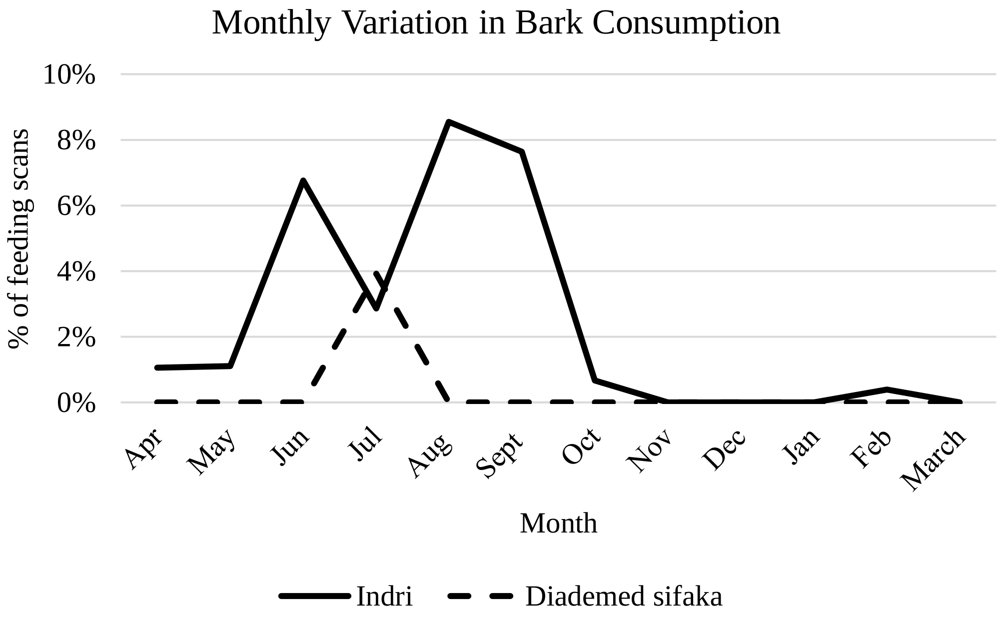

Figure 4-4. Monthly percentage of feeding records devoted to bark consumption for indri and diademed sifakas at BNR.

Geophagy

Geophagy was observed in both lemur species, but did not occur often. Indri were observed consuming soil on 22 occasions and diademed sifakas consumed soil on 16 occasions. Geophagic events peaked in April and from October to December for diademed sifakas and from September to March for indri (Figure 4-5).

Indri and diademed sifakas exhibited an inverse relationship with bark consumption and geophagy. Indri consumed both soil and bark in September, October, and February but in September and October when soil consumption rose, bark consumption declined. Diademed sifakas were only observed eating bark in July; a month when no soil was consumed. We observed diademed sifaka geophagy from September-February and in April.

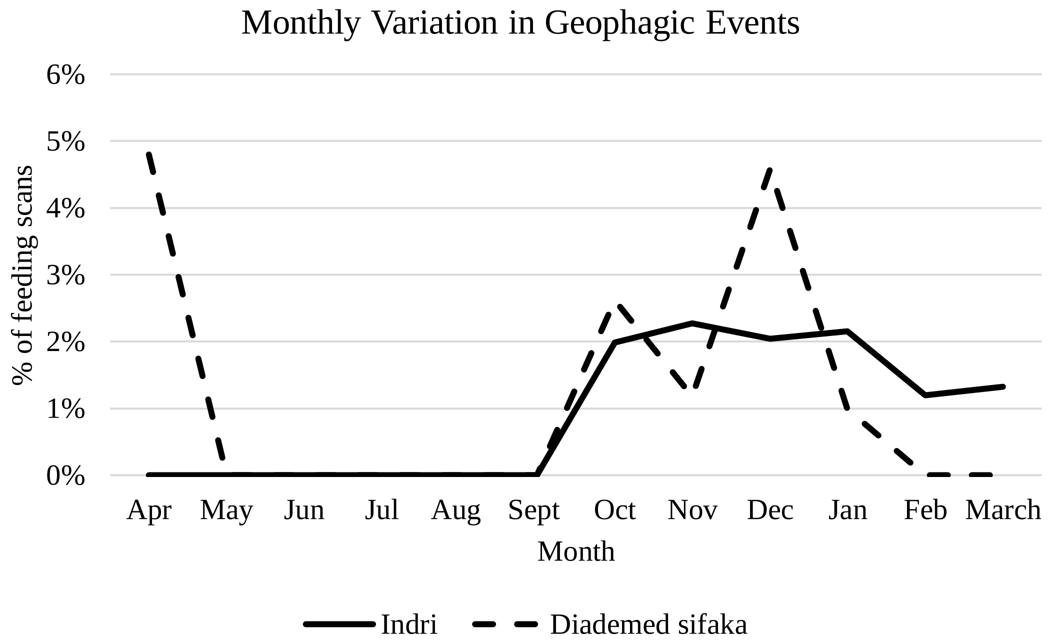

Figure 4-5. Monthly percentage of feeding records devoted to soil consumption for indri and diademed sifakas at BNR.

Flowers

The diets of both lemur species contained flowers each month. Indri were observed to feed on flowers from 23 identified plant species and diademed sifakas from 21 plant species. Indri flower consumption peaked in April to May and September to October (Figure 4-6). Diademed sifakas flower consumption increased in May, but showed a dietary peak from July to October (Figure 4-6). The top five species of flower consumed by indri were *Symphonia pauciflora, Haematodendron glabrum, Mauloutchia humblotii, Ocotea racemosa,* and *Symphonia louveli*. These comprised over half (56.2%) of all observed flower feeding occurrences (N = 26, 15, 14, 14 and 13 occurrences respectively). For diademed sifakas, the top five plant species, *Bakarella clavata, Sorendea madagascarensis, Syzygium* sp3, *Tinopsis* sp1, and *Symphonia pauciflora* accounted for 54.1% of all occurrences of flower feeding (N = 17, 13, 6, 4, and 3 occurrences respectively). Flower dietary overlap occurred in four plant species overall (Table 4-8). Nine flower species were unidentified.

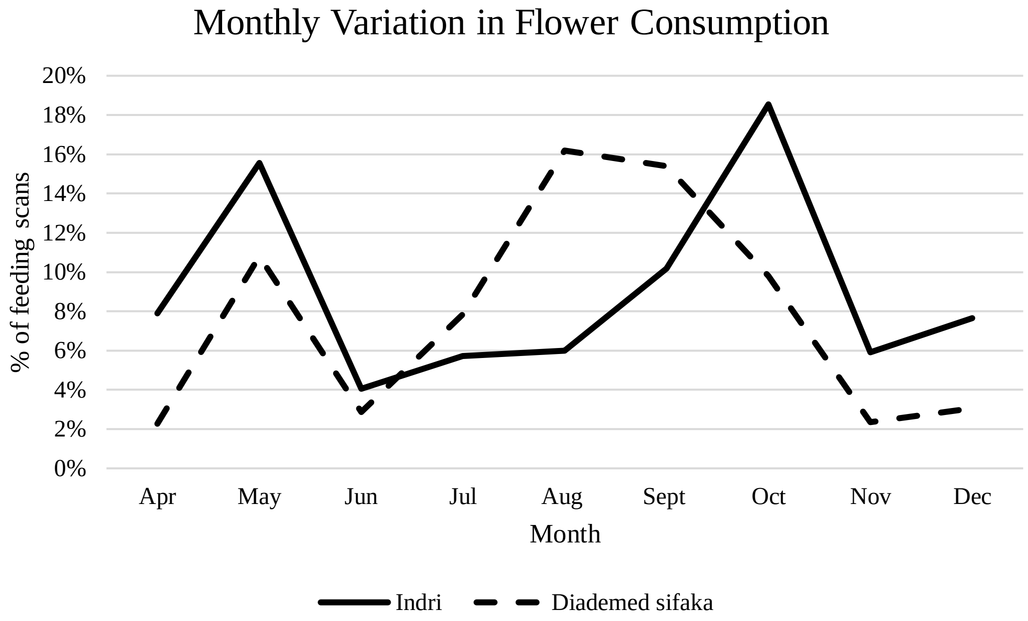

Figure 4-6. Monthly percentage of feeding records devoted to flower consumption for indri and diademed sifakas at BNR.

Table 4-8. Overlapping plant species where flowers were consumed and overall number of flower feeding occurrences per plant species.

	Indri	**Diademed sifaka**	**Total**
Bronchoneura sp1	6	1	7
Cryptocarya sp1	3	2	5
Mauloutchia humblotii	14	1	15
Symphonia pauciflora	26	3	29

Fruits

Fruit feeding was highest in December to January, March to May, and July to August for diademed sifakas and from July to September and in December for indri (Figure 4-7). Fruit comprised a higher proportion of the diademed sifakas in all months but February and June when fruit consumption was nearly equal. Diademed sifakas consumed fruits from a wider variety of plant species (N = 31) than indri (N = 20). Both lemur species consumed fruit from five overlapping species (Table 4-9).

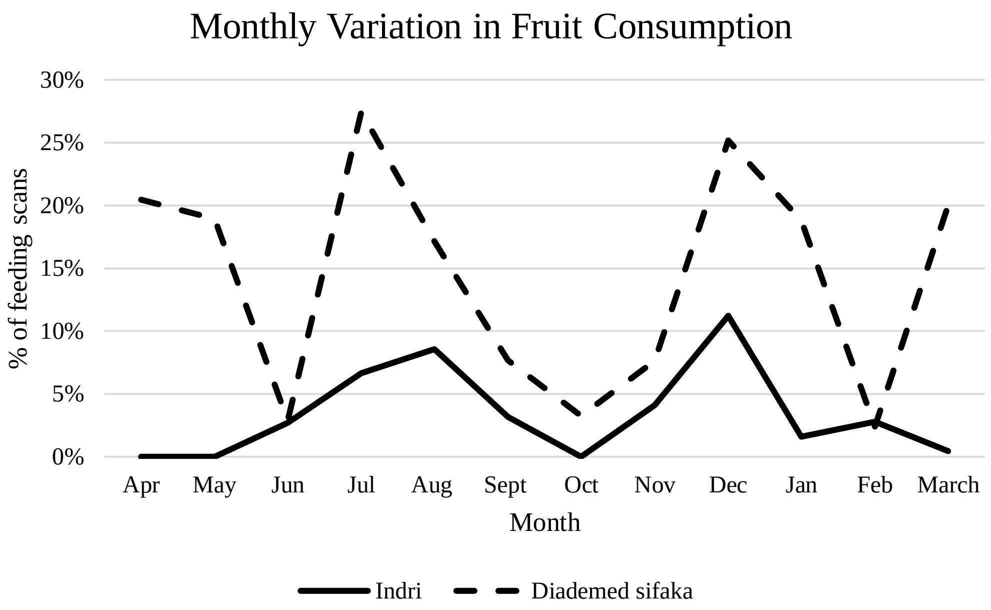

Figure 4-7. Monthly percentage of feeding records devoted to fruit consumption for indri and diademed sifakas at BNR.

Table 4-9. Overlapping plant species where fruit was consumed and overall number of fruit feeding occurrences per plant species.

Species	**Indri**	**Diademed sifaka**	**Total**
Haematodendron glabrum	4	1	5
Mammea bongo	1	2	3
Ocotea sp1	3	1	4
Symphonia louveli	5	2	7
Symphonia pauciflora	10	7	17

Seeds

We also observed temporal variation in seed consumption for both lemur species. Seed consumption began to rise for indri in December and was at its highest from January-February whereas diademed sifakas seed consumption rose in September-November, were highest from

December-March and rose again from May-June (Figure 4-8). Overall diademed sifakas fed on seeds more often than indri in all months except April and July. Diademed sifakas fed on seeds from more plant species (N = 25) than indri (N = 15). While they fed on seeds from four of the same tree species, in each case, either indri or diademed sifakas were recorded feeding from the overlapping tree once and the other lemur species fed from the same tree species multiple times (Table 4-10).

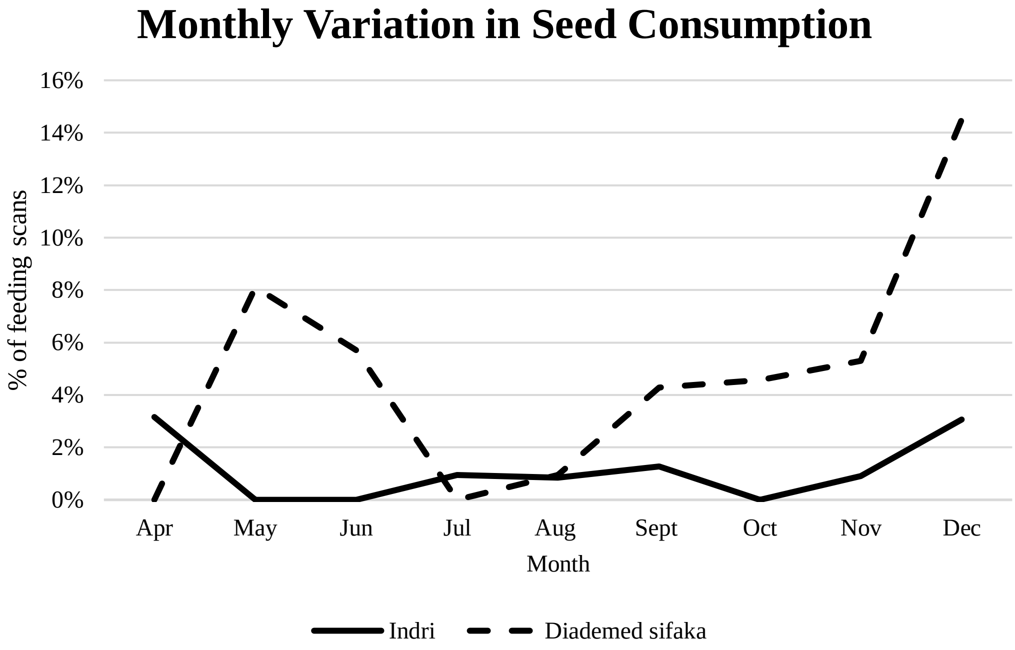

Figure 4-8. Monthly percentage of feeding records devoted to seed consumption for indri and diademed sifakas at BNR.

Table 4-10. Overlapping plant species where seeds were consumed and number of seed feeding occurrences per plant species.

Species	**Indri**	**Diademed sifaka**	**Total**
Haematodendron glabrum	14	1	15
Mammea bongo	1	3	4
Symphonia louveli	1	4	5
Symphonia pauciflora	1	6	7

Petioles

Both species demonstrated temporal variation in leaf petiole feeding. Petioles comprised a larger part of indri diets than diademed sifakas but a relatively small part of each species' overall diet. Petiole feeding peaked from June-September for indri and July-September for diademed sifakas (Figure 4-9). Indri consumed petioles from a greater number of plant species (N = 11) than diademed sifakas (N = 2) and they only overlapped in the consumption of petioles from one plant species, *Rheedia sp.*. We only recorded one instance of diademed sifakas feeding on petioles from this species and five instances for indri.

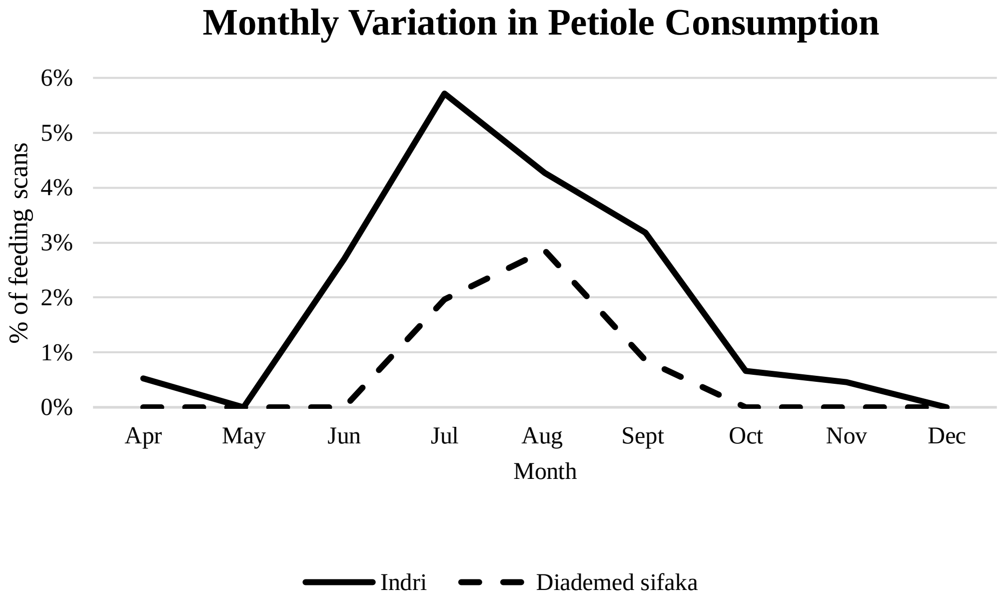

Figure 4-9. Monthly percentage of feeding records devoted to petiole consumption for indri and diademed sifakas at BNR.

Mature Leaves

Mature leaf feeding increased from May-August for diademed sifakas and June-September for diademed sifakas (Figure 4-9). Indri consumed mature leaves from more plant species (N = 20) than diademed sifakas (N = 13) and they overlapped in the consumption of mature leaves from five plant species. Overlap of mature leaves from *Rheedia sp.* was greatest with seven instances of indri and 12 instances of diademed sifaka feeding (Table 4-11).

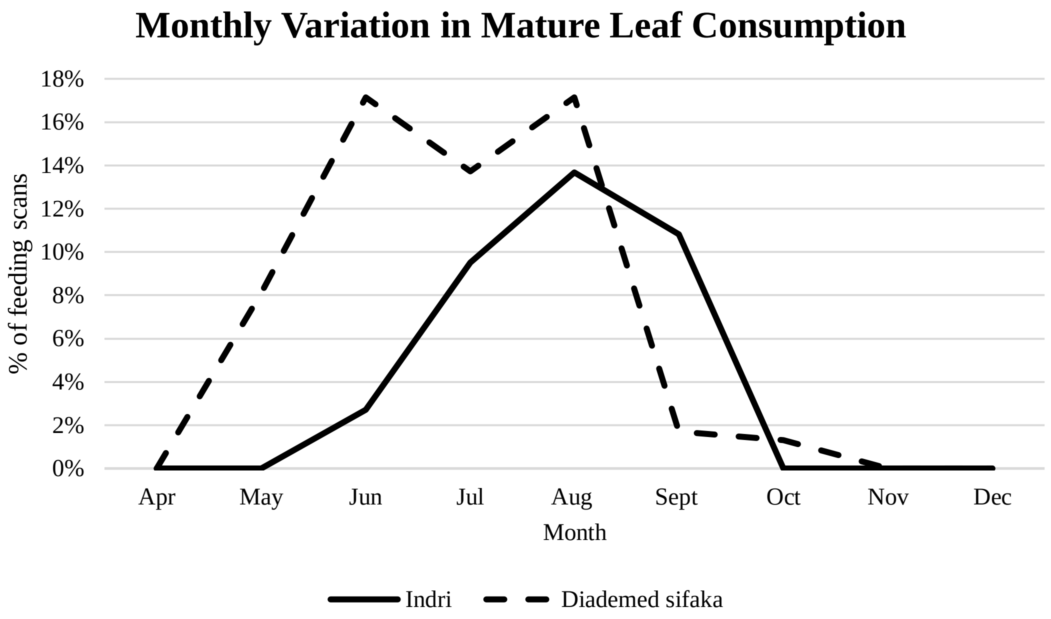

Figure 4-10. Monthly percentage of feeding records devoted to mature leaf consumption for indri and diademed sifakas at BNR.

Table 4-11. Overlapping plant species where mature leaves and overall number of mature leaf feeding occurrences per plant species.

Species	**Indri**	**Diademed sifaka**	**Total**
Potameia crassifolia	9	1	10
Cryptocarya sp2	1	1	2
Polyscias	4	1	5
Rheedia sp.	5	12	17
Symphonia pauciflora	1	2	3

Young Leaves

Young leaves comprised the highest proportion of both species' diets with some temporal variation. Young leaf consumption was lowest in July and August for both species (Figure 4-11). In all months but September, young leaves accounted for a larger proportion on the indri diet than the diademed sifakas diet. The two lemur species overlapped in eating young leaves from 38 plant species to varying degrees (Table 4-12).

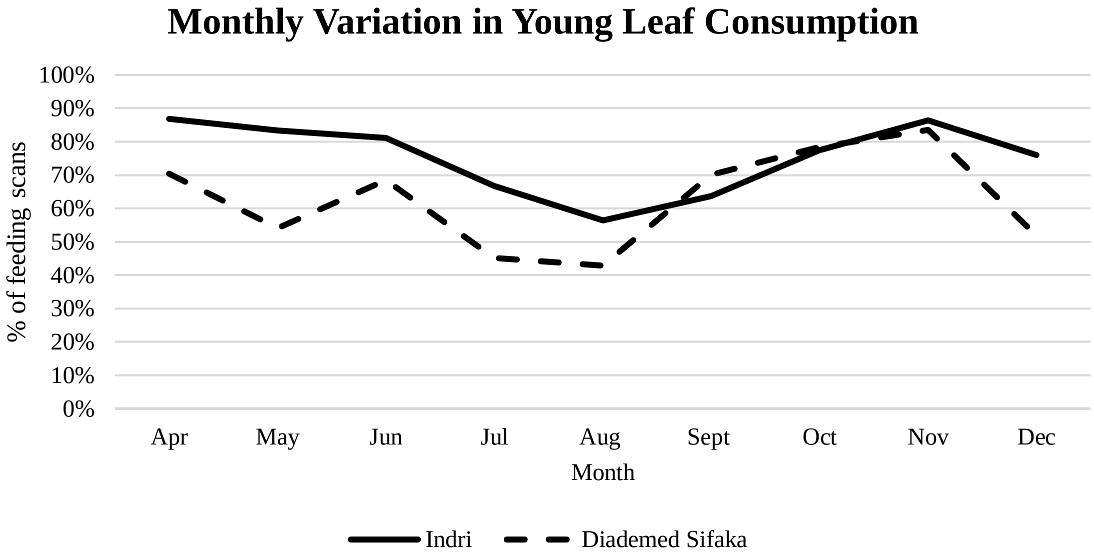

Figure 4-11. Monthly percentage of feeding records devoted to young leaves consumption for indri and diademed sifakas at BNR.

Table 4-12. Overlapping plant species where young leaves were consumed and overall number of young leaf feeding instances per plant species.

Species	**Indri**	**Diademed sifaka**	**Total**
Cryptocarya sp2	141	14	155
Cryptocarya sp1	119	12	131
Aspidostemon spp	97	2	99
Uapaca louveli	90	1	91
Rheedia sp.	85	44	129

Bronchoneura sp1	84	5	89
Symphonia louveli	82	26	108
Mauloutchia humblotii	80	4	84
Ocotea racemosa	79	6	85
Symphonia pauciflora	78	49	127
Haematodendron glabrum	71	12	83
Ocotea sp2	56	11	67
Potameia crassifolia	56	6	62
Mammea bongo	47	19	66
Beilschmiedia sp2	45	7	52
Cynometra spp	29	32	61
Treculia spp	27	15	42
Trophis spp	25	13	38
Potameia sp.	19	4	23
Isolona sp1	18	6	24
Symphonia sp1	18	3	21
Treculia sp	16	15	31
Calophyllum sp1	12	1	13
Michronychia tsiramiramy	12	1	13
Treculia sp1	10	10	20
Uapaca sp	10	1	11
Symphonia sp2	9	1	10
Streblus spp 1	5	13	18
Cryptocarya sp5	5	1	6
Polyscias	4	12	16
Noronhia sp	4	4	8
Noronhia verticilata	3	5	8
Stadmania sp1	2	3	5
Sorendea madagascariensis	1	32	33
Oncostemum sp1	1	9	10
Stadmania sp3	1	9	10
Polyscias sp2	1	4	5

4.4.4 Niche Breadth and Overlap

Standardized mean monthly niche breadth (B_A) was 0.015 (range = 0.071 – 0.279, SD = .075) for indri and 0.061 (range = 0.128 – 0.719, SD = 0.182) for diademed sifakas. Dietary overlap (*O*) varied throughout the year (mean = 0.0014 +/-SD 0.12, range: 0.0002 to 0.0037) (Figure 4-12). Overlap was highest in October and November. They fed on flowers from the same species in September, October, January, and May and on fruits and from the same tree species from November to January. Seed overlap occurred from December through March. In nearly all instances, one of the two lemur species fed on the on the food source several times during the month while the other lemur species was only observed feeding on the same plant species and part once. The greatest overlap occurred on the fruits of *Symphonia pauciflora* in November and December when indri and diademed sifakas fed on the fruits nine and seven time respectively.

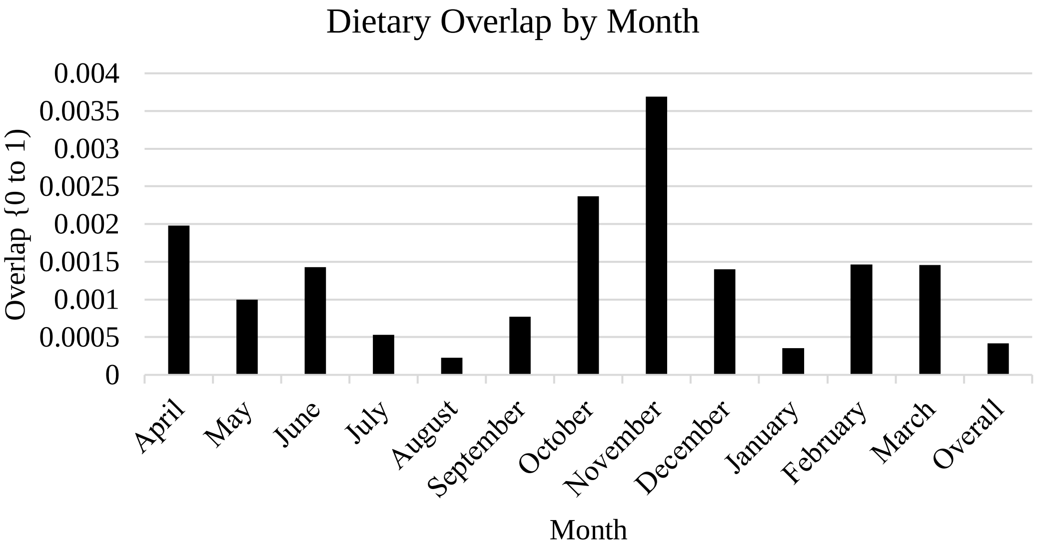

Figure 4-12. Pianka's measure of dietary overlap based on plant species and part consumed calculated by month and for the entire study period. This is measured on a scale of 0 (no overlap) to 1(complete dietary overlap).

4.4.4 Phenological Patterns of Resource Availability

Availability of plant parts varied throughout the year (Figure 4-13). Young leaves were available throughout the year but were at their highest availability from January to March and had the lowest availability from June through August. Fruits were also available in all months but at their lowest level of availability from October through December. Flowers were most abundantly available from November through February. Dietary overlap between indri and diademed sifakas was not significantly correlated with the availability of young leaves, fruits, or flowers.

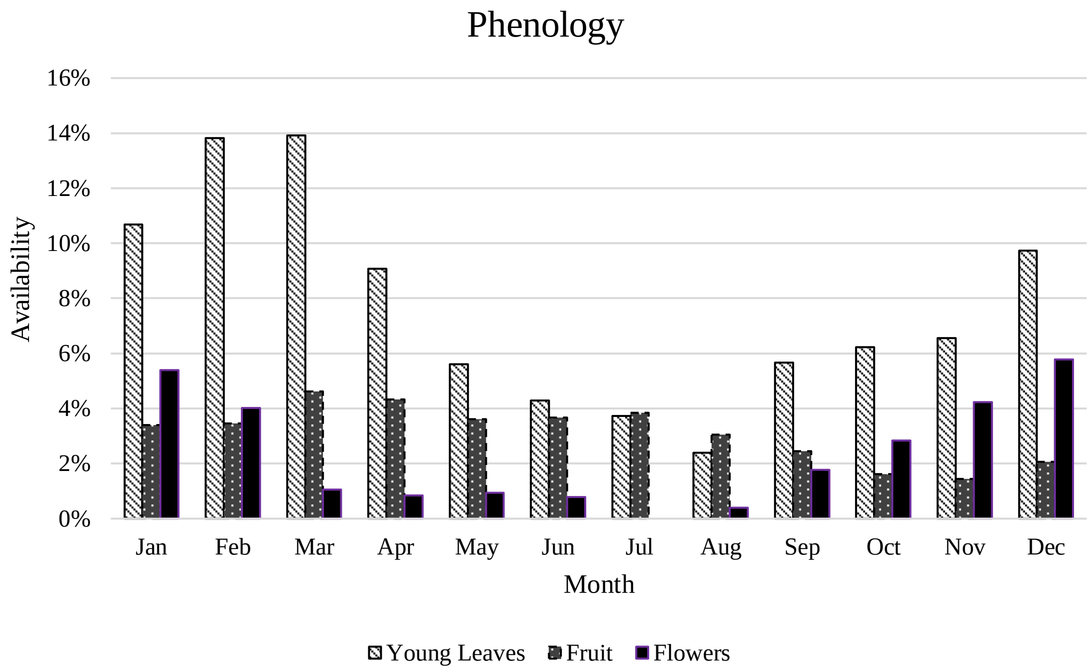

Figure 4-13. Plant part availability by month for young leaves, fruits, and flowers (Phenological data courtesy of Sarah Federman).

I found significant correlations between plant part availability and consumption. For indri, I found a positive correlation between the availability of young leaves and the consumption of both young leaves and seeds and seeds and a negative correlation between young leaf availability and the consumption of mature leaves, petioles, and bark (Table 4-13). When the young leaves increased in availability, consumption of young leaves and seeds increased while the consumption of mature leaves, petioles, and bark decreased. There was also a negative correlation between flower feeding and the consumption of mature leaves and bark. For diademed sifakas, I found a statistically negative correlation between young leaf availability and the consumption of flowers, mature leaves, and petioles and a positive correlation between young leaf availability and seed consumption (Table 4-14). There was also a significant positive correlation between flower availability and seed consumption and a negative correlation between flower availability and mature leaf consumption.

Table 4-13. Indri correlation between consumption of plant parts and monthly availability. Values in bold indicate significance where $P < 0.05$.

		Consumption						
		Young leaves	**Fruit**	**Flowers**	**Seeds**	**Mature leaves**	**Petiole**	**Bark**
Young leaves	***rs* =**	**0.6014**	-0.2465	-0.3818	**0.7254**	**-0.7614**	**-0.7403**	**-0.84**
	P =	**0.0428**	0.4398	0.22	**0.0102**	**0.0057**	**0.0082**	**0.0012**
Fruits	***rs* =**	0.3846	-0.331	-0.4308	0.1831	0.02496	-0.04983	0.1424
	P =	0.2183	0.2935	0.1627	0.5693	0.9414	0.8795	0.6565
Flowers	***rs* =**	0.1331	0.07055	-0.01754	0.4303	**-0.6189**	-0.5669	**-0.763**
	P =	0.6784	0.8285	0.959	0.1629	**0.0354**	0.0579	**0.0057**

Table 4-14. Diademed sifaka correlation between consumption of plant parts and monthly availability. Values in bold indicate significance where $P < 0.05$.

		Consumption						
		Young leaves	**Fruit**	**Flowers**	**Seeds**	**Mature leaves**	**Petiole**	**Bark**
Young leaves	***rs* =**	0.4125	0.01414	**-0.6422**	**0.6823**	**-0.7528**	**-0.6111**	-0.3274
	P =	0.1827	0.9652	**0.0244**	**0.0145**	**0.0047**	**0.0348**	0.2988
Fruits	***rs* =**	-0.2098	0.3846	-0.1538	-0.1296	0.08975	-0.01836	0.3057
	P =	0.5137	0.2183	0.6353	0.687	0.781	0.9636	0.5
Flowers	***rs* =**	0.3468	-0.1189	-0.4821	**0.7734**	**-0.6494**	-0.4926	-0.5431
	P =	0.2695	0.7129	0.1125	**0.0032**	**0.0223**	0.1037	0.068

4.4.5 Vertical Stratification During Feeding

While both indri and diademed sifakas primarily fed on all food types in the continuous canopy level (level 4) they do exhibit some stratigraphic differences while feeding on different plant parts. Indri fed on young leaves, flowers, and seeds in the emergent canopy level (level 5) while sifakas were not observed feeding at that level (Figure 4-14, Figure 4-15). I found the largest stratigraphic divergence pattern between these two lemur species when feeding on seeds. Diademed sifakas ate seeds while on the ground (level 1) or in the understory level (2) whereas indri fed on seeds only in the continuous and emergent canopy. Diademed sifakas were observed sitting on the ground and feeding on seeds from large fallen fruits from *Symphonia pauciflora* and *Treculia* sp.. Indri only descended to the ground to consume soil.

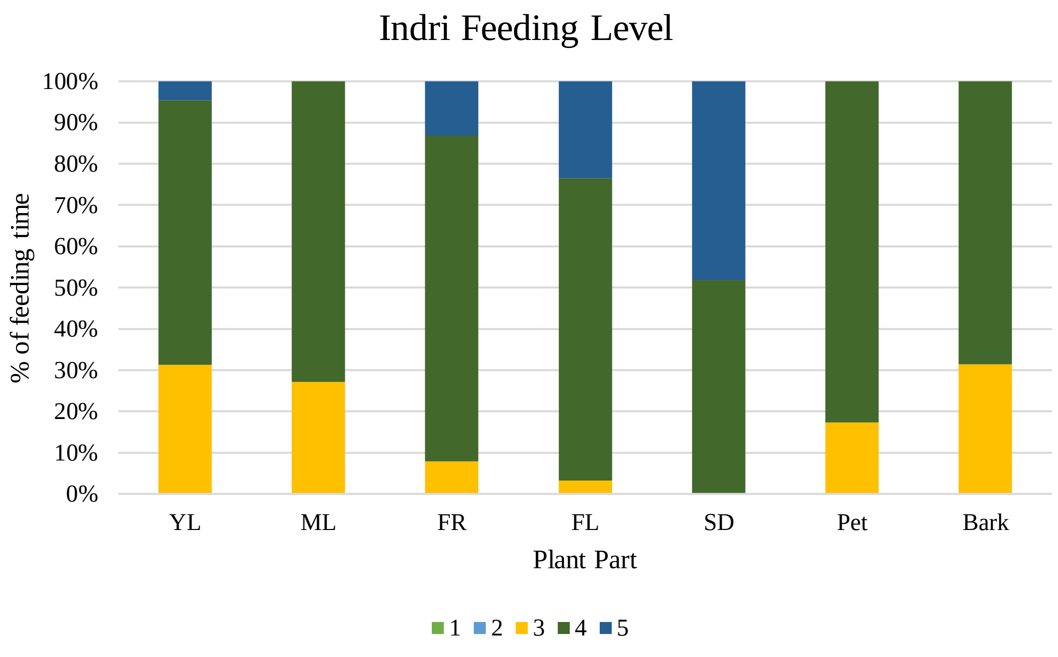

Figure 4-14. Percent of time spent feeding on plant parts in different stratigraphic forest levels for indri. YL = young leaves, ML = mature leaves, FR = fruit, FL = flowers, SD = seeds, PET = petioles.

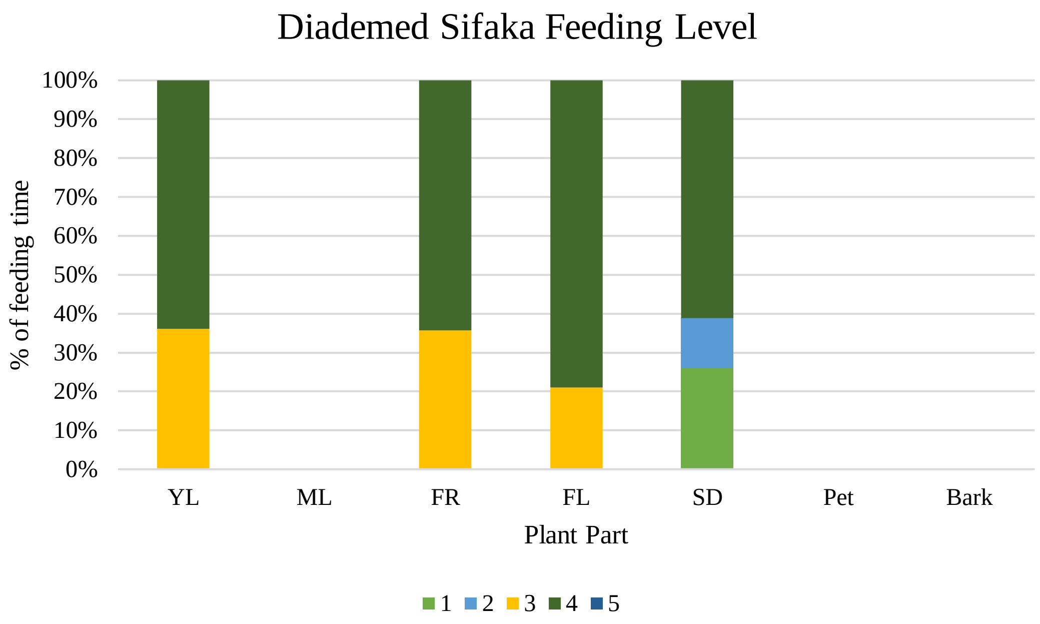

Figure 4-15. Percent of time spent feeding on plant parts in different stratigraphic forest levels for diademed sifakas. YL = young leaves, ML = mature leaves, FR = fruit, FL = flowers, SD = seeds, PET = petioles.

4.5 Discussion

4.5.1 Overview

At BNR, indri and diademed sifakas exhibit patterns of niche separation through several aspects of their dietary choices. Results with this study are consistent with the current knowledge of indri and diademed sifaka feeding patterns in that both species are folivores but indri exhibit a higher degree of folivory than diademed sifakas. Diademed sifakas have greater dietary diversity in the overall number of plant species in their diet and in the types of plants they consume. Indri almost exclusively fed from trees whereas diademed sifakas exploited a variety of plant types. Close to 1/5 of feeding occurrences were from non-trees. Both species also exhibited differences in preferences for feeding in different forest levels whereby indri fed primarily in the continuous canopy but also utilized the emergent canopy. Diademed sifakas also feed primarily in the continuous canopy but descend to the ground and understory to feed on seeds.

4.5.2 Dietary Diversity

Differences in dietary diversity at BNR were consistent with reports of indri and diademed sifaka feeding at other sites (Blanchard 2007; Powzyk 1997; Powzyk and Mowry 2003). This supports the prediction that indri will consume more leaves and diademed sifakas, while still considered folivorous, consumed more fruits and seeds. These differences correspond with expectations of dietary preferences based on their gut and molar morphology (Chapter1). The plant families that both species preferred were among the most abundant at BNR (Armstrong et al. 2011). These overall dietary patterns (percent of different plant parts in the diet) and the plant families in each species' diet are consistent with reports from other sites and, for indri, at BNR (Britt et al. 2002; Irwin 2006; Pollock 1977; Powzyk 1997; Powzyk and Mowry 2003).

For indri, consumption of young leaves was comparable but slightly higher than what Britt et al. (2002) reported at BNR and higher than reported by Powzyk (1997). Britt et al. (2002) found that indri consumed a higher proportion of mature leaves than previous studies. Results from this present study, while still higher than reports from Mantadia, were less than that reported by Britt et al. (2002). This indicates two important points: 1) indri exhibit some degree of dietary flexibility throughout their species range, and 2) indri can adapt to inter-annual fluctuations in resource availability. Their degree of dietary plasticity between sites and longitudinally requires further investigation.

The prediction that diademed sifakas feed from a wider variety of non-tree plants was supported in that diademed sifakas fed from non-tree plants in almost 20% of overall feeding occurrences whereas indri overwhelmingly fed from trees. Results from a nutritional analysis of food samples from Mantadia indicate that the diet of diademed sifakas is overall higher in fat and water soluble carbohydrates when compared to indri. Diademed sifakas may consume a wide variety of food types to obtain necessary nutrients and minerals for survival. For example, Powzyk (1997) reported that ferns were an important part of the diademed sifaka diet and found that these had a relatively high percent of protein relative to immature leaves from non-ferns. Powzyk (1997) posited that consumption of fern leaves may be a way for diademed sifakas to obtain protein seasonally when they spent long amounts of time feeding on fruit. At BNR, diademed sifakas were only observed to feed on ferns in February, April, and August. These periods did not correspond with an increase in fruit consumption.

Results from this study support the prediction that diademed sifakas feed from a greater number of plant species than indri. Powzyk reported that diademed sifakas fed from at least 172 species for diademed sifakas and 76 species for indri. She was, however, able to identify some ferns to the species level. Ferns from my study were too high in the canopy for sample collection. Irwin (2006) reported that the diademed sifakas at Tsinjoarivo fed from 165 food species. The Tsinjoarivo sifakas in the study inhabit both continuous and fragmented forests where they are likely exposed to a greater taxonomic variety of potential food sources. At BNR, Britt et al. (2002) identified a minimum of 42 indri food species but stated that this number was likely an underestimation of their actual dietary diversity as the identification of plant species can be difficult in the field and that a vernacular name for a type of tree often applies to several tree species. For example, Britt *et. al.* (2002) and Powzyk (1997) identified *Haematodendron* *glabrum* (family: Myristicaceae) as a potential "keystone" species for indri. The vernacular name for this tree species is "Rara". During our data collection at BNR we discovered that trees called "Rara" represented four different species from the family Myristicaceae family. Indri commonly fed from several plant parts from all four species in this family lending support to the notion that this plant family is an important resource for indri but that *Haematodendron glabrum* is unlikely a "keystone" species on its own.

4.5.3 Feeding on Non-Vegetative Items

The two primary hypotheses to explain geophagy in primates are 1) to reduce digestive issues from the consumption of secondary compounds from other food sources; and 2) to provide minerals not found in other sources in the diet (Krishnamani and Mahaney 2000; Mananey and Krishnamani 2003). Other potential explanations are to alleviate diarrhea and reduce parasites (Krishnamani and Mahaney 2000). Semel (2015) tested these hypotheses in diademed sifakas at Tsinjoarivo. Parasite loads were low in this population and no bouts of diarrhea were observed during his data collection and were unlikely explanations for geophagy (Semel 2015). Semel (2015) did find that diademed sifakas consumed foods that were higher in toxins in the hours before soil consumption than toxin levels in foods on days when no soil was consumed but the relationship was not significant. This trend supports the hypothesis that the diademed sifakas at Tsinjoarivo consumed soil to alleviate digestive issues from the consumption of plant secondary compounds but it also highlights the need for further investigation. Powzyk (1997) conducted a nutritional analysis of a bark sample from Mantadia and found that it was low in protein, calcium, and other minerals. The sample was high in fiber and may have provided some digestive benefit but the ultimate cause for bark consumption remains speculative.

The greater dietary diversity exhibited by diademed sifakas relative to indri is consistent with expectations that species that consume more fruits and seeds will exploit a wider variety of foods than more folivorous primates (Clutton-Brock and Harvey 1977). This differentiation of dietary profiles serves to reduce the potential for interspecific competition for a specific food source and helps maintain the sympatric coexistence of these confamilial indriids.

4.5.4 Species Overlap

Indri and diademed sifakas exhibited varying degrees of dietary overlap throughout the year that corresponded with fluctuations in resource availability. Dietary overlap was lowest when young leaves were least available. This supports the importance of young leaves in the diets of these sympatric indriids as they decrease potential resource competition by diverging their diets most in times low young leaf abundance.

Young Leaves

Tree species in which overlap was the greatest and that were fed from most often were: *Rheedia sp., Symphonia pauciflora* (Clusiaceae), *Symphonia louveli* (Clusiaceae), *Treculia sp.* (Moraceae), and *Cynometra spp*. (Fabaceae). These tree species are relatively abundant in the forest and represent some of the most abundant plant families present at BNR (Armstrong et al. 2011). While folivores are selective about the leaves in their diets, this resource type is generally more abundant overall and consistently available throughout the year than fruits, seeds, and flowers (Hemingway and Bynum 2005; van Schaik et al. 1993). Overlap in abundant foods like young leaves is less likely to result in resource competition as young leaves are generally not a limited resource.

Fruit

There was a small degree of overlap in fruit feeding but this only occurred in 5 species that are commonly found in the forest. Additionally, there were few feeding occurrences overall by either lemur species on these trees. The highest degree of overlap was the fruit of *Symphonia pauciflora* (Clusiaceae) (indri: N = 10 feeding occurrences; diademed sifaka: N = 7 feeding occurrences). In these cases, the possibility of interspecific competition was generally reduced via vertical stratification. Diademed sifakas often fed on these fruits after they had fallen to the ground while indri consumed the fruits primarily by plucking them from the tree directly and feeding in the continuous canopy (see below for further discussion).

Flowers, Seeds, Mature Leaves, and Leaf Petioles

A small degree of overlap occurred for flowers, seeds, mature leaves, and petioles. Overlap occurred rarely relative to the frequency of feeding on these plant parts. As with young leaves and fruits, overlapping tree species are commonly found in the forest and represent the most common plant families at BNR.

Overall, the greatest overlap occurred in feeding on fruits, flowers, and seeds from two species of *Symphonia* (Clusiaceae) trees. These trees are generally large in size and abundant in at BNR (Armstrong 2009; Armstrong et al. 2011). Additionally, black-and-white ruffed lemurs have been reported to feed from these tree species at BNR (Britt 2000; Schmidt et al. 2010). While brown lemur (*Eulemur albifrons*) resource use has not been the subject of intense study at BNR, rufous lemurs (*Eulemur rufus*) and red-bellied lemurs (*Eulemur rubriventer)* have been reported to feed on *Symphonia sp.* trees at Ranomafana (Overdorff 1993). Overlap occurred in non-limiting, superabundant tree species at BNR. Other lemur species as well as non-primates (birds, rodents, etc.) may also feed from these trees but further investigation is required to determine the extent to which this occurs. In summary, indri, diademed sifakas, other lemurs, and likely other birds and mammals use these trees as food sources.

Compared to other sympatric folivorous primate species, the overlap in food resources between indri and diademed sifakas observed in this study are quite low. For example, overlapping congeneric howler monkeys in Argentina overlapped in nearly half of the plant species and parts consumed (Agostini et al. 2010). These species maintained sympatry by overlapping on abundant non-limiting food sources (Agostini et al. 2010). At Mantadia, indri and diademed sifaka resource overlap was also low (~2-9%) and, when overlap occurred, it was primarily in the consumption of young leaves from the same tree species (Powzyk 1997). I found the same pattern at BNR. Clearly, these two species exploit food items in the forest differently and I found no evidence of resource competition.

4.5.5 Interspecific Encounter in a Feeding Context and Strategies for Maintaining Sympatry

While competition for food resources has been reported for some sympatric folivores, I found little evidence to support feeding competition between indri and diademed sifakas at BNR. We observed one instance of interspecific encounter in a feeding context. This occurred on 3 March 2014 at 11:20. The indri group Southwest was feeding on young leaves in a *Cryptocarya* sp. tree when the Central diademed sifaka group approached and displaced the indri. The indri group moved approximately 20 meters away and began feeding on young *Ocotea racemosa* leaves. There was no physical contact or vocalizations from either species. The Central group began feeding on fruit from a *Symphonia* sp. tree adjacent to the original indri feeding tree cluster. Both lemur species fed on fruit from 2 *Symphonia* species in November and December but we did not record any observations of indri feeding on these fruits later than December. Tree species from this genus have relatively high IVI, abundance, and dominance scores (Armstrong 2009). The abundance of *Symphonia* sp. and assertion that fruits and flowers are not limiting resources at BNR is further evidenced by reports that black and white ruffed lemurs feed on the fruits and flowers from these trees at BNR (Britt 2000; Schmidt et al. 2010). Brown lemur feeding ecology at BNR would aid in a better understanding of the diurnal/cathemeral lemur community ecology and should be considered for future research.

The abundance of this plant genus, *Symphonia*, in the forest combined with the lack of an aggressive encounter and the proximity maintained by the indri after they were displaced all support the notion that these two species have strategies to avoid interspecific feeding competition. When overlap occurs, generally they show temporal variation in that they rarely feed from the same plant species and part at the same time of year. This supports the hypothesis that one mechanism to maintain sympatry is dietary differentiation. Powzyk (1997) also reported that most overlap of plant species and part occurred in young leaves and, overall, rates of overlap were low.

4.5.6 Intraspecific Encounters in a Feeding Context

We observed two intraspecific encounters between the South and Central diademed sifaka groups on 14 and 20 February 2014. In both cases, the Central group traveled into the territory of the South group. Members from both groups chased each other and the adult males from each group briefly engaged in a physical altercation on the ground. After the contact aggression event, the Central group traveled back toward their own territory. This occurred when *Syzygium* sp. (Family: Myrtaceae) was fruiting and encounters were near these fruiting trees. Diademed sifaka groups fed on the fruits and seeds of these trees from December to

February and generally traveled to parts of their home range that were rarely visited at other times of the year (Chapter 5). The intergroup aggressive encounters and travel costs incurred to reach this food source supports the notion that this is an important resource during this time of year for diademed sifakas.

4.5.7 Temporal Variation

The prediction that indri and diademed sifakas would exhibit temporal variation in the type the plant parts (and non-vegetative items) consumed was supported. Results from the phenological analyses and previous studies show that temporal fluctuations in resource availability occur at BNR (Britt et al. 2002). Indri and diademed sifaka diets consist primarily of young leaves throughout the year. Young leaf availability was lowest in the cool, rainy winter months (May-August). During this time, both lemur species diversified the types of plant parts they consume. When young leaves are less abundant, both species exhibit a slight dip in the amount of young leaves in their diets. They also increase the amount of mature leaves, fruits, petioles, flowers, and bark consumed. This pattern is consistent with the report from Britt et al. (2002) at BNR which suggests that general fluctuations in plant part availability. This is also consistent indri and diademed sifaka reports from Analamazatora (Pollock 1977), Mantadia (Powzyk 1997; Powzyk and Mowry 2003), and Tsinjoarivo (Irwin 2006).

Indri varied their dietary composition throughout the year but fed from the four Myristicaeae tree species and from *Cryptocarya* species in all months. From August to December they increased feeding on *Mammea bongo, Rheedia sp.*, three *Ocotea* species, and two *Symphonia* species. They clearly shift their diet throughout the year as a strategy to cope with differences in resource availability but no clear “keystone” or “fallback” food sources were apparent.

Diademed sifaka dietary composition also varied. For example, when young leaves were least available, diademed sifakas fed from leaves and flowers from more lianas, ferns, and epiphytes than at other times of the year.   In August, when young leaves were least available, *Bakarella clavata* flowers comprised a higher portion of diademed sifaka diets than any other month. They fed on leaves and flowers from this species from August to September. Irwin (2006) reported that, at Tsinjoarivo, diademed sifakas increase flower consumption from August to October and particularly focus on flowers from *Bakarella clavata*. They also increased feeding on the fruits and young leaves of *Diospyros sp.* and a tree with the local name Ompa in these months. Both indri and diademed sifakas fed on the young leaves of *Mammea bongo* from August to December. As with the indri, diademed sifaka diets varied throughout the year whereby they fed from some plant species in nearly all months and other species were only consumed in specific months. Clear “keystone” or “fallback” foods were not identified but the increase in feeding from lianas, ferns, and epiphytes times of decreased young leaf availability is a likely coexistence strategy with indri. Indri nearly exclusively fed from trees so the ability of diademed sifakas to shift their diet to non-trees in times of food scarcity is advantageous for maintaining sympatry while reducing competition for resources.

The proportion of fruits in the diet of the diademed sifakas was lowest in June and February. Two non-mutually exclusive explanations likely explain this difference. First, days of observation for diademed sifakas were low in these months due to illness, weather, and availability of researchers and guides therefore overall dietary diversity may be underrepresented in these months. Secondly, in June, the diademed sifakas moved less and spent more time resting due to cold and rainy weather on observation days. They increased their consumption of mature leaves and petioles in June. The increase in lower quality foods coupled with the decrease in movement are consistent with patters of diet and activity budgets in primates and many other animals.

4.6 Conclusions and Future Directions

Summary of main findings:

- A higher proportion of the indri diet consisted of leaves relative to diademed sifakas.
- Indri fed from fewer overall plant species than diademed sifakas.
- Indri fed almost exclusively from trees whereas diademed sifakas fed from trees, lianas, epiphytes, and ferns.
- Both lemur species fed on bark in the cold, rainy months, and soil throughout the rest of the year.
- Both species also increased feeding on petioles and mature leaves in the cold, rainy months. This corresponded with a time of low young leaf availability.
- Dietary overlap was low between lemur species.
- When indri and diademed sifakas fed on the same plant part from the same tree species, they were abundant trees at BNR that also serve as food resources for other animal species.
- Indri primarily fed in the continuous canopy level whereas diademed sifakas fed in the continuous canopy and under canopy levels.
- Indri only came to the ground to consume soil whereas diademed sifakas consumed soil, along with fallen fruits and seeds.

The overall dietary profiles of indri and diademed sifakas at BNR indicate that these two species employ several strategies for maintaining coexistence. Their dietary overlap was low and, when they overlapped in feeding on the same plant part from the same tree species, they employed three main strategies that minimize the potential for interspecific competition: 1) vertical stratification of feeding preferences, and 2) overlapping in feeding from abundant resources, and 3) temporal variation in feeding on fruits and seeds from the same plant species. This last point is a particularly important avenue for further research. This temporal separation in feeding shows that the feeding and overall coexistence strategies of these two species are more nuanced than previously thought. Finally, the observation that diademed sifakas increased the percent of non-trees in their diet coupled with the nearly exclusive use of trees as food sources when young leaf availability is decreased is clearly an important facet of niche separation for indri and diademed sifakas at BNR. In the future, a more fine-grained approach to the analysis of overlapping food species with consideration for types of plants, vertical stratification, and degree of temporal overlap in resources warrants consideration.

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Chapter 5: Comparison of home range and daily path length between *Indri indri* and *Propithecus diadema* in Betampona Nature Reserve, Madagascar

5.1 Introduction

Primates exhibit species-specific patterns of home range size and daily travel patterns. A home range refers to the area that a primate group uses to feed, travel, and rest (Burt 1943). Daily path length (DPL) is the horizontal distance traveled from sleeping site to sleeping site. Many factors can influence home range size and ranging patterns such as group size, resource availability, seasonality, habitat quality, and population density. Differences in space use and ranging behaviors allow animals to both exist with conspecifics and other sympatric species. Differences in habitat use between closely related, sympatric species has been considered a mechanism for maintaining coexistence (Schoener 1974; Schreier et al. 2009; Sussman 1979).

A consistent primate-wide trend is that more folivorous primates have smaller home ranges as their food sources tend to be more uniformly distributed and are closer in spatial proximity to each other (Clutton-Brock and Harvey 1977). Frugivorous primates must travel farther to reach patchily distributed fruit resources and so home range size and daily path length increase (Clutton-Brock and Harvey 1977; Milton and May 1976). Within species, frugivorous primates tend to exhibit a wider range of variation in home range size both between groups and throughout the year (Milton and May 1976; Oates 1987).

Many primates adjust their ranging patterns seasonally to cope with fluctuating climatic conditions or resource availability (Hemingway and Bynum 2005; van Schaik and Brockman 2005). Tropical rainforest primates tend to move less in cold, rainy months and more in warmer, drier months (Clutton-Brock and Harvey 1977; Hemingway and Bynum 2005). Some primates increase their home ranges and daily path lengths to find food in times of food scarcity ("energy maximizers"), whereas others adopt an "energy minimizing" strategy and decrease movement and increase resting (Hemingway and Bynum 2005; Hill 2005; Milton 1980; Milton and May 1976). As most primates do not migrate seasonally, they must use other methods for dealing with fluctuating temperatures, amounts of rainfall and resource availability (Hemingway and Bynum 2005). Within a primate community, species exhibit varied responses to these seasonal changes (Hemingway and Bynum 2005; van Schaik et al. 2005).

When sympatric primates are ecologically similar, they employ several mechanisms of niche separation whereby they utilize resources and their environment differently to avoid competition for resources (Hutchinson 1957; Schoener 1974; Tokeshi 1999). One of the principal niche separation mechanisms is differential habitat use (Schoener 1974). Specifically, when folivorous primates ("energy minimizers") coexist, they exhibit species-specific patterns of ranging and habitat use that reduces the possibility of interspecific competition (Hladik 1977; Oates 1987). When home ranges overlap, the two species may use the space in their home range with differing areas of intensity. Areas of a home range that are used more often than expected if the entire range were used homogeneously are called "core" areas (Kaufmann 1962; Samuel and Green 1988). Sympatric closely related primates can temporally partition their habitat to minimize direct encounters of simultaneous spatial and temporal overlap (Agostini et al. 2010; Vandercone et al. 2013).

Indri and diademed sifakas are sympatric folivorous primates that overlap throughout 90% of their species ranges (Powzyk 1997). Both species are territorial and group home ranges do not overlap (Powzyk 1997; Powzyk and Mowry 2003). Due to their ecological similarity and the large degree of species overlap, sympatric Indri and diademed sifakas are an excellent model to examine spatial coexistence strategies through direct comparisons of home range use, core area overlap, and daily path length. Simultaneous monitoring of both species can also show how they differentially adjust their ranging in response to shifting climates and food resource availability.

Estimates of both indri and diademed sifaka home range sizes vary among sites. While both species inhabit both pristine and disturbed forests throughout their species ranges, diademed sifakas have demonstrated the most variation in home range size and overall ecological flexibility (Irwin 2006; Irwin 2008).

One limitation in our current understanding of indri and diademed sifaka home ranges is that only the MCP has been used to measure home range size in all studies but Irwin (2008) and Blanchard (2007). As with the indri, Blanchard's study (2007) represents one diademed sifaka group that was followed for nine months. The MCP method measures the smallest polygon from a set of GPS points with no angle exceeding 180 degrees. This method has been widely used in studies of primate ranging and endorsed by the IUCN to measure habitat areas of species because of simplicity and ability to provide cross-site comparisons (IUCN 2001). While useful, this method overestimates overall home range size and does not provide consideration for the intensity to which certain areas are used (Burgman and Fox 2003; Worton 1995). Kernel density estimations (KDE) of home range size allow for a more fine-grained understanding of home range use by measuring the intensity to which areas are used (Worton 1995). This is a particularly useful and informative tool in the study of niche separation and coexistence strategies of sympatric species as it provides valuable information on specific areas of overlap between species.

Three long-term studies have documented indri ranging behavior at three different sites, each of which differs in the degree of habitat disturbance. The earliest study of indri was conducted at near the southern extent of their species' range at Analamazaotra, a small (~800 ha) forest patch that has been subjected to selective logging and can be considered to have the highest degree of anthropogenic disturbance of the three indri study sites (Junge et al. 2011; Pollock 1977). Analamazaotra is surrounded by *Eucalyptus* plantations and the two indri study groups were separated by a road (Junge et al. 2011; Pollock 1977). Indri MCP home ranges at this site were 17.7 and 18 ha which are the smallest reported home range sizes for this species (Pollock 1977). At Mantadia which is located 20 km north of Analamazaotra, Powzyk (1997) studied two groups of indri in a large (~10,000 ha) montane rain forest which is pristine and undisturbed by humans (Powzyk 1997; Powzyk and Mowry 2003). Indri MCP home ranges at Mantadia are 34 and 40 ha which is twice as large as those reported from Analamazaotra and the largest reported for this species (Powzyk 1997). Glessner and Britt (2005) followed three groups of indri in the southern portion of Betampona and reported an average MCP home range size at 27 ha (21, 24, and 36 ha by group) for this species. Of these three sites, Betampona, which is also the focus of my research is intermediate in terms of size (2228 ha) and level of anthropogenic disturbance (see Chapter 2 for more detailed site description). Blanchard (2007) also contributed to the existing body of indri home range literature with a nine-month (February to October) study of one indri group at Mantadia and reported a smaller MCP home range than Powzyk (1997) at 13.2 ha.

Diademed sifaka ranging has been studied where they are allopatric at Tsinjoarivo as well as at Mantadia where they overlap with indri (Irwin 2008; Powzyk 1997). The Tsinjoarivo sifakas had much larger MCP home ranges in continuous forest habitats (83.1 and 75.98 ha) than in forest fragments (21.22 and 47.33 ha) (Irwin 2008). Their home ranges in fragmented habitats were equal or smaller to sifaka populations in the pristine forests of Mantadia where they coexist with indri. Differential use of particular areas within home ranges has not been examined in these taxa with the exception of Tsinjoarivo.

The aim of this chapter is to examine strategies of indri and diademed sifakas to maintain coexistence across different ecological contexts. I report intra- and inter-specific patterns of home range size, home range use, and DPL for these primate populations at Betampona, and compare these findings to other populations when comparative data are available.as. Intra- and interspecific areas of home range overlap and the intensity of home range use are also used to examine mechanisms of niche separation. I also examine the effect of seasonality on DPL. In addition to broadening our understanding of indri and diademed sifaka ranging behavior, this study aims to contribute to broader theoretical discussions of coexistence strategies and factors driving variation within and between species across study sites.

5.2 Hypotheses and Predictions

When primates with similar dietary patterns coexist, they avoid resource competition via niche partitioning. The most common niche partitioning mechanisms are 1) dietary divergence, 2) lack of spatial overlap, 3) use of different levels in the forest (Schreier et al. 2009). Primates that are more folivorous tend to have smaller overall home ranges and daily path lengths (Clutton-Brock and Harvey 1977; Milton and May 1976). I hypothesize that, if primate-wide trends regarding the relationship between morphology, diet, home range size, and daily path length remain consistent for indri and diademed sifakas, then niche differentiation strategies can be predicted from their differences in morphology. Based on the current body of literature, indri and diademed sifaka home range sizes and daily path lengths differ interspecifically and also fluctuate throughout the year (Blanchard 2007; Irwin 2006; Pollock 1975; Pollock 1977; Powzyk 1997). Building on general primate-wide trends related to diet and ranging patterns, along with knowledge of indri and diademed sifaka home range size and DPL from other sites, I propose the following hypotheses and predictions:

H_1: Primates that consume more fruits and seeds in their diet need to travel farther to find these patchily distributed resources relative to primates that feed on a higher proportion of leaves. As such, they tend to have larger home ranges and longer daily path lengths. Previous research has shown that indri and diademed sifakas have species-specific differences in home range size, with indri home ranges being smaller than those of diademed sifakas.

$P_{1.1}$: Indri home ranges will be smaller than diademed sifaka home ranges.

H_2: Territorial primates do not overlap with conspecifics in the parts of their home ranges that are actively defended (Krebs and Davies 1978) Indri and diademed sifakas are reported to be territorial primates (Blanchard 2007; Pollock 1975; Powzyk 1997). Indri and diademed sifakas are reported to be territorial primates (Blanchard 2007; Pollock 1975; Powzyk 1997). If these species are territorial, then home ranges will not overlap intraspecifically but will overlap interspecifically.

$P_{2.1}$: Intraspecific home ranges will not overlap.

$P_{2.2}$: Interspecific home ranges will overlap.

H_3: Indri and diademed sifakas have been characterized as sympatric confamilial primates that maintain coexistence through niche separation (Powzyk 1997; Powzyk and Mowry 2003). If differentiation of habitat preferences is one of their strategies to maintain coexistence, then they will overlap less in core areas than less intensively used areas of their home ranges.

$P_{3.1}$: The percent of interspecific core area overlap (50% kernel) will be lower than overlap in other areas of their home range (95% kernel and MCP).

H_4: Based on the knowledge that indri are more folivorous than diademed sifakas and, as such, do not need to travel as far to reach patchily distributed food sources, indri DPL will be shorter than that of diademed sifakas.

$P_{4.1}$: DPL of indri will be significantly shorter than diademed sifakas.

H_5: Indri and diademed sifakas decrease their daily active period in cold, rainy months. DPL will also decrease during this time.

$P_{5.1}$: Both species will reduce daily path length in cold, rainy months.

5.3 Methods

Data collection methods, study site, and focal groups are described in detail in Chapter 2. Here I outline methodologies specific to this chapter.

All spatial analyses were conducted using ArcGIS 10.1. To facilitate between-site comparisons of home range size, I determine MCPs for each study group based on daily travel paths recorded during this study at 15-minute intervals. I also calculated home range size using KDE with a 95% contour to determine home range size and a 50% contour to delineate core areas (cell size: 20 m^2, bandwidth: 20 m) (Worton 1995).

I used GPS points collected at 15-minute intervals throughout daily follows of focal groups to calculate DPL. I calculated DPL on days where we were able to follow groups from sleeping site to sleeping site or on days that we were able to collect GPS track log data before 7:00 in the morning through 16:30 in the afternoon. DPL values represent the horizontal distance traveled by a group throughout the day (see Chapter 3 for vertical use of the vertical strata in the forest). To examine the effect of seasonality on lemur ranging behavior, I averaged DPL calculations from the cold, rainy months of May to August; the warm, dry months of September to November; and the warm, rainy months of December to March. I excluded April from the seasonal analyses because it is a time of transition from the warm, rainy season to the cold, rainy season and also due to low sample size of daily follows for diademed sifakas (N = 1) during that month. Comparisons are made for home range size and DPL between sites when comparable methodologies and time scales are available.

5.4 Results

5.4.1 Home Range Size per Group and Species Average

Diademed sifaka group home ranges were larger, on average, than indri home ranges based on MCP and KDE analyses (Table 5-1;Table 5-2). Indri MCP home ranges were 21.17 ha on average with a wide range of variation (N = 6 groups, range = 13 – 32 ha), with the two-southernmost groups having the smallest home ranges and the northern groups within more pristine habitats having the largest home ranges (Table 5-1; Figure 5-1). When compared to other study sites, the average indri home range for these six groups was smaller than Mantadia, but larger than Analamazatora (Pollock 1977; Powzyk 1997). Blanchard (2007) reported a small home range for one indri group at Mantadia (13.2 ha) from February to October.

Table 5-1. Home range size estimates for each indri group and site averages for Betampona, Mantadia, and Analamazaotra.

Study Group	**MCP (ha)**	**95% Kernel (ha)**	**50% Kernel (ha)**	**Group Size**	**Source**
SE	16	6.36	1.24	2	Current Study
SW	13	6.75	1.69	2	Current Study
CE	18	5.53	2.38	2.5	Current Study
CW	18	5.04	1.15	3	Current Study
NE	32	9.64	3.69	2 to 4*	Current Study
NW	30	10.76	3.44	3.5	Current Study
BNR 1	21			3	Glessner and Britt 2005
BNR 2	24			4	Glessner and Britt 2005
BNR 3	36			2	Glessner and Britt 2005
Mantadia 1	13.2	8**		3	Blanchard 2007
Mantadia 2	34			2	Powzyk 1997
Mantadia 3	40			2	Powzyk 1997
Analamazaotra 1	17.7			5	Pollock 1975
Analamazaotra 2	18			2.5	Pollock 1975
Current study	21.17	7.35	2.26	2.6*	
BNR	27			3	Glessner and Britt 2005
Mantadia (2007)	13.2	8**		3	Blanchard 2007
Mantadia (1997)	37			2	Powzyk 1997
Analamazaotra	17.85			3.75	Pollock 1975

* Indri group NE was not included in group size averages. See text for further details regarding the demographic composition of group NE.

** Blanchard’s (2007) KDE analysis includes all GPS points with 18 m^2 cell sizes.

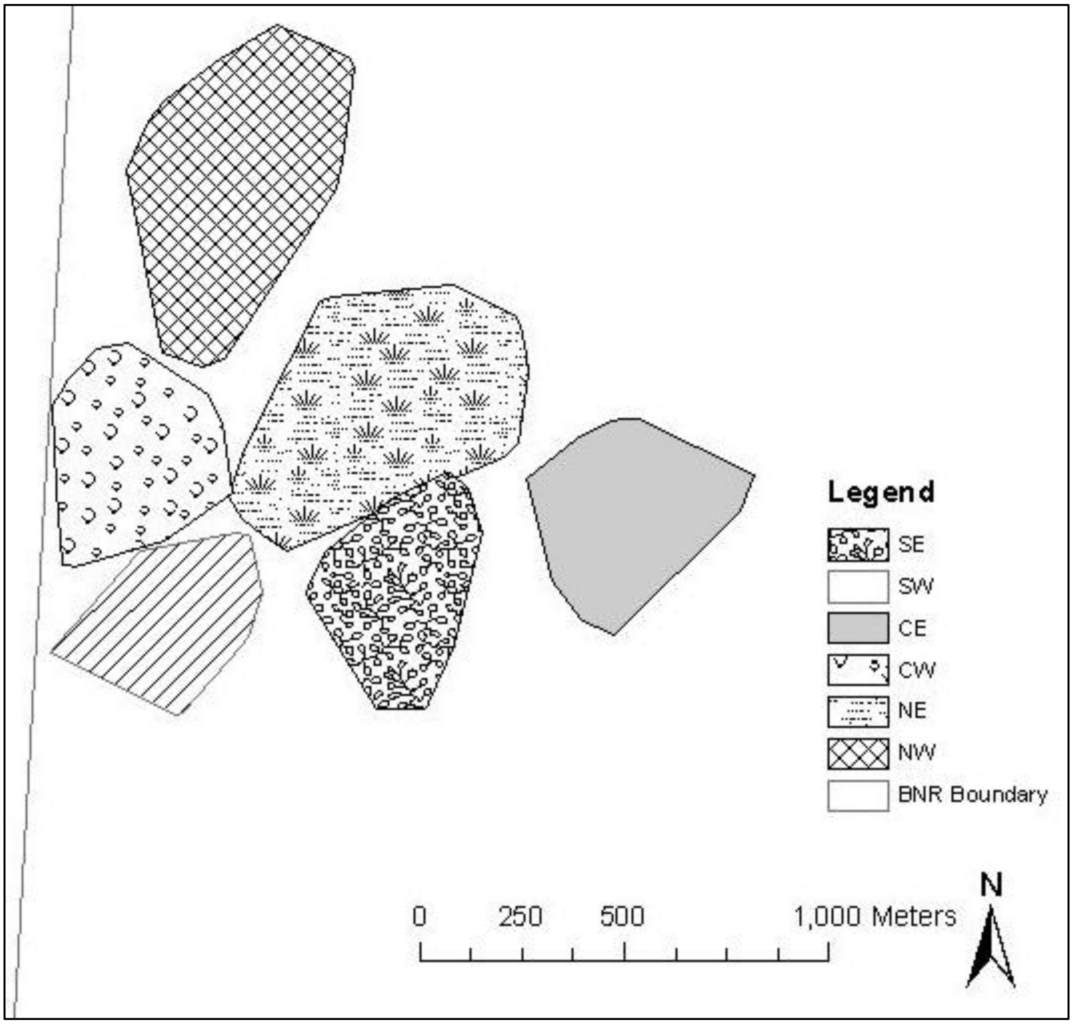

Figure 5-1. Indri group locations at BNR based on MCP analysis.

It is important to note that the NE indri group composition fluctuated throughout the study period. One adult male was radio collared, and observed with three separate adult females on different days. The adult male associated primarily with two females, one collared female (AF1) in the eastern portion of his home range and another collared female (AF2) in the western portion of his range. The two females did not overlap spatially or temporally, which is expressed in the large NE home range size (Figure 5-2). The eastern female (AF1) was with a juvenile and subadult from February through July 2013. The subadult and juvenile were not seen with AF1 after July 2013 and their whereabouts are unknown. In November 2013, we found the NE adult male with a third collared female (AF3) and an infant. The only individual with a radio collar was the adult male so we were only able to reliably find and follow him. Home range analyses for this group represented the size of the male's home range, but the extent of the home ranges including females was undetermined.

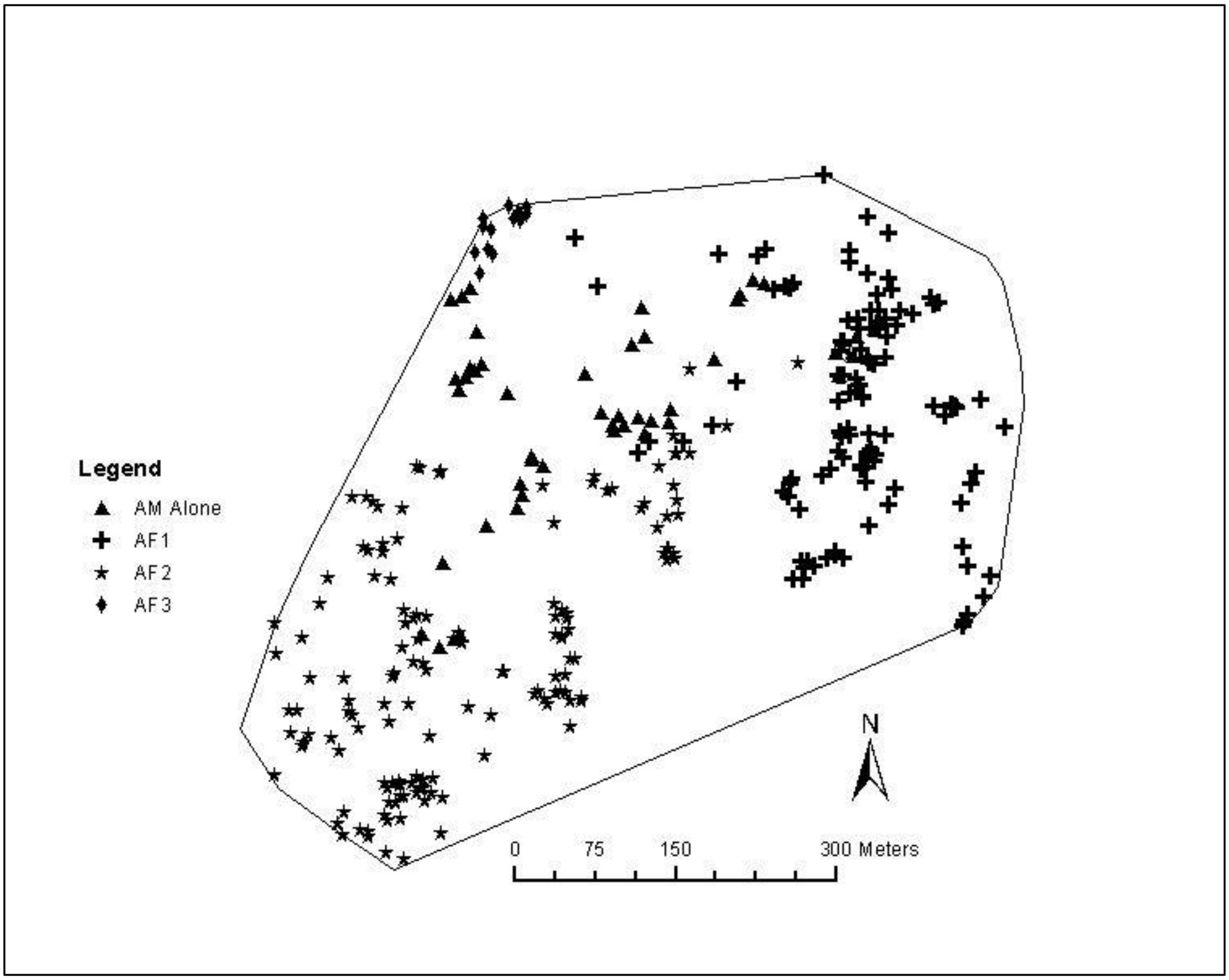

Figure 5-2. Indri group NE locations based on group composition. Points here represent locations of feeding trees.

I found the same south-to-north spatial gradient pattern for the diademed sifaka groups where the southernmost group had the smallest home range (37ha), followed by the central group

(51 ha) (Figure 5-3, Table 5-2). The north group's home range was the largest (54 ha) but the Central and North group home range sizes were more alike than either group's home range size was to the South group. Diademed sifaka home ranges were, on average, larger than those reported at Mantadia and in the fragmented Tsinjoarivo site but smaller than the continuous forest at Tsinjoarivo for both the MCP and KDE measures.

Table 5-2. Diademed sifaka home range size at Betampona, Mantadia, and Tsinjoraivo.

Study Group	**MCP (ha)**	**95% Kernel (ha)**	**50% Kernel (ha)**	**Group Size**	**Source**
South	37	12.69	1.80	2	Current Study
Central	51	18.40	3.19	3	Current Study
North	54	9.45	4.88	4	Current Study
Mantadia 1	27	12.8		7	Blanchard 2007
Mantadia 2	42			6	Powzyk 1997
Mantadia 3	33			3	Powzyk 1997
Tsinjoarivo Cont 1	83.18	72.24	8.56	5.5	Irwin 2006
Tsinjoarivo Cont 2	75.98	79.29	13.42	5.5	Irwin 2006
Tsinjoarivo Frag 1	21.22	19.61	3.53	4	Irwin 2006
Tsinjoarivo Frag 2	40.06	36.78	5.86	5	Irwin 2006
Current study	47.33	13.51	3.29	3	
Mantadia (2007)	27	12.8		7	Blanchard 2007
Mantadia (1997)	37.5			4.5	Powzyk 1997
Tsinjoarivo Cont	79.58	75.65	10.99	5.5	Irwin 2006
Tsinjoarivo Frag	30.34	30.64	4.7	4.5	Irwin 2006

* Blanchard's (2007) KDE analysis includes all GPS points with 18 m^2 cell sizes.

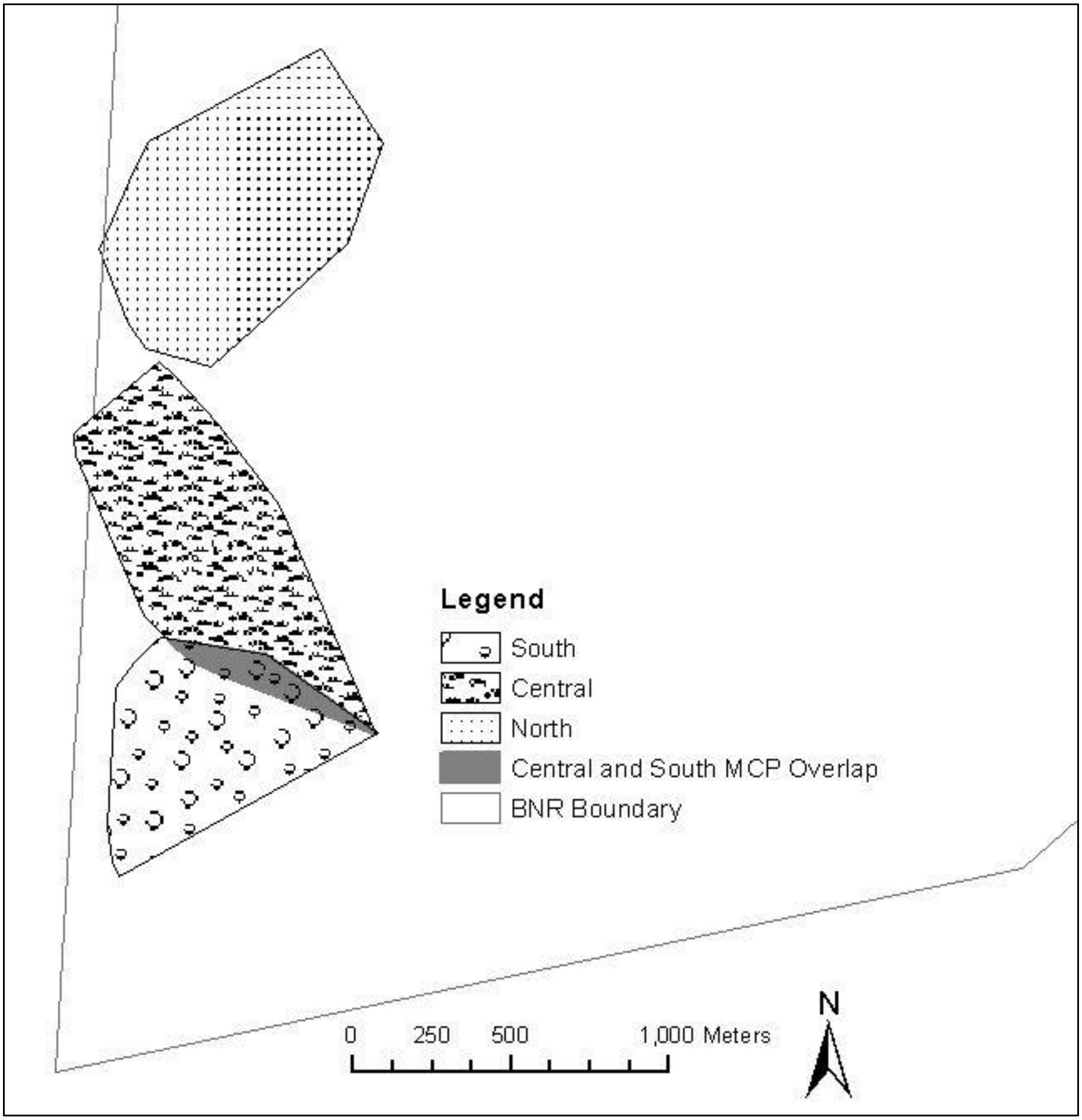

Figure 5-3. Diademed sifaka group locations at BNR based on MCP analysis.

Both species maintained territorial boundaries as evidenced by the low amount of home range overlap between groups. Intraspecifically, I found very small areas of overlap between indri groups SE and CE and between CE and CW from the MCP analysis but no KDE home range or core area overlap. The diademed sifaka Central and North groups did not overlap

(Figure 5-4). There was, however, overlap between the Central and South Diademed sifaka groups (MCP: 4.48ha, 95% kernel: 0.59 ha overlap, 50% kernel: 0.0014 ha overlap) (Figure 5-4). While the two Diademed sifaka groups rarely overlapped in both space and time, we observed two intraspecific aggressive encounters (See Chapter 4 for a full description of the encounter) (see Figure 5-4).

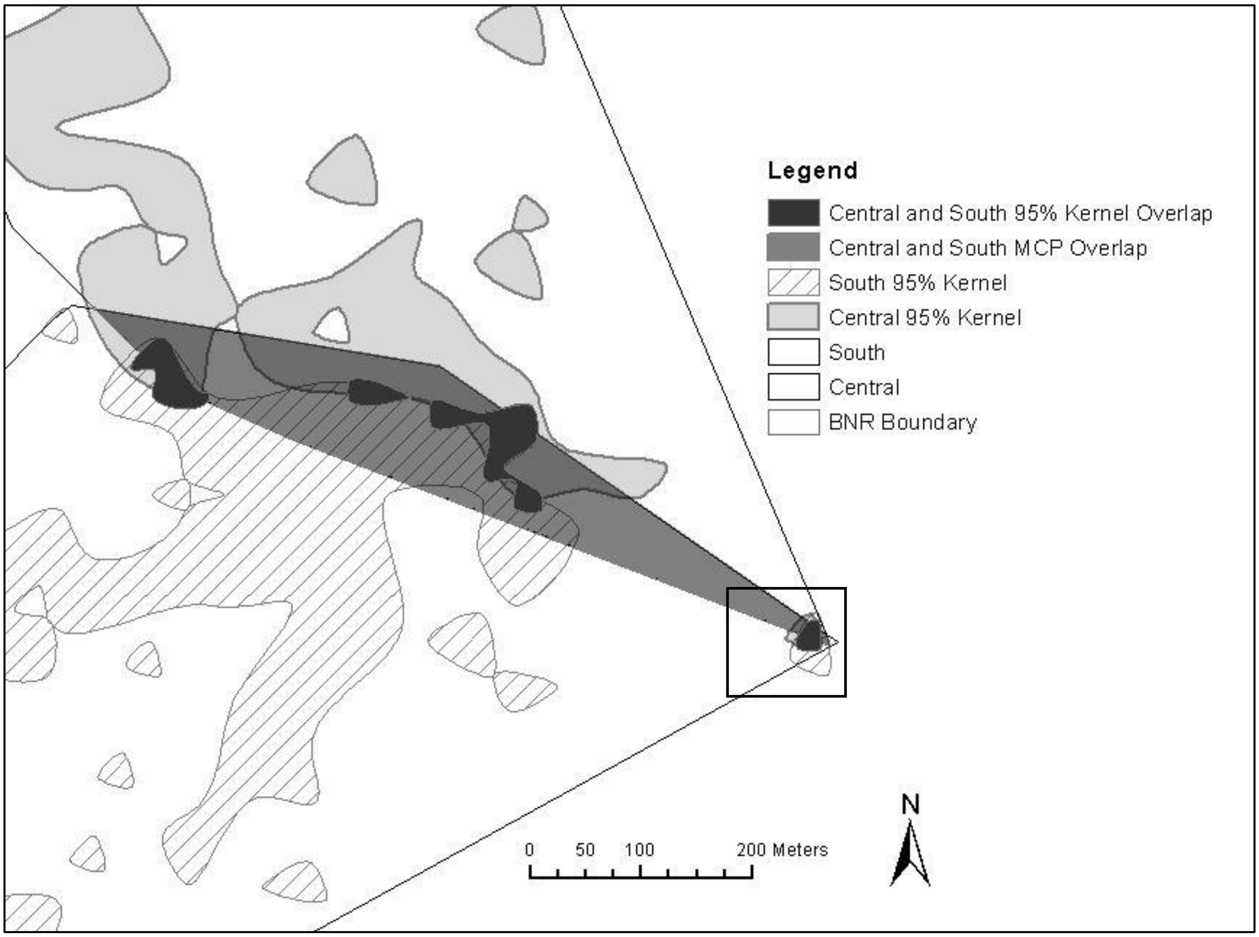

Figure 5-4. Diademed sifaka area of overlapping home ranges between the South and Central groups. The area in the black box in the eastern extent of both groups' ranges indicates the location of two intraspecific aggressive encounters. See Chapter 4 for a detailed discussion of this encounter.

I found interspecific home range overlap between the Central diademed sifaka group and the SW and CW indri groups and between the North diademed sifaka group and the NW indri group (Table 5-3). While none of the diademed sifaka study groups in this study overlapped with the eastern indri groups that we studied, we did encounter other sifakas while in the home range of the CE and NE groups. We did not encounter sifakas while in the SE home range and it is unclear if sifakas inhabit that region.

Table 5-3. Amount of home range and core area overlap between indri and diademed sifakas. Values indicate that the entire indri home range was encompassed by the diademed sifaka group.

	Diademed sifaka/Indri Group Name		
	Central/SW	**Central/CW**	**North/NW**
MCP Overlap (ha	13	18	30
% Diademed sifaka overlap	25.49	35.29	55.56
% Indri overlap	100	100	100
95% Kernel Overlap (ha)	4.4	1.69	4.29
% Diademed sifaka overlap	23.91	9.18	39.88
% Indri overlap	65.19	33.53	39.88
50% Kernel Overlap (ha)	0.12	0.06	0.34
% Diademed sifaka overlap	3.76	1.88	6.97
% Indri overlap	7.11	5.22	9.89

The KDE analysis illustrated that home ranges were not used uniformly by either species of lemur. I found differing intensities of use within the home range of each group as well as distinct core areas (50% kernel) (Figure 5-6). While, on average, the core area occupied by diademed sifakas was larger than indri, the ratio of core area to the overall home range was similar (indri: 30%, diademed sifakas: 27.7%). Neither species appeared to avoid forest edge habitats as groups that inhabited home ranges near the border of the reserve (all diademed sifaka groups and the western indri groups) utilized areas near the boundary of BNR.

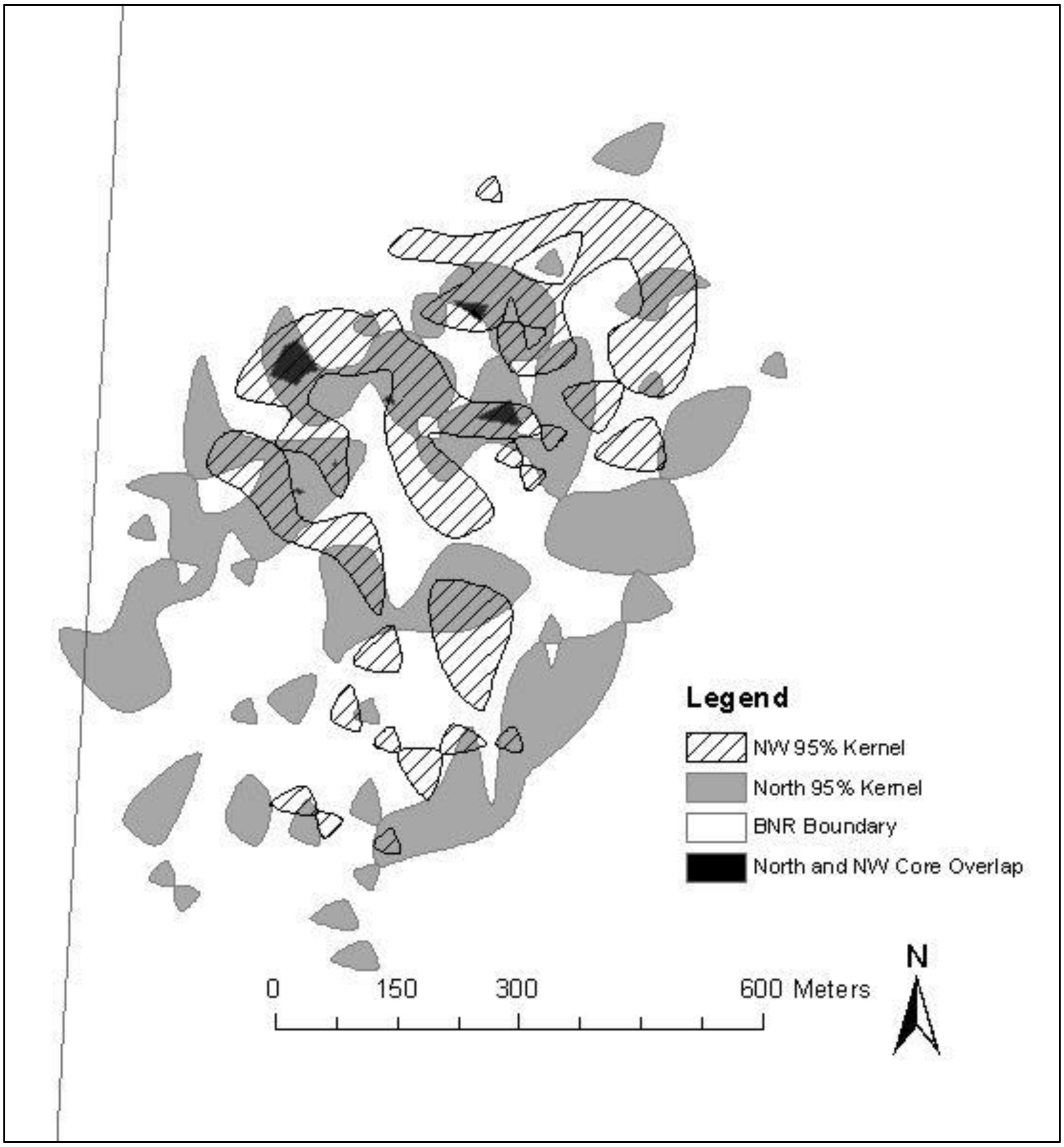

Figure 5-5. Graphical representation of sifaka (North group) and indri (NW group) home range overlap. The 95% kernel home range is represented for each species along with core area overlap.

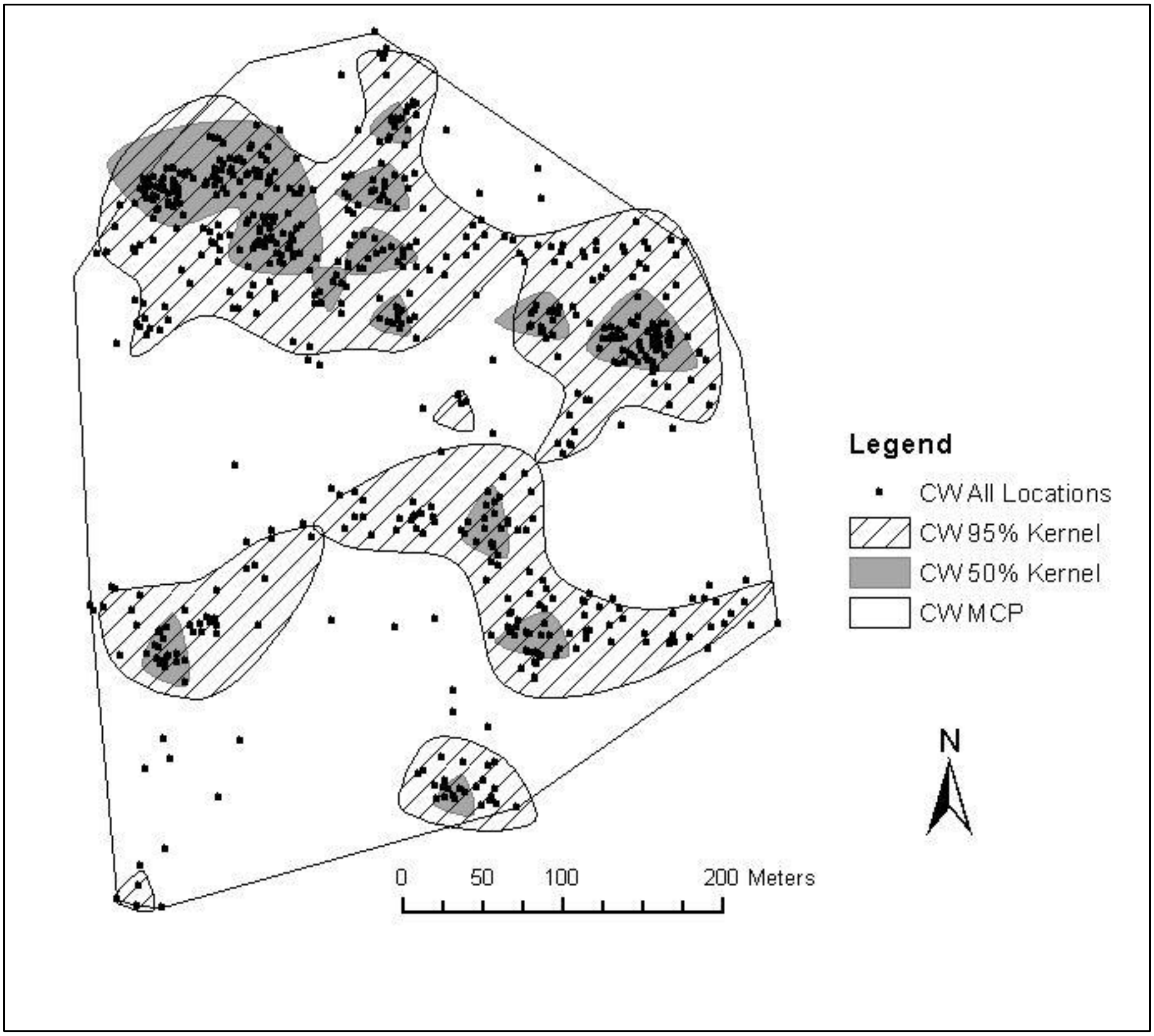

Figure 5-6. Example of areas of differing intensity of home range use. In this example, all GPS points, the 95% kernel home range, 50% kernel core areas, and MCP home range for indri group CW are depicted.

5.4.2 Daily Path Length Per Group and Species Averages

Average DPL was significantly longer for diademed sifakas than for indri ($U = 609$, $p < 0.0001$) (Table 5-4 and Table 5-5). Within species, I found no statistically significant between-group differences in DPL (Kruskal-Wallis test: Indri, $H = 4.122$, $p = 0.5319$; Diademed sifakas, H = 2.935, p = 2.935) (Figure 5-7 and Figure 5-8). Diademed sifakas exhibited more overall variation in DPL than indri (diademed sifaka: 593-2332, indri: 344-1409) (Figure 5-9).

Indri average DPL (733 m) and the range of variation in DPL were very similar to groups from the year-long study at Mantadia (759 m) (Powzyk 1997). Blanchard, however, (2007) reported shorter DPL estimates (482 m) in a study of one indri group at Mantadia from February to October. When only these months were considered, I found that the indri at BNR still had a longer DPL (N = 78 days, average DPL = 740.4 m).

I also compared average DPL for diademed sifakas at Mantadia (Blanchard 2007; Powzyk 1997) and both the continuous and fragmented sites at Tsinjoarivo (Irwin 2006; Irwin 2008). Average DPL values at BNR were longer than both sites at Tsinjoarivo and Blanchard's (2007) group at Mantadia but shorter than the average reported by Powzyk (1997) at Mantadia. The average DPL for diademed sifakas at BNR from February to October was slightly shorter than the annual average at 1166 m (N = 26 days) but still longer than Blanchard's (1997) estimates from Mantadia.

Table 5-4. Indri DPL, standard deviation, range, and sampling effort by group and by study site.

Study Group	**Mean DPL (m)**	**SD**	**Range**	***N***	**Source**
SE	794.1	268.2	439 - 1329	18	Current study
SW	714.7	249.4	339 - 1063	16	Current study
CE	633.5	279.9	344 - 1129	13	Current study
CW	705	198.8	402 - 1000	21	Current study
NE	794.9	285.5	344 - 1324	19	Current study
NW	739.1	262.7	385 - 1409	17	Current study
Mantadia 1	482	171.9	250-947	26	Blanchard 2007
Mantadia 2	814		330 - 1550	59	Powzyk 1997
Mantadia 3	704		335 - 1340	34	Powzyk 1997
BNR	733	256.5	344-1409	103	Current study
Mantadia (2007)	466	171.9	250-947	26	Blanchard 2007

Mantadia (1997)	759	241.33	330-1540	93	Powzyk 1997

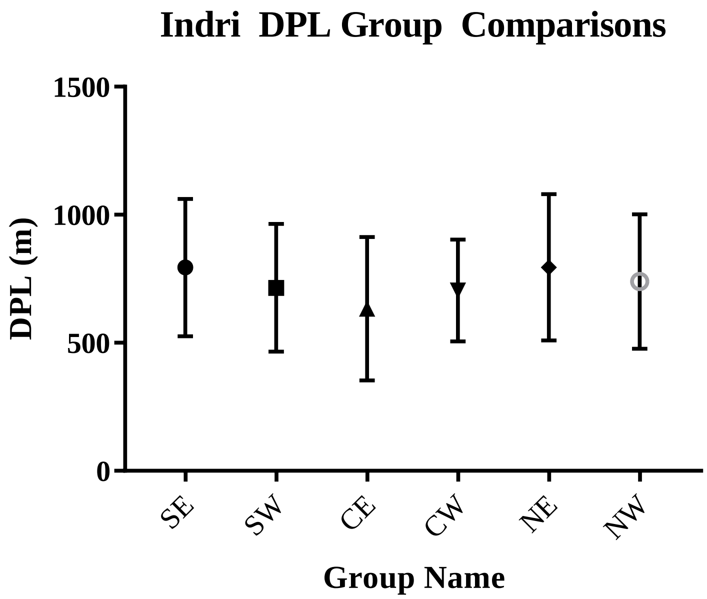

Figure 5-7. Indri DPL group comparisons with mean and range represented.

Table 5-5. Diademed sifaka DPL in meters, standard deviation, range, and sampling effort by group and study site.

Study Group	Mean DPL (m)	SD	Range	*N*	Source
South	1361	528.4	601 - 1956	8	Current study
Central	1130	338.3	610 - 2068	19	Current study
North	1402	453.4	934 - 2332	13	Current study
Mantadia 1	1650	450.92	600 - 2575	39	Blanchard 2007
Mantadia 2	1595	241.33	330-1540	25	Powzyk 1997
Mantadia 3	902	326.9	489-1708	23	Powzyk 1997
Tsinjoarivo Cont 1	1046	208	342 - 1439	66	Irwin 2006, 08
Tsinjoarivo Cont 2	935	204	464 - 1539	56	Irwin 2006, 08
Tsinjoarivo Frag 1	769	na	600 - 2575	39	Irwin 2006, 08
Tsinjoarivo Frag 2	917	na	755 - 2470	25	Irwin 2006, 08
BNR	1248	146.6	593 - 2332	41	Current study
Mantadia (2007)	902	326.9	489-1708	23	Blanchard 2007
Tsinjoarivo Cont	987	79.49	412-2014	125	Irwin 2006, 08
Tsinjoarivo Frag	837	104.7	342-1539	122	Irwin 2006, 08
Mantadia (1997)	1623	450.92	600-2575	64	Powzyk 1997

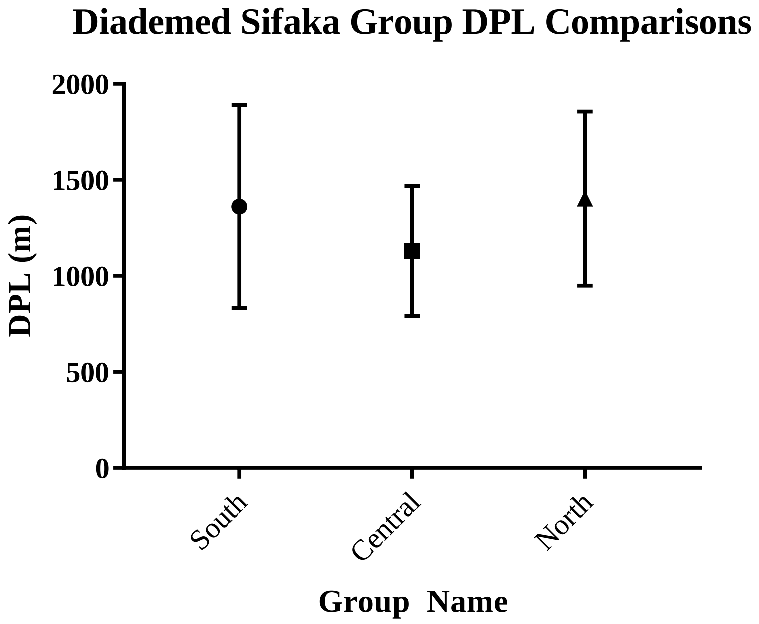

Figure 5-8. Diademed sifaka DPL group comparisons with mean and range represented.

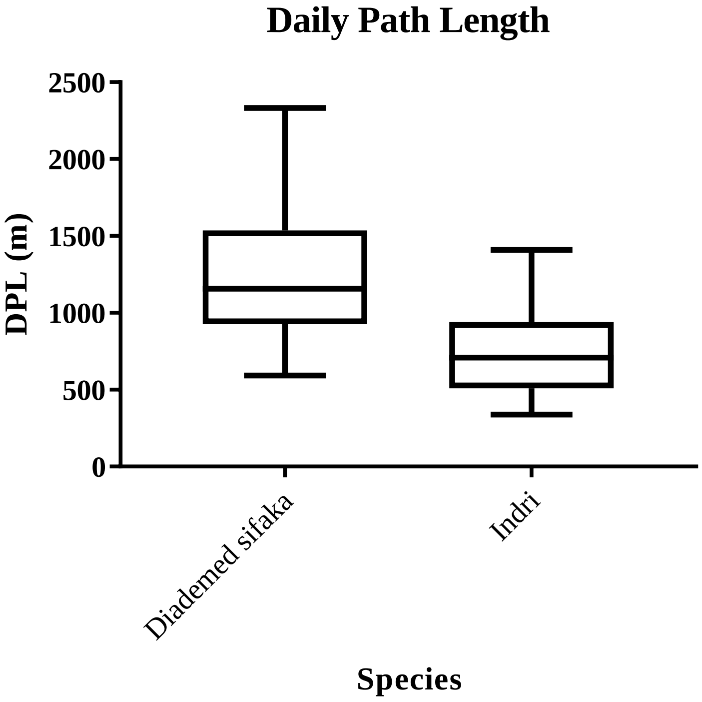

Figure 5-9. Comparison of DPL for diademed sifakas and indri at BNR.

5.4.3 Relationship Between DPL with Temperature and Rainfall

Diademed sifaka DPL varied less from May to August but I found no significant seasonal differences (Kruskal-Wallis test: H = 5.052, n.s.) (Figure 5-10). Indri varied less in DPL between seasons than diademed sifakas and I found no significant differences between seasons (One way ANOVA, F = 0.9346, n.s.). Mean DPL was longest between December and March for both species. The overall longest DPL was recorded in December for diademed sifakas (2332 m) and in February for indri (1409 m).

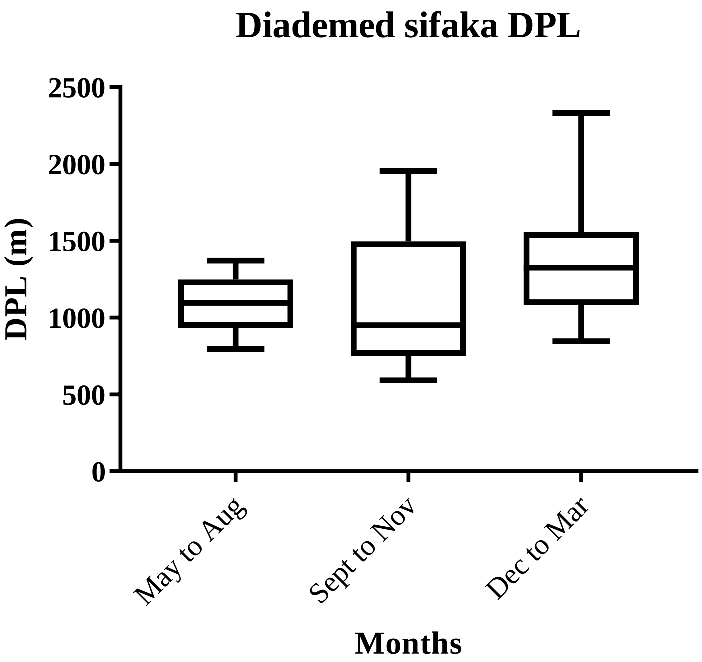

Figure 5-10. Daily path length comparisons across seasons for diademed sifakas at BNR.

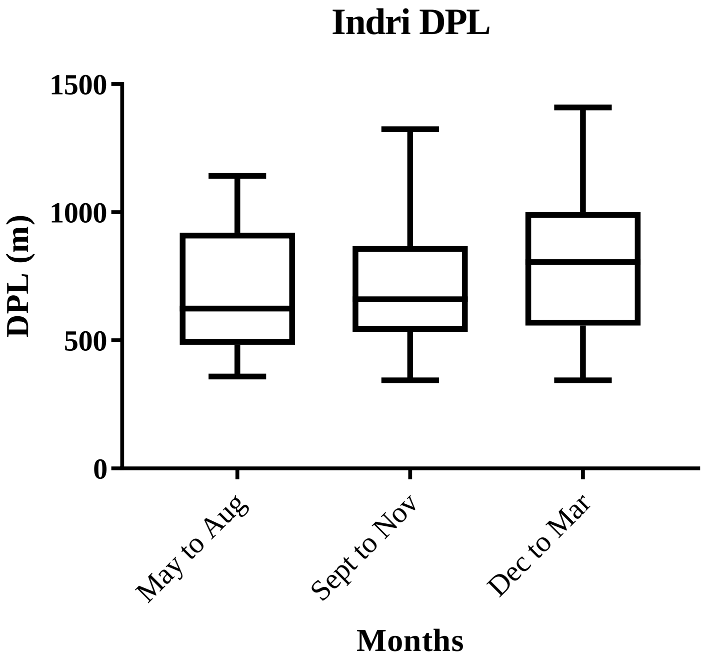

Figure 5-11. Daily path length comparisons between seasons for indri at BNR.

5.5 Discussion

5.5.1 Overview

Ecologically similar, sympatric primates employ several mechanisms of niche separation to maintain coexistence. Differences in habitat preferences and home range use can allow primates to overlap in space but avoid direct overlap by occupying those areas at different times. Indri and diademed sifakas exhibited species-specific patterns in both home range size and daily path length. As predicted by their diet composition, diademed sifakas occupied larger home ranges than indri. As predicted, the more frugivorous diademed sifaka had larger home ranges and longer daily path lengths. This follows the general primate-wide trend that, because fruits are more widely dispersed than leaves, home range size increases with a species' degree of frugivory (Clutton-Brock and Harvey 1977). Intraspecific home range was low supporting the hypothesis that these species are territorial. While interspecific home range overlap occurred these two species did not use their home ranges homogeneously. Overlap in core areas was low (<10%) which strongly suggests that indri and diademed sifakas exhibit differential habitat use as a coexistence strategy.

5.5.2 Home Range Overlap

Home ranges overlapped between indri and diademed sifakas considerably, but the two species rarely used these overlap areas as the same time. Additionally, the percent of non-core area overlap was greater than in the more intensively used core areas. This demonstrates both spatial and temporal differences in habitat use in these two species. We observed one interspecific encounter during the period of data collection (see Chapter 4). In contrast, we commonly observed groups of brown lemurs (*Eulemur albifrons*) and black and white ruffed lemurs (*Varecia variegata*) within 30 meters of the indri and diademed study groups. Both species are frugivorous and are not considered competitors for resources with either indri or diademed sifakas. This regular interspecific overlap occurred several times per day and a *Eulemur* or *Varecia* group would occasionally remain in sight for several hours during our daily follows of indri and diademed sifakas. On one occasion, a group of brown lemurs was traveling through a large tree crown where a group of diademed sifakas were feeding. One *Eulemur* physically climbed over a sifaka while the sifaka was feeding with no agonistic or affiliative response from either species. This co-occurrence was not considered a polyspecific association as groups did not feed or travel together, but both species tolerated the presence of each other without any indication of agonistic or affiliative behavior (Cords 1990). We also occasionally observed lesser bamboo lemurs (*Hapalemur griseus*) near indri and diademed sifaka groups but they were generally in the understory layer of the canopy. Bamboo lemurs are also not considered competitors for resources as they primarily feed on bamboo (Tan 1999).

While indri and diademed sifakas overlapped in many areas of their home range, they clearly temporally differed in home range use relative to the *Varecia, Eulemur,* and *Hapalemur* species at BNR. The low rate of intergroup encounters between indri and diademed sifakas relative to the other diurnal (or cathemeral) lemurs previously mentioned supports this notion. While no aggressive interspecific encounters were observed, an indri group was displaced by a diademed sifaka group on one occasion during this study (See Chapter 4). The KDE provided a more nuanced view of home range and core area use for these species. At BNR, core area overlap is small which greatly reduces the opportunity for overlap in space and time.

At Mantadia, Blanchard (2007) reported interspecific encounters between indri and red-bellied lemurs (*E. rubriventer*) and bamboo lemurs (*H. griseus*) where the indri appeared to be unaffected by the presence of another lemur species. The same pattern of avoidance was reported between diademed sifakas and both red-bellied and bamboo lemurs (Blanchard 2007). Of the three interspecific encounters between indri and diademed sifakas at Mantadia varied. In one instance, Powzyk (1997) reported one affiliative interspecific encounter (see Chapter 3). Powzyk (1997) also reported that another diademed sifaka group would “often” chase an indri group with an overlapping territory. Blanchard (2007) described observed one interspecific encounter that involved an indri group that chased a diademed sifaka group. The difference in interspecific interactions between indri and diademed sifakas when compared to other lemur species indicates both spatial and temporal habitat differentiation as a coexistence strategy.

5.5.3 Species Differences in Home Range Use

Both species exhibited clear preferences for some areas over others as evidenced by the KDE. Intraspecifically, home range overlap was very low which is a consistent trend for territorial primates (Mitani and Rodman 1979). Indri use group long calls as a territorial spacing mechanism (Geissmann and Mustchler 2006; Giacoma et al. 2010; Pollock 1975) whereas sifakas scent mark around boundaries and occasionally engage in intergroup encounters (Day et al. 2009; Powzyk 1997). The prediction that group home ranges would not overlap intraspecifically was supported for indri but not for diademed sifakas. Indri intergroup encounter rates are rare but have been reported in Analamazaotra where anthropogenic disturbance is high (Pollock 1977). At Mantadia, Powzyk (1997) reported an indri intergroup encounter where "agitation calls" were used to displace one group from a feeding tree. In another instance, Powzyk (1997) observed two indri groups resting within 50 m of a neighboring group.

Diademed sifakas intergroup encounters are not common but do occur near territorial boundaries (Powzyk 1997). At BNR, two interspecific group encounters were observed in December 2013 between the Central and South diademed sifaka groups. The adult males from each group physically wrestled on the ground while the other group member chased each other. The Central group initiated the event and retreated afterward in both instances. While no groups were feeding at the time of the encounter, this was a territorial dispute over nearby feeding trees that were fruiting at the time (*Syzygium* sp.).

Both indri and diademed sifaka home range sizes were smaller for groups in the southern part of BNR. The two northernmost indri groups had particularly large home ranges. The NE group home range size is likely the result of the unique grouping pattern observed where one adult male spent time with at least three non-overlapping females. Group size has been used to explain differences in home range size in primates as larger groups require more resources (Clutton-Brock and Harvey 1977; Milton and May 1976). The home range of the adult male, therefore, had to provide sufficient food resources for a minimum of four adult indri. The large home range for the NW group is more difficult to explain as it included two adults, one subadult, and one infant (born in June 2013). Two explanations are possible 1) the other indri home ranges provide sufficient resources in a smaller area, or 2) the population density of indri in the northern areas of the reserve is lower than in the south. Indri population density estimates have varied widely at BNR from 2.6-3.2 individuals/km^2 (Welch and Katz 1992) to 13.2 individuals/km^2 (Glessner and Britt 2005) and have primarily been conducted in the southern area of the reserve. Longitudinal monitoring of these groups and the addition of groups in the north of BNR are an important avenue for future research to determine factors that influence indri home range size.

Diademed sifakas also exhibited the same pattern where the South group had the smallest home range based on MCP analysis. When home range was assessed using KDE, the North group had the smallest 95% kernel home range but the largest 50% kernel core area. The mean DPL for each group was similar for each group. Three non-mutually exclusive explanations are possible; 1) territorial defense, 2) resource distribution differences, or 3) group size. Powzyk (1997) found that the diademed sifakas at Mantadia traveled to most territorial boundaries every four to eight days. The intergroup encounters between diademed sifakas observed at BNR supports the notion that territorial defense is necessary. The South group's small home range but consistent DPL relative to the other groups may be the result of more frequently traveling to territorial boundaries. As mentioned above, resource distribution may be a factor in home range size. The South group had the smallest core area of the three groups. Sufficient resources may be distributed patchily but in a smaller overall area than in the home ranges of the other groups. As mentioned above, in some primates, there is a positive relationship between group size and home range size. The South group was the smallest with only two individuals whereas the Central group consisted of 3-4 individuals. The North group had 4 individuals. A combination of these factors is likely but can only be determined through more intensive monitoring of these groups at BNR.

5.5.4 Seasonality in Home Range Use and Daily Path Length

The prediction that indri and diademed sifakas would decrease their daily path length in in cold, rainy months was partially supported. Diademed sifakas had less variation in their DPL in the cold, rainy months from May to August. Indri DPL decreased slightly during this time but, varied more widely from day-to-day. Powzyk (1997) also found that indri DPL varied less throughout the year than diademed sifakas This marked decrease in DPL for diademed sifakas and slight decrease in DPL for indri in the cold, rainy months corresponded with a decrease in seed feeding, and an increase in bark, petiole, and mature leaf feeding for both lemur species. Resting also increased and the length of the daily active period decreased during these months. These activity and dietary changes during this time of year are consistent with reports from Mantadia (indri and diademed sifakas) and Tsinjoarivo (diademed sifakas only) (Blanchard 2007; Irwin 2008; Powzyk 1997). The more dramatic fluctuations observed for diademed sifakas relative to indri indicate that they were more heavily impacted by seasonal changes in temperature, rainfall, and resource availability. This observed seasonal change is consistent with an “energy minimizing” strategic response to the increase in the consumption of lower quality foods (Clutton-Brock and Harvey 1977; Milton and May 1976).

5.5.5 Comparisons with Other Sites

Diademed sifakas exhibited greater variability in home range size and daily path length between sites than indri. They also inhabit forest fragments (Irwin 2006; 2008) and secondary forest habitats and are able to adjust to a wider variety of habitats than indri. At BNR, indri were only found in the primary forest whereas diademed sifakas are found in both primary and secondary forest. While indri have been reported to exist in areas with some degree of anthropogenic disturbance, they exhibited clear preference for the primary forest at BNR. It is unclear whether the botanical composition of the secondary forest lacks sufficient resources for indri or if the population density is low enough for indri groups to only inhabit the primary forest but warrants further investigation.

The diademed sifakas in the continuous forest at Tsinjoarivo (Irwin 2008) had much larger home ranges than I found at BNR or those reported by Powzyk (1997) at Mantadia. Irwin (2008) attributed this to the continuous forest sifakas feeding on rare and widely dispersed fruit trees. Diademed sifakas have demonstrated ecological flexibility and can survive in environments with varying population densities and resource availability (Irwin 2006; Irwin 2008). The degree to which these factors contribute to diademed sifaka home range size warrants further study as the population densities of the sifakas at all three study sites is unknown.

5.5.6 Conclusions and Future Directions

Summary of main findings:

- Diademed sifakas had larger home ranges than indri.

- Intraspecific home range overlap did not occur for indri and was small for two diademed sifaka groups.
- The area of diademed sifaka home range overlap was also the site of two aggressive inter-group encounters in December 2013.
- Both species exhibited preference for certain areas of their home ranges and used these areas more intensively than the rest of their home range. These areas of preference were referred to as core areas.
- Interspecifically, home ranges overlapped but the proportion of overlap in core areas was lower than overlap in the rest of their home ranges.
- While indri and diademed sifakas overlap spatially, they rarely occupy the same space at the same time.
- DPL was shorter for indri than diademed sifakas.
- Diademed sifaka DPL was shorter and had a wider range of variation in the cold, rainy months whereas indri DPL remained more stable throughout the year.

Overall patterns of home range use at BNR are similar to other study sites. When indri and diademed sifakas are sympatric, they maintain coexistence in three main ways 1) while their home ranges overlap, their core area overlap is small, 2) they rarely temporally overlap, and 3) diademed sifakas use a wider variety of habitats (primary and secondary forest) and are more ecologically flexible than indri. Results from BNR have yielded new insight into the overall species-wide trends for the spatial requirements and preferences for these indriids.

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Chapter 6: Summary and Conclusions

6.1 Overview

In this study, I examined how two closely related but morphologically distinct lemurs, indri and diademed sifakas, that reside the same habitat, maintain coexistence. This study represents a more comprehensive depiction of the behavior and ecology of these sympatric species than previous studies. Further, new research methods and analytical approaches enabled me to document several aspects of their ranging and sociality more precisely. Additionally, I have incorporated between-site comparisons to enhance our understanding of the behavioral variation and ecological flexibility exhibited by these critically endangered primates.

My primary objective for this research was to identify the coexistence strategies of these confamilial indriids at BNR to compare my findings with studies of indri and diademed sifakas at other sites and determine what mechanisms promote equilibrium of coexistence between these primates. I used activity patterns, dietary profiles, home ranges, and daily path lengths to assess potential differentiation of niches. I found species-specific differences in activity budgets, diets, home range size, and daily path length. Activity patterns, feeding, and ranging patterns of each species fluctuated throughout the year. In this chapter, I summarize the main findings and I discuss how these findings relate to previous research. I then examine how findings from this study relate to interpreting morphological characteristics of these folivorous primates. I also discuss the conservation implications of my research. Finally, I contextualize my findings in a broader anthropological framework and discuss their relevance to the interpretation of the primate fossil record and variation in morphology.

6.2 Summary of Main Findings

6.2.1 Activity Budget

The aim of Chapter 3 was to determine the degree of niche differentiation between sympatric indri and diademed sifakas through assessment of inter- and intra-specific differences in activity patterns, seasonal changes in activity, sex differences in rates of activity, and species-specific vertical stratification in forest use for specific activities. My research is the most comprehensive study of the activity budgets of indri (N = 6 groups, 18 individuals) and diademed sifakas (N = 3 groups, 9 individuals) to date, as it encompasses the largest sample of groups/individuals followed throughout an entire annual cycle. As predicted, activity patterns did not differ significantly between groups of the same species. Resting and feeding were the most commonly observed behaviors for both species. Diademed sifakas rested less often in the morning and late afternoon than indri, but rested more than indri in the middle of the day. The prediction that diademed sifakas would spend more time engaging in locomotion was supported, whereas predictions that they would spend less time resting and more time feeding than indri were not supported. Both species increased their daily active period as temperatures increased. The prediction that daily active period would significantly decrease with increased rainfall was supported for diademed sifakas, but not for indri. I found statistically and biologically significant differences in the amount of time spent and activities performed in different forest levels. Indri spent the majority of their time in the continuous canopy, whereas diademed sifakas spent the majority of time in both the continuous canopy and under canopy. Diademed sifakas spent more time on the ground than indri. Members of all sifaka groups were observed to feed, rest, and play on the ground. On the rare occasions that indri descended to the ground, they were only observed engaging in geophagy. Overall coexistence strategies as they relate to activity patterns for indri and diademed sifaka include divergent daily activity patterns, length of daily active period, and use of different forest strata.

6.2.2 Dietary Profiles

In this chapter, my primary objectives were to determine species differences in diets and potential dietary overlap for limited resources to identify mechanisms of resource partitioning between indri and diademed sifakas that facilitate maintenance of coexistence. To do this, I collected detailed behavioral and ecological data on species-specific feeding preferences, degree of resource overlap, and resource availability throughout an annual cycle at BNR. My predictions that diademed sifakas would feed from more plant species, a greater diversity of plant types, and on more fruits and seeds relative to indri were supported. This was consistent with previous reports of indri and diademed sifaka feeding behavior as well as with an overall primate-wide trend that more folivorous primates tend to have lower dietary diversity than more frugivorous primates.

Overall, there was relatively little overlap in food resources used by these sympatric lemurs. They overlapped in feeding from the same part of the same tree species on non-limiting, superabundant food sources at BNR. I also documented niche differentiation between diademed sifakas and indri in the use of different vertical strata they use while feeding from different plant parts. While both species primarily fed in the continuous canopy, indri often utilized the emergent canopy for feeding on leaves, flowers, and seeds. In contrast, diademed sifakas were not observed feeding in the emergent canopy during this study. Diademed sifakas fed from fruits, seeds and soil while on the ground whereas indri only descended to the ground to consume soil. In sum, these differences in diet and forest strata use minimize competition between species and contribute to the successful coexistence between indri and diademed sifakas.

6.2.3 Home Range Use and Ranging Patterns

In this chapter, my objective was to determine whether sympatric diademed sifakas and indri spatially differentiated their niches to minimize competition. Home range size estimates for each of the study groups were determined using two methods: MCP, and 95% KDE. Core areas within the group home ranges were determined using KDE analysis with the core threshold set at 50%. The prediction that diademed sifakas would have larger home ranges than indri was supported. Both indri and diademed sifakas are considered territorial species, but the degree to which they enforce their territorial boundaries may depend on factors such as population density and resource availability (Glessner and Britt 2005; Irwin 2006; Irwin 2008a; Pollock 1975; Powzyk 1997).

The estimated extent of home range overlap between species varied depending on the measure used. MCP analyses are commonly used to determine home ranges, but do not take into account differential use of particular regions within the home range as can be accomplished using KDE. As expected due to the assumptions of each method, the degree of overlap between lemur species was higher when estimated by the 95% KDE. Both species had distinct core areas of preferred habitat within their home range, but the extent of core area overlap was low between species. This highlights the importance of scale when analyzing home range use and species overlap patterns. When I used the MCP analysis, indri and diademed sifakas appeared to have considerable spatial overlap but, when the more fine-grained KDE approach was employed, a new pattern developed. These two species, in fact, used areas of their home ranges with varying intensities and exhibited clear preferences for some areas over others.

I observed one interspecific group encounter between indri and diademed sifakas whereby a group of indri were displaced by a diademed sifaka group. The indri group moved approximately 20 m away and began feeding on young leaves. Neither group vocalized or made physical contact during the interspecific encounter. The observation of frequent spatio-temporal overlap between indri or diademed sifakas with other lemur species and rarity of indri and diademed sifaka encounters with each other supports the notion that both spatial and temporal segregation in home range use contribute to the maintenance of coexistence between these two folivorous primates at BNR.

A small degree of within species overlap occurred between adjacent groups of the same species. As expected, the MCP approach showed more intraspecific overlap than the 95% KDE analysis. There was also very little overlap between core areas of neighboring groups in the same species (0.06% to 9.89% of overall core area). Although infrequent, I observed encounters between groups of the same species. For diademed sifakas, two groups had a small area of overlap where two aggressive intraspecific encounters occurred during the study period. These occurred in December 2013, when *Syzygium* sp. (Myrtaceae) was fruiting and all three diademed sifaka groups were observed to feed on the fruits and seeds of this tree species at this same time of year. Both encounters involved contact aggression and resulted in one group retreating into their own territory. Powzyk (1997) also reported intraspecific encounters near territorial boundaries for diademed sifakas. Intraspecifically, indri groups did not overlap. Indri intergroup encounters have been reported at Mantadia (Powzyk 1997) and Analamazaotra (Pollock 1975), but none were observed at BNR during data collection for the current study. Powzyk (1997) reported that, in one indri intergroup encounter, groups vocalized at each other and one group finally displaced another from a feeding tree. In the other encounter, two groups fed within 50 m of each other (Powzyk 1997).

My prediction that average DPL would be longer for diademed sifakas than indri was supported. However, diademed sifakas showed a dramatic decrease in their DPL during the cold, rainy months of May through August. In contrast, Indri DPL remained relatively stable throughout the year. The intense fluctuations in diademed sifaka DPL indicate that they were more heavily impacted by seasonal changes in temperature and rainfall than indri. May through August is a period of lower fruit availability when diademed sifakas and indri increased their consumption of lower quality foods (such as mature leaves, leaf petioles, and bark). The combination of these factors indicates that diademed sifakas exhibit a greater degree of flexibility in adjusting their activity and ranging patterns to respond to seasonal differences in resource availability when compared to indri.

6.2.4 Syntheses of Main Findings

In addition to making new observations of these sympatric lemurs, my results confirm many of the previously reported strategies for indri and diademed sifaka coexistence. My compilation of activity budgets showed a high degree of similarity across sites, with resting and feeding being the most commonly observed activities for both species (Blanchard 2007; Irwin 2006; Pollock 1975; Powzyk 1997). Overall dietary patterns at BNR were comparable to other sites, whereby diademed sifakas consumed significantly more fruits and seeds than indri and indri primarily consumed young leaves. However, analysis at a finer scale showed that diademed sifaka food preferences varied more than indri as evidenced by greater differences in plant species and plant families in their dietary profiles at BNR, Mantadia, and Tsinjoarivo (Britt et al. 2002; Irwin 2006; Irwin 2008b; Powzyk 1997; Powzyk and Mowry 2003; current study Chapter 4). I found that indri at BNR consumed bark more often and from a greater diversity of tree species than previously reported (Powzyk 1997). My study did not confirm sex differences in feeding reported by Powzyk (1997), which could be due to demographic circumstances within my study period (see Chapter 2 for study group demographic composition).

The more detailed spatial analysis conducted in this study revealed intriguing differences between groups and species, which is likely due to a combination of social and ecological factors. Home range sizes were similar between BNR and Mantadia (Powzyk 1997) for diademed sifakas, but were considerably smaller at BNR than in the continuous forest at Tsinjoarivo (Irwin 2006). Indri home ranges were closer to those reported by Pollock (1975) at Analamazaotra for four out of the six study groups. The two northernmost indri groups were closer in size to those at Mantadia (Powzyk 1997). My review of diademed sifaka ranging behavior showed that they have greater ecological flexibility to exist in fragments and in secondary forest areas (Irwin 2006; Irwin et al. 2010b; current study) than indri. Based on their dietary profiles and use of high canopy forest, it is not surprising that indri were most often found ranging in primary rainforest habitats at BNR, though they have been reported to exist in anthropogenically disturbed habitats (Pollock 1975) and even in forest fragments as small as ~200 ha (Britt et al. 1999) at other sites.

In summary, all the interspecific differences that I found between indri and diademed sifakas at BNR relate to their species-specific behavioral and morphological characteristics. Indri exhibit a more folivorous and less flexible dietary regime than diademed sifakas. These species differences directly relate to the activity and home range patterns observed at BNR and at other sites. This study also supports links between specific morphological features and diet in indri and diademed sifakas. In the next section, I outline how these interactions support the successful coexistence of these particular folivores and yield insights for other sympatric primates.

6.3 Strategies of Coexistence

While my dissertation has focused on comparing two sympatric primate species, it is essential to consider the role of these primates in the broader ecosystem. The presence of other primate species, potential predators, and non-primates with similar ecological profiles (e.g. birds, bats, and other mammals) can impact the way an animal uses its environment. When closely related (congeneric or confamilial) species exist in sympatry, they exhibit mechanisms of coexistence such as dietary divergence, differential habitat use, use of different forest strata, reduction of temporal overlap, and differences in activity budgets. At some sites, the presence of one species may even impact the population density of another (Rodman 1978; Ruhiyat 1983; Schreier et al. 2009). Some species, rather than avoiding temporal overlap, form polyspecific associations and even feed and forage together in times of resource scarcity (e.g. Freed 1996; Freed 2006; Porter et al. 2007). These polyspecific associations have been observed for frugivorous and gummivorous primates but not for folivores (Schreier et al. 2009). I conducted a review of sympatric folivorous primate studies and found that the most common coexistence strategy in closely related, folivorous primates is reduction in dietary overlap followed by differences in ranging patterns, use of different forest types and differential use of levels in the forest (Table 6-1). Group size also differs between these sympatric species where one species will have relatively small groups, and the other will have larger groups (Table 6-1). At all sites, a minimum of two main coexistence strategies have been reported.

Madagascar has many particularly informative ecosystems to facilitate the study of community ecology and more specifically the coexistence strategies of sympatric primates. This is, in part, due to its long geographic isolation from mainland Africa and high rates of endemic flora and fauna (Ganzhorn et al. 1999; Grubb 2003). The island's vast variety in ecosystems, from the arid west and south to the rainforests in the east makes it one of the most species-rich countries on the planet (Ganzhorn et al. 1999). In the eastern rainforests of Madagascar lemur communities tend to consist of more species relative to the dry forests in the west and south of the island (Ganzhorn et al. 1999; Sussman 2002). When only diurnal and cathemeral species are considered (species that may overlap spatially and temporally), up to three species of frugivorous lemurs (Overdorff 1996; Razafindratsima et al. 2014), two folivorous (Powzyk 1997; Powzyk and Mowry 2003), and up to three species of bamboo lemur (Tan 1999) have been reported to coexist. In each of these studies, a combination of non-mutually exclusive coexistence strategies has been reported.

Table 6-1. Summary of confamilial or congeneric, diurnal, crepuscular or cathemeral, sympatric primate studies and reported coexistence strategies.

Region and Study Site	Primate Species	Group Size	Reported Niche Separation Strategies	Sources
Africa				
Côte d'Ivoire, Taï Forest	*Procolobus verus*	2 - 20	Diet, Forest Strata	1 - 4
	Colobus polykomos	4 - 11		
	Procolobus badius	60 - 80		
Uganda, Kibale	*Procolobus badius*	60 - 80	Diet, Forest Type	4 - 8
	Colobus guereza	6 - 10		
Democratic Republic of Congo, Botsima, Salonga	*Colobus angolensis*	3 - 7	Diet, Ranging	2 - 3
	Procolobus badius	60 - 80		
Democratic Republic of Congo, Ituri Forest	*Colobus angolensis*	3 - 7	Ranging, Forest Type	3, 7 - 8
	Colobus guereza	6 - 10		

Ghana	*Colobus polykomos*	4 - 11	Diet, Vertical Stratification	2 - 4
	Procolobus badius	60 - 80		
Sierra Leone, Tiwai Island	*Procolobus verus*	2 - 20	Diet, Ranging	1 - 3
	Colobus polykomos	4 - 11		
	Procolobus badius	60 - 80		
Americas				
Argentina, Atlantic Forest	*Alouatta caraya*	2 - 20	Diet, Ranging	9 - 11
	Alouatta guarbia clamitans	2 - 14		
Asia				
India, Tripura Forest	*Trachypithecus phayrei*	8 - 22	Diet, Ranging	12 - 13
	Trachypithecus pileatus	3 - 13		
Thailand, Huai Kha Khaeng Forest	*Trachypithecus phayrei*	8 - 22	Diet, Ranging, Forest type	12, 14
	Trachypithecus cristatus	9 - 40		
Indonesia, Kutai Forest	*Presbytis rubicunda*	2 - 13	Diet, Population Density	4, 15 - 16
	Presbytis comata	3 - 20		
Malaysia, Barham River	*Trachypithecus obscurus*	5 - 20	Diet, Forest Strata, Substrate Size, Forest Type	17 - 19
	Presbytis melalophos	2 - 8		
Sri Lanka, Kaludiyapokuna Forest Reserve	*Semnopithecus entellus*	2 - >100	Diet, Ranging	20 - 21
	Trachypithecus vetulus	2 - 14		
Madagascar				
Ranomafana	*Hapalemur griseus*	3 - 9	Diet, Activity Patterns	22 - 23
	Hapalemur aureus	2 - 4		
	Hapalemur simus	1 - 3		

Mantadia	*Indri*	2 - 5	Diet, Vertical Stratification, Ranging	24 - 27
	Propithecus diadema	2 - 7		
Betampona Nature Reserve	*Indri*	2 - 5	Diet, Vertical Stratification, Ranging	Current study
	Propithecus diadema	2 - 7		

Sources: 1. (Oates and Anadu 1989); 2. (DaSilva 1994); 3. (Maisels et al. 1994); 4. (Davies et al. 1988); 5. (Struhsaker and Leland 1979); 6. (Chapman and Chapman 2000); 7. (Oates 1977); 8. (Wasserman and Chapman 2003); 9. (Agostini et al. 2010b); 10. (Agostini et al. 2010a); 11. (Agostini et al. 2012); 12. (Stanford 1988); 13. (Stanford 1991); 14. (Brotoisworo and Dirgayusa 1991); 15. (Supriatna et al. 1986); 16. (Ruhiyat 1983); 17. (Curtin 1980); 18. (MacKinnon and MacKinnon 1980); 19. (Kool 1993); 20. (Vandercone et al. 2012); 21. (Vandercone et al. 2013); 22. (Mittermeier et al. 2010); 23. (Tan 1999); 24. (Reed 1999); 25. (Powzyk 1997); 26. (Powzyk and Mowry 2003); 27. (Blanchard 2007)

At BNR, I found that indri and diademed sifakas employed several coexistence strategies. These included differences in activity budgets, divergent diets, dietary overlap on superabundant resources, differential use of forest levels, and minimal spatio-temporal overlap. These strategies are consistent with the morphological differences between these lemur species. Indri are more morphologically specialized for a folivorous diet and exhibit behavioral, dietary, and ranging patterns consistent with other energy minimizing primate species such as howler monkeys (*Alouatta*) (e.g. Milton 1980; Milton 1998), black and white colobus monkeys (*Colobus guereza*) (e.g. Bennett and Davies 1994; Curtin and Olson 1984; Gautier-Hion 1978; Oates 1987; Struhsaker and Leland 1979) and dusky leaf monkeys (*Presbytis obscura*) (e.g. Curtin and Chivers 1978; Curtin 1976; Fleagle 1977; Fleagle 1978). While diademed sifakas were still primarily folivorous, they consumed more high-energy foods such as fruits and seeds than indri. They exhibited more of an energy maximizing strategy relative to indri. Other folivorous primates that exhibit more diademed sifaka-like strategies include (but are not limited to) red colobus monkeys (*Colobus badius*) (e.g. Gebo and Chapman 1995; Struhsaker and Leland 1979), the mitered leaf monkey (*Presbytis melalophos*) (e.g. Curtin 1976; Fleagle 1977; Fleagle 1978)   and the banded leaf monkey (*P. femoralis*) (e.g. Bennett and Davies 1994; Curtin and Chivers 1978; Curtin 1976; Davies et al. 1988). The general pattern that has emerged when sympatric primates co-occur is that one will exhibit a higher degree of folivory and the other primate species will have a more catholic diet that includes greater dietary diversity, and more fruits and seeds relative to the highly specialized folivore. In summary, the trend seen in other sympatric folivorous primates throughout the world was consistent in this research project where one species (diademed sifakas) exhibited several energy maximizing strategies relative to indri who exhibited a more energy minimizing strategy.   It is important to note that these between-species comparisons were made relative to each other. Folivores, in general, exhibit an energy minimizing strategy relative to more frugivorous primates.

6.4 Conservation Implications

Madagascar has experienced massive deforestation. Since the 1950s, researchers have used satellite imagery to assess deforestation rates (Green and Sussman 1990; Harper et al. 2007). Over 80% of the country's rainforests have been destroyed leading to habitat loss and fragmentation for many lemur species (Green and Sussman 1990; Harper et al. 2007). BNR is one of the last remaining tracts of eastern lowland rainforest (Green and Sussman 1990). BNR is a strict nature reserve with access restricted to researchers with scientific permits from Madagascar National Parks (MNP) the government agency responsible for the oversight of all protected areas. The Madagascar Fauna and Flora Group (MFG) works with MNP as an active conservation presence in and around the reserve. Even with the presence of these two conservation groups, people living in the villages surrounding BNR have been found hunting or setting traps inside the reserve. As an isolated forest patch, species within the reserve face many conservation threats including the threat of genetic isolation (Nunziata et al. 2016) and loss of primary rainforest to invasive plant species (Ghulam 2014), hunting (Golden and Comaroff 2015). This makes active conservation efforts in this area vital to the survival of lemurs and many other species in the reserve (Freeman et al. 2014).

This expanded knowledge of the behavioral plasticity and ecological requirements of indri and diademed sifakas reported in this thesis will assist in the development of more effective and well-informed conservation management plans for these two critically endangered primates. The need for *in situ* conservation programs throughout each species' range is critical because neither of these particular lemur species exists in captivity. Further, indri and diademed sifaka populations in areas of higher anthropogenic disturbance have been reported to have higher parasite loads although the fitness consequences of these infections remain unknown (Irwin et al. 2010a; Junge et al. 2011).

As populations become more fragmented, genetic isolation also becomes a greater thread as evidenced by the genetic distinctiveness already reported for indri at BNR relative to other populations (Nunziata et al. 2016). Nunziata et al. (2016) warned that this genetic isolation of indri at BNR will likely pose a conservation threat for this indri population without conservation intervention. They suggested finding ways to introduce gene flow to increase the genetic diversity of indri at BNR (Nunziata et al. 2016). Genetic diversity is currently unknown for the diademed sifaka population at BNR and genetic assessment for population viability should be considered a conservation priority. Based on the findings from the current study combined with previous research, diademed sifakas exhibit a greater degree of ecological flexibility than indri as evidenced by their greater between-site dietary diversity (see Chapter 4; Irwin 2006; Irwin

2008b) and ability to inhabit fragmented and secondary forests (Irwin 2008a). This may assist in conservation of diademed sifakas at BNR as it is likely that they are able to inhabit more areas within the reserve than indri, but this is counterbalanced by their larger average home range size (47.33 ha) which indicates overall population sizes are undoubtedly low and that these primates may be more susceptible to edge effects.

Maintenance of the currently forested areas of BNR and the continued reforestation of the 100 m ZOP around the reserve's border are essential to the conservation of indri and diademed sifakas in this area. However, the lack of gene flow and overall low populations numbers combined with a subsequent loss of genetic diversity in these populations is a serious consideration for conservation planning. The MFG has conducted one of the first primate restocking programs with the black-and-white ruffed lemurs at BNR (Britt et al. 2003; Britt et al. 2004). Thorough population surveys of indri and diademed sifakas are recommended, with potential translocation of individuals from genetically distinct populations a last resort to maintain genetic diversity in these lemurs in the wild.

6.5 Broader Significance and Relevance to Human Evolution

Extant sympatric primate studies are beneficial to our understanding of the evolution of hominins, interactions between sympatric hominins and other primates, and the place of hominins in paleoecological communities (Wood and Schroer 2012). Currently, humans are the only extant hominin species but early hominin species likely existed in sympatry. While it is difficult to state the degree of overlap and subsequent interactions between extant hominin species, evidence such as finding hominin fossils from > 1 species at the same site that from the same time period indicates that co-occurrence. It is likely that overlap occurred among early *Homo* and *Paranthropus* at Omo (Suwa et al. 1996), Swartkrans (Grine 1981) Sterkfontein

(Reed 1997), and Drimolen (Keyser et al. 2000). In the Turkana basin, *H. habilis* and *H. erectus* experienced a long period of co-occurrence (Spoor et al. 2007; Wood 1991). At Koobi Fora, *Paranthropus boisei, H. habilis, H. rudolfensis,* and *H. ergaster* all likely came into contact (Spoor et al. 2007; Wood 1991). The coexistence of early hominins is still somewhat controversial but recent genetic analyses have confirmed that gene flow occurred between modern humans and Neandertals as well as the Denisovians (Kuhlwilm et al. 2016; Reich et al. 2010; Sankararaman et al. 2012). Not only did they come into contact but they also interbred. Using multiple lines of evidence such as genetics (when possible), dental microwear, stable isotope analysis, paleo-environmental reconstructions, and observations of extant sympatric primates, researchers have been able to infer coexistence strategies of potentially sympatric hominins.

Dental microwear patterns of fossil hominin teeth and stable isotope analyses of hominin enamel have been compared with extant primate species with known dietary profiles to gain insight into the overall diets and dietary diversity of early hominins (Ungar and Sponheimer 2011). Dental microwear analyses have shown that even different species of *Paranthropus*, with their extremely derived cranial morphology relative to other hominins, exhibited species-specific feeding patterns (Scott et al. 2014; Strait et al. 2013).

Just as potentially co-occurring hominins exhibit differences in diet, they also differed in their habitat use. For example, *Australopithecus* species likely inhabited more wooded regions whereas *Paranthropus* specimens have been found in fossil assemblages associated with open habitats and wetlands (Behrensmeyer and Reed 2013; Reed 1997). Early *Homo* is associated with more arid, open habitats (Reed 1997). *Paranthropus* likely also inhabited areas associated with *Australopithecines* and early *Homo* but the ability of *Paranthropus* to exploit wetlands would have assisted in the maintenance of sympatry with other hominins via habitat partitioning (Reed 1997).

Primatology is finally entering an era in which between-site comparisons for a growing number of primate species is now yielding important insights on the behavioral and ecological variability within species. Non-human and human primate species did not evolve in isolation, but in dynamic environments and in sympatry with potential competitors. African apes are the most often non-human used models used to examine how closely related sympatric hominins were able to maintain coexistence (Macho and Lee-Thorp 2014; Stanford 2006). While sympatric gorillas and chimpanzees may provide insight into questions related to sympatric hominin coexistence strategies due to their phylogenetic relationship with humans and their geographic location, a broader perspective is certainly warranted. That said, invoking comparative approaches that include several primate species residing in different environments can illuminate; 1) common sympatric primate coexistence strategies, 2) environmental or phylogenetic patterns in coexistence strategies, and 3) coexistence strategies not necessarily exhibited by great apes. This current study and other research on sympatric primates can contribute valuable insights into the factors that have shaped not only the evolutionary histories of particular species, but how the presence of one species impacts the evolution of another species. The behavioral and ecological patterns I found are reflected in each species' distinct morphologies and can be coupled with the patterns of intraspecific variation that I observed between-sites to yield deeper and more insightful connections between primate behavior, ecology, and morphology. This, in turn enhances our ability to interpret the hominin fossil record and construct valid models of the past primate communities. In summary, the combination of behavioral, ecological, and morphological studies of extant primates yield valuable insights to reconstructing the behavioral ecology of paleospecies of non-human and human primates (see Scott et al. 2012; Strait et al. 2013; Sussman and Hart 2015; Ungar and Sponheimer 2011; Wood and Schroer 2012).

6.6 Future Directions

As with most scientific studies, the research presented in this dissertation highlighted areas for further investigation. At BNR, longitudinal data on indri and diademed sifakas are necessary to determine the amount of inter-annual variation in the behavior, diets, home ranges, and demography of the groups included in this study.

The inclusion of the behavioral ecology of the brown lemurs and bamboo lemurs at BNR is essential to enhance our understanding of the dynamics of the diurnal/cathemeral lemurs at this site. For example, diademed sifakas, indri, and black and white ruffed lemurs have all been reported to feed on fruits, seeds, and flowers from *Symphonia* sp. (Britt 2000; Schmidt et al. 2010). Brown lemurs at Ranomafana also feed from trees in this genus (Overdorff 1993). The addition detailed dietary information for brown lemurs here will not only enhance our understanding of the lemur community at this reserve, it will also yield necessary information regarding the behavioral and ecological variation in this species. There is currently no indication of dietary overlap between bamboo lemurs and indriids but they have yet to be the subject of long term, in depth study of their dietary profiles. Finally, in order to understand species-wide trends in the behavioral ecology of indri and diademed sifakas as well as their behavioral and ecological variation, and research from new study sites throughout each species' range.

The addition of more groups in the north of the reserve is necessary to gain an understanding of intraspecific variation in the behavioral ecology of these lemurs. Future research would also benefit from using GPS or radio collars on more than one individual in a group. This would be particularly useful to more fully comprehend one of the most intriguing findings from this study, the demography of the indri NE group. This group exhibited a flexible grouping pattern; something that has never been previously reported. In this group, the adult male visited several females but females did not overlap in space or time. It would be extremely valuable to study this group in more depth to answer questions about whether or not the females in the group associate with other males when they are not with the adult male in this study. This is a previously unreported grouping pattern for indri and requires further investigation.

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Appendix 1

List of All Plant Species Consumed During Study Perion

Species or common name and part consumed	Plant Family	Indri	Diademed sifaka
		# of feeding instances	
Abrahamia spp	Anacardiaceae		
Flowers			1
Petioles			1
Seeds			2
Young leaves			10
Albizia gummifera	Fabaceae		
Young leaves			16
Allophyllus cobe	Sapindaceae		
Fruits			1
Young leaves			2
Ambohita			
Flowers			1
Ambonambona faranikely			
Young leaves			1
Ambovitsika keliravina			
Young leaves			1
Ampaly			
Fruits			1
Ampana beravina			
Young leaves			1
Ampy liana			
Flowers			1
Fruits			1
Antafonana boribory ravina			
Flowers		1	
Young leaves		1	
Antafonana farany kelyravina			
Young leaves		1	
Aphloia theaformis	Aphloiaceae		
Young leaves			1

Species or common name and part consumed	**Plant Family**	**Indri**	**Diademed sifaka**
		# of feeding instances	
Aspidostemon perrieri	Lauraceae		
Flowers		1	
Young leaves		18	
Aspidostemon spp	Lauraceae		
Bark		1	
Flowers		5	
Young leaves		97	2
Azinina farany keliravina			
Young leaves		3	
Bakarella clavata	Loranthaceae		
Flowers			17
Young leaves			4
Beilschmiedia sp2	Lauraceae		
Bark		2	
Flowers		2	
Fruits			1
Mature leaves		2	
Petioles		1	
Young leaves		45	7
Bronchoneura sp	Myristicaceae		
Flowers		2	
Fruits		2	
Seeds		10	
Young leaves		5	
Bronchoneura sp1	Myristicaceae		
Flowers		6	1
Fruits		3	
Mature leaves		2	
Seeds		5	
Young leaves		84	5
Bronchoneura voury	Myristicaceae		
Young leaves		1	
Calophyllum sp1	Clusiaceae		
Flowers		2	
Fruits		1	
Seeds			3
Young leaves		12	1

Species or common name and part consumed	**Plant Family**	**Indri**	**Diademed sifaka**
		# of feeding instances	
Canarium sp1	Burseraceae		
Seeds		1	
Young leaves		2	
Chrysophyllum spp	Sapotaceae		
Fruits			2
Cryptocarya	Lauraceae		
Mature leaves		1	
Young leaves		1	
Cryptocarya sp1	Lauraceae		
Flowers		3	2
Fruits		2	
Mature leaves		1	
Seeds		1	
Young leaves			1
Cryptocarya sp2	Lauraceae		
Flowers		6	
Fruits		7	
Mature leaves		1	1
Petioles		1	
Seeds		6	
Cryptocarya sp3	Lauraceae		
Young leaves		4	
Cryptocarya sp5	Lauraceae		
Young leaves		5	1
Cynometra spp	Fabaceae		
Young leaves		29	32
Dalbergia graveana	Fabaceae		
Young leaves			2
Dillenia spp	Dilleniaceae		
Young leaves			1
Diospyros sp1	Ebenaceae		
Fruits			3
Young leaves			6

Species or common name and part consumed	**Plant Family**	**Indri**	**Diademed sifaka**
		# of feeding instances	
Dracaena sp1	Convallariceae		
Seeds		3	
Young leaves		1	
Eugenia sp1	Myrtaceae		
Fruits			2
Fanalatay			
Fruits			1
Faucherea sp1	Sapotaceae		
Flowers			1
Fruits			1
Young leaves			3
Faucherea sp2	Sapotaceae		
Fruits			1
Ficus politoria	Moraceae		
Fruits			7
Mature leaves			1
Young leaves			1
Ficus sp2	Moraceae		
Fruits			1
Gaertnera sp1	Rubiaceae		
Bark		1	
Mature leaves		1	
Grewia sp1	Malvaceae		
Fruits			1
Haematodendron glabrum	Myristicaceae		
Flowers		15	
Fruits		4	1
Mature leaves		1	
Petioles		1	
Seeds		14	1
Young leaves		71	14

Species or common name and part consumed	**Plant Family**	**Indri**	**Diademed sifaka**
		# of feeding instances	
Hazoambovahy liana			
Fruits		3	9
Seeds			3
Young leaves		1	1
Mature leaves			1
Hazobarovana			
Young leaves			1
Hazombato keliravina			
Flowers			1
Young leaves			1
Hazomboangy tsy kely tsy maventy			
Young leaves			2
Hazombovahy			
Fruits		1	
Hildegardia sp1	Malvaceae		
Flowers			1
Young leaves			1
Hildegardia sp2	Malvaceae		
Flowers			2
Isolona sp1	Annonaceae		
Flowers		1	
Mature leaves		1	
Young leaves		17	6
Young leaves		1	
Macaranga sp1	Euphorbiaceae		
Young leaves			12
Mature leaves			1
Mammea bongo	Clusiaceae		
Fruits		1	2
Seeds		1	3
Young leaves		47	19
Mandresy epiphyte			
Fruits			3
Young leaves		1	2

Species or common name and part consumed	**Plant Family**	**Indri**	**Diademed sifaka**
		# of feeding instances	
Mauloutchia humblotii	Myristicaeae		
Flowers		14	1
Mature leaves		5	
Seeds		9	
Young leaves		80	4
Memecylon spp	Melastomataceae		
Flowers			2
Seeds			2
Young leaves			1
Michronychia tsiramiramy	Anacardiaceae		
Young leaves		12	1
Millettia sp1	Fabaceae		
Mature leaves		1	
Mokaranana			
Young leaves			1
Nonoka epiphyte			
Young leaves			3
Noronhia grandifolia	Oleaceae		
Young leaves			1
Noronhia sp	Oleaceae		
Flowers			1
Fruits			1
Young leaves		4	4
Noronhia verticilata	Oleaceae		
Young leaves		3	5
Ocotea racemosa	Lauraceae		
Bark		9	
Flowers		14	
Fruits		8	
Mature leaves		4	
Petioles		3	
Seeds		8	1
Young leaves		79	6

Species or common name and part consumed	**Plant Family**	**Indri**	**Diademed sifaka**
		# of feeding instances	
Ocotea sp1	Lauraceae		
Bark		4	
Flowers		3	
Fruits		3	1
Mature leaves		1	
Petioles		1	
Seeds		1	
Young leaves		26	
Ocotea sp2	Lauraceae		
Bark		2	1
Flowers		3	
Fruits		3	
Seeds			1
Young leaves		56	12
Ompa			
Fruits			15
Seeds			10
Young leaves			5
Oncostemum sp1	Myrsinaceae		
Flowers			1
Mature leaves			2
Young leaves		1	9
Oncostemum sp2	Myrsinaceae		
Young leaves			2
Petchia sp1	Apocynaceae		
Fruits			1
Seeds			1
Mature leaves			1
Young leaves			39
Petchia sp2	Apocynaceae		
Fruits			1
Seeds			1
Young leaves			5
Petchia spp	Apocynaceae		
Young leaves			16

Species or common name and part consumed	**Plant Family**	**Indri**	**Diademed sifaka**
		# of feeding instances	
Pittosporum ochrosiaefolium	Pittosporaceae		
Flowers			2
Mature leaves			2
Seeds			1
Young leaves			11
Pittosporum sp2	Pittosporaceae		
Young leaves			3
Polyscias	Araliaceae		
Fruits			5
Mature leaves		4	1
Young leaves		4	12
Polyscias sp2	Araliaceae		
Flowers			2
Fruits			1
Young leaves		1	4
Potameia sp.	Lauraceae		
Bark		1	
Mature leaves		1	
Petioles		2	
Seeds		1	
Young leaves		19	4
Potameia crassifolia	Lauraceae		
Bark		13	
Flowers		2	
Mature leaves		9	1
Petioles		2	
Young leaves		56	6
Rheedia sp.	Clusiaceae		
Bark		1	
Flowers		3	1
Fruits		2	
Mature leaves		5	12
Petioles		5	1
Young leaves		85	44
Robanga liana			
Flowers			1
Young leaves			42
Petioles			2

Species or common name and part consumed	**Plant Family**	**Indri**	**Diademed sifaka**
		# of feeding instances	
Sary			
Flowers		4	
Sorendea madagascariensis	Anacardiaceae		
Flowers			13
Fruits			6
Seeds			2
Young leaves		1	32
Stadmania sp1	Sapindaceae		
Flowers			1
Fruits			1
Young leaves		2	3
Stadmania sp2	Sapindaceae		
Young leaves			4
Stadmania sp3	Sapindaceae		
Seeds			3
Young leaves		1	9
Stadmania sp4	Sapindaceae		
Fruits			1
Young leaves			7
Streblus spp 1	Moraceae		
Fruits			1
Young leaves		5	13
Suregada sp1	Euphorbiaceae		
Flowers			1
Mature leaves			1
Seeds			1
Young leaves			4
Symphonia louveli	Clusiaceae		
Flowers		13	
Fruits		5	2
Mature leaves		1	
Seeds		1	5
Young leaves		82	26

Species or common name and part consumed	**Plant Family**	**Indri**	**Diademed sifaka**
		# of feeding instances	
Symphonia pauciflora	Clusiaceae		
Flowers		26	3
Fruits		10	7
Mature leaves		1	2
Seeds		1	6
Young leaves		78	49
Symphonia sp1	Clusiaceae		
Flowers		3	
Mature leaves		1	
Seeds			6
Young leaves		18	3
Symphonia sp2	Clusiaceae		
Flowers		1	
Seeds			1
Young leaves		9	1
Syzygium emirnensis	Myrtaceae		
Fruits			3
Seeds			1
Syzygium sp1	Myrtaceae		
Fruits		1	
Seeds			5
Young leaves		3	
Syzygium sp2	Myrtaceae		
Flowers		1	
Fruits		2	1
Petioles		1	
Seeds			1
Young leaves		1	
Syzygium sp3	Myrtaceae		
Flowers			6
Fruits			18
Seeds			6
Young leaves			4

Species or common name and part consumed	Plant Family	Indri	Diademed sifaka
		# of feeding instances	
Tina sp1	Sapindaceae		
Mature leaves			1
Young leaves			3
Tinopsis sp1	Sapindaceae		
Flowers			4
Fruits		2	
Young leaves			2
Tongatra			
Mature leaves			1
Treculia sp	Moraceae		
Fruits		1	5
Seeds			3
Young leaves		16	15
Treculia sp1	Moraceae		
Fruits			4
Seeds			1
Young leaves		10	10
Treculia sp2	Moraceae		
Fruits			2
Young leaves			7
Treculia spp (Mailardia)	Moraceae		
Fruits		1	4
Seeds			1
Young leaves		27	15
Trophis spp	Moraceae		
Flowers			1
Fruits			2
Seeds			4
Young leaves		25	13
Trova maventy ravina			
Young leaves			1
Uapaca amplifolia	Euphorbiaceae		
Flowers		4	
Mature leaves			1
Petioles		1	
Seeds		2	
Young leaves		28	

Species or common name and part consumed	**Plant Family**	**Indri**	**Diademed sifaka**
		# of feeding instances	
Uapaca louveli	Euphorbiaceae		
Bark		1	
Flowers		5	
Fruits		2	
Mature leaves		1	
Petioles		3	
Young leaves		90	1
Vahimbahilena liana			
Mature leaves			3
Young leaves			2
Vahivy liana			
Fruits			1
Vazy liana			
Young leaves			1
Voankarabo fotsy liana			
Young leaves			2
Voronboron'ala			
Fruits			1
Young leaves			4
Xylopia spp.	Annonaceae		
Mature leaves			1
Young leaves			1
Zanthoxylum sp1	Rutaceae		
Seeds			1
Young leaves			2