Development of feeding in ring-tailed lemurs

by

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ABSTRACT

Fundamental hypotheses about the life history, complex cognition and social dynamics of humans are rooted in feeding ecology – particularly in the experiences of young animals as they grow. However, the few existing primate developmental data are limited to only a handful of species of monkeys and apes. Without comparative data from more basal primates, such as lemurs, we are limited in the scope of our understanding of how feeding has shaped the evolution of these extraordinary aspects of primate biology.

I present a developmental view of feeding ecology in the ring-tailed lemur (*Lemur catta*) using a mixed longitudinal sample (infant through adult) collected at the Beza Mahafaly Special Reserve in southwestern Madagascar from May 2009 to March 2010. I document the development of feeding, including weaning, the transition to solid food, and how foods are included in infant diets. Early in juvenility ring-tailed lemurs efficiently process most foods, but that hard ripe fruits and insects require more time to master. Infants and juveniles do not use many of the social learning behaviors that are common in monkeys and apes, and instead likely rely both on their own trial and error and simple local enhancement to learn appropriate foods. Juvenile ring-tailed lemurs are competent and efficient foragers, and that mitigating ecological risks may not best predict the lemur juvenile period, and that increases in social complexity and brain size may be at the root of primate juvenility. Finally, from juvenility through adulthood, females have more diverse diets than males. The early emergence of sex differences in dietary diversity in juvenility that are maintained throughout adulthood indicate that, in addition to reproductive costs incurred by females, niche partitioning is an important aspect of sex differential feeding ecology, and that ontogenetic studies of feeding are particularly valuable to understanding how selection shapes adult, species-typical diets.

Overall, lemur juvenility is a time to play, build social relationships, learn about food, and where the kernels of sex-typical feeding develop. This study of the ontogeny of feeding ecology contributes an important phylogenetic perspective on the relationship between juvenility and the emergent foraging behaviors of developing animals

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CHAPTER 1. INTRODUCTION

This dissertation is about how infant and juvenile ring-tailed lemurs learn what to eat, how juvenile feeding influences lemur life history, and how the ecological differences between male and female ring-tailed lemurs develop. Food and its acquisition are one of the most powerful selective pressures in biology and have driven the evolution of an enormous diversity of social organizations and morphology in primates. Food, and its distribution in time and space, is at the center of socio-ecological models used to describe the various social organizations of primates, from fission fusion community dynamics to the unusual case of the female dominance in the Malagasy lemurs (Wrangham, 1980). Food quality and availability set the pace of development and are a primary correlate of metabolic rate and of brain size (Leigh, 1994; Fish and Lockwood, 2003; Godfrey et al., 2004). Processing and extracting food has driven the outlandish cranial and dental adaptations in the robust australopithecines as well as the unique dental and manual organization of the aye-aye. Additionally, the challenges of collecting and processing of food fostered the technological innovations that allowed humans to move away from primate-typical life histories into a pace of life history, social complexity, and biological dominance that is, in the very least, unusual for even a very brainy mammal. In short, “the whole of nature … is a conjugation of the verb to eat, in the active and the passive” (Inge, 1927).

Food and feeding ecology have had major roles in the diversity of primate evolution, and the comparative study of primate feeding ecology is one of the best paths to discovering processes that have shaped human evolution and the origin of human social complexity. The successful development of the individual’s behaviors associated with feeding is a key predictor of survival and reproductive success in primates (Altmann, 1991; Hauser, 1993; Altmann, 1998). However, the actual developmental patterns associated with feeding ecology, particularly in the lemurs, remain poorly understood. Consequently, it is not known how the processes of primate development vary across clades, and how the developmental interaction of sociality and ecology affect individual fitness.

The ontogeny of feeding and primate life history

The development of feeding is complex and involves maturation across cognitive, behavioral, and physical developmental axes. Young animals must learn what are appropriate food resources, learn how to execute the correct behaviors that are necessary to collect those foods, and have the strength and dexterity to process them. Each of these aspects of foraging can exert varying pressure on infants and juveniles to either learn quickly and reach feeding competency as soon as possible, or potentially to grow slowly and accumulate knowledge and skill pools that are necessary to be an effective and competitive forager as an adult. To understand how changes in an individual's biology and its social environment shape the emergence of group and species-typical feeding ecology, it is necessary to know what behaviors young animals use to develop feeding, how infant and juvenile ecologies differ from adults, and then how these are all shaped by changes in physical size, strength and coordination, as well as cognitive maturation and the influence that other individuals and social regulations have on these changes.

For any animal, learning to feed itself is obviously one of the most important skills to acquire to survive into adulthood. In some cercopithecine monkeys the timing of when they learn to do this, the composition of their diet as this is done, and the behaviors that are used to learn about diet have long lasting effects into adulthood (Hauser, 1993; Altmann, 1998). These effects reach beyond the immediacy of surviving and reach into extended life history characters, including the reproductive success of an individual's offspring. In one of the most comprehensive studies of juvenile primate feeding ecology, Altmann (1998) demonstrated that protein surplus and energetic deficits of juvenile female baboons directly impacted a female's subsequent reproductive success. This was not only in the age at first reproduction and the number of offspring produced, but more importantly, a juvenile female's feeding ecology predicted the quality and survival of those offspring to subsequent reproductive success. Early, successful juvenile feeding competency then has long-lasting effects on the body mass, survivorship, and reproduction of a female's lineage.

Dietary composition and nutritional intake are not the only aspects of the development of feeding that determine success to adulthood. The successful execution of specific behaviors during infancy and juvenility also predict juvenile mortality (Hauser, 1993). Co-feeding is one of these behaviors, and is the close, coordinated, and simultaneous feeding with another individual. In vervet monkeys, the percentage of total feeding time spent that infants and juveniles spent co-feeding with their mother predicts their age at death (Hauser, 1993). In this species, the use of co-feeding by infants and juveniles to learn about diet has significant effects on mortality, either through the increased likelihood that young animals learn appropriate food items or by keeping offspring close to their mothers during vulnerable feeding and foraging bouts.

Currently, examples of how the feeding ecology impacts survival to adulthood and reproductive success are limited to several of catarrhine monkey species (e.g., Hauser, 1993; Altmann, 1998). These catarrhine examples show that feeding ecology and behavior of juveniles is one of the most important places to begin to understand broad life history patterns across primates as it seems to be a particularly sensitive period in life to perturbations in social interactions and dietary composition. The primate juvenile period (from weaning to the age at first reproduction) is often viewed as one of phenotypic limbo (Janson and van Schaik, 1993; Pagel and Harvey, 1993), but it is a vulnerable time with significant risks. Delaying reproduction and extending the growth period can have significant fitness costs as individuals are smaller and are at greater risk of predation and starvation. Multiple hypotheses have tried to explain the evolution of primate juvenility, with some viewing juvenility as a non-adaptive consequence of constraints imposed by other aspects of primate life history and biology, including brain mass, metabolic demands, and demography and mortality schedules (Cole, 1954; Charnov, 1993; Pagel and Harvey, 1993; Godfrey et al., 2004). Alternatively, other hypotheses propose long juvenile periods are a direct product of selection that enhances learning opportunities and refines social skills (Joffe, 1997; Ross and Jones, 1999), or are a result of selection slowing the growth process to compensate for ecological incompetence to minimize starvation risks (Janson and van Schaik, 1993).

This latter hypothesis, the Ecological Risk Aversion Hypothesis (ERAH Janson and van Schaik, 1993) has been a particularly attractive framework for understanding the evolution of the long primate juvenility period. It brings aspects of constraint-based hypotheses into behavioral and ecological context. The primary assumption of the ERAH is that juveniles are less efficient foragers than adults, and to minimize predation risk juveniles forage closer the center of the social group and to other group members. This increases feeding competition, and to compensate and minimize starvation risk, juveniles grow slowly. By prolonging development, juveniles reduce the proportional energy devoted to growth and therefore reduce the risk of starvation under periodic food shortages.

The ERAH has been primarily supported through interspecific comparisons in the growth and life histories of frugivores and folivores. In these comparisons, the predictability of resources can influence growth patterns. More consistently available resources, such as leaves, permit faster growth rates and earlier ages at maturation than patchily distributed or unpredictable foods (i.e., fruit). Because of the consistent and predictable availability of leaves, folivorous haplorhines grow faster than closely related and comparably sized frugivores (Leigh, 1994). Consequently, frugivorous haplorhines have comparatively longer juvenile periods (Breuer et al, 2010) than folivores. However, when the behavioral foundations of the ERAH are explored within a given species, the feeding and foraging patterns typically do not conform to the ERAH’s predictions (e.g., Hanya, 2003; Stone, 2007; Bezanson, 2009; Schmitt, 2010). In strepsirrhines the pattern is less clear. Contrary to the ERAH, folivorous indriids grow slower than frugivorous lemurids. However, there are no comparative developmental behavioral data from the lemurs that can test the comparative nature of the ERAH or if these differences in growth patterns relative to food type between haplorrhines and strepsirrhines are a consequence of the somewhat unusual ecological conditions of Madagascar. Further behavioral data are needed from the lemurs to understand if, like in the catarrhine monkeys, juvenile feeding ecology has dramatic and long-lasting effects into adulthood and if primate juvenility is a key life history stage that then shapes later reproductive success.

Learning what, when, where, and how to eat

Development of feeding and foraging competency can require more time and learning in primates than in other mammalian orders due to broad dietary composition and selectivity of food items, as well as foods that require skill to extract (Altmann and Alberts, 1987; Ross and Jones, 1999; Deaner et al., 2003). Some primate foraging tasks require a minimum amount of physical maturation, coordination and skill, and local ecological knowledge (Boinski and Fragaszy, 1989), and after reaching nutritional independence, juveniles of some species need considerable time to develop the strength and coordination needed to process complex foods (Corp and Byrne, 2002; Gunst et al, 2010). This may be a time of trial and error learning, or one that occurs through social learning processes. A variety of behaviors have been identified in primates that are associated with social learning, and include begging, scrounging, and co-feeding as well as direct transfers of food from one individual to another (Rapaport and Brown, 2008). These behaviors are commonly found in monkeys and apes, but the frequency of use of these social learning behaviors by strepsirrhines is unknown. Without developmental social learning data from strepsirrhines, the role that social learning has played in shaping the evolution of primate social groups remains unclear (reviewed in Rapaport and Brown, 2008).

Adult lemurids are capable of learning from each other to some extent (Kendal et al, 2010; Dean et al, 2011; Stoinski et al, 2011), but it is unknown what behaviors are used in adult social learning in these species. Likewise it is unknown if social learning is common or crucial to the development of feeding ecology in lemurs, as has been shown in vervet monkeys (Hauser, 1993). The only strepsirrhine that has been shown to require long periods of learning and skill refinement is the aye-aye (*Daubentonia madagascariensis*). The complex extractive foraging behaviors for which *D. madagascariensis* shows anatomical and behavioral specialization (Krakauer, 2006), appears to take considerable time to master (Krakauer, 2006), and correspondingly the aye-aye has a higher relative brain size when compared to other lemurs (MacLean et al., 2009). However, the aye-aye specializes on a percussive foraging behavior to find hidden food items. Most lemurs are generalist foragers that include a diverse array of food items in their diets and do not specialize on cryptic or difficult to process foods. It is unknown if these species, including the ring-tailed lemur, also need long periods of learning to master feeding and foraging or if social learning processes are necessary to guide them to nutritional independence and foraging proficiency.

The development of sex differences in primate feeding

Extended developmental periods may also be required to learn sex-specific dietary compositions and feeding ecology, with social processes guiding growing animals into sex-typical feeding ecology. Sex-typical foraging behavior is a specialized subset of foraging that may require social modeling and input to develop. Sex differences in feeding may be a response to increased costs of reproduction to females or as a niche partitioning strategies, but likely require social modeling to develop fully. However, few comparative data from primates are available to test hypotheses associated with the ontogeny of feeding behavior, particularly in how social interactions shape feeding ecology, and if there is predictable variation between males and females. An ontogenetic perspective on feeding can simultaneously evaluate a cost-based framework for the evolution of sex differences in feeding as well as identify the social mechanisms that shape feeding ecology and subsequent life history patterns.

Adult sex differences in diet and foraging behavior have been documented in all primate clades that live in permanent social groups (Gautier-Hion, 1980; Boinski, 1988; Sugardjito, 1992; Rose, 1994; Sauther, 1994; Michels, 1998; Bean, 1999; Hemingway, 1999; van Schaik et al., 1999; Nakagawa, 2000; Field and McGraw, 2001; Vasey, 2002; Baker and Wardle, 2003; Agostini and Visalberghi, 2005). In some cases, sex differences in feeding can be explained as physiological consequences of 1) differences in body mass and metabolic rate or 2) as response to increased costs incurred by females during gestation and lactation (Clutton-Brock, 1977; Rose, 1994). In these two scenarios, sex differential feeding is closely tied to physiology and diet, with sex differences appearing as males and females reach adult body mass (1) or when females begin to reproduce (2). Alternatively, sex differences in feeding may be a niche partitioning strategy (3) that facilitates permanent social groups composed of multiple males and females. If niche partitioning helps to drive sex differences in feeding, then sex differences should appear early in life and will be reinforced throughout development. Successful niche partitioning may require social learning throughout the juvenile and subadult period to effectively establish the ecological differences between females and males. In this case same-sex associations reinforce sex differences and contribute a strong social learning component to sex differential feeding ecology in feeding (Agostini and Visalberghi, 2005). However, in many species the development of feeding is a self-motivated trial and error process (Buchler, 1980; Whitehead, 1986; Boinski, 1988; Wiens and Zitzmann, 2003), while some foraging tasks require a social partner to learn efficiently (Rapaport and Brown, 2008). Identifying when sex differences begin to develop in development can reveal their underlying evolutionary causation and the behavioral and social mechanisms (if any) used in the development of ecological differences between males and females. Understanding the relationships among feeding ecology, social learning, and sex-based ecological differences within a developmental framework is necessary to contextualize the suite of behavioral and life history features that characterize primates.

Juvenile feeding ecology is particularly important to many aspects of primate biology, and past work on the ecology of primate juveniles has focused on monkeys and, to a lesser degrees, on apes. Comparative data on the development of feeding ecology beyond weaning in wild strepsirrhines are rare, with single studies on *Eulemur fulvus* (Tarnaud, 2004) and *Nycticebus coucang* (Wiens and Zitzmann, 2003) contributing the bulk of the comparative data. Comparisons to the generalist strepsirrhines are necessary to understand the how feeding and the development of these behaviors have shaped primate evolution. Ring-tailed lemurs are eclectic omnivores that feed from a broad dietary menu and develop relatively quickly for a primate. Compared to similarly sized monkeys (e.g., *Cebus spp.*, 2.2-2.6 kg), ring-tailed lemurs (2.4-2.6 kg) reach sexual maturity quickly. The ring-tailed lemur juvenile period spans 18 months in captivity to 30 months in the wild. The social and physical development of captive ring-tailed lemurs has been well-explored (Klopfer and Klopfer, 1970; Klopfer, 1972; Pereira, 1993,1995; Palagi et al., 2002), but much less is known about how this occurs in an ecological context, (but see Gould, 1990) and little is known about the ecology of wild juvenile lemurs and their transition to adulthood. While the ontogeny of feeding ecology has been relatively well described in monkeys and apes, in the strepsirrhines it is less clear when food classes enter the diet, how this is mediated through social interactions, and how these relate to changes in physical size, strength, and coordination

In this dissertation I present a developmental view of feeding ecology in the ring-tailed lemur using a mixed longitudinal sample (infant through adult) of ring-tailed lemurs at the Beza Mahafaly Special Reserve in southwestern Madagascar to understand how feeding ecology changes throughout development, how social processes shape juvenile and adult feeding ecology and the emergence of sex differences in feeding, and if ecological risk aversion has a prominent effect on the duration of lemur juvenility.

Study Site – The Beza Mahafaly Special Reserve

The Beza Mahafaly Special Reserve is located in southwestern Madagascar (23.65647°S, 44.62897°E; Fig. 1-1) and was established in 1978 through a collaborative agreement among the local Mahafaly villages, the Université d'Antananarivo, Washington University, and Yale University (Ratsirarson, 2003). In 1986 the reserve was given the status of Special Reserve by the government of Madagascar and throughout its history has been administered by the Ecole Supérieure des Sciences Agrononomiques, Département des Eaux et Forêt at the Universite d'Antananarivo (ESSA-Forêt), the World Wildlife Foundation, and in 2004 Beza was transferred to the protection of Madagascar National Parks (Sussman and Ratsirarson, 2006). Beginning in 2007, as part of President Marc Ravolomanana's 2003 Durban Vision, Beza was expanded from its original 280 Ha in two non-contiguous parcels (Parcel 1 and 2) to incorporate over 3,500 Ha of protected area (Fig 1-2), with additional land designated for sustainable use, service and ecotourism, and restoration purposes (Youssef, 2010).

The primary study area, Parcel 1, grades from dry deciduous and Dideraceae dominated desert spiny forest in the west to a gallery forest dominated by *Tamarindus indica* in the east (Sussman and Rakotozafy, 1994). This west to east moisture gradient (dry to wet) is coincident with an increasingly tall and more enclosed canopy, increasing average tree stem diameter, and decreasing diversity in tree species per hectare (Sussman and Rakotozafy, 1994). Beza's climate is highly seasonal, with a cold dry (May-September) and a hot wet (October – April) season where 80% of the annual average of 615 mm of rain falls each year (Lawler et al., 2009). Temperature and rainfall measurements taken in camp show that this study period was hot and dry with average high temperatures of 35.7°C (dry season) and 45.8°C (wet season) and experienced half the amount of rain that typically falls during equivalent times in other years (Fig. 1-3; this study: 265mm, Beza average for June-March: 500mm; (Ratsirarson, 2003; Sussman and Ratsirarson, 2006).

Study population

The ring-tailed lemur (*Lemur catta*) is an IUCN Red List (A1C: Vulnerable and Declining) primate endemic to the forests of Southwestern Madagascar (Sauther et al., 1999). They live in large multi-male, multi-female groups of 9-22 individuals that form linear dominance hierarchies where, among adults, typically all females are dominant to all males. Births are highly seasonal and synchronous, with all females in a group giving birth within a one to two-week period of one another (Jolly et al., 2006).

Ring-tailed lemurs are eclectic frugivore-folivores that spend half of their feeding and foraging time on the ground (Sussman, 1977) and 95% of total observed feeding time is spent on substrate lower than 10 meters (O'Mara, unpublished data). Ring-tailed lemur foods do not require extensive processing, although some fruits such as *Tamarindus indica* may require a minimum of strength or post-canine occlusal surface area to open (Cuozzo and Sauther, 2004; Millette et al., 2009). Ring-tailed lemurs maintain a non-transitive dominance hierarchy with low linearity (Martin and Bateson, 1993) where, contrary to the typical mammalian pattern, females dominate males in all contexts (Pereira and Kappeler, 1997). Reproduction is photoperiod controlled, highly seasonal and synchronized to resource availability (Sauther, 1991; Jolly et al., 2002). Gestation typically occurs during the cold-dry season (May – September), with most infants born during the transition to the hot wet season (September – October). Ring-tailed lemurs lactate through the wet season (October – December) and wean their offspring during maximum food availability, particularly of young leaves (December – February). They experience a recovery period (March-April) before a very brief mating period (May) where females are receptive for a period of 6-24 hours (Sauther, 1991). First year mortality averages 50% (Gould et al., 2003) but was as high as 71% in the 2008 birth cohort (Meredith & O'Mara unpublished data).

Ring-tailed lemurs are an ideal contrast to developmental studies on monkeys an apes to their behavioral and ecological plasticity, relatively fast development, absence of sexual size dimorphism, and large multi-male multi-female social system. Their large social groups, eclectic feeding ecology, and high degree of terrestriality make ring-tailed lemurs comparable to many well-studied haplorhines, particularly baboons, macaques, and vervets, and provide an interesting contrast due to their female dominant social groups.

Seven study groups (mean size: 13, range: 8-19 individuals, including 6-14 adults) were sampled across the habitat gradient and included the collared, long-term study groups Red, Green, Orange, Yellow, Teal, Blue, and Purple (Figure 1-4). Group demographics are given in Table 1-1. Age classes are defined as Infant 1 (0-12 weeks), Infant 2 (13-24 weeks), Juvenile 1 (25 weeks – 1 year), Juvenile 2 (1-2 years), Subadult (2-3 years), and Adult (3 years and older). Description of each age stage are given in Appendix A. Birth dates are known for the individuals born into each of the study groups since 2006, but birth dates, exact ages, and matrilineal relationships are not known for females older than 4 years old and adult males who transfer between groups. Individuals were recognized through a combination of collars bearing numbered tags, natural markings, and in some cases, less than 1cc of dye (Nyanzol-D, Greenville Colorants) was applied to their fur.

Food availability

Phenology transects (Figure 1-5) were used to monitor the potential availability of plant resources. Twenty-one 2m x 30m phenology transects were distributed throughout the ranges of the study groups. In these transects woody plants with a diameter at breast height (DBH) greater than 2cm were individually tagged and identified to species totaling 402 individuals from 44 species. The DBH, total height, canopy height and canopy width were recorded for each individual. Every two weeks the proportional phenophase for young leaves and leaf buds, mature leaves, unripe fruit, ripe fruit, flower buds and flowers was ranked for each tagged plant on a 0-4 scale based on the presence of the phase relative to the estimated overall availability of sites within the crown. A score of zero indicated phase absence, 1=25%, 2=50%, 3=75%, 4=100% present. A one square meter plot located in the center of each transect was used to monitor ground cover with the same phase scale (0-4) indicating the presences of mature and young leaves in the herbaceous layer (Figure 1-6).

Goals and organization of the dissertation

My goal is to present an ontogenetic perspective on how ring-tailed lemurs develop the knowledge and behaviors that are related to feeding themselves, and how this process potentially structures life history and social relationships in this species. Chapter 2 provides a general description of the development of feeding in ring-tailed lemurs from nursing through weaning and nutritional independence as a juvenile and adult. The development of foraging behavior and of feeding ecology is essential for a juvenile to successfully progress from weaning to nutritional competency. Development of primate foraging competency can require more extensive learning due to broad dietary inclusion and selectivity of food items, as well as foods that require skill to extract (Altmann and Alberts, 1987; Ross and Jones, 1999; Deaner *et al.*, 2003). The skills necessary for some primate foraging tasks also require a minimum amount of physical maturation, coordination and skill, and local ecological knowledge (Boinski and Fragaszy, 1989), which may not be present until late in juvenility or until adulthood. In this chapter I show how and when individual food classes enter the diet of growing ring-tailed lemurs. These foods vary in their availability, physical properties, and particularly for insects, coordination required to capture or extract them.

In Chapter 3 I test how infant and juvenile lemurs use potential social information in the development of feeding. Infants and juveniles can use both social and individual learning strategies as they develop species-typical feeding ecology. In monkeys and apes, learning from mothers and other group mates is critical to survive weaning, with behaviors such as co-feeding playing particularly strong roles in determining post-weaning survival (Hauser, 1993; Altmann, 1998). Experiments have shown that adult lemurs are capable of social learning, but it is unknown how social information is incorporated throughout development or what social learning strategies are used. This chapter describes the diversity of behaviors that may be related to social learning (Rapaport and Brown, 2008), and tests the use of two behavioral classes that are assumed to facilitate social learning: co-feeding and behavioral synchrony (i.e., local enhancement).

Chapter 4 presents the first data from a lemur species applied to the behavioral and ecological predictions of Ecological Risk Aversion Hypothesis (ERAH: Janson and van Schaik, 1993). There is a general mismatch between the available behavioral support for the ERAH and the well-defined growth profiles in the monkeys and apes. Monkeys and apes grow in ways that are predicted by ERAH (Leigh, 1994; Breuer et al., 2009), but show very mixed results in their support of the behavioral patterns predicted by the ERAH that are necessary to produce these patterns (Stone, 2007; Bezanson, 2009; Gunst et al., 2010; Schmitt, 2010). Strepsirrhine primates do not show growth patterns depicted by ERAH (Godfrey et al., 2004), but there are no or few behavioral data to contextualize these patterns. The ontogeny of feeding from gregarious juvenile strepsirrhines such as the ring-tailed lemur contribute an important phylogenetic perspective on the relationship between the duration of the juvenile period and the emergent foraging behaviors of developing animals.

Finally, Chapter 5 addresses the ontogeny of adult sex differences in feeding. Sex differences in feeding ecology are common across mammalian taxa and may range from complete ecological and spatial separation of males and females to more subtle differences in the composition in and emphasis on foods eaten (Clutton-Brock, 1977; Beck et al., 2005; Ruckstuhl, 2007; Dunbar and Shi, 2008). Three hypotheses have been proposed for the origin and maintenance of sex differences in primate feeding: (1) sexual size dimorphism, (2) costs of reproduction, and (3) ecological competition avoidance or niche partitioning (Clutton-Brock, 1977; Rose, 1994). Recently, it has been shown across a wide survey of primates that sexual size dimorphism likely has a minimal effect on sex differences in ecology (Kamilar and Pokempner, 2008). This further emphasizes how costs of reproduction or intraspecific niche partitioning, or both, may drive ecological differences between males and females, but there have been few studies that have tested niche partitioning as a fundamental factor in sex differential feeding. Using developmental data I show when sex differences in ring-tailed lemur feeding appear and how they are related to costs of reproduction and niche partitioning.

Figure 1-1. The original two Parcels (P1, P2) of Beza Mahafaly Special Reserve. Map from Sussman and Ratsirarson (2006).

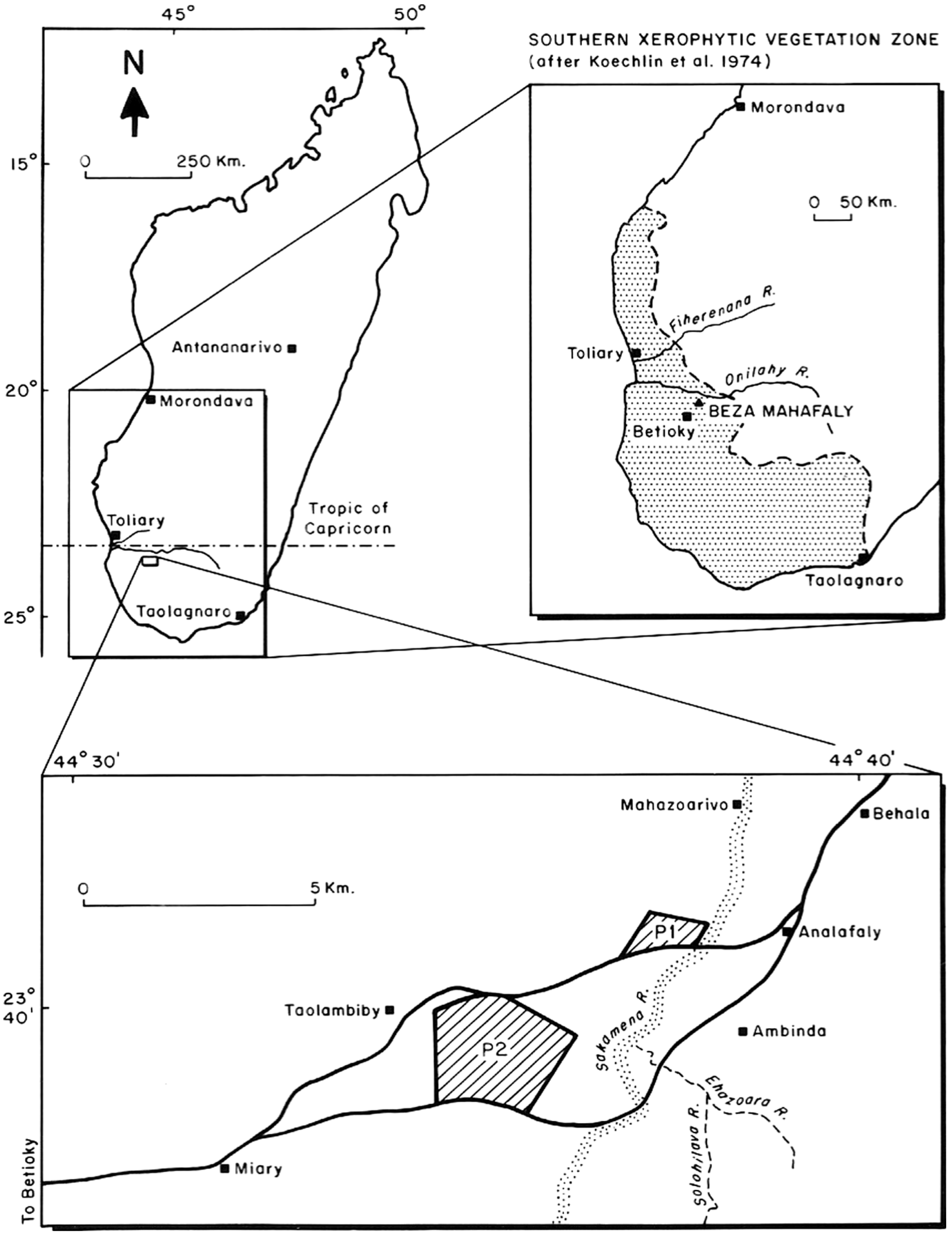
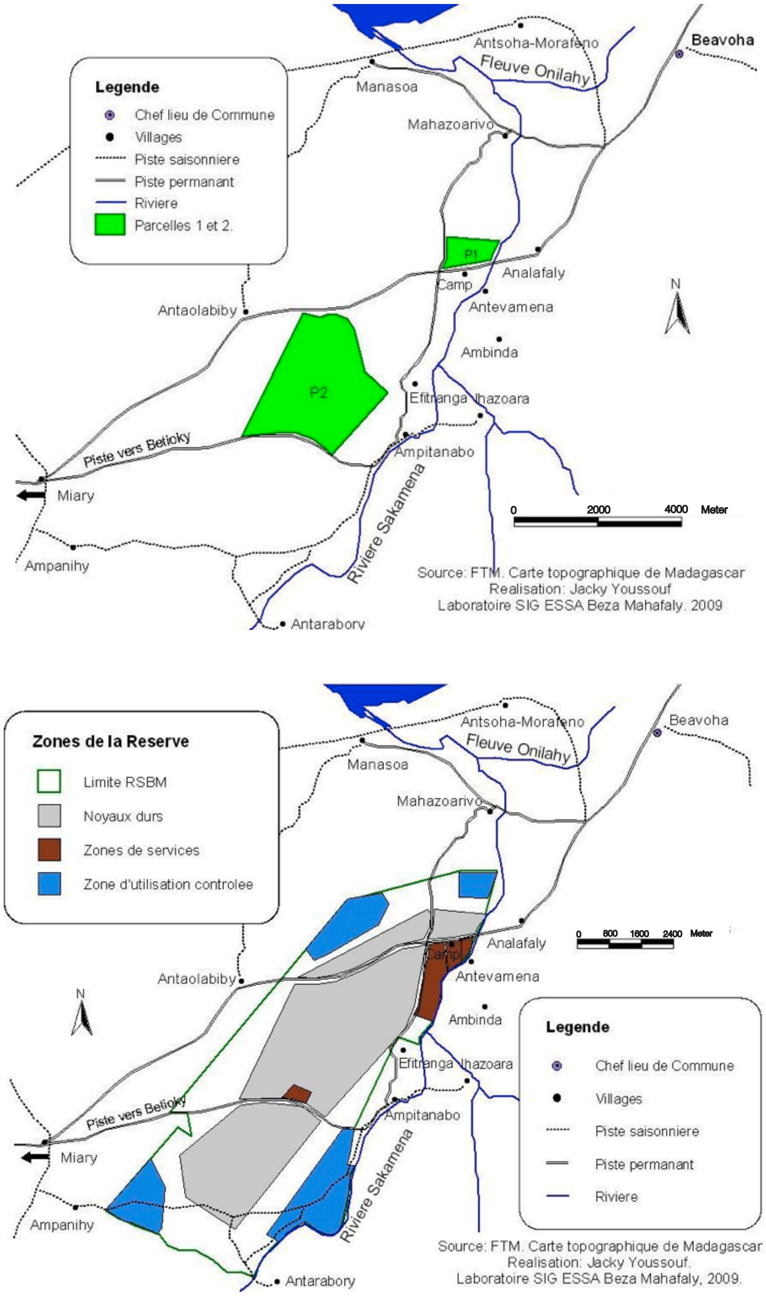


Figure 1-2. Expansion of Beza Mahafaly Special Reserve showing various use areas. The original two parcels are shown in green (top), and in the bottom panel the new extent of the reserve is outlines in green, with fully protected areas (Noyaux durs - grey), community sustainable use areas (Zone d'utilisation controlee – blue), and service and ecotourism zones (Zones de service – brown). Maps by IAJ Youssef (2010) and used with permission.



Source: FTM. Carte topographique de Madagascar
Realisation: Jacky Youssouf
Laboratoire SIG ESSA Beza Mahafaly. 2009

Source: FTM. Carte topographique de Madagascar
Realisation: Jacky Youssouf.
Laboratoire SIG ESSA Beza Mahafaly, 2009.

Figure 1-3. Two week mean maximum (filled circles) and mean minimum (open circle) temperature ±SD and monthly rainfall (red line, right axis) for the study period May 2009 – March 2010.

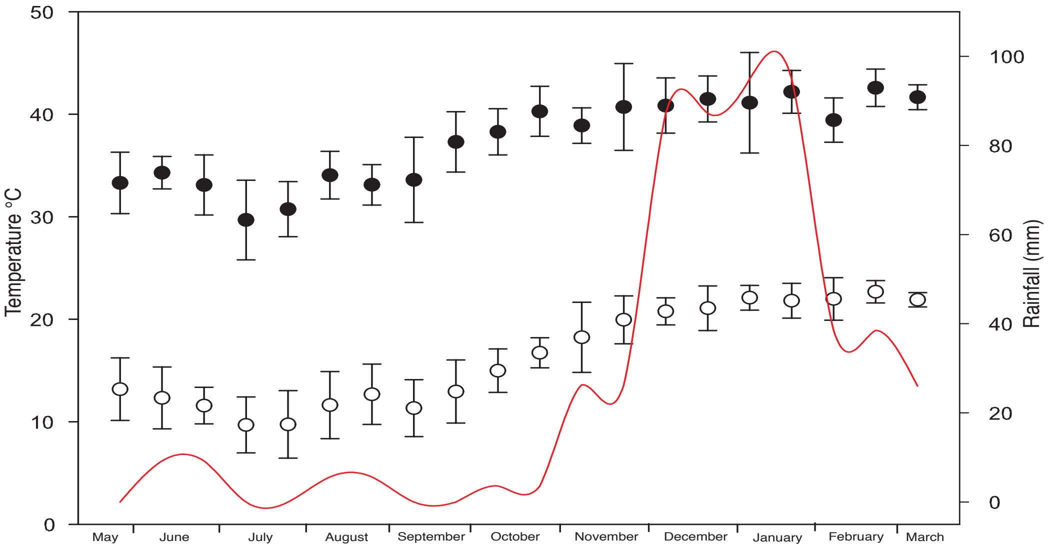


Figure 1-4. Ranges of the study groups. Color-coded circles are GPS coordinates taken every 30 minutes while following each group. Camp is marked by a star.

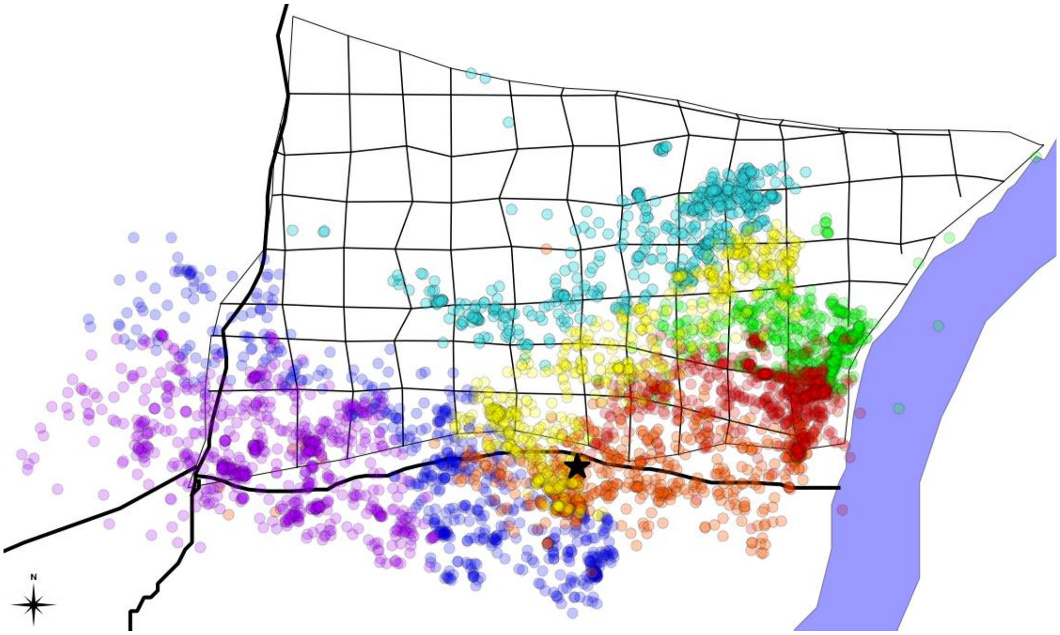


Figure 1-5. Phenology transect locations. Circles indicate the two ends of the transects, and camp by a star.

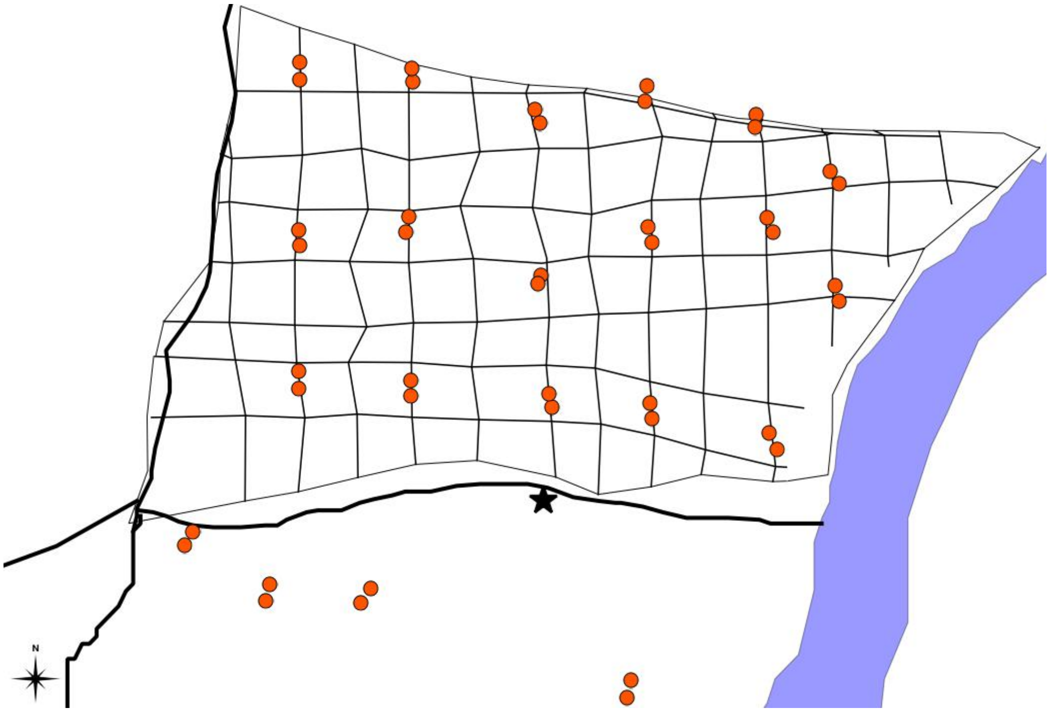


Figure 1-6. Food availability index for flowers, ripe fruit, unripe fruit, and young leaves for the bimonthly phenology assessments. Mature leaves are not shown. Monthly rainfall in the bottom panel is from Figure 3.

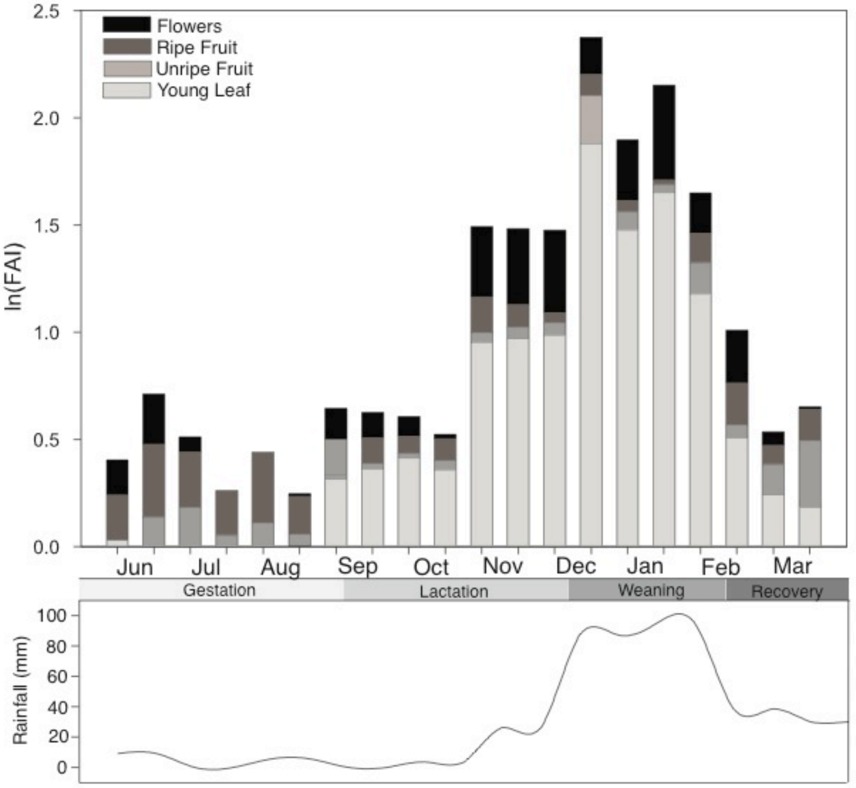


Table 1-1. Demographics of the study groups at the end of the study with the year of birth indicated in square brackets. Values in parentheses indicate the number of individuals in each category at the beginning of the study.

		Red	Green	Yellow	Teal	Orange	Blue	Purple
Infant to Juvenile	F	0	0 (2)	2 (3)	0 (2)	2 (3)	1 (3)	2 (2)
[2009]	M	0 (3)	1 (3)	0 (1)	1 (1)	2 (3)	2 (4)	2 (3)
Juvenile	F	1 (1)	0 (0)	0 (0)	1 (1)	2 (2)	1 (1)	0 (1)
[2008]	M	0 (1)	0 (1)	1 (1)	0 (0)	0 (0)	0 (0)	0 (0)
Juvenile to Subadult	F	0 (0)	0 (0)	0 (0)	0 (0)	2 (2)	0 (0)	0 (0)
[2007]	M	0 (0)	0 (0)	0 (0)	1 (1)	1 (1)	0 (0)	2 (2)
Subadult to Adult	F	0 (0)	1 (1)	0 (0)	1 (1)	1 (2)	1 (1)	0 (0)
[2006]	M	2 (2)	1 (2)	1 (1)	0 (0)	1 (1)	0 (2)	2 (2)
Adult	F	4 (4)	4 (4)	4 (4)	3 (3)	5 (6)	6 (6)	6 (6)
	M	3 (3)	5 (3)	4 (2)	2 (2)	5 (5)	4 (4)	4 (4)

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CHAPTER 2: THE ONTOGENY OF RING-TAILED LEMUR FEEDING

INTRODUCTION

Feeding and foraging are the largest daily energy expenditures for a primate, and can constitute a significant portion of the overall daily time budget (Cant and Temerin, 1980; Wrangham, 1980). The development of foraging behavior and of feeding ecology is essential for a juvenile to successfully progress from weaning to nutritional competency, and eventually into a competitive role within the social group. Males and females must assume those behaviors typified by their species in order to succeed, incorporating the knowledge of sometimes highly disparate sex-typical feeding ecologies and their proper execution. This places juveniles in a precarious position whereby exploitation of individual innovation and social observation of diet type and temporal patterning must be executed without placing themselves in direct competition with adult members of the social group.

Development of feeding and foraging competency can require more time and learning in primates than in other mammalian orders due to broad dietary inclusion and selectivity of food items, as well as foods that require skill to extract (Altmann and Alberts, 1987; Ross and Jones, 1999; Deaner et al., 2003). The abilities necessary for some primate foraging tasks require a minimum amount of physical maturation, coordination and skill, and local ecological knowledge (Boinski and Fragaszy, 1989), and after reaching nutritional independence, juveniles of some species need considerable time to develop the strength and coordination needed to process complex foods. For chimpanzees (*Pan troglodytes schweinfurthii*) to process and eat the fruit of *Saba florida* they must remove the edible sarcocarp from around large seeds embedded in a tough inedible matrix. Successful removal of the fruit requires substantial strength and dexterity, and typically follows a well-defined behavioral sequence (Corp and Byrne, 2002). Infant chimpanzees are able to process these fruits by two years of age, but they do not achieve adult mastery and sequence fidelity until two years later (Corp and Byrne, 2002). On food resources that primarily require strength to process (*Maximiliana maripa* palm fruit), brown capuchins (*Cebus apella*) show adult behaviors by two years of age and reach adult proficiency by 3 years of age (Gunst et al., 2010). For foods that require more complex perceptual processing (e.g., finding and extracting beetle larvae), capuchins do not show adult proficiency until well into adulthood at six years of age (Gunst et al., 2008). Likewise, the aye-aye (*Daubentonia madagascariensis*) requires long periods of observation and co-feeding with their mothers to master the extractive foraging behaviors for which this lemur shows anatomical and behavioral specialization (Krakauer, 2006), and which shows a slightly higher relative brain size when compared to other lemurs (MacLean et al., 2009).

While the ontogeny of feeding ecology has been relatively well described in monkeys and apes, in strepsirrhines it is less clear how and when food types enter the diet and how social interactions influence the development of skills and knowledge related to feeding. In the lemurids, the use of social information through co-feeding in the development of feeding behaviors does not seem to be as crucial as in monkeys or apes, although there may be significant local enhancement that draws attention to a particular locale in the environment and its food resources (Chapter 3; Krakauer, 2006). Brown lemurs (*Eulemur fulvus*) will synchronize their feeding with their mothers and have high dietary overlap with her, but it is not known if this differs relative to other group members, or how social coordination in this species varies by activity and context (Tarnaud, 2004). It is unclear if social facilitation influences the development of diet in the solitary strepsirrhines. In a study of a single wild juvenile solitary slow loris (*Nycticebus coucang*) the juvenile shows high dietary concordance with its mother, although no social interaction during feeding was observed (Wiens and Zitzmann, 2003). Instead of behavioral observation and social facilitation guiding dietary development, odor transfer via breath or milk, similar to what has been reported for rodents (Galef and Sherry, 1973), may be more important in the slow loris and other less gregarious nocturnal primates.

The development of several lemur populations has been documented from birth until weaning (Table 2-1), but with the exception of brown lemurs (Tarnaud, 2004,2008), little is known how wild juvenile lemurs transition to adult diets. The main developmental stages of captive brown, ring-tailed, and ruffed lemur infants have been described from birth to three months old. In general, ring-tailed lemurs meet behavioral developmental landmarks sooner than these other lemurs (Klopfer and Klopfer, 1970; Klopfer, 1974; Klopfer and Dugard, 1976). They begin exploring their environment and interacting with other group members sooner than other lemurids, although weaning and nutritional independence is similarly timed among these species (Klopfer and Klopfer, 1970; Leigh and Terranova, 1998; Wright, 1999). However, little is known of how wild juvenile lemurs continue their development through adulthood and if a generalized lemurid developmental pattern exists.

Here I describe the overall pattern of the ontogeny of feeding ecology in ring-tailed lemurs from infancy through adulthood. Using behavioral data collected from a mixed longitudinal sample of ring-tailed lemurs at the Beza Mahafaly Special Reserve, Madagascar I show how various food classes enter the diet, when infants are weaned, and how processing skills develop for both difficult to process and difficult to capture foods. In general, adult-like proficiency in most areas of feeding are achieve by early juvenility in ring-tailed lemurs, but strength and skill-based food processing takes more practice and achieving near-adult size and dentition.

METHODS

Study Site. Data were collected from May 2009 to March 2010 at the Beza Mahafaly Special Reserve (Beza) in southwest Madagascar (23.65647°S, 44.62897°E) where the biology, behavior, and ecology of adult ring-tailed lemurs have been studied since 1987 (Sauther, 1998; Yamashita, 2002; Gould et al., 2003; Sussman and Ratsirarson, 2006; Sauther and Cuozzo, 2009). The primary study area, Parcel 1, grades from gallery forest dominated by *Tamarindus indica* in the east to drier deciduous and Dideraceae dominated desert spiny forest as one moves west away from the Sakamena river (Sussman and Rakotozafy, 1994). This east to west moisture gradient is coincident with a lower and more open canopy, smaller average tree stem diameter, and increasing diversity in tree species per hectare (Sussman and Rakotozafy, 1994).

Beza's climate is highly seasonal, with a cold dry (May-September) and a hot wet (October – April) season where 80% of the annual average of 615 mm of rain falls each year (Lawler et al., 2009). This study period was hot and dry with average high temperatures of 35.7°C (dry season) and 45.8°C (wet season) and with only half the amount of rain that typically falls during equivalent times in other years (this study: 265mm, Beza average for June-March: 500mm; (Ratsirarson, 2003; Sussman and Ratsirarson, 2006).

Study population. Ring-tailed lemurs are eclectic frugivore-folivores that spend half of their feeding and foraging time on the ground (Sussman, 1977) and 95% of total observed feeding time is spent on substrates lower than 10 meters (O'Mara, unpublished data). Ring-tailed lemur foods do not require extensive processing, although some fruits such as *Tamarindus indica* may require a minimum of strength (bite force) or post-canine occlusal surface area to open (Cuozzo and Sauther, 2004; Millette et al., 2009). Reproduction is photoperiod controlled, highly seasonal and synchronized to resource availability (Sauther, 1991; Jolly et al., 2002). Gestation typically occurs during the cold-dry season (May – September), with most infants born during the transition to the hot wet season (September – October). Ring-tailed lemurs lactate through the wet season (October – December) and wean their offspring during maximum food availability, particularly of young leaves (December – February). They experience a recovery period (March-April) before a very brief mating period (May) where females are receptive for a period of 6-24 hours (Sauther, 1991).

More than 2,300 observation hours were completed by five observers on a mixed longitudinal sample of ring-tailed lemurs from early infancy through adulthood (Appendix A) of 78 individuals from seven study groups (Table 2-2). Birth dates are known for the individuals born into each of the study groups since 2006, but birth dates, exact ages, and matrilineal relationships are not known for females older than 4 years old and adult males who transfer between groups. Individuals were recognized through a combination of collars bearing numbered tags, natural markings, and in some cases, less than 1cc of dye (Nyanzol-D, Greenville Colorants) was applied to their fur. Interobserver reliability was periodically assessed to maintain a minimum of 85% agreement using Cohen's Kappa statistic included in the JWatcher package (Coelho and Bramblett, 1981). All methods were approved by the IACUC at Arizona State University (08-983R) and by Madagascar National Parks (138/09, 257/09**)** and conformed to the Principles for the Ethical Treatment of Non-Human Primates of the American Society of Primatologists

Behavioral Sampling. Continuous and instantaneous sampling methods (Altmann, 1974) were used simultaneously to sample feeding and its social context during 12-minute focal animal sampling sessions (FAS). Subjects were chosen from among the seven study groups to maintain a sex and rank balanced sample within each age category. These individuals were selected for observation following a stratified random protocol where an infant or juvenile was followed every other or every third observation. Each social group was observed in rotating two-day blocks for between four and eight days per month. All feeding, foraging, bite counts, and aggressive behaviors were recorded continuously in JWatcher (www.jwatcher.ucla.edu). Nursing was defined as any time that an infant was in mouth contact with a lactating female's nipple. This then includes all times when the infant was ingesting milk as well as when they were resting (Appendix B).

General activity. General activity of the focal (feed, forage, rest, move, stand, groom, other) was recorded instantaneously at three-minute intervals during each FAS session. At these three-minute intervals the identity, activity, and categorical distance to the nearest neighbor (touching, within arm's reach, within one meter, within three meters, and greater than three meters away were also recorded.

Feeding and foraging. To be included in analysis of the continuous and instantaneously recorded variables, individuals must have contributed a minimum of three observation sessions in a given day. Each individual contributed between four and eight FAS per day (Table 2-2). Feeding was defined as the ingestion of food and foraging was defined as the active searching for and processing of food items and includes sniff, lick, and crack. Plant parts were divided into unripe fruit, ripe fruit, young leaves, mature leaves, flowers and flower buds. Ring-tailed lemurs also include arthropods, soil, and wood into their diet. Arthropods were identified to species when possible and minimally to taxonomic order. Plants were identified to species with help of local experts (Mr. Elahavelo and Mr. Herman Mananjo), by Mr. Rokiman Lestara (Tsimbazaza Botanical Gardens, Antananarivo), and through digital voucher images from the Missouri Botanical Gardens TROPICOS database (www.tropicos.org). Bite counts were conducted each individual throughout the twelve-minute FAS sessions to measure intake rates. We attempted to measure bite count rates at least twice per individual per day (Table 2-3). These intake rates are then used as a measure of ingestion rate and feeding efficiency (Johnson and Bock, 2004). Most fruits and young leaves, which constitute the bulk of ring-tailed lemur diet, are ingested in a single bite by all age categories (Sauther, 1992). Bite count rates were calculated for each individual from each bout of feeding each food type. Average bite count rates were then calculated for each day when counts were taken.

Analysis

To measure the dietary overlap of total food species and their constituent parts among individuals, a dietary overlap index (R) was calculated for all individual pairs within each group during these two-week blocks. R was calculated as $R = \frac{\Sigma(p_{ij} \times p_{ik})}{\sqrt{\Sigma p_{ij}^2 \times \Sigma p_{ik}^2}}$, where p_{ij} and p_{ik} are the proportion of item i in the diet of individuals j and k (Pianka, 1973).

Both continuously and instantaneously recorded data are summarized as proportions of total observations per individual per day. This generates a mixed-longitudinal data set of individual-days with the intent of preserving any individual level variability in behavior (Machlis et al., 1985; Dagosto, 1994). Generalized linear mixed models (GLMMs) were then fit to the mixed longitudinal data in the *lme4* package in R 2.13 (R Core Development Team, 2011). Untransformed proportional data were modeled using logistic mixed models with a binomial distribution and logit link identity (Jaeger, 2008; Warton and Hui, 2011). Traditional repeated measure designs are encumbered by balanced sample requirements that can rarely be met using observational data from wild animals. Generalized linear mixed models have the advantage of being able to process unbalanced, multi-way repeated measures designs through the inclusion of random effects in the model (Bolker et al., 2009). For all models, individual animal identity and a time factor (reproductive season) were included as random effects. The significance of the fixed factors (e.g., age, sex) was evaluated by comparing two nested models differing in a single factor (Huchard et al., In Press; Pinheiro and Bates, 2009). A likelihood ratio test (X^2) of these two nested models was then used to evaluate the significance of individual factors (Lewis et al., 2011). When factors did not significantly contribute to the fit of the model they were removed from the analysis. For models with significant main effects, subsequent Tukey's post-hoc tests identified differences among factor level pairwise comparisons, typically age-sex levels. All significance was evaluated at $\alpha=0.05$.

RESULTS

Food exploration and weaning. Infant ring-tailed lemurs began exploring potential solid foods as early as 2-3 weeks in this study. These typically were not items eaten by the group as they were sticks, waxy leaves, etc., and likely were only used as objects as part of individual play bouts. On average, infants begin to feed on young leaves at four weeks of age, when their premolars are beginning to come into occlusion (Figs. 2.1 and 2.2), mature leaves and flowers at five weeks, and tougher to process fruits (e.g., *Tamarindus indica, Strychnos madagascariensis*) at seven weeks into their diets, which is slightly earlier than the ages reported by Gould (1990) for each of these food categories. Weaning, defined by a marked increase in maternal rejection rates and a decrease in nursing, begins at 16 weeks and is completed by the end of 24 weeks (Fig. 1). Occasional nursing occurs until 27 weeks and no nursing behavior was observed by the end of the seventh month. This period of time coincides with the eruption of the first permanent lower molar (M1) and a rapid increase in dental eruption (Fig 2-2). Infants have passed into juvenility and full nutritional independence by 28 weeks of age. As has been previously shown (Sauther, 1998), weaning coincides with maximum food availability, with a substantial increase in the availability of young leaves and flowers (Chapter 5; Fig 2-3). Juveniles then can transition to feeding on ripe fruit as it becomes available throughout the subsequent dry season.

Allonursing was observed in six of the seven study groups at varying frequencies. Of the 22 infants who were studied, 12 of them (54.5%) were observed to nurse from a female who wasn't their mother at least once (Table 2-4). Infants nursed from females who had living infants and those whose infants had recently died. Three of the adult females who allonursed (27.3%) had recently lost their infants, although one of these females also nursed other infants while her own was alive. Females who lost an infant nursed more infants more regularly than other females in their groups. For example, two females from different groups both lost their infants when they were 7 and 8 weeks old, respectively. These females routinely nursed other infants in the group until well past when these infants were weaned from their own mothers. During the weaning transition allonursing may account for almost 90% of nursing observations in a single day, but typically is 10-16% of nursing during weaning/post weaning. The genetic relationship between adult females who allonursed and the infants they supported is unknown.

Infants have closer nearest neighbors than juveniles, subadults, and adults when they feed and forage. Infants have higher proportions of nearest neighbors within one meter, in contact and within arm's reach (Fig 2-4: Touch: X^2=78.726, df=11, $p<0.001$; Reach X^2=59.555, df=11, $p<0.001$; 1 m X^2=65.564, df=11, $p<0.001$; 1-3 m X^2=44.101, df=11, $p<0.001$; >3 m X^2=119.09, df=11, $p<0.001$). As infants grow into juvenility they transition to adult-like spacing patterns except for attaining adult-like sex differences in spacing at Juvenile 1, with typical distances between nearest neighbors of 1 and 3 meters away (Chapter 5). Infants have their mother as their nearest neighbor while feeding and foraging more often than other group members (Fig 2-5), but after weaning juveniles have their mothers as nearest neighbors for less than 20% of feeding and foraging time (X^2 = 106.42, df=3, p<0.001; Fig 2-5).

All age classes of ring-tailed lemurs have moderate dietary overlap among individuals within a social group (Fig 2-6). Dietary overlap, both with an individual's mother (X^2=5.561, df=4, p=0.234) and among other group members (X^2=8.521, df=5, p=0.130), is consistent among all age categories. There are no differences within age categories between an individual's dietary overlap with older and with same age or younger group members (Fig. 6; X^2=17.247, df=10, p=0.069). However, young juveniles generally have higher dietary overlap with group members, but this is only significant for dietary overlap with group members that are older than the focal individual (X^2=10.18, df=4, p=0.0375).

Food handling and processing. Including nursing, young infants spend more time than older age categories feeding relative to foraging, but this quickly transitions to levels consistent with older age categories by infant 2 (Fig 2-7; X^2= 652.3, df=5, p<0.001). Growing ring-tailed lemurs also quickly approach adult-like ingestion rates for all foods except for ripe fruit and flowers (Fig 2-8; X^2= 207.92, df=30, p<0.001; Chapter 3). Adult-level proficiency for both ripe fruit and flower ingestion is not reached until subadulthood when animals have reached nearly adult body size and strength as well as have begun integrating themselves into the adult dominance hierarchy.

As much as 30% of a group's total feeding time is focused on the ripe fruit of *Tamarindus indica* (Head et al., in review). The ripe fruit of *T. indica* is a difficult food to process. Its hard outer shell, tough fibrous interior and sticky pulp make processing this fruit time intensive for lemurs with either few teeth erupted or highly eroded dentition (Millette et al., 2009) as well as young animals with less-developed jaw musculature.

Infants through young Juvenile 1 spend more time cracking fruit than ingesting the pulp (Fig 2-9; F=7.901 df=5, 84; $p<0.001$), as well as more time cracking the fruit than licking it (Fig 2-9; F=2.472 df=5, 97; p=0.037). Juvenile 1 have higher ratios for both of these behaviors, which is unsurprising given that they are still responsible for meeting their own nutritional needs at a smaller body size and lower dental surface area than adults (Fig 2-2).

Ring-tailed lemurs were not observed to engage in any complex food processing behaviors. Arthropods comprise a small proportion of ring-tailed lemur diet (Appendix C), but most insects that these lemurs eat require some level of skill and coordination to capture. Ring-tailed lemurs fed on beetles, cicadas, spiders, lepidoptera larvae (Fig 2-10A & B), and the sugary secretions ("honeydew") of a white fly nymph (*Aleuromarginatus millettiae*, Fig 2-11). The only flying insects that ring-tailed lemurs were observed to capture were cicadas (Fig 2-10C, *Yanga heathii*) and jewel beetles (Fig 2-10D, *Lampropepla rothschildii*). Jewel beetles were seen occasionally throughout the year, and cicadas are only available during the early wet season (October – November) during which time they experience an explosive emergence and breeding season. Because of the seasonal availability of cicadas, opportunities to practice capturing flying insects may be limited.

Insects, including cicadas, jewel beetles, and larval Lepidoptera are seasonal and are not often eaten. Infants and young juveniles were never observed to capture flying insects and only fed on flying insects that were caught by older group members (typically their mother). Older juveniles were less successful than adults and subadults (Fig 2-12, X^2= 6.2, df=2, p=0.045). However, within adults, there was large individual variation in their capture success, with some individuals never successfully catching cicadas and the most expert females successful on 60% of observed attempts.

DISCUSSION

Soon after weaning, ring-tailed lemur juveniles forage and feed in very adult-like ways. They show spacing and time invested in feeding relative to foraging that is similar to all older age categories. With exception of ripe fruits and flowers, juveniles also show adult-like feeding efficiency and ingestion rates. Offspring show the same dietary overlap with their mothers as with other group members. However, processing foods that require strength, such as *T. indica*, or a skill such as capturing flying insects are not reached until later in juvenility or subadulthood. With these exceptions, juvenile ring-tailed lemurs forage and feed like adults and then are able to use the juvenile period to refine skills, develop social relationships, and divert energy to build body mass for an environment with unpredictable food availability.

Gould (1990) divided wild infant ring-tailed lemur development into three stages of primate social development: neonatal (mother-focused), exploration, and peer socialization (Poirier, 1971; Fragaszy and Mitchell, 1974). Many of the behavioral landmarks identified by Gould (1990) were observed at slightly early ages in this population (Table 2-1), with the exception of weaning. Gould (1990) identified the beginning of weaning at 8 weeks, which coincided with an increase in overall rejection rates. The rejection profiles between Gould (1990) and this study are similar, with peak rejection rates from the nipple for both studies at 16 weeks (Fig 2-1). While there is an increase in rejection rates at 8-10 weeks, when combined with the changes in nursing and feeding and foraging, weaning does not begin in this population until 12-14 weeks, which is nearly one month later than has been previously reported at Berenty (Table 2-1; Gould 1990). Differences in weaning time in these two populations may reflect effects of water and food provisioning that have occurred at Berenty but are absent at Beza. A consistent decrease in the proportion of time spent suckling relative to time feeding and foraging on solid foods does not occur until 16 weeks (Fig 2-1), which coincides, in captivity, with the emergence of the first molar (Fig 2-2), a commonly used dental marker of weaning and the transition to nutritional independence (Eaglen, 1985). However, the first molar emergence appears to be later than 16 weeks in this wild population (Cuozzo and Sauther, 2006; M.L. Sauther, personal communication). Infants in this sample do not consistently reduce their time spent nursing until after 20 weeks of age (Table 2-1). The completion of weaning around 24 weeks is similar to that seen in captive ring-tailed lemurs (Palagi et al., 2002), wild *Eulemur fulvus* (19 weeks: Tarnaud 2004) and *Eulemur flavifrons* (25 weeks: (Volampeno et al., 2011).

In a study of four mother-offspring pairs of *Eulemur fulvus,* Tarnaud (2004) identified four phases marked by changes in the focus of food and the dietary overlap and coordination with mother. Phase one includes nursing with limited exploration (0-3 mo). Phase 2 (4 & 5 mo) involved independent feeding and social weaning where the offspring spent more time feeding than their mothers during the middle portion of the day, with mothers exhibiting a burst of feeding activity at the end of the day which the infants did not show. During phase three (immediate post-weaning: 6 & 7 mo) feeding of mother and offspring *E. fulvus* is largely coordinated, with large dietary overlap. In the late post-weaning Phase 4 (10-12 months) are independent and do not synchronize their behavior with their mother. Ring-tailed lemur infants and juveniles advance through these stages at earlier ages than do brown lemurs, which is consistent with differences in overall social development in these two species (Klopfer and Klopfer, 1970). Both captive and wild ring-tailed lemur infants and juveniles explore their ecological and social environments earlier than *E. fulvus*, with juvenile ring-tailed lemurs more often feeding and foraging with group members than they do with their mothers (Fig 2-5).

Over the course of a year, adult and subadult ring-tailed lemurs consume an average of 35.7 ± 2.06 plant species, infants 22.5 ± 2.46 plant species, young juveniles 34 ± 3.69 plant species, and older juveniles 38 ± 1.71 plant species. Juveniles have more diverse diets than all other age categories (Chapter 4), with the major increase in dietary diversity is at 35-40 weeks of age, approximately mid-way through the young juvenile period, and does not drop until adulthood. This pattern of high juvenile diet diversity is also found in brown lemurs, where 20-40% of the plant species that mother-juvenile pairs ate were exclusive to the juvenile only (Tarnaud, 2004). Infant ruffed lemurs (*Varecia rubra*) willingly explore their environment early on as well, trying new foods that are presented to them. However, infant and juvenile aye-ayes are much more reluctant to try new foods without the social facilitation of their mothers (Krakauer, 2006). Based on these three species, it appears that lemurid infants and juveniles are highly motivated to explore and build their diets through trial and error and limited social facilitation (Chapter 3). The larger dietary diversity observed in juvenility is then gradually reduced up until adulthood.

By the end of their first year, ring-tailed lemurs have a nearly full adult dentition (Fig 2-2), with complete eruption of permanent dentition by 16 months (Schwartz et al., 2002). At this point (Juvenile 2), ring-tailed lemurs take the same amount of time to process tough foods as adults, exemplified by *Tamarindus indica* (Fig 2-6). However, in a similar manner to fruit foraging and processing by juvenile *Cebus apella* (Gunst et al., 2010), juvenile ring-tailed lemur ripe fruit ingestion rates are lower than adults until they are nearly adult sized (Fig 2-5). This time lag between processing and ingestion efficiency may be due to strength differences between subadults and the smaller juveniles. To bite and ingest *T. indica*, the sticky pulp (and usually a large seed) must be pulled from the fibrous interior and then chewed and swallowed (Sauther, 1992). Juvenile jaw musculature may not be strong enough to do this as quickly as adult-size animals. However, these data are currently lacking and further study of the ontogeny of jaw length and gape size relative to bite strength will help contextualize this lag between processing and ingestion efficiency.

Ring-tailed lemurs were not observed to engage in any type of extractive foraging or complex food handling. Capture of flying insects is the most skill-intensive food processing executed by ring-tailed lemurs. Mastery of this skill is not achieved until adulthood (Fig 2-12), and there is a large amount of variation in the success rates of individual lemurs. The most successful animals tended to be adult females who would force a cicada to fly, track it to where it landed, and then jump onto it with both hands. Attempts at grabbing the insects while in flight were rarely successful. Capture of

Lepidoptera larvae (caterpillars) in trees also required some skill. When disturbed, these caterpillars would drop from the tree crown on a silk thread and out of reach of the lemurs. Ring-tailed lemurs either had to detect the caterpillars directly on the leaf surfaces or grab them as soon as they tried to escape. Adults were more successful than any other age category, and proficiency wasn't achieved in caterpillar capture until subadulthood (Fig 2-12).

Compared to similarly sized monkeys (e.g., *Cebus spp.*, 2.2-2.6 kg), ring-tailed lemur (2.4-2.6 kg) development is rapid. The ring-tailed lemur juvenile period spans 18 months in captivity to 30 months in the wild. This is considerably shorter than the length of the juvenile period in *Cebus spp.* or *Cercopithecus campbelli* (2.2-2.7 kg) that may spend 4 to 5 years as juveniles (Jones et al., 2009). Despite marked differences in the length of the juvenile period, a general pattern in the development of primate juvenile foraging behavior is present. As in some of the more frugivorous monkey species, including *Cebus* (Bezanson, 2009; Gunst et al., 2010), *Saimiri* (Boinski and Fragaszy, 1989; Stone, 2007), and *Papio* species (Johnson and Bock, 2004), the general patterns of ring-tailed lemur feeding behaviors are developed early during the juvenile period. Along with the early ontogeny of feeding, patterns of juvenile positional behavior in some of these species, including ring-tailed lemurs, also reflect adult patterns (Bezanson, 2009; Wolf, 2011). This is contrary to more folivorous monkeys, including *Alouatta palliata,* that develop feeding behaviors and positional behavior patterns slowly and do not show adult-like foraging behavior until they have reached nearly adult size (Whitehead, 1986; Bezanson, 2009). Whitehead (1986) assigns the slow development of feeding in *A. palliata* as a cautious tactic to learn the appropriate leaf type to avoid high concentrations of secondary compounds. In the primate species that attain adult-like foraging early in juvenility, they still require a significant amount of time to become proficient at complicated foraging and food processing tasks (Corp and Byrne, 2002; Johnson and Bock, 2004; Lonsdorf, 2005; Gunst et al., 2010). While ring-tailed lemurs do not forage for hidden or more cognitively demanding foods, they do require several years to become efficient at insect capture. Overall it seems that juvenile lemurs assume the majority of adult-typical foraging behaviors soon after weaning. There is likely strong pressure to reach proficiency in important foraging tasks to meet the energetic and nutritional needs of their own growth and development. In an highly seasonal environment, such as Beza Mahafaly, there is strong pressure for juveniles to learn to feed themselves quickly and effectively and for females to wean offspring as quickly as possible so that they can recover body condition in preparation of the next year’s reproduction. More complicated skills that focus on obtaining high-value foods take more time to be refined. It is still unknown how the development of feeding, the weaning transition, and juvenility are linked to the energetic balance of juveniles as they move toward adulthood. As comparative behavioral and ecological data are collected on juvenile primates, future work that includes physiological and energetic markers will provide new and invaluable insight into primate juvenility, and how the energetics of juvenility sets the pace for primate life history and the social complexity that is so common across the primate order.

Figure 2-1. Percent of total feeding time in nursing (black) and feeding on solid food (grey). Hourly maternal rejection rate is shown by the red line.

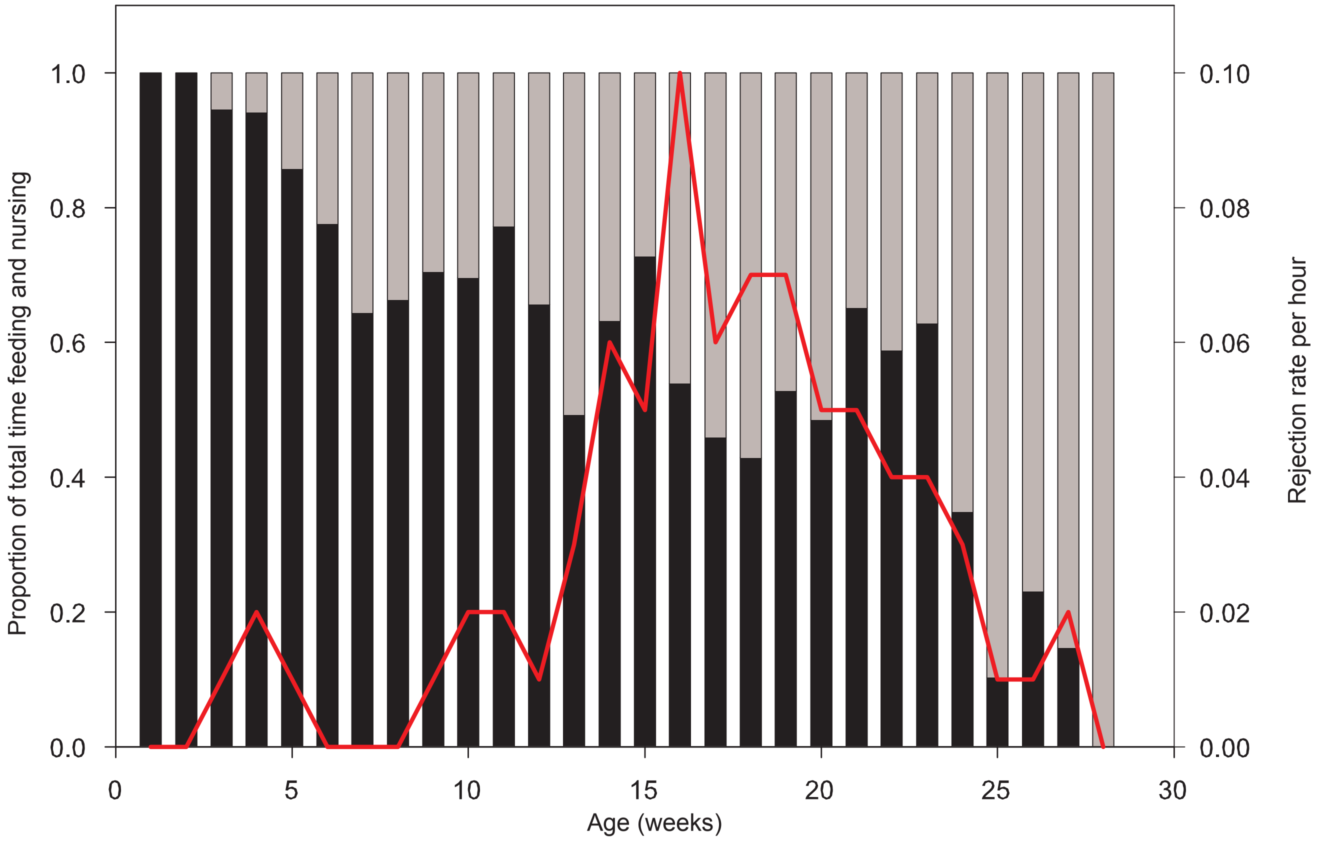

Figure 2-2. Eruption of permanent molars and premolars in ring-tailed lemurs. Age along the horizontal axis is given in weeks, with a schematic representation of dental developmental stage from Schwartz et al (Schwartz et al., 2002) on the vertical axis and illustrated with the horizontal lines that increase throughout development. Permanent premolars begin eruption at 4 weeks of age, with permanent molars beginning at 16 weeks. Data are compiled from Eaglen (1986) and Godfrey et al (2004)

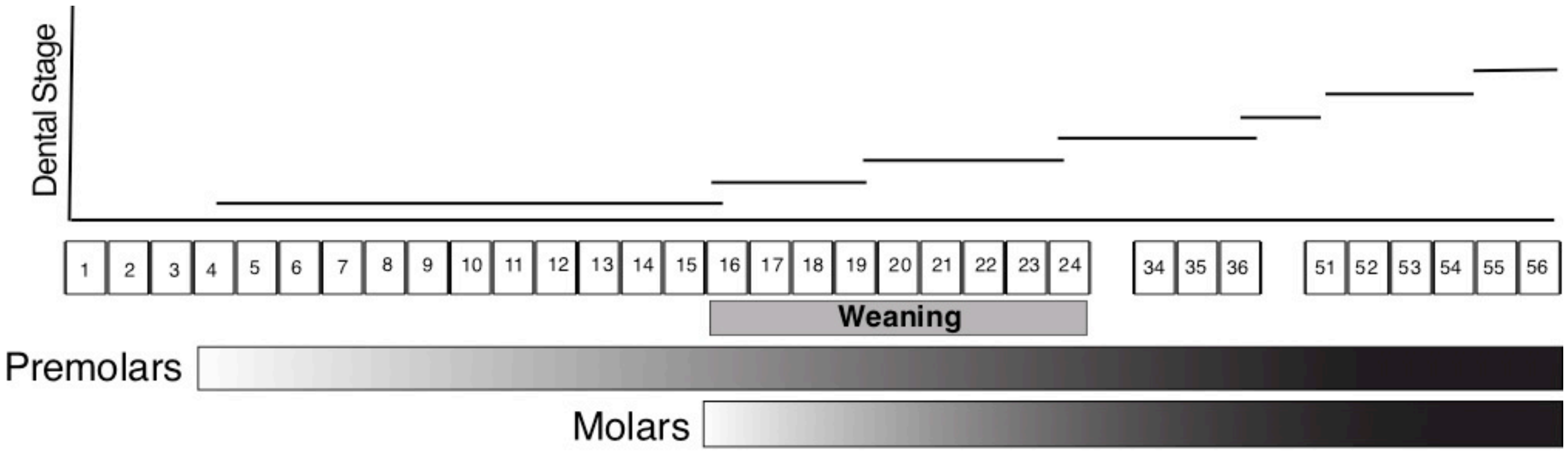

Figure 2-3. Food availability index (FAI) and monthly rainfall throughout the study period as described in Chapter 5. Peak food availability coincides with weaning of infants.

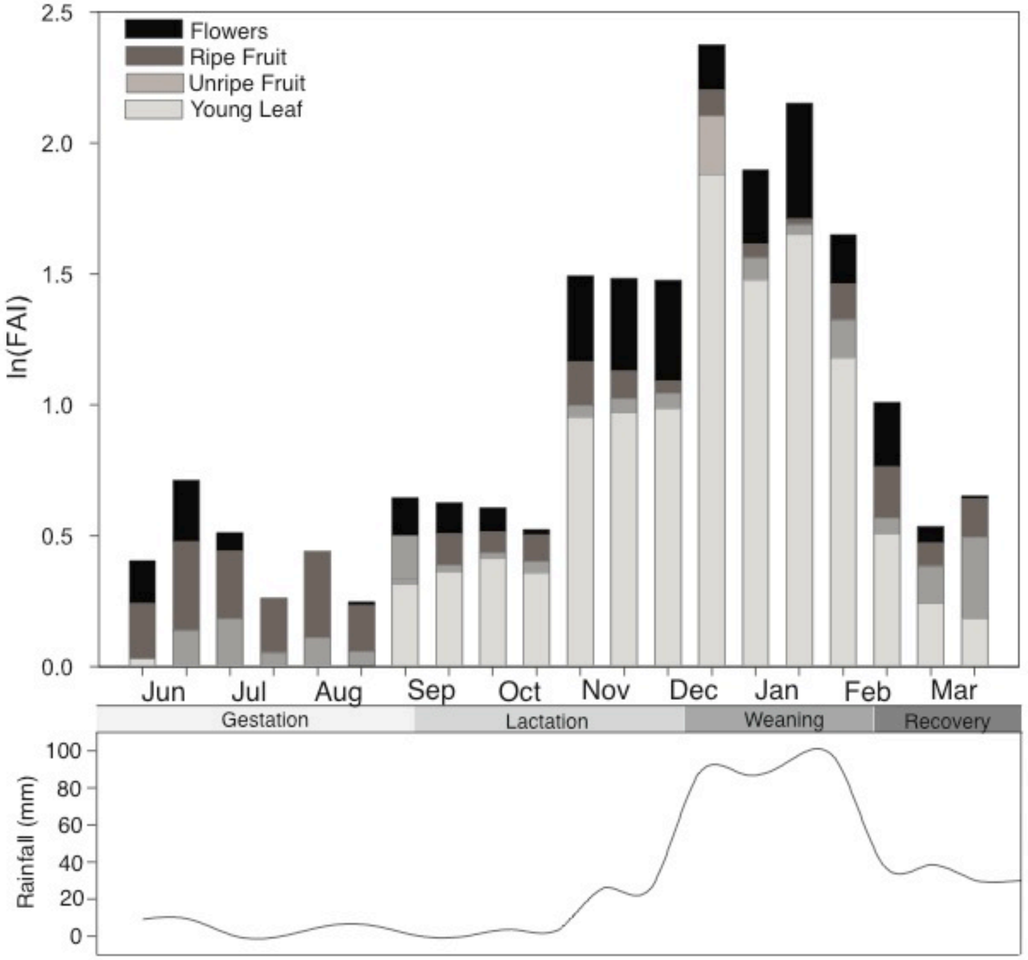

Figure 2-4. Mean distance to nearest neighbor while focal is feeding and foraging. Means are from GLMM of the effects of age-sex class on mean proportions of observations within each distance category to nearest neighbor and are adjust so that all proportions equal 100%. Infant 1 and Infant 2 show significantly different spatial associations than do all older age classes.

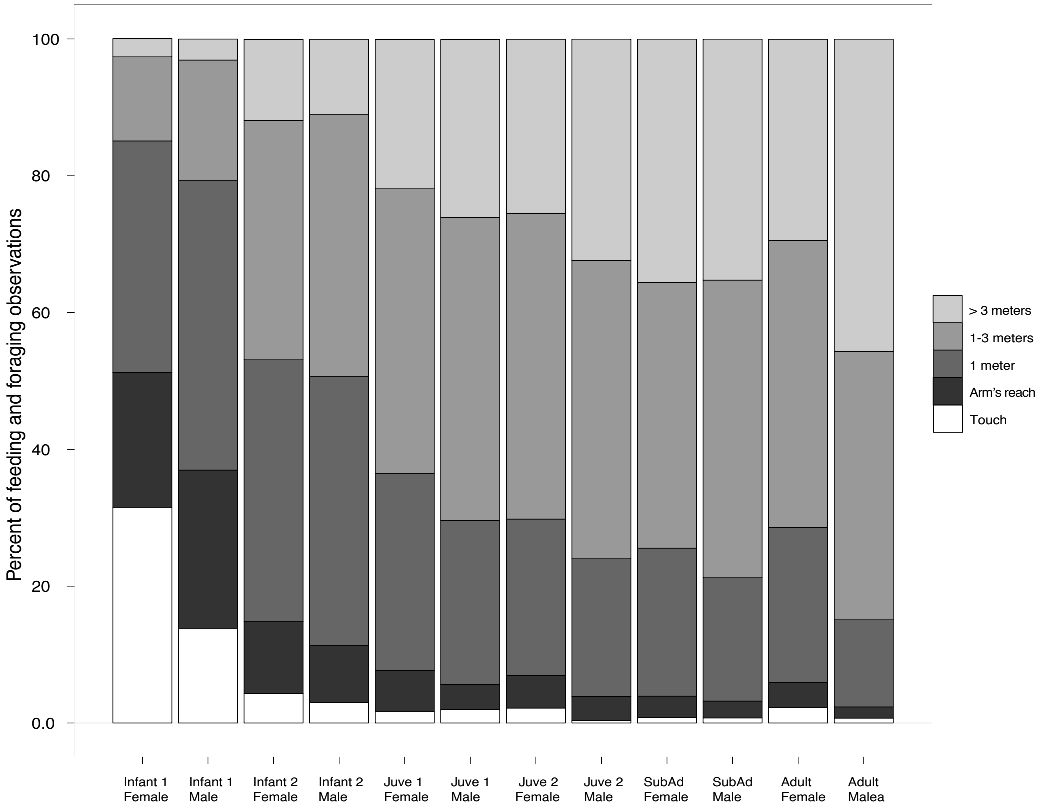

Figure 2-5. Mean proportion of time (±SE) that infants and juveniles have their mother as their nearest neighbor while feeding (including nursing) and foraging.

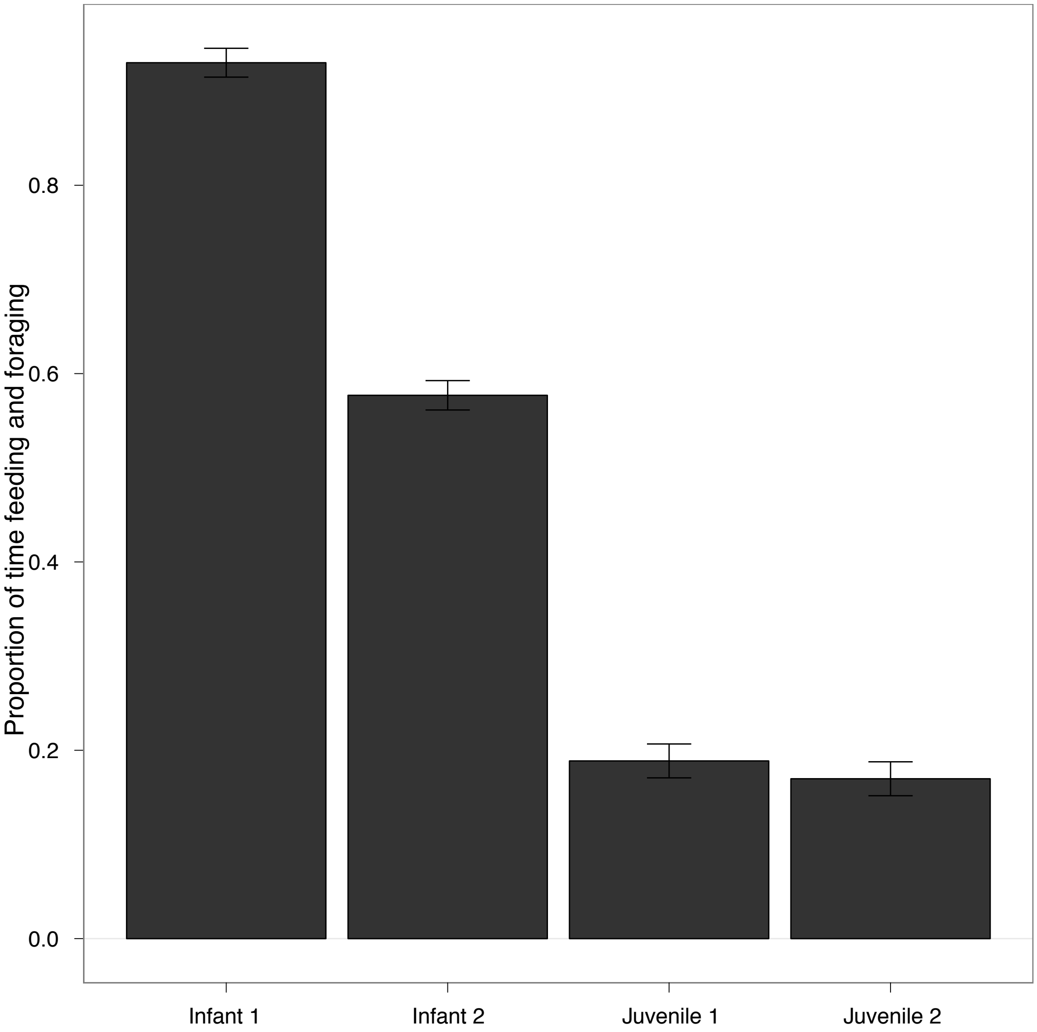

Figure 2-6. Mean dietary overlap index (±SE) between offspring and older group members (black) and between same age or younger group members (grey). The asterisk indicates that Juvenile 1 have significantly higher dietary overlap with older group members than do other age classes.

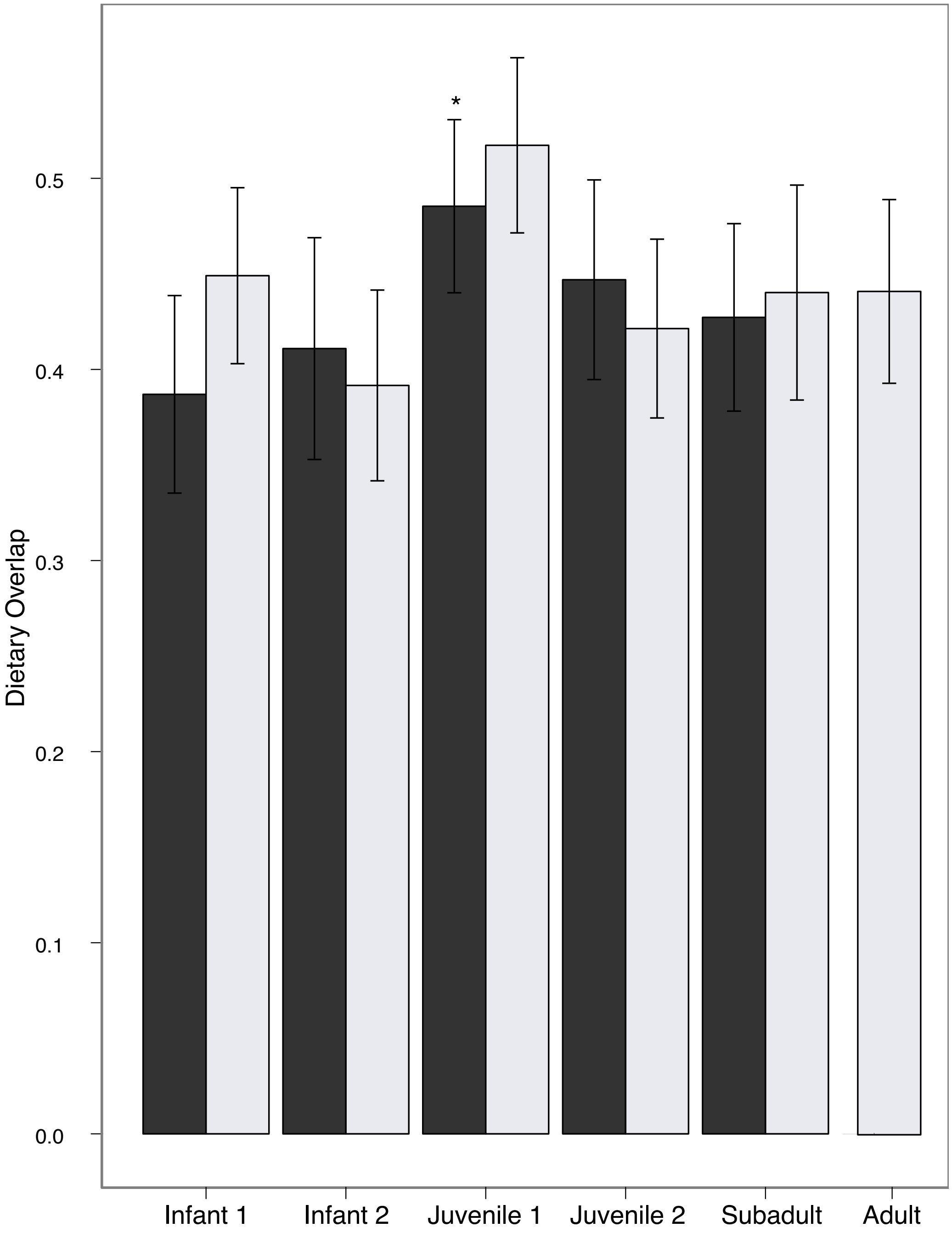

Figure 2-7. Mean ratio of time spent feeding to time spent foraging. The horizontal bar joins age classes with means that are not significantly different from one another (Infant 2 through Adult). Asterisks indicate that Infant 1 has a higher ratio than all other age classes.

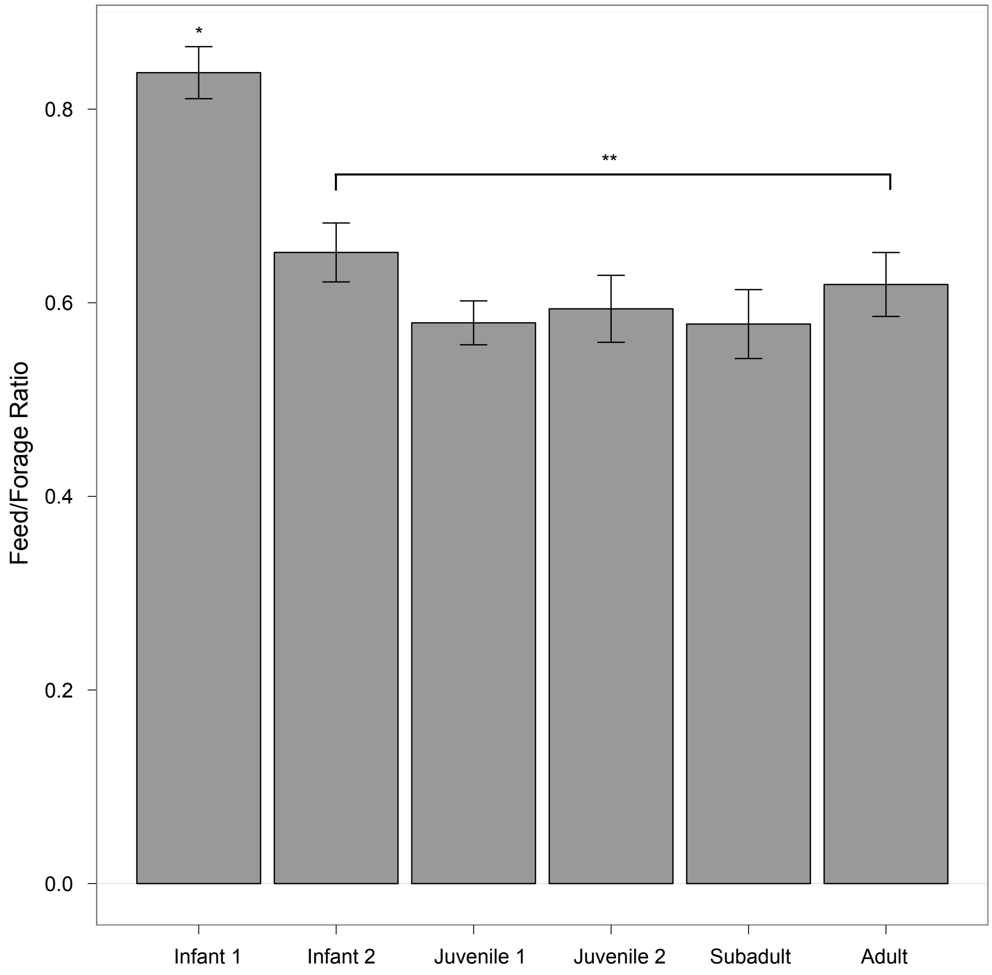

Figure 2-8. Ingestion rates (bite counts) by age classes for major food classes in ring-tailed lemur diet (means + SE). Vertical bars join age classes that are not different from one another and asterisks mark age class groups that are significantly different. NA denotes foods where bite counts were not collected due to low seasonal availability or absence during infancy.

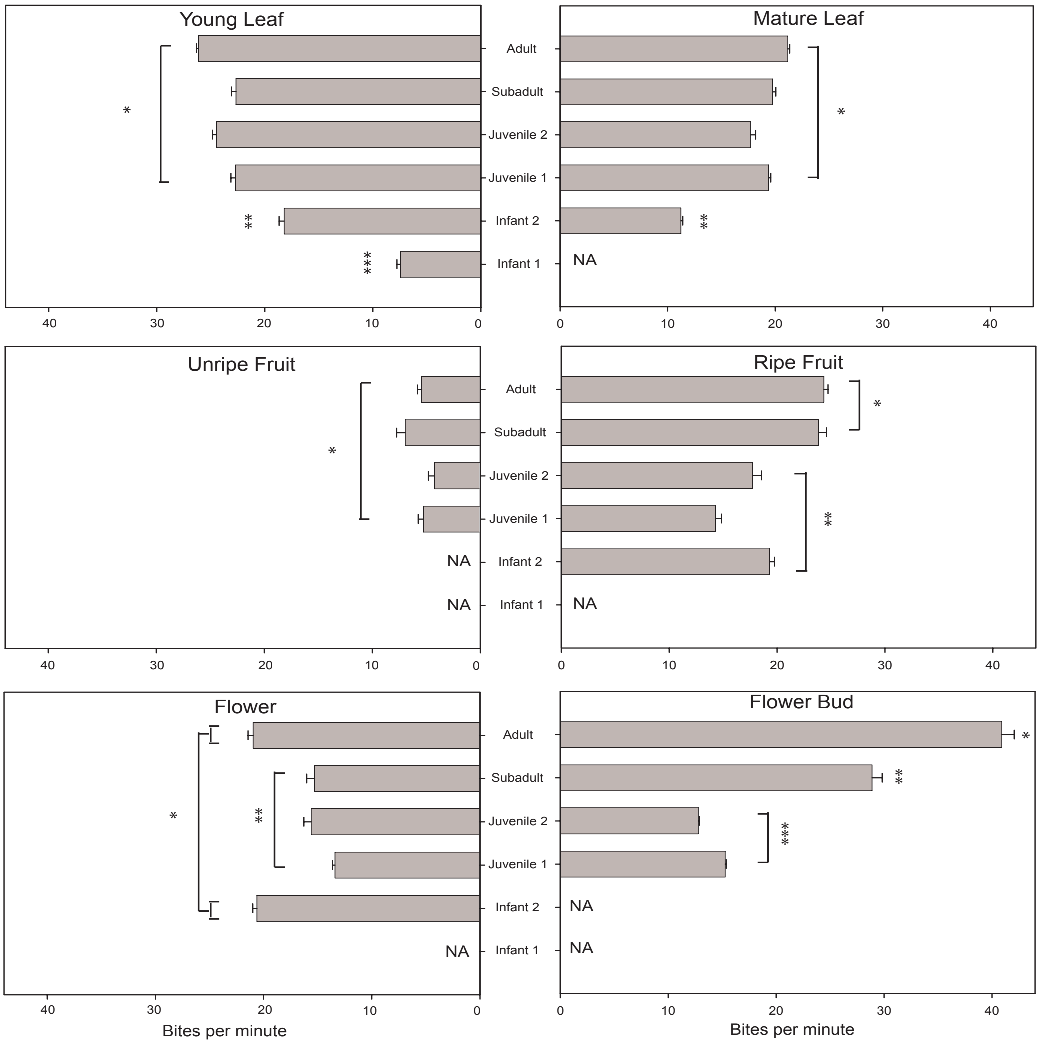

Figure 2-9. Processing ratios for ripe *Tamarindus indica* fruit. Mean ratios (±SE) of cracking:fruit ingestion (black; F=7.901 5, 84; p<0.001) and cracking:licking fruit pods (grey; F=2.472 5,97; p=0.037).

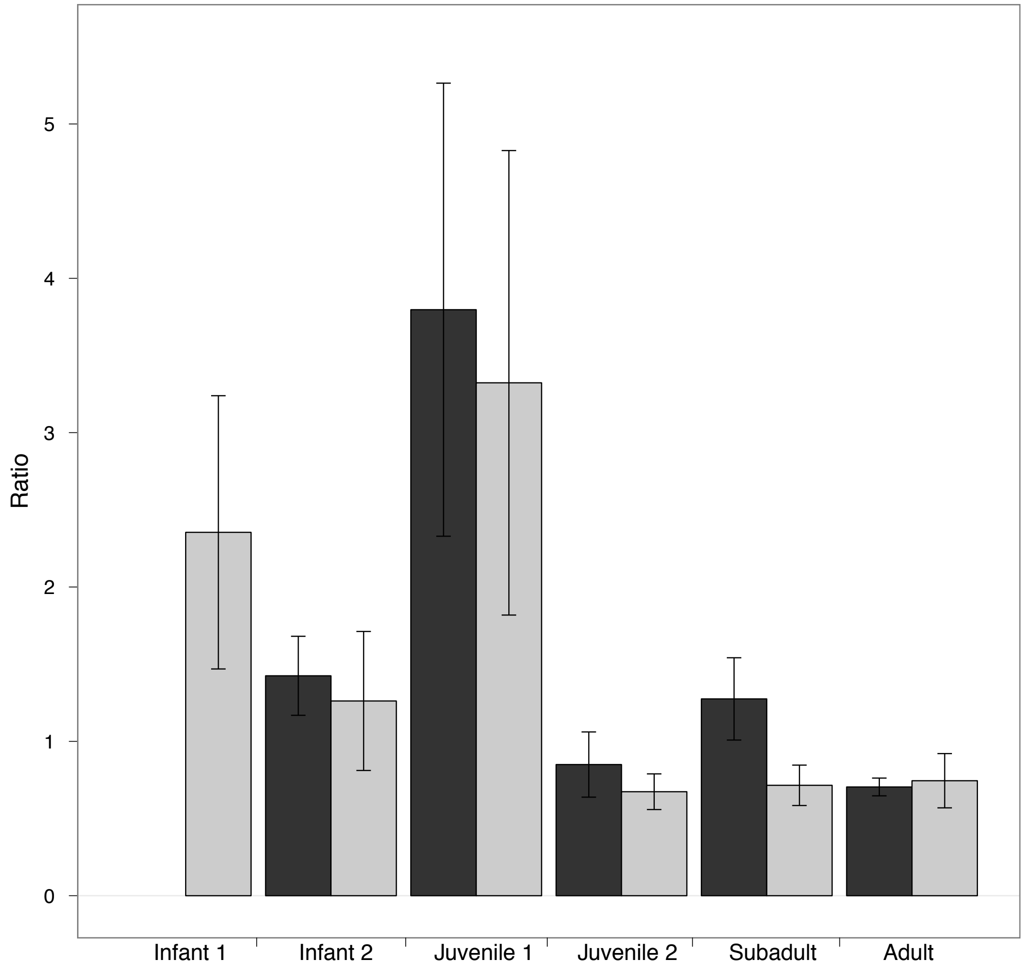

Figure 2-10. Arthropod foods of *Lemur catta*: A, unknown Lepidoptera larva, B, unknown Lepidoptera larva, C *Yanga heathii*, D *Lampropepla rothschildii*

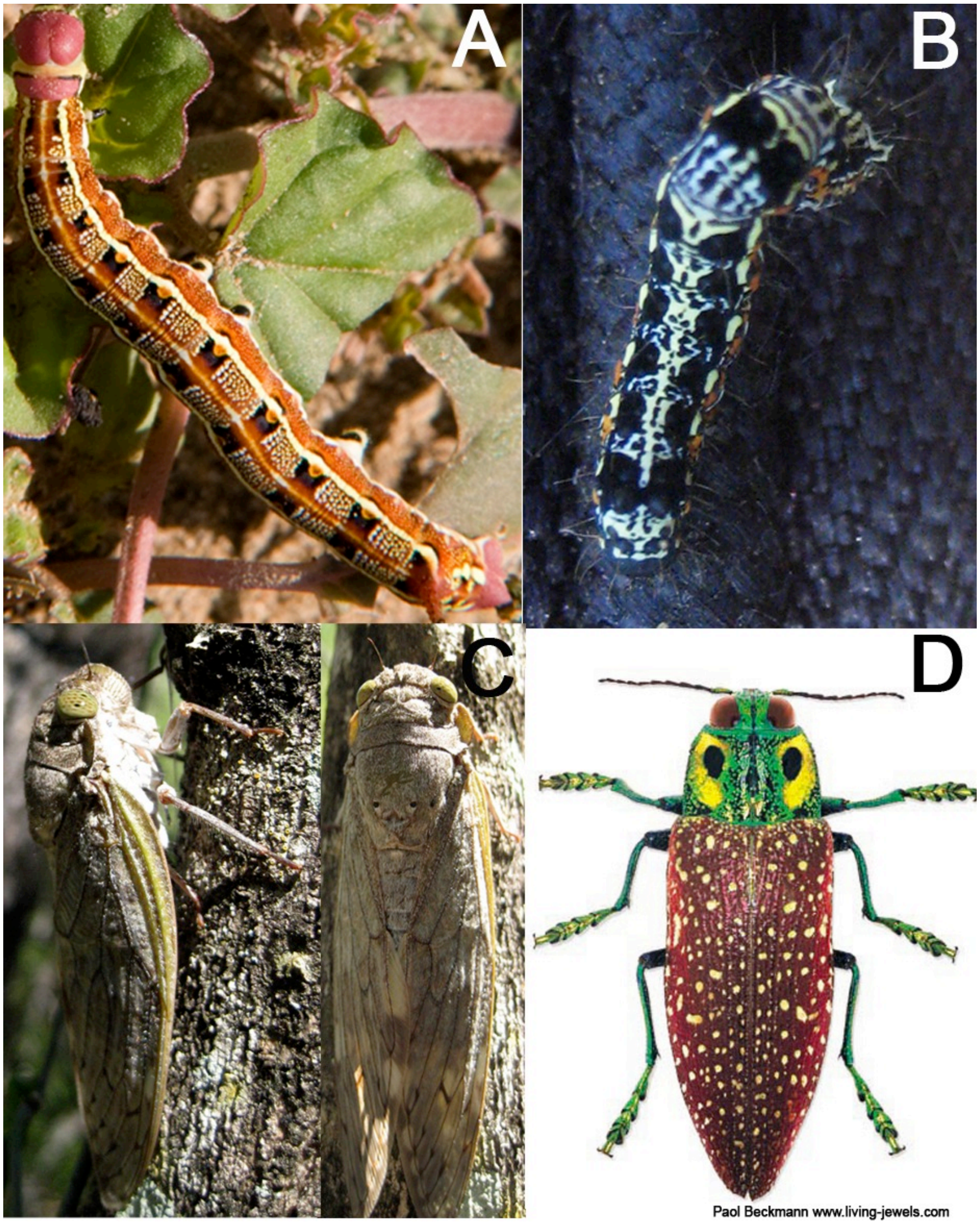

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Figure 2-11. Whitefly nymph (*Aleuromarginatus millettiae*) infestations on the leaves of *Tamarindus indica* (left) and a high-contrast image of a nymph (right).

Figure 2-12. Mean capture success rates (±SE) of caterpillars (black) and flying insects (grey). The number of FAS for each age category where insect foraging was observed is below the bars.

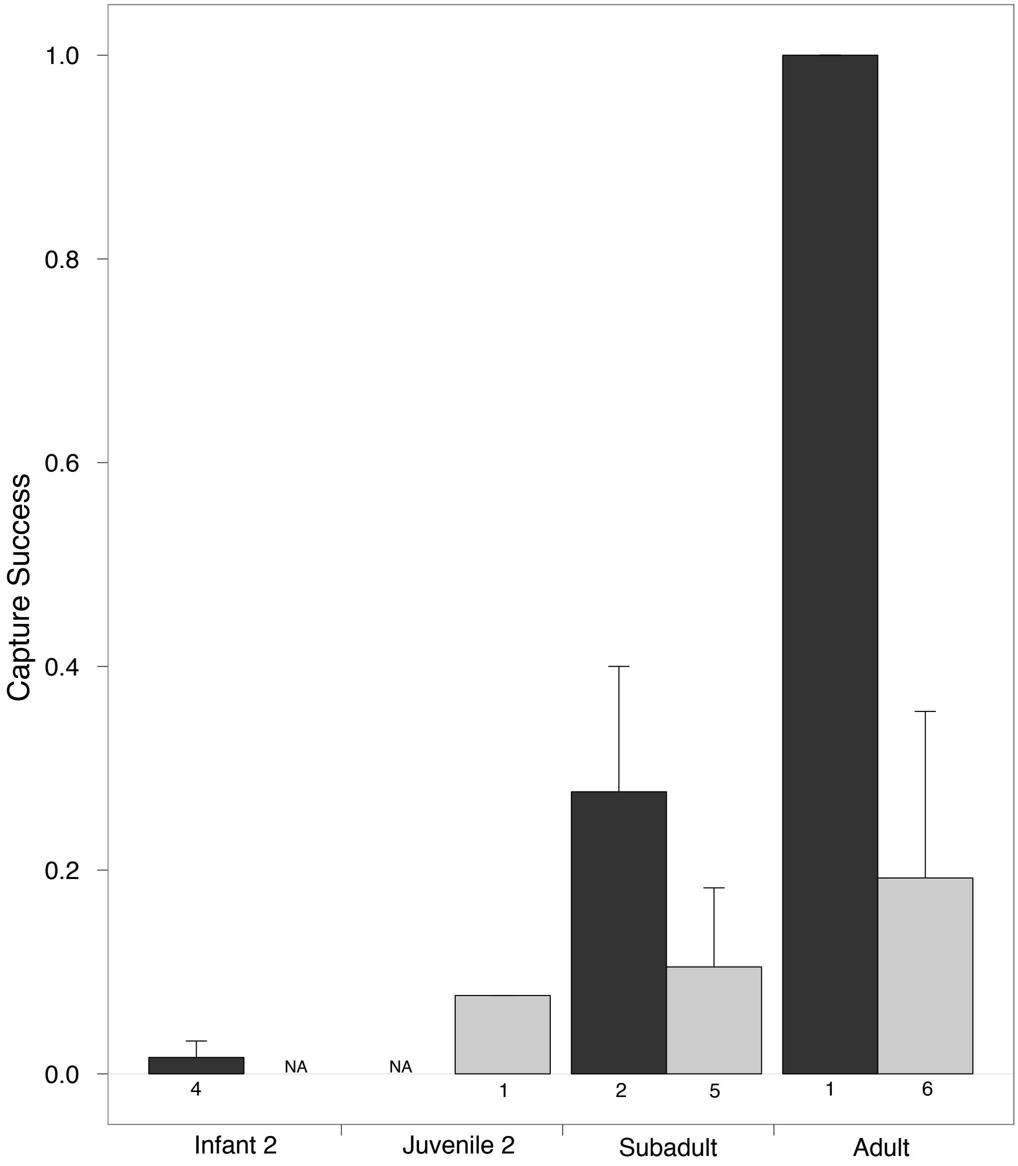

Table 2-1. Age of behavioral landmarks (first appearance except as noted) in the ontogeny of feeding in the ring-tailed lemur and brown lemur

Behavioral Landmark	***L. catta*** (wild) This study	***L. catta*** (wild) Gould 1990	***L. catta*** (captive) Klopfer & Klopfer 1970	***Eulemur fulvus*** (wild) Tarnaud 2004
Duration of study (*mixed longitiduinal)	Birth – Adult*	Birth – 16 weeks	Birth – 14 weeks	Birth – 1 year
Food exploration	2-3 weeks	4 weeks	31 days	
Food ingestions	4 weeks	6 weeks	56 days	6 weeks
Ingesting young leaves	4 weeks	6 weeks		6 - 7weeks
Ingesting mature leaves	5 weeks	6 weeks		
Ingesting flowers	5 weeks	6 weeks		
Ingesting fruit	7 weeks	6 weeks		
Weaning start	16 weeks	8 weeks	69 d	13-20 weeks
Weaning complete	24 weeks	16 weeks	14 weeks?	19 weeks
Last observed suckling	27 weeks			28 weeks
Feeding time exceeds suckling	16 weeks	11 weeks		15-18 weeks
Immature diet similar to adult	Early Juvenility			39-52 weeks
High overlap with mother's diet	Early Infancy			13-20 weeks

Table 2-2. Sample sizes for age-sex categories across the reproductive. Sample sizes are given as number of individuals (N), total numbers of hours (Hours) and the mean number of hours (± SE) each individual was observed per day across the study period. Number of individuals includes animals who progressed through age categories. Blank cells indicate an age-sex category that was not observed during the particular season.

Age - Sex	Variable	Gestation	Lactation	Weaning	Recovery
Infant 1 Female	**N / Hours**		**14 / 93.4**		
	Mean ± SE		1.015 ± 0.064		
Infant 1 Male	**N / Hours**		**12 / 93.4**	**1 / 5.6**	
	Mean ± SE		1.112 ± 0.061	1.867 ± 0.657	
Infant 2 Female	**N / Hours**		**8 / 48.8**	**8 / 36**	**4 / 17.6**
	Mean ± SE		0.841 ± 0.066	1.5 ± 0.104	1.6 ± 0.162
Infant 2 Male	**N / Hours**		**10 / 60.4**	**10 / 42**	**2 / 9.8**
	Mean ± SE		0.915 ± 0.072	1.5 ± 0.136	1.633 ± 0.209
Juvenile 1 Female	**N / Hours**	**6 / 112.4**	**4 / 26.4**		**4 / 13.4**
	Mean ± SE	1.405 ± 0.078	2.4 ± 0.318		1.489 ± 0.183
Juvenile 1 Male	**N / Hours**	**3 / 25.8**	**1 / 6.4**		**5 / 14**
	Mean ± SE	1.433 ± 0.194	2.133 ± 0.593		1.273 ± 0.153
Juvenile 2 Female	**N / Hours**	**3 / 32**	**6 / 118.8**	**4 / 17.6**	**4 / 18**
	Mean ± SE	0.821 ± 0.081	1.467 ± 0.094	1.467 ± 0.176	1.5 ± 0.249
Juvenile 2 Male	**N / Hours**	**6 / 84.4**	**2 / 41**	**1 / 5.8**	**1 / 5.6**
	Mean ± SE	1.068 ± 0.07	2.05 ± 0.166	1.933 ± 0.24	1.867 ± 0.067
Subadult Female	**N / Hours**	**1 / 0.4**	**3 / 54.8**	**3 / 18.6**	**3 / 8.6**
	Mean ± SE	0.2 ± 0	0.979 ± 0.076	1.431 ± 0.192	1.075 ± 0.1
Subadult Male	**N / Hours**	**7 / 66.8**	**8 / 165.2**	**6 / 23.6**	**6 / 16.8**
	Mean ± SE	0.768 ± 0.042	1.412 ± 0.07	1.311 ± 0.146	1.292 ± 0.133
Adult F – NR	**N / Hours**	**23 / 235.8**	**23 / 336**	**23 / 71.8**	**23 / 49.8**
	Mean ± SE	0.753 ± 0.032	0.919 ± 0.050	0.99 ± 0.068	1.020 ± 0.062
Adult Male	**N / Hours**	**11 / 82.2**	**17 / 178.8**	**16 / 38.6**	**14 / 37.4**
	Mean ± SE	0.709 ± 0.043	0.774 ± 0.028	0.99 ± 0.081	1.039 ± 0.067

Table 2-3. Mean number of bite count observation sessions per individual per day and the total number of bite counts observed per age class.

Age Category	Mean Number Per Individual Per Day	Total
Infant 1	1.40	60
Infant 2	1.58	104
Juvenile 1	2.40	144
Juvenile 2	2.00	175
Subadult	1.84	178
Adult	1.70	588

Table 2-4. Allonursing by infants in ring-tailed lemurs, who they nursed from (target) and whether the adult female still had an infant that was alive.

Group	Infant	Infant's Age (weeks)	Number of days nursing on target	Target of allonursing	Target's baby alive?
Orange	I300	21-26	5	154	yes
	I154	21	1	268	Yes
		21	1	316	No – died day before
	I268	11, 14	1	171	Yes
			1	316	Yes
	I368	7	1	316	Yes
Blue	I137	13	1	332	Yes
Green	I23	11-22	7	9	No – started immediately after baby missing and continued for 2.5 months
	I167	10	2	9	No
Purple	I207	13	1	334	Yes
	I334	16	1	214	Yes
Teal	I144	8-16	7	312	No – died day before and continued for 2 months
	I202	8-22	9	312	No – died day before and continued for 2 months
Yellow	I319	5	1	157	Yes
		9	1	155	Yes

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CHAPTER 3. SOCIAL INFLUENCES ON THE DEVELOPMENT OF RING-TAILED LEMUR FEEDING

SUMMARY

Infants and juveniles can use both social and individual learning strategies as they develop species-typical feeding ecology. In monkeys and apes, learning from mothers and other group mates is critical to survive weaning, with behaviors such as co-feeding playing particularly strong roles in determining post-weaning survival. Experiments have shown that adult lemurs are capable of social learning, but it is unknown how social information is incorporated throughout development or what social learning strategies are used. To address this question, I collected data on feeding and social behavior from all age-sex categories of ring-tailed lemurs (*Lemur catta*) living in seven social groups at the Beza Mahafaly Special Reserve, Madagascar. Here I describe the behaviors that may lead to social learning in ring-tailed lemurs and test the hypothesis that, like monkeys, lemurs will have strong social influences on the development of feeding, particularly in the use of co-feeding, that will lead to high degrees of mother-offspring dietary overlap and equal dietary diversity among mothers and offspring. I found that infants and juveniles show low levels of co-feeding (the simultaneous feeding with another individual within one meter that followed an approach), and do not routinely use many of the social learning behaviors that are observed in monkeys and apes such as begging or food transfers. While the frequency of this intentional behavior of co-feeding is low, a more generalized behavioral synchrony of an individual and its nearest neighbor during feeding is used often, particularly when the nearest neighbor is older than the infant or juvenile. Additionally, juveniles have the most diverse diets within a social group, which indicates that they are engaging in more dietary exploration than older group members. Social learning may be common and important to the development of feeding behaviors in monkeys and apes, but these data show that the use of social behaviors are likely less important in the ontogeny of lemur feeding, and may further indicate major differences in

the way that social complexity and the use of social information has shaped strepsirrhines and haplorhine evolution.

INTRODUCTION

Learning from others enables the accumulation of complex behaviors and knowledge and is the foundation of human culture. Social learning is found across a wide diversity of animals and is a common strategy to develop group and species-specific feeding behavior (Thorpe, 1963; Hauser, 1993; Rose, 1994; Galef, 1995; Galef and Giraldeau, 2001; Agostini and Visalberghi, 2005; Lonsdorf, 2005; Hoppitt and Laland, 2008; Thornton and Clutton-Brock, 2011; van Schaik and Burkart, 2011). Learning from experienced individuals may be the most risk aversive strategy for growing animals to develop adult diets, particularly when complex knowledge or handling skills must be attained (Janson and van Schaik, 1993), and use of social information can have far ranging impacts on an individual’s survival and development. There may then be strong selection on the use of social learning in infants and juveniles, and these young individuals should maximize their exposure to the behavior of others if they are to effectively learn necessary adult skills. However, relying on social learning is not always advantageous (Toelch et al., 2009; Rendell et al., 2010), and it is unknown how developing individuals balance the use of social information against their own trial and error learning.

Learning what, where, and how to eat is critical to survive until adulthood. This pressure can be so strong that in some primates, juveniles who fail to emulate their mother’s diet soon after weaning typically do not survive (Hauser, 1993). To develop their diet, infants and juveniles explore and use trial-and-error type learning, they learn from the behavior of others, or use a mix of individual and social learning that is usually dependent on resource type and social context (Galef and Giraldeau, 2001). Young animals can spend a large proportion of time co-feeding with an experienced partner (Hauser, 1993; Gosset and Roeder, 2001; Allen and Clarke, 2005; Ueno, 2005), scrounge discarded food items (Caldwell and Whiten, 2003; Wiens and Zitzmann, 2003; Humle and Snowdon, 2008; Amita et al., 2010), and less commonly receive food directly from relatives (Corp and Byrne, 2002; Rapaport and Ruiz-Miranda, 2006; Thornton and McAuliffe, 2006). It is unknown how common these behaviors are in strepsirrhines.

The use of social learning has variable returns that depend on stability of both the social and physical environment. Strict reliance upon social learning may only be advantageous in stable environments, while individual exploration and trial and error are better strategies in unpredictable environments (Galef and Giraldeau, 2001). Humans are more likely to incorporate the behavior of their group mates into their decision making process when the social groups are stable than when social environments fluctuate (Toelch et al., 2009; Rendell et al., 2010). Likewise, the use of social learning may be adaptive only in environments with predictable resources (Hoppitt and Laland, 2008) and when the previous quality of someone's knowledge can be evaluated based on its age and the stability of the environment (Rendell et al., 2010). Otherwise, individual learning and exploration are likely favored to keep up with resources in rapidly changing landscapes. In these cases, knowledge gained through trial and error is more stable than either waiting for a social demonstrator or attempting to apply previous knowledge to a novel circumstance. Growing and vulnerable animals must be particularly tuned to when socially acquired versus personally discovered information will be the most beneficial. Likewise, using a more diverse social array of non-related individuals may be more advantageous when the environment is unpredictable and changes faster than the generation time (Laland and Kendal, 2003). Extensive learning from non-relatives may allow the rapid diffusion of new behaviors and improve feeding efficiency at ephemeral resources whereas learning from one's mother and other close relatives may be necessary to develop fundamental skills (Thornton and Clutton-Brock, 2011).

This is particularly the case for primate species that have long life spans and an elongated juvenile period. They exploit a wide range of diets with large variation in seasonal availability and complexity of food processing (Rapaport and Brown, 2008).

Social learning is common in monkeys and apes (Whiten, 2000), but the extent to which strepsirrhines use the behavior of conspecifics to inform dietary choices throughout development is unknown. Adult lemurs have been shown to solve two-action feeding puzzles in a manner consistent with social learning (Kendal et al., 2010; Dean et al., 2011; Stoinski et al., 2011), and captive ring-tailed lemurs have spontaneously developed an innovative foraging behavior (using their tails as a sponge) that spreads throughout a group (Hosey et al., 1997). It has yet to be shown what social learning behaviors are used by infant and juvenile lemurs as well as how common social learning is in wild individuals. Understanding the full extent to which social learning shapes the feeding behavior in these primates, particularly in wild individuals that face a full range of ecological challenges, will identify how social processes shape behavioral development.

The ring-tailed lemur (*Lemur catta*) is an ideal species to explore behaviors that facilitate social learning. Ring-tailed lemurs live in large multi-male, multi-female social groups analogous to those found in the better-studied monkeys and apes (Jolly, 1966). They are the most monkey-like of the lemurs in their social cognitive capabilities (Maclean et al., 2008; Sandel et al., 2011), and have been shown to learn behaviors socially through diffusion analysis (Hosey et al., 1997; Kendal et al., 2010), although the behavioral strategies used in this type of learning have yet to be described. In this study I test if the same social learning behaviors and strategies that shape the development of feeding in monkeys and apes are also common in the ontogeny of ring-tailed lemur feeding. If social learning, particularly co-feeding, is under the same type of selection as seen in some monkeys (Hauser, 1993), I predict that infants and juveniles will actively seek out individuals who are feeding, and that co-feeding will comprise a large proportion of infant and juvenile feeding time. Young animals will feed and forage in closer proximity to other group members and approach individuals who are feeding more often than individuals who are engaged in other behaviors. Additionally, behavioral synchrony with an individual's nearest neighbor will be higher during foraging and feeding than during other social behaviors including travel and grooming. If social learning, rather than exploration and trial-and-error, is the primary way that young individuals learn about food, then infants and juveniles will also show high dietary overlap with adults and equal dietary diversity.

METHODS

Study Site

Data were collected from May 2009 through March 2010 at the Beza Mahafaly Special Reserve (Beza) in southwestern Madagascar (23.65647°S, 44.62897°E) where the biology, behavior, and ecology of adult ring-tailed lemurs have been studied since 1987 (Sauther, 1998; Yamashita, 2002; Gould et al., 2003; Sussman and Ratsirarson, 2006; Sauther and Cuozzo, 2009). The primary study area, Parcel 1, grades from gallery forest dominated by *Tamarindus indica* in the east to drier deciduous and Dideraceae dominated desert spiny forest to the west (Sussman and Rakotozafy, 1994). This east to west moisture gradient is coincident with a lower and increasingly more open canopy, diminishing average stem diameter, and increasing diversity in tree species per hectare (Sussman and Rakotozafy, 1994).

Beza's climate is highly seasonal, with a cold dry (May-September) and a hot wet (October – April) season where 80% of the annual average of 615 mm of rain falls each year (Lawler et al., 2009). This study period was unusually hot and dry with average high temperatures of 35.7°C (dry season) and 45.8°C (wet season) and half the typical amount of rain that falls during equivalent times in other years (this study: 265mm, Beza average for June-March: 500mm; (Ratsirarson, 2003; Sussman and Ratsirarson, 2006).

Study population

Ring-tailed lemurs are frugivore-folivores that spend half of their feeding and foraging time on the ground (Sussman, 1977) and 95% of total observed feeding time is spent on substrates lower than 10 meters (O'Mara, unpublished data). Ring-tailed lemur foods do not require extensive processing, although some fruits such as *Tamarindus indica* may require a minimum of strength or post-canine occlusal surface area to open. Contrary to the typical mammalian pattern, females dominate males in all contexts (Pereira and Kappeler, 1997). Dominant females control access to small food patches and limit who may feed in close proximity (generally within three meters), to themselves their infants, juveniles, and, occasionally, other preferred social partners. Reproduction is photoperiod controlled, highly seasonal, and synchronized to resource availability (Sauther, 1991; Jolly et al., 2002). First year mortality averages 50% (Gould et al., 2003) but was as high as 71% in the 2008 birth cohort (Meredith & O'Mara unpublished data).

Over 2,300 observation hours were completed by five observers on a mixed longitudinal sample (infants through adults) of 78 individuals from seven study groups (Table 3-1). This included 18 mother-offspring pairs: 12 mothers with infants, four mothers with Juvenile 1 or Juvenile 2 aged offspring, and two mothers and their older juvenile or subadults. Some mothers had surviving offspring from more than one breeding year for at least part of the study. Infants begin moving independently and foraging from their mothers at six weeks of age, are responsible for their own travel by 14 weeks, and are fully weaned by 25 weeks (Gould, 1990; Chapter 2). Birth dates are known for the individuals born into each of the study groups since 2006, but birth dates and exact ages are not known for females older than 4 years and adult males who transfer between groups. Interobserver reliability was periodically assessed to maintain a minimum of 85% agreement using Cohen's Kappa statistic included in the JWatcher package (Coelho and Bramblett, 1981). All infants and juveniles had mothers in the group throughout the duration of study. All methods were approved by the IACUC at Arizona State University and by Madagascar National Parks.

Behavioral Sampling

Continuous and instantaneous sampling methods were used simultaneously to sample feeding and its social context. Subjects were chosen from among the seven study groups and selected for observation according to a stratified random protocol where an infant or juvenile was followed every other or every third observation. Each social group was observed in rotating two-day blocks for between four and eight days per month.

Feeding behavior. All feeding and foraging behaviors were continuously recorded in JWatcher (www.jwatcher.ucla.edu) during 12-minute focal animal observation sessions (FAS)(Altmann, 1974). To be included in analysis, individuals must have contributed a minimum of three FAS in a given day, with each individual typically observed between 4-8 times per day (Table 3-1). Feeding behaviors (Appendix B) included feed (defined as the ingestion of food), food explore (placing item in mouth but not eating it), forage (active searching for and processing of food items), sniff, sniff mouth, lick, crack, and co-feed (defined below). Additional social learning behaviors included beg, steal, scrounge, and transfer food (Rapaport and Brown, 2008). These behaviors, however, were not used by ring-tailed lemurs or were observed once and are excluded from analysis. Approaches to within one meter initiated by the focal animal were also recorded continuously as approaches targeted at an individual who is feeding and foraging versus one who is engaged in any other behavior. Plant foods were identified to species with help of local experts (Mr. Elahavelo and Mr. Herman Mananjo), by Mr. Rokiman Lestara (Tsimbazaza Botanical Gardens, Antananarivo), and through digital voucher images from the Missouri Botanical Gardens TROPICOS database (www.tropicos.org).

Co-feeding and Neighbor Synchrony. Two different measures of socially-motivated feeding behavior were used. Co-feeding is an intentional feeding association that approximates seeking out a partner to feed with or learn from. As a specific feeding association, co-feeding was defined as simultaneous feeding with another individual within one meter that followed an approach (Hauser, 1993; Ueno, 2005). The inclusion of an approach into this definition was to add a measure of interest in the behavior or identity in the individual who was approached. Initially, co-feeding was sub-categorized as feeding on the same part of the same species, a different part of the same species, or a different species. Because of the relative rarity of co-feeding in this dataset (less than 10% of total feeding time), and that 95% of all co-feeding observations were of feeding on the same part of the same species, these sub-categories were grouped together for this analysis.

A more generalized measure of feeding synchrony was also included to measure unintentional and non-directional information transfer that would be consistent with both local and stimulus enhancement learning strategies. To measure generalized behavioral synchrony, both the focal's and its nearest neighbor's general activity (nurse, feed, forage, rest, move, stand, engaged in social behaviors, other) were recorded instantaneously at three-minute intervals during the FAS. During these instantaneous samples, the focal's categorical distance to the nearest neighbor (touching, within arm's reach, within one meter, within three meters, and greater than three meters away) and position within the tree (ground; lower, middle, upper portion of crown; interior, middle, exterior of crown) were also recorded.

Dietary diversity, evenness, and overlap. Three indices were constructed to measure the dietary diversity, dietary evenness, and dietary overlap of the focal animals in two-week blocks. Dietary diversity was calculated using the Inverse Simpson's Diversity index, D, where $D=\mathbf{1}/(\Sigma p_i^2)$ and p_i^2 is the squared proportion of total time feeding in these two-week blocks on each item (species + part)(Begon et al., 1996; Irwin, 2008). D originates from a value of 1 (diet of 1 item), with higher values reflecting a more diverse diet. Dietary evenness (E_D) was calculated as $E_D=D/s$ where D is the Inverse Simpson's Diversity Index and s is the maximum number of food items utilized in the two-week block (Begon et al., 1996). The evenness value ranges from 0 to 1. A low evenness value indicates a diet where many of the food items are used in unequal proportions. An index of dietary overlap (R) was calculated for all individual pairs within each group during these two-week blocks. R was calculated as $R = \frac{\Sigma(p_{ij} \times p_{ik})}{\sqrt{\Sigma p_{ij}{}^2 \times \Sigma p_{ik}{}^2}}$, where p_{ij} and p_{ik} are the proportion of item *i* in the diet of individuals *j* and *k* (Pianka, 1973).

Analysis

Both continuously and instantaneously recorded data are summarized as proportions of total FAS per individual per day, and diversity, evenness, and overlap indices data were summarized per individual per two-week block. This generates a mixed-longitudinal data set of individual-days with the intent of preserving any individual level variability in behavior (Machlis et al., 1985; Dagosto, 1994). Generalized linear mixed models (GLMMs) were then fit to the mixed longitudinal data in the *lme4* package in R 2.13 (R Core Development Team, 2011). Traditional repeated measure designs are encumbered by balanced sample requirements that can rarely be met using observational data from wild animals. Generalized linear mixed models have the advantage of being able to process unbalanced, multi-way repeated measures designs through the inclusion of random effects in the model (Bolker et al., 2009). Untransformed proportional data were modeled using logistic mixed models with a binomial distribution and logit link identity (Jaeger, 2008; Warton and Hui, 2011). For all models, individual animal identity and a time factor (reproductive season) were included as random effects. The significance of the fixed factors (e.g., age, sex) was evaluated by comparing two nested models differing in a single factor (Huchard et al., In Press; Pinheiro and Bates, 2009). A likelihood ratio test of these two nested models (X^2) was then used to evaluate the significance of individual factors (Lewis et al., 2011). When factors did not significantly contribute to the fit of the model they were removed from the analysis. For models with significant main effects, subsequent Tukey's post-hoc tests identified differences among factor level pairwise comparisons, typically age-sex levels. All significance was evaluated at $\alpha=0.05$.

RESULTS

Is social learning important in the development of feeding ecology? Infants feed and forage on solid foods with closer nearest neighbors than do other age categories (Table 3-2). Infants are in contact, within reach, and within one meter of their nearest neighbor more than are all age categories (Table 3-2; Touch: X^2=78.726, df=11, p<0.001; Reach

X^2=59.555, df=11, p<0.001; 1 m X^2=65.564, df=11, p<0.001), and correspondingly are less often found at large distances from their nearest neighbor (1-3 m X^2=44.101, df=11, p<0.001; >3 m X^2=119.09, df=11, p<0.001). As infants are weaned, they transition to adult-like spacing patterns while feeding and foraging, with typical distances among nearest neighbors between 1 and 3 meters away (Table 3-2). When the proportion of approaches toward an individual who is feeding or foraging is compared to the proportion of approaches to an individual who is engaged in any other behavior, infants are less likely than adults to approach another individual who is feeding and foraging (Fig 3-1, X^2=20.501 df=5, p=0.001). Average feeding and foraging time is less than 30% of the total time budget (Chapter 5), and this test shows that at all ages, ring-tailed lemurs are more likely to approach another group member while the partner is feeding than during other activities. Since the null hypothesis has the proportion of the two types of approaches as equivalent (rather than that approaches are distributed in proportion to the time partners are feeding and foraging), this is a very conservative test.

The total proportion of feeding time that ring-tailed lemurs engage in co-feeding is low (generally less than 10% of total feeding time for each age class); therefore all categories of co-feeding (feeding on the same part of the same species, on a different part of the same species, or on a different species) were grouped together. Co-feeding on the same part of the same plant species accounts for over 95% of the time of co-feeding. Co-feeding was then divided into the proportion of feeding time co-feeding with an individual's mother and time co-feeding with other group members, with co-feeding with other group members was adjusted by dividing the time spent co-feeding by the number of potential adult and subadult partners in the group. There are no significant differences in total proportion of feeding time engaged in co-feeding among age categories (Fig 3-2; X^2=6.177, df=5, p=0.2894; means: Infant 1=11.15%, Infant 2=5.34%, Juvenile 1=6.34%, Juvenile 2=7.75%, Subadult=9.58%, Adult=7.24%). Infants and juveniles co-feed more with their mother than with other group members (Fig 3-2, X^2=57.704, df=7, p<0.001), and young infants show slightly higher frequencies of co-feeding with mother than older age categories, except for subadults (Fig. 2). Subadults maintain close associations with their mothers as they approach sexual maturity, and co-feed slightly more with their mothers than younger group members, but this difference is not significant.

While the proportion of time co-feeding is low, behavioral synchrony with an individual's nearest neighbor during feeding and foraging is high (Fig 3-3). Individuals in all age categories show higher proportions of synchrony with their nearest neighbor during feeding and foraging than during other active (i.e., non-rest) behaviors (X^2=1507.3, df=11, p<0.001). Infants in particular show the strongest difference between synchrony in feeding and synchrony for their other activities (Fig 3-3), and infants are less likely to be in synchrony with their nearest neighbor during non-feeding activities than are juveniles and older group members (Fig 3-3, X^2=316.69, df=5, p<0.001).

The relative age of the focal's nearest neighbor has the strongest effect on whether the two animals will be feeding at the same time (Fig 3-3). Individuals are more likely to be in synchrony with their nearest neighbor during feeding and foraging when that neighbor is older than the focal (X^2=25.083, df=15, p=0.048). During this time they are more often feeding on the same food item than not (X^2=65.031, df=1, p<0.001). There are no significant effects of either the focal's sex (X^2=1.060, df=1, p=0.480), or whether the nearest neighbor is of the same sex (X^2=0.873 df=1, p=0.350). However, this relationship changes for other active behaviors. Young individuals are more likely to be synchronized with their nearest neighbor during other activities (move, stand, groom, general social behaviors, and other) when that neighbor is younger (X^2=329.47, df=15, p<0.001). There are no significant effects of the focal's sex (X^2=3.02, df=1, p=0.082), but there is a weak effect of whether the nearest neighbor is of the same sex (X^2=4.2737 df=1, p=0.039). Overall, the strongest determinant of the synchrony between focal and nearest neighbor is their relative age, and during non-feeding behaviors there is a minor effect of sex.

There is no difference among age categories in their dietary overlap index with their mothers (Chapter 2, X^2=5.561, df=4, p=0.234) or in the overlap with all other group members (X^2=8.521, df=5, p=0.1298). There is also no significant difference in dietary overlap within each age category (X^2=11.588, df=10, p=0.314). Juveniles and subadults have the most diverse (X^2=52.342, df=5, $p<0.0001$), and least even diets (X^2= 18.427, df=5, p=0.002) within a social group (Fig 3-4). Consequently, adults have the most even diets, with all other age classes showing relatively the same dietary evenness.

Do ring-tailed lemurs use the same social learning behaviors as monkeys and apes? Most of the social learning behaviors or tactics that have been observed in monkeys and apes were not found in ring-tailed lemurs. Voluntary food transfers or food offering were never observed, and ring-tailed lemurs do not show a stereotyped begging vocalization or gestures. Infants would occasionally sniff their mother's mouth while she was feeding on an item, but this did not occur regularly and was limited to novel foods such as insects or while feeding on soil. Scrounging, or feeding immediately on a discarded food item was also rare. Instead, animals would scavenge on fruits that had been long discarded by other individuals or even other social groups. This typically occurred with the ripe fruit of *Tamarindus indica*. The hard shell of this fruit makes accessing the sticky pulp on the inside a considerable challenge, and ring-tailed lemurs forage for discarded fruit pods on the ground, scavenging any remaining fruit in previously opened pods (Sauther, 1992). Young juveniles were rarely observed to steal food from others (2 instances in this sample). In the first example, a juvenile male stole a spider web out of the hands of a subadult female who was eating it, ran away and then quickly consumed the spider web. In a different social group a young juvenile female offspring of the dominant female showed a rare, but consistent behavior where she would approach an individual subordinate to her mother (target) and attempt to co-feed or share the target's food. If the target resisted, the juvenile would give a series of loud submissive calls directed at the target's mouth that drew her mother's attention. Her mother would then aggress at the target and the juvenile would come away with her desired food item. This juvenile female was the only individual observed to use this type of manipulation, and she also used this technique several times in her infancy (S.L. Meredith, personal communication), as well during young juvenility. While an uncommon tactic, this type of manipulative theft may be used to supplement an infant and juvenile's dietary knowledge. More commonly though, young animals would synchronize their feeding behavior with their nearest neighbor and co-feed with other group members.

DISCUSSION

Ring-tailed lemurs in this environment do not seek out social information to shape the development of feeding with the same strength and frequency observed in monkeys and apes. Instead, individuals may rely on a response facilitation or local enhancement strategy and feed when a nearest neighbor feeds, particularly when that nearest neighbor is older. Infant and juvenile ring-tailed lemurs were not observed to use most of the stereotype learning behaviors that have been described for other primates (Rapaport and Brown, 2008). While social learning by adult ring-tailed lemurs has been inferred through dual-action puzzle experiments in both captive and wild settings (Kendal et al., 2010), it is interesting that the capacity for social learning displayed in experimental manipulations does not reflect common behavioral patterns in a wild population. These experiments indicate that the rigid dominance hierarchy in ring-tailed lemurs may limit learning opportunities to members of the same social clique (Kendal et al., 2010). Because of this, agonistic exclusion from social learning opportunities may make social learning an infrequent strategy for the adoption of new foods into ring-tailed lemur diets. Among primates, the use of diverse and stereotyped social learning behaviors is likely limited to the monkeys and apes. In ring-tailed lemurs, the limited use of social learning behaviors may either reflect cognitive and energetic constraints of brain size (Isler and van Schaik, 2009), or may be a consequence of ring-tailed lemur social hierarchy.

Consistent with other studies on infant and juvenile foraging behavior, younger ring-tailed lemurs have closer nearest neighbors while they are feeding and foraging for solid foods (Table 3-2). Feeding closely with a nearest neighbor is typical for most primate infants (Watts, 1985; Hauser, 1993; Ueno, 2005), and in addition to providing social learning opportunities, having close neighbors provides enhanced predator protection. This decrease in distance among individuals during feeding association has been hypothesized to have direct impacts on primate life history through the elongation of the juvenile period (Janson and van Schaik, 1993,1993,1993). Close proximity during feeding increases feeding competition as well the likelihood of social facilitation, and may explain the high levels of nearest neighbor feeding synchrony (Fig 3-3), and the high dietary overlap among group members.

Co-feeding in ring-tailed lemurs is not common, but is at its peak early in infancy and was observed at low levels throughout nutritional dependency (Fig. 2). Early infancy is a period when infants are beginning to explore new foods, placing food and non-food items in their mouth, particularly during play bouts (Gould, 1990). This play behavior may constitute an important aspect of trial-and-error learning and individual exploration in the early stages of feeding development (Chapter 2). Young ring-tailed lemurs co-feed more with their mother than with any other individual within the group (Fig 3-2). However, when all other group members are grouped together, there is no difference in the amount of time spent co-feeding with mom and the amount of time co-feeding with everyone else (X^2=0.007, df=5, p=0.933). As in other primates, ring-tailed lemur mothers are particularly important learning partners for infants. Like the ruffed lemur that shows no observed co-feeding (Krakauer, 2006), ring-tailed lemur co-feeding does not approach the high proportion of total feeding time and may reflect an overall lemurid pattern. This is contrary to the large proportion of co-feeding that has been observed in vervet monkeys (35-55%; Hauser, 1993), macaques (60-100%; Ueno, 2005), and in the specialized extractive forager, the aye-aye (20 – 40%; Krakauer, 2006). Consequently, it is likely that the strong selection on social learning early in development that is present in monkeys is absent in ring-tailed lemurs. Ring-tailed lemurs may use other social information to guide the development of feeding. The act of a neighbor feeding may induce infants and juveniles to feed as well, and may provide much of the social information used by infant and juveniles.

The strongest evidence for the use of social learning during feeding is the age-based differences in the way that individuals biased their synchrony with their neighbors in feeding and foraging versus other types of behaviors. Young animals are more likely to synchronize their feeding with their nearest neighbor if that neighbor is older than they are (Fig 3-3). Synchrony in feeding for infants and juveniles, particularly with their mothers, is an important part of feeding development in many primate species, and infants and juveniles preferentially synchronize their behavior with older group members (Altmann, 1980; Nicholson, 1982; King, 1991,1994; Tarnaud, 2004). In contrast, ring-tailed lemurs are more likely to synchronize other behaviors such as grooming, play, and travel with a neighbor who is the same age or younger than themselves (Fig 3-3). The information encoded in observing an older, experienced individual feed may have a higher value than that gained by synchronizing with a younger group member, a phenomenon that has been demonstrated in rats (Galef and Giraldeau, 2001). The reliability of feeding near an older group member likely stimulates an infant or juvenile to feed (e.g., response facilitation (Sherwin et al., 2002). Because of the size of feeding patches (e.g., a tree crown, a patch of herbaceous vines), and the high seasonality of resources in southwestern Madagascar, lemurs that are within 1-3 meters of each other are usually feeding on the same food item. The synchrony of feeding behavior is at minimum a local enhancement feeding strategy where individuals are becoming familiar with a food. Further work is needed to understand if these behaviors are actually facilitating learning, how generalizable the information is that infants and juveniles acquire, and how long this information is retained.

This synchrony of feeding is likely responsible for the rapid development of adult-like diets in lemurs, as high levels of synchrony between nearest neighbors are also found in brown lemurs (Tarnaud, 2004,2008) and there is strong social facilitation in the ontogeny of aye-aye foraging (Krakauer, 2006). However, unlike adult ring-tailed lemurs, adult brown lemurs (*Eulemur fulvus*) and black lemurs (*E. macaco macaco*) do not seem to use social information to change their foraging behaviors (Glander and Rabin, 1983; Gosset and Roeder, 2001). Pairwise dietary overlap values among ring-tailed lemurs are at adult levels from early infancy, which is earlier than in brown lemurs where significant overlap develops in late infancy (Tarnaud, 2004). This may mean that within a social group, there is a relatively moderate overlap among all group members and intragroup feeding competition is low and that infants and juveniles potentially use older individuals as social models. Alternatively, the limited food availability restricts the potential for large variation in dietary composition and the dietary overlap observed is at a stable level to facilitate permanent group living. While this dietary overlap among individuals remains consistent throughout development, juveniles have more diverse diets than do other age categories (Fig 3-4). After coming through a period of conservative infancy, ring-tailed lemur juveniles appear motivated to explore their environments through trial-and-error processes. This is reflected in the increase in juvenile dietary diversity and is consistent with other primate species (Watts, 1985; Hanya, 2003; Tarnaud, 2004). In captive trials, young ring-tailed lemurs are the first to explore and learn new foraging techniques (Feldman and Klopfer, 1972; Kappeler, 1987), and their increased dietary diversity in the wild reflects this motivation observed in captivity. Controlled choice tests of food neophilia throughout development will be necessary to assess how motivation to explore changes throughout development; however, the results presented here suggest that dietary diversity increases in juvenility and that this change is not completely contingent on social information.

If the environment of southwestern Madagascar is as unpredictable as rainfall data suggests (Dewar and Richard, 2007; Lawler et al., 2009), there may not be strong selection for reliance upon stereotyped social learning behavior in ring-tailed lemurs. While large brains are not a requirement for social learning (e.g,, guppies: (Stanley et al., 2008), ants: (Leadbeater et al., 2006), bats: (Page and Ryan, 2006)), it is a general trend within primates that more behaviorally complex species also have larger and more complex brains. Increasingly large brains require large amounts of energy (Isler and van Schaik, 2009), and in a resource-limited environment such as Madagascar, brain size may be energetically constrained. However, the use of social learning may be flexible and called into action when resources and social stability permit. Social learning through feeding synchrony with an experienced older neighbor may be the most effective way to develop feeding knowledge in the intolerant social hierarchy of ring-tailed lemurs. The seasonal and year-to-year variability in the nature of resources available is such that a growing individual may not be exposed to resource types within the span of one or two years – the ages when females appear to be more tolerant of their young. Synchrony with a nearest neighbor may expose juvenile and adolescent lemurs to the range of food possibilities. Behavioral synchrony, combined with a strong motivation to explore new resources may mitigate juvenile starvation risks in similar ways that co-feeding functions in other primate species.

The unpredictable environment of southern Madagascar may make generalizable knowledge and flexible learning especially valuable. Future work on social learning in ring-tailed lemurs should incorporate if the information that ring-tailed lemurs use is specific to the food and situation observed or can be generalized across multiple situations. The potential for information transfer through more active, offspring-directed co-feeding is low. However, basic response facilitation or local enhancement may be the most common method for ring-tailed lemurs to learn about resources through synchronized feeding behavior. In a species such as the ring-tailed lemur with a strong dominance hierarchy, synchrony of behavior may ensure a direct benefit from passively transmitted feeding information while maintaining distances that minimize agonistic encounters.

Figure 3-1. Mean proportion of approaches that are directed toward a conspecific that is feeding or foraging (±SE). Letters above the bars join age classes with the same mean, and age classes with different letters are significantly different from each other.

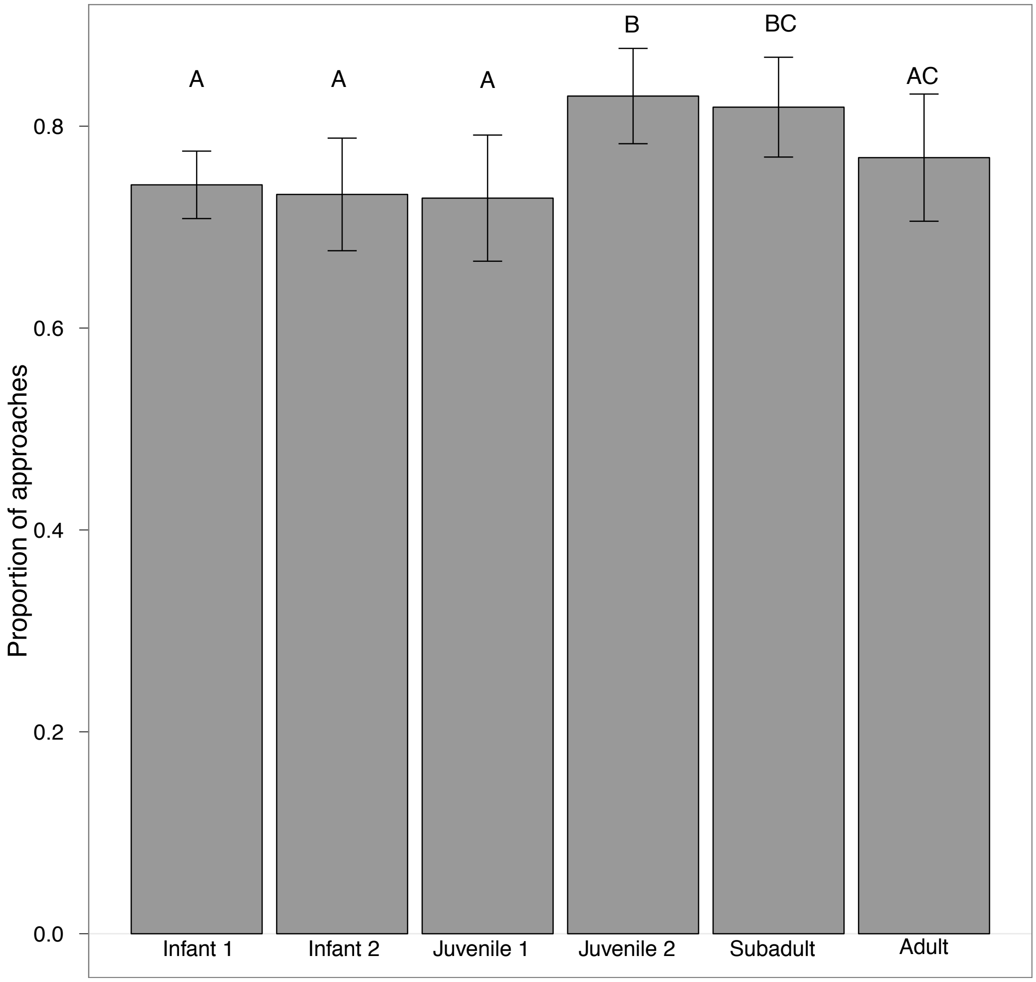

Figure 3-2. Mean percent of time co-feeding on solid foods with a focal's mother (black) and with other subadult and adult group members (grey). Because the proportion of co-feeding is low, standard errors are lower than 0.01% and are not shown.

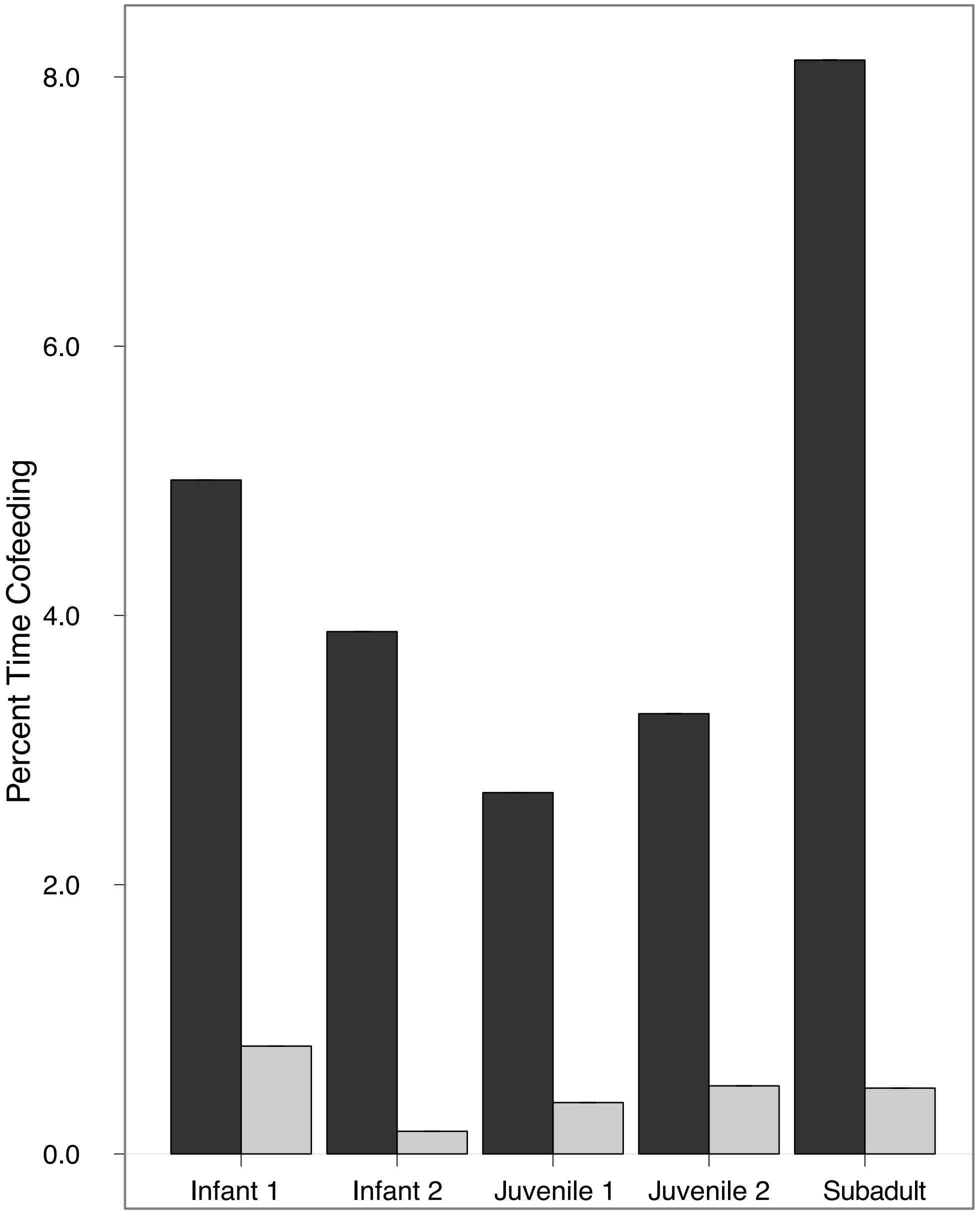

Figure 3-3. Mean proportion (±SE) of feeding and foraging (black) and other active behaviors (grey) that an individual is in synchrony with their nearest neighbor.

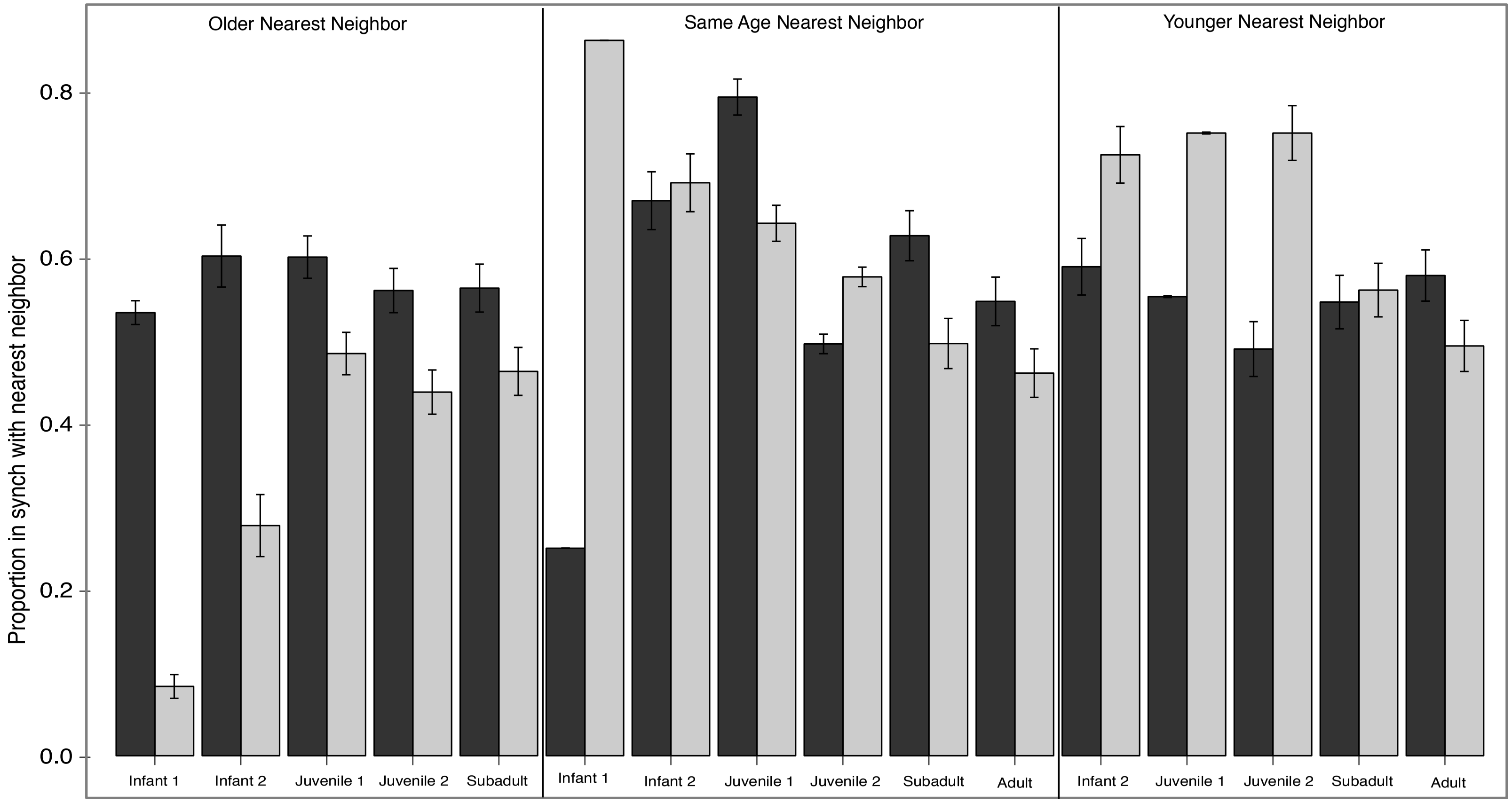

Figure 3-4. Mean Simpson's inverse diversity (black) and dietary evenness (grey) indices ± SE. Dietary diversity scores that are not significantly different across age categories are joined by the same letter below the bars. Dietary evenness scores that are not significantly different are indicated by the same number of asterisks.

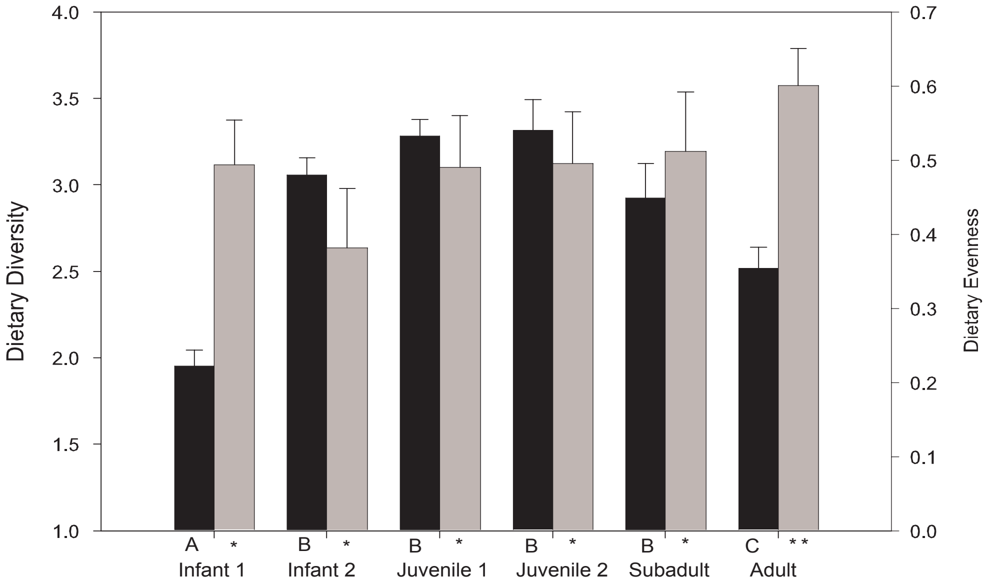

Table 3-1. Sample sizes for age-sex categories across the reproductive seasons. Sample sizes are given as number of individuals (N), total numbers of hours (Hours) and the mean number of hours (± SE) each individual was observed per day across the study period. Number of individuals includes animals who progressed through age categories. Blank cells indicate an age-sex category that was not observed during the particular season.

Age - Sex	**Variable**	**Gestation**	**Lactation**	**Weaning**	**Recovery**
Infant 1 Female	**N / Hours**		**14 / 93.4**		
	Mean ± SE		1.015 ± 0.064		
Infant 1 Male	**N / Hours**		**12 / 93.4**	**1 / 5.6**	
	Mean ± SE		1.112 ± 0.061	1.867 ± 0.657	
Infant 2 Female	**N / Hours**		**8 / 48.8**	**8 / 36**	**4 / 17.6**
	Mean ± SE		0.841 ± 0.066	1.5 ± 0.104	1.6 ± 0.162
Infant 2 Male	**N / Hours**		**10 / 60.4**	**10 / 42**	**2 / 9.8**
	Mean ± SE		0.915 ± 0.072	1.5 ± 0.136	1.633 ± 0.209
Juvenile 1 Female	**N / Hours**	**6 / 112.4**	**4 / 26.4**		**4 / 13.4**
	Mean ± SE	1.405 ± 0.078	2.4 ± 0.318		1.489 ± 0.183
Juvenile 1 Male	**N / Hours**	**3 / 25.8**	**1 / 6.4**		**5 / 14**
	Mean ± SE	1.433 ± 0.194	2.133 ± 0.593		1.273 ± 0.153
Juvenile 2 Female	**N / Hours**	**3 / 32**	**6 / 118.8**	**4 / 17.6**	**4 / 18**
	Mean ± SE	0.821 ± 0.081	1.467 ± 0.094	1.467 ± 0.176	1.5 ± 0.249
Juvenile 2 Male	**N / Hours**	**6 / 84.4**	**2 / 41**	**1 / 5.8**	**1 / 5.6**
	Mean ± SE	1.068 ± 0.07	2.05 ± 0.166	1.933 ± 0.24	1.867 ± 0.067
Subadult Female	**N / Hours**	**1 / 0.4**	**3 / 54.8**	**3 / 18.6**	**3 / 8.6**
	Mean ± SE	0.2 ± 0	0.979 ± 0.076	1.431 ± 0.192	1.075 ± 0.1
Subadult Male	**N / Hours**	**7 / 66.8**	**8 / 165.2**	**6 / 23.6**	**6 / 16.8**
	Mean ± SE	0.768 ± 0.042	1.412 ± 0.07	1.311 ± 0.146	1.292 ± 0.133
Adult F – NR	**N / Hours**	**23 / 235.8**	**23 / 336**	**23 / 71.8**	**23 / 49.8**
	Mean ± SE	0.753 ± 0.032	0.919 ± 0.050	0.99 ± 0.068	1.020 ± 0.062
Adult Male	**N / Hours**	**11 / 82.2**	**17 / 178.8**	**16 / 38.6**	**14 / 37.4**
	Mean ± SE	0.709 ± 0.043	0.774 ± 0.028	0.99 ± 0.081	1.039 ± 0.067

Table 3-2. Mean percent of feeding observations on solid foods within each distance categories (±SE). Means are from GLMM of the effects of age-sex class on mean proportions of observations within each distance category to nearest neighbor. Bold values indicate significant difference from adults, and asterisks indicate sex differences within an age category.

Age	Sex	Touch	Reach	1 meter	1-3 meters	>3 meters
Infant 1	F	**31.46±0.00**	**19.77±5.28**	**33.86±0.00**	**12.29±9.05**	**2.68±0.03**
	M	**13.76±0.47**	**23.22±6.70**	**42.38±0.07**	**17.56±12.23**	**3.06±0.27**
Infant 2	F	**4.34±0.59**	**10.47±3.96**	**38.28±0.10**	**35.01±14.47**	**11.84±0.78**
	M	**3.01±0.40**	**8.36±2.96**	**39.25±0.08**	**38.38±13.88**	**10.95±0.74**
Juvenile 1	F	1.64±0.46	6.02±3.01	28.85±0.05	41.58±14.42	21.85±0.53
	M	1.98±0.41	3.65±1.82	23.99±0.03	44.31±12.00	25.99±0.59
Juvenile 2	F	2.18±0.52	4.74±2.12	22.89±0.06	44.67±10.24	25.47±0.52
	M	0.39±0.41	3.5±1.42	20.12±0.03	43.62±8.21	32.35±0.32
Sub-adult	F	0.83±0.09	3.1±1.79	21.64±0.05	38.83±12.50	35.58±0.66
	M	0.74±0.14	2.47±0.93	18.02±0.03	43.52±6.81	35.22±0.36
Adult	F	2.23±0.22	3.69±0.81*	22.68±0.02*	41.93±4.95	29.42±0.25*
	M	0.72±0.08	1.63±0.41*	12.74±0.01*	39.22±3.18	45.67±0.19*

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CHAPTER 4. ECOLOGICAL RISK AVERSION AND JUVENILE RING-TAILED LEMUR FEEDING AND FORAGING

SUMMARY

The extended primate juvenile period is hypothesized to be a result of the interaction between feeding ecology and sociality. The Ecological Risk Aversion Hypothesis (ERAH, Janson and van Schaik 1993) has contextualized juvenility as a strategic life history shift that minimizes both predation and starvation risk. Behavioral support for the ERAH in primates has been mixed. The ERAH is not supported by somatic growth patterns in the strepsirrhines, and behavioral evidence from gregarious strepsirrhine species, primarily lemurs, is lacking to fully understand the relationship between strepsirrhine juvenility and ecological risk. To test the behavioral predictions of the ERAH and the generalizability of risk aversion in the evolution of primate juvenility, I collected a mixed-longitudinal sample of observations on feeding and foraging behavior from ring-tailed lemurs (*Lemur catta*) at the Beza Mahafaly Special Reserve, Madagascar. Like many monkeys and apes, ring-tailed lemur juveniles show a mix of behavioral traits predicted by the ERAH, but in general do not meet the ERAH's predictions. Contrary to the ERAH, juvenile ring-tailed lemurs do not show spatial patterning that would minimize predation risk more than do adults, as they do not forage closer to conspecifics or in center of group, have higher dietary diversity, and are equally efficient at finding and eating leaves. As predicted by the ERAH, juveniles are less efficient than adults at processing fruits and feeding on flowers, and received more aggression than other group members. Using ring-tailed lemurs as an example, like many New World monkeys, it does not appear that lemurs show the same developmental tradeoffs as Old World monkeys and apes in the way that they execute their own foraging behavior relative to increased social proximity, lower feeding efficiency, and low dietary diversity. Ecological risk aversion may have broader impacts on growth and development in Old World monkeys and apes than in other primates as a consequence of increases in brain size and social complexity.

INTRODUCTION

The extended juvenile period is one of the major life history shifts that characterizes primates and sets them apart from other mammals (Harvey and Purvis, 1999). The juvenile period (from weaning to age at first reproduction) is a vulnerable time. Delaying reproduction and extending the growth period can have significant fitness costs as individuals are smaller and are at greater risk of predation and starvation. Multiple hypotheses have tried to explain the evolution of primate juvenility, with some viewing juvenility as a non-adaptive consequence of constraints imposed by other aspects of primate life history and biology, including brain mass, metabolic demands, and demography (Cole, 1954; Charnov, 1993; Pagel and Harvey, 1993; Godfrey et al., 2004). Alternatively, juvenility is a direct product of selection that enhances learning opportunities and refines social skills (Joffe, 1997; Ross and Jones, 1999). The Ecological Risk Aversion Hypothesis, (ERAH) (Janson and van Schaik, 1993) attempts to bridge these two perspectives by incorporating growth, development, and energetics of juvenility in an ecological context. It proposes that the extended primate juvenile period, particularly in monkeys and apes, results from a tradeoff between decreasing mortality risk through close social associations with group members and subsequent increased feeding competition due to this close association. Low feeding proficiency of the young then requires decreased growth rates to minimize starvation risks borne by less competent and experienced feeders. There is mixed support for the behavioral foundations of the ERAH in the haplorhines, and there are no comparative behavioral data are available from the gregarious strepsirrhines (i.e., lemurs) that can test the comparative nature of the ERAH.

The primary assumption of the ERAH is that juveniles are less efficient foragers than adults, and to minimize predation risk juveniles forage closer the center of the social group and to other group members. This increases feeding competition, and to compensate and minimize starvation risk, juveniles grow slowly. By prolonging development, juveniles reduce the proportional energy devoted to growth and therefore reduce the risk of starvation under periodic food shortages. The predictability of food resources will also influence growth patterns, with more consistently available resources, such as leaves, permitting faster growth rates and earlier ages at maturation than patchily distributed or unpredictable foods. Because of the consistent and predictable availability of leaves, folivorous primates should grow faster than closely related and comparably sized frugivores, and frugivores should have comparatively longer juvenile periods.

Predictions generated by the ERAH for primate growth (Table 4-1) are supported mostly in the catarrhines. For their body sizes, folivorous catarrhines grow faster, for shorter durations, and reach sexual maturity earlier than do comparably sized frugivores (Leigh, 1994; Breuer et al., 2009). However, when extended to other primate taxa, the ERAH does not adequately explain primate growth and development. Growth patterns of New World monkeys are better explained by reproductive strategies (Garber and Leigh, 1997), and social complexity and grouping dynamics (Schmitt, 2010). Furthermore, growth in lemurs may be more closely tied to maternal investment in an unpredictable environment, and lemurs with frugivores growing faster and maturing earlier than folivores (Godfrey et al., 2004; O'Mara et al., 2012).

Tests of the behavioral predictions of the ERAH (Table 4-1) are inconclusive in monkeys and apes, and no comparable data are available from lemurs, which are the only gregarious strepsirrhines. In many species, juveniles are not less efficient foragers than adults nor do they spend more time foraging than adults (Fragaszy, 1986,1990; Hanya, 2003; MacKinnon, 2006; Stone, 2006,2007b; Bezanson, 2009). For example, squirrel monkeys infants were as successful as adults in insect capturing by 6 months of age (Stone, 2006,2007a), young *Cebus capucinus* juveniles are equally efficient foragers as adults (Bezanson, 2009), but on food resources that require strength to process, brown capuchins (*Cebus apella*) show all adult behaviors by two years of age and reach adult proficiency by late juvenility at 3 years of age (Gunst et al., 2008,2010). In studies where juvenile foraging efficiency is lower than adults, lowered efficiency is hypothesized to be a consequence of cognitive constraints on finding food (Johnson and Bock, 2004), limitations imposed by strength (Gunst et al., 2010), or refinement of motor and spatial skills (Lonsdorf, 2005) and not of competitive agonism from adults. For foods that require more complex perceptual processing (finding and extracting beetle larvae), *C. apella* do not show adult proficiency until well into adulthood at six years of age (Gunst et al., 2008,2010). In all of these cases, however, adult efficiency and behavioral patterns are reached by the beginning of late juvenility. Juveniles may forage closer to the center of the group (Robinson, 1981; Janson, 1990), but not necessarily closer to another group member to minimize predation risk (Bidner, 2003; Stone, 2007a).

The ERAH also predicts that as a consequence of inexperience in foraging, juvenile dietary diversity will be lower than that of adults. Increased dietary diversity, however, may be a compensatory mechanism to increased feeding competition to introduce juveniles to the array of food possibilities. Compared to adults, juvenile diets often show more breadth in both species composition and part of a food species used, and diets become more focused as the animal ages (Hauser, 1993; Altmann, 1998; Tarnaud, 2004). In baboons (*Papio cynocephalus*), this dietary diversity is positively correlated with amount of play and later reproductive success (Altmann, 1998). Juveniles may incorporate items not typically considered food by adults. These items may be eaten once in exploration, or may be incorporated into the diet for a period of time and lost as the animal approaches adulthood (Watts, 1985). Increased dietary diversity may also reflect heightened neophilia and a trial-and-error learning strategy in juveniles who show less caution when presented with novel foods or situations (Watts, 1985; Whitehead, 1986; Fragaszy et al., 1997; Johnson, 2000; Visalberghi et al., 2003; Fragaszy and Visalberghi, 2004).

There is then a mis-match between the available behavioral support for the ERAH and the well-defined growth profiles relative to diet in the monkeys and apes. Monkeys and apes grow in ways that are predicted by ERAH but do not show the behavioral patterns predicted by the ERAH to produce these patterns. Strepsirrhine primates do not show growth patterns predicted by ERAH, and there are no or few behavioral data to contextualize these patterns (Table 4-1). Behavioral examples on the ontogeny of feeding from gregarious juvenile strepsirrhines can then contribute an important phylogenetic perspective on the relationship between the duration of the juvenile period and the emergent foraging behaviors of developing animals.

This study presents developmental behavioral data on the ontogeny of feeding ecology in ring-tailed lemurs (*Lemur catta*) from infancy through adulthood. Ring-tailed lemurs are highly gregarious, diurnal lemurs that provide an ideal contrast to haplorrhine primates that live in large social groups (Jolly, 1998; Sandel et al., 2011). They are eclectic frugivores-folivores with broad taxonomic dietary composition. By comparing the development of feeding across all age stages, I evaluate if the ways ring-tailed lemur juveniles forage and feed are consistent with the predictions of the ERAH. If juvenile ring-tailed lemurs forage and feed in ways that are consistent with ERAH then they should show lower feeding efficiencies, forage closer to their nearest neighbor, and forage closer to the center of individual tree crowns to minimize predator exposure than do adults. Concomitant to their foraging inexperience, juvenile dietary diversity will be lower than that of adults and dietary evenness will be higher than adults in the social group. However, I show that ring-tailed lemur juveniles do not meet most of the predictions of the ERAH and instead show very adult-like foraging patterns early in development.

METHODS

Data were collected from May 2009 to March 2010 at the Beza Mahafaly Special Reserve (Beza) in southwest Madagascar (23.65647°S, 44.62897°E) where the biology, behavior, and ecology of adult ring-tailed lemurs have been studied since 1987 (Sauther, 1998; Yamashita, 2002; Gould et al., 2003; Sussman and Ratsirarson, 2006; Sauther and Cuozzo, 2009). The primary study area, Parcel 1, grades from gallery forest dominated by *Tamarindus indica* in the east to drier deciduous and Dideraceae dominated desert spiny forest as one moves west away from the Sakamena river (Sussman and Rakotozafy, 1994). This east to west moisture gradient is coincident with a lower and more open canopy, smaller average tree stem diameter, and increasing diversity in tree species per hectare (Sussman and Rakotozafy, 1994).

Beza's climate is highly seasonal, with a cold dry (May-September) and a hot wet (October – April) season where 80% of the annual average of 615 mm of rain falls each year (Lawler et al., 2009). This study period was hot and dry with average high temperatures of 35.7°C (dry season) and 45.8°C (wet season) and with only half the amount of rain that typically falls during equivalent times in other years (this study: 265mm, Beza average for June-March: 500mm; (Ratsirarson, 2003; Sussman and Ratsirarson, 2006).

Study population

Ring-tailed lemurs are eclectic frugivore-folivores that spend half of their feeding and foraging time on the ground (Sussman, 1977) and 95% of total observed feeding time is spent on substrate lower than 10 meters (O'Mara, unpublished data). Ring-tailed lemur foods do not require extensive processing, although some fruits such as *Tamarindus indica* may require a minimum of strength or post-canine occlusal surface area to open (Cuozzo and Sauther, 2004; Millette et al., 2009).

Ring-tailed lemurs maintain a non-transitive dominance hierarchy with low linearity (Martin and Bateson, 1993) where, contrary to the typical mammalian pattern, females dominate males in all contexts (Pereira and Kappeler, 1997). Reproduction is photoperiod controlled, highly seasonal and synchronized to resource availability (Sauther, 1991; Jolly et al., 2002). Gestation typically occurs during the cold-dry season (May – September), with most infants born during the transition to the hot wet season (September – October). Ring-tailed lemurs lactate through the wet season (October – December) and wean their offspring during maximum food availability, particularly of young leaves (December – February). They experience a recovery period (March-April) before a very brief mating period (May) where females are receptive for a period of 6-24 hours (Sauther, 1991). First year mortality averages 50% (Gould et al., 2003) but was as high as 71% in the 2008 birth cohort (Meredith & O'Mara unpublished data). A full complement of predators, including wild cats (*Felis sp.*), feral dogs (*Canis familiaris*), foosa (*Cryptoprocta ferox*), and harrier hawks (*Polyboroides radiatus*) were either observed directly or signs were found within the study area (Sauther, 1989; Brockman, 2003; Goodman, 2003; Brockman et al., 2008). Wild cats were observed twice to prey on infant ring-tailed lemurs during the study.

With the help of several field assistants, more than 2,300 observation hours were completed on 78 individuals from seven study groups (Table 4-2; mean group size: 13, range: 8-19 individuals, including 6-14 adults). Birth dates are known for the individuals born into each of the study groups since 2006, but birth dates, exact ages, and matrilineal relationships are not known for females older than 4 years old and adult males who transfer between groups. Individuals were recognized through a combination of collars bearing numbered tags, natural markings, and in some cases, less than 1cc of dye (Nyanzol-D, Greenville Colorants) was applied to their fur. Interobserver reliability was periodically assessed to maintain a minimum of 85% agreement using percent agreement and Cohen's Kappa statistic included in the JWatcher package (Coelho and Bramblett, 1981). All methods were approved by the IACUC at Arizona State University (08-983R) and by Madagascar National Parks (135/07; 257/09**)** and conformed to the Principles for the Ethical Treatment of Non-Human Primates of the American Society of Primatologists.

Behavioral Sampling

Continuous and instantaneous sampling methods (Altmann, 1974) were used simultaneously to sample feeding and its social context during 12-minute focal animal sampling sessions (FAS). All feeding, foraging, bite counts, and aggressive behaviors were recorded continuously in JWatcher (www.jwatcher.ucla.edu). Subjects were chosen from among the seven study groups to maintain a sex and rank balanced sample within each age category. These individuals were then selected for observation following a stratified random protocol where an infant or juvenile was followed every other or every third observation. Each social group was observed in rotating two-day blocks for between four and eight days per month.

Spacing, risk, and general activity. General activity of the focal individual (feed, forage, rest, move, stand, engaged in social behaviors, other) was recorded instantaneously at three-minute intervals during each FAS session. At these three-minute intervals the identity, activity (as above), and categorical estimate of distance to the nearest neighbor (touching, within arm's reach, within one meter, within three meters, and greater than three meters away), height to the nearest meter, and position within the tree crown based on a 3x3 grid (interior, middle, exterior; lower, middle, upper) were also recorded. The location in this grid was then used to assess potential predation risk. Ring-tailed lemurs emit two alarm calls for distinct predator classes (Sauther, 1989): one for aerial predators (yap) and one for terrestrial predators (shriek). Both the outer edges of a tree crown and the ground were considered high risk foraging areas because of the risk of hawk and cat predation, respectively (Janson, 1998). All other areas were classed together as low risk. Agonistic encounters (aggression and submission given and received) were recorded as events during the focal observation sessions and were graded on the intensity of the interaction. Here, only aggression that would disrupt feeding and foraging was included (e.g., move to displace, spat, lunge, cuff). Aggression is summarized as the number of aggressive instances over the total time of observation to give hourly rates of aggression

Feeding and foraging. To be included in analysis of the continuous and instantaneously recorded variables, individuals must have contributed a minimum of three observation sessions in a given day, with each individual contributing between four and eight 12-minute FAS per day when their group was followed (mean number of FAS/day (F/M): Infant 1: 5.0/5.4, Infant 2: 5.6/5.8, Juvenile 1: 7.7/7.3, Juvenile 2: 6.4/6.6, Subadult: 5.1/5.7, Adult: 4.1/4.0). Feeding was defined as the ingestion of food and foraging as the active searching for and processing of food items and includes sniffing, licking, and cracking (Appendix B). Plant parts were divided into unripe fruit, ripe fruit, young leaves, mature leaves, flowers and flower buds. Ring-tailed lemurs also include arthropods, soil, and wood into their diet. Arthropods were identified to species when possible and minimally to taxonomic order. Plants were identified to species with help of local experts (Mr. Elahavelo and Mr. Herman Mananjo), by Mr. Rokiman Lestara (Tsimbazaza Botanical Gardens, Antananarivo), and through digital voucher images from the Missouri Botanical Gardens TROPICOS database (www.tropicos.org). Bite counts were conducted each individual throughout the twelve-minute FAS sessions to measure intake rates. We attempted to measure bite count rates at least twice per individual per day (Mean 1.2 – 2.4/individual/day, Chapter 2). These intake rates are then used as a measure of ingestion rate and feeding efficiency (Johnson and Bock, 2004). Most fruits and young leaves, which constitute the bulk of ring-tailed lemur diet, are ingested in a single bite by all age categories (Sauther, 1992). Average bite count rates were then calculated for each individual per day of observation.

Dietary diversity and dietary overlap were calculated for each individual focal animal in two-week blocks. Dietary diversity was calculated using the Inverse Simpson's Diversity index, D, where $D=\mathbf{1}/(\Sigma p_i^2)$ and p_i^2 is the squared proportion of total time feeding in these two-week blocks on each item (Begon et al., 1996; Irwin, 2008). D originates from a value of 1 (diet of 1 item), with higher values reflecting a more diverse diet. Dietary evenness (E_D) was calculated as $E_D=D/s$ where D is the Inverse Simpson's Diversity Index and s is the maximum number of food items utilized in the two-week block (Begon et al., 1996). Dietary evenness ranges from 0 to 1, with a low evenness value indicating a diet where food items are used in unequal proportions.

Analysis

Both continuously and instantaneously recorded data are summarized as proportions of total observations per individual per day. This generates a mixed-longitudinal data set of individual-days with the intent of preserving any individual level variability in behavior

(Machlis et al., 1985; Dagosto, 1994). Generalized linear mixed models (GLMMs) were then fit to the mixed longitudinal data in the *lme4* package in R 2.13 (R Core Development Team, 2011). Untransformed proportional data were modeled using logistic mixed models with a binomial distribution and logit link identity (Jaeger, 2008; Warton and Hui, 2011). Traditional repeated measure designs are encumbered by balanced sample requirements that can rarely be met using observational data from wild animals. Generalized linear mixed models have the advantage of being able to process unbalanced, multi-way repeated measures designs through the inclusion of random effects in the model (Bolker et al., 2009). For all models, individual animal identity and a time factor (reproductive season) were included as random effects. The significance of the fixed factors (e.g., age, sex) was evaluated by comparing two nested models differing in a single factor (Huchard et al., In Press; Pinheiro and Bates, 2009). A likelihood ratio test of these two nested models (X^2) was then used to evaluate the significance of individual factors (Lewis et al., 2011). When factors did not significantly contribute to the fit of the model they were removed from the analysis. For models with significant main effects, subsequent Tukey's post-hoc tests identified differences among factor level pairwise comparisons, typically age-sex levels. All significance was evaluated at α=0.05

RESULTS

*Spacing and risk while feeding and foraging***.** Young infants feed and forage in areas of lower risk exposure to predation more than do than older individuals (Fig 4-1, X^2=19.355, df=5, p=0.002). By Infant 2 there are no differences among these older age groups (Fig 4-1, X^2=1.1548, df=4, p=0.8855). Infants have closer nearest neighbors than juveniles, subadults, and adults during feeding and foraging, including higher proportions of nearest neighbors within one meter than all other ages (including in touch and in reach, Table 4-3). As infants are weaned, they transition to adult-like spacing patterns by early juvenility, with typical distances among nearest neighbors between 1 and 3 meters away (Table 4-3). Juveniles do not differ significantly from adults in the distance to their nearest neighbors while feeding and foraging (Table 4-3).

Feeding efficiency and competency. As expected, infants show high ratios of time feeding to foraging, and devote a larger proportion of their time to feeding (including nursing) than to foraging relative to other age classes (Fig 4-2; X^2= 652.3, df=5, p<0.001). The long nursing bouts that comprise infant feeding decrease as the infants age, and by their transition to Infant 2, infants are showing the same ratio of time feeding to foraging as adults. While infants begin to ingest food as early as three weeks of age, across the twelve weeks of young infancy, infants nurse for an average of 65 ± 0.02% of feeding time. This drops to 22.7 ± 0.05% of total feeding time in late infancy prior to weaning. All other age classes do not differ in the ratio of the proportion of time spent feeding divided by the proportion of time spent foraging.

Feeding efficiency, measured through bite count rates, increases with age across all food types (Fig 4-3; X^2= 207.92, df=30, p<0.001). Infants and young juveniles are generally less efficient feeders than adults, but there is large variation in the efficiency of feeding by food part (Fig 4-3). By late juvenility (Juvenile 2), efficiency differences in the processing of leaves disappear. However, juvenile feeding efficiency on both ripe fruits and flowers are lower than that of adults. Adult-level proficiency in ripe fruit feeding is not reached until subadulthood, while adults are faster feeders on flowers than all other age categories except infants

The study population ate a minimum of 137 plant species from 55 families and six arthropod species (Appendix D), with each social group consuming at least 60 plant species from 33 families. Older infants, juveniles, and subadults all have more diverse diets than do adults (Fig 4-4; X^2=52.342, df=5, p<0.0001, O'Mara Chapter 3). Per group, the mean number of plant species consumed for adults and subadults is 35.7 ± 2.06 species, for infants 22.5 ± 2.46 species, for young juveniles 34 ± 3.69 species, and for older juveniles 38 ± 1.71 species. The major increase in dietary diversity is at 35-40 weeks of age, approximately mid-way through the young juvenile period, and does not drop until adulthood. Correspondingly, infants, juveniles, and subadults show less dietary evenness than do adults and nursing infants (Fig 4-4; X^2= 18.427, df=4, p=0.041).

*Aggression and competition during feeding and foraging***.** Ring-tailed lemurs are organized in a highly regulated dominance hierarchy where older animals dominate younger group members. Accordingly, young animals experience higher rates of aggression directed at them while feeding and foraging than do adults (Fig 4-5, X^2=98.609; df=11, p<0.001). Infant males receive the most aggression (4.67 ± 0.27 events per hour) and adult females receive the least (0.98 ±0.70 events per hour). Aggression directed at an individual while feeding or foraging does not affect the ingestion rate of each food type (X^2=9.381; df=5, p=0.110). There is a significant interaction between sex and age revealing that while at any age males have more aggression directed at them than do females, this only becomes significant in adults (X^2=46.612; df=6, p<0.001).

DISCUSSION

The Ecological Risk Aversion Hypothesis (Janson & van Schaik 1993) posits that “slow and steady wins the race.” It predicts that young primates will minimize predation risk by foraging closer to the center of the group. These young and inexperienced animals will have a more restricted diet than adults and will be less efficient foragers due to smaller size and less strength, lack of experience, and cognitive immaturity. These growing individuals have higher relative energetic costs for traveling than adults (Steudel, 2000), yet still must devote significant energetic resources to growth and development. They will receive more food-related agonism and be displaced from feeding positions more easily than adults. Consequently, juveniles must grow slowly to mitigate the starvation risk induced by increased feeding competition due to close proximity to other higher ranking and more efficient foragers (Table 4-1). Ring-tailed lemur juvenile foraging patterns do not support these predictions.

Once they are weaned, juveniles do not position themselves closer to other group members while foraging than do adults, but maintain a distance of 1-3 meters from their nearest neighbor while feeding. This distance may be an anti-predator strategy, regardless of age, that optimizes a tradeoff of anti-predation tactics with minimizing feeding competition. Alternatively this may place growing animals (and all group members) in a more effective spatial position to learn socially from other group members. When foraging in trees, juveniles also do not forage in a more predator sensitive manner. The distance to a nearest neighbor decreases as animals move higher in the canopy as well as further toward the edge of the tree crown. These peripheral areas are high-risk areas for aerial predators including the Madagascar harrier-hawk (*Polyboroides radiatus*). It is unknown which class of predator preys on ring-tailed lemurs more frequently, but ring-tailed lemurs show distinct alarm calls and behavioral responses to both aerial and terrestrial predators (Sauther, 1989). Foraging on the ground may be more risky than in the trees, and during this study I observed wild cats (*Felis sp.*) prey on infant ring-tailed lemurs twice. In both instances the cats were hidden on the ground near where lemurs were foraging. When an infant came within striking distance the cat quickly pounced, grabbed the lemur by the back of the neck in what seemed to be a fatal bite, and then rapidly carried off its prey. If this type of predation event is common for these lemurs, then foraging closer to your neighbors while on the ground may be the best risk-averse strategy.

The behavioral measures here show that at least by older juvenility, juveniles are equally efficient feeders to adults and that they have more diverse diets than adults, but have diets that are equal in the frequency of plant parts used. However, feeding efficiency on ripe fruit and flowers remains low until a nearly adult body size, as well as adult dentition, is reached (Fig 4-3). The ripe fruit of *Tamarindus indica* can comprise as much as much as 30% of a group's diet within a given season (Head et al., In Review). *Tamarindius indica* ripe fruit is covered by a hard shell, with a tough fibrous interior and sticky pulp surrounding a large seed (Yamashita, 2002; Sauther and Cuozzo, 2009). The mechanical challenges of this fruit may require longer processing time by juveniles who have fewer teeth and a lower post-canine occlusal surface area than adults (Eaglen, 1985; Godfrey et al., 2001). The eruption of adult post-canine dentition is completed just after the first year (Eaglen, 1985), but it may require the development of mature jaw musculature and a sufficiently high bite forces to effectively process these fruits. The lower juvenile ingestion rates of flowers and flower buds are explained less by morphology than by social displacement from this resource. Flowers and flower buds become a highly sought after resource when they appear during seasons of low overall food abundance (Sauther, 1998). Juveniles are more easily displaced from these resources than other group members, lowering their feeding efficiency.

Juveniles did not show lower ratios of feeding to foraging than adults (Fig 4-2). Young ring-tailed lemurs did have more diverse and less even diets than older group members. This diversity likely arises through food exploration, as well as an increased distance from other group members while foraging during the early and late juvenile stages (Fig 4-2). This pattern has been found in primates spanning all body sizes, relative durations of juvenility, and dietary types for both time spent feeding [*Saimiri sciureus*: (Stone, 2006); *Gorilla gorilla berengei* (Watts, 1985); *Macaca fuscata*: (Hanya, 2003); *Cebus capucinus*: (Janson and Boinski, 1992), *C. apella*: (Janson and van Schaik, 1993)] and equal or greater dietary diversity and composition [*Saimiri sciuerus*: (Stone, 2007a); *Chlorocebus sabaeus*: (Harrison, 1983); *G. g. berengei*: (Watts, 1985); *Eulemur fulvus*: (Tarnaud, 2004)].

In primate species where juveniles devote more time to foraging relative to feeding it is generally due to limitations in strength, cognition, or fine motor skills [extractive foraging of *Cebus apella*: (Gunst et al., 2008); mixed grass and root foraging in *Papio ursinus*: (Johnson and Bock, 2004); termite fishing in *Pan troglodytes schweinfurthii*: (Lonsdorf, 2005)]. This is also true of ring-tailed lemurs. Juveniles are less adept than adults at catching seasonally available flying insects such as cicadas, and do not open hard and large fruits such as *Crateva excelsa,* a spherical fruit with a diameter of 3.5 cm, until they are in later juvenility, likely due to a limitation in both gape and canine size. However, most high-ranking females were also not observed to open these fruits and instead waited for males and low-ranking females to crack the fruits and then displaced these lower-ranking group members in an apparent producer-scrounger model (Hirsch, 2007; King et al., 2009). Further testing of producer-scrounger dynamics will be valuable in understanding how sex, age, and dominance rank influence an individual's foraging strategy.

Juvenile ring-tailed lemurs experience higher rates of aggression directed at them during foraging than adults; however, rates of aggression may not be an adequate measure of feeding competition. Chacma baboon juveniles receive more aggression than their adult counterparts, but this does not decrease their feeding efficiency (Johnson and Bock, 2004). This same pattern is found in ring-tailed lemurs. The threat of displacement and aggression may also depend on the quality of the resource being eaten. Adult vervet monkeys will differentially abandon resources based on the quality of the food type, with animals staying in a high-quality feeding patch (exudates or fruits) until a dominant animal is very close, but fleeing low quality resources (grasses) when a dominant animal is far away (Hauser, 1993). Juvenile vervet monkeys use this same pattern and are no more likely to abandon high-quality resources than are adults (Hauser, 1993). The current dataset cannot address the question of the persistence of juveniles on a prized resource relative to adults, and measurements of displacement distances to food resources would be ideal to compare the relative value of a given resource and how juvenile ring-tailed lemurs perceive feeding competition (Hauser, 1993; Vogel and Janson, 2007). Based on the already high rates of aggression and no decrease in bite rate, I predict that like vervet monkeys, juvenile ring-tailed lemurs are no more likely than adults to abandon a resource until a threat of physical, aggressive displacement is imminent. Understanding how these relate to one another may clarify how feeding competition is manifested across age categories within a ring-tailed lemur social group.

Aggressive behavior by a group member may not be adequate to instill fear or stress in juveniles while feeding. Older juvenile ring-tailed lemurs have lower fecal glucocorticoid levels, a general measure of physiological stress, compared to adults (O'Mara, 2008). At this point it is unclear if these low values are indicative that juveniles are neither nutritionally nor socially stressed or if they pass through a hyporesponsive period where it is difficult to elicit a glucocorticoid response to any external stimulus (Lupien et al., 2009). Aggression directed at individuals does not necessarily elevate glucocorticoids, and in ring-tailed lemurs lower-ranking females who receive higher rates and intensity of aggression directed at them have lower glucocorticoid levels than top ranking females (Cavigelli et al., 2003). Fecal glucocorticoid levels have been shown to reflect mortality risk in adults (Pride, 2005), and the lower glucocorticoid levels of older juveniles may also indicate a downshift in mortality risk during this life stage. Future analyses of glucocorticoid samples collected concurrently with these behavioral data will further contextualize the response to potential risk perceived by this population and quantify how juvenile lemurs respond physiologically to increased levels of agonism.

Contrary to the ERAH, more frugivorous lemurids, such as the ring-tailed lemur, grow faster, have larger infants and reproduce sooner than folivorous indriids (Godfrey et al., 2004). However, dental development does conform to the ERAH and folivorous lemurs develop adult dentition faster than frugivores (Godfrey et al., 2004). Mortality data across the lemur radiation do not indicate juvenile folivorous lemurs, relative to frugivorous ones, are at lower risk of death or morbidity due to starvation as would be predicted by ERAH. Infant lemurs experience high mortality regardless of dietary category (Frugivores: *Eulemur fulvus rufus*: 35.7-50% (Overdorff et al., 1999); *Eulemur rubriventer*: 50% (Overdorff, 1991); *Lemur catta*: 30-70% (Gould et al., 2003); this study); Folivores: *Propithecus diadema*: 43% (Wright, 1995); *Propithecus verreauxi* 48% (Richard et al., 2002)). Juvenile mortality rates are not typically reported, but for the Beza Mahafaly population, juvenile mortality is reported as 6% (Gould et al 1999) and 36% (this study).

More complete demographic records that reflect juvenile mortality specifically will help clarify the degree of ecological risk that juvenile lemurs face.

Diet composition does affect starvation resilience in lemurs. During an extended drought period at Beza Mahafaly (1991-1993), ring-tailed lemur infant and juvenile mortality was 80% and 50%, respectively (Gould et al., 2003) and *Propithecus verreauxi verreauxi* infant mortality was 66% (Richard et al., 2002). While there was an overall increase in mortality in these sympatric species, likely due to starvation effects, consistent with the ERAH, the folivorous *P. v. verreauxi* showed lower overall population loss than did the frugivorous ring-tailed lemurs.

The unpredictable environment of Madagascar (Wright, 1999; Dewar and Richard, 2007) may have removed the lemurs from the playing field of juvenile ecological risk aversion and into an arena where maternal investment dictates growth. Godfrey and colleagues (2004) propose that lemurids and indriids evolved different solutions to Madagascar's environmental instability. Indriids employ a 'low maternal input, slow returns' strategy where few infants are produced, but they grow slowly and can survive on low quality foods. In contrast, lemurids follow a 'high maternal input, fast returns' strategy where more and faster-growing infants are birthed, but these infants require higher quality foods and are not resilient to fluctuations in food availability. Where indriids may take a 'slow and steady' approach to growth and reproduction, lemurids consistently play 'catch-up' (Godfrey et al., 2004).

Juvenility in primates may not simply be a consequence of minimizing ecological risk, but may be an adaptation to learning complex foraging tasks, spatial maps, or social rules (Joffe, 1997; Ross and Jones, 1999; Walker et al., 2006). These "needing to learn" or "social intelligence" hypotheses require social and ecological complexity that must be learned to become a successful adult. However, infants and juveniles must focus on what it takes to be a successful infant and juvenile before becoming an adult (Bezanson and Morbeck, In Press). The behavioral repertoire of an adult may not be the most adaptive set of behaviors for a juvenile, and could potentially impede the development of cognitive and physical maturity. Juvenility is a period of life where individuals acquire the behavioral skills that are necessary as an adult, and is generally characterized by a progressive refinement of skill and knowledge. However, juveniles tend to show behavioral repertoires unusual for adults. They spend large amounts of energy in play, have diverse diets, and use positional behavior modes that are either rare or absent in adults (Pereira, 1993; Bezanson, 2009; Lewis Graham, 2011). Primates living in the largest social groups tend to have the longest relative juvenile periods (Joffe, 1997), although these are typically accompanied by increases in brain size and ecological complexity that all are correlated with extended juvenility (Walker et al., 2006). Predation and memory may also have had a strong influence on slowing primate growth and extending the juvenile period. In fish, slow growth rates facilitate learning and extended memory of predator cues (Brown et al., 2011). Learning and remembering the appropriate behavioral response and refining appropriate detection images to a diverse guild of predators may be a complex aspect of development. If predation exerts strong pressure on juvenility, as argued by the ERAH, then cognitive resolution of predation may require an extended juvenile period as well.

The life history phase of juvenility is not a homogenous stage of life (Pereira and Leigh, 2003). There are complex development changes in behavior and physiology that make understanding juvenility as a single phase difficult, and considering it as such may make predictions from the ERAH difficult to test without detailed data that span the behavioral shifts within the juvenile period. With increases in brain and social and behavioral complexity in monkeys and apes, ecologically risk aversive foraging may have a broader impact on growth and development. Increases in social complexity and concomitant increases in brain size may regulate the overall growth of haplorhine primates and set the pace for juvenility. To understand the full extent of these impacts future work that integrates the energetics and physiology of development within an ecological context will better test if juveniles do use behaviorally risk aversive strategies and if these help mitigate starvation risks and energetic deficits. However, using ring-tailed lemurs as an example, it does not appear that a need to minimize risk while foraging has impacted variability in the way that lemur species grow (Godfrey et al., 2004) or in the way that they execute their own foraging behavior.

Figure 4-1. Mean percent of feeding and foraging observations (± SE) spent in locations of high predation risk. Asterisks show that Infant 1 are in high-risk areas less than all other age class, which do not differ from each other.

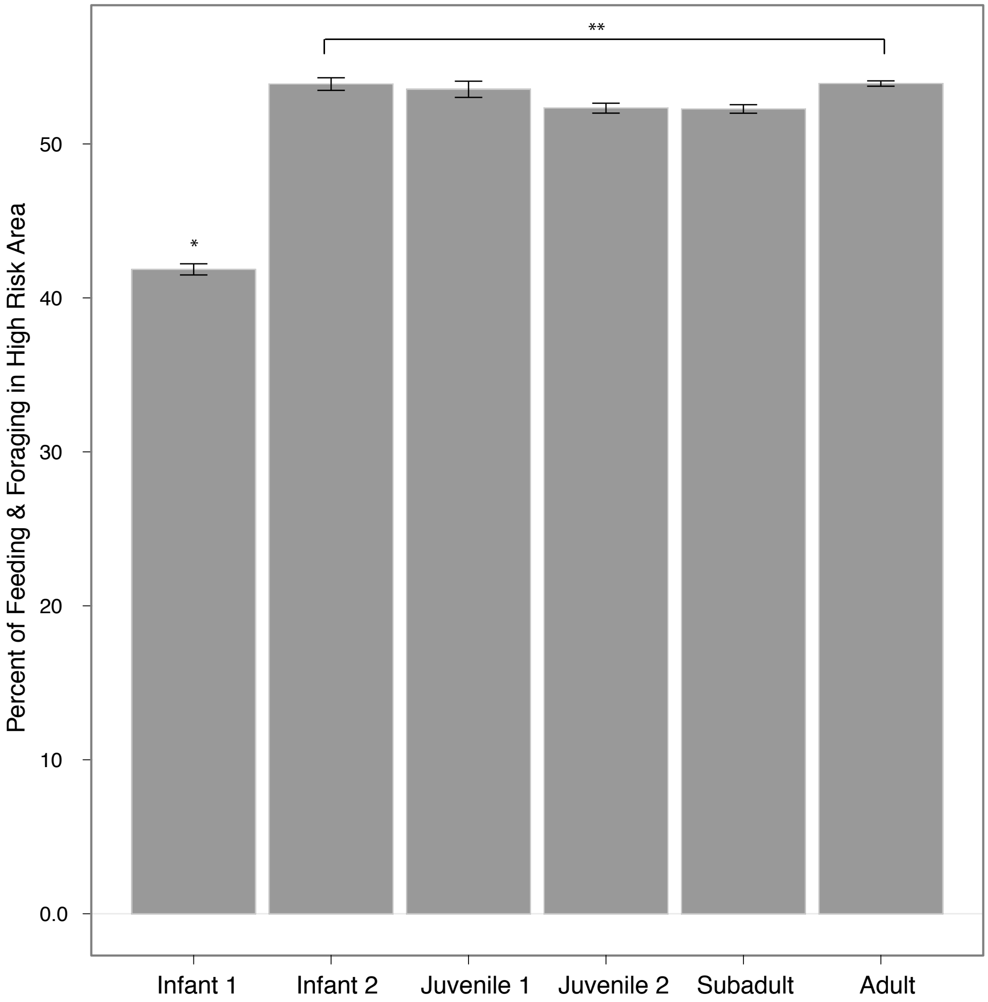

Figure 4-2. Mean ratio of time spent feeding (including nursing) to time spent foraging (±SE). The Horizontal bar joins age categories of equal means asterisks mark age class groups that are significantly different.

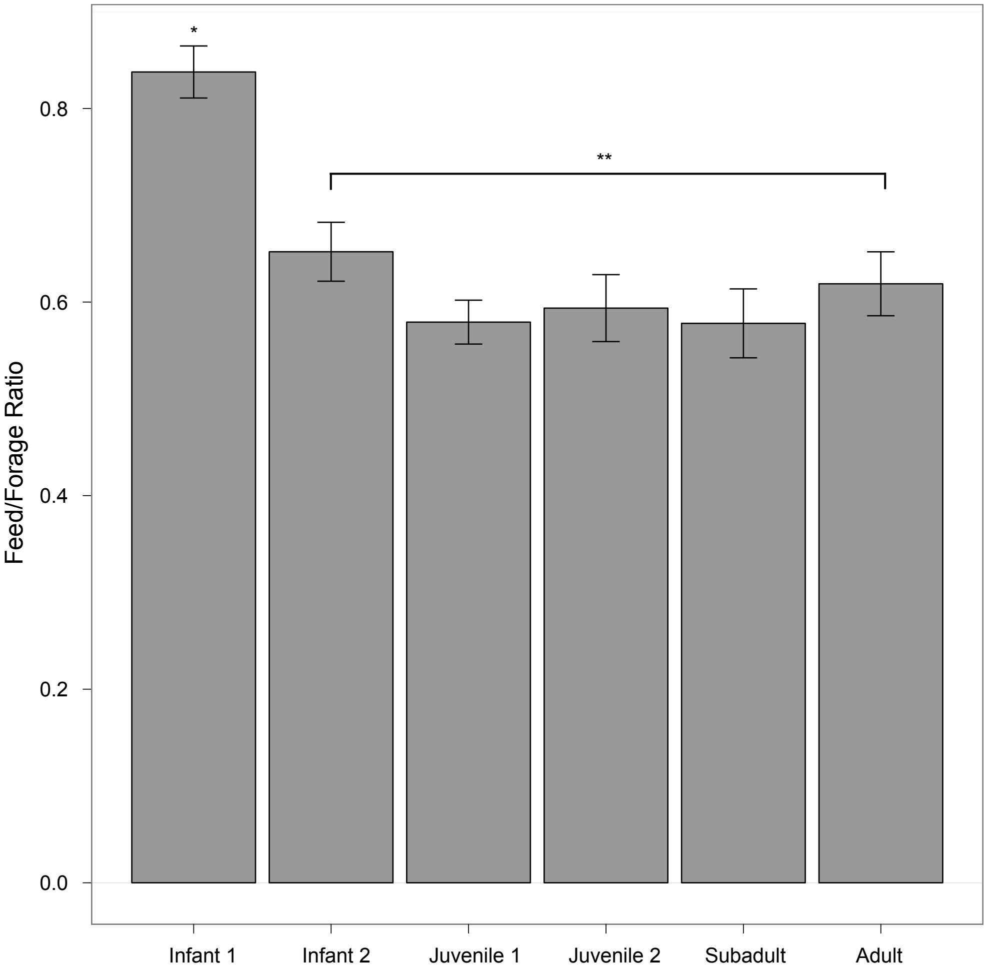

Figure 4-3. Ingestion rates (bite counts) by age classes for major food classes in ring-tailed lemur diet (means + SE). Vertical bars join age classes that are not different from one another and asterisks mark age class groups that are significantly different. NA denotes foods where bite counts were not collected due to low seasonal availability or absence during infancy.

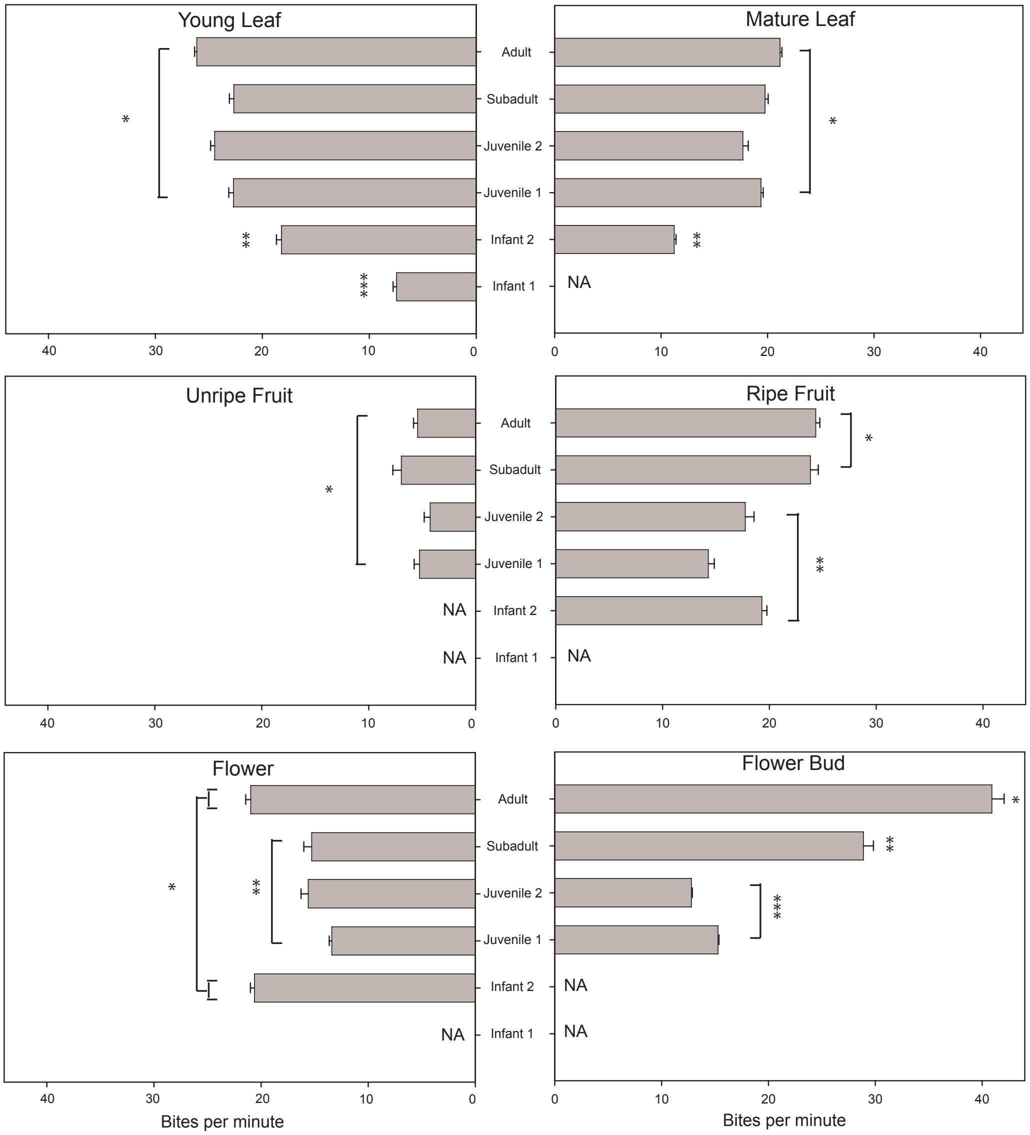

Figure 4-4. Mean Simpson's inverse diversity (black) and dietary evenness (grey) indices ± SE. Dietary diversity scores that are equal across age categories are joined by the same letter below the bars. Equal dietary evenness scores are indicated by the same number of asterisks.

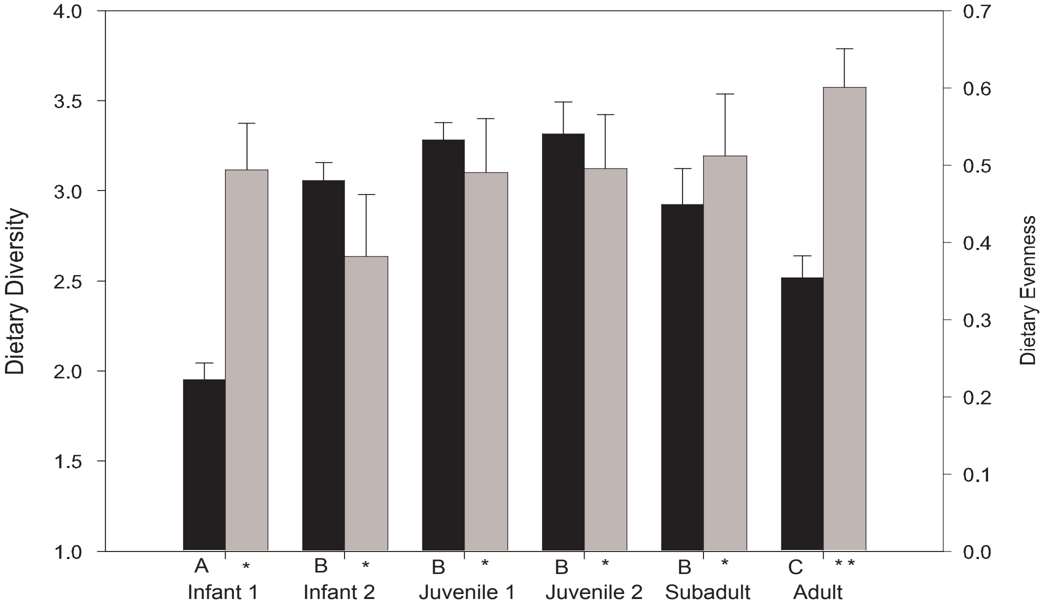

Figure 4-5. Mean rates of aggression (±SD) directed at a focal while feeding or foraging. Females are in black, males in grey. The asterisk indicates sex differences in aggression received. Letters below the bars indicate age-sex classes that are not different from one another.

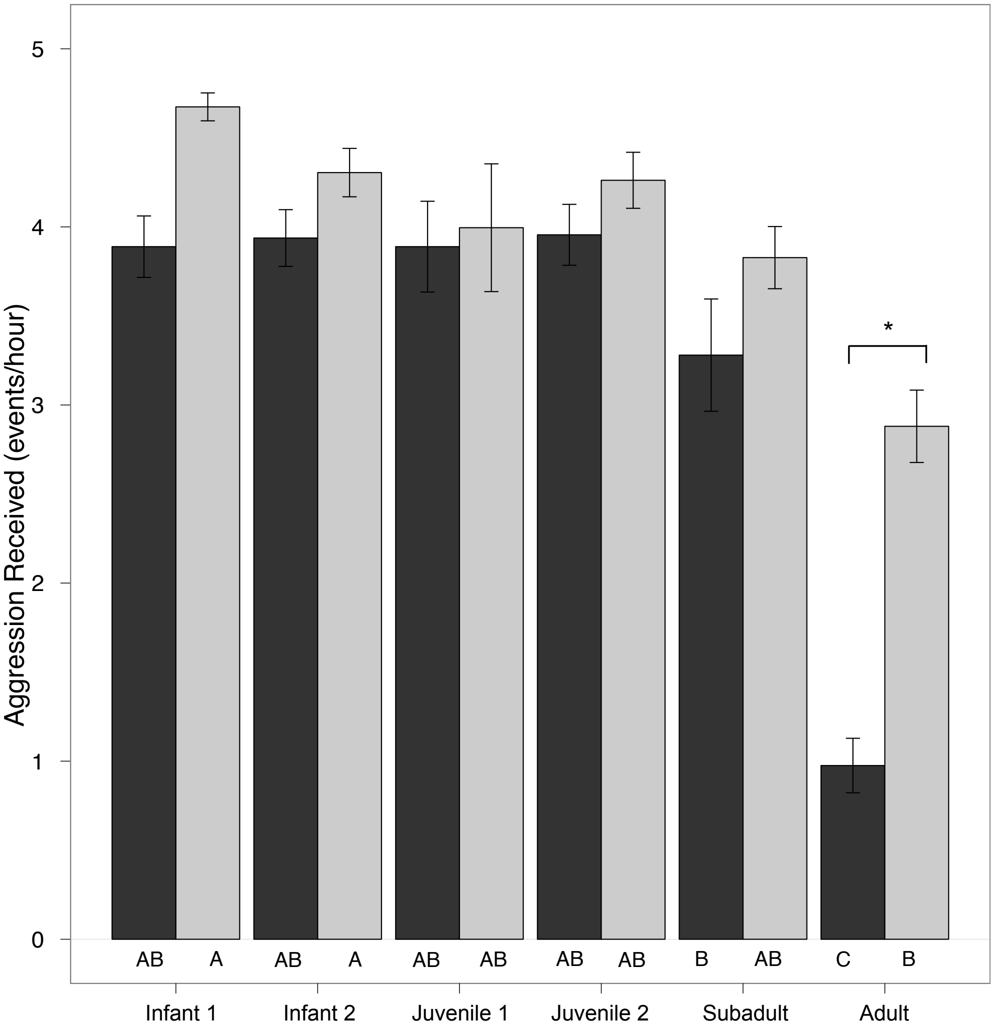

Table 4-1. Behavioral and growth predictions of the ERAH and ring-tailed lemur outcomes. Bold type indicates congruence between ERAH predictions and the behavior and growth of juvenile ring-tailed lemurs.

Predication Class	**ERAH Prediction**	**Ring-tailed lemur**
Spacing	Juveniles forage close to nearest neighbor	Juveniles do not forage closer to nearest neighbors than adults
	Juveniles forage in low-risk areas	Juveniles forage in high risk areas similar to adults
Feeding Efficiency	Juveniles are inexperienced and less efficient feeders	Juvenile feed:forage ratios are equal to adults
	Juveniles have low feed:forage ratios	**Juvenile bite count rates are lower than adults for ripe fruits and flowers** and equal for other foods
	Juveniles have low ingestion rates	
Feeding Competition	Juveniles receive higher rates of aggression than adults and experience higher levels of feeding competition	**Juveniles receive higher rates of aggression than adult**
Dietary Diversity	Juveniles are inexperienced foragers and will have less diverse diets than adults.	Juveniles have more diverse diets than adults.
Growth	Frugivorous species grow slower than folivorous species	Frugivorous lemurids grow faster than folivorous indriids[1]
Dental Eruption	Folivorous species erupt permanent teeth earlier than frugivorous species	**Folivorous indriids erupt permanent teeth earlier than frugivorous lemurids**[1]

1) Godfrey et al 2004

Table 4-2. Sample size for the number of individuals, total observation hours per age-sex category, the mean number of focal animal samples (FAS) per day, and the mean number of hours (± SE) each individual was observed per day across the study period. Number of individuals includes animals who have passed from one age category to the next.

Age Category	**Sex**	**Number of Individuals**	**Total Hours**	**Mean FAS/day**	**Mean ± SE hours per day**
Infant 1 (0-12 weeks)	F	14	93.4	5.0	1.015 ± 0.064
	M	12	99	5.4	1.138 ± 0.063
Infant 2 (13-24 weeks)	F	8	102.4	5.6	1.101 ± 0.063
	M	10	112.2	5.8	1.122 ± 0.068
Juvenile 1 (25 -52 weeks)	F	4-6	152.2	7.7	1.522 ± 0.079
	M	1-3	46.2	7.3	1.444 ± 0.135
Juvenile 2 (1 – 2 years)	F	3-6	186.4	6.4	1.294 ± 0.066
	M	1-6	136.8	6.6	1.303 ± 0.073
Subadult (2 – 3 years)	F	3	82.4	5.1	1.043 ± 0.067
	M	6-8	272.4	5.7	1.159 ± 0.045
Adult (3+ years)	F	23-26	693	4.1	0.822 ± 0.016
	M	11-17	337	4.0	0.799 ± 0.022

Table 4-3. Mean percent of feeding observations within each distance categories (±SE). Means are from GLMM of the effects of age-sex class on mean proportions of observations within each distance category to nearest neighbor (Touch: X^2=78.726, df=11, p<0.001; Reach X^2=59.555, df=11, p<0.001; 1 m X^2=65.564, df=11, p<0.001; 1-3 m X^2=44.101, df=11, p<0.001; >3 m X^2=119.09, df=11, p<0.001). Bold values indicate significant difference from adults, and asterisks indicate sex differences within an age category

Age	Sex	Touch	Reach	1 meter	1-3 meters	>3 meters
Infant 1	F	**31.46±0.00**	**19.77±5.28**	**33.86±0.00**	**12.29±9.05**	**2.68±0.03**
	M	**13.76±0.47**	**23.22±6.70**	**42.38±0.07**	**17.56±12.23**	**3.06±0.27**
Infant 2	F	**4.34±0.59**	**10.47±3.96**	**38.28±0.10**	**35.01±14.47**	**11.84±0.78**
	M	**3.01±0.40**	**8.36±2.96**	**39.25±0.08**	**38.38±13.88**	**10.95±0.74**
Juvenile 1	F	1.64±0.46	6.02±3.01	28.85±0.05	41.58±14.42	21.85±0.53
	M	1.98±0.41	3.65±1.82	23.99±0.03	44.31±12.00	25.99±0.59
Juvenile 2	F	2.18±0.52	4.74±2.12	22.89±0.06	44.67±10.24	25.47±0.52
	M	0.39±0.41	3.5±1.42	20.12±0.03	43.62±8.21	32.35±0.32
Subadult	F	0.83±0.09	3.1±1.79	21.64±0.05	38.83±12.50	35.58±0.66
	M	0.74±0.14	2.47±0.93	18.02±0.03	43.52±6.81	35.22±0.36
Adult	F	2.23±0.22	3.69±0.81*	22.68±0.02*	41.93±4.95	29.42±0.25*
	M	0.72±0.08	1.63±0.41*	12.74±0.01*	39.22±3.18	45.67±0.19*

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CHAPTER 5. THE ONTOGENY OF SEX DIFFERENCES IN RING-TAILED LEMUR FEEDING ECOLOGY: COSTS OF REPRODUCTION AND NICHE PARTITIONING

SUMMARY

Sex differences in primate feeding ecology are a common phenomenon, but for most species it is unknown when in development they appear and how they are related to metabolic and ecological strategies of males and females. They may function to minimize feeding competition within a group or may simply be a behavioral response that compensate for fluctuating physiological costs, particularly to females during reproduction. Clutton-Brock (1977) proposed three potential scenarios for the evolution of sex differences in feeding ecology: (1) sexual size dimorphism, (2) costs of reproduction, and (3) ecological competition avoidance or niche partitioning. As a primate-wide pattern, sexual size dimorphism does not reliably predict sex differences in feeding, emphasizing a need for a better understanding of how female reproductive costs and niche partitioning structure ecological sex differences. Based on the ontogeny of sex differences in feeding ecology I show that both reproductive costs and niche partitioning determine sex differences in the feeding ecology of ring-tailed lemurs (*Lemur catta*) at the Beza Mahafaly Special Reserve. Sex differences in dietary overlap among group members are most prevalent in adults during lactation, the most energetically expensive portion of mammalian reproduction when females ingest higher proportions of young leaves and ripe fruit than do males or non-reproductive females. From juvenility through adulthood, females have more diverse diets than males and feed from a greater number of plant species. Consistent sex differences in feeding do not develop until adulthood and are primarily related to female reproductive costs. The early emergence of sex differences in dietary diversity in juvenility that are maintained throughout adulthood indicate that niche partitioning is an important and overlooked aspect of sex differential feeding ecology, and that ontogenetic studies of feeding are particularly valuable to understanding how selection shapes adult, species-typical diets.

INTRODUCTION

Sex differences in adult feeding ecology are common across mammalian taxa and may range from complete ecological and spatial separation of males and females to more subtle differences in the composition and emphasis in foods (Clutton-Brock, 1977; Beck et al., 2005; Ruckstuhl, 2007; Dunbar and Shi, 2008). Within the primate order, sex differences in feeding ecology are common for species that live in mixed sex social groups. They comprise differences between males and females in dietary composition (Gautier-Hion, 1980; Boinski, 1988; Sugardjito, 1992; Rose, 1994; Sauther, 1994; Michels, 1998; Bean, 1999; Hemingway, 1999; van Schaik et al., 1999; Nakagawa, 2000; Field and McGraw, 2001; Vasey, 2002; Baker and Wardle, 2003), substrate use (Fleagle and Mittermeier, 1980; Gautier-Hion, 1980; Ménard and Vallet, 1986; McGraw, 1998), and in the skills associated with the acquisition and processing of food (van Schaik and Pradhan, 2003; Agostini and Visalberghi, 2005; de A. Moura and Lee, 2010).

Three hypotheses have been proposed for the origin and maintenance of adult sex differences in primate feeding: (1) sexual size dimorphism, (2) costs of reproduction, and (3) ecological competition avoidance or niche partitioning (Clutton-Brock, 1977; Rose, 1994). Sexual size dimorphism likely has a minimal effect on ecological separation between males and females (Kamilar and Pokempner, 2008), but previous studies were unable to separate sex differences related to each of these factors. Most commonly, confounds of sexual size dimorphism or a study period that excluded some phases of reproduction precluded tests of how each of these three factors influence the both the timing and degree of ecological separation between males and females (Gautier-Hion, 1980; Harrison, 1983; Boinski, 1988; Rose, 1994). Understanding when sex differences occur in development can reveal their underlying causation. Niche partitioning is most likely responsible for sex differences early in life, whereas fluctuations in sex differential feeding ecology in adults are most likely linked to female reproductive costs. Here I use a mixed longitudinal sample of infant through adult ring-tailed lemurs (*Lemur catta*) to test how costs of reproduction and niche partitioning shape the development of sex differences in feeding ecology.

Sex and sexual size dimorphism can have profound effects on differences in metabolism and substrate use of males and females, thus directly impacting sex differences in feeding (Kleiber, 1965; Fleagle and Mittermeier, 1980; Gautier-Hion, 1980; Jarman, 1983; Ménard and Vallet, 1986; McGraw, 1998). In most sexually size dimorphic species males are larger than females. Despite the physiological and substrate use differences in dimorphic species, recent work in primates has shown that sexual size dimorphism alone is not a substantial predictor for ecological differences between the sexes (Kamilar and Pokempner, 2008), emphasizing a need for a better understanding of how female reproductive costs and niche partitioning structure ecological sex differences. A developmental approach can identify how differential male and female growth trajectories are correlated with subsequent changes in feeding ecology in a way that past studies of adults only have been unable to do.

Increased metabolic costs associated with reproduction may be the most significant factor affecting sex differences in feeding. If these costs drive sex differences, then the developmental timing of sex divergent metabolism should show that sex differences in feeding would not develop until adulthood or until body size or reproductive output changes between males and females. While males of many species have higher basal metabolic rates and dietary requirements than females due to differences in relative muscle mass and composition (Garn et al., 1953; Arciero et al., 1993; Raichlen et al., 2010), pregnant and lactating females undergo a dramatic increase in metabolic requirements and need a higher nutrient intake (especially protein and energy) than males to compensate (Trivers, 1972; Tilden and Oftedal, 1997). Reproductive costs to females are greatest during lactation when mothers are the primary source of both nutrition and transport for their offspring (Altmann and Samuels, 1992; Dufour and Sauther, 2002). To accommodate this elevation in metabolism, females may increase intake of rare and crucial nutrients and decrease intake of superabundant items throughout their reproductive cycle (Simpson et al., 2004). Alternatively, females may instead choose to conserve energy as much as possible to compensate for their reproductive costs and minimize their active time feeding (Sauther, 1994).

While sex differences in feeding due to costs of reproduction are seasonal and correlated with gestation and lactation, sex difference due to niche partitioning should be present throughout the year and develop early in ontogeny. Sex differences via niche partitioning are predicted to be present in species that fulfill three major feeding scenarios (Clutton-Brock, 1977). First, in species that are territorial and feed from a centralized site such as a nest, sleeping hole, or sleeping tree, niche partitioning would lower travel costs. Second, niche partitioning would be expected in specialists rather than generalists, especially in species where feeding rate is limited by search time rather than handling time. Finally, sex differences in feeding ecology are expected through niche partitioning in species where the adult sex ratio of the social group is approximately even. To maintain cohesiveness, these multi-male, multi-female groups may need to minimize feeding competition by partitioning the species' feeding niche.

To discern between sex differences that are due to reproductive costs or differences that arise as part of a niche partitioning strategy, I use a mixed longitudinal sample collected from infant through adult ring-tailed lemurs to identify when and how sex differences in feeding ecology develop. The ring-tailed lemur is a monomorphic primate that lives in large, multi-male multi-female social groups. It is ideal to discriminate between the roles of costs of reproduction and niche partitioning in sex differences in feeding because potential confounds due to sexual size dimorphism are absent (Kappeler, 1996; Godfrey and Jungers, 2002). Additionally, ring-tailed lemurs live in a seasonal environment and their reproductive cycles are highly synchronized, enabling me to dissect differences in feeding ecologies due to cost of reproduction from those due to niche partitioning. Seasonal variation in food availability and potentially high costs of reproduction present a situation where reducing overlap and competition between males and females throughout the year would be advantageous to females competing for limited resources.

Ring-tailed lemur females are dominant to all males, thus males must adjust their feeding strategies to accommodate their low social position and the relative ease with which an adult female ejects them from a feeding site. Because each female is only in estrous for a 6-24 hour period once per year (Sauther, 1991), each reproductive opportunity is particularly valuable to male ring-tailed lemurs. Female dominance and female feeding priority in ring-tailed lemurs may function to maximize the ecological differences between males and females throughout the year. Alternatively, because of the highly limited resources there may not be sufficient ecological space to partition, and sex differences will be concentrated during lactation – the time of peak metabolic differences between males and females.

High reproductive costs have been used to explain sex differences in the dietary composition and amount of time spent feeding and resting by ring-tailed lemurs (Rasamimanana and Rafidinarivo, 1993; Sauther, 1994). Across all seasons of female reproduction (mating through weaning of offspring), males principally focus on ripe fruit resources while females' diets fluctuating according to reproductive stage. Gestating females eat more fruits and flowers than do males, and lactating females differ from both males and non-reproductive females primarily in their emphasis on young leaves and proportional increase of time spent resting. Interestingly, adult females that are not pregnant or lactating show similar dietary compositions to adult males (Sauther, 1994). It is unclear if these differences reflect an age-graded development of adult feeding, as young females entering their first or second breeding season are less likely to become pregnant, or if this pattern in non-reproductive females truly illustrates feeding differences relative to reproductive state.

Niche partitioning may be an important, but yet undescribed feeding strategy for the ring-tailed lemur. Consistent with Clutton-Brock's (1977) predictions for niche partitioning, they live in large multi-male, multi-female groups that have a relatively even sex ratio. They show varying levels of territoriality and forage out from stable sleeping sites (Mertl-Millhollen, 2000; Mertl-Millhollen et al., 2003). If niche partitioning drives sex differences then males and females should differ early in development, most likely at the time of weaning as adult feeding ecologies are acquired and function to minimize intragroup feeding competition. Differential feeding ecologies will then be maintained throughout development to adulthood and across the year, with fluctuations in the intensity of these differences based on availability of resources and interactions with female reproductive state.

Using a mixed-longitudinal sample of ring-tailed lemurs, I document the ontogeny of adult feeding ecology from birth through sexual maturation and reproduction. I demonstrate that adult feeding ecologies are acquired early in juvenility, and show that the ecology of adult males and females varies throughout development and across a year, and that sex differences in feeding are consequence of both costs of reproduction and niche partitioning. Sex differences in this species are strongest during lactation, but early in development males and female maintain differentially diverse diets. Because of the high seasonality in food availability, niche partitioning may maintain maximum dietary space, preparing females for costly reproductive events and minimizing feeding competition.

METHODS

Study Site

Data were collected from May 2009 to March 2010 at the Beza Mahafaly Special Reserve (Beza) in southwest Madagascar (23.65647°S, 44.62897°E) where the biology, behavior, and ecology of adult ring-tailed lemurs have been studied since 1987 (Sauther, 1998; Yamashita, 2002; Gould et al., 2003; Sussman and Ratsirarson, 2006; Sauther and Cuozzo, 2009). The primary study area, Parcel 1, grades from dry deciduous and Dideraceae dominated desert spiny forest in the west to a gallery forest dominated by

Tamarindus indica (Sussman and Rakotozafy, 1994). This west to east moisture gradient (dry to wet) is coincident with an increasingly tall and more enclosed canopy, increasing average tree stem diameter, and decreasing diversity in tree species per hectare (Sussman and Rakotozafy, 1994).

Beza's climate is highly seasonal, with a cold dry (May-September) and a hot wet (October – April) season where 80% of the annual average of 615 mm of rain falls each year (Lawler et al., 2009). This study period was hot and dry with average high temperatures of 35.7°C (dry season) and 45.8°C (wet season) and experienced half the amount of rain that typically falls during equivalent times in other years (this study: 265mm, Beza average for June-March: 500mm; (Chapter 1; (Ratsirarson, 2003; Sussman and Ratsirarson, 2006).

Phenology transects were used to monitor the potential availability of plant resources. Twenty-two 2m x 30m phenology transects were distributed throughout the ranges of the study groups. In these transects woody plants with a diameter at breast height (DBH) greater than 2cm were individually tagged and identified to species totaling 402 individuals from 44 species. The DBH, total height, canopy height and canopy width were recorded for each individual. Every two weeks the proportional phenophase for young leaves and leaf buds, mature leaves, unripe fruit, ripe fruit, flower buds and flowers was ranked for each tagged plant on a 0-4 scale based on the presence of the phase relative to the estimated overall availability of sites within the crown. A score of zero indicated phase absence, 1=25%, 2=50%, 3=75%, 4=100% present. A one square meter plot located in the center of each transect was used to monitor ground cover with the same phase scale (0-4) indicating the presences of mature and young leaves in the herbaceous layer.

Study population

Ring-tailed lemurs are eclectic frugivore-folivores that spend half of their feeding and foraging time on the ground (Sussman, 1977) and 95% of total observed feeding time is spent on substrate lower than 10 meters (O'Mara, unpublished data). Ring-tailed lemur foods do not require extensive processing, although some fruits such as *Tamarindus indica* may require a minimum of strength or post-canine occlusal surface area to open (Cuozzo and Sauther, 2004; Millette et al., 2009). The capture of insects, which comprise a minority of ring-tailed lemur diet, require skill that is not attained until adulthood, but infants and young juveniles are often allowed to feed from large insects captured by their mothers (e.g., *Yanga heathii, Lampropepla rothschildi,* Chapter 2).

Ring-tailed lemurs maintain a non-transitive dominance hierarchy with low linearity (Martin and Bateson, 1993) where, contrary to the typical mammalian pattern, females dominate males in all contexts (Pereira and Kappeler, 1997). Reproduction is photoperiod controlled, highly seasonal and synchronized to resource availability (Sauther, 1991; Jolly et al., 2002). Wild ring-tailed lemurs typically gestate a single offspring for an average of 138.7 days (Koyama et al., 2001). Two females in this study were observed to mate and give birth, and they gestated offspring for 142 and 143 days. I divided the study into reproductive seasons that were based on the median reproductive timing of the animals observed in this study. Seasons are identified as Gestation (May – September), Lactation (September – December), Weaning (December – February), and Recovery (March – April) (Fig.1). While reproduction within a group is timed to a single one to two week period, females who do not become pregnant often cycle again, which means that there are some females who reproduce out of synchrony with the rest of the group. These females (e.g., gestating females in Lactation) experience different food availability than the majority of females during each reproductive phase, and are therefore presented separately within each season. First year offspring mortality averages 50% (Gould et al., 2003) but was as high as 71% in the 2008 birth cohort that comprises the Juveniles in this study (Meredith & O'Mara unpublished data).

With the help of several field assistants, over 2,300 observation hours were completed on a total of 78 individuals from seven study groups (Table 5-1) with ranges that overlap to some degree (Chapter 1). Age classes are defined as Infant 1 (0-12 weeks), Infant 2 (13-24 weeks), Juvenile 1 (25 weeks – 1 year), Juvenile 2 (1-2 years), Subadult (2-3 years), and Adult (3 years and older). Birth dates are known for the individuals born into each of the study groups since 2006, but birth dates, exact ages, and matrilineal relationships are not known for females older than 4 years old and adult males who transfer between groups. Interobserver reliability was periodically assessed to maintain a minimum of 85% agreement using Cohen's Kappa statistic included in the JWatcher package (Coelho and Bramblett, 1981). All methods were approved by the IACUC at Arizona State University (08-983R) and by Madagascar National Parks (135/07; 257/09**)** and conformed to the Principles for the Ethical Treatment of Non-Human Primates of the American Society of Primatologists.

Behavioral Sampling

Continuous and instantaneous focal sampling methods were used simultaneously to sample feeding and its social context. Subjects were chosen from among the seven study groups for observation according to a stratified random protocol where an infant or juvenile was the focal every other or every third observation. All feeding and foraging behaviors were continuously recorded in JWatcher (www.jwatcher.ucla.edu) during 12-minute focal animal sampling sessions (Altmann, 1974). To be included in analysis of the continuous and instantaneously recorded variables, individuals must have contributed a minimum of three observation sessions in a given day, with each individual typically observed between 4-8 times per day when their group was observed (Table 5-1). Feeding was defined as the ingestion of food and foraging was defined as the active searching for and processing of food items and includes sniff, lick, and crack (Appendix B). Plant parts were divided into unripe fruit, ripe fruit, young leaves, mature leaves, and flowers and flower buds. Ring-tailed lemurs also include insects, soil, and wood into their diet. These items were recorded individually, with insects identified to species when possible and minimally to taxonomic order. Plant species were identified with help of local experts (Mr. Elahavelo and Mr. Herman Mananjo), by Mr. Rokiman Lestara (Tsimbazaza

Botanical Gardens, Antananarivo), and through digital voucher images from the Missouri Botanical Gardens TROPICOS database (www.tropicos.org). Bite counts were conducted each individual throughout the twelve-minute FAS sessions to measure intake rates. We attempted to measure bite count rates at least twice per individual per day (Chapter 2). These intake rates are then used as a measure of ingestion rate and feeding efficiency (Johnson and Bock, 2004). Most fruits and young leaves, which constitute the bulk of ring-tailed lemur diet, are ingested in a single bite by all age categories (Sauther, 1992). Bite count rates were calculated for each individual on each food type. I observed no sex differences in ingestion rates (measured through bite counts). This, along with the lack of dimorphism in ring-tailed lemurs, indicates that comparisons of time spent feeding are adequate to test for sex differences in feeding.

General activity of the focal (feed, forage, rest, move, stand, groom, other) was instantaneously recorded at three-minute intervals during all focal sessions. To evaluate an energy conservation strategy executed by females, time spent in rest and social grooming were grouped together as energy conservation behavior (ECB). The focal individual's height to the nearest meter and position within the tree crown based on a 3x3 grid (ground; lower, middle, upper; interior, middle, exterior) were also recorded at these instantaneous time points.

To estimate changes in the availability of plant food resources, a food availability index (FAI) was calculated for each food part for each tagged tree in the phenology transect. The FAI is the natural log of each phenophase score (0-4) multiplied by the tree's crown volume. This gives a measure of availability for each food part based on the size of the tree crown and the presence of each part within it.

Dietary diversity was calculated for each individual focal animal in two-week blocks that correspond to the phenology surveys. Dietary diversity was calculated using the Inverse Simpson's Diversity index, D, where $D=\mathbf{1}/(\Sigma p_i^2)$ and p_i^2 is the squared proportion of total time feeding in these two-week blocks on each item (Begon et al., 1996; Irwin, 2008). D originates from a value of 1 (diet of 1 item), with higher values reflecting a more diverse diet.

Analysis

With the exception of biweekly indices, data were summarized per individual per day, generating a mixed-longitudinal data set of individual-days. This approach preserves any daily variation in the development of feeding present at the individual level. Generalized linear mixed models (GLMMs) were then fit to the mixed longitudinal data. Traditional repeated measure designs are encumbered by balanced sample requirements that can rarely be met using observational data from wild animals. Generalized linear mixed models have the advantage of being able to process unbalanced, multi-way repeated measures designs through the inclusion of random effects in the model (Bolker et al., 2009). GLMMs were fit to the data in the *lme4* package in R 2.13 (R Core Development Team, 2011). In all models, individual animal identity and a time factor (reproductive season) were included as random effects. Much of the data presented are summarized as proportions of a total (e.g., proportion of time feeding). Logistic mixed models with a binomial distribution and logit link identity were fit to proportional data directly (Jaeger, 2008; Warton and Hui, 2011). The significance of the fixed factors (e.g., age-sex category) was evaluated by comparing two nested models differing in a single factor (Huchard et al., In Press; Pinheiro and Bates, 2009). A likelihood ratio test of these two nested models (X^2) was then used to evaluate the significance of individual factors (Lewis et al., 2011). When factors did not significantly contribute to the fit of the model they were removed from the analysis. Subsequent Tukey's post-hoc tests identified differences among factor level pairwise comparisons, typically age-sex levels. When no random effects were present (e.g., number of plants eaten by an age class), a general linear model (F) was fit to the data. Significance for all tests was evaluated at α=0.05.

RESULTS

Seasonality in Food availability. Food availability varies greatly throughout the year, with peak FAI coinciding with an overall increase in precipitation (Fig. 1). The availability of resources drives subsequent seasonal differences in lemur diet. The increase in the FAI is a consequence of young leaf flush that begins in September with the transition to the wet season. Ripe fruit is at its peak availability at the end of the wet season and continues through the beginning of the dry season (March – September).

Sex differences in activity levels. There are no sex effects on intake rate (bites/min) across all food types (X^2 = 1.151, df=1, p=0.283). Sex differences that are present in ring-tailed lemur feeding are then a result of differences in the time spent feeding and not due to differences in intake rates. There is a significant effect of season on the proportion of time spent feeding by all age-sex classes (Fig. 2; X^2= 9.4091. df=3, p=0.024). As the year progressed, all ring-tailed lemurs increase the proportion of time spent feeding, with peak feeding in the Recovery season when juveniles have been weaned, adults are preparing for the mating season, and food is past its peak in availability (Fig 5-2).

There is no change in feeding efficiency (i.e., the ratio of time spent feeding to time spent foraging) across seasons (X^2=2.462, df=3, p=0.481). There are sex differences in the amount of time spent feeding to time foraging that are influenced by age and the reproductive status of females (X^2=28.508, df=13, p=0.008). In general, males are more efficient than females (i.e., they show higher ratios and thus spend more time feeding relative to foraging), but this does not develop until subadulthood (Fig 5-3). Adult males are more efficient, but are there are no differences in between males and females who are gestating and lactating.

To evaluate the use of an energy conservation strategy by females, rest and grooming were grouped together as energy conservation behavior (ECB), and there are no sex differences among adults in the proportion of total time spent in ECB (X^2 = 16.742, df=13, p=0.211; lactating females: 59.4%, gestating females: 62.7%, non-reproducing females: 61.7%, males: 61.9%). However, when ECB is separated into its rest and grooming components, lactating females rest for a significantly lower proportion of time compared to other adults, particularly during Weaning and Recovery seasons (Fig 5-4), and all females rest less than males during the Lactation season. This reflects a trade-off between inactive rest and grooming. During the Lactation season, females devote more time to grooming and socialization that is centered on new offspring, and adult males are typically excluded from these interactions. During Gestation and Lactation seasons all reproductive classes for females spend the same proportion of time in rest as males (Gestation season: X^2 =3.890, df=3, p= 0.262; Lactation season: X^2 = 5.721, df=3, 0.126).

Sex differences in diet composition and crown use. Ring-tailed lemurs fed from 137 plant species comprising 55 families, and on six arthropod species from four orders (Appendix D). There are significant sex differences in plant part dietary composition only in adults during the Lactation season (LRT X^2= 59.442, df= 9, p<0.001, Fig. 5). This is confirmed through GLMMs that show significant age-sex differences in the percentage of time feeding on ripe fruit, mature leaves, young leaves, and flowers (Tables 2 & 3). Similar to Sauther (1994), lactating females, non-reproductive females, and adult males are more similar to each other during the Lactation season than they are to gestating females (Table 3). Lactating females ingest a higher proportion of young leaves and ripe fruit during the Lactation season than males and other females, and females who are gestating during this time eat a higher proportion of mature leaves and flowers than males and other females (Fig. 5, see Appendix C for full seasonal diet composition values). The only sex differences in non-adults are in flower composition of Juvenile 1. The single male Juvenile 1 consumed considerably more flowers than Juvenile 1 females (91.66% vs 38.62% of observations), and both sexes of Juvenile 1 consume more flowers than all other ages. In general, the adult pattern of plant part dietary composition is reached by juvenility. During the Lactation season when adult sex differences are present (Table 5-2), non-adults show the same dietary composition as do adult males and non-reproductive adult females, indicating that increased reproductive costs do drive both age and sex differences during the Lactation season.

Dietary diversity is a function of the number of species eaten and the number of parts from those species. Except for Infant 1, young animals have more diverse diets than adults, and sex differences in dietary diversity begin to appear in the late Juvenile period (Juvenile 2, Fig 5-6). Some adult females have more diverse diets than males across all seasons (Fig 5-6, X^2=60.749, df=13, p<0.001), but the differences vary by season and among female reproductive stages. During the Gestation season, females in early lactation have more diverse diets than all other adults (lactating female: 2.72 ± 0.01, gestating female: 2.51 ±0.01, non-reproductive female: 2.47 ± 0.14, male: 2.42 ± 0.08), with no significant differences among gestating females, non-reproductive females, and males.

The adult sex differences in diversity scores are mainly due to a greater number of species eaten by females than males. There are significant differences among seasons in mean number of plant species eaten (X^2=36.689, df=3, p<0.001). The increase in number of plants species eaten parallels the FAI, with the lowest number of species eaten per day during Gestation and maximum during Weaning (Gestation: 3.31 ± 0.12, Lactation: 4.29 ±0.10, Weaning: 4.98 ± 0.22, Recovery: 4.54 ±0.30, Fig. 1 for FAI). Across all seasons, Lactating and non-reproducing females feed from a greater number of plant species than do males or gestating females (F=5.44, df=3,593; p=0.001; lactating females: 3.70 ± 0.15, non-reproductive females: 3.76 ± 0.18, gestating females: 3.02 ± 0.15, males: 3.35 ± 0.13). During Lactation, Weaning, and Recovery seasons there are no differences among the dietary diversity scores of female reproductive stages (Fig. 6). Sex differences in the number of plant species eaten do not appear until subadulthood when females transition into sex-typical dominance (F= 2.800, df= 1,144; p=0.028; subadult females: 5.57 ± 0.49, subadult males: 4.60 ± 0.26).

There few spatial differences in the way that adult males and females feed and forage, but gestating females do use the upper sections of tree crowns more than other females and males (X^2=18.931, df=9, p=0.026; Gestating females: 24.5% of total time, non-reproductive females: 10.4%, lactating females: 14.4%, males: 15.4%). Gestating females increase feeding on flowers and ripe fruit, two resources that are most readily found in the upper levels within a tree crown. Below the upper crown level, males and all reproductive stages of females feeding and foraging for equal proportions of time on the ground (X^2=8.723, df=9, p=0.463), the lower level of tree crown (X^2=8.766, df=9, p=0.459) and mid crown (X^2=6.905, df=9, p=0.647). There are no sex differences in the proportion of time spent in the interior and periphery of tree crowns (interior: X^2=3.147, df=9, p=0.958; periphery: X^2=2.7932, df= 9, p=0.9719). There are no sex differences in non-adults, but young infants forage closer to the center of a tree crown than do older age categories (X^2=19.355, df=5, p=0.002), but show the same crown use as juveniles, subadults, and adults by Infant 2 (X^2=1.1548, df=4, p=0.886).

DISCUSSION

Sex differences in primate feeding ecology are commonly attributed to a consequence of sexual dimorphism, increased costs to females during reproduction, or to a niche partitioning strategy (Clutton-Brock, 1977). This ontogenetic study of the development of sex differences in ring-tailed lemur feeding suggests that a combination of both increased physiological costs of reproduction and niche partitioning are responsible for the sex differences in the feeding ecology of this monomorphic primate. Consistent with a reproductive costs hypothesis, major sex differences in dietary composition (i.e., plant part emphasis) are only present in adults when females lactate, but females do not engage in an energy conservation strategy more than males. However, consistent with niche partitioning, sex differences in dietary diversity develop in juvenility and continue throughout adulthood. Niche partitioning in this species may only contribute a minor role to sex differences in feeding due to the generalist and flexible diet that is typical of ring-tailed lemurs (Clutton-Brock, 1977). Niche partitioning early in development that is then reinforced during elevated reproductive costs to females are responsible for sex differences in ring-tailed lemur feeding.

Previous work suggests that gestating and lactating lemurs follow an energy conservation strategy to compensate for reproductive costs, since they rested more than males or non-reproductively active females (Rasamimanana and Rafidinarivo, 1993; Sauther, 1994). Sex differences that point to an energy conservation strategy are not apparent during this study. This could be related to the higher daily maximum temperatures and low rainfall that occurred during this study compared to averages for this site. It is possible that lactating females engage in conserving energy, but they are not doing this more than males or non-reproductively active females who rest more than lactating females. However, there is a general increase in the proportion of overall time that all age-sex categories devote to feeding and foraging across the study period (Fig 5-2). The increase in time feeding across these seasons may be related to a lower overall food availability during this study, when compared to other years. Future comparisons of ring-tailed lemur feeding across multiple years may be able to identify how fluctuations in weather patterns affect food availability and its subsequent impact on ring-tailed lemur feeding and resting behaviors.

This study confirms the previous pattern of sex differences in adult ring-tailed lemur feeding (Sauther, 1994). Sex differences are not a result of spending more or less time eating, but of a shift in emphasis on plant parts and food species eaten. Gould and colleagues (2011) failed to find any sex differences in their study of ring-tailed lemurs during early gestation and early lactation. The small social groups in their study live in a spiny forest habitat with low population density that had recently experienced a severe drought. The absence of sex differences in feeding in desert spiny forests may reflect the dietary flexibility of the ring-tailed lemur and that when food resources are particularly restricted or unstable, sex differences in feeding may be minimal (Gould et al., 2011). These smaller groups living in low population density may not be under the same pressures to partition the feeding niche that affect lemurs living in larger groups or in areas with higher population density.

Sex differences in the dietary composition of individual plant parts are only present during the Lactation season. While the number of observation hours are not equal across seasons (Table 5-1), the pattern of results and strength of the likelihood ratio tests do not indicate that the failure to find sex differences in these other season are related to sampling issues (Table 5-2), rather this reflects the behavior of these animals. The presence of sex differences in dietary composition during the Lactation season is likely a consequence of increased costs to females during reproduction that are coincident with a season of low food availability. At Beza Mahafaly, ring-tailed lemur females gestate during the period of lowest food availability, lactate during increasing food abundance, and time weaning to maximum food availability (Fig 5-1; (Sauther, 1991,1998). The early portion of the Lactation season has the lowest FAI (Fig 5-1). The rising metabolic costs associated with lactation result in females shifting their dietary emphasis and feeding on more young leaves and ripe fruit than males and non-reproductive females (Fig 5-5; (Ganzhorn, 1989; Yamashita, 2008; Ganzhorn et al., 2009).

Reproduction is closely synchronized within ring-tailed lemur social groups, but some females fall out of synchrony and come into a second estrous if they do not become pregnant during the first mating season (Sauther, 1991). In this study, females who are offset in their reproduction and still gestating during the Lactation season show interesting differences from the more synchronized females within a group, and eat a greater proportion of flowers and mature leaves (Fig 5-5). These females who are delayed in reproduction eat even more flowers than females who gestate during the typical Gestation season (Fig. 5; X^2=7.36, df=1, p=0.007). Even though flowers are in relatively low availability, competition with lactating females may push gestating females to feed from other, perhaps less desirable, resources (mature leaves), or foods that may expose animals to increased predation risk (e.g., flowers on the crown periphery). The fitness consequences of this late reproduction are not yet known, and will be explored in the future.

The development of sex differences in dietary diversity in juvenility are consistent with niche partitioning also playing a role in the overall structure of sex differences in ring-tailed lemur feeding. While dietary composition of plant parts does not differ among males and females outside of the lactation season, throughout development and across reproductive states females have more diverse diets than males. These diverse female diets indicate that partitioning of the feeding niche starts at weaning when young animals move into full competitiveness with group members. Females do not begin to exert dominance until they are subadults when an increase in estradiol activates sex-typical dominance behavior (Meredith & O'Mara, unpublished data), and female priority of access to resources may allow females to exploit a more selective and varied diet, where males are pushed to the periphery of a feeding group and may have to narrow their diets to what is abundantly available (Jolly, 1984; Kappeler, 1990; White et al., 2007). Lactating females feed from a greater number of plant species and have the highest diversity index (plant species + plant part) values for adults.

Lactation is the most energetically expensive aspect of reproduction to female mammals (Blaxter, 1971; Pond, 1977; Dufour and Sauther, 2002), not only because of the energetic costs of lactation, but also due to mothers carrying their growing infants. During this study, subjectively assessed female body condition decreased noticeably throughout lactation, with lactating females' coats progressively thinning and becoming duller accompanied by apparent weight loss (O'Mara personal observation; Pereira, 1993; Jolly, 2008). Dietary separation between adult females and males only during the Lactation season may be insufficient to maintain a high enough body condition to allow the typical annual reproduction by female ring-tailed lemurs (Sauther, 1991; Koyama et al., 2001). Subtle niche partitioning across all seasons may provide females the added ecological space that they need to play body condition 'catch up' (Godfrey et al., 2004) and maintain an income breeding strategy (Richard et al., 2002; Gould et al., 2003; Houston et al., 2007).

Of Clutton-Brock's (1977) three primary hypotheses for the evolution of sex differences in primate feeding ecology (sexual size dimorphism, costs of reproduction, and niche partitioning), costs of reproduction reliably predict the presence of sex differences in feeding in many primates (Fragaszy, 1986; Rose, 1994; Sauther, 1994). Costs of reproduction are the driving force behind sex differences in ring-tailed lemur feeding. However, this study shows that niche partitioning is present outside of major reproductive costs and emphasizes that these are not two mutually exclusive hypotheses accounting for sex difference in diet. While increased costs of reproduction amplify female nutritional needs, niche partitioning likely helps to maintain a sufficiently wide niche space that reduces intersexual feeding competition and facilitates annual income-based reproduction.

Figure 5-1. Food availability index, rainfall and reproductive phases or seasons. Reproduction, particularly weaning, is timed to maximum food availability when there is a large flush of young leaves. Note that mature leaves are excluded from the figure, as they are consistently available throughout the year and comprise a small proportion of ring-tailed lemur diet.

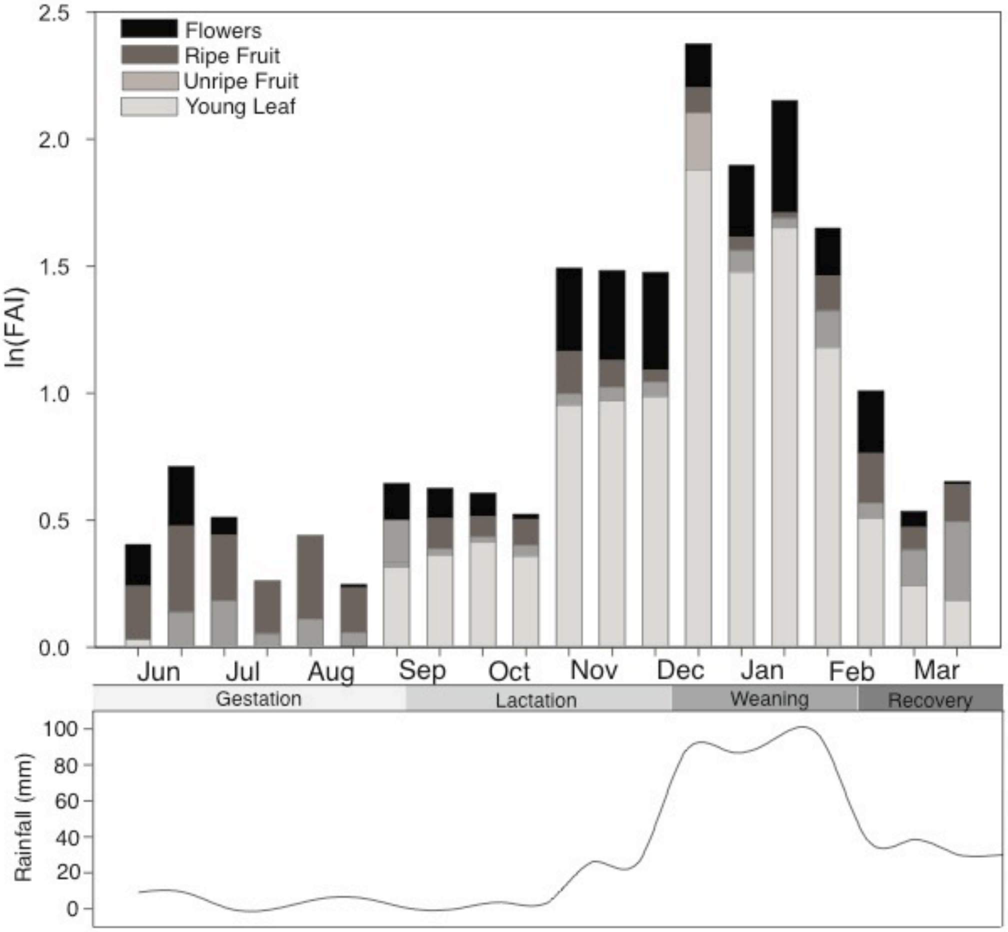

Figure 5-2. Mean proportion of total observation time engaged in feeding behaviors for all age-sex categories across seasons. Females are noted by closed and shaded symbols, males by open symbols. There are no sex differences in the proportion of time spent feeding, but all age classes increase the amount of time feeding across the year.

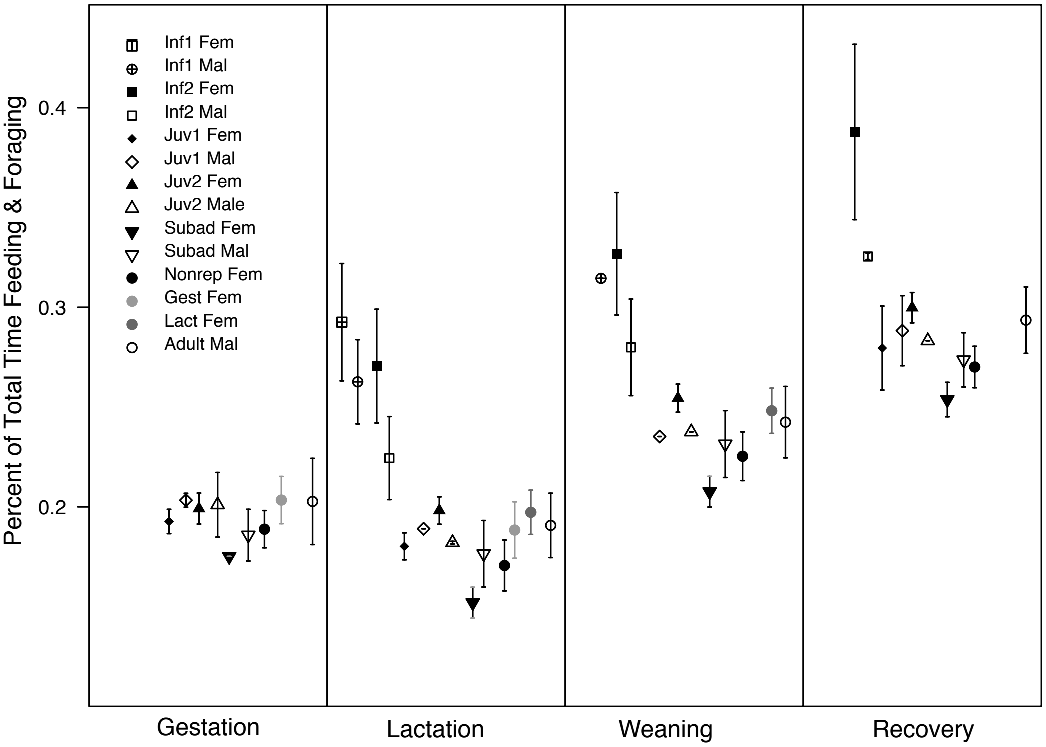

Figure 5-3. Feeding efficiency. Mean ratio of proportion of time feeding divided by proportion of time foraging (±SE). Higher ratios indicate higher efficiency.

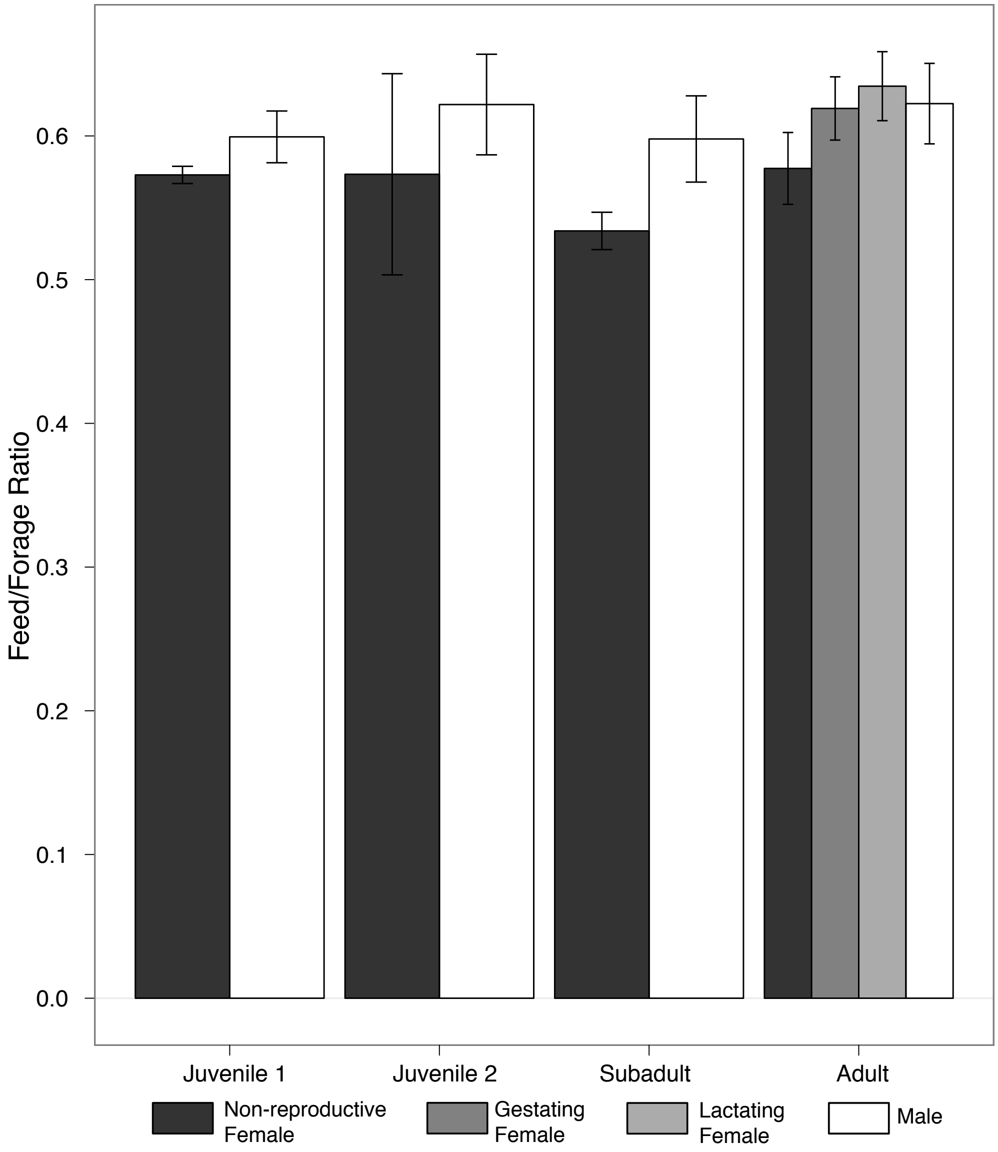

Figure 5-4. Mean (±SE) percent of total time in rest only in each reproductive season. Significant pairwise sex differences within age categories are denoted by an asterisk. Double pronged bars show pairwise differences between sexes and among female reproductive stages. For example, during the Lactation season all females are significantly different from males but in the Weaning season, non-reproductive females do not differ from males, but these two groups differ significantly from lactating females.

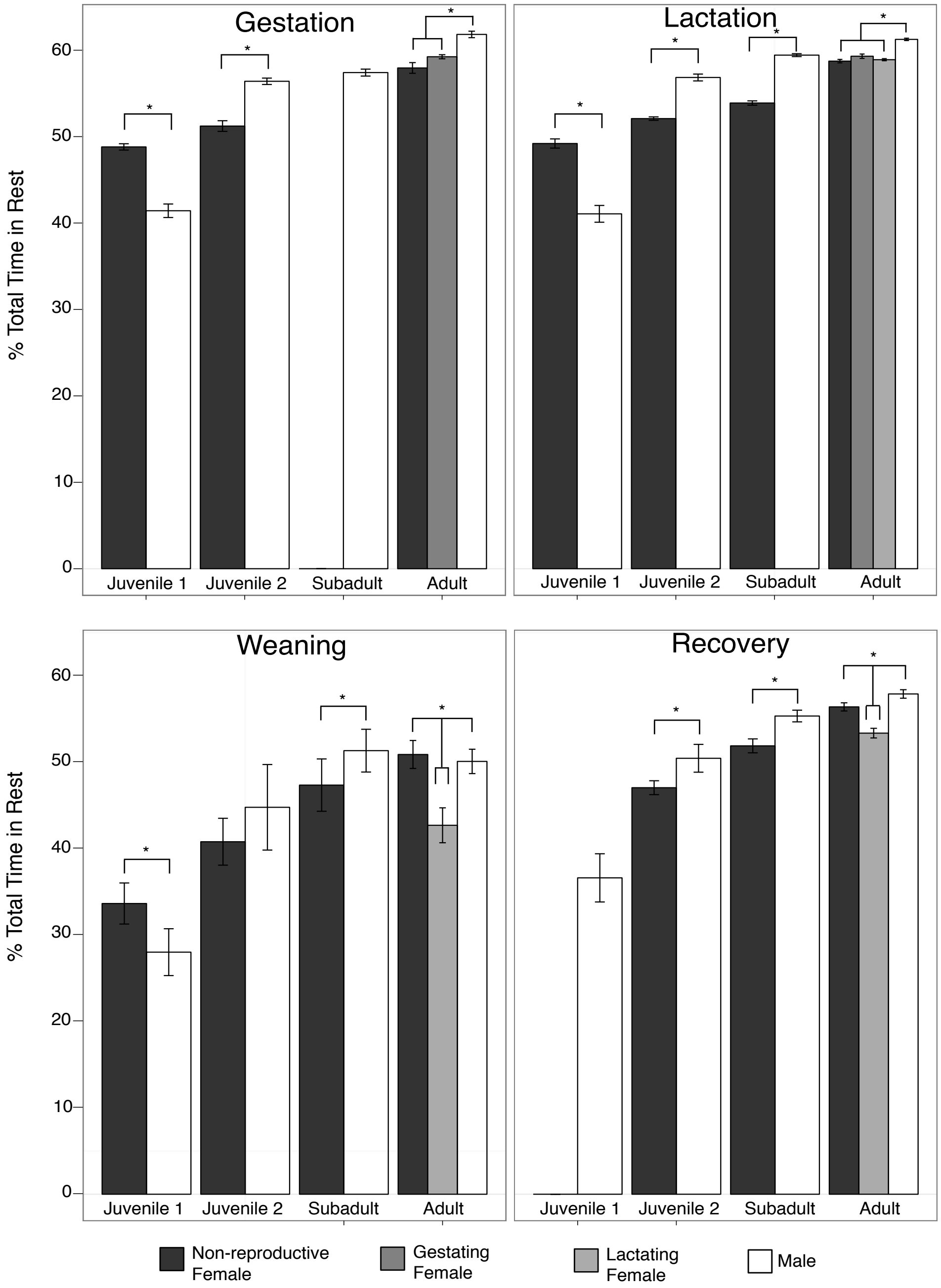

Figure 5-5. Dietary composition of food part for all age-sex categories during the Lactation seasons, excluding nursing time. Significant sex differences among adults are only present during lactation (Table 5-2). Age-sex abbreviations are: I1 – Infant 1, I2 – Infant 2, J1- Juvenile 1, J2 – Juvenile 2, SA – Subadult, AF.G – Gestating female, AF.L- Lactating female, AF – Adult non-reproductive female, AM – Adult male).

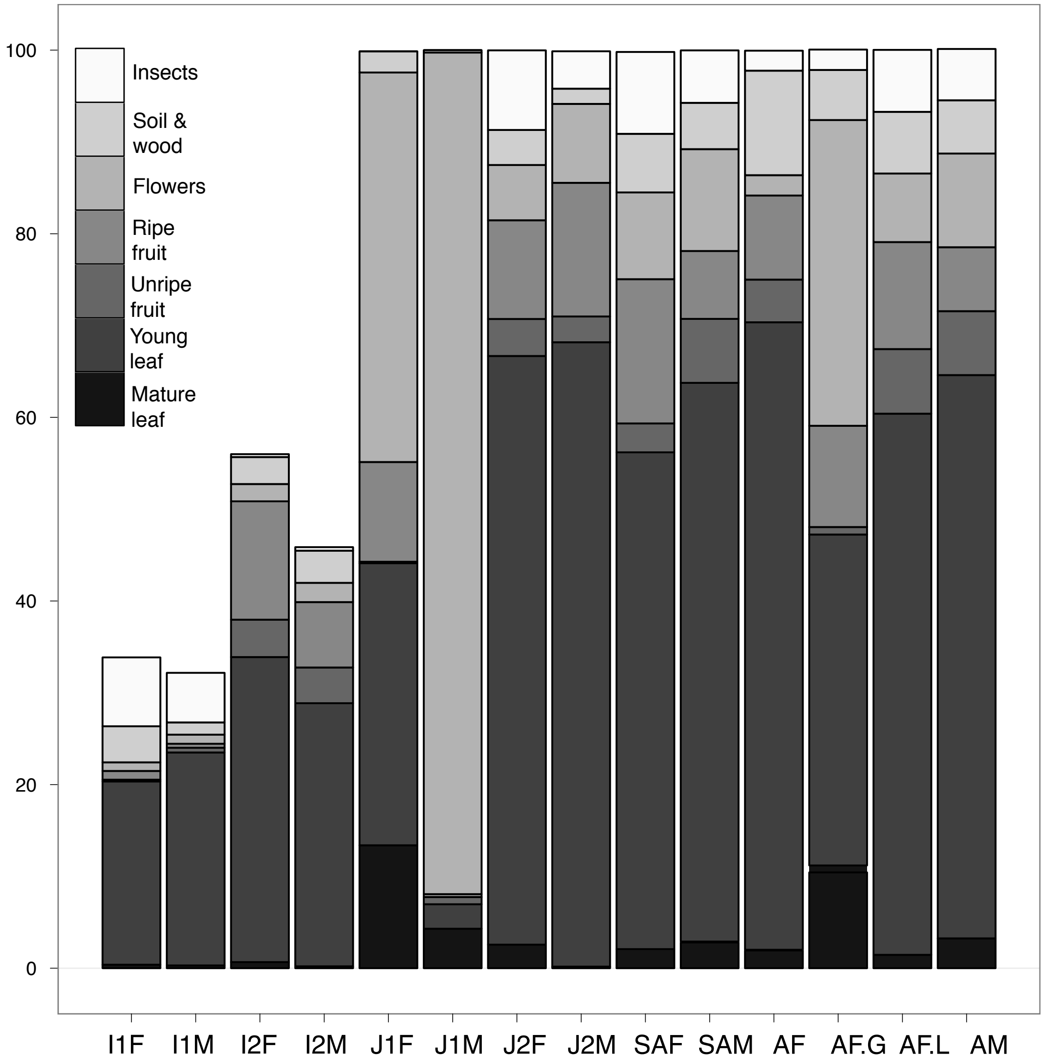

Figure 5-6. Simpson's inverse dietary diversity index for solid foods. Asterisks denote significant differences among sexes or female reproductive categories within an age category.

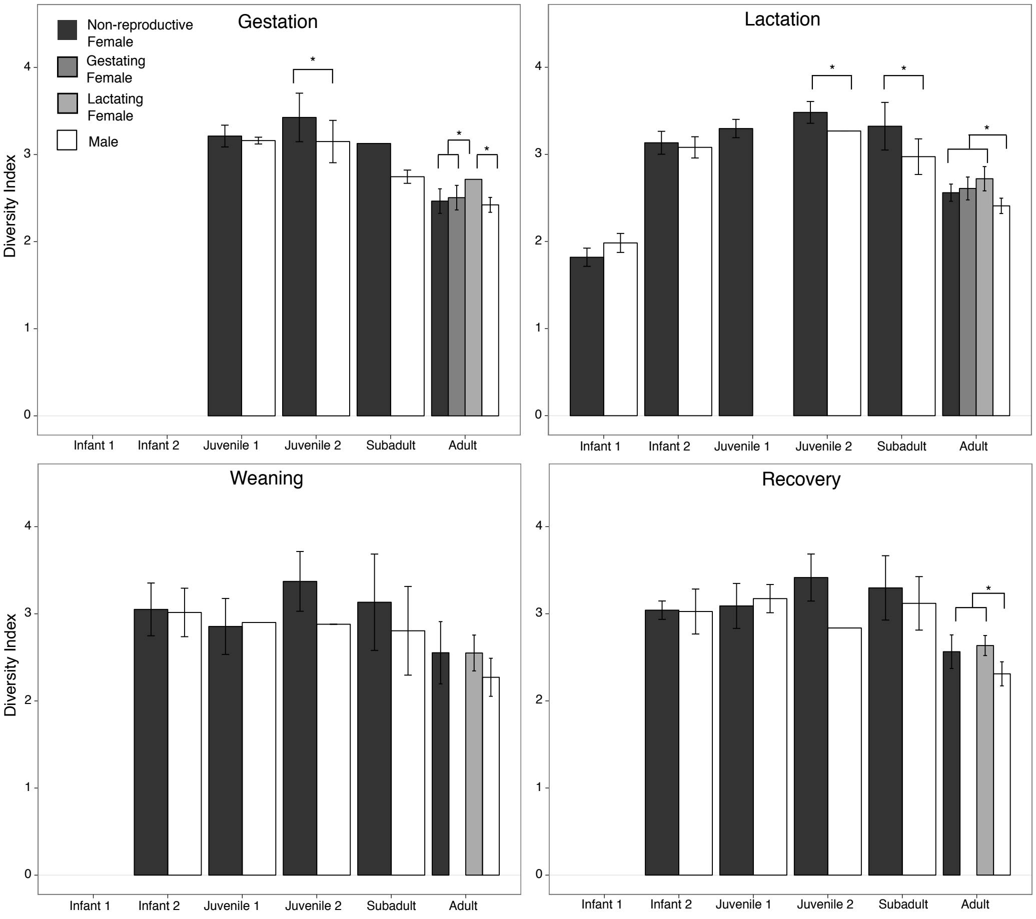

Table 5-1. Sample sizes for age-sex categories across the reproductive seasons including non-reproductive females (F – NR), gestating females (F – Gest), and lactating females (F – Lact). Sample sizes are given as number of individuals (N), total numbers of hours (Hours) and the mean number of hours (± SE) each individual was observed per day across the study period. Number of individuals includes animals who have passed from one age category to the next. Blank cells indicate an age-sex category that was not observed during the particular season.

Age - Sex	**Variable**	**Gestation**	**Lactation**	**Weaning**	**Recovery**
Infant 1 Female	**N / Hours**		**14 / 93.4**		
	Mean ± SE		1.015 ± 0.064		
Infant 1 Male	**N / Hours**		**12 / 93.4**	**1 / 5.6**	
	Mean ± SE		1.112 ± 0.061	1.867 ± 0.657	
Infant 2 Female	**N / Hours**		**8 / 48.8**	**8 / 36**	**4 / 17.6**
	Mean ± SE		0.841 ± 0.066	1.5 ± 0.104	1.6 ± 0.162
Infant 2 Male	**N / Hours**		**10 / 60.4**	**10 / 42**	**2 / 9.8**
	Mean ± SE		0.915 ± 0.072	1.5 ± 0.136	1.633 ± 0.209
Juvenile 1 Female	**N / Hours**	**6 / 112.4**	**4 / 26.4**		**4 / 13.4**
	Mean ± SE	1.405 ± 0.078	2.4 ± 0.318		1.489 ± 0.183
Juvenile 1 Male	**N / Hours**	**3 / 25.8**	**1 / 6.4**		**5 / 14**
	Mean ± SE	1.433 ± 0.194	2.133 ± 0.593		1.273 ± 0.153
Juvenile 2 Female	**N / Hours**	**3 / 32**	**6 / 118.8**	**4 / 17.6**	**4 / 18**
	Mean ± SE	0.821 ± 0.081	1.467 ± 0.094	1.467 ± 0.176	1.5 ± 0.249
Juvenile 2 Male	**N / Hours**	**6 / 84.4**	**2 / 41**	**1 / 5.8**	**1 / 5.6**
	Mean ± SE	1.068 ± 0.07	2.05 ± 0.166	1.933 ± 0.24	1.867 ± 0.067
Subadult Female	**N / Hours**	**1 / 0.4**	**3 / 54.8**	**3 / 18.6**	**3 / 8.6**
	Mean ± SE	0.2 ± 0	0.979 ± 0.076	1.431 ± 0.192	1.075 ± 0.1
Subadult Male	**N / Hours**	**7 / 66.8**	**8 / 165.2**	**6 / 23.6**	**6 / 16.8**
	Mean ± SE	0.768 ± 0.042	1.412 ± 0.07	1.311 ± 0.146	1.292 ± 0.133
Adult F – NR	**N / Hours**	**8 / 26.2**	**11 / 83.2**	**15 / 42.4**	**15 / 34.2**
	Mean ± SE	0.609 ± 0.052	0.785 ± 0.036	1.06 ± 0.064	1.036 ± 0.062
Adult F – Gest	**N / Hours**	**23 / 209.6**	**12 / 58.2**		
	Mean ± SE	0.782 ± 0.031	1.188 ± 0.064		
Adult F – Lact	**N / Hours**		**21 / 194.6**	**10 / 29.4**	**16 / 15.6**
	Mean ± SE		0.76 ± 0.027	0.98 ± 0.076	0.821 ± 0.063
Adult Male	**N / Hours**	**11 / 82.2**	**17 / 178.8**	**16 / 38.6**	**14 / 37.4**
	Mean ± SE	0.709 ± 0.043	0.774 ± 0.028	0.99 ± 0.081	1.039 ± 0.067

Table 5-2. Likelihood ratio tests for logistic GLMMs that test the significance of age-sex categories on the use of individual plant parts in each reproductive season. Bold type indicates a significant overall test for differences among age-sex differences in dietary composition. A † indicates plant parts where significant sex differences are present in adults. Lactating females ingest more young leaves and ripe fruit during the Lactation season than males and other females. Gestating females eat a higher proportion of mature leaves and flowers than males and other females. .

Reproduction Season	Food part	Chi-square	df	p
Gestation	Ripe fruit	5.59	8	0.6931
	Unripe fruit	11.318	8	0.1843
	Mature leaf	7.5292	8	0.4808
	Young leaf	4.0697	8	0.8508
	Flowers	8.4182	8	0.3937
	Soil	9.6067	8	0.2937
	Insect	5.773	8	0.6726
Lactation	**Ripe fruit †**	**40.705**	**13**	**<0.001**
	Unripe fruit	17.451	13	0.1795
	Mature leaf †	**55.122**	**13**	**<0.001**
	Young leaf †	**113.78**	**13**	**<0.001**
	Flower †	**173.97**	**13**	**<0.001**
	Soil	17.073	13	0.196
	Insect	20.066	13	0.0936
Weaning	Ripe fruit	6.6157	10	0.7612
	Unripe fruit	4.3512	10	0.9301
	Mature leaf	4.0089	10	0.9469
	Young leaf	10.585	10	0.3908
	Flower	2.0116	10	0.9963
	Soil	2.9018	10	0.9836
	Insect	13.71	10	0.1866
Recovery	Ripe fruit	3.8779	10	0.9527
	Unripe fruit	5.9591	10	0.8187
	Mature leaf	4.5607	10	0.9185
	Young leaf	10.755	10	0.3769
	Flower	**25.448**	**10**	**0.0046**
	Soil	8.314	10	0.5982
	Insect	11.35	10	0.3309

Table 5-3. Post hoc age-sex comparisons for the significant dietary composition models during the Lactation season from Table 5-2. Letters within a row indicate mean consumption of a plant phase that are not significantly different across all age-sex categories. Sex differences within an age category are in bold

	Inf 1 Fem	Inf 1 Mal	Inf 2 Fem	Inf 2 Mal	Juv 1 Fem	Juv 1 Mal	Juv 1 Fem	Juv 2 Mal	Sub Fem	Sub Mal	NR Adult Fem	Gest Adult Fem	Lact Adult Fem	Adult Mal
Ripe Fruit	a	a	b	ab	ab	ab	ab	ab	b	ab	**ab**	**ab**	**b**	**ab**
Mature Leaves	a	a	a	a	bc	ab	ac	ab	ac	ac	**a**	**b**	**a**	**ac**
Young Leaves	b	ab	ab	ab	bc	bc	c	ac	ac	c	**c**	**ab**	**c**	**c**
Flowers	b	ab	bc	bc	**d**	**e**	bc	bc	bc	c	**bc**	**d**	**bc**	**ac**

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CHAPTER 6. DISCUSSION

Feeding ecology and lemur life history and development

An extended juvenile period sets primates apart from all other mammals. Multiple hypotheses describe the evolution of primate juvenility, with some explaining it as a non-adaptive consequence of constraints imposed by other aspects of primate life history and physiology, including brain mass, metabolic demands, and demography (Cole, 1954; Charnov, 1993; Pagel and Harvey, 1993; Godfrey et al., 2004). Others have moved beyond these physiological and demographic constraint models to explain juvenility as a direct product of selection that enhances learning opportunities and refines social skills (Needing to Learn Hypotheses (NTLH): Joffe, 1997; Ross and Jones, 1999) or as a time of reduced growth that is a tactic to minimize starvation and predation risks (Ecological Risk Aversion Hypothesis (ERAH): Janson and van Schaik, 1993). The work presented here cannot test the physiological constraint-based hypotheses for primate juvenility, but contributes to evaluating the behavior and ecology based explanations for an extended juvenile period.

The NTLH proposes that juveniles are inexperienced foragers and need extended time to learn the necessary ecological and social skills to become an adult, and this energetic pressure has forced a slow maturation process (Case, 1978; Joffe, 1997; Ross and Jones, 1999). The ERAH joins the behavioral aspects of NTL to constraint-based perspectives on growth, development, and energetics of juvenility in an ecological context. It proposes that the extended primate juvenile period, particularly in monkeys and apes, results from a tradeoff between decreasing mortality risk through close social associations with group members and consequent increased feeding competition due to this close association (Janson and van Schaik, 1993). Low feeding proficiency of the young then requires decreased growth rates to minimize starvation risks borne by less competent and experienced feeders. The major difference between these two hypotheses is that in the NTLH there is a significant learning component, particularly to feeding, with a progressive, accumulative increase in proficiency across the juvenile period.

There are only a few studies that have focused on the ecology of wild juvenile lemurs, making generalizations about lemur development difficult. However, this study shows that the behavior and ecology of juvenile ring-tailed lemurs are not consistent with predictions of either the NTLH or the ERAH. Juvenility in ring-tailed lemurs does not appear to be directly related to either the need to learn particular skills or to minimize ecological risk (Chapters 2-4). Ring-tailed lemurs are like most other primates, where juveniles are efficient at locating and processing most food items. However, some large, tough ripe fruits and insects are an exception to this (Chapter 2), similar to foods that require extractive foraging and complex processing used by other primate species (Corp and Byrne, 2002; Gunst et al., 2008,2010). Some fruits require the development of adequate jaw strength to process quickly, and the capture of flying insects may take up to three years to perfect (Chapter 2). Infant and juvenile ring-tailed lemurs do not seek out learning opportunities in the same frequency that catarrhine monkeys do, but use simple local enhancement strategies to time their feeding with group members and likely learn appropriate food types and locations in this way (Chapter 3). Juvenile lemurids including *Lemur, Eulemur,* and *Varecia* are motivated explorers of their environments, have diverse diets, and do not appear to rely heavily on social information in the development of feeding ecology (Chapter 3; (Krakauer, 2006; Tarnaud, 2008). Social learning other than basic local enhancement may not be particularly important in the development of lemur feeding ecology, but soon after weaning juvenile ring-tailed lemurs have the most diverse diets in a social group (Chapter 3). Juvenile ring-tailed lemurs are exploring their environment at this time which is likely spurred by an increase in received aggression that pushes them away from preferred feeding positions (Chapter 4). If juvenility is not a time for learning ecological skills, then lemurid juveniles may use this time to refine social skills and build energetic reserves for their growth into sexual maturity and reproduction in a resource-limited and unpredictable environment.

What then is lemur juvenility about? Most of the information about lemur juveniles comes from captive studies, and the majority of those have focused on lemurid species, particularly the ring-tailed lemur. As in all mammals, lemur juvenility is a time to play, build social relationships, and learn about food. Unlike many haplorhines, lemur infants and juveniles sort out their own dominance relationships without influence of their mother’s rank (Pereira, 1995; O'Mara, personal observation). Juvenile lemurids are innovative and motivated to explore their environments (Anderson et al., 1992; Krakauer, 2006). Juvenility in lemurs is also a time to develop sex-appropriate feeding and social behaviors. From early in juvenility, females exploit more diverse diets from males, and this continues throughout their lives (Chapter 5). Juvenile males receive more aggression than juvenile females and all other adults, a pattern that continues throughout adulthood (Chapter 4). Similarly, sex-typed ring-tailed lemur social behavior does not emerge until juvenility and is likely a result of internal physiological changes throughout development rather than as a result of the extrinsic social environment (Meredith, 2012).

From emerging work on New World monkeys, it seems that in many ways primate juvenility is less tightly correlated with ecological constraints than with complexity of behavior. Juvenile capuchin, squirrel, spider, and woolly monkeys all show adult levels of foraging efficiency and risky behavior, and in some cases adult positional behavior and movement patterns . Comparative work between two sympatric atelin species (*Ateles belzebuth* and *Lagothrix poeppiggi*) points to differences in the relative social complexity of these two species rather than their ecology as driving the differences in the length of their juvenile periods (Schmitt, 2010). The flexible fission-fusion social system of *Ateles* may place large constraints on amount and type of social interactions a juvenile may have (Pusey, 1983). The development of proper social skills and relationships may then take a long time, and without these appropriate skills juveniles may fail to gain a position within the dominance hierarchy, or in extreme cases, be a target of lethal aggression (Valero et al., 2006; Vick, 2008; Talebi et al., 2009). This pressure on the development of social behavior during juvenility may be extreme in these flexible social organizations, but illustrates that there can be significant social risks to development in addition to ecological ones.

As an alternative to the behavioral and ecological explanations of juvenility, growing and maintaining an energetically expensive brain may have been the original regulator of juvenility in primates (Charnov and Berrigan, 1993; Ross and Jones, 1999). Brains are energetically expensive organs that require a high and continuous energy supply (Mink et al., 1981; Isler and van Schaik, 2009). If social complexity is the primary correlate of increased brain size within the primate clade (Joffe, 1997; Dunbar, 1998), then as primate brain sizes increased, so did the amount of energy that must have been devoted to maintaining them. If we take lemurs as an approximation of a basal, gregarious primate then two things stand out relative to the energetic trends across primates: lemurs have low basal metabolic rates (BMR) and a brain that requires a disproportionately high amount of energy to maintain relative to catarrhine primates (Müller, 1985; Kappeler, 1996; van Woerden et al., 2012). Strepsirrhines allocate similar proportions of total metabolic energy to maintaining their brains as do humans, which is unsual considering the smaller, less complex brains of strepsirrhines (van Woerden et al., 2012). It is unknown if strepsirrhine brains are more energetically demanding than other mammals because of their low BMR, or if the relatively higher energy use compared to catarrhines reflects their smaller overall body size. However, the size of strepsirrhine brains are constrained by the effects of environmental seasonality (van Woerden et al., 2010), where catarrhines brains have increased in size relative to environmental seasonality and act as a cognitive buffer to variation in food availability (van Woerden et al., 2012). The relatively large amount of energy required by a strepsirrhine brain may have imposed a slow growth period, and helps to explain not only the primate juvenile period, but also many of the unusual aspects of lemur biology including low levels of sexual size dimorphism and female dominance, (Young et al., 1990; Leigh and Terranova, 1998; Wright, 1999).

The work presented in this dissertation does not provide strong support for ecological or learning constraints on the duration of lemur juvenility. It may be that social complexity, its influence on brain size and subsequent influence on the energetics of development, are likely the foundation of primate juvenility. However, we still know comparatively little about what it means to be a juvenile and how their energetic allocations to growth and maintenance shift as they develop and assume a position within the adult social environment. Future work that includes physiological and energetic markers of development across primates will provide invaluable insight into primate juvenility, and how the energetics of juvenility set the pace for primate life history.

Sex differential feeding ecology and the evolution of female dominance in lemurs

Female social dominance is unusual among group-living mammals, with only a handful of examples outside of the lemurs (Sherman et al., 1991; Kano, 1992; Kappeler, 1993; Glickman et al., 1997). Lemurs show an unusual suite of features including torpor, high degrees of folivory for their small body size, low or reversed sexual size dimorphism, small groups comprising relatively equal numbers of males and females, intense female breeding competition, and female dominance to males (Kappeler and Schaffler, 2008). This suite of features in lemurs is hypothesized to be either a product of phylogenetic inertia via evolutionary disequilibrium (Evolutionary Disequilibrium Hypothesis: EVDH) or it is a result of selection to mitigate high reproductive costs in an unpredictable environment (Energetic Constraints Hypothesis; ECH). Among this suite of features, female dominance in lemurs has been particularly problematic to explain. The development of sex differences in feeding can offer some insight into the ecological and behavioral basis of female dominance from the perspective of both the EVDH and ECH. They illustrate how males and females balance the costs associated with shifting social, activity, and ecological niches and how these are amplified by Madagascar’s unpredictable resource environment (Chapter 5).

Evolutionary Disequilibrium. The evolutionary disequilibrium hypothesis (EVDH) proposes the extant diurnal lemurs historically were nocturnal, pair-bonded species (van Schaik and Kappeler, 1996; Kappeler, 1999). The extinction of large raptors (Goodman, 1994a,b) and at least 17 large diurnal lemurs coincided with human colonization of the island (Godfrey and Jungers, 2002), and opened a wealth of diurnal niches that the extant lemurs are currently in the process of occupying. The EVDH explains the monomorphic body size of most lemurs, and to some extent the variable social structure and tendency towards pair bonds (or dyads) within the social aggregations of many *Eulemur* species (Overdorff, 1998a; Ostner and Kappeler, 1999). While this hypothesis does not directly address the evolution of female social dominance, female social dominance to males is considered to be a relic of these historically pair-bonded species of monomorphic body size. Female dominance begins with males and females that are the same size and are evenly matched competitors for resources. Because females incur the bulk of reproductive costs they have more to lose and compete more intensely for resources and displace males (Dunham, 2008). Female dominance would then an inevitable consequence of asymmetrical costs between males and females in a monomorphic mammal species (cost asymmetry hypothesis: (Dunham, 2008). While there are no data or model-based tests of the cost asymmetry hypothesis, female priority of access to food would then have to cascade into the pervasive social dominance typified by ring-tailed lemurs (Kappeler, 1990). Female dominance is then a consequence of phylogenetic inertia where lemurs retained female dominance as they moved into diurnal activity patterns and formed larger social groups in response to predation and intergroup competition.

It is currently unknown how the degree of sex differences in feeding correlates with primate social structure and complexity. Sex differences in feeding are most likely to be found in multi-male, multi-female social groups (Clutton-Brock, 1977). However sex differences in feeding have been reported for a single species of pair-bonded primate, the indri (Pollock, 1977) but may also be present in the siamang (Chivers, 1974). Intragroup competition between males and females may be much different in pair bonded species than in those with larger social groups and may not necessitate large dietary separation between males and females. Sex differences in feeding have yet to be identified in dyads within a larger social aggregation, such as in *Eulemur fulvus* (Overdorff, 1998b) or even if these dyadic relationships shift based on ecological conditions (Ostner and Kappeler, 1999) or how this changes the competitive relationships between males and females.

Costs of reproduction in an unpredictable environment. More traditionally, female dominance in lemurs has been identified as a strategy where females can monopolize resources to help alleviate potentially high costs of reproduction in an unpredictable resource environment (Jolly, 1984; Young et al., 1990). The high prenatal growth rates in lemurs relative to other primates of their body size supports this hypothesis (Young et al., 1990). The energy conservation hypothesis (ECH: Jolly, 1966; Richard, 1987) has been extended to account for the suite of unusual lemur features including low or absent sexual size dimorphism, low basal metabolic rates, female dominance, small group size, and photoperiod estrous synchrony (Wright, 1999). The strength of this hypothesis is in its near universal application to each of these unusual aspects of lemur biology. Energetic constraints and their influence on the highly competitive nature of females within a social group help to explain the emphasis on intragroup competitive intelligence in lemurs rather than some of the more empathetic and cooperative cognitive abilities of monkeys and apes (Fichtel and Kappeler, 2010). The major challenges to energetic conservation paradigm have been that the environment of Madagascar does not experience unusual seasonality when compared to other primate habitats, and that the energetic costs of lemurs are not unusual relative to those of other primates, particularly the galagos and lorises (Kappeler, 1996; Tilden and Oftedal, 1997; von Engelhardt et al., 2000). Absent the extreme energetic costs, there is little pressure for female dominance over males to evolve.

While lemurs may not experience unusual energetic costs for primates of their body size (Kappeler, 1996), the ecological context of these reproductive characters is missing.

Primate species in many areas of the world experience the same degree of seasonality as in Madagascar, without requiring female dominance (van Schaik and Kappeler, 1996). However, the reliability and predictability of rainfall and subsequent resources may be more relevant than absolute degree of seasonality. Madagascar experiences some of the most unpredictable rainfall in the world (Dewar and Richard, 2007), and the interannual variation in rainfall may make long periods of low food availability more common in Madagascar. Seasonality and food availability has restricted brain size evolution in lemurs more than in other primates (van Woerden et al., 2010,2012). In catarrhines, large brains act as a cognitive buffer in seasonal environments (van Woerden et al., 2012), but in the case of the lemurs brain sizes are constrained by high seasonality.

Lemurs devote a disproportionate amount of their metabolic budget to maintaining their brains, relative to catarrhines (van Woerden et al., 2012), and this restricts potential energy available for reproduction. Even if their costs of reproduction are not unusual when compared to other primates, the large amount of energy devoted to maintaining their brains may put lemurs at a significant disadvantage if they are to maintain an income based reproductive strategy (Richard et al, 2002; Godfrey et al, 2004). This is further compounded in the ring-tailed lemur in that despite the variation in food availability across the year (Chapter 5) ring-tailed lemurs consume a diet that is nutritionally and energetically balanced between the wet and the dry seasons (Yamashita, 2008). By maintaining a consistent amount of energy and protein intake between each season, it is possible that ring-tailed lemur females go into energetic and protein deficits by reproducing and lactating when food availability is at its lowest. Sex differences in feeding ecology then allow them to recover from these deficits as the lactation period ends and lemurs move into a recovery and mating season (Chapter 5).

Evolutionary Disequilibrium vs Energetic Conservation? It is difficult to say how the development of sex differences can support the EVDH, especially if female dominance relies on monomorphism and competitive assessment relative to differential costs of reproduction (Dunham, 2008). Because costs of reproduction are still invoked in this hypothesis, predictions that support EVDH are not likely to differ substantially from the ECH. The EVDH relies on the phylogenetic inertia of a hypothetical lemur historical biology. Feeding ecology is likely more plastic than other traits, especially the evolution of body size and sexual dimorphism. Male and female lemurs grow at the same rate for the same duration of time to nearly identical adult body masses and do not reflect the diversity of growth patterns to monomorphism found in other smaller, nocturnal strepsirrhines (Leigh and Terranova, 1998; O'Mara et al., 2012). The canalization of lemurid growth indicates large energetic constraints on their overall biology (Leigh and Terranova, 1998).

Sex differences in lemur feeding ecology lend further support to an overall energy conservation strategy. In the ring-tailed lemur, which is the most extreme example of female dominance in the lemurs (Jolly, 1998), sex differences in feeding begin at weaning with niche partitioning between males and females in their overall dietary diversity. These initial sex differences expand during lactation and contract to lower levels throughout the year (Chapter 5). Sex differences in lemur feeding are variable in their presence and strength. In both ring-tailed lemurs and ruffed lemurs (*Varecia rubra*), distinct sex differences in diet composition are present during lactation (Chapter 5; (Vasey, 2002), but sex differences in diet are mostly absent in the white-headed lemur (*Eulemur albifrons*). Sex differences during gestation and lactation in ruffed lemurs are so distinct that the sexes are more similar to same sex white-headed lemurs than they are to each other, similar to the pattern in sympatric guenon species (Gautier-Hion, 1980). At least for the lemurids, in light of high energetic expenditure to maintain their brains and unpredictable food availability, both female dominance and sex differential niche partitioning are necessary to facilitate their annual, income based reproductive strategy. Female dominance may allow for partitioning the feeding niche in ring-tailed lemurs and provide an essential buffer to females, particularly during early lactation when the physiological costs of lactating females increase and sex differences in feeding amplify.

Feeding ecology and the conservation of ring-tailed lemurs

Perhaps deceptively, ring-tailed lemurs are a primate of low conservation priority. They are ecologically flexible primates and are found from the mountains of the Andringitra massif to the gallery and spiny forests of Beza Mahafaly, and the cactus-dominated hedges of the southern tip of Madagascar (Goodman et al., 2006; Kelley, 2011). They breed readily in captivity and are one of the most recognizable species in Madagascar and in zoos throughout the world. However, the habitats that harbor ring-tailed lemurs are rapidly being destroyed or degraded. In these degraded habitats, ring-tailed lemurs exploit more diverse diets then groups in gallery forests (Whitelaw, 2010), but these habitats have significant negative impacts on ring-tailed lemurs. Animals in disturbed areas have smaller home ranges but must travel further to find food. They rest less, groom less, and show low group cohesion in these ranges when compared to groups in gallery forests (Whitelaw, 2010). How this impacts mortality and reproductive success is unknown, but if ring-tailed lemurs exist already on a limited energy budget then severe degradation will likely curtail their success in these habitats.

Ring-tailed lemur survival and reproductive success have responded quickly to droughts and hurricanes that have dramatically reduced population density in the past (Gould et al., 2003). Recent work exploring the genetic evidence for a population bottleneck for ring-tailed lemurs in southwestern Madagascar is equivocal. (Parga et al., 2012). Ring-tailed lemurs have a history of population crashes and recovery (Gould et al., 2003). Following the 1991-1992 drought at BMSR the ring-tailed lemur population in the gallery forest dropped by 50% over the next three years including an exceptionally high adult and juvenile mortality (29% and 57%, respectively)(Gould et al., 1999). The mortality of juveniles and adults are usually low at Beza (6% for juveniles, 3% for adults). Drought conditions likely eliminated the herbaceous ground cover that ring-tailed lemur juveniles at Beza rely on during the weaning process. Despite the high mortality, the population quickly recovered with increases in the number of females by 13-15% each year. This demographic resiliency of the ring-tailed lemur may make anything but the most extreme of population bottlenecks difficult to detect using current genomic tools (Parga et al., 2012).

Their income breeding strategy, however, may only be possible when food resources allow the niche partitioning and sex differences in feeding ecology that help to compensate for female costs of reproduction in a relatively unpredictable environment (Chapter 5). As ring-tailed lemurs are forced into more marginal and degraded habitats, the niche space may be narrowed and eliminate some of the ecological buffer needed by females. As a consequence, demographic recovery for this species may be slow or may not occur at all. However, growing lemurs show high dietary diversity (Chapters 3 & 4) and their inclination to explore new foods may facilitate their behavioral and ecological flexibility.

Both ring-tailed lemurs and sifaka (*Propithecus verreauxi verreauxi*) are culturally protected at Beza under a traditional taboo system (Loudon et al., 2006). While Beza has been expanded to encompass a significant area of land (Chapter 1), it will take time to see if this has positive benefits to the Beza Mahafaly ecosystem. During the course of this study the largest conservation challenges were livestock grazing and timber poaching. Despite barbed wire fences surrounding the protected area, cattle, goats, and sheep were repeatedly seen in Parcel 1. Cattle are the primary source of wealth in this area and throughout Madagascar, and play central roles in cultural transactions and reciprocity. Livestock were usually brought into the reserve at night, both to graze and to protect them from cattle thieves. Timber poaching, particularly for *Alluaudia procera* and *Cedrelopsis grevei*, was less of a problem in Parcel 1, but was seen to a far greater extent in the drier areas of Parcel 2 and the expansion areas of the reserve. The Madagascar National Parks (MNP) staff and the KASTI (Komiten'ny Ala sy ny Tontolo Iainana, or forest and environment committee), continue to work to prevent these incursions, primarily through community outreach, and to a lesser extent, through economic sanctions. The full impact of livestock grazing in the reserve is not known, but these grazers nearly completely denude the understory and ground cover where they forage. This has a significant impact on lemur feeding ecology. Both ring-tailed lemurs and sifaka feed on the leaves of these understory plant species, particularly during periods of low food availability and high heat stress. Vines and low shrubs comprised 8-10% of overall ring-tailed lemur diet during this study. These vines are also an important food source during weaning and contributed 30% to feeding time of infants as they are weaned to juvenility. Without the presence of these foods during weaning, it is unlikely that infants will be able to successfully navigate the process to juvenility.

While there have been local taboos against harming or eating both ring-tailed lemurs and sifaka (Loudon et al., 2006), the influx of people from other areas in Madagascar to this region could potentially have the effect of degrading these cultural laws that have so far helped to protect the diurnal lemurs of the area. In fact, MNP wildlife rangers at Beza note that this seems to be the case for other economically and culturally important species, including the radiated tortoise (*Asterochelys radiata* - Critically Endangered, 2011 IUCN Red List). This is a species where the taboos against collection have been more variable, but as immigration to the area increases the population of these tortoises outside of the reserve is decreasing quickly as animals are easily captured for food and for the pet trade.

Despite it richness in biodiversity, Madagascar remains one of the poorest nations in the world. It has a per capita Gross National Income of $824 per year, 67.8% of the population lives below the national poverty line, and it is ranked 151 of 187 countries in the United Nations Development Programme's 2011 Human Development Index (http://hdrstats.undp.org). The Human Development Index is a composite of multiple variables measured along three primary axes: a long and healthy life, access to knowledge, and a decent standard of living. The 2011 HDI of Madagascar (0.480) is only slightly higher than that of Sub-Saharan Africa (0.463) and the lowest worldwide values (0.456). Recent political instability and the resulting political and economic sanctions have only pushed Madagascar deeper into poverty and desperation that has resulted in logging, poaching, and degradation of many of the protected areas of the country. This has hollowed out much of former President Marc Ravelomanana's 2003 Durban Vision that expanded protected areas in Madagascar to over 6 million Ha, or 10% of the country's land area. While the borders of protected areas expanded, the actual protection within those borders has not.

With a median age of 22 years (F: 22.4, M: 21.2; Youssef, 2010), the population living in and around Beza is young. Fertility rates and recruitment in these communities are not known, but subjectively it appears that these communities are growing and new villages are being established throughout the region. The population growth rate of Madagascar is currently the 12th highest in the world, with a 2010 growth rate of 2.97% (IndexMundi.com). Rapid population increase and low education levels will likely continue to be a major challenge. Currently 20% of school-aged children near Beza attend school regularly, with only 8% of eligible children completing 9th grade (Youssef, 2010). This is substantially lower than the national expected years of schooling (10.7) and the national mean of 5.2 years of school attended (http://hdrstats.undp.org). A rapidly increasing population, high population recruitment, and low education levels will place increasing pressure on the reserve while eroding the traditional sets of taboos that have protected much of the reserve wildlife. Much remains to be done in terms of economic development and enrichment in Madagascar. Without it, and substantial increases in education, the forests and biodiversity will continue to suffer.

Too often, descriptions of conservation and the future of Madagascar are grim with little hope for the future. However, the long history of positive, integrative conservation efforts at Beza Mahafaly means that there is much to look forward to in the coming years. The dedicated team of MNP staff and rangers, ecological monitoring team, long-term primate researchers and their students, and the collective KASTI are a model for community-based, cooperative conservation. In this relatively unstable time of Madagascar's history, the lemurs of Beza Mahafaly will continue to be under good care.

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APPENDIX A

AGE CLASS DEFINITIONS

Age class definitions for ring-tailed lemurs in this study.

Age class	Age	Description
Infant 1	0-12 weeks	Completely dependent on mother for feeding and travel. Movement consists mostly of relatively uncoordinated hopping and playing with other young infants. Some food exploration and initial ingestion takes place.
Infant 2	13-24 weeks	Beginning to feed and forage with adult-like patterns. Still spending considerable time nursing toward the weaning transition, but mothers begin to consistently reject offspring nursing attempts.
Juvenile 1	25 weeks – 1 year	Nursing has largely stopped. Spending more time with age-mates and less time with mother. Approximately 30-50% adult body size
Juvenile 2	1-2 years	Approximately one-half to three-quarters 50-75% of adult body size. Foraging like an adult but spending considerable proportions of time with age-peers. Large proportions of play behavior with younger infants and age mates.
Subadult	2-3 years	Adult body size but not showing the same frequency of the secondary sex typical behaviors such as scent marking. Still participate in play bouts with younger animals and age mates. Males can still be dominant to females at this age.
Adult	3 years and older	Fully adult. Little play behavior with other individuals. Females completely dominant to males.

APPENDIX B

ETHOGRAM

Ethogram for this study. All feeding behaviors are modified by the food being eaten or foraged. * indicates that the behavior can be expressed by the focal or that it can be directed at the focal

Continuously recorded behaviors

Behavior	**Definition**
Approach while eating/foraging *	Directed movement to within 0.5 meters of another individual while they are eating or foraging
Approach outside of feeding *	Directed movement to within 0.5 meters of another individual
Leave dyad/group *	Can also be directed at focal
Feed	Ingest food. Modified by species identity and food part
Forage	Active searching for food
Drink	Ingest water
Lick	Touches tongue to item
Crack/bite attempt	Places item in mouth, closes jaws and perforates item
Nurse	Mouth to nipple contact. Includes suckling.
Rejected	Rejected from a feeding or nursing attempt. Includes levels of increasing aggression including block, move away, and contact aggress (e.g., bite)
Beg	Direct look, gesture, or sound at an individual with food with apparent intent of getting food donated, dropped, or transferred
Scrounge	Immediately feed on food discarded by another individual
Co-feed	Simultaneous feeding after an approach. Includes levels same species same part, same species different part, different species different part. Modified by species identity and part
Resist	Attempt to not give food. Could include turning away, holding on to food
Food explore/put in mouth	Placing items in mouth but not ingesting
Food reject	Spit out item in mouth
Show interest in food	Inspecting and watching food or another individual feeding
Grab	Capture attempt on arthropod

Continuously recorded behaviors

Behavior	Definition
Sniff mouth	Inspects another individual’s mouth with nose
Sniff	Inspects potential food item with nose
Touch another's food	Puts hand on another individual’s food
Steal food	Forcibly take food from another
Mark	Impregnate scent on substrate. Levels denoted as anogenital, wrist, tail, and tail waive
Play	Play via Potter Stewart’s definition. Divided into solo, object, and social play
Aggress *	Can also be directed at focal. Divided into levels stare, move to lunge, chase, and contact/bite
Submit *	Can also be directed at focal. Divided into levels look away, move, jump & flee, and receive contact
Out of sight	Animal cannot be seen

Instantaneously recorded behaviors

Behavior	Definition
Feed	Ingest food. Divided into ripe fruit, unripe fruit, young leaves, mature leaves, flowers, flower buds, soil, wood, arthropod, other
Forage	Searching for food
Groom	Includes levels autogroom, receive grooming, and mutual grooming
Sniff	Inspects potential food item with nose
Lick	Touches tongue to item
Crack	Places item in mouth, closes jaws and perforates item
Move	Movement that is not directly related to finding food
Stand	Standing stationary
Vigilance	Actively visually inspecting the environment, but not for food
Rest	No movement, not actively searching, could be sleeping
Rest in proximity	Resting within arm’s reach of another individual
Other	Engaged in some other behavior. Accompanied by a comment describing it.

APPENDIX C

DIET COMPOSITION BY AGE-SEX CATEGORY PER SEASON

Dietary composition for each age-sex category per reproductive season. Means are from logistic mixed regression models that test the effect of age-sex category on the percent of each food type within a season with animal identity as a random factor.

Age	**Sex**	**Season**	**Food Type**	**Mean**	**SE**
Infant 1	Female	Lactation	Mature Leaves	0.382	0.164
			Young Leaves	19.965	0.602
			Unripe Fruit	0.187	0.211
			Ripe Fruit	0.953	0
			Flowers	0.937	0
			Insects	7.501	0.111
			Soil/Wood	3.929	0.136
Infant 1	Male	Lactation	Mature Leaves	0.305	0.172
			Young Leaves	23.194	0.631
			Unripe Fruit	0.51	0.221
			Ripe Fruit	0.439	0
			Flowers	0.993	0
			Insects	5.401	0.116
			Soil/Wood	1.331	0.143
		Weaning	Mature Leaves	0	0
			Young Leaves	35.633	6.515
			Unripe Fruit	0	NA
			Ripe Fruit	5.695	10.369
			Flowers	0.036	0
			Insects	0	0
			Soil/Wood	6.258	2.846
Infant 2	Female	Lactation	Mature Leaves	0.668	0.203
			Young Leaves	33.224	0.744
			Unripe Fruit	4.073	0.26
			Ripe Fruit	12.889	0
			Flowers	1.885	0
			Insects	0.314	0.137
			Soil/Wood	2.94	0.168
		Recovery	Mature Leaves	0.376	0.022
			Young Leaves	10.308	NA
			Unripe Fruit	0	0.022
			Ripe Fruit	68.216	1.601
			Flowers	0	0
			Insects	0	0
			Soil/Wood	6.404	0.196
		Weaning	Mature Leaves	1.364	0

Age	Sex	Season	Food Type	Mean	SE
			Young Leaves	18.854	1.881
			Unripe Fruit	0	NA
			Ripe Fruit	52.748	2.993
			Flowers	0.829	0
			Insects	0.013	0
			Soil/Wood	2.22	0.821
Infant 2	Male	Lactation	Mature Leaves	0.208	0.19
			Young Leaves	28.659	0.698
			Unripe Fruit	3.889	0.244
			Ripe Fruit	7.123	0
			Flowers	2.095	0
			Insects	0.381	0.128
			Soil/Wood	3.508	0.158
		Recovery	Mature Leaves	0.041	0.026
			Young Leaves	21.551	NA
			Unripe Fruit	0.657	0.026
			Ripe Fruit	61.482	1.849
			Flowers	0	0
			Insects	0	0
			Soil/Wood	3.446	0.227
		Weaning	Mature Leaves	0.377	0
			Young Leaves	18.952	1.807
			Unripe Fruit	0.036	NA
			Ripe Fruit	45.541	2.876
			Flowers	1.289	0
			Insects	0.299	0
			Soil/Wood	2.646	0.789
Juvenile 1	Female	Gestation	Mature Leaves	14.441	0.619
			Young Leaves	31.936	0.864
			Unripe Fruit	10.112	NA
			Ripe Fruit	10.182	0
			Flowers	23.822	0
			Insects	0	0
			Soil/Wood	7.007	0
		Lactation	Mature Leaves	12.189	0.47
			Young Leaves	27.97	1.723
			Unripe Fruit	0.143	0.602
			Ripe Fruit	9.887	0
			Flowers	38.62	0
			Insects	0	0.317
			Soil/Wood	2.1	0.389

Age	Sex	Season	Food Type	Mean	SE
		Recovery	Mature Leaves	2.011	0.017
			Young Leaves	14.804	NA
			Unripe Fruit	0.137	0.017
			Ripe Fruit	73.307	1.256
			Flowers	0.56	0
			Insects	0	0
			Soil/Wood	3.055	0.154
	Male	Gestation	Mature Leaves	17.708	1.304
			Young Leaves	45.598	1.821
			Unripe Fruit	10.12	NA
			Ripe Fruit	11.091	0
			Flowers	7.02	0
			Insects	0	0
			Soil/Wood	2.908	0
		Lactation	Mature Leaves	4.299	0.9
			Young Leaves	2.67	3.299
			Unripe Fruit	0.78	1.153
			Ripe Fruit	0.321	0
			Flowers	91.664	0
			Insects	0	0.607
			Soil/Wood	0.267	0.746
		Recovery	Mature Leaves	0.301	0.019
			Young Leaves	16.321	NA
			Unripe Fruit	0.247	0.019
			Ripe Fruit	68.713	1.365
			Flowers	0	0
			Insects	0	0
			Soil/Wood	1.945	0.167
		Weaning	Mature Leaves	0	0
			Young Leaves	21.344	9.213
			Unripe Fruit	0	NA
			Ripe Fruit	78.657	14.663
			Flowers	0	0
			Insects	0	0
			Soil/Wood	0	4.024
Juvenile 2	Female	Gestation	Mature Leaves	28.814	0.91
			Young Leaves	21.038	1.27
			Unripe Fruit	19.836	NA
			Ripe Fruit	10.761	0
			Flowers	9.53	0
			Insects	0	0

Age	Sex	Season	Food Type	Mean	SE
			Soil/Wood	10.021	0
		Lactation	Mature Leaves	2.438	0.173
			Young Leaves	60.89	0.635
			Unripe Fruit	3.829	0.222
			Ripe Fruit	10.21	0
			Flowers	5.716	0
			Insects	8.234	0.117
			Soil/Wood	3.626	0.143
		Recovery	Mature Leaves	0.206	0.018
			Young Leaves	26.788	NA
			Unripe Fruit	0.898	0.018
			Ripe Fruit	69.604	1.307
			Flowers	0	0
			Insects	0	0
			Soil/Wood	2.505	0.16
		Weaning	Mature Leaves	0.068	0
			Young Leaves	36.875	2.66
			Unripe Fruit	0	NA
			Ripe Fruit	57.087	4.233
			Flowers	1.096	0
			Insects	1.167	0
			Soil/Wood	3.707	1.162
	Male	Gestation	Mature Leaves	17.813	0.631
			Young Leaves	31.585	0.88
			Unripe Fruit	9.81	NA
			Ripe Fruit	11.488	0
			Flowers	17.038	0
			Insects	0.512	0
			Soil/Wood	8.282	0
		Lactation	Mature Leaves	0.175	0.349
			Young Leaves	64.682	1.278
			Unripe Fruit	2.67	0.447
			Ripe Fruit	13.846	0
			Flowers	8.175	0
			Insects	3.875	0.235
			Soil/Wood	1.577	0.289
		Recovery	Mature Leaves	0	0.036
			Young Leaves	16.994	NA
			Unripe Fruit	0	0.036
			Ripe Fruit	79.486	2.614
			Flowers	1.754	0

Age	Sex	Season	Food Type	Mean	SE
			Insects	0	0
			Soil/Wood	1.766	0.321
		Weaning	Mature Leaves	1.5	0
			Young Leaves	5.369	5.319
			Unripe Fruit	0	NA
			Ripe Fruit	93.13	8.466
			Flowers	0	0
			Insects	0	0
			Soil/Wood	0	2.323
Subadult	Female	Gestation	Mature Leaves	0	5.533
			Young Leaves	0	7.725
			Unripe Fruit	0	NA
			Ripe Fruit	0	0
			Flowers	0	0
			Insects	0	0
			Soil/Wood	0	0
		Lactation	Mature Leaves	1.934	0.21
			Young Leaves	50.273	0.771
			Unripe Fruit	2.925	0.269
			Ripe Fruit	14.598	0
			Flowers	8.781	0
			Insects	8.283	0.142
			Soil/Wood	5.932	0.174
		Recovery	Mature Leaves	0.815	0.022
			Young Leaves	34.968	NA
			Unripe Fruit	0	0.022
			Ripe Fruit	52.227	1.601
			Flowers	0.293	0
			Insects	0	0
			Soil/Wood	11.697	0.196
		Weaning	Mature Leaves	0.825	0
			Young Leaves	39.9	2.555
			Unripe Fruit	0.06	NA
			Ripe Fruit	53.659	4.067
			Flowers	0.126	0
			Insects	0	0
			Soil/Wood	5.429	1.116
	Male	Gestation	Mature Leaves	17.681	0.611
			Young Leaves	31.153	0.853
			Unripe Fruit	8.02	NA
			Ripe Fruit	15.174	0

Age	Sex	Season	Food Type	Mean	SE
			Flowers	15.984	0
			Insects	0	0
			Soil/Wood	7.11	0
		Lactation	Mature Leaves	2.806	0.145
			Young Leaves	58.746	0.533
			Unripe Fruit	6.727	0.186
			Ripe Fruit	7.138	0
			Flowers	10.711	0
			Insects	5.516	0.098
			Soil/Wood	4.871	0.12
		Recovery	Mature Leaves	0.056	0.018
			Young Leaves	15.093	NA
			Unripe Fruit	0	0.018
			Ripe Fruit	72.423	1.307
			Flowers	0	0
			Insects	2.546	0
			Soil/Wood	9.882	0.16
		Weaning	Mature Leaves	0.852	0
			Young Leaves	32.775	2.172
			Unripe Fruit	1.8	NA
			Ripe Fruit	57.791	3.456
			Flowers	1.709	0
			Insects	0	0
			Soil/Wood	5.073	0.949
Adult	Female	Gestation	Mature Leaves	32.141	0.935
			Young Leaves	21.773	1.306
			Unripe Fruit	8.082	NA
			Ripe Fruit	19.489	0
			Flowers	12.433	0
			Insects	0.015	0
			Soil/Wood	0.353	0
		Lactation	Mature Leaves	1.934	0.161
			Young Leaves	65.767	0.589
			Unripe Fruit	4.472	0.206
			Ripe Fruit	8.812	0
			Flowers	2.133	0
			Insects	2.095	0.108
			Soil/Wood	10.953	0.133
		Recovery	Mature Leaves	0.389	0.011
			Young Leaves	32.027	NA
			Unripe Fruit	1.244	0.011

Age	Sex	Season	Food Type	Mean	SE
			Ripe Fruit	61.139	0.801
			Flowers	0	0
			Insects	0	0
			Soil/Wood	4.938	0.098
		Weaning	Mature Leaves	0.838	0
			Young Leaves	37.788	1.457
			Unripe Fruit	0.513	NA
			Ripe Fruit	52.272	2.318
			Flowers	1.013	0
			Insects	0	0
			Soil/Wood	7.576	0.636
	Gestating Female	Gestation	Mature Leaves	20.945	0.358
			Young Leaves	26.769	0.5
			Unripe Fruit	10.301	NA
			Ripe Fruit	15.613	0
			Flowers	16.298	0
			Insects	0.004	0
			Soil/Wood	5.342	0
		Lactation	Mature Leaves	10.439	0.227
			Young Leaves	33.609	0.834
			Unripe Fruit	0.761	0.291
			Ripe Fruit	10.283	0
			Flowers	31.05	0
			Insects	2.07	0.153
			Soil/Wood	5.086	0.188
	Lactating Female	Lactation	Mature Leaves	1.38	0.098
			Young Leaves	55.796	0.358
			Unripe Fruit	6.658	0.125
			Ripe Fruit	11.033	0
			Flowers	7.067	0
			Insects	6.388	0.066
			Soil/Wood	6.362	0.081
		Recovery	Mature Leaves	0.698	0.015
			Young Leaves	22.339	NA
			Unripe Fruit	5.743	0.015
			Ripe Fruit	69.295	1.067
			Flowers	0.035	0
			Insects	1.112	0
			Soil/Wood	0.778	0.131
		Weaning	Mature Leaves	0.494	0
			Young Leaves	36.924	1.682

Age	Sex	Season	Food Type	Mean	SE
			Unripe Fruit	1.566	NA
			Ripe Fruit	56.766	2.677
			Flowers	1.154	0
			Insects	0.006	0
			Soil/Wood	3.089	0.735
	Male	Gestation	Mature Leaves	16.974	0.551
			Young Leaves	30.777	0.769
			Unripe Fruit	5.946	NA
			Ripe Fruit	14.749	0
			Flowers	16.204	0
			Insects	1.033	0
			Soil/Wood	4.021	0
		Lactation	Mature Leaves	2.996	0.105
			Young Leaves	56.536	0.384
			Unripe Fruit	6.417	0.134
			Ripe Fruit	6.416	0
			Flowers	9.405	0
			Insects	5.15	0.071
			Soil/Wood	5.345	0.087
		Recovery	Mature Leaves	0.96	0.01
			Young Leaves	28.2	NA
			Unripe Fruit	1.383	0.01
			Ripe Fruit	67.224	0.744
			Flowers	0	0
			Insects	0	0
			Soil/Wood	2.232	0.091
		Weaning	Mature Leaves	0.73	0
			Young Leaves	36.135	1.475
			Unripe Fruit	0.926	NA
			Ripe Fruit	54.749	2.348
			Flowers	0.4	0
			Insects	0.007	0
			Soil/Wood	6.326	0.644

APPENDIX D

IDENTIFIED FOOD SPECIES INGESTED BY EACH AGE-SEX CATEGORY IN EACH STUDY GROUP. 1 = PRESENCE, 0 = ABSENCE

			Blue						
Family	**Species**	**Common name**	**Inf Fem**	**Inf Mal**	**Juv 1 Fem**	**Juv 2 Fem**	**Juv 2 Mal**	**Sub & Adult Fem**	**Sub & Adult Mal**
Plants									
Acanthaceae	Ecobilum sp.		0	0	0	0	0	0	0
Acanthaceae	Justica		0	0	0	0	0	1	0
Acanthaceae	Neuracanthus		0	1	0	0	0	0	0
Acanthaceae	Ruellia		0	0	0	0	0	0	0
Acanthaceae	unknown Acanthaceae	tsake	0	0	0	0	0	0	0
Amaranthaceae	Achyranthes aspera	tsipotike	0	1	1	0	0	1	0
Amaranthaceae	Amaranthus spinosa		0	0	0	0	0	0	0
Apocynaceae	Camptocarpus crassifolius	tamboro	0	0	0	0	0	0	0
Apocynaceae	Cryptostegia	lombiry	0	0	0	0	0	0	0
Apocynaceae	Cynanchum	try	1	1	0	0	0	1	0
Apocynaceae	Gonocrypta	kompitse	0	0	0	0	0	1	0
Apocynaceae	Landolphia	piravola	0	1	0	0	0	1	0
Apocynaceae	Marsdenia aff truncata	bokabe	0	0	0	0	0	0	0
Apocynaceae	Marsdenia sp		0	0	0	0	0	0	0
Apocynaceae	Pentopetia	tsompia	1	1	1	0	0	1	0
Apocynaceae	Secamone pachystigma	angalora	0	0	0	0	0	0	1
Aristolochiaceae	Aristolochia bernieri	tontonga	0	0	0	0	0	0	0
Asteraceae	Bidens bipinnata		0	0	0	0	0	0	0
Bignoniaceae	Rhigozum madagascariense	hazontaha	0	0	0	0	0	0	0
Boraginaceae	Coridia ainensis	malainarety	0	0	1	0	0	1	0
Burseraceae	Commiphora grandifolia	daromangily	0	0	0	0	0	0	0
Burseraceae	Commiphora marchandi	darosiky	0	0	0	0	0	0	0
Cactaceae	Opuntia dilleri	raketa	0	0	0	0	0	0	0
Capparaceae	Cadaba virgata	ndriamainty	0	0	0	0	0	0	0
Capparaceae	Capparis chrysomea	roihavitse	0	0	1	0	0	0	0
Capparaceae	Crateva excelsa	akaly	0	0	0	0	0	1	0
Capparaceae	Crateva sp1		0	0	0	0	0	0	0

			Blue						
Family	**Species**	**Common name**	**Inf Fem**	**Inf Mal**	**Juv 1 Fem**	**Juv 2 Fem**	**Juv 2 Mal**	**Sub & Adult Fem**	**Sub & Adult Mal**
Capparaceae	Maerua filiformis	somangy	0	0	1	0	0	1	1
Capparaceae	Maerus nuda	soamangy	0	0	0	0	0	0	0
Celastraceae	Gymnosporia linearis	filofilodrano	0	0	0	0	0	0	0
Celastraceae	Hippocratea angustifolia	vahipinde	0	0	0	0	0	1	1
Combretaceae	Combretum aff villosum	tamenaka	0	0	0	0	0	0	0
Combretaceae	Terminalia seyrigii	taly	0	0	0	0	0	0	0
Convolvulaceae	Ipomea batatus	bageda	0	0	0	0	0	0	0
Convolvulaceae	Ipomea cairica	velae	0	0	0	0	0	0	0
Convolvulaceae	Ipomea mojagensis	valae	0	0	1	1	1	1	1
Convolvulaceae	Ipomea sp1		0	0	0	0	0	0	0
Convolvulaceae	Metaporana parvifolia	kililo	1	1	1	0	0	1	1
Convolvulaceae	Rapona multifolia		0	0	0	0	0	0	0
Convolvulaceae	Rapona tiliifolia		0	0	0	0	0	0	0
Convolvulaceae	Unknown	teloravina	0	0	0	0	0	0	0
Crassulaceae	Kalanchoe	mongy	0	0	0	0	0	0	0
Cucurbitaceae	Corallocarpus grevei	saritaboara	0	0	0	0	0	1	0
Cucurbitaceae	Lemurosicyos	taboarandolo	0	0	0	0	0	0	0
Cucurbitaceae	Seyrigia multiflora	tsiridambo	1	0	0	0	0	1	0
Cucurbitaceae	Xerosicyos danguyi	tapisabola	0	0	0	0	0	0	0
Dideraceae	Alluaudia procera	fantsiolotra	0	0	0	0	0	0	0
Dioscoreaceae	Dioscorea fandrae	oviala	1	0	0	0	0	1	0
Dioscoreaceae	Dioscorea nako	nako	1	0	0	0	0	1	0
Dioscoreaceae	Dioscorea sp1		1	1	0	0	0	1	1
Ebenaceae	Diospyros latispa	maintifototse	0	0	1	0	0	1	0
Euphorbiaceae	Acalypha decaryana	tainaiaiamena	0	0	0	0	0	0	0
Euphorbiaceae	Acalypha sp.		1	1	1	0	0	1	1
Euphorbiaceae	Alchornea	tanatanga	0	0	0	0	0	0	0
Euphorbiaceae	Croton geayi	kelehagnitse	0	0	0	0	0	0	0

			Blue						
Family	**Species**	**Common name**	**Inf Fem**	**Inf Mal**	**Juv 1 Fem**	**Juv 2 Fem**	**Juv 2 Mal**	**Sub & Adult Fem**	**Sub & Adult Mal**
Fabaceae	Acacia bellula	tratriotse	0	0	1	0	0	1	1
Fabaceae	Acacia polyphylla	robontsy	0	0	0	0	0	0	0
Fabaceae	Acacia rovumae	kasia	0	0	0	0	0	1	0
Fabaceae	Alantsilodendron humbertii		0	0	0	0	0	0	1
Fabaceae	Albizzia arenicola	halimboron'ala	1	0	0	0	0	0	0
Fabaceae	Bauhina		0	0	0	0	0	0	0
Fabaceae	Clitoria sp.		0	0	0	0	0	0	0
Fabaceae	Tamarindus indica	kily	1	1	1	1	0	1	1
Hemiptera	Aleuromarginatus millettiae		1	1	1	0	0	1	1
Hernandiaceae	Gyrocarpus americana	kapaipoty	1	0	1	0	0	1	1
Lamiaceae	Clerodendrum sp. Cf. emirnense	forimbitike	0	0	0	0	0	0	1
Lauraceae	Ocotea tricantha	maroanake	0	1	0	0	0	0	1
Loganiaceae	Strychnos madagascariensis	bakoa	1	1	1	0	0	1	1
Malvaceae	Abutilon sp.		0	0	0	0	0	0	0
Malvaceae	Byttneria voululi	sarihasy	0	0	0	0	0	1	1
Malvaceae	Grewia		1	0	0	0	0	0	0
Malvaceae	Grewia franciscana	tainkafotse	1	0	1	0	0	1	1
Malvaceae	Grewia grevei	kotipoke	1	1	1	0	0	1	1
Malvaceae	Grewia leucophylla	tratramborondreo	1	0	1	0	0	0	0
Malvaceae	Grewia sp1	selibohoka	0	0	0	0	0	0	0
Malvaceae	Grewia sp2	vololo	0	0	0	0	0	0	0
Malvaceae	Grewia trifolia	sely	0	0	1	0	0	1	0
Malvaceae	Grewia tulearensis	maintifototse	1	1	0	0	0	1	1
Meliaceae	Cedrelopsis grevei	katrafay	1	1	1	0	0	1	1
Meliaceae	Quivisianthe papinae	valiandro	1	0	1	0	0	1	1
Meliaceae	Turrae sp1	malainarete	0	0	0	0	0	0	0
Meliaceae	Turrae sp2	mote	0	0	0	0	0	0	0
Moracea	Ficus cocculifolia	adabo	0	0	0	0	0	0	0

			Blue						
Family	**Species**	**Common name**	**Inf Fem**	**Inf Mal**	**Juv 1 Fem**	**Juv 2 Fem**	**Juv 2 Mal**	**Sub & Adult Fem**	**Sub & Adult Mal**
Nyctaginaceae	Boerhavia coccinea	Boerhaavea	0	0	0	0	0	0	0
Nyctaginaceae	Boerhavia diffusa	beamena	0	0	0	0	0	0	0
Nyctaginaceae	Commicarpus commersoni	bea	0	0	0	0	0	1	1
Olacaceae	Anacolosa pervilleana	tanjaka	0	0	0	0	0	0	0
Oleaceae	Norhonia		1	0	0	0	0	1	0
Oleaceae	Norhonia sp1	mantsandro	0	0	0	0	0	0	0
Oleaceae	Norhonia sp2	tsilaitse	0	0	0	0	0	0	0
Opiliaceae	Pentarhopalopilia	fofotse	1	0	0	0	0	0	0
Papaveraceae	Argemone mexicana	fatiboay	0	0	0	0	0	0	0
Phyllanthaceae	Antidesma petiolare	voafogne	0	0	0	0	0	0	0
Phyllanthaceae	Bridelia	hary	1	0	0	0	0	1	0
Phyllanthaceae	Flueggea obovata	tsikembakemba	0	0	0	0	0	1	0
Phyllanthaceae	Phyllanthus angavensis	sanira	0	0	0	0	0	0	0
Physenaceae	Physena sessiliflora	fandriandrambo	0	0	0	0	0	0	0
Poaceae	grass		1	0	0	0	0	1	1
Poaceae	Sporobols maximus	ahidalo	0	0	0	0	0	0	0
Rhamnaceae	Colubrina sp		0	0	0	0	0	0	0
Rhamnaceae	Gouana	masokara	0	0	0	0	0	0	0
Rhamnaceae	Rhamnaceae		0	0	0	0	0	0	0
Rubiaceae	Enterospermum pruinosum	mantsake	0	0	1	0	0	1	0
Rubiaceae	Gardenia	volivaza	0	0	0	0	0	0	0
Rubiaceae	Paederia grandidieri		0	0	0	0	0	0	0
Rubiaceae	Paederia thouarsiana		0	0	0	0	0	0	0
Salvadoraceae	Azima tetracantha	filofilo	0	1	1	0	0	1	1
Salvadoraceae	Salvadora angustifolia	sasavy	1	1	1	0	0	1	1
Scrophulariaceae	Buddleja sp.		0	0	1	0	0	1	1
Sphaerosepalaceae	Rhopalocarpus lucidus	tsiongake	0	0	0	0	0	0	0
Stilbaceae	Nuxia		0	0	0	0	0	0	0

			Blue						
Family	**Species**	**Common name**	**Inf Fem**	**Inf Mal**	**Juv 1 Fem**	**Juv 2 Fem**	**Juv 2 Mal**	**Sub & Adult Fem**	**Sub & Adult Mal**
Talinaceae	Talinella grevei	dango	1	1	1	0	0	1	1
Xanthorrhoeaceae	Aloe divercata	vahontsoi	1	0	1	0	0	1	0
Unknown	unk		1	0	0	0	0	1	0
Unknown	unk102		0	0	0	0	0	0	0
Unknown	unk119		0	0	0	0	0	0	0
Unknown	unk123		1	0	0	0	0	1	0
Unknown	unk126		0	0	0	0	0	0	0
Unknown	unk135		0	0	0	0	0	0	0
Unknown	unk137		0	1	0	0	0	0	0
Unknown	unk4		0	0	0	0	0	0	0
Unknown	unk42		0	0	0	0	0	0	0
Unknown	unk44		0	0	1	0	0	0	0
Unknown	unk45		0	0	0	0	0	0	0
Unknown	unk57		0	0	0	0	0	0	0
Unknown	unk61		0	0	0	0	0	0	0
Unknown	unk78		0	0	0	0	0	0	0
Unknown		tsakohnako	1	1	1	0	0	1	1
Arthopods									
Araneae	spiderweb		0	0	0	0	0	0	0
Buprestidae	Lampropela rothschildi		0	0	0	0	0	1	0
Cicadidae	Yanga heathii		0	0	0	0	0	1	0
Lepidoptera	unknown	field caterpillar	0	0	0	0	0	0	0
Lepidoptera	Unknown	G. grevei caterpillar	0	0	0	0	0	0	0
Cultigens									
Anacardiaceae	Mangifera indica	mango	0	0	1	0	0	1	1
Cucurbitaceae	melon	saritaboara	0	0	0	0	0	0	0
Solanaceae	Solanum lycopersicum	voatabiha	0	0	0	0	0	0	0
Human refuse									

			Blue						
Family	**Species**	**Common name**	**Inf Fem**	**Inf Mal**	**Juv 1 Fem**	**Juv 2 Fem**	**Juv 2 Mal**	**Sub & Adult Fem**	**Sub & Adult Mal**
	trash		0	0	0	0	0	0	0
Cucurbitaceae	squash	taboara	0	0	0	0	0	1	0
Passifloraceae	Passiflora edulis		0	0	0	0	0	0	0
Bromeliaceae	Ananas comosus	pineapplie	0	0	0	0	0	0	0

			Green						
Family	**Species**	**Common name**	**Inf Fem**	**Inf Mal**	**Juv 1 Mal**	**Juv 2 Fem**	**Juv 2 Mal**	**Sub & Adult Fem**	**Sub & Adult Mal**
Plants									
Acanthaceae	Ecobilum sp.		0	0	0	0	0	0	0
Acanthaceae	Justica		0	0	0	1	0	1	0
Acanthaceae	Neuracanthus		0	1	0	1	1	1	1
Acanthaceae	Ruellia		0	0	0	0	1	0	0
Acanthaceae	unknown Acanthaceae	tsake	0	0	0	0	0	1	1
Amaranthaceae	Achyranthes aspera	tsipotike	0	1	0	1	1	1	1
Amaranthaceae	Amaranthus spinosa		0	0	0	0	0	0	0
Apocynaceae	Camptocarpus crassifolius	tamboro	0	0	0	0	1	1	1
Apocynaceae	Cryptostegia	lombiry	0	0	0	0	0	0	0
Apocynaceae	Cynanchum	try	0	0	0	0	0	0	0
Apocynaceae	Gonocrypta	kompitse	0	0	0	0	0	1	1
Apocynaceae	Landolphia	piravola	0	1	0	1	1	1	1
Apocynaceae	Marsdenia aff truncata	bokabe	0	0	0	0	0	0	0
Apocynaceae	Marsdenia sp		0	0	0	0	0	0	0
Apocynaceae	Pentopetia	tsompia	0	1	0	1	1	1	1
Apocynaceae	Secamone pachystigma	angalora	0	1	1	1	1	1	1
Aristolochiaceae	Aristolochia bernieri	tontonga	0	0	0	0	0	0	1
Asteraceae	Bidens bipinnata		0	0	0	0	0	0	0
Bignoniaceae	Rhigozum madagascariense	hazontaha	0	0	0	0	0	0	0
Boraginaceae	Coridia ainensis	malainarety	0	0	0	0	0	0	0
Burseraceae	Commiphora grandifolia	daromangily	0	0	0	0	0	0	0
Burseraceae	Commiphora marchandi	darosiky	0	0	0	0	0	0	0
Cactaceae	Opuntia dilleri	raketa	0	0	0	0	0	0	0
Capparaceae	Cadaba virgata	ndriamainty	0	0	0	0	0	1	0
Capparaceae	Capparis chrysomea	roihavitse	0	0	0	0	0	0	0
Capparaceae	Crateva excelsa	akaly	0	1	0	1	1	1	1
Capparaceae	Crateva sp1		0	0	0	0	0	0	0

			Green						
Family	**Species**	**Common name**	**Inf Fem**	**Inf Mal**	**Juv 1 Mal**	**Juv 2 Fem**	**Juv 2 Mal**	**Sub & Adult Fem**	**Sub & Adult Mal**
Capparaceae	Maerua filiformis	somangy	0	1	0	0	0	0	1
Capparaceae	Maerus nuda	soamangy	0	0	0	0	0	0	0
Celastraceae	Gymnosporia linearis	filofilodrano	0	0	0	0	0	0	0
Celastraceae	Hippocratea angustifolia	vahipinde	0	0	0	0	0	0	1
Combretaceae	Combretum aff villosum	tamenaka	0	0	0	1	1	1	1
Combretaceae	Terminalia seyrigii	taly	0	0	0	1	0	0	0
Convolvulaceae	Ipomea batatus	bageda	0	0	0	0	0	0	0
Convolvulaceae	Ipomea cairica	velae	0	0	0	0	0	1	0
Convolvulaceae	Ipomea mojagensis	valae	0	0	0	1	1	1	1
Convolvulaceae	Ipomea sp1		0	0	0	1	1	1	1
Convolvulaceae	Metaporana parvifolia	kililo	0	1	0	1	1	1	1
Convolvulaceae	Rapona multifolia		0	0	0	0	0	0	0
Convolvulaceae	Rapona tiliifolia		0	0	0	0	0	0	0
Convolvulaceae	Unknown	teloravina	0	0	0	0	0	0	1
Crassulaceae	Kalanchoe	mongy	0	0	0	0	0	0	0
Cucurbitaceae	Corallocarpus grevei	saritaboara	0	0	0	0	0	0	0
Cucurbitaceae	Lemurosicyos	taboarandolo	0	0	0	0	0	0	0
Cucurbitaceae	Seyrigia multiflora	tsiridambo	0	0	0	0	0	0	0
Cucurbitaceae	Xerosicyos danguyi	tapisabola	0	0	0	0	0	0	0
Dideraceae	Alluaudia procera	fantsiolotra	0	0	0	0	0	0	0
Dioscoreaceae	Dioscorea fandrae	oviala	0	1	1	1	1	1	1
Dioscoreaceae	Dioscorea nako	nako	0	0	0	0	0	0	0
Dioscoreaceae	Dioscorea sp1		0	1	0	1	1	1	1
Ebenaceae	Diospyros latispa	maintifototse	0	0	0	0	0	0	0
Euphorbiaceae	Acalypha decaryana	tainaiaiamena	0	0	0	0	0	0	0
Euphorbiaceae	Acalypha sp.		0	1	0	0	0	0	0
Euphorbiaceae	Alchornea	tanatanga	0	0	0	0	1	0	0
Euphorbiaceae	Croton geayi	kelehagnitse	0	0	0	0	0	0	0

			Green						
Family	**Species**	**Common name**	**Inf Fem**	**Inf Mal**	**Juv 1 Mal**	**Juv 2 Fem**	**Juv 2 Mal**	**Sub & Adult Fem**	**Sub & Adult Mal**
Fabaceae	Acacia bellula	tratriotse	0	0	0	0	0	0	0
Fabaceae	Acacia polyphylla	robontsy	0	0	0	0	0	0	0
Fabaceae	Acacia rovumae	kasia	0	0	0	0	0	0	0
Fabaceae	Alantsilodendron humbertii		0	0	0	0	0	0	0
Fabaceae	Albizzia arenicola	halimboron'ala	0	0	0	0	0	0	0
Fabaceae	Bauhina		0	0	0	1	0	0	0
Fabaceae	Clitoria sp.		0	0	0	0	0	0	0
Fabaceae	Tamarindus indica	kily	1	1	1	1	1	1	1
Hemiptera	Aleuromarginatus millettiae		0	0	0	1	1	1	1
Hernandiaceae	Gyrocarpus americana	kapaipoty	0	1	0	1	0	1	1
Lamiaceae	Clerodendrum sp. Cf. emirnense	forimbitike	0	0	0	0	0	0	0
Lauraceae	Ocotea tricantha	maroanake	0	0	0	0	0	0	0
Loganiaceae	Strychnos madagascariensis	bakoa	0	0	0	1	0	0	0
Malvaceae	Abutilon sp.		0	0	0	0	0	0	0
Malvaceae	Byttneria voululi	sarihasy	0	1	0	1	0	0	1
Malvaceae	Grewia		0	0	0	0	0	0	0
Malvaceae	Grewia franciscana	tainkafotse	0	0	0	0	1	0	0
Malvaceae	Grewia grevei	kotipoke	0	1	0	0	0	0	0
Malvaceae	Grewia leucophylla	tratramborondreo	0	1	0	1	1	1	0
Malvaceae	Grewia sp1	selibohoka	0	0	0	0	0	0	0
Malvaceae	Grewia sp2	vololo	0	0	0	0	0	0	0
Malvaceae	Grewia trifolia	sely	0	0	0	0	0	0	0
Malvaceae	Grewia tulearensis	maintifototse	0	0	0	0	1	0	0
Meliaceae	Cedrelopsis grevei	katrafay	0	1	0	1	1	1	1
Meliaceae	Quivisianthe papinae	valiandro	0	1	0	1	1	1	1
Meliaceae	Turrae sp1	malainarete	0	0	0	0	1	0	0
Meliaceae	Turrae sp2	mote	0	0	0	0	0	0	0
Moracea	Ficus cocculifolia	adabo	0	0	0	0	1	1	0

			Green						
Family	**Species**	**Common name**	**Inf Fem**	**Inf Mal**	**Juv 1 Mal**	**Juv 2 Fem**	**Juv 2 Mal**	**Sub & Adult Fem**	**Sub & Adult Mal**
Nyctaginaceae	Boerhavia coccinea	Boerhaavea	0	0	0	0	0	0	0
Nyctaginaceae	Boerhavia diffusa	beamena	0	0	0	1	0	0	0
Nyctaginaceae	Commicarpus commersoni	bea	0	0	0	0	1	0	0
Olacaceae	Anacolosa pervilleana	tanjaka	0	0	0	0	0	0	0
Oleaceae	Norhonia		0	0	0	0	0	1	0
Oleaceae	Norhonia sp1	mantsandro	0	0	0	0	1	0	0
Oleaceae	Norhonia sp2	tsilaitse	0	1	0	1	0	1	1
Opiliaceae	Pentarhopalopilia	fofotse	0	0	0	0	0	0	0
Papaveraceae	Argemone mexicana	fatiboay	0	0	0	1	1	1	0
Phyllanthaceae	Antidesma petiolare	voafogne	0	1	0	1	1	1	1
Phyllanthaceae	Bridelia	hary	0	1	0	1	0	1	0
Phyllanthaceae	Flueggea obovata	tsikembakemba	0	1	0	1	1	1	1
Phyllanthaceae	Phyllanthus angavensis	sanira	0	0	0	0	0	0	0
Physenaceae	Physena sessiliflora	fandriandrambo	0	0	0	0	0	0	0
Poaceae	grass		0	0	0	0	0	0	0
Poaceae	Sporobols maximus	ahidalo	0	0	1	1	0	1	0
Rhamnaceae	Colubrina sp		0	0	0	0	0	0	0
Rhamnaceae	Gouana	masokara	0	0	0	0	0	1	0
Rhamnaceae	Rhamnaceae		0	0	0	0	0	0	0
Rubiaceae	Enterospermum pruinosum	mantsake	0	1	1	1	0	1	1
Rubiaceae	Gardenia	volivaza	0	0	0	0	0	0	1
Rubiaceae	Paederia grandidieri		0	0	0	0	0	0	0
Rubiaceae	Paederia thouarsiana		0	0	0	1	0	0	0
Salvadoraceae	Azima tetracantha	filofilo	0	1	0	1	0	0	1
Salvadoraceae	Salvadora angustifolia	sasavy	0	1	0	1	1	1	1
Scrophulariaceae	Buddleja sp.		0	0	0	1	0	0	0
Sphaerosepalaceae	Rhopalocarpus lucidus	tsiongake	1	0	0	0	0	0	0
Stilbaceae	Nuxia		0	1	0	0	0	0	1

			Green						
Family	**Species**	**Common name**	**Inf Fem**	**Inf Mal**	**Juv 1 Mal**	**Juv 2 Fem**	**Juv 2 Mal**	**Sub & Adult Fem**	**Sub & Adult Mal**
Talinaceae	Talinella grevei	dango	0	1	0	1	1	1	1
Xanthorrhoeaceae	Aloe divercata	vahontsoi	0	0	0	0	0	0	0
Unknown	unk		0	0	0	1	1	1	1
Unknown	unk102		0	0	0	0	0	0	0
Unknown	unk119		0	0	0	0	0	0	0
Unknown	unk123		0	0	0	0	0	0	0
Unknown	unk126		0	0	0	0	0	0	0
Unknown	unk135		0	0	0	0	0	0	0
Unknown	unk137		0	0	0	0	0	0	0
Unknown	unk4		0	0	0	0	0	1	0
Unknown	unk42		0	0	0	0	0	0	0
Unknown	unk44		0	0	0	0	0	0	0
Unknown	unk45		0	0	0	1	0	0	0
Unknown	unk57		0	0	0	0	0	0	0
Unknown	unk61		0	0	0	0	0	0	0
Unknown	unk78		0	0	0	0	0	0	0
Unknown		tsakohnako	0	0	0	0	0	0	0
Arthopods									
Araneae	spiderweb		0	0	0	0	0	0	0
Buprestidae	Lampropela rothschildi		0	0	0	0	0	0	0
Cicadidae	Yanga heathii		0	0	0	0	0	0	1
Lepidoptera	unknown	field caterpillar	0	0	0	0	0	0	0
Lepidoptera	Unknown	G. grevei caterpillar	0	0	0	0	0	0	0
Cultigens									
Anacardiaceae	Mangifera indica	mango	0	0	0	0	0	0	0
Cucurbitaceae	melon	saritaboara	0	0	0	0	0	0	0
Solanaceae	Solanum lycopersicum	voatabiha	0	0	0	0	0	0	0
Human refuse									

			Green						
Family	**Species**	**Common name**	**Inf Fem**	**Inf Mal**	**Juv 1 Mal**	**Juv 2 Fem**	**Juv 2 Mal**	**Sub & Adult Fem**	**Sub & Adult Mal**
	trash		0	0	0	0	0	0	0
Cucurbitaceae	squash	taboara	0	0	0	0	0	0	0
Passifloraceae	Passiflora edulis		0	0	0	0	0	0	0
Bromeliaceae	Ananas comosus	pineapplie	0	0	0	0	0	0	0

			Orange						
Family	**Species**	**Common name**	**Inf Fem**	**Inf Mal**	**Juv 1 Fem**	**Juv 2 Fem**	**Juv 2 Mal**	**Sub & Adult Fem**	**Sub & Adult Mal**
Plants									
Acanthaceae	Ecobilum sp.		0	0	0	0	0	0	0
Acanthaceae	Justica		0	0	0	0	0	0	0
Acanthaceae	Neuracanthus		0	1	0	0	1	0	0
Acanthaceae	Ruellia		0	0	0	0	0	0	0
Acanthaceae	unknown Acanthaceae	tsake	0	0	1	0	0	0	0
Amaranthaceae	Achyranthes aspera	tsipotike	1	1	1	1	1	1	1
Amaranthaceae	Amaranthus spinosa		0	0	0	0	0	0	0
Apocynaceae	Camptocarpus crassifolius	tamboro	1	1	0	1	1	1	0
Apocynaceae	Cryptostegia	lombiry	0	0	0	0	0	1	0
Apocynaceae	Cynanchum	try	0	0	0	0	0	0	0
Apocynaceae	Gonocrypta	kompitse	0	0	1	1	1	1	1
Apocynaceae	Landolphia	piravola	1	1	1	0	0	0	1
Apocynaceae	Marsdenia aff truncata	bokabe	0	0	0	0	0	0	1
Apocynaceae	Marsdenia sp		0	0	0	0	0	0	0
Apocynaceae	Pentopetia	tsompia	1	1	1	1	1	1	1
Apocynaceae	Secamone pachystigma	angalora	1	1	1	0	1	1	1
Aristolochiaceae	Aristolochia bernieri	tontonga	0	0	0	0	0	0	0
Asteraceae	Bidens bipinnata		0	0	0	0	0	0	0
Bignoniaceae	Rhigozum madagascariense	hazontaha	1	0	0	0	0	0	0
Boraginaceae	Coridia ainensis	malainarety	0	1	0	1	0	0	0
Burseraceae	Commiphora grandifolia	daromangily	0	0	0	0	0	0	0
Burseraceae	Commiphora marchandi	darosiky	0	0	0	0	0	0	1
Cactaceae	Opuntia dilleri	raketa	0	0	0	0	0	0	0
Capparaceae	Cadaba virgata	ndriamainty	0	0	0	0	0	0	0
Capparaceae	Capparis chrysomea	roihavitse	1	0	1	1	1	1	0
Capparaceae	Crateva excelsa	akaly	0	0	0	0	0	0	1
Capparaceae	Crateva sp1		0	0	0	0	0	0	0

			Orange						
Family	Species	Common name	Inf Fem	Inf Mal	Juv 1 Fem	Juv 2 Fem	Juv 2 Mal	Sub & Adult Fem	Sub & Adult Mal
Capparaceae	Maerua filiformis	somangy	1	1	1	1	0	0	0
Capparaceae	Maerus nuda	soamangy	0	0	0	0	0	0	0
Celastraceae	Gymnosporia linearis	filofilodrano	0	0	0	0	0	0	0
Celastraceae	Hippocratea angustifolia	vahipinde	2	1	1	0	1	0	0
Combretaceae	Combretum aff villosum	tamenaka	0	0	1	0	0	0	0
Combretaceae	Terminalia seyrigii	taly	0	0	0	0	0	0	0
Convolvulaceae	Ipomea batatus	bageda	0	0	1	1	1	1	0
Convolvulaceae	Ipomea cairica	velae	0	0	0	0	0	0	0
Convolvulaceae	Ipomea mojagensis	valae	1	0	1	1	1	1	1
Convolvulaceae	Ipomea sp1		0	0	0	0	1	0	0
Convolvulaceae	Metaporana parvifolia	kililo	1	1	1	1	1	1	1
Convolvulaceae	Rapona multifolia		0	0	0	0	0	0	0
Convolvulaceae	Rapona tiliifolia		0	0	0	0	0	0	0
Convolvulaceae	Unknown	teloravina	0	0	1	1	0	1	0
Crassulaceae	Kalanchoe	mongy	0	0	1	1	0	0	0
Cucurbitaceae	Corallocarpus grevei	saritaboara	0	0	1	0	0	0	0
Cucurbitaceae	Lemurosicyos	taboarandolo	0	0	0	0	0	0	0
Cucurbitaceae	Seyrigia multiflora	tsiridambo	0	0	0	0	0	0	0
Cucurbitaceae	Xerosicyos danguyi	tapisabola	0	0	0	0	0	0	0
Dideraceae	Alluaudia procera	fantsiolotra	0	0	0	0	0	0	0
Dioscoreaceae	Dioscorea fandrae	oviala	1	1	1	1	1	1	0
Dioscoreaceae	Dioscorea nako	nako	0	1	1	1	0	1	0
Dioscoreaceae	Dioscorea sp1		1	1	1	1	1	1	0
Ebenaceae	Diospyros latispa	maintifototse	0	0	0	0	0	0	0
Euphorbiaceae	Acalypha decaryana	tainaiaiamena	0	0	0	0	0	0	0
Euphorbiaceae	Acalypha sp.		1	1	1	1	1	1	1
Euphorbiaceae	Alchornea	tanatanga	0	0	0	0	0	0	0
Euphorbiaceae	Croton geayi	kelehagnitse	1	1	0	0	0	0	0

			Orange						
Family	**Species**	**Common name**	**Inf Fem**	**Inf Mal**	**Juv 1 Fem**	**Juv 2 Fem**	**Juv 2 Mal**	**Sub & Adult Fem**	**Sub & Adult Mal**
Capparaceae	Maerua filiformis	somangy	1	1	1	1	0	0	0
Capparaceae	Maerus nuda	soamangy	0	0	0	0	0	0	0
Celastraceae	Gymnosporia linearis	filofilodrano	0	0	0	0	0	0	0
Celastraceae	Hippocratea angustifolia	vahipinde	2	1	1	0	1	0	0
Combretaceae	Combretum aff villosum	tamenaka	0	0	1	0	0	0	0
Combretaceae	Terminalia seyrigii	taly	0	0	0	0	0	0	0
Convolvulaceae	Ipomea batatus	bageda	0	0	1	1	1	1	0
Convolvulaceae	Ipomea cairica	velae	0	0	0	0	0	0	0
Convolvulaceae	Ipomea mojagensis	valae	1	0	1	1	1	1	1
Convolvulaceae	Ipomea sp1		0	0	0	0	1	0	0
Convolvulaceae	Metaporana parvifolia	kililo	1	1	1	1	1	1	1
Convolvulaceae	Rapona multifolia		0	0	0	0	0	0	0
Convolvulaceae	Rapona tiliifolia		0	0	0	0	0	0	0
Convolvulaceae	Unknown	teloravina	0	0	1	1	0	1	0
Crassulaceae	Kalanchoe	mongy	0	0	1	1	0	0	0
Cucurbitaceae	Corallocarpus grevei	saritaboara	0	0	1	0	0	0	0
Cucurbitaceae	Lemurosicyos	taboarandolo	0	0	0	0	0	0	0
Cucurbitaceae	Seyrigia multiflora	tsiridambo	0	0	0	0	0	0	0
Cucurbitaceae	Xerosicyos danguyi	tapisabola	0	0	0	0	0	0	0
Dideraceae	Alluaudia procera	fantsiolotra	0	0	0	0	0	0	0
Dioscoreaceae	Dioscorea fandrae	oviala	1	1	1	1	1	1	0
Dioscoreaceae	Dioscorea nako	nako	0	1	1	1	0	1	0
Dioscoreaceae	Dioscorea sp1		1	1	1	1	1	1	0
Ebenaceae	Diospyros latispa	maintifototse	0	0	0	0	0	0	0
Euphorbiaceae	Acalypha decaryana	tainaiaiamena	0	0	0	0	0	0	0
Euphorbiaceae	Acalypha sp.		1	1	1	1	1	1	1
Euphorbiaceae	Alchornea	tanatanga	0	0	0	0	0	0	0
Euphorbiaceae	Croton geayi	kelehagnitse	1	1	0	0	0	0	0

			Orange						
Family	**Species**	**Common name**	**Inf Fem**	**Inf Mal**	**Juv 1 Fem**	**Juv 2 Fem**	**Juv 2 Mal**	**Sub & Adult Fem**	**Sub & Adult Mal**
Nyctaginaceae	Boerhavia coccinea	Boerhaavea	1	0	0	0	0	0	0
Nyctaginaceae	Boerhavia diffusa	beamena	0	0	1	0	0	0	0
Nyctaginaceae	Commicarpus commersoni	bea	1	0	1	1	0	0	1
Olacaceae	Anacolosa pervilleana	tanjaka	0	0	0	0	0	0	0
Oleaceae	Norhonia		0	0	0	1	0	1	0
Oleaceae	Norhonia sp1	mantsandro	0	1	0	0	0	0	0
Oleaceae	Norhonia sp2	tsilaitse	0	0	0	0	0	0	0
Opiliaceae	Pentarhopalopilia	fofotse	0	0	0	0	0	0	0
Papaveraceae	Argemone mexicana	fatiboay	0	0	0	0	0	0	0
Phyllanthaceae	Antidesma petiolare	voafogne	0	0	0	0	0	0	0
Phyllanthaceae	Bridelia	hary	1	0	0	0	0	0	0
Phyllanthaceae	Flueggea obovata	tsikembakemba	0	0	0	0	0	0	0
Phyllanthaceae	Phyllanthus angavensis	sanira	0	0	0	1	0	0	0
Physenaceae	Physena sessiliflora	fandriandrambo	0	0	0	0	1	0	0
Poaceae	grass		0	0	0	1	0	0	0
Poaceae	Sporobols maximus	ahidalo	0	0	0	0	0	0	0
Rhamnaceae	Colubrina sp		0	0	0	0	0	0	0
Rhamnaceae	Gouana	masokara	0	0	0	0	0	0	0
Rhamnaceae	Rhamnaceae		0	0	0	0	0	0	0
Rubiaceae	Enterospermum pruinosum	mantsake	1	0	0	1	1	0	0
Rubiaceae	Gardenia	volivaza	0	0	0	0	0	0	0
Rubiaceae	Paederia grandidieri		0	0	0	0	0	0	0
Rubiaceae	Paederia thouarsiana		0	0	0	0	0	0	0
Salvadoraceae	Azima tetracantha	filofilo	0	0	1	1	0	0	0
Salvadoraceae	Salvadora angustifolia	sasavy	1	1	1	1	1	1	1
Scrophulariaceae	Buddleja sp.		1	0	1	1	0	1	0
Sphaerosepalaceae	Rhopalocarpus lucidus	tsiongake	0	0	0	1	0	0	0
Stilbaceae	Nuxia		0	0	0	0	0	0	0

			Orange						
Family	**Species**	**Common name**	**Inf Fem**	**Inf Mal**	**Juv 1 Fem**	**Juv 2 Fem**	**Juv 2 Mal**	**Sub & Adult Fem**	**Sub & Adult Mal**
Talinaceae	Talinella grevei	dango	1	1	1	1	1	1	1
Xanthorrhoeaceae	Aloe divercata	vahontsoi	0	0	0	0	0	0	1
Unknown	unk		0	0	1	1	1	0	0
Unknown	unk102		0	0	0	0	0	0	0
Unknown	unk119		0	0	0	0	0	0	0
Unknown	unk123		0	0	0	0	0	0	0
Unknown	unk126		1	0	0	0	0	0	0
Unknown	unk135		0	0	0	0	0	0	0
Unknown	unk137		0	0	0	0	0	0	0
Unknown	unk4		0	0	0	0	0	0	0
Unknown	unk42		0	0	0	0	0	0	0
Unknown	unk44		0	0	0	0	0	0	0
Unknown	unk45		0	0	0	0	0	0	0
Unknown	unk57		0	1	0	1	0	0	0
Unknown	unk61		0	0	1	0	0	0	0
Unknown	unk78		0	0	0	0	0	0	0
Unknown		tsakohnako	0	0	0	0	0	1	0
Arthopods									
Araneae	spiderweb		0	0	0	0	0	0	0
Buprestidae	Lampropela rothschildi		0	0	0	0	0	0	0
Cicadidae	Yanga heathii		1	1	0	1	1	1	1
Lepidoptera	unknown	field caterpillar	0	0	0	1	1	1	0
Lepidoptera	Unknown	G. grevei caterpillar	0	0	1	1	1	1	1
Cultigens									
Anacardiaceae	Mangifera indica	mango	1	1	1	1	1	1	0
Cucurbitaceae	melon	saritaboara	1	1	0	0	0	0	0
Solanaceae	Solanum lycopersicum	voatabiha	0	0	0	1	0	0	0
Human refuse									

			Orange						
Family	**Species**	**Common name**	**Inf Fem**	**Inf Mal**	**Juv 1 Fem**	**Juv 2 Fem**	**Juv 2 Mal**	**Sub & Adult Fem**	**Sub & Adult Mal**
	trash		1	1	1	1	1	1	1
Cucurbitaceae	squash	taboara	0	1	0	0	0	0	0
Passifloraceae	Passiflora edulis		0	0	1	0	0	0	0
Bromeliaceae	Ananas comosus	pineapplie	0	0	0	0	1	0	0

			Purple					
Family	**Species**	**Common name**	**Inf Fem**	**Inf Mal**	**Juv 1 Fem**	**Juv 2 Mal**	**Sub & Adult Fem**	**Sub & Adult Mal**
Plants								
Acanthaceae	Ecobilum sp.		0	0	0	1	0	0
Acanthaceae	Justica		0	0	0	0	0	0
Acanthaceae	Neuracanthus		0	0	0	0	0	0
Acanthaceae	Ruellia		0	0	0	0	0	0
Acanthaceae	unknown Acanthaceae	tsake	0	0	0	0	0	0
Amaranthaceae	Achyranthes aspera	tsipotike	0	0	0	0	0	0
Amaranthaceae	Amaranthus spinosa		0	0	0	1	0	0
Apocynaceae	Camptocarpus crassifolius	tamboro	0	0	0	0	0	0
Apocynaceae	Cryptostegia	lombiry	0	0	0	0	0	0
Apocynaceae	Cynanchum	try	0	0	0	0	0	1
Apocynaceae	Gonocrypta	kompitse	0	0	0	0	0	1
Apocynaceae	Landolphia	piravola	1	1	0	1	1	0
Apocynaceae	Marsdenia aff truncata	bokabe	0	0	0	0	0	0
Apocynaceae	Marsdenia sp		0	0	1	0	1	0
Apocynaceae	Pentopetia	tsompia	0	0	0	0	0	0
Apocynaceae	Secamone pachystigma	angalora	1	0	0	1	1	1
Aristolochiaceae	Aristolochia bernieri	tontonga	0	0	0	0	0	0
Asteraceae	Bidens bipinnata		0	0	0	0	0	0
Bignoniaceae	Rhigozum madagascariense	hazontaha	0	0	0	0	0	0
Boraginaceae	Coridia ainensis	malainarety	0	0	0	0	0	0
Burseraceae	Commiphora grandifolia	daromangily	0	1	0	0	0	0
Burseraceae	Commiphora marchandi	darosiky	0	0	0	0	0	0
Cactaceae	Opuntia dilleri	raketa	0	0	0	0	0	0
Capparaceae	Cadaba virgata	ndriamainty	0	0	0	0	0	0
Capparaceae	Capparis chrysomea	roihavitse	0	0	0	1	1	1
Capparaceae	Crateva excelsa	akaly	0	0	0	1	1	1
Capparaceae	Crateva sp1		0	0	0	0	0	0

			Purple					
Family	**Species**	**Common name**	**Inf Fem**	**Inf Mal**	**Juv 1 Fem**	**Juv 2 Mal**	**Sub & Adult Fem**	**Sub & Adult Mal**
Capparaceae	Maerua filiformis	somangy	0	0	0	1	1	0
Capparaceae	Maerus nuda	soamangy	0	0	0	1	0	0
Celastraceae	Gymnosporia linearis	filofilodrano	0	0	0	0	0	0
Celastraceae	Hippocratea angustifolia	vahipinde	0	0	0	0	0	0
Combretaceae	Combretum aff villosum	tamenaka	0	0	0	0	0	0
Combretaceae	Terminalia seyrigii	taly	0	1	0	1	0	0
Convolvulaceae	Ipomea batatus	bageda	0	0	0	0	0	0
Convolvulaceae	Ipomea cairica	velae	0	0	0	0	0	0
Convolvulaceae	Ipomea mojagensis	valae	0	1	1	1	1	1
Convolvulaceae	Ipomea sp1		0	0	0	0	1	1
Convolvulaceae	Metaporana parvifolia	kililo	1	1	1	1	1	1
Convolvulaceae	Rapona multifolia		0	0	0	0	0	0
Convolvulaceae	Rapona tiliifolia		0	0	0	0	0	0
Convolvulaceae	Unknown	teloravina	0	0	0	0	0	0
Crassulaceae	Kalanchoe	mongy	0	0	0	0	0	0
Cucurbitaceae	Corallocarpus grevei	saritaboara	0	0	0	0	0	0
Cucurbitaceae	Lemurosicyos	taboarandolo	0	0	0	1	0	1
Cucurbitaceae	Seyrigia multiflora	tsiridambo	1	1	1	1	1	1
Cucurbitaceae	Xerosicyos danguyi	tapisabola	0	0	0	0	0	1
Dideraceae	Alluaudia procera	fantsiolotra	0	0	1	1	1	1
Dioscoreaceae	Dioscorea fandrae	oviala	0	1	1	1	1	1
Dioscoreaceae	Dioscorea nako	nako	0	1	1	1	1	1
Dioscoreaceae	Dioscorea sp1		1	1	0	1	1	1
Ebenaceae	Diospyros latispa	maintifototse	0	0	0	0	0	0
Euphorbiaceae	Acalypha decaryana	tainaiaiamena	0	0	0	0	0	0
Euphorbiaceae	Acalypha sp.		1	1	0	1	1	0
Euphorbiaceae	Alchornea	tanatanga	0	0	0	0	0	0
Euphorbiaceae	Croton geayi	kelehagnitse	1	1	0	0	1	0

			Purple					
Family	**Species**	**Common name**	**Inf Fem**	**Inf Mal**	**Juv 1 Fem**	**Juv 2 Mal**	**Sub & Adult Fem**	**Sub & Adult Mal**
Fabaceae	Acacia bellula	tratriotse	0	0	1	1	1	1
Fabaceae	Acacia polyphylla	robontsy	0	0	0	0	0	0
Fabaceae	Acacia rovumae	kasia	0	0	0	0	0	0
Fabaceae	Alantsilodendron humbertii		0	0	0	0	0	0
Fabaceae	Albizzia arenicola	halimboron'ala	0	0	0	0	0	0
Fabaceae	Bauhina		0	0	0	0	0	0
Fabaceae	Clitoria sp.		0	0	0	0	0	0
Fabaceae	Tamarindus indica	kily	1	1	1	1	1	1
Hemiptera	Aleuromarginatus millettiae		1	1	0	1	1	1
Hernandiaceae	Gyrocarpus americana	kapaipoty	1	1	1	1	1	1
Lamiaceae	Clerodendrum sp. Cf. emirnense	forimbitike	0	0	0	0	0	1
Lauraceae	Ocotea tricantha	maroanake	1	1	0	1	1	1
Loganiaceae	Strychnos madagascariensis	bakoa	0	0	0	0	0	1
Malvaceae	Abutilon sp.		0	0	0	0	0	0
Malvaceae	Byttneria voululi	sarihasy	0	0	0	0	0	0
Malvaceae	Grewia		0	0	0	0	0	0
Malvaceae	Grewia franciscana	tainkafotse	0	0	1	1	0	1
Malvaceae	Grewia grevei	kotipoke	0	0	0	1	0	0
Malvaceae	Grewia leucophylla	tratramborondreo	1	1	0	0	0	0
Malvaceae	Grewia sp1	selibohoka	1	0	1	1	0	0
Malvaceae	Grewia sp2	vololo	0	0	0	0	0	0
Malvaceae	Grewia trifolia	sely	0	0	0	0	0	0
Malvaceae	Grewia tulearensis	maintifototse	1	1	0	1	1	0
Meliaceae	Cedrelopsis grevei	katrafay	1	1	0	1	1	1
Meliaceae	Quivisianthe papinae	valiandro	0	0	1	1	1	1
Meliaceae	Turrae sp1	malainarete	0	0	0	1	0	0
Meliaceae	Turrae sp2	mote	0	0	0	0	0	0
Moracea	Ficus cocculifolia	adabo	0	0	0	0	0	0

			Purple					
Family	**Species**	**Common name**	**Inf Fem**	**Inf Mal**	**Juv 1 Fem**	**Juv 2 Mal**	**Sub & Adult Fem**	**Sub & Adult Mal**
Nyctaginaceae	Boerhavia coccinea	Boerhaavea	0	0	0	0	0	0
Nyctaginaceae	Boerhavia diffusa	beamena	0	0	0	0	0	0
Nyctaginaceae	Commicarpus commersoni	bea	0	0	0	1	1	0
Olacaceae	Anacolosa pervilleana	tanjaka	1	1	0	1	0	1
Oleaceae	Norhonia		0	0	0	0	0	0
Oleaceae	Norhonia sp1	mantsandro	0	0	0	0	0	0
Oleaceae	Norhonia sp2	tsilaitse	0	0	0	0	0	0
Opiliaceae	Pentarhopalopilia	fofotse	1	1	0	1	1	1
Papaveraceae	Argemone mexicana	fatiboay	0	0	0	0	0	0
Phyllanthaceae	Antidesma petiolare	voafogne	0	0	0	0	0	0
Phyllanthaceae	Bridelia	hary	1	0	0	0	0	0
Phyllanthaceae	Flueggea obovata	tsikembakemba	0	0	0	0	0	0
Phyllanthaceae	Phyllanthus angavensis	sanira	0	0	0	0	0	0
Physenaceae	Physena sessiliflora	fandriandrambo	0	0	0	0	0	0
Poaceae	grass		1	1	0	1	1	1
Poaceae	Sporobols maximus	ahidalo	0	0	0	0	0	0
Rhamnaceae	Colubrina sp		0	0	0	0	0	0
Rhamnaceae	Gouana	masokara	0	0	0	0	0	0
Rhamnaceae	Rhamnaceae		0	0	0	0	0	0
Rubiaceae	Enterospermum pruinosum	mantsake	0	1	1	1	1	1
Rubiaceae	Gardenia	volivaza	0	0	0	0	0	0
Rubiaceae	Paederia grandidieri		0	0	0	0	0	0
Rubiaceae	Paederia thouarsiana		0	0	0	0	0	0
Salvadoraceae	Azima tetracantha	filofilo	1	0	0	1	0	0
Salvadoraceae	Salvadora angustifolia	sasavy	1	1	1	1	1	1
Scrophulariaceae	Buddleja sp.		0	0	0	1	1	1
Sphaerosepalaceae	Rhopalocarpus lucidus	tsiongake	0	1	0	1	1	0
Stilbaceae	Nuxia		0	0	0	1	0	0

			Purple					
Family	**Species**	**Common name**	**Inf Fem**	**Inf Mal**	**Juv 1 Fem**	**Juv 2 Mal**	**Sub & Adult Fem**	**Sub & Adult Mal**
Talinaceae	Talinella grevei	dango	1	1	0	1	1	1
Xanthorrhoeaceae	Aloe divercata	vahontsoi	0	0	0	0	0	0
Unknown	unk		0	1	0	1	1	1
Unknown	unk102		0	0	0	0	0	1
Unknown	unk119		0	0	0	1	0	0
Unknown	unk123		0	0	0	0	0	0
Unknown	unk126		0	0	0	0	0	0
Unknown	unk135		1	0	0	0	0	0
Unknown	unk137		0	0	0	0	0	0
Unknown	unk4		0	0	0	0	0	0
Unknown	unk42		0	0	0	0	1	0
Unknown	unk44		0	0	0	0	0	0
Unknown	unk45		0	0	0	0	0	0
Unknown	unk57		0	0	0	0	0	0
Unknown	unk61		0	0	0	0	0	0
Unknown	unk78		0	0	0	0	0	0
Unknown		tsakohnako	0	0	0	0	0	0
Arthopods								
Araneae	spiderweb		0	0	0	0	0	0
Buprestidae	Lampropela rothschildi		0	0	0	0	0	0
Cicadidae	Yanga heathii		0	0	0	0	0	0
Lepidoptera	unknown	field caterpillar	0	0	0	0	0	0
Lepidoptera	Unknown	G. grevei caterpillar	0	0	0	0	0	0
Cultigens								
Anacardiaceae	Mangifera indica	mango	0	0	0	0	0	0
Cucurbitaceae	melon	saritaboara	0	0	0	0	0	0
Solanaceae	Solanum lycopersicum	voatabiha	0	0	0	0	0	0
Human refuse								

			Purple					
Family	**Species**	**Common name**	**Inf Fem**	**Inf Mal**	**Juv 1 Fem**	**Juv 2 Mal**	**Sub & Adult Fem**	**Sub & Adult Mal**
	trash		0	0	0	0	0	0
Cucurbitaceae	squash	taboara	0	0	0	0	0	0
Passifloraceae	Passiflora edulis		0	0	0	0	0	0
Bromeliaceae	Ananas comosus	pineapplie	0	0	0	0	0	0

			Red					
Family	**Species**	**Common name**	**Inf Fem**	**Inf Mal**	**Juv 1 Fem**	**Juv 1 Mal**	**Sub & Adult Fem**	**Sub & Adult Mal**
Plants								
Acanthaceae	Ecobilum sp.		0	0	0	0	0	0
Acanthaceae	Justica		0	0	0	0	1	0
Acanthaceae	Neuracanthus		0	0	0	0	0	1
Acanthaceae	Ruellia		0	0	0	0	0	0
Acanthaceae	unknown Acanthaceae	tsake	0	0	0	0	0	0
Amaranthaceae	Achyranthes aspera	tsipotike	1	1	1	0	1	1
Amaranthaceae	Amaranthus spinosa		0	0	0	0	0	0
Apocynaceae	Camptocarpus crassifolius	tamboro	0	0	0	0	1	0
Apocynaceae	Cryptostegia	lombiry	0	0	1	0	0	1
Apocynaceae	Cynanchum	try	0	0	0	0	0	0
Apocynaceae	Gonocrypta	kompitse	0	0	1	0	1	1
Apocynaceae	Landolphia	piravola	0	0	1	0	1	1
Apocynaceae	Marsdenia aff truncata	bokabe	0	0	0	0	0	0
Apocynaceae	Marsdenia sp		0	0	0	0	0	0
Apocynaceae	Pentopetia	tsompia	1	1	1	0	1	1
Apocynaceae	Secamone pachystigma	angalora	1	1	1	0	1	1
Aristolochiaceae	Aristolochia bernieri	tontonga	0	0	0	0	0	0
Asteraceae	Bidens bipinnata		0	0	0	0	0	0
Bignoniaceae	Rhigozum madagascariense	hazontaha	0	0	0	0	0	0
Boraginaceae	Coridia ainensis	malainarety	0	0	0	0	0	0
Burseraceae	Commiphora grandifolia	daromangily	0	0	0	0	0	0
Burseraceae	Commiphora marchandi	darosiky	0	0	0	0	0	0
Cactaceae	Opuntia dilleri	raketa	0	0	0	0	0	0
Capparaceae	Cadaba virgata	ndriamainty	0	0	1	0	0	0
Capparaceae	Capparis chrysomea	roihavitse	0	0	0	0	0	0
Capparaceae	Crateva excelsa	akaly	1	1	1	0	1	1
Capparaceae	Crateva sp1		0	1	0	0	0	0

			Red					
Family	**Species**	**Common name**	**Inf Fem**	**Inf Mal**	**Juv 1 Fem**	**Juv 1 Mal**	**Sub & Adult Fem**	**Sub & Adult Mal**
Capparaceae	Maerua filiformis	somangy	0	0	1	0	1	1
Capparaceae	Maerus nuda	soamangy	0	0	0	0	0	0
Celastraceae	Gymnosporia linearis	filofilodrano	0	0	0	0	0	0
Celastraceae	Hippocratea angustifolia	vahipinde	1	1	0	0	1	0
Combretaceae	Combretum aff villosum	tamenaka	0	0	1	0	1	1
Combretaceae	Terminalia seyrigii	taly	0	0	0	0	0	0
Convolvulaceae	Ipomea batatus	bageda	0	0	1	0	1	0
Convolvulaceae	Ipomea cairica	velae	0	0	0	0	0	0
Convolvulaceae	Ipomea mojagensis	valae	0	0	1	0	1	1
Convolvulaceae	Ipomea sp1		0	0	1	1	1	1
Convolvulaceae	Metaporana parvifolia	kililo	1	1	1	0	1	1
Convolvulaceae	Rapona multifolia		0	0	0	0	0	0
Convolvulaceae	Rapona tiliifolia		0	0	0	0	0	0
Convolvulaceae	Unknown	teloravina	0	0	1	0	1	1
Crassulaceae	Kalanchoe	mongy	0	0	0	0	0	0
Cucurbitaceae	Corallocarpus grevei	saritaboara	0	0	0	0	0	0
Cucurbitaceae	Lemurosicyos	taboarandolo	0	0	1	0	1	0
Cucurbitaceae	Seyrigia multiflora	tsiridambo	0	0	1	0	0	0
Cucurbitaceae	Xerosicyos danguyi	tapisabola	0	0	0	0	0	0
Dideraceae	Alluaudia procera	fantsiolotra	0	0	0	0	0	0
Dioscoreaceae	Dioscorea fandrae	oviala	0	0	0	0	1	1
Dioscoreaceae	Dioscorea nako	nako	0	0	0	0	0	1
Dioscoreaceae	Dioscorea sp1		0	0	1	0	1	1
Ebenaceae	Diospyros latispa	maintifototse	0	0	0	0	0	0
Euphorbiaceae	Acalypha decaryana	tainaiaiamena	0	0	0	0	0	0
Euphorbiaceae	Acalypha sp.		0	0	1	0	1	1
Euphorbiaceae	Alchornea	tanatanga	0	0	0	0	0	0
Euphorbiaceae	Croton geayi	kelehagnitse	0	0	0	0	1	0

			Red					
Family	**Species**	**Common name**	**Inf Fem**	**Inf Mal**	**Juv 1 Fem**	**Juv 1 Mal**	**Sub & Adult Fem**	**Sub & Adult Mal**
Fabaceae	Acacia bellula	tratriotse	0	0	0	0	0	0
Fabaceae	Acacia polyphylla	robontsy	0	0	0	0	1	1
Fabaceae	Acacia rovumae	kasia	0	0	0	0	0	0
Fabaceae	Alantsilodendron humbertii		0	0	0	0	0	0
Fabaceae	Albizzia arenicola	halimboron'ala	0	0	0	0	0	0
Fabaceae	Bauhina		0	0	0	0	0	0
Fabaceae	Clitoria sp.		0	0	0	0	0	0
Fabaceae	Tamarindus indica	kily	1	1	1	1	1	1
Hemiptera	Aleuromarginatus millettiae		0	0	1	0	1	1
Hernandiaceae	Gyrocarpus americana	kapaipoty	0	1	1	0	1	1
Lamiaceae	Clerodendrum sp. Cf. emirnense	forimbitike	0	0	0	0	0	1
Lauraceae	Ocotea tricantha	maroanake	0	0	0	0	0	0
Loganiaceae	Strychnos madagascariensis	bakoa	1	0	0	0	1	1
Malvaceae	Abutilon sp.		0	0	0	0	0	0
Malvaceae	Byttneria voululi	sarihasy	0	0	1	0	0	1
Malvaceae	Grewia		0	0	0	0	0	0
Malvaceae	Grewia franciscana	tainkafotse	0	0	1	0	0	0
Malvaceae	Grewia grevei	kotipoke	0	0	0	0	0	0
Malvaceae	Grewia leucophylla	tratramborondreo	0	0	0	0	0	0
Malvaceae	Grewia sp1	selibohoka	0	0	0	0	0	0
Malvaceae	Grewia sp2	vololo	0	0	0	0	0	0
Malvaceae	Grewia trifolia	sely	0	0	0	0	1	0
Malvaceae	Grewia tulearensis	maintifototse	0	0	0	0	0	0
Meliaceae	Cedrelopsis grevei	katrafay	1	1	1	0	1	1
Meliaceae	Quivisianthe papinae	valiandro	0	0	1	0	1	1
Meliaceae	Turrae sp1	malainarete	0	0	0	0	0	1
Meliaceae	Turrae sp2	mote	0	0	0	0	0	1
Moracea	Ficus cocculifolia	adabo	0	0	0	0	0	0

			Red					
Family	**Species**	**Common name**	**Inf Fem**	**Inf Mal**	**Juv 1 Fem**	**Juv 1 Mal**	**Sub & Adult Fem**	**Sub & Adult Mal**
Nyctaginaceae	Boerhavia coccinea	Boerhaavea	0	0	0	0	1	1
Nyctaginaceae	Boerhavia diffusa	beamena	0	0	0	0	0	0
Nyctaginaceae	Commicarpus commersoni	bea	0	0	1	0	1	0
Olacaceae	Anacolosa pervilleana	tanjaka	0	0	1	0	0	0
Oleaceae	Norhonia		0	1	0	0	1	0
Oleaceae	Norhonia sp1	mantsandro	0	1	0	0	0	0
Oleaceae	Norhonia sp2	tsilaitse	0	0	0	0	0	0
Opiliaceae	Pentarhopalopilia	fofotse	0	0	0	0	0	0
Papaveraceae	Argemone mexicana	fatiboay	0	0	0	0	0	0
Phyllanthaceae	Antidesma petiolare	voafogne	0	0	0	0	1	0
Phyllanthaceae	Bridelia	hary	0	0	0	0	0	0
Phyllanthaceae	Flueggea obovata	tsikembakemba	0	0	1	0	0	1
Phyllanthaceae	Phyllanthus angavensis	sanira	0	0	1	0	1	1
Physenaceae	Physena sessiliflora	fandriandrambo	0	0	0	0	0	0
Poaceae	grass		0	0	0	0	0	0
Poaceae	Sporobols maximus	ahidalo	0	0	1	0	0	0
Rhamnaceae	Colubrina sp		0	0	0	0	0	0
Rhamnaceae	Gouana	masokara	0	0	0	0	1	0
Rhamnaceae	Rhamnaceae		0	0	0	0	0	0
Rubiaceae	Enterospermum pruinosum	mantsake	0	1	1	1	1	0
Rubiaceae	Gardenia	volivaza	0	0	1	0	1	1
Rubiaceae	Paederia grandidieri		0	0	0	0	0	0
Rubiaceae	Paederia thouarsiana		0	0	0	0	0	0
Salvadoraceae	Azima tetracantha	filofilo	1	1	1	0	0	0
Salvadoraceae	Salvadora angustifolia	sasavy	0	1	1	0	1	1
Scrophulariaceae	Buddleja sp.		0	0	1	0	0	0
Sphaerosepalaceae	Rhopalocarpus lucidus	tsiongake	0	0	0	0	0	0
Stilbaceae	Nuxia		0	0	0	0	1	0

			Red					
Family	**Species**	**Common name**	**Inf Fem**	**Inf Mal**	**Juv 1 Fem**	**Juv 1 Mal**	**Sub & Adult Fem**	**Sub & Adult Mal**
Talinaceae	Talinella grevei	dango	1	1	1	0	1	1
Xanthorrhoeaceae	Aloe divercata	vahontsoi	0	0	0	0	0	0
Unknown	unk		0	0	1	1	1	1
Unknown	unk102		0	0	0	0	0	0
Unknown	unk119		0	0	0	0	0	0
Unknown	unk123		0	0	0	0	0	0
Unknown	unk126		0	0	0	0	0	0
Unknown	unk135		0	0	0	0	0	0
Unknown	unk137		0	0	0	0	0	0
Unknown	unk4		0	0	0	0	0	0
Unknown	unk42		0	0	0	0	0	0
Unknown	unk44		0	0	0	0	0	0
Unknown	unk45		0	0	0	0	0	0
Unknown	unk57		0	0	0	0	0	0
Unknown	unk61		0	0	0	0	0	0
Unknown	unk78		0	0	0	0	0	0
Unknown		tsakohnako	0	0	0	0	0	0
Arthopods								
Araneae	spiderweb		0	0	0	0	0	0
Buprestidae	Lampropela rothschildi		0	0	0	0	0	0
Cicadidae	Yanga heathii		1	0	0	0	1	1
Lepidoptera	unknown	field caterpillar	0	0	0	0	0	0
Lepidoptera	Unknown	G. grevei caterpillar	0	0	0	0	0	0
Cultigens								
Anacardiaceae	Mangifera indica	mango	0	0	0	0	1	0
Cucurbitaceae	melon	saritaboara	0	0	0	0	0	0
Solanaceae	Solanum lycopersicum	voatabiha	0	0	0	0	1	0
Human refuse								

			Red					
Family	**Species**	**Common name**	**Inf Fem**	**Inf Mal**	**Juv 1 Fem**	**Juv 1 Mal**	**Sub & Adult Fem**	**Sub & Adult Mal**
	trash		0	0	0	0	0	0
Cucurbitaceae	squash	taboara	0	0	0	0	0	0
Passifloraceae	Passiflora edulis		0	0	0	0	0	0
Bromeliaceae	Ananas comosus	pineapplie	0	0	0	0	0	0

			Teal					
Family	**Species**	**Common name**	**Inf Fem**	**Inf Mal**	**Juv 1 Fem**	**Juv 2 Mal**	**Sub & Adult Fem**	**Sub & Adult Mal**
Plants								
Acanthaceae	Ecobilum sp.		0	0	0	0	0	0
Acanthaceae	Justica		0	0	0	0	0	0
Acanthaceae	Neuracanthus		0	1	1	1	1	1
Acanthaceae	Ruellia		0	0	0	0	0	0
Acanthaceae	unknown Acanthaceae	tsake	0	0	0	0	0	0
Amaranthaceae	Achyranthes aspera	tsipotike	0	1	1	1	1	0
Amaranthaceae	Amaranthus spinosa		0	0	0	0	0	0
Apocynaceae	Camptocarpus crassifolius	tamboro	0	1	1	1	1	0
Apocynaceae	Cryptostegia	lombiry	0	0	1	1	1	1
Apocynaceae	Cynanchum	try	0	1	0	0	0	0
Apocynaceae	Gonocrypta	kompitse	0	0	1	1	1	0
Apocynaceae	Landolphia	piravola	0	1	1	1	1	0
Apocynaceae	Marsdenia aff truncata	bokabe	0	0	0	0	0	0
Apocynaceae	Marsdenia sp		0	0	0	0	0	0
Apocynaceae	Pentopetia	tsompia	0	1	1	1	1	1
Apocynaceae	Secamone pachystigma	angalora	1	1	1	1	1	1
Aristolochiaceae	Aristolochia bernieri	tontonga	0	0	0	0	0	0
Asteraceae	Bidens bipinnata		0	0	0	0	0	0
Bignoniaceae	Rhigozum madagascariense	hazontaha	0	0	0	0	0	0
Boraginaceae	Coridia ainensis	malainarety	0	0	0	0	0	0
Burseraceae	Commiphora grandifolia	daromangily	0	0	0	0	0	0
Burseraceae	Commiphora marchandi	darosiky	0	0	0	0	0	0
Cactaceae	Opuntia dilleri	raketa	0	0	0	0	0	0
Capparaceae	Cadaba virgata	ndriamainty	0	0	0	0	0	0
Capparaceae	Capparis chrysomea	roihavitse	0	0	1	0	1	1
Capparaceae	Crateva excelsa	akaly	0	1	0	1	1	1
Capparaceae	Crateva sp1		0	0	0	0	0	0

			Teal					
Family	**Species**	**Common name**	**Inf Fem**	**Inf Mal**	**Juv 1 Fem**	**Juv 2 Mal**	**Sub & Adult Fem**	**Sub & Adult Mal**
Capparaceae	Maerua filiformis	somangy	0	0	1	1	1	0
Capparaceae	Maerus nuda	soamangy	0	0	0	0	0	0
Celastraceae	Gymnosporia linearis	filofilodrano	0	0	0	0	0	0
Celastraceae	Hippocratea angustifolia	vahipinde	0	0	0	0	0	0
Combretaceae	Combretum aff villosum	tamenaka	0	0	0	0	0	0
Combretaceae	Terminalia seyrigii	taly	0	0	0	0	0	0
Convolvulaceae	Ipomea batatus	bageda	0	0	0	0	0	0
Convolvulaceae	Ipomea cairica	velae	0	0	0	0	0	0
Convolvulaceae	Ipomea mojagensis	valae	0	0	1	1	1	1
Convolvulaceae	Ipomea sp1		0	0	1	0	0	0
Convolvulaceae	Metaporana parvifolia	kililo	1	1	1	1	1	1
Convolvulaceae	Rapona multifolia		0	0	1	0	0	0
Convolvulaceae	Rapona tiliifolia		0	0	0	1	0	0
Convolvulaceae	Unknown	teloravina	0	0	1	0	0	0
Crassulaceae	Kalanchoe	mongy	0	0	0	0	0	0
Cucurbitaceae	Corallocarpus grevei	saritaboara	0	0	0	0	0	0
Cucurbitaceae	Lemurosicyos	taboarandolo	0	0	0	0	0	0
Cucurbitaceae	Seyrigia multiflora	tsiridambo	1	0	1	0	0	0
Cucurbitaceae	Xerosicyos danguyi	tapisabola	0	0	0	0	0	0
Dideraceae	Alluaudia procera	fantsiolotra	0	0	0	0	0	0
Dioscoreaceae	Dioscorea fandrae	oviala	1	1	1	1	1	0
Dioscoreaceae	Dioscorea nako	nako	0	0	1	1	0	0
Dioscoreaceae	Dioscorea sp1		1	1	1	1	1	0
Ebenaceae	Diospyros latispa	maintifototse	0	0	0	0	0	0
Euphorbiaceae	Acalypha decaryana	tainaiaiamena	0	0	0	0	1	0
Euphorbiaceae	Acalypha sp.		0	0	0	0	1	0
Euphorbiaceae	Alchornea	tanatanga	0	0	0	0	0	0
Euphorbiaceae	Croton geayi	kelehagnitse	0	0	0	0	0	0

			Teal					
Family	**Species**	**Common name**	**Inf Fem**	**Inf Mal**	**Juv 1 Fem**	**Juv 2 Mal**	**Sub & Adult Fem**	**Sub & Adult Mal**
Fabaceae	Acacia bellula	tratriotse	0	0	1	1	1	1
Fabaceae	Acacia polyphylla	robontsy	0	0	0	0	1	0
Fabaceae	Acacia rovumae	kasia	0	0	0	0	0	0
Fabaceae	Alantsilodendron humbertii		0	0	0	0	0	0
Fabaceae	Albizzia arenicola	halimboron'ala	0	0	0	0	0	0
Fabaceae	Bauhina		0	0	0	0	0	0
Fabaceae	Clitoria sp.		0	0	0	1	0	0
Fabaceae	Tamarindus indica	kily	1	1	1	1	1	1
Hemiptera	Aleuromarginatus millettiae		1	1	1	1	1	1
Hernandiaceae	Gyrocarpus americana	kapaipoty	1	0	1	1	1	1
Lamiaceae	Clerodendrum sp. Cf. emirnense	forimbitike	0	0	0	0	0	0
Lauraceae	Ocotea tricantha	maroanake	0	0	0	0	0	0
Loganiaceae	Strychnos madagascariensis	bakoa	0	0	0	1	0	0
Malvaceae	Abutilon sp.		0	0	0	0	0	0
Malvaceae	Byttneria voululi	sarihasy	0	1	0	0	0	0
Malvaceae	Grewia		0	0	0	0	0	0
Malvaceae	Grewia franciscana	tainkafotse	1	0	1	1	1	0
Malvaceae	Grewia grevei	kotipoke	0	0	1	0	1	0
Malvaceae	Grewia leucophylla	tratramborondreo	0	1	1	0	0	0
Malvaceae	Grewia sp1	selibohoka	0	1	1	1	0	0
Malvaceae	Grewia sp2	vololo	0	0	0	0	0	0
Malvaceae	Grewia trifolia	sely	0	0	0	1	0	0
Malvaceae	Grewia tulearensis	maintifototse	1	0	0	1	0	0
Meliaceae	Cedrelopsis grevei	katrafay	1	1	1	1	1	1
Meliaceae	Quivisianthe papinae	valiandro	0	0	1	1	1	1
Meliaceae	Turrae sp1	malainarete	0	0	0	0	1	0
Meliaceae	Turrae sp2	mote	0	0	0	0	0	0
Moracea	Ficus cocculifolia	adabo	0	0	0	0	0	0

			Teal					
Family	**Species**	**Common name**	**Inf Fem**	**Inf Mal**	**Juv 1 Fem**	**Juv 2 Mal**	**Sub & Adult Fem**	**Sub & Adult Mal**
Nyctaginaceae	Boerhavia coccinea	Boerhaavea	0	0	0	0	0	0
Nyctaginaceae	Boerhavia diffusa	beamena	0	0	0	0	0	0
Nyctaginaceae	Commicarpus commersoni	bea	0	0	0	0	0	0
Olacaceae	Anacolosa pervilleana	tanjaka	1	0	0	0	1	0
Oleaceae	Norhonia		0	0	0	0	0	0
Oleaceae	Norhonia sp1	mantsandro	0	0	0	0	0	0
Oleaceae	Norhonia sp2	tsilaitse	0	0	0	0	0	0
Opiliaceae	Pentarhopalopilia	fofotse	0	0	0	0	0	0
Papaveraceae	Argemone mexicana	fatiboay	0	0	0	0	0	0
Phyllanthaceae	Antidesma petiolare	voafogne	0	0	0	0	0	0
Phyllanthaceae	Bridelia	hary	0	0	1	0	0	0
Phyllanthaceae	Flueggea obovata	tsikembakemba	0	1	1	1	1	0
Phyllanthaceae	Phyllanthus angavensis	sanira	0	0	0	0	0	0
Physenaceae	Physena sessiliflora	fandriandrambo	0	0	0	0	0	0
Poaceae	grass		1	1	1	0	0	0
Poaceae	Sporobols maximus	ahidalo	1	1	0	1	1	1
Rhamnaceae	Colubrina sp		0	0	0	0	0	0
Rhamnaceae	Gouana	masokara	0	0	0	0	0	0
Rhamnaceae	Rhamnaceae		0	1	1	0	0	0
Rubiaceae	Enterospermum pruinosum	mantsake	1	1	1	1	1	1
Rubiaceae	Gardenia	volivaza	0	0	0	1	0	0
Rubiaceae	Paederia grandidieri		0	0	1	0	0	0
Rubiaceae	Paederia thouarsiana		0	0	0	0	0	0
Salvadoraceae	Azima tetracantha	filofilo	0	0	0	0	1	0
Salvadoraceae	Salvadora angustifolia	sasavy	1	1	1	1	1	1
Scrophulariaceae	Buddleja sp.		0	0	0	1	1	0
Sphaerosepalaceae	Rhopalocarpus lucidus	tsiongake	0	1	1	0	0	0
Stilbaceae	Nuxia		0	0	0	0	1	0

			Teal					
Family	**Species**	**Common name**	**Inf Fem**	**Inf Mal**	**Juv 1 Fem**	**Juv 2 Mal**	**Sub & Adult Fem**	**Sub & Adult Mal**
Talinaceae	Talinella grevei	dango	1	1	1	1	1	1
Xanthorrhoeaceae	Aloe divercata	vahontsoi	0	0	0	0	0	0
Unknown	unk		1	1	1	1	1	1
Unknown	unk102		0	0	0	0	0	0
Unknown	unk119		0	0	0	0	0	0
Unknown	unk123		0	0	0	0	0	0
Unknown	unk126		0	0	0	0	0	0
Unknown	unk135		0	0	0	0	0	0
Unknown	unk137		0	0	0	0	0	0
Unknown	unk4		0	0	0	0	0	0
Unknown	unk42		0	0	0	0	0	0
Unknown	unk44		0	0	0	0	0	0
Unknown	unk45		0	0	0	0	0	0
Unknown	unk57		0	0	0	0	0	0
Unknown	unk61		0	0	0	0	0	0
Unknown	unk78		0	0	0	0	1	0
Unknown		tsakohnako	0	0	1	1	0	1
Arthopods								
Araneae	spiderweb		0	0	1	0	0	0
Buprestidae	Lampropela rothschildi		0	0	0	0	0	0
Cicadidae	Yanga heathii		1	1	1	1	1	0
Lepidoptera	unknown	field caterpillar	0	0	0	0	0	0
Lepidoptera	Unknown	G. grevei caterpillar	0	0	0	0	0	0
Cultigens								
Anacardiaceae	Mangifera indica	mango	0	0	0	0	0	0
Cucurbitaceae	melon	saritaboara	0	0	0	0	0	0
Solanaceae	Solanum lycopersicum	voatabiha	0	0	0	0	0	0
Human refuse								

			Teal					
Family	**Species**	**Common name**	**Inf Fem**	**Inf Mal**	**Juv 1 Fem**	**Juv 2 Mal**	**Sub & Adult Fem**	**Sub & Adult Mal**
	trash		0	0	0	0	0	0
Cucurbitaceae	squash	taboara	0	0	0	0	0	0
Passifloraceae	Passiflora edulis		0	0	0	0	0	0
Bromeliaceae	Ananas comosus	pineapplie	0	0	0	0	0	0

Family	Species	Common name	Yellow Inf Fem	Inf Mal	Juv 1 Mal	Sub & Adult Fem	Sub & Adult Mal
Plants							
Acanthaceae	Ecobilum sp.		0	0	0	0	0
Acanthaceae	Justica		0	0	0	0	0
Acanthaceae	Neuracanthus		0	0	0	0	0
Acanthaceae	Ruellia		0	0	0	0	0
Acanthaceae	unknown Acanthaceae	tsake	0	0	0	0	0
Amaranthaceae	Achyranthes aspera	tsipotike	0	0	0	1	1
Amaranthaceae	Amaranthus spinosa		0	0	0	0	0
Apocynaceae	Camptocarpus crassifolius	tamboro	1	0	1	1	1
Apocynaceae	Cryptostegia	lombiry	0	1	0	0	0
Apocynaceae	Cynanchum	try	1	0	1	0	0
Apocynaceae	Gonocrypta	kompitse	0	0	0	1	1
Apocynaceae	Landolphia	piravola	0	0	0	1	0
Apocynaceae	Marsdenia aff truncata	bokabe	0	0	0	0	0
Apocynaceae	Marsdenia sp		0	0	0	0	0
Apocynaceae	Pentopetia	tsompia	1	1	1	1	1
Apocynaceae	Secamone pachystigma	angalora	0	0	1	1	1
Aristolochiaceae	Aristolochia bernieri	tontonga	0	0	1	0	0
Asteraceae	Bidens bipinnata		0	0	0	1	0
Bignoniaceae	Rhigozum madagascariense	hazontaha	0	0	0	1	0
Boraginaceae	Coridia ainensis	malainarety	0	0	0	1	0
Burseraceae	Commiphora grandifolia	daromangily	0	0	0	0	0
Burseraceae	Commiphora marchandi	darosiky	0	0	0	0	0
Cactaceae	Opuntia dilleri	raketa	1	0	0	0	0
Capparaceae	Cadaba virgata	ndriamainty	0	0	0	0	0
Capparaceae	Capparis chrysomea	roihavitse	1	0	1	0	0
Capparaceae	Crateva excelsa	akaly	1	1	1	1	1
Capparaceae	Crateva sp1		0	0	0	0	0

			Yellow				
Family	**Species**	**Common name**	**Inf Fem**	**Inf Mal**	**Juv 1 Mal**	**Sub & Adult Fem**	**Sub & Adult Mal**
Capparaceae	Maerua filiformis	somangy	1	0	1	1	1
Capparaceae	Maerus nuda	soamangy	0	0	0	0	0
Celastraceae	Gymnosporia linearis	filofilodrano	0	0	1	1	0
Celastraceae	Hippocratea angustifolia	vahipinde	1	0	1	1	1
Combretaceae	Combretum aff villosum	tamenaka	0	0	1	1	1
Combretaceae	Terminalia seyrigii	taly	0	0	0	0	0
Convolvulaceae	Ipomea batatus	bageda	0	0	0	1	0
Convolvulaceae	Ipomea cairica	velae	0	0	0	0	0
Convolvulaceae	Ipomea mojagensis	valae	0	0	1	1	1
Convolvulaceae	Ipomea sp1		0	0	0	0	0
Convolvulaceae	Metaporana parvifolia	kililo	1	1	1	1	1
Convolvulaceae	Rapona multifolia		0	0	0	0	0
Convolvulaceae	Rapona tiliifolia		0	0	0	0	0
Convolvulaceae	Unknown	teloravina	0	0	0	0	0
Crassulaceae	Kalanchoe	mongy	0	0	0	0	0
Cucurbitaceae	Corallocarpus grevei	saritaboara	0	0	0	0	0
Cucurbitaceae	Lemurosicyos	taboarandolo	0	0	0	0	0
Cucurbitaceae	Seyrigia multiflora	tsiridambo	0	0	0	0	0
Cucurbitaceae	Xerosicyos danguyi	tapisabola	0	0	0	0	0
Dideraceae	Alluaudia procera	fantsiolotra	0	0	0	0	0
Dioscoreaceae	Dioscorea fandrae	oviala	1	0	1	1	1
Dioscoreaceae	Dioscorea nako	nako	0	0	0	1	0
Dioscoreaceae	Dioscorea sp1		1	1	1	1	1
Ebenaceae	Diospyros latispa	maintifototse	0	0	0	0	0
Euphorbiaceae	Acalypha decaryana	tainaiaiamena	0	0	1	0	0
Euphorbiaceae	Acalypha sp.		0	0	0	0	0
Euphorbiaceae	Alchornea	tanatanga	1	0	0	0	0
Euphorbiaceae	Croton geayi	kelehagnitse	0	0	0	0	0

			Yellow				
Family	**Species**	**Common name**	**Inf Fem**	**Inf Mal**	**Juv 1 Mal**	**Sub & Adult Fem**	**Sub & Adult Mal**
Fabaceae	Acacia bellula	tratriotse	0	0	1	1	1
Fabaceae	Acacia polyphylla	robontsy	0	0	0	0	0
Fabaceae	Acacia rovumae	kasia	1	0	0	0	0
Fabaceae	Alantsilodendron humbertii		0	0	0	0	0
Fabaceae	Albizzia arenicola	halimboron'ala	0	0	0	0	0
Fabaceae	Bauhina		0	0	0	0	0
Fabaceae	Clitoria sp.		0	0	0	1	0
Fabaceae	Tamarindus indica	kily	1	1	1	1	1
Hemiptera	Aleuromarginatus millettiae		1	0	1	1	1
Hernandiaceae	Gyrocarpus americana	kapaipoty	1	1	1	1	1
Lamiaceae	Clerodendrum sp. Cf. emirnense	forimbitike	0	0	0	1	1
Lauraceae	Ocotea tricantha	maroanake	0	0	0	0	0
Loganiaceae	Strychnos madagascariensis	bakoa	1	1	1	1	1
Malvaceae	Abutilon sp.		0	0	0	0	1
Malvaceae	Byttneria voululi	sarihasy	1	0	1	1	0
Malvaceae	Grewia		0	0	0	0	0
Malvaceae	Grewia franciscana	tainkafotse	1	0	0	1	1
Malvaceae	Grewia grevei	kotipoke	0	0	1	0	0
Malvaceae	Grewia leucophylla	tratramborondreo	1	1	1	1	1
Malvaceae	Grewia sp1	selibohoka	0	0	0	0	0
Malvaceae	Grewia sp2	vololo	0	0	1	0	0
Malvaceae	Grewia trifolia	sely	0	0	0	0	0
Malvaceae	Grewia tulearensis	maintifototse	1	1	0	1	0
Meliaceae	Cedrelopsis grevei	katrafay	1	1	1	1	1
Meliaceae	Quivisianthe papinae	valiandro	1	0	1	1	1
Meliaceae	Turrae sp1	malainarete	0	0	0	0	0
Meliaceae	Turrae sp2	mote	0	0	0	0	0
Moracea	Ficus cocculifolia	adabo	0	0	0	0	0

			Yellow				
Family	**Species**	**Common name**	**Inf Fem**	**Inf Mal**	**Juv 1 Mal**	**Sub & Adult Fem**	**Sub & Adult Mal**
Nyctaginaceae	Boerhavia coccinea	Boerhaavea	0	0	0	0	0
Nyctaginaceae	Boerhavia diffusa	beamena	0	0	0	0	0
Nyctaginaceae	Commicarpus commersoni	bea	1	0	1	1	1
Olacaceae	Anacolosa pervilleana	tanjaka	1	1	1	1	1
Oleaceae	Norhonia		0	0	0	0	0
Oleaceae	Norhonia sp1	mantsandro	0	0	0	0	0
Oleaceae	Norhonia sp2	tsilaitse	0	0	0	0	0
Opiliaceae	Pentarhopalopilia	fofotse	0	0	0	0	0
Papaveraceae	Argemone mexicana	fatiboay	0	0	0	0	0
Phyllanthaceae	Antidesma petiolare	voafogne	0	0	0	0	0
Phyllanthaceae	Bridelia	hary	0	0	0	0	0
Phyllanthaceae	Flueggea obovata	tsikembakemba	0	0	0	0	0
Phyllanthaceae	Phyllanthus angavensis	sanira	0	0	0	0	0
Physenaceae	Physena sessiliflora	fandriandrambo	0	0	0	0	0
Poaceae	grass		0	0	0	0	0
Poaceae	Sporobols maximus	ahidalo	0	0	1	0	0
Rhamnaceae	Colubrina sp		0	0	0	0	1
Rhamnaceae	Gouana	masokara	0	0	1	0	1
Rhamnaceae	Rhamnaceae		0	0	0	0	0
Rubiaceae	Enterospermum pruinosum	mantsake	0	1	1	1	1
Rubiaceae	Gardenia	volivaza	0	0	0	0	0
Rubiaceae	Paederia grandidieri		0	0	0	0	0
Rubiaceae	Paederia thouarsiana		0	0	0	0	0
Salvadoraceae	Azima tetracantha	filofilo	1	0	0	1	0
Salvadoraceae	Salvadora angustifolia	sasavy	1	1	1	1	1
Scrophulariaceae	Buddleja sp.		0	0	1	1	1
Sphaerosepalaceae	Rhopalocarpus lucidus	tsiongake	0	0	0	0	0
Stilbaceae	Nuxia		0	0	0	0	0

			Yellow				
Family	**Species**	**Common name**	**Inf Fem**	**Inf Mal**	**Juv 1 Mal**	**Sub & Adult Fem**	**Sub & Adult Mal**
Talinaceae	Talinella grevei	dango	1	1	1	1	1
Xanthorrhoeaceae	Aloe divercata	vahontsoi	0	0	0	0	0
Unknown	unk		0	0	0	1	1
Unknown	unk102		0	0	0	0	0
Unknown	unk119		0	0	0	0	0
Unknown	unk123		0	0	0	0	0
Unknown	unk126		0	0	0	0	0
Unknown	unk135		0	0	0	0	0
Unknown	unk137		0	0	0	0	0
Unknown	unk4		0	0	0	0	0
Unknown	unk42		0	0	0	0	0
Unknown	unk44		0	0	1	0	0
Unknown	unk45		0	0	0	0	0
Unknown	unk57		0	0	0	0	0
Unknown	unk61		0	0	0	0	0
Unknown	unk78		0	0	0	0	0
Unknown		tsakohnako	0	0	0	0	0
Arthopods							
Araneae	spiderweb		0	0	0	1	0
Buprestidae	Lampropela rothschildi		0	0	0	0	0
Cicadidae	Yanga heathii		1	0	1	1	0
Lepidoptera	unknown	field caterpillar	0	0	0	0	0
Lepidoptera	Unknown	G. grevei caterpillar	0	0	0	0	0
Cultigens							
Anacardiaceae	Mangifera indica	mango	0	0	1	1	1
Cucurbitaceae	melon	saritaboara	0	0	0	0	0
Solanaceae	Solanum lycopersicum	voatabiha	0	0	0	0	0
Human refuse							

			Yellow				
Family	**Species**	**Common name**	**Inf Fem**	**Inf Mal**	**Juv 1 Mal**	**Sub & Adult Fem**	**Sub & Adult Mal**
	trash		0	0	0	1	0
Cucurbitaceae	squash	taboara	0	0	0	0	0
Passifloraceae	Passiflora edulis		0	0	0	0	0
Bromeliaceae	Ananas comosus	pineapplie	0	0	0	0	0

APPENDIX E

INSTITUTIONAL ANIMAL CARE AND USE COMMITTEE (IACUC) APPROVAL

Institutional Animal Care and Use Committee (IACUC)
Arizona State University

Tempe, Arizona 85287-1103
(480) 965-2179 FAX: (480) 965-7772

Animal Protocol Review

Protocol Number:	08-983R
Protocol Title:	Development of Sex Differences in Ring-Tailed Lemur Feeding Ecology
Principal Investigator:	Leanne Nash
Date of Action:	03/27/2008

The animal protocol review was considered by the Committee and the following decisions were made:

☒ The original protocol was APPROVED as presented.
☐ The revised protocol was APPROVED as presented.
☐ The protocol was APPROVED with RESTRICTIONS or CHANGES as noted below. The project can only be pursued, subject to your acceptance of these restriction or changes. If you are not agreeable, contact the IACUC Chairperson immediately.
☐ The Committee requests CLARIFICATIONS or CHANGES in the protocol as described in the attached memorandum. The protocol will be reconsidered when these issues are clarified and the revised protocol is submitted.
☐ The protocol was approved, subject to the approval of a WAIVER of provisions of NIH policy as noted below. Waivers require written approval from the granting agencies.
☐ The protocol was DISAPPROVED for reasons outlined in the attached memorandum.
☐ The Committee requests you to contact ________________ to discuss this proposal.
☐ A copy of this correspondence has been sent to the Vice President for Research.
☐ Amendment was approved as presented.

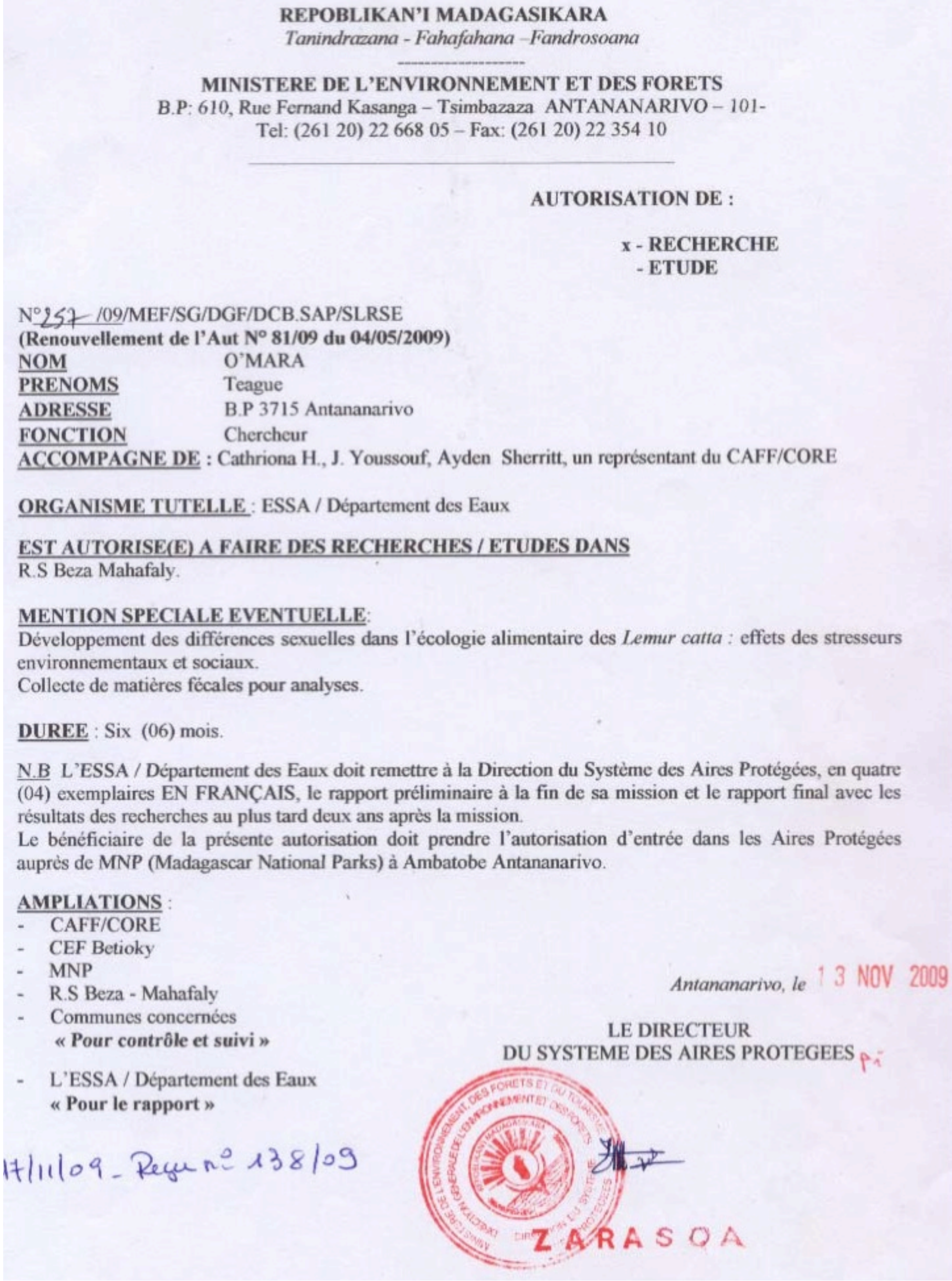
RESTRICTIONS, CHANGES OR WAIVER REQUIREMENT: None
Approved # of Animals: 48 Ring-Tailed Lemur **Pain Level:** C
Approval Period: 03/27/2008 - 03/26/2011
Granting Agency: National Science Foundation
Proposal Number: 0824572
Proposal Title: Development of sex differences in ring-tailed lemur feeding ecology: Effects of social and environmental stressors

Signature: ______________________________ Date: 3/28/08
IACUC Chair or Designee

Original: Principal Investigator
cc: IACUC Office
IACUC Chair
ORSPA/SPS

APPENDIX F

MADAGASCAR NATIONAL PARKS PERMIT



REPOBLIKAN'I MADAGASIKARA
Tanindrazana - Fahafahana –Fandrosoana

MINISTERE DE L'ENVIRONNEMENT ET DES FORETS
B.P: 610, Rue Fernand Kasanga – Tsimbazaza ANTANANARIVO – 101-
Tel: (261 20) 22 668 05 – Fax: (261 20) 22 354 10

AUTORISATION DE :

x - RECHERCHE
- ETUDE

N°257 /09/MEF/SG/DGF/DCB.SAP/SLRSE
(Renouvellement de l'Aut N° 81/09 du 04/05/2009)
NOM O'MARA
PRENOMS Teague
ADRESSE B.P 3715 Antananarivo
FONCTION Chercheur
ACCOMPAGNE DE : Cathriona H., J. Youssouf, Ayden Sherritt, un représentant du CAFF/CORE

ORGANISME TUTELLE : ESSA / Département des Eaux

EST AUTORISE(E) A FAIRE DES RECHERCHES / ETUDES DANS
R.S Beza Mahafaly.

MENTION SPECIALE EVENTUELLE:
Développement des différences sexuelles dans l'écologie alimentaire des *Lemur catta :* effets des stresseurs environnementaux et sociaux.
Collecte de matières fécales pour analyses.

DUREE : Six (06) mois.

N.B L'ESSA / Département des Eaux doit remettre à la Direction du Système des Aires Protégées, en quatre (04) exemplaires EN FRANÇAIS, le rapport préliminaire à la fin de sa mission et le rapport final avec les résultats des recherches au plus tard deux ans après la mission.
Le bénéficiaire de la présente autorisation doit prendre l'autorisation d'entrée dans les Aires Protégées auprès de MNP (Madagascar National Parks) à Ambatobe Antananarivo.

AMPLIATIONS :
- CAFF/CORE
- CEF Betioky
- MNP
- R.S Beza - Mahafaly
- Communes concernées
  « Pour contrôle et suivi »
- L'ESSA / Département des Eaux
  « Pour le rapport »

Antananarivo, le 13 NOV 2009

LE DIRECTEUR
DU SYSTEME DES AIRES PROTEGEES Pi

ZARASOA

17/11/09 - Reçu n° 138/09