Infant Development and Maternal Strategies in the Two Largest Lemurs: The Diademed Sifaka (*Propithecus diadema*) and the Indri (*Indri indri*).

by

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B.Sc., The University of British Columbia, 2002
M.Sc., Texas A&M University, 2007

A Dissertation Submitted in Partial Fulfillment
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University of Victoria

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ABSTRACT

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At least half of the world's primate species are currently threatened with extinction. Slow life histories combined with rapid habitat loss and hunting in recent years has heightened the extinction risk for many species, including the two largest extant lemurs, the diademed sifaka (*Propithecus diadema*) and the indri (*Indri indri*). Both species belong to the taxonomic family Indriidae, have similar adult weights, and occur in sympatry in certain areas of the montane rainforests of eastern Madagascar. Both species are adapted for folivory however *I. indri* spend considerably more time feeding on leaves than do *P. diadema* resulting in several energy-saving adaptations in *I.indri*. In this dissertation, I explore infant development and maternal strategies of these critically endangered primates with the goal of increasing our knowledge of reproduction and ontogeny in both species. Although previous studies have elucidated key differences in adult behaviour, there is a dearth of information on infants and lactating females in either of these two species. Between June and December of 2011 and 2012, I collected continuous time focal animal data, in Maromizaha forest, to examine behavioural patterns of 12 infants and their mothers from 0 – 33 weeks. In addition, I developed a framework to define and quantify the weaning process and facilitate comparisons across different species and studies. *P. diadema* infants developed feeding competency and independent locomotion faster than did *I. indri* infants however both species were consistently feeding independently more than they were suckling by week 20. The process of feeding ontogeny in *I. indri* was likely accelerated by coprophagy, as all infants of this species consumed their mother’s feces regularly from 10 – 15 weeks old. Lactating females of both species spent more time feeding in mid-lactation when maternal investment was the highest. The prolonged inter-birth interval in *I. indri* is suggested as another adaptation that reduces energetic expenditures. In addition, the protracted period of close contact with their mother may offer infant *I. indri* more time for social learning of the mother’s diet and the group song and for developing competency in vertical clinging and leaping without a tail for balance and support.

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For the lemurs of Maromizaha,
May you always flourish in this enchanting forest

1 - INTRODUCTION

1.1 Extinction risk, Madagascar, and the challenges facing lemur conservation

Approximately one quarter of the world's 5,506 mammal species are now threatened with a high, very high, or extremely high risk of extinction (IUCN 2013). The ultimate causes of extinction are human population density and growth (McKee et al. 2004; McKee et al. 2013). In countries where there are high densities of human inhabitants and in particular in areas where the number of people are growing, the suitable habitat remaining for wild species is becoming dramatically reduced and increasingly fragmented (Fahrig 2003; Woog et al. 2006). Moreover, the quality of the resources available to wildlife species frequently has deteriorated due to human alteration and removal of natural vegetation for agricultural areas and human habitation (McKee et al. 2004; McKee et al. 2013). In countries where human poverty is significant, many animals are additionally threatened by direct hunting for food or for monetary incentives (Brashares et al. 2004).

At least half of the world's primate species are currently listed as Critically Endangered, Endangered or Vulnerable by IUCN Red List criteria (IUCN 2013). Habitat loss and hunting are the two major direct threats to primate conservation (Oates 2013) and there are an increasing number studies documenting declining primate populations worldwide (ex. Uganda, Chapman et al. 2012; India, Srivastava et al. 2001; Madagascar, Schwitzer et al. 2014). There is an urgent need for change and for action if we are to prevent human-caused extinctions in the near future (Oates 2013; McKee et al. 2013). Of the 25 most endangered primates in the world five species are from Africa, six are from Madagascar, nine are from Asia and five are from the Neotropics (Mittermeier et al.

2012). As a country, Madagascar is home to more endangered primates than any other country in the world (Mittermeier et al. 2012).

The island nation of Madagascar is considered to be one of, if not the highest priority biodiversity hotspot in the world (Schwitzer et al. 2014). Having been isolated from other landmasses for the past 88 million years and from mainland Africa for at least 130 million years, Madagascar exhibits an extremely high level of endemism at the species, genus and family levels (Tattersall & Sussman 1975). The island is home to 480 endemic genera and 26 endemic families, more than any other place on earth (Schwitzer et al. 2013). All of Madagascar's 103 primate taxa are endemic, and these represent 20% of all the primate species in the world (Schwitzer et al. 2014). Brazil is the only country with more primate taxa than Madagascar. However at 587,015 km^2 the latter has only 7% of the former's land area leading to a much higher concentration of species (Schwitzer et al. 2013). In addition, due to the large-scale deforestation, only 10 – 20% of Madagascar's surface area remains as natural forest, and therefore all 103 species inhabit areas that when combined, approximately totals the size of Nova Scotia, Canada's second smallest province (Nova Scotia is 55,284 km^2 and according to Schwitzer et al. 2013, the remaining suitable habitat for lemurs is estimated to be between 50,000-60,000 km^2).

As predicted by McKee et al. (2004), high human population density, population growth and poverty, coupled with species richness, has led to a high, very high, or extremely high extinction risk for many species primates in Madagascar, as it has for primates in Africa (ex. Chapman et al. 2012) and Asia (ex. Srivastava et al. 2001). Currently, of the 103 known lemur taxa, 24 are Critically Endangered, 49 are Endangered and 20 are Vulnerable (IUCN 2014). The illegal hunting of lemurs for bushmeat (Jenkins et al. 2011) combined with the rapid loss of their habitat due to mining, slash and burn agriculture, and the illegal logging of rosewood and ebony are the main reasons why many species are threatened with extinction by the end of the decade (Schwitzer et al. 2013; Schwitzer et al. 2014). According to Rakotomanana et al. (2013), the primary conservation challenges for Madagascar in the next decade will include stopping illegal hunting, supporting the country's protected area (PA) network, and promoting science as a tool to support conservation. Schwitzer et al. (2014) explain how lemur conservation has been additionally threatened by the 2009 political crisis and the instability that it has caused, including the withdrawal of international aid from the country. There is hope that President Hery Rajaonarimampianina, elected in December of 2013, will bring effective governance back to Madagascar and that this will, in turn, facilitate the resumption of international aid and conservation programs. Indeed, in May 2014 the World Bank announced that it would provide Madagascar with $400 million in financial support over the next three years (Reuters Africa), and the World Wildlife Fund (WWF) and Madagascar National Parks (MNP) have formed a new partnership aimed at protecting Madagascar’s unique biodiversity (wwf.panda.org/wwf_news/?221892/New-era-for-environmental-protection-in-Madagascar).

In addition to the threats inherent with inhabiting areas with rapid human population increases and the associated loss of habitat, many primates possess specific life-history characteristics that also put them at a higher risk of extinction. For example, mammalian taxa that reproduce slowly, and thus produce few offspring over the course of their lifetime, have a reduced reproductive effort and are consequently more susceptible to population declines (Jones 2011). For example Hector's dolphins (*Cephalorhynchus hectori*), Amur tigers (*Panthera tigris altaica*) and black rhinoceros (*Diceros bicornis*) only produce offspring every 2 – 3 years and are all highly endangered (IUCN 2013). Primates, in general, begin reproducing later, have long lives and each female produces few offspring over a lifetime (Harvey & Clutton-Brock 1985; Bielby et al. 2007; Jones 2011). In gorillas (*Gorilla* spp.), for example, females only give birth to one infant approximately every six years and each infant is at least 3.8 years old when weaned (Stoinski et al. 2013). These slow life-history traits coupled with rapid habitat loss and hunting, have contributed to dramatic declines in gorilla populations and they are currently at an extremely high risk of extinction in the near future (IUCN 2013).

Within the lemurs, members of the taxonomic family Indriidae, have relatively slow life-history strategies (Wright 1999; Richard et al. 2002; Godfrey et al. 2004). The larger members of this group face additional extinction risks due to their relatively large body size, specialized diet, and relatively slow life histories (Richard et al. 2002; Pochron et al. 2004; Cardillo et al. 2006; Tomiya 2013; Sax et al. 2013). While all indriids give birth to only one offspring at a time, the longest interbirth intervals amongst the indriids and amongst the lemurs, is for the indri (*Indri indri*), where females only produce one offspring every two to three years over an unknown life span (Mittermeier et al. 2008). Again, low reproductive effort coupled with rapid habitat loss and the recent escalation of hunting of both *I.indri* and *Propithecus diadema* (the largest sifaka species) has pushed these two species further towards extinction in recent years (Jenkins et al. 2011) and they are now both listed as Critically Endangered, or at an extremely high risk of extinction

(IUCN 2014). *I. indri*, in particular, are now considered one of the 25 most endangered primates in the world (Mittermeier et al. 2012).

1.2 Conservation strategies for lemurs threatened with extinction

In order to halt, and eventually to reverse the rapid decline of wild lemurs, several conservation measures were recommended in the 2013 Lemur Action Plan (Schwitzer et al. 2013). The two largest species of lemur are also those with the lowest reproductive effort and therefore likely face a high extinction risk. Here, I will focus on three conservation strategies and suggest how dedicated research, such as the work I present in this manuscript, could potentially contribute towards the implementation and eventual success of conservation action plans for lemurs in general, and for indri and for sifaka species specifically.

a) Identify, Protect and Create Suitable Habitat: The most important way that we can assist in the recovery of endangered species is by protecting what remains of their habitat. The first step in many cases is to identify the existing distribution of a threatened species. Then, by studying the movement patterns and feeding behaviours of wild groups, we can identify the physical conditions (ex. elevation range, temperatures, rainfall) and key resource requirements for an area to successfully sustain a group (Sax et al. 2013). For example, dietary studies have been key to successful conservation and re-introduction programs for ruffed lemurs (*Varecia variegata*) (Britt & Iambana 2003; King et al. 2013). Understanding the size and characteristics of an observed home range can assist in determining how large protected areas must be, while detailed information on diet and feeding behaviours can assist in determining what types of vegetation are required for the area to support a particular species. Additionally, this information could be used to identify other areas that could potentially be inhabited by a particular species if the required conditions were met (fundamental niche; Sax et al. 2013). For example, in areas where the required food and space resources are available, but numbers of indri have been reduced below the carrying capacity of the area due to hunting, or even locally extirpated, it is possible that indri could be reintroduced to these areas once hunting is stopped. Also, in areas where habitat has been degraded, particularly around the outer edges of forest fragments, knowledge of the particular plants required by a species could be useful in determining which plants should be the focus of reforestation efforts (Britt et al. 2002). For example, in south-central Madagascar, where a matrix of human-made savannah, rice cultivation, and villages separate small forest fragments of mixed xerophytic and semi-tropical rupicolous outcrop vegetation, dietary studies of ring-tailed lemurs (*Lemur catta*) were recently used to inform reforestation projects in the area (Gould et al. *in prep*).

b) Understand Requirements for Successful Reproduction: In addition to uncovering the physical conditions and resources needed for a threatened species to *occur* in a particular area, it is also important that we understand the specific requirements for successful reproduction if we are to attempt to increase the overall numbers of these animals. Long-term research can potentially reveal the particular environmental conditions that correlate with more or fewer births in a certain year, or within a specific forest. Likewise, dedicated investigations into the infancy period, including feeding ontogeny of infants and strategies employed by lactating females to raise their infants, could help us to better predict what causes the high rate of mortality observed in most lemur species, in most years (Wright 1995; Richard et al. 2002; Pochron et al. 2004;

Morelli et al. 2009). Thus far, we have yet to be successful in the captive breeding of most indriid species (Schwitzer et al. 2013). Attempts to keep indri in captivity in the 1970's were unsuccessful, and it is suspected that this is partly due to the our incomplete understanding of the specific intestinal flora required by specialized folivores to digest particular plants in the captive environment (Janzen 1978; Thalmann et al. 1993; Britt et al. 2002). Lemurs that eat more leaves tend to be more difficult to keep and breed in captivity (ex. *Lepilemur* spp., *Avahi* spp., and *Propithecus* spp) however positive results in breeding programs for *P. verreauxi* and *P. coquereli*, suggest we should re-visit the viability of a captive breeding program for *I. indri* and for other indriid species (Schwitzer et al. 2013). A more comprehensive view of how infants develop the specialized diet of adults in the wild could be beneficial in future attempts to breed these two species in captivity.

c) Develop Captive Breeding Programs: Although the first priority should always be to identify, protect, and eventually to expand the amount of wild habitat available to a threatened species, captive breeding programs have been proven to facilitate conservation efforts to sustain and increase the sizes of threatened populations (Conde et al. 2011; Lacy 2013). When integrated with other types of efforts, breeding programs can make valuable contributions by sustaining insurance populations and by providing reserves for the eventual restocking of wild populations (Schwitzer et al. 2013). Currently, within the three genera and 19 species in the lemur family Indriidae, there are only breeding programs for two species of *Propithecus* (*P. coquereli* and *P. coronatus*) and no other indriids exist in captivity (Schwitzer et al. 2013). The last golden-crowned sifaka (*P. tattersalli*) and diademed sifaka (*P. diadema*) in captivity both died in 2008 and

2012 respectively, after spending almost their entire lives at the Duke Lemur Center and failing to produce offspring. Of the world's 60 captive Coquerel's sifaka, all are owned by the Duke Lemur Center and roughly half of these are currently on loan to other facilities as part of the breeding program for this species (DLC 2014). In Europe, a breeding program for the crowned sifaka was established in 2007 and thus far, 42 infants have been born as part of this program, although 40% have died within a few days of birth (Roullet 2013). Through focused studies of indri and sifaka in the wild, we could potentially develop a better understanding of the resources and conditions required by females to reproduce successfully and for infants to survive to reproductive age (Britt et al. 2003; Custance et al. 2002). These types of studies could contribute towards the development of species-specific breeding programs at regional lemur breeding facilities within Madagascar and eventually at international facilities (King et al. 2013).

1.3 Infant Development in Primates

Newborn primates are completely dependent on their mothers for both nourishment and for transport in their first stages of infancy. The transitions to independent acquisition of nourishment and to independent locomotion are gradual, and these may begin in the first weeks (ex. *Lemur catta*, Gould 1990; *Nycticebus coucang*, Wiens & Zitzmann 2003), months (ex. *Symphalangus syndactylus*, Lappan 2009) or years (ex. *Pongo pygmaeus wurmbii*, van Noordwijk et al. 2013) of life.

The significant variation observed between, and sometimes within species, can largely be explained by six factors known to influence the speed at which an infant develops from birth through to independence. The first of these factors is phylogeny or common ancestry (Stearns 1983; Kappeler 1996). For example, species within a genus will have similar speeds of development compared with those that are more distantly related phylogenetically (Stearns 1983; Godfrey et al. 2004). The second factor affecting the speed of infant development is adult size, with larger bodied species usually taking longer to reach independence than do smaller species (Kappeler 1996; Lee 1997). The feeding ecology of a species also tends to influence the speed of infant development. For example, folivorous haplorhines tend to grow more quickly than do similarly sized frugivorous haplorhines (ex. howler monkeys, *Alouatta* sp. develop more quickly than the sympatric spider monkeys, *Ateles* sp.; Leigh 1994; Godfrey et al. 2001) while folivorous lemurs tend to grow more slowly than do similarly sized frugivorous lemurs (ex. indriids develop more slowly than lemurids; Godfrey et al. 2004). Godfrey et al. (2004) suggested that the slower pace of growth in folivorous lemurs was part of an overall slower life-history strategy adapted to optimize food resources in an environment with fluctuating resource availability. These authors suggest folivorous lemurs in the family Indriidae employ a slow but consistent life-history strategy while more frugivorous lemurs employ a 'catch-up' strategy with faster growth during infancy but yearly variations in reproduction (Godfrey et al. 2004).

The specific habitat of a population may also affect infant development. For example, Bornean orangutans tend to develop much faster than do Sumatran orangutans (van Noordwijk et al. 2009) and infant *L. catta* at Beza Mahafaly Special Reserve are born over one month later than infants at Berenty Reserve (Gould 1990; O'Mara 2012). One possible explanation for these discrepancies between habitats is the relative amount, or quality of food resources available at each site. For example, *L. catta* studied at Berenty inhabited an area with abundant fruit trees where the animals frequently supplemented their diet with foods scavenged from human garbage and also occasionally with foods provided directly by tourists (L. Gould personal communication). Conversely, animals inhabiting nearby spiny forest habitat and those at Beza Mahafaly, were not in close contact with, or fed by tourists, suggesting that this particular discrepancy in infant development is due to the additional food resources available at the Berenty field site (O'Mara 2012; L. Gould personal communication). The type of locomotion primarily employed, and the associated level of arboreality may also influence the length of time it takes for infants to become independent. For example, in the more terrestrial *L. catta*, infants develop relatively quickly (Gould 1990) compared with the similarly sized, but more arboreal *E. fulvus* (Sussman 1977; Tarnaud 2004) and *E. flavifrons* (Volampeno et al. 2011). Another variable predicted to affect the speed of infant development in primates is the type of social organization employed by the group (Coussi-Korbel & Fragazy 1995; Overdorff 1996; Galef & Giraldeau 2001). Haplorhine primates that live in highly despotic, non-tolerant groups (ex. rhesus macaques) tend to develop more slowly than those living in more egalitarian or tolerant societies (ex. titi monkeys) (Coussi-Korbel & Fragazy 1995). Furthermore, within haplorhines species, those with a high occurrence of allomaternal care (including infant transport, babysitting and food provisioning by individuals other than the mother), tend to grow faster and be weaned at a younger age (Ross & MacLarnon 2000; Ross 2003). While this correlation is not observed within the lemuriformes (Tecot et al. 2013), there are some cases where allomaternal care does appear to influence the speed of development of infants. For example, Overdorff (1996) found that *E. rufifrons* infants were slower to pass certain developmental markers than sympatric, similarly sized and very closely related, *E.*

rubriventer and suggested that the difference is correlated to differences in levels of allomaternal care. In this comparison, *E. rubriventer* males provided allomaternal care through infant transport while *E. rufifrons* males did not (Overdorff 1996). The resulting interplay of these different variables contributes to the complex process of infant development exhibited by each species, and occasionally by particular populations.

The term *weaning*, a key consideration when considering infant development and maternal strategies, has traditionally been applied both generally, to include the entire suite of behavioural, nutritional, morphological and physiological developments that the infant experiences, and more specifically, as the precise period when the change from suckling to independent feeding occurs (Galef 1981; Martin 1984). Therefore, the age at '*weaning*' has been defined inconsistently in the literature as either the cessation of all suckling, when suckling becomes infrequent, when infants are no longer carried by the mother, or when infants are no longer in contact with the mother for the majority of their time (Lee 1997). To add to such confusion, the use of the term '*weaned*' is frequently not defined, making interspecies and inter-study comparisons either imprecise or inaccurate (Martin 1984; Lee 1997). One major aim of my study was to test the applicability of using three pre-defined phases of development, as an operational tool for defining and quantifying the processes of feeding ontogeny, weaning and behavioural development in two separate primate species.

This type of comparative study is useful for undertaking questions about the specific adaptations of particular primates (McClarnon 1999). Simultaneous comparative studies of sympatric species are especially valuable as they control for variability between environments, food availability, and climate, and instead allow the researcher to focus at the species specific level. The two species (*Indri indri* and *Propithecus diadema*) that I will be comparing in this manuscript share several important traits: 1) they are closely related phylogenetically, both belonging to the lemur family Indriidae (see Mittermeier et al. 2008 for recent classification), 2) they both weigh approximately 6–7 kg as adults (Glander & Powzyk 1995), 3) they both have highly folivorous diets (Powzyk & Mowry 2003), 4) they both use vertical clinging and leaping as their primary mode of locomoting (Napier & Walker 1967; Demes et al. 1996), and 5) in some areas their home ranges overlap and they occur in sympatry, thus in some places they share the same habitat (Powzyk 1997). *I. indri* and *P. diadema* differ however in the social organization of their respective groups and in how much feeding time they dedicate to folivory (Powzyk & Mowry 2003). *I. indri* live in monogamous groups whereas *P. diadema* live in more despotic, rank-based groups and this difference may contribute to faster development in *I. indri*, if following the above case example of *E. rubriventer* and *E. rufifrons*. Furthermore, if these two species follow the trend presented by Godfrey et al. (2004), that more folivorous lemurs develop more slowly than more frugivorous species, I might expect to see slower development in the more folivorous *I. indri*.

Long term studies of *I. indri* were conducted within the Analamazaotra forests by Pollock in the 1970's (Pollock 1975a; Pollock 1975b; Pollock 1986), at Mantadia by Powzyk in the 1990's (Powzyk 1997; Powzyk and Mowry 2003; Powzyk and Thalmann 2003; Powzyk and Mowry 2006), and most recently at Betampona by Britt in 2000 and 2001 (Britt et al. 2002). Long term studies of *P. diadema* have been conducted at Mantadia by Powzyk in the 1990's (Powzyk 1997; Powzyk and Mowry 2003; Powzyk and Thalmann 2003), and more recently at Tsinjoarivo by Irwin (Irwin 2006a; Irwin

2006b; Irwin 2008; Irwin et al. 2010; Table 1.1). In the following sections I will introduce each study species separately, and then I will present my study site.

Table 1.1 Characteristics of four field sites where studies of *Indri indri* and *Propithecus diadema* have previously taken place

Site Name	Latitude Longitude	Area (ha)	Elevation (m)	Rainfall (mm)	Temperature (˚C)	Study Species (length of study)
Betampona Reserve	17˚15'-17˚55' S 49˚12'-49˚15' E	2228	275-650 Low altitude	4129	21	*I. Indri* (12 mo.) 2000-2001[1]
Mantadia NP	18˚48' S 48˚26' E	10000 (site ~ 100)	1000-1220 Mid altitude	3721	10-30	*I. Indri* and *P. diadema* (17 mo.) 1993-1995[2]
Tsinjoarivo Forest	19˚40'-19˚43' S 47˚45'-47˚51' E	Not specified	1400-1650 High altitude	2008 - 2632	8-27	*P. diadema* (12 mo.) 2003[3]
Analamazaotra Forests	18˚56' S 48˚24' E	Not specified	928-1300 Mid altitude	1708	19	*I. Indri* (12 mo.) 1972-1973[4]

[1] Britt et al. 2002
[2] Powzyk 1997
[3] Irwin 2006a
[4] Pollock 1975a

1.4 Study Species 1– Diademed Sifaka (*Propithecus diadema*)

P. diadema are the largest of the nine allopatric species of sifaka, and one of the two largest bodied lemurs alive today, with an average weight of 6.5 kg and adult weights of up to 7.5 kg (Glander & Powzyk 1995; Gordon et al. 2013). They are the most colourful of the *Propithecus* (Mittermeir et al. 2008) with a pelage that is slate gray to silvery gray on the head, face, hands and feet, white on the ventral surface and parts of the limbs, tail, head and back, and gold/yellow on the back, tail, head and parts of the limbs (Figure 1.1).

Figure 1.1 Diademed sifaka juvenile (left), mother and infant (middle) and female sitting in tree fern (right) in Maromizaha

These sifaka are endemic to the eastern rainforests of Madagascar, where they live in multi-male, multi-female groups of three to nine individuals (Powzyk 1997; Irwin 2006). Their home ranges at Mantadia were 20 – 50 ha (Powzyk & Mowry 2003) and Irwin (2008) found that at Tsinjoarivo, home ranges were considerably smaller in fragmented (37 ha) than in continuous (70 – 80 ha) forests. Although rare, infanticide, or killing of infants by conspecifics, has been documented in some species of sifaka (Richard et al. 2002; Morelli et al. 2009) including three infants within a translocated population of *P. diadema* (Day et al. 2009). Generally, rates of agonism are relatively low between group members and aggressive interactions tend to be seasonal (Erhart & Overdorff 2008).

All sifaka are anatomical folivores with morphological adaptions for consuming large amounts of structural plant cell wall material including a relatively long gastrointestinal tract and an enlarged and sacculated cecum (Campbell et al. 2000), and the mixed diet of *P. diadema* tends to include a greater proportion of foliage than that of other eastern sifaka (Irwin 2006b). The diet of *P. diadema* at Mantadia was composed of 44% leaves, 31% seeds, 15% flowers and 6% fruit, (Powzyk & Mowry 2003) while that of Tsinjoarivo sifaka was composed of 53% leaves, 24% fruits (both with and without seeds), 7% only seeds, and 15% flowers (Irwin 2006; Irwin 2008). The range of this species extends from the Mangoro River in the north, to south of Maroantsetra and the Antainambalana River and whereas it was once widespread through this area, it is currently not seen in areas it was found in recent years (Mittermeier et al. 2008).

1.5 Study Species 2– Indri (*Indri indri*)

Indri (*Indri indri*), are the only extant species in the genus (Mittermeier et al. 2008; Figure 1.2). Inhabiting eastern rainforests from near Sambava in the north, to the Mangoro River in central-eastern Madagascar, *I. indri* are highly arboreal and the only extant lemurs with very short and vestigial tails, a morphological trait that was common in the extinct giant lemurs that were much larger and likely spent more time on the ground (Godfrey & Jungers 2003; Mittermeier et al. 2008). The pelage of *I. indri* is mostly black with varying amounts of white on the top of the head, limbs and at the base of the back, although northern populations are almost entirely black (Thalmann et al. 1993). Adults of this species weigh 5.83 - 8.8 kg and females are approximately a kilogram heavier than males (Glander & Powzyk 1995; Britt et al. 2002). *I. indri* are the largest bodied primate to use vertical clinging and leaping (VCL) as their primary form of locomotion (Napier & Walker 1967; Demes et al. 1996) and it takes over one year for young to master this difficult technique (Pollock 1986b).

Figure 1.2 Indri male (left), mother and infant (middle) and two-year old juvenile (right) in Maromizaha

Indri live in territorial groups of two to five individuals composed of a breeding pair and their offspring (Pollock 1986a; Powzyk 1997; Glessner & Britt 2005). Infants stay with their group for at least three years (this study) however it is still unknown how old individuals must be when they leave their natal group. Females have the longest reported interbirth interval amongst the lemurs, giving birth in May or in June to a single infant every 2–3 years (Pollock 1975a; this study). While *I. indri* are generally classified as monogamous, mating pairs do change (Pollock 1975b) and at least one instance of extra pair copulation (Bonadonna et al. 2013), and one instance of female takeover by infanticide (Ratolojanahary & Dolch 2013) have been documented. As in most species of lemurs, females are dominant and exhibit feeding priority over males (Pollock 1979). Rates of agonism are extremely low between group members (Erhart & Overdorff 2008) and aggressive interactions between groups are rare, particularly in pristine forests (Pollock 1975b; Powzyk & Mowry 2006). In contrast to physical contests, *I. indri* tend to defend their territories using a very conspicuous loud call that persists for 40–250 seconds and can be heard 3–4 km away from the source (Pollock 1986a).

I. indri are highly folivorous (Pollock 1975a) with 72% and 82% of their feeding time dedicated to leaves at Mantadia National Park (Powzyk & Mowry 2003) and Betampona Reserve respectively (Britt et al. 2002). Unlike the African and Asian colobine monkeys, who possess specialized gut anatomy adapted for the challenges of folivory, *I. indri*, like howler monkeys (*Alouatta* spp.) must expend considerable physiological energy breaking down plant material including toxins and secondary compounds (Milton 1981; Langer 2003). To compensate for the amount of energy needed for digesting a diet dominated by leaves, *I. indri* spend a large amount (45 – 59 %) of their time resting (Powzyk 1997; Britt et al. 2002) as do other highly folivorous primates including *A. palliata* (63%; Raguet-Schofield 2010) and *Lepilemur mustelinus* (80%; Hladik & Charles-Dominique1974). In addition, *I. indri* rarely engage in energetically costly behaviours such as play or scent-marking (Powzyk 1997) and the daily distances they tend to travel are less than half that of the sympatric and similarly sized *Propithecus diadema* (Powzyk 1997).

Although there have been longer-term studies of both *I. indri* and *P. diadema* ecology and behaviour (Pollock 1975a; Powzyk 1997; Britt et al. 2002; Irwin 2006a), to date no one has specifically studied infant development or the strategies of lactating females in these enigmatic and iconic species. Both species are currently listed as Critically Endangered (IUCN 2014) due to the illegal hunting of these animals for bushmeat (Jenkins et al. 2011) combined with the very rapid loss of their rainforest habitat due primarily to mining, slash and burn agriculture, the illegal logging of rosewood and ebony and illegal rum production (Irwin & Ravelomantsoa 2004; Schwitzer et al. 2013). While the protection and expansion of suitable habitat and the elimination of hunting are the two most important strategies to prevent their extinction, a greater knowledge and understanding of the infancy period including early ontogeny of diet and feeding behaviours would be highly beneficial in the successful application of integrated conservation strategies such as captive breeding, translocations and re-introductions (Britt et al. 2002; Custance et al. 2002; Britt & Iambana 2003). One goal of my research is to contribute a more detailed understanding of *I. indri* and *P. diadema* diet and feeding ontogeny to support the development of captive breeding programs for these species. Ultimately, these insurance populations could facilitate the eventual re-introduction and re-population of areas where *I. indri* and *P. diadema* could exist, when hunting is eliminated and the area protected (fundamental niche; Sax et al. 2013).

1.6 Study Site

I studied the feeding and social behaviours of wild indri (*Indri indri*) and diademed sifaka (*Propithecus diadema*) infants and their mothers in Maromizaha forest (18°57'S, 48°36'E) where these two species live in sympatry. This small protected forest is located 140 km east of the nation's capital of Antananarivo, and approximately 6.5 km east of Analamazaotra Reserve, near the village of Anevoka on Route Nationale 2, a major highway running from the capital city of Antananarivo to the eastern port of Toamasina (Figure 1.3). As a research site for primatology, Maromizaha has only been used sporadically and relatively little work has been conducted here. From September 1972 until the end of July 1973, Pollock (1975b) monitored six groups of indri within Maromizaha as part of his larger study of indri in Perinet (now called Analamazaotra and

Andasibe). Much later, in 2009, Giacoma and her students began studying the vocalizations of indri in Maromizaha, as part of her larger study in Analamazaotra Reserve and Mitsinjo (Giacoma et al. 2010; Sorrentino et al. 2013; Torti et al. 2013). As part of an international collaboration between the University of Torino (Italy), the University of Antananarivo, the University of Toamasina, the University of the Comoros and the Zoological Society of San Diego, in 2010, a multi-purpose centre was built at 40 minutes walking distance from Route Nationale 2. This research center was constructed with major financial contributions from Parco Natura Viva - Breeding Centre for Endangered Species (Bussolengo, Italy) (Schwitzer et al. 2013).

Figure 1.3 The location of the small village of Anevoka, in the eastern mountains of Madagascar (Google Earth 2013)

As part of the Ankeniheny-Zahamena rainforest corridor conservation initiative Maromizaha is an important link between forests to the north and to the south (Figure 1.4), (CAZ; Schwitzer et al. 2013). In 2001, legal logging within the forest ceased, agricultural development was limited, and an area of approximately 1,600 ha (16 km^2) was designated as a New Protected Area within Madagascar's larger protected area network (Zimmerman & Randrianambinina 2005). From 2001 – 2005 the private NGO NAT (Foundation for Conservation in the Tropics) managed the area in cooperation with the Direction des Eaux et Forêts, in Antananarivo, Madagascar (Zimmerman & Randrianambinina 2005). Maromizaha is currently managed by GERP (Groupe d'Etude et de Recherche sur les Primates de Madagascar) a Malagasy NGO, and a zoning strategy has been employed to designate the intended use for each part of the protected area (Figure 1.5). The area is composed of approximately 820 ha of intact hard wood forest and 360 ha of regenerated forest, with the remaining classified as degraded habitat (see below for predominant vegetation in Maromizaha). Although the area is legally protected, there is ongoing deforestation occurring along the area's perimeter where forest is burned for charcoal production and agriculture and trees are selectively removed for construction (personal observation). Since the perimeter is not routinely monitored, it is impossible to know how significant this deforestation is, except that it is occurring, and therefore Maromizaha forest is slowly diminishing in overall size.

Figure 1.4 The location of Maromizaha forest in relation to the village of Anevoka and Route Nationale 2 (Google Earth 2013)

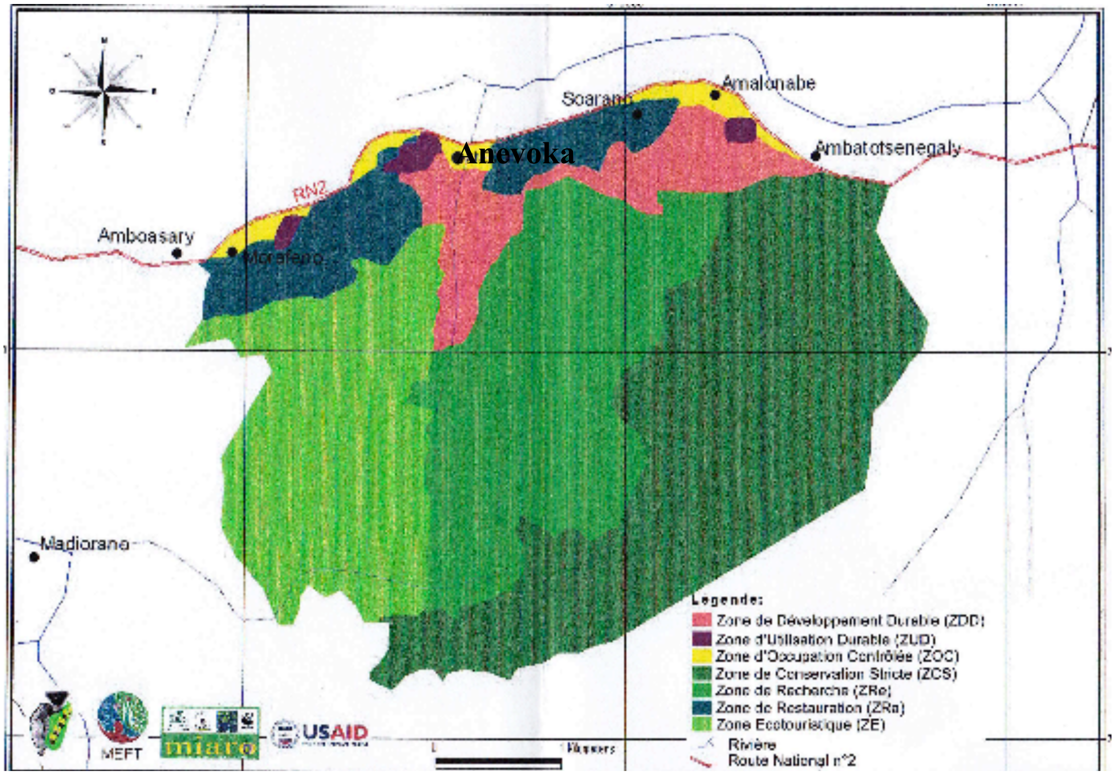

Figure 1.5 Map of Maromizaha protected area, including zoning for sustainable development, ecotourism, restoration, research and strict conservation, produced by GERP in 2009.

The other name for Maromizaha (which translate as 'see a lot'), is Forêt d'Arbres de Dragon (The Dragon Tree Forest). The terrain is mountainous with elevations ranging from 800 – 1200 m, and a series of closely spaced mountain ridges, valleys and small streams. The vegetation is similar to what has been recorded in the nearby Mantadia National Park, with several large *Canarium* sp., *Faucherea* sp., *Uapaca* sp., *Cryptocaria* sp. *Syzygium* sp., *Chrysophyllum* sp. and *Tina* sp. trees, and dozens of smaller species of trees, lianas and vines (Powzyk & Mowry 2003). Maromizaha is unique however, in possessing several large dragon trees (*Dracaena* spp.) of the plant family Liliaceae. There is no dry season, and annual rainfall is significant. Mine was the first study to record temperature and rainfall data for this site (Appendix I). For 2012, rainfall was

3163 mm, with close to one third falling in January and February combined. This is similar to the nearby Mantadia National Park, and Ranomafana National Park further south, where the yearly average rainfall is 3000 mm (Powzyk 1997; King et al. 2011). February 2012 was also when Cyclone Giovanna struck the area, killing several large trees and leaving all trees defoliated (R.M. Randrianarison personal communication /unpublished data). The average temperature (at 7:30 am) during the study period was 16°C (min=12.6, max=19.1), and the overall maximum and minimum temperatures were 36.8°C and 7.6°C respectively. The hottest months of the year were November – February and the coldest were July – September (Appendix I).

Maromizaha is home to at least 77 bird, 60 amphibian and 20 reptile species (Woog et al. 2006). So far, 13 lemurs have been documented in the protected area, including the Critically Endangered indri (*Indri indri*), diademed sifaka (*Propithecus diadema*), and southern black-and-white ruffed lemur (*Varecia variegata editorum*), the Endangered weasel sportive lemur (*Lepilemur mustelinus*) and aye-aye (*Daubentonia madagascarensis*), the Vulnerable eastern wooly lemur (*Avahi laniger*), red-bellied lemur *(Eulemur rubriventer*), gray bamboo lemur (*Hapalemur griseus*), red mouse lemur (*Microcebus rufus*), Goodman's mouse lemur (*Microcebus lehilahytsara*) and hairy-eared dwarf lemur (*Allocebus trichotis*), the Near Threatened common brown lemur (*Eulemur fulvus*), and the Data Deficient greater dwarf lemur (*Cheirogaleus major*) (Schwitzer et al. 2013; See Appendix II for a list of lemur species documented during my study). In June of 2010, I conducted a pilot study in Maromizaha, and I have returned to work in this forest in 2011, 2012 and 2013.

1.7 Objectives and Significance

This is the first project to investigate early feeding ontogeny, infant development, infant survival and the behaviours of lactating females in *P. diadema* and in *I. indri*. Throughout this manuscript I explore how ecology, including diet, social organization and locomotory tactics may influence the complex processes of infant development in these and other mammalian taxa. I also introduce a three-phase framework for determining the main stages of the weaning process that can be applied to other species. The findings I present lend to a growing body of knowledge on how infants and mothers within the primate order cope with the early challenges of feeding ontogeny and contributes to the small body of knowledge we have on the ecology and life-history strategies of these two lesser known primates. In addition, the results of my study may be useful in the development of conservation action plans for these and other endangered species. In Chapter 2, I present the first data on infant development and survivorship in *P. diadema*. I also demonstrate the applicability of the three phases of weaning as an operational tool for defining and quantifying the processes of feeding ontogeny and weaning in a primate. In addition, I apply these three phases of feeding ontogeny to other behavioural aspects of development for *P. diadema*, and compare the proportion of time infants spend resting, observing, playing, allogrooming, self-grooming and locomoting independently by phase. In Chapter 3, I present the first data on feeding ontogeny and diet in wild *I. indri* infants. I again apply the three phases of feeding ontogeny to other behavioural aspects of development for *I. indri*, including changes in the proportion of time infants spend resting, observing, playing, allogrooming, self-grooming and locomoting independently, and compare this to what I found for *P. diadema* in Chapter 2.

In this chapter I also examine the possibility for more complex social learning mechanisms in *I. indri* and compare this to what has been found for other primates. In Chapter 4, I begin to elucidate the variables that affect the development of certain key behaviours in *P. diadema* and *I. indri* in their first six months of life. Infant behaviours are categorized either as active or passive, and either social or non-social and I test how key behaviours could potentially be influenced by four specific variables including species, group size, season and phase (age) of the infant. I also examine the similarities and differences between the two species for each of their main behaviours within each of the three phases as designated in Chapters 1 and 2. Finally, in Chapter 5, I present the first data on maternal strategies employed by lactating *P. diadema* and *I. indri* in the first six months of their infant's life. I investigate the variables that affect the proportion of time *P. diadema* and *I. indri* mothers dedicate to each of the main behaviours over the corresponding three stages of lactation and I examine the relative cost of each stage of lactation.

Throughout these chapters, I address ways that my results could further my ultimate goal of contributing valuable information towards the conservation of these two species. By identifying the specific environmental conditions and resources required for successful reproduction, we will be better positioned to identify, protect and expand suitable habitat for *P. diadema* and *I. indri*. In addition, a focused understanding of the infancy period for these two species will undoubtedly be helpful in the development of captive breeding and translocation programs.

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2 - PHASES OF WEANING, EARLY ONTOGENY AND SURVIVAL OF DIADEMED SIFAKA (*PROPITHECUS DIADEMA*) INFANTS AT MAROMIZAHA FOREST

2.1 Introduction

Early feeding ontogeny in primates includes a complex suite of behavioural developments associated with an infants' transition from complete dependence on the mother for nourishment to independent acquisition of nourishment (Lee 1997). The term *weaning*, a key consideration in this transition process, has been applied both generally, to include the entire suite of behavioural, nutritional, morphological and physiological developments that the infant experiences, and more specifically, as the precise period when the change from suckling to independent feeding occurs (Galef 1981; Martin 1984). Therefore, the age at '*weaning*' has been defined inconsistently in the literature as either the cessation of all suckling, when suckling becomes infrequent, when infants are no longer carried by the mother, or when infants are no longer in contact with the mother for the majority of their time (Lee 1997). To add to this confusion, the term '*weaned*' is frequently not even defined in the literature, making interspecies and inter-study comparisons either imprecise or inaccurate (Martin 1984; Lee 1997; Godfrey et al. 2001).

Martin (1984) suggested that by operationalizing Trivers' (1972; 1974) concepts of parental investment and parent-offspring conflict, we would be better able to quantify the complex processes of weaning in a particular species, and thus be better equipped to compare these processes between species and between studies. For example, by calculating the relative energetic investment of a mother towards her infant, or the relative energetic investment of an infant towards its own development over discrete periods of time, we are able to determine a specific rate of parental investment in their offspring or infant investment in their own independent development per unit of time. Since the mother's milk must provide all of the energy required to support the infant's basal metabolism, thermo-regulation, somatic growth and locomotor activity until the infant begins to ingest solid foods, the proportion of time infants suckle each week is an effective measure of rate of parental investment, whereas the proportion of time infants feed independently each week is an effective measure of the rate of an infant’s investment in their own development (Randolph et al. 1977; Martin 1984). Similarly, the proportion of time infants are carried per unit of time represents another rate of parental investment, whereas the proportion of time infants are independent represents another rate of an infant’s investment in their own development.

In this Chapter I will demonstrate an effective method for analyzing the gradual process of feeding ontogeny and for subsequently identifying three distinct phases, based on the relative energetic investment of infants and mothers over the course of the weaning period. The pre-set definitions allow for clear and objective distinctions between the phases that can then be compared between species, populations, and studies. The three phases of weaning employed throughout here, and throughout this manuscript encompass and represent the total time that infants are receiving nourishment from their mothers relative to the time they are consuming solid foods. In contrast, most traditional definitions of weaning are based on one-off documentations of when a particular behaviour was first (ex. ingestion of solid foods) or last (ex. suckling) observed, and are therefore subjective to the schedule of the observer and likely highlight outlying events as opposed to overall patterns in the data. Given that weaning in primates is gradual and non-uniform and not in actuality demarcated by one-off events, the three phases provide set criteria that are significantly more biologically relevant to the overall process of feeding ontogeny. If this method is eventually used to quantify infant development in other species of primates, we will be able to further elucidate and compare the adaptive significance of particular schedules of infant development across a broader set of conditions and variables, and thus have a greater understanding of the infancy period in primates.

Weaning, or the overall change from suckling to independent feeding in primates is relatively gradual (Lee 1997), and may begin in the first weeks (ex. *Lemur catta*, Gould 1990; *Nycticebus coucang*, Wiens & Zitzmann 2003), months (ex. *Symphalangus syndactylus*, Lappan 2009) or years (ex. *Pongo pygmaeus wurmbii*, van Noordwijk et al. 2013) of life. The pace at which this process unfolds can also be non-uniform, with occasional regressions to more suckling for some days or weeks as the infant begins to feed independently more often. While several studies have focused on infant development in haplorhine primates, relatively few have concentrated on infant development in lemurs (Gould 1990). Exceptions include *Lemur catta* (Gould 1990; Meredith 2011; O'Mara 2012), *Eulemur fulvus* (Tarnaud 2004), *Eulemur rufifrons* and *Eulemur rubvriventer* (Overdorff 1991; Overdorff 1996), *Eulemur flavifrons* (Volampeno et al. 2011), *Varecia variegata* (Morland 1990) and *Varecia rubra* (Vasey 2007). As was previously mentioned, definitions for what entails weaning are often unclear or inconsistent between studies (Martin 1984; Lee 1997), making comparisons between species and studies challenging. In Table 2.1, I have synthesized the most comprehensive data presented for infant development in *L. catta*, *Eulemur* spp. and *V, rubra*, and extracted parameters often used to describe weaning and infant development.

Table 2.1 Ecology and infant developmental schedules in six species of wild lemur

	Lemur catta	*Eulemur fulvus*	*Eulemur rufifrons*	*Eulemur rubriventer*	*Eulemur flavifrons*	*Varecia rubra*
Adult size	≤2.2 kg[5]	1.2–2.5 kg[5]	1.2–2.5 kg[5]	1.2–2.5 kg[5]	1.2–2.5 kg[5]	3.3–3.6 kg[6]
Adult diet	Opportunistic omnivore[7]	Frugivorous[2]	Frugivorous[9]	Frugivorous[3]	Frugivorous[11]	Frugivorous[6]
Social organization	Multi-male/multi-female	Multi-male/multi-female	Multi-male/multi-female[3]	Monogamous groups[3]	Multi-male/multi-female[11]	Multi-male/multi-female[6]
Infant first off mother	2 weeks[1]	3 weeks[2]	3-4 weeks or 26 days[3]	1-2 weeks or 10 days[3]	4 weeks[11]	1-2 weeks or 8 days[6]
Play with other group members	3 weeks with mother, 6 weeks with peers[1]	11 weeks[2]	6 weeks or 42 days[3]	3-4 weeks or 26 days[3]	7 weeks[11]	6 weeks with siblings in stash site[6]
Locomote independently	6 weeks[1,10]	8 weeks[2]	7-8 weeks or 55 days[3]	6 weeks or 42 days[3]	10 weeks[11]	10-16 weeks[6]
Eat solid food	6 weeks[1] 4 weeks[10]	6-8 weeks[2]	7-8 weeks or 55 days[3]	5-6 weeks or 40 days[3]	10 weeks[11]	5-6 weeks[6]
Rejected by mother (nipple)	8 weeks[1]	17 weeks[2]	13-14 weeks or 96 days[3]	15-16 weeks or 110 days[3]	11 weeks[11]	Not reported
Rejected by mother (riding)	12 weeks[1,10] Responsible for own travel by 14 weeks[1,10]	20-27 weeks	8 weeks or 56 days[3]	4-5 weeks or 30 days[3]	Not reported	10 weeks[6]
Male care	1 week[12]	Not reported	Never observed[3]	2-3 weeks/ 4-5 weeks or 20/32 days[3]	6 weeks[11]	2 weeks[6]
Time spent feeding > time spent suckling	11 weeks[1] 16 weeks[10]	19 weeks[2]	Not reported	Not reported	Not reported	11-16 weeks[6]
‘Fully weaned’	25 - 27 weeks[1,10]	7 months[2]			25 weeks[11]	18 weeks[6]

[1]Gould 1990, [2]Tarnaud 2004, [3]Overdorff 1996, [4]Vasey 2006, [5]Mittermeier et al. 2008, [6]Vasey 2007, [7]Sauther et al. 1999, [9]Overdorff 1993, [10]O’Mara 2012, [11]Volampeno et al. 2011, [12]Gould 1992,

The significant variation observed between, and sometimes within species, can mostly be explained by six factors known to influence the speed at which an infant develops from birth through to independence. The first of these factors is phylogeny or common ancestry (Stearns 1983; Kappeler 1996). For example, species within a genus will have similar speeds of development compared with those that are more distantly related phylogenetically (Stearns 1983; Godfrey et al. 2004). The second factor affecting the speed of infant development is adult size, with larger bodied species usually taking longer to reach independence than do smaller species (Kappeler 1996; Lee 1997). The feeding ecology of a species also tends to influence the speed of infant development. For example, folivorous haplorhines tend to grow more quickly than do similarly sized frugivorous haplorhines (ex. howler monkeys, *Alouatta* sp. develop more quickly than the sympatric spider monkeys, *Ateles* sp.; Leigh 1994; Godfrey et al. 2001) while folivorous lemurs tend to grow more slowly than do similarly sized frugivorous lemurs (ex. indriids develop more slowly than lemurids; Godfrey et al. 2004). Godfrey et al. (2004) suggested that the slower pace of growth in folivorous lemurs was part of an overall slower life-history strategy adapted to optimize food resources in an environment with fluctuating resource availability. These authors suggest folivorous lemurs in the family Indriidae employ a slow but consistent life-history strategy while more frugivorous lemurs employ a 'catch-up' strategy with faster growth during infancy but yearly variations in reproduction (Godfrey et al. 2004).

The specific habitat of a population may also affect infant development. For example, Bornean orangutans tend to develop much faster than do Sumatran orangutans (van Noordwijk et al. 2009) and infant *L. catta* at Beza Mahafaly Special Reserve are born one month later than are infants at Berenty Reserve (Gould 1990; O'Mara 2012). One possible explanation for these discrepancies between habitats is the relative amount, or quality of food resources available at each site. For example, *L. catta* studied at

Berenty inhabited an area with abundant fruit trees where the animals frequently supplemented their diet with foods scavenged from human garbage and also occasionally with foods provided directly by tourists (L. Gould personal communication). Conversely, animals inhabiting nearby spiny forest habitat and those at Beza Mahafaly, were not in close contact with, or fed by tourists, suggesting that this particular discrepancy in infant development is due to the additional food resources available at the Berenty field site (O'Mara 2012; L. Gould personal communication). The type of locomotion primarily employed, and the associated level of arboreality may also influence the length of time it takes for infants to become independent. For example, in the more terrestrial *L. catta*, infants develop relatively quickly (Gould 1990) compared with the similarly sized, but more arboreal *E. fulvus* (Sussman 1977; Tarnaud 2004) and *E. flavifrons* (Volampeno et al. 2011). Another variable predicted to affect the speed of infant development in primates is the type of social organization employed by the group (Coussi-Korbel & Fragazy 1995; Overdorff 1996; Galef & Giraldeau 2001). Haplorhine primates that live in highly despotic, non-tolerant groups (ex. rhesus macaques) tend to develop more slowly than those living in more egalitarian or tolerant groups (ex. titi monkeys) (Coussi-Korbel & Fragazy 1995). Furthermore, within haplorhines species, those with a high occurrence of allomaternal care (including infant transport, babysitting and food provisioning by individuals other than the mother), tend to grow faster and be weaned at a younger age (Ross & MacLarnon 2000; Ross 2003). While this correlation is not observed within the lemuriformes (Tecot et al. 2013), there are some cases where allomaternal care does appear to influence the speed of development of infants. For example, Overdorff (1996) found that *E. rufifrons* infants were slower to pass certain developmental markers than sympatric, similarly sized and very closely related, *E. rubriventer* and suggested that the difference is correlated to differences in levels of allomaternal care. In this comparison, *E. rubriventer* males provided allomaternal care through infant transport while *E. rufifrons* males did not (Overdorff 1996). The resulting interplay of these different variables contributes to the complex process of infant development exhibited by each species, and occasionally by particular populations.

Relatively little quantitative data currently exists for infant development in the larger bodied species of lemurs. The extant sifaka include nine allopatric species from the genus *Propithecus* and the taxonomic family Indriidae (see Mittermeier et al. 2008 for recent classification). The smallest sifaka are *P. verreauxi* weighing 2.8 kg on average (Richard et al. 2002) and inhabiting very dry regions to the south and west of Madagascar. The larger sifaka, *P. edwardsi*, *P. candidus* and *P. diadema*, inhabit the eastern rainforests, and are twice the weight of *P. verreauxi* (Gordon et al. 2013). Jolly (1966) and Richard (1976) were the first to document infant development in a *Propithecus* species. They each studied populations of *Propithecus verreauxi*, inhabiting two different study sites. Even though both researchers were studying the same species, there were notable differences between the ages that infants were reported to first venture off the mother, begin dorsal riding, and receive attention by males in these two studies (Richard 1976). It is possible that some of these discrepancies were associated with the relative number of predators and level of human intervention between the two sites. It is also likely that some differences are associated with the problems in reporting ‘firsts’. In primates especially, behaviours may be first observed to occur long before they are incorporated as a significant aspect of the overall activity budget of the infant (Martin

1984). Sifaka species inhabiting the eastern rainforest of Madagascar are more difficult to observe than western sifaka, owing to their very dense, steep and mountainous habitat (mean elevations 794 – 1530 m; Gordon et al. 2013) and to their lower population densities (Irwin 2006b) thus observing the behaviours of infants is particularly challenging. Wright (1995) was the first to undertake a long-term study of a rainforest sifaka, *P. edwardsi*, beginning in 1986 and several aspects of infant survival (Wright 1995; Pochron et al. 2004; King et al. 2005; Morelli et al. 2009) and growth patterns (King et al. 2011) have since been reported. Patel (2011) began a long-term study of *P. candidus* in 2000 and his work has illuminated certain aspects of allocare in this rainforest sifaka (Patel 2007). Wright (1995) reported that infant *P. edwardsi* were receiving half of their nourishment through independent feeding on solid foods by six months of age, and Patel (personal communication/unpublished data) found that *P. candidus* infants had ceased suckling by 6 – 7 months. Overall, however, there is a great need for more comprehensive and detailed studies of infant developmental phases in sifaka in general, and in rainforest sifaka in particular. To ease and facilitate interspecies and inter-study comparisons, it is imperative that data be collected and presented with functional and operational definitions for the phases of weaning.

Sifaka reproduce relatively slowly compared to haplorhine primates of similar size (Pochron et al. 2004). The earliest that female *P. verreauxi* and *P. edwardsi* are able to reproduce is three or four years but reproduction is usually not successful until the females are six or seven years old (Wright 1995; Richard et al. 2002; Pochron et al. 2004; Morelli et al. 2009; King et al. 2011). All sifaka only give birth to one infant every 1 – 3 years (*P. verreauxi*, Richard et al. 2002; *P. edwardsi*, Wright 1995; *P. candidus*, Patel

2006). The milk of most lemurs is very low in energy and lipids (Tilden & Oftedal 1997; Power et al. 2006) and neonates are exceptionally small relative to the size of adults (Kappeler 1996; Tecot et al. 2013). For example, in their first week of life, *P. edwardsi* infants weigh only 100 – 200 g, or 3% of their mother's mass (King et al. 2011). Infant mortality is very high in both *P. verreauxi* and *P. edwardsi* with 48% (Richard et al. 2002) and 52% (Morelli et al. 2009) of infants dying before they reach one year respectively. Both Richard et al. (2002) and Wright (1995) have proposed that sifaka follow a bet-hedging strategy (Stearns 1976) to cope with Madagascar's intensely variable and unpredictable environmental conditions (Wright 1999). By frequently producing small and weak young, and investing relatively little energy in each offspring, over a long life-expectancy period (until over 18 years in *P. verreauxi*, Richard et al. 2002 and *P. edwardsi*, King et al. 2005) this strategy provides females a high chance of reproducing in a year when environmental conditions are favourable, but does not require too much energetic investment in any one particular offspring that has a high probability of dying due to unpredictable environmental conditions (Wright 1995; Richard et al. 2002), predation (Pochron et al. 2004; Irwin et al. 2009), or infanticide (Morelli et al. 2009; Day et al. 2009). Similar to folivorous haplorhines, the pace of dental development is very fast in sifaka and other indriids relative to their overall growth, and relative to similarly sized frugivorous lemurids (Godfrey et al. 2004; King et al. 2011). *P. edwardsi* infants have their full complement of deciduous teeth by the time they are three months old, and by one year, while they are slightly more than half the mass of adults, they already have their full complement of permanent mandibular molars (King et al. 2011). Godfrey et al. (2001) suggested that the fast pace of dental development in these folivorous indriids is an adaptation that: 1) allows infants to eat solid foods relatively early, 2) provides infants with the dentition required to become independently responsible for their own nourishment relatively early, 3) prepares these young folivores for the mechanical requirements for processing high fiber foods in the first postweaning season of scarce resources (when they are 8–9 months old), and thus 4) increases the chances of infant survival.

P. diadema are the largest of the sifaka, and one of the two largest bodied lemurs alive today, with an average weight of 6.5 kg (Glander & Powzyk 1995) and maximum weights of up to 7.5 kg (Gordon et al. 2013). These sifaka are endemic to the eastern rainforests of Madagascar, where they live in multi-male, multi-female groups of three to nine individuals (Powzyk 1997; Irwin 2006). Their home ranges at Mantadia were 20 – 50 ha (Powzyk & Mowry 2003) and Irwin (2008) found that at Tsinjoarivo, home ranges were considerably smaller in fragmented (37 ha) than in continuous (70 – 80 ha) forests. All sifaka are anatomical folivores with morphological adaptions for consuming large amounts of structural plant cell wall material including a relatively long gastrointestinal tract and an enlarged and sacculated cecum (Campbell et al. 2000), and the mixed diet of *P. diadema* tends to include a greater proportion of foliage than that of other eastern sifaka (Irwin 2006b). The diet of *P. diadema* at Mantadia was composed of 44% leaves, 31% seeds, 15% flowers and 6% fruit, (Powzyk & Mowry 2003) while that of Tsinjoarivo sifaka was composed of 53% leaves, 24% fruits (both with and without seeds), 7% only seeds, and 15% flowers (Irwin 2006; Irwin 2008). The range of this species extends from the Mangoro River in the north, to south of Maroantsetra and the Antainambalana River and whereas it was once widespread throughout this area, it is currently not seen in areas it was found in recent years (Mittermeier et al. 2008). The illegal hunting of these animals for bushmeat (Jenkins et al. 2011) combined with the rapid loss of their rainforest habitat due to mining, slash and burn agriculture, and the illegal logging of rosewood and ebony (Schwitzer et al. 2014) and illegal rum production (Irwin & Ravelomantsoa 2004) are the main reasons why this species is Critically Endangered and at risk of extinction (Schwitzer et al. 2013).

My aim in this chapter is to capture and quantify the gradual and non-uniform pace of feeding ontogeny, in wild diademed sifaka (*Propithecus diadema*) infants. To do this, I further modified Martin's (1984) operational view of weaning to consist of three distinct phases. In Phase 1, infants are suckling for more time, per week, than they are feeding independently. In Phase 2, infants are fluctuating between spending more time suckling, and more time feeding on solid foods, per week. Finally, in Phase 3 infants are feeding on solid foods for more time, per week, than they are suckling. My objectives for this chapter are; 1) to present the first data on infant development in the Critically Endangered diademed sifaka, 2) to test the applicability of the above three phases as an operational tool for defining and quantifying the processes of feeding ontogeny and weaning in a primate, and 3) to apply these three phases of feeding ontogeny to other behavioural aspects of development including changes in the proportion of time infants spend resting, observing, playing (either independent exploration or with other group members), allogrooming, self-grooming and locomoting independently and 4) to present the first data on infant survivorship in *P. diadema*.

Given that *P. diadema* are: 1) large in body size relative to other lemurs, 2) highly folivorous, and 3) members of the lemur family Indriidae, I predicted that *P. diadema* infants would develop nutritional independence later than the smaller and more frugivorous lemurids (Table 2.1). As *P. diadema* are highly arboreal vertical clingers and leapers, I also expected that they would have slower physical development than lemurs that do not exhibit this kind of locomotion. Finally, given that infant survivorship is very low in almost all lemur studies where it has been examined, I predicted that *P. diadema* would exhibit low infant survivorship at my study site as well.

2.2 Methods

Study Area

I studied the behaviours of *P. diadema* infants in Maromizaha forest (18°57'S, 48°36'E), a New Protected Area, located 140 km east of the nation's capital of Antananarivo, near the village of Anevoka. This montane rainforest is part of the Ankeniheny-Zahamena rainforest corridor conservation initiative (CAZ; Schwitzer et al. 2013) and includes a protected area encompassing approximately 1,600 ha, composed of 820 ha of intact hard wood forest and 360 ha of regenerated forest, with the remaining classified as degraded habitat. My study area is within mid-altitude rainforest and the *P. diadema* groups that I studied are found at elevations ranging from 970 – 1223m. The annual rainfall for 2012 was 3163 mm, with close to one third falling in January and February combined (Appendix I). February 2012 was also when cyclone Giovanna struck the area, leaving all trees defoliated and several large trees dying. The average temperature (at 7:30 am) during the study period was 16°C (min=12.6, max=19.1), and the overall maximum and minimum temperatures were 36.8°C and 7.6°C respectively (Appendix I). The hottest months of the year were November-February and the coldest were July-September (Appendix I). This study took place in the cold (July-September) and hot (October-December) seasons of 2011 and 2012 and is part of my larger study comparing infant development and maternal strategies in *I. indri* and *P. diadema* inhabiting Maromizaha forest.

Study Subjects

With the help of five trained assistants (see Acknowledgements), I collected behavioural data for eight *P. diadema* infants from June – December 2011 and June – December 2012. In addition, bi-weekly monitoring and observations of groups continued from January – June 2012. All eight infants belonged to one of four focal groups ranging in size from four to nine individuals and each group was habituated in the three months preceding data collection (Table 2.2).

Table 2.2 Mother-infant dyads within four groups of *P. diadema* over two successive birth seasons in Maromizaha forest

Dyad ID	Group	Group Size	Mother	Infant	Birthday
1	PD1	7	Mavo	Orana	July 9, 2011
2	PD1	7	Zoma	Tara	October 13, 2011
3	PD2	9-7	Rambo	Voa	June 27, 2011
4	PD2	9-7	Tandra	Kintana	June 27, 2011
5	PD3	8	Orkide	Siramamy	July 1, 2011
6	PD4	4	Volana	Faly	July 2, 2011
7	PD1	9	Mavo	Namana	June 24, 2012
8	PD3	9	Orkide	Rahona	July 22, 2012

Each group was monitored at least once per week and therefore the dates of each birth are known to within one week. We often knew the actual day of an infant's birth, due to absence one day and presence the next, but in cases where there was a full week between observations of the group, we estimated the birthdate to be in the middle of the preceding week. Seven of the eight births occurred between June 24 and July 22, and one infant was born on October 13. One mother-infant dyad (Dyad ID 3; Table 2.2) disappeared from PD2 when the infant was only five weeks old and therefore data on this dyad were excluded from further analyses. All of the remaining seven infants had survived past two years as of September 2013. Focal mother-infant dyads were identifiable by distinguishing fur colouration and natural body markings to ears and/or tails. Five of the seven infants were the only infants in their groups that year. Since only one group had two infants for longer than five weeks, and since one infant was three months older than the other, it was easy to distinguish the two infants in PD1 from one another.

Behavioural Sampling

I collected over 540 hours of behavioural data on seven infant *P. diadema*, in two consecutive birth seasons (2011 and 2012). Focal groups were located each day with the assistance of local guides and all-day follows of each infant were conducted for approximately two days each week. Depending on how long it took to find the animals, and the conditions on the particular day, focal follows commenced between 5:30–8:00 and ended between 15:00–17:30. Continuous and instantaneous sampling methods (Altmann 1974) were used to sample suckling, independent feeding, resting, observing, playing, allogrooming, and self-grooming behaviours (see Table 2.3 for definitions of infant behaviours). Time, to the nearest second, was recorded every time the behavioural state of the infant changed for longer than 10 seconds.

Table 2.3 Ethogram describing the infant behaviours recorded for focal observations of *P. diadema* at Maromizaha

Behaviour	Definition
Suckling	Infant's face is in contact with the mother's nipple
Independent Feeding	Infant is harvesting with hands and/or mouth, and chewing or ingesting, a plant item
Resting	Infant is not moving, eyes are either closed, or, if open they are not focused on anything in the environment
Observing	Infant is not moving, eyes/gaze and attention are focused on something specific in the environment, including other group members, sounds/movement in the trees/air/ground, and the observer
Playing	Infant is moving/active but not engaged in other active behaviours (feeding, allo, or self-grooming). Play behaviour includes individual exploration and exaggerated movements, and rough and tumble play and chases, and approach/retreat play with other individuals (Poirier 1974). Play behaviour is often accompanied by play face (Jolly 1966; Chevalier-Skolnikoff 1974)
Allogrooming	Infant is using the mouth/toothcomb to pick through and clean the fur of another individual
Self-Grooming	Infant is using the mouth/toothcomb to pick through and clean/lick the fur on its own body

Data Analysis

Data were summarized as proportions of observed time that infants spent suckling, independent feeding, resting, observing, playing, allogrooming, and self-grooming behaviours per focal follow session. To determine the precise week when infants transitioned from one phase to the next, I plotted suckling and independent feeding data as proportions of consumption time, per age of the infants, per week. The end of Phase 1 was predetermined to be the last week that infants were consistently suckling for more than 50% of their consumption time (time spent suckling and independent feeding combined). I predetermined that Phase 2 would end when there were no longer any weeks when the proportion of consumption time that infants spent suckling exceeded the proportion of consumption time spent feeding independently. I defined Phase 3 as beginning when the infants were feeding independently for more than 50% of their consumption time, consistently, for the remainder of the study. After determining the three phases of development for *P. diadema* infants by applying these pre-set criteria to the data, I categorized each focal follow session as being one of Phase 1, 2 or 3, depending on the age of the infant (in weeks) at the time of the session. To statistically compare the behaviours of *P. diadema* throughout these three phases of development, while accounting for overall observed time, I performed chi-square analyses of potential differences on the proportions of time infants were engaged in each behavioural state, during each developmental phase. I quantified and compared the proportion of observed time that infants spent in each of the three main positions (ventral, dorsal and independent) by week and by phase. I also examined the proportion of observed time that infants spent in physical contact with either their mothers or another group member, and compared this to the proportion of time infants spent physically independent (no physical contact with another individual), by phase. I used Spearman's correlation test to examine whether there was a relationship between the infant's age and the proportion of time they spent independent and feeding independently. All statistical analyses were performed in R 3.0.2 (R Core Development Team 2013).

Research authorizations for this study were obtained from the Malagasy Direction Générale des Forêts (DGF) du Ministère de l'Environnement et des Forêts (MEF). This research was strictly observational and was in compliance with the Ethical Treatment of Non-Human Primates as described by the American Society of Primatologists. Furthermore, all research described in this manuscript complies with protocols approved by the University of Victoria's Animal Care Committee.

2.3 Results

A total of 541 hours of behavioural data were collected for seven *P. diadema* infants, aged 0 – 25 weeks old. For comparisons by phase, I used 167 focal follow sessions and a total of 520 hours of behavioural data.

Schedule of Development for *P. diadema* infants

When first born, *P. diadema* were completely white and they gradually gained their colouration as they aged. Infants were first observed ingesting solid foods at three weeks and were not observed suckling past 31 weeks. For the first three weeks, infants were almost always in the mother's ventral position. They were first observed travelling short distances on their mother's back, in the dorsal position at three weeks. Sifaka infants were first observed independent (no physical contact with another individual) at five weeks and playing with other group members in week seven but then not again until week nine.

Defining Phases of Weaning for *P. diadema*

In total, infants spent over 150 hours of observed time either suckling or feeding independently. Figure 1 shows the proportion of this overall consumption time that infants were suckling and feeding independently by age, in weeks. For the first three weeks, infants received close to 100% of their nourishment from their mothers. Infants were suckling for a greater proportion of their consumption time until week 13. This was therefore defined as the end of Phase 1. Between weeks 14 and 19, there were some ages when the proportion of consumption time that infants spent suckling exceeded the proportion of consumption time spent feeding independently and vice versa. This period was defined as Phase 2. Beginning in week 20, infants were consistently feeding independently for a greater proportion of their consumption time through the rest of the study. This was therefore defined as Phase 3. This trend continued, and from bi-weekly observations in January – June 2012, I determined that no infants were observed suckling past 31 weeks.

I found a strong positive correlation between *P. diadema* infant age in weeks and proportion of consumption time dedicated to individual feeding (Spearman rank correlation, r = 0.96, N = 25 weeks, P < 0.001; Figure 2.1).

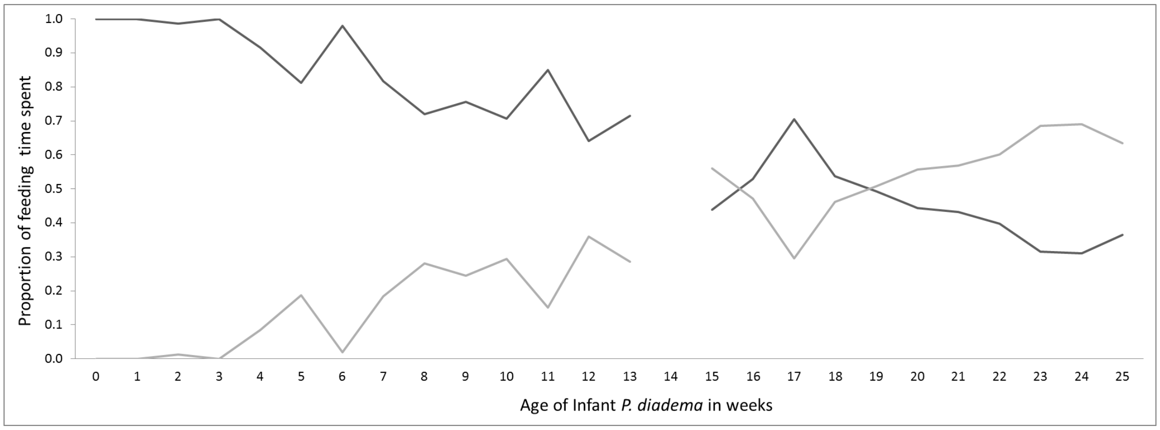

Figure 2.1 Proportion of observed feeding time that infant *P. diadema* (N=7) spent suckling (black) and feeding independently (grey) by week, from birth to 25 weeks. Week 14 was excluded from this figure due to small sample size for infants at this age.

Each focal follow session was subsequently categorized according to the weaning phase definitions as follows: Phase 1 included sessions when infants were 0 – 13 weeks old, Phase 2 included sessions when infants were 14 – 19 weeks old, and Phase 3 included sessions when infants were 20 – 25 weeks old. Figure 2.2 shows the proportion of consumption time (suckling + independent feeding) that infants suckled and fed independently, by each phase.

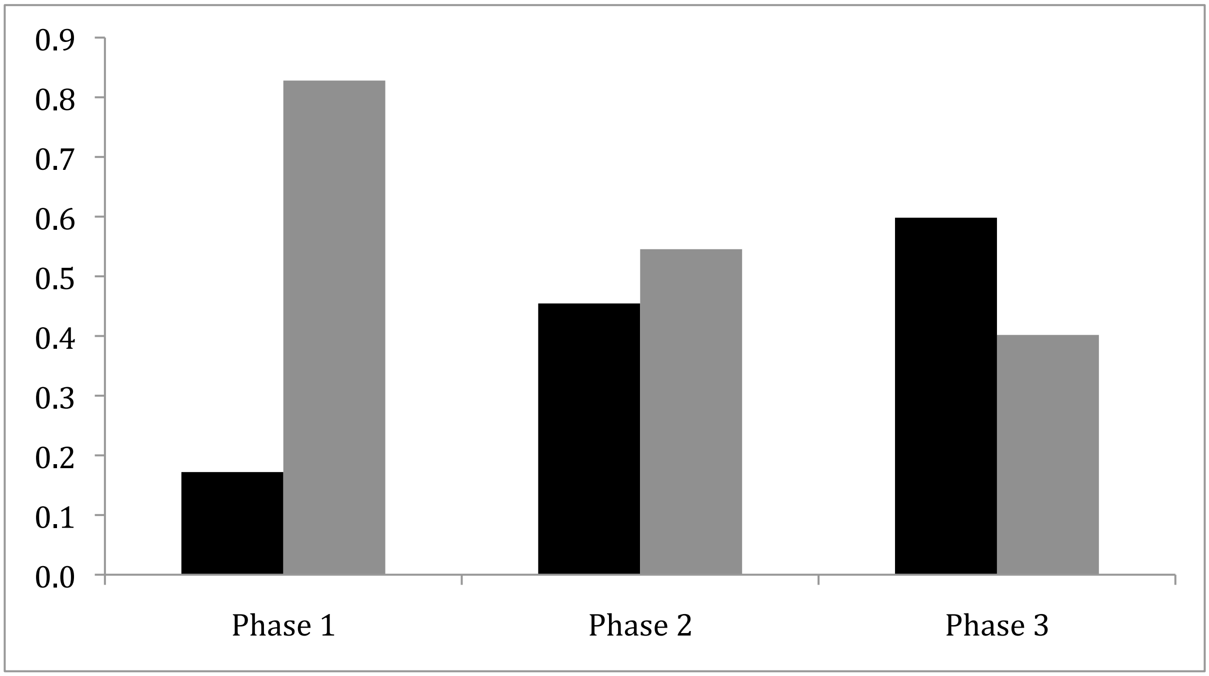

Figure 2.2 Proportion of observed consumption time (suckling + independent feeding) that *P. diadema* infants suckled (grey) and fed independently (black) during each of the three developmental phases. Phase 1 includes weeks 0 – 13 (40 hours of consumption time), Phase 2 includes weeks 14 – 19 (50 hours of consumption time), and Phase 3 includes weeks 20 – 25 (60 hours of consumption time).

When examining infant feeding behaviours as part of the overall activity budget (including all behaviours, not exclusively time spent feeding), *P. diadema* infants spent a significantly greater proportion of their overall observed time consuming food (suckling + independent feeding) in Phase 2 than they did in Phase 1 ($\chi^2 = 1224.99$, $P < 0.001$), and significantly more time consuming food (suckling + independent feeding) in Phase 3 than they did in Phase 2 ($\chi^2 = 194.82$, $P < 0.001$; Figure 2.3). However, while infants spent a significantly greater proportion of time feeding independently in Phase 2 than they did in Phase 1 ($\chi^2 = 1408.20$, $P < 0.001$) and in Phase 3 than they did in Phase 2 ($\chi^2 = 276.63$, $P < 0.001$; Figure 2.4), suckling did not follow a distinct pattern. Infants suckled for a greater proportion of time in Phase 2 than they did in Phase 1 ($\chi^2 = 188.78$, $P < 0.001$; Figure 2.5) and this proportion of time spent suckling remained constant throughout

Phase 3. Such suckling behaviour demonstrates that the increase in consumption time by infants in Phase 3 is completely dependent on the additional time infants spent feeding independently in this phase, and not influenced by a change in the overall proportion of time spent suckling.

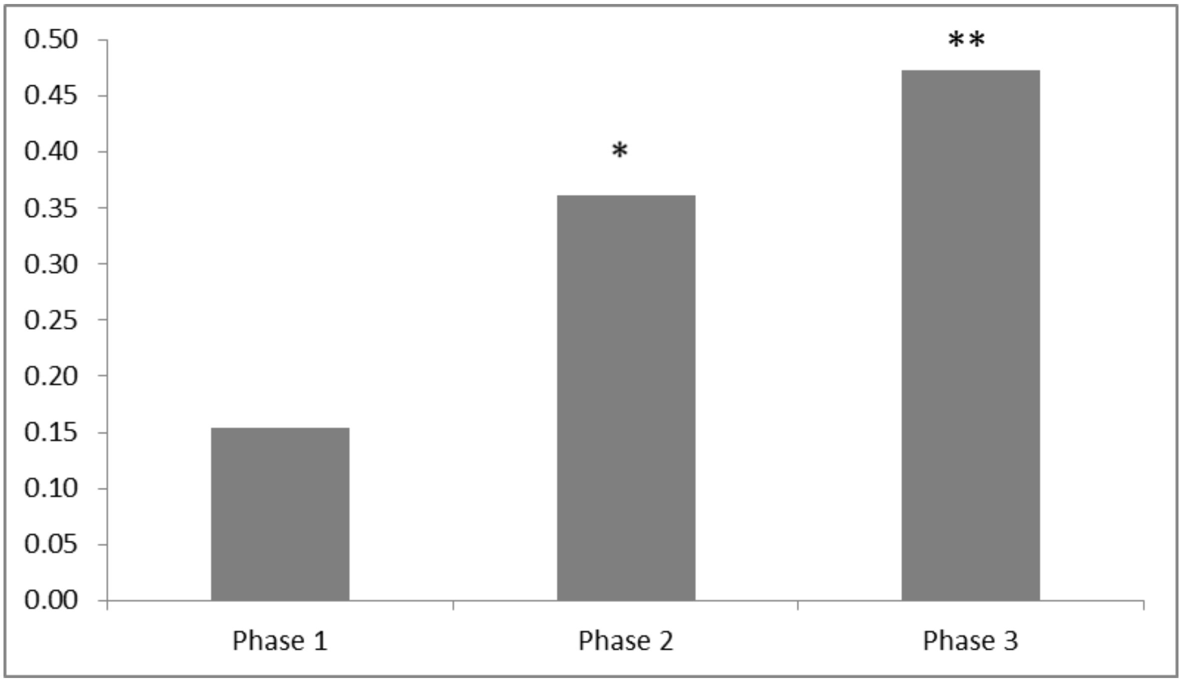

Figure 2.3 Total proportion of observed time that *P. diadema* infants consumed food (suckling + independent feeding) during each of the three developmental phases. *P. diadema* spent a significantly greater proportion of time consuming food in each phase. Asterisks denote a significant difference between that phase and the preceding phase.

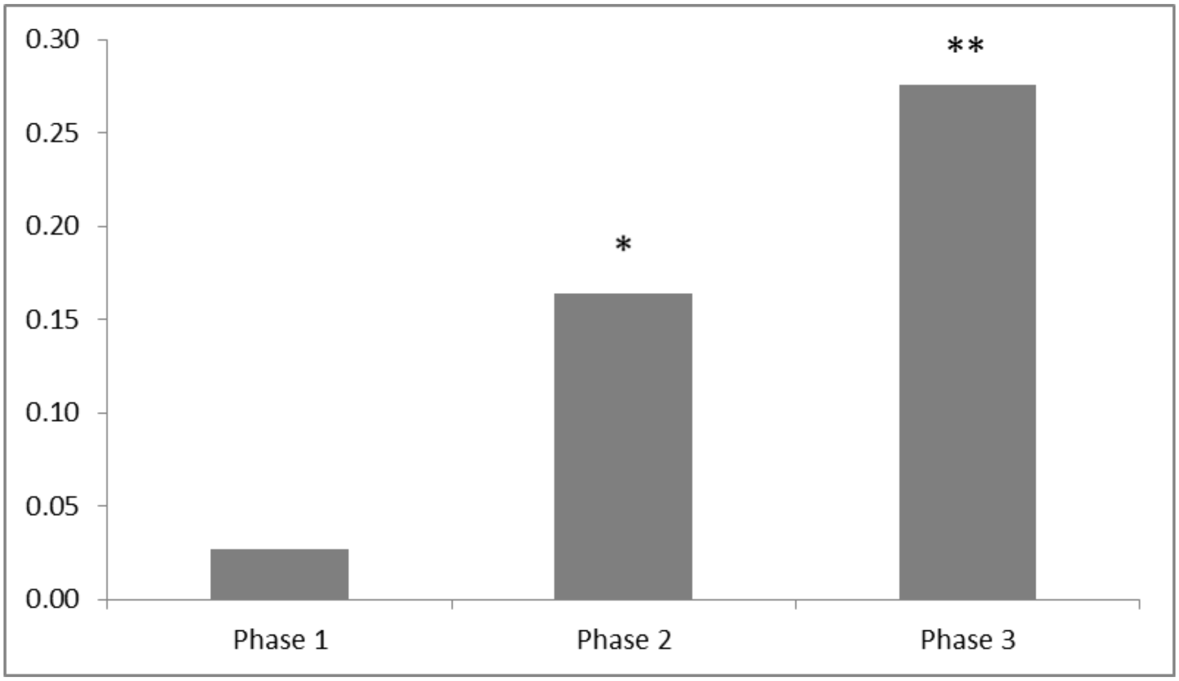

Figure 2. 4 Total proportion of observed time that *P. diadema* infants fed independently during each of the three developmental phases. *P. diadema* infants spent a significantly greater proportion of time feeding independently in each phase. Asterisks denote a significant difference between that phase and the preceding phase.

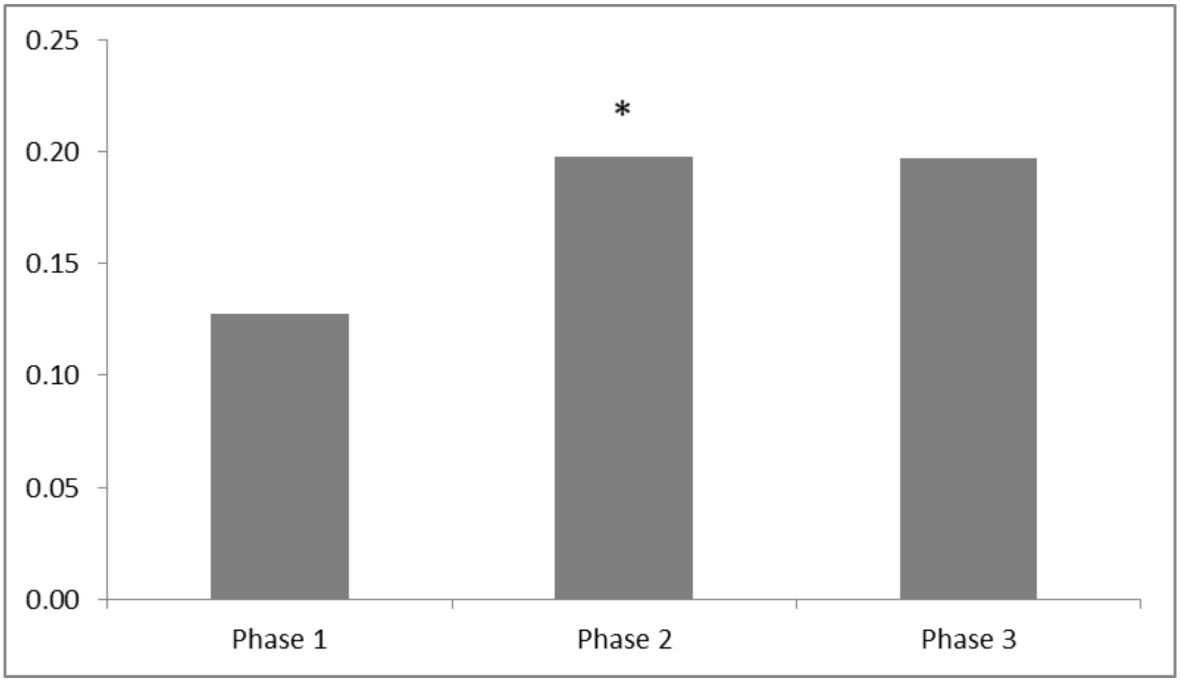

Figure 2. 5 Total proportion of observed time that *P. diadema* infants were suckling in each of the three developmental phases. *P. diadema* spent a significantly greater proportion of time suckling in Phase 2 but not in Phase 3. Asterisks denote a significant difference between that phase and the preceding phase.

Physical Contact with Mother

P. diadema infants spent 100% of their time in physical contact with their mothers in the first three weeks and progressively spent less time in contact with her as they aged. Infants spent 7%, 30% and 50% of their time independent (not in physical contact with their mothers) in Phases 1, 2, and 3 respectively. Infants spent significantly more time independent in Phase 2 than they did in Phase 1 ($\chi^2 = 2734.40$, $P < 0.001$), and significantly more time independent in Phase 3 than they did in Phase 2 ($\chi^2 = 679.80$, $P < 0.001$; Figure 2.6).

I found a strong positive correlation between *P. diadema* infant age in weeks and proportion of observed time spent independent (Spearman rank correlation, r = 0.92, N = 25 weeks, P < 0.001).

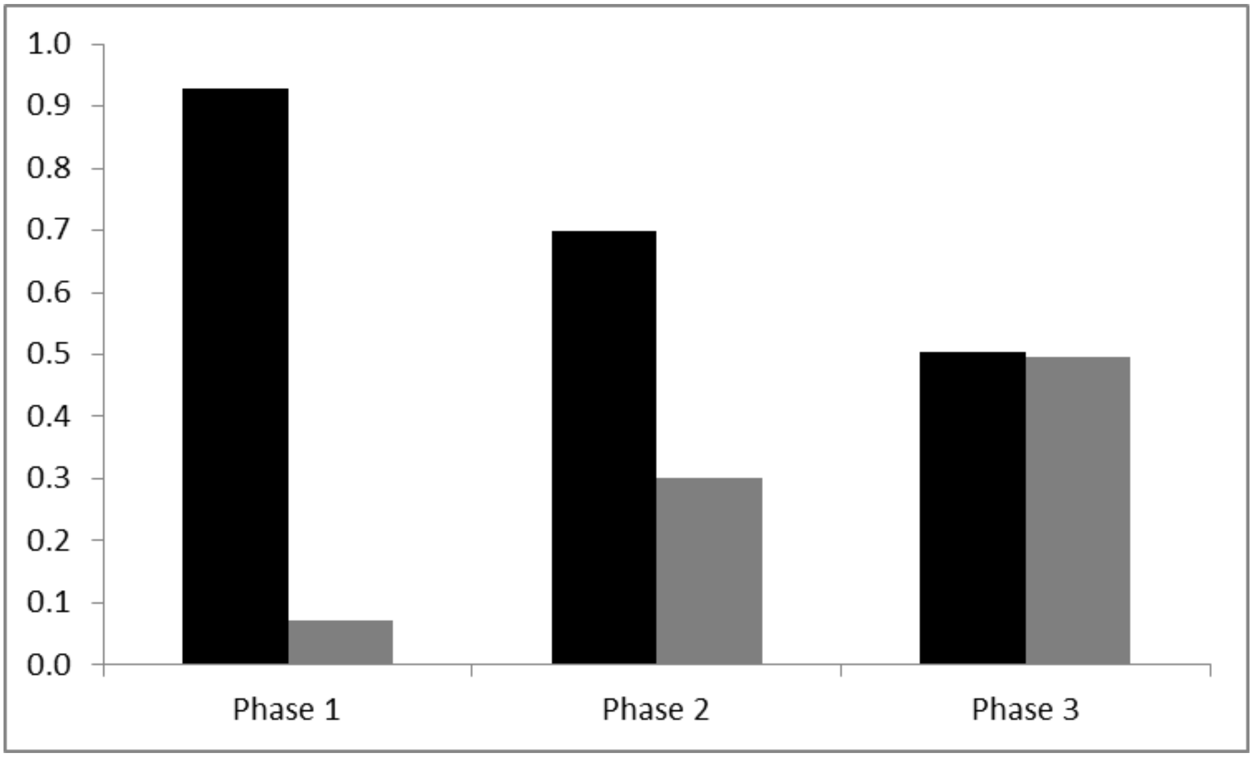

Figure 2.6 Proportion of observed time that *P. diadema* infants (N=7) were in physical contact with their mothers or non-mothers (black) and independent (grey) during each of the three developmental phases.

Position of the Infant

P. diadema infants were classified as either in the mother's ventral position, dorsal position or independent throughout this study. Infants spent 88%, 50% and 34% of their time in the ventral position in Phases 1, 2, and 3 respectively. Infants spent significantly less time in ventral position in Phase 2 than they did in Phase 1 (χ^2 = 4958.61, $P < 0.001$), and significantly less time in ventral position in Phase 3 than they did in Phase 2 (χ^2 = 394.62, $P < 0.001$; Figure 2.7). In Phase 2, infants spent 20% of their time in dorsal position, compared to only 5% in Phase 1 (χ^2 = 1575.90, $P < 0.001$). In Phase 3, infants spent 16% of their time in dorsal position, which was significant less than they did in Phase 2 (χ^2 = 53.49, $P < 0.001$; Figure 2.7).

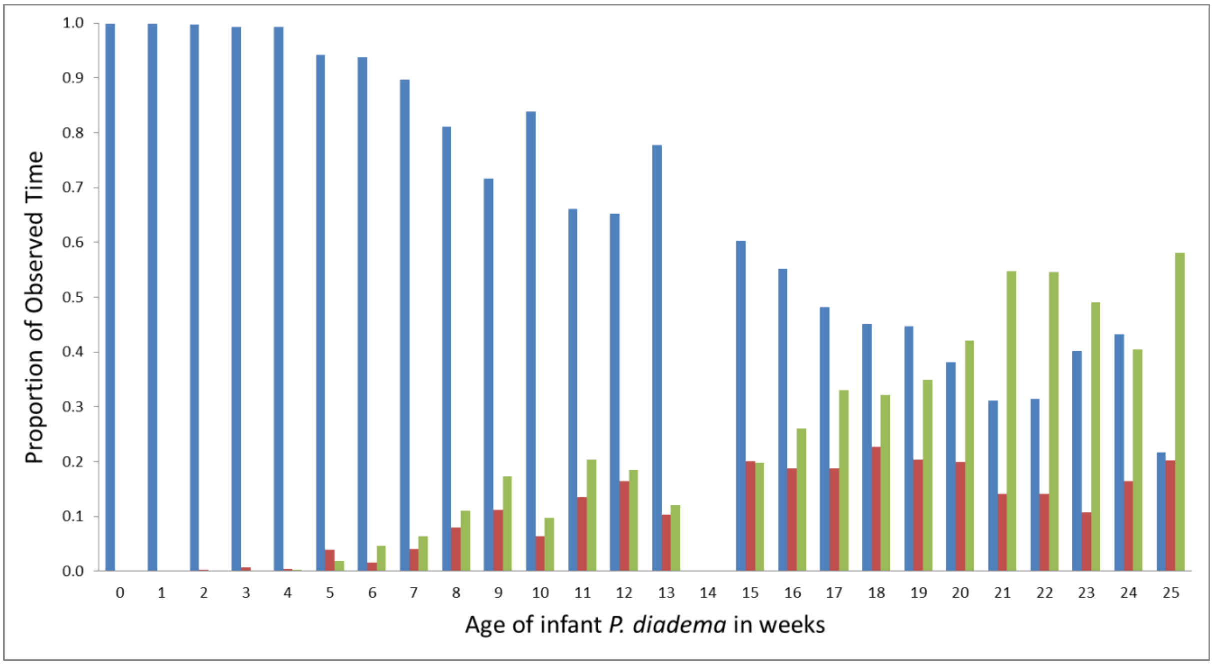

Figure 2.7 Proportion of observed time that *P. diadema* infants (N=7) were in the ventral position (blue), the dorsal position (red) or independent (green) by week from birth to 25 weeks. Week 14 was excluded from this figure due to the small sample size for infants at this age.

Behavioural Changes by Phase

Table 2.4 displays the percentage of time that infants were suckling, feeding independently, resting, observing, playing, self-grooming and allogrooming with other group members by individual phase, as defined by the stages of feeding ontogeny, and overall, from birth to 25 weeks. The results in this table illustrate the detailed developmental information that is potentially lost when behaviours are generalized across phases. For example, the time that *P. diadema* infants spent feeding independently overall, is significantly different than the time they spent feeding independently in Phase 1 ($\chi^2 = 1206.30$, $P < 0.001$), Phase 2 ($\chi^2 = 71.95$, $P < 0.001$) and Phase 3 ($\chi^2 = 1118.62$, $P < 0.001$; Table 2.4).

Table 2.4 Percentage of observed time *P. diadema* infants engaged in each behaviour throughout the first 25 weeks (overall), and by individual phase.

Behaviour	Overall (%)	Phase 1 (%)	Phase 2 (%)	Phase 3 (%)
Suckling	16.2	12.7	19.7	19.7
Feeding independently	12.6	2.7	16.4	27.6
Resting	15.7	27.7	3.9	3.7
Observing	27.6	26.4	28.0	29.5
Playing	24.8	28.7	28.7	14.3
Self-grooming	1.9	1.2	2.2	2.9
Allogrooming	0.8	0.4	0.7	1.4

P. diadema infants spent a significantly greater proportion of time observing in Phase 2 than they did in Phase 1 ($\chi^2 = 6.32$, $P < 0.02$), and in Phase 3 than they did in Phase 2 ($\chi^2 = 4.20$, $P < 0.05$; Figure 2.8). Infants were resting for a greater proportion of their time in Phase 1 than they were in Phase 2 ($\chi^2 = 1709.99$, $P < 0.001$; Figure 2.9) but there was no significant difference in the proportion of time infants spent resting in Phases 2 and 3. As the proportion of time infants spent observing increased, the proportion of time spent resting decreased. This suggests a gradual change from resting behaviour by infants, defined as infants not moving and with eyes closed, or not focused/observant of anything in the environment, to more observant behaviour, including watching/directing attention to other individuals in the group, sounds/movement in the trees/air/ground, and/or the observer.

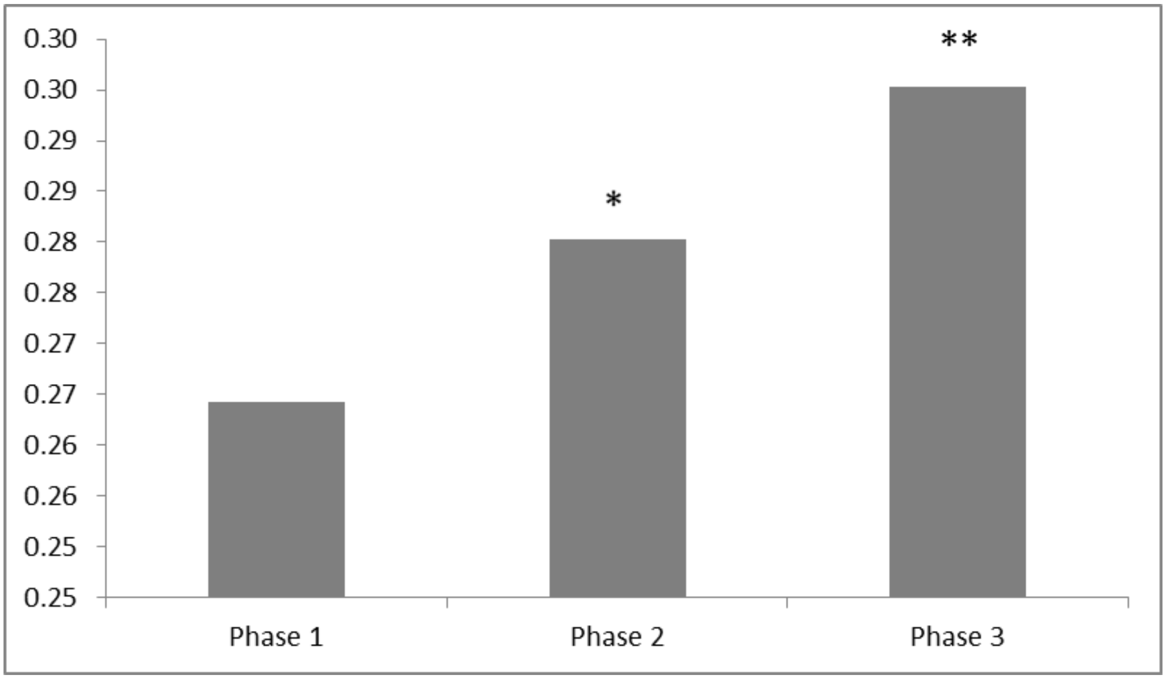

Figure 2.8 Total proportion of observed time that *P. diadema* infants were observing during each of the three developmental phases. *P. diadema* infants spent a significantly greater proportion of their time observing in each phase. Asterisks denote a significant difference between that phase and the preceding phase.

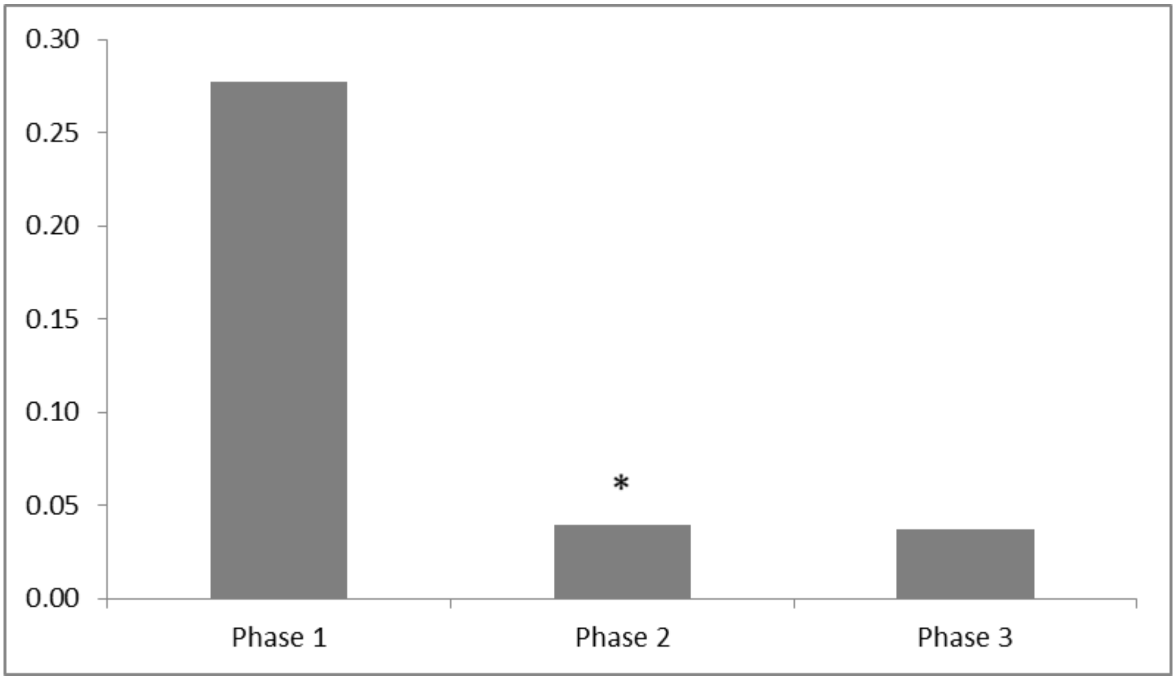

Figure 2.9 Total proportion of observed time that *P. diadema* infants rested during each of the three developmental phases. *P. diadema* spent significantly less time resting in Phases 2 & 3 compared to Phase 1. Asterisks denote a significant difference between that phase and the preceding phase.

P. diadema infants spent the smallest proportion of their time playing in Phase 3 ($\chi^2 = 482.90$, $P < 0.001$; Figure 2.10), but there was no difference between time spent playing in Phases 1 and 2. In addition to frequent active movement and exploration all over the body of their mothers, infant *P. diadema* also frequently engaged in distinct VCL (vertical clinging and leaping) development behaviours that appeared to be facilitated by the mothers. The following anectdotal observations summarize this particular behaviour. During these observations, a mother would position herself and her infant in a specific place with supports that enabled the infant to utilize thick lianas or small vertical branches to 'practice' VCL. The mother would observe and monitor her infant while the infant would spend over 10 minutes repeating the following behaviour sequence: The infant would first climb up on the mother's back, then reach for the vertical support, grasp the vertical support with one hand and one foot, and then the other hand and foot so that the infant was in the vertical clinging position. Next, the infant would reach for the dorsal side of the mother, grasp her fur with one hand and one foot, and then the other hand and foot so that the infant was back in the dorsal position where it started the behaviour sequence. Early on, infants frequently repeated the specific sequence 12 or more times, and in one session, an infant repeated the same sequence 87 times. I first recorded this behaviour when the infants were five weeks old. As the infants aged, the reach, grasp, transfer and cling pattern became quicker and more fluid so that eventually the infants were actually leaping to and from the vertical support. In the beginning the distance between the mother and the vertical support was only 10 cm, however this distance increased as the infant developed. As the infants got older, they would sometimes ‘embellish’ the behaviour sequence by climbing up and down the vertical support and eventually they would repeat the same sequence from and back to the mother but go to different supports instead of constantly returning to the same spot. Infants were recorded repeating the sequence of leaps to three different supports, returning to the mother and then repeating the sequence to the same three spots for several minutes of observation time. The mother was always very close and observant of her infant in the beginning and in instances when the infant could not reach the mother to get back she would gently reach out and pull the infant to her again. Mothers frequently appeared to facilitate this behaviour by positioning herself in an ideal spot with appropriate supports to allow the infant to practice safely.

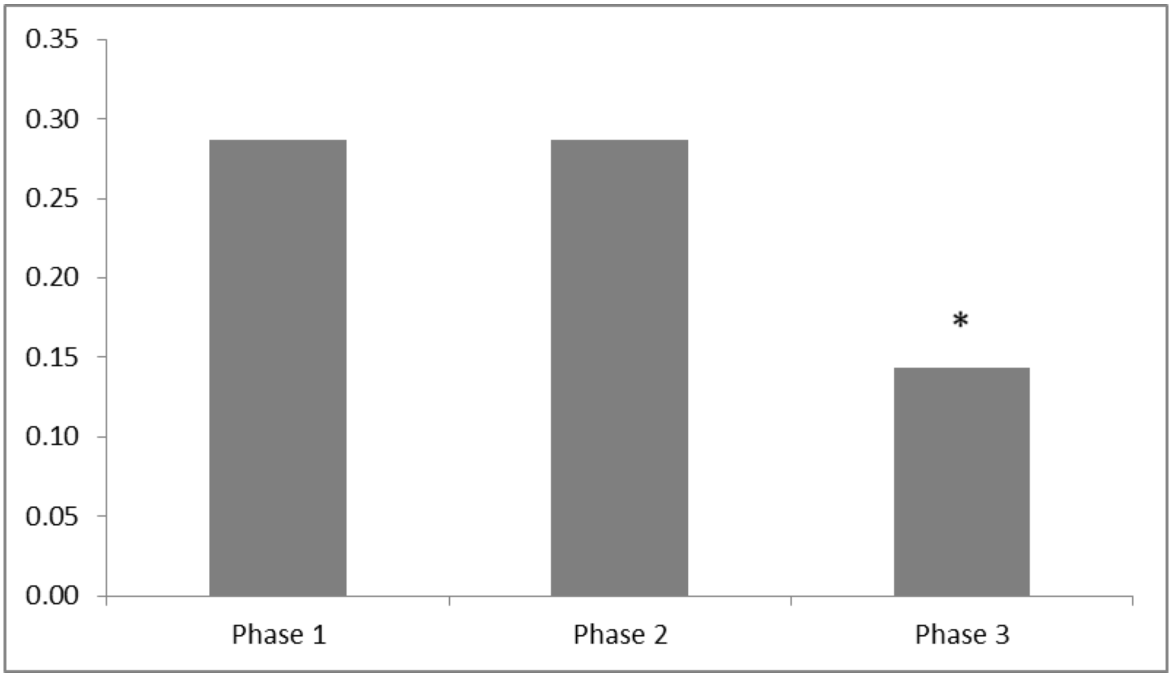

Figure 2.10 Total proportion of observed time that *P. diadema* infants spent playing during each of the three developmental phases. *P. diadema* spent a significantly smaller proportion of time playing in Phase 3 than Phases 1 & 2. Asterix denote a significant difference between that phase and the preceding phase.

P. diadema infants spent a significantly greater proportion of time self-grooming in Phase 2 than they did in Phase 1 ($\chi^2 = 38.28$, $P < 0.001$), and in Phase 3 than they did in Phase 2 ($\chi^2 = 6.14$, $P < 0.02$; Figure 2.11). They also spent a significantly greater proportion of time allogrooming with other group members in Phase 2 than they did in Phase 1 ($\chi^2 = 5.22$, $P < 0.03$), and in Phase 3 than they did in Phase 2 ($\chi^2 = 22.89$, $P < 0.001$; Figure 2.12).

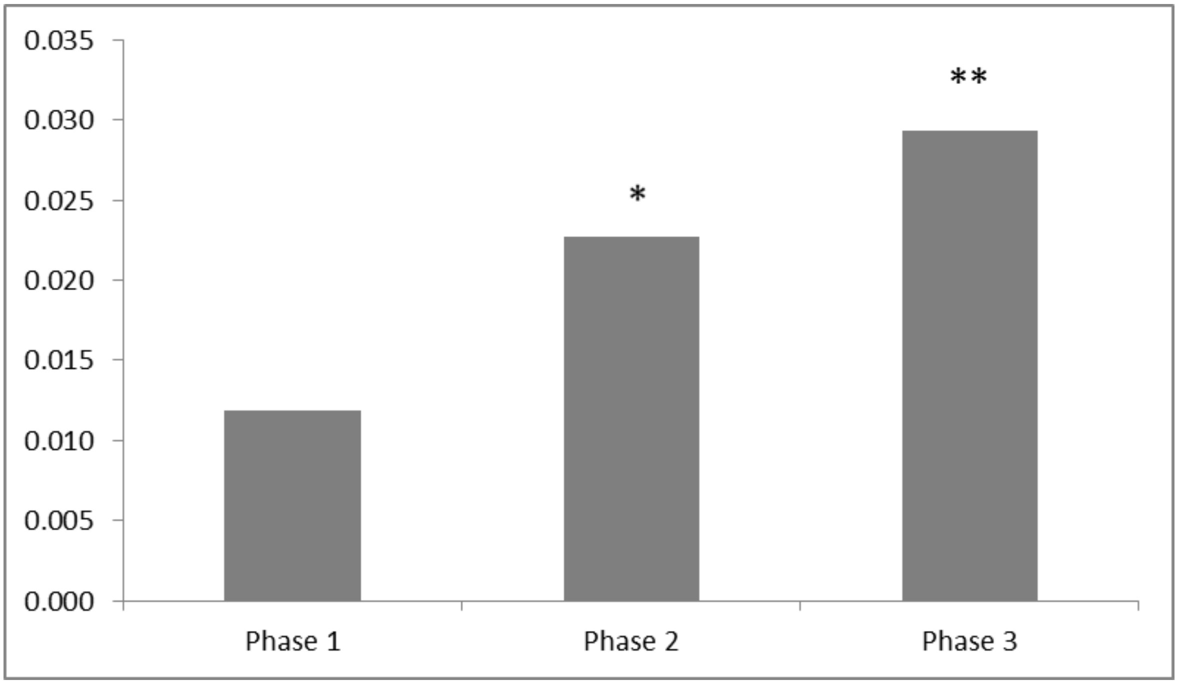

Figure 2.11 Total proportion of observed time that *P. diadema* infants spent self-grooming during each of the three developmental phases. *P. diadema* spent a significantly greater proportion of time self-grooming in each phase. Asterisks denote a significant difference between that phase and the preceding phase.

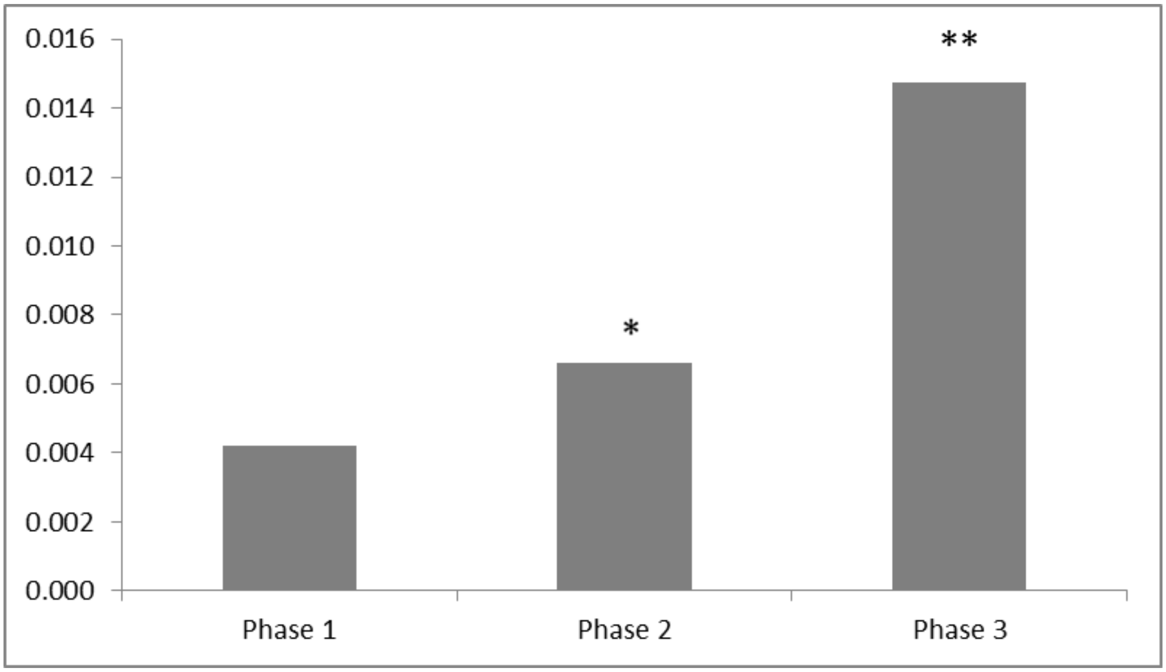

Figure 2.12 Total proportion of observed time that *P. diadema* infants spent allogrooming with other group members during each of the three developmental phases. *P. diadema* spent a significantly greater proportion of time allogrooming in each phase. Asterisks denote a significant difference between that phase and the preceding phase.

2.4 Discussion

My study presents the only data on the distinct phases of weaning, ontogeny of behaviours and infant survival in the Critically Endangered diademed sifaka (*P. diadema*). I also introduced a three-phase framework for determining the main stages of the weaning process that can be applied to other species. The findings I present lend to a growing body of knowledge on how infants and mothers within the primate order cope with the early challenges of feeding ontogeny and contributes to the small body of knowledge we have on the ecology and life-history strategies of this lesser known species. By using a three-phase framework, I was able to further quantify and compare the proportion of time that infants spent suckling, feeding independently, resting, observing, playing (either independent exploration or with other group members), allogrooming, self-grooming and locomoting independently, in each of the three distinct phases of weaning.

Three Phases of Weaning for *P. diadema*

Weaning, defined generally as the change from dependent to independent acquisition of nourishment, is a gradual process for primates (Lee 1997). It is therefore impractical to use the first observation of ingesting solid food or the last observation of suckling to measure the boundaries of feeding ontogeny, as infants will begin feeding independently, and continue to occasionally suckle, at ages when these behaviours contribute relatively negligible nourishment to the overall diet the infant (Martin 1984). I recorded these developmental markers for *P. diadema* infants to compare with previous studies, but I also divided focal follow sessions into three pre-defined stages, according to suggestions put forth by Martin (1984) and Lee (1997) and measured the relative length of time that infants spent in each phase. This resulted in three distinct phases of weaning summarized below.

Phase 1 - From birth to 13 weeks old, *P. diadema* were suckling, rather than feeding independently to obtain most of their nourishment and hence I defined this as the first phase of weaning. *P. diadema* infants ate their first solid foods at three weeks, at the same age that independent feeding was first reported for one *P. edwardsi* infant (Grieser 1992) and for *P. verreauxi* (Richard 1976), but markedly earlier than what has been reported for *L. catta* (Gould 1990), *E. fulvus* (Tarnaud 2004), *E. rufifrons* (Overdorff 1996), *E. rubriventer* (Overdorff 1996), *E. flavifrons* (Volampeno et al. 2011) and *Varecia rubra* (Vasey 2007; Table 2.1). Like other folivorous primates, *P. diadema* infants exhibit rapid dental development and are consequently able to begin processing solid foods at an earlier age than the more frugivorous lemurids, who exhibit slower dental development, but faster growth overall (Godfrey et al. 2001; Godfrey et al. 2004). Early consumption of solid foods, in conjunction with consuming milk from their mothers may be necessary for infants to develop the gut microflora and the enzymes required for the effective digestion their highly folivorous diet. It is also possible that the dilute milk supplied by folivorous mothers is lacking in some essential nutrient that the infants are only able to ingest through the consumption of solid foods. We currently lack data on the properties of *Propithecus* milk (Hinde & Milligan 2011) however future studies in this area may help uncover the adaptive explanations for why these infants begin consuming solid foods at such a young age.

Phase 2 - Between 14 and 19 weeks, *P. diadema* infants were alternating between suckling and feeding independently as their main source of nourishment (Figure 2.1).

This phase illustrates the gradual and non-uniform transition from dependence on the mother for most of their nourishment to independent consumption of solid foods in this species. It also suggests that there could be other important, non-nourishment benefits to infants suckling during this phase in particular, including maintaining mother-infant contact for comfort, safety from predators and for warmth on rainy days (Altmann 1980). Although this phase was less than half the length of Phase 1 (in weeks), it was marked by a significant reduction in the proportion of time that infants spent suckling and a significant increase in the time infants spent feeding independently.

Phase 3 - *P. diadema* infants were feeding on solid foods for at least 50% of their observed consumption time beginning in week 20 and consistently until week 25 when regular observations ended. According to the proportion of time spent feeding independently, I defined this as Phase 3, and the final phase of weaning. By these same criteria, Phase 3 began at 19 weeks for *E. fulvus* (Tarnaud 2004), 11-16 weeks for *L. catta* (Gould 1990; O'Mara 2012) and for *Varecia rubra* (Vasey 2007), and *by* week 26 in *P. edwardsi* and *P. tattersalli* (Wright 1995). Therefore, I was correct in my prediction that *P. diadema* infants would develop nutritional independence later than the smaller and more frugivorous lemurids (Table 2.1). In some studies, the age that infants are reported as 'weaned' is based on the age at which they were last observed suckling although this is usually considerably later than when infants are responsible for most of their own nourishment. For example, *Varecia rubra, E. flavifrons*, *E. fulvus* and *L. catta* were last observed suckling in week 18 (Vasey 2007), week 25 (Volampeno et al. 2011), week 30 (Tarnaud 2004) and weeks 25–27 (Gould 1990; O'Mara 2012) respectively. In *P. candidus*, infants were considered weaned (no longer observed suckling) at approximately 6–7 months (E. Patel unpublished data/personal communication) however some *P. edwardsi* infants continued to suckle during the day up until 12 months (Wright 1995). Wright (1995) also discovered that two relatively young *P. edwardsi* mothers were secreting milk when they had offspring that were 1.5 old, and suggested that in some cases infants *may* continue to suckle at night until they are two years old. However, lactation this late is not common and a greater sample size is needed to better understand the conditions under which this occurs (P. Wright, personal communication). While I was not able to observe *P. diadema* infants at night, I did not observe any suckling during the day past 31 weeks. Between weeks 20 and 25, infants spent 60% of their consumption time and 28% of their observed time overall feeding independently, demonstrating that they were likely receiving most of their nourishment independently well before the age they were last seen suckling. I suggest that it is in this last weaning phase that nutritional responsibility switches from the mother to the infant, regardless of infrequent suckling events that may continue until a later age. I recommend that infant feeding data for other sifaka species be organized according to these criteria so that we might compare the particular similarities and differences in early feeding ontogeny within the genus *Propithecus*.

Ontogeny of Non-Feeding Behaviours

By using the specific, pre-determined criteria detailed above for defining the beginning of each phase of weaning, I was able to expand upon this conceptual framework to further quantify and compare the proportion of time that infants spent independent, and in certain non-feeding behaviours in each of the three distinct phases of weaning. Again, I recorded developmental 'firsts' for *P. diadema* infants to compare with previous studies, but I also divided focal follow sessions into the three pre-defined phases to show differences between different periods of development.

Time spent independent - In Phase 1, *P. diadema* infants were mostly in the mother's ventral position, but began travelling short distances in the dorsal position in their third week. Similarly, *P. verreauxi* began dorsal riding in week four (Richard 1976) and one *P. edwardsi* infant was observed dorsal riding in week three (Grieser 1992). The first time I observed a *P. diadema* infant independent (no physical contact) for more than 10 seconds was in the fifth week. This is slightly later than what has been reported for *E. fulvus* (Tarnaud 2004), *E. rufifrons* (Overdorff 1996), *E. flavifrons* (Volampeno et al. 2011) and *P. edwardsi* (Grieser 1992) and more than three weeks later than what was observed in *L. catta* (Gould 1990), *E. rubriventer* (Overdorff 1996), *Varecia rubra* (Vasey 2007) and *P. verreauxi* (Richard 1976; Table 2.1). Overall, *P. diadema* infants spent 7%, 30% and 50% of their time independent in Phases 1, 2, and 3 respectively, with Phase 3 beginning at week 20 and continuing until week 25. Although not summarized in the same way, other sifaka species showed similar patterns, while *L. catta* (Gould 1990) and *E. flavifrons* (Volampeno et al. 2011) spent a greater proportion of their time independent at an earlier age, thus confirming my prediction that *P. diadema* would have slower physical development than lemurs than do not exhibit VCL. For example, infant *P. verreauxi* were independent for 35% of their time at five months (22 weeks), and 63% of their time by six months (26 weeks) (Richard 1976), and *P. edwardsi* infants travelled independently for 80% of observed time by the seventh month (30 weeks) (Wright 1995). In comparison, *E. flavifrons* were not in contact with their mothers for 50% of their time in week 13 and for 20% of their time in week 25 (Volampeno et al. 2011) while *L. catta* were in contact with their mothers for less than 50% of their time by week eight, and less than 20% by week 14 (Gould 1990). In accordance with my prediction, independent locomotion in *P. diadema* developed at a later age than in species that do not exhibit vertical clinging and leaping (Napier & Walker 1967; Demes et al. 1996). Pollock (1986b) reported that *Indri indri* infants were not able to exhibit adult competency in VCL until they were over one year old. Since falls are assumed to be a leading cause of infant mortality in highly arboreal lemurs (Morland 1990; Richard et al. 2002), infant *P. diadema* presumably reduce the probability of injury or death due to falls, by prolonging the time spent being carried (Ross 2001; Ross 2003).

Time spent observing - Observational learning is an important behaviour for developing infants (Coussi-Korbel & Fragaszy 1995; Galef & Giraldeau 2001; Rapaport & Brown 2008; Jaeggi et al. 2010; O'Mara & Hickey 2012). For example, infant howler monkeys (*Alouatta palliata*) observe the behaviour of other individuals in the group before feeding on a new species of leaves (Whitehead 1986) and in most instances of feeding, adult feeding precedes infant feeding (Whitehead 1986). This cautionary approach to eating leaves is hypothesized to be an adaptation for learning to select particular species that are lower in secondary compounds (Whitehead 1986) and I expect that this is important in *P. diadema* as well, since the adult diet and plants available in their habitat also include high levels of secondary compounds (Powzyk & Mowry 2003). Visual attention to any elements in the environment, including sudden or unfamiliar sounds and movement may also be a precursor to the vigilant anti-predator behaviours of adults. Dominant females in groups of *L. catta* were more frequently vigilant of potential predators, unknown sources of noise and audible sounds from conspecifics in other social groups than were other members of their own group (Gould 1996; Gould et al. 1997) and infants may learn these behaviours by observing their mothers. In my study, infants gradually spent more time observing as they got older, and spent the most time observing during Phase 3 when they were also feeding on solid foods for most of their consumption time. The time individuals spend observing during early infancy may be critical to the development of adult feeding behaviours in *P. diadema*. In addition, infants may learn important anti-predator and social behaviours by observing their environments and other individuals in their group at a young age. Further investigation into the behaviours of mothers and the specific food items she consumes while infants are observing, would be helpful in understanding the relative importance of observational learning in *P. diadema* development.

Time spent playing - I observed the first social play in *P. diadema* at seven weeks, but then this behaviour was not observed again until nine weeks. This is similar to six weeks reported for one *P. edwardsi* infant (Grieser 1992) but later than for two infant *P. verreauxi* who were observed playing together at 3 – 4 weeks (Richard 1976) and when *L. catta* began social play at five weeks (Gould 1990). The individuals that played with infants in my study were either juveniles or adults as there was very rarely an opportunity for an infant to play with another infant. In all but one of the groups that I observed, there was only one infant in the group. In the one group with two infants (PD1-2011) there was a three month age difference between the two infants and I did not observe any play between the two infants. Infant *P. diadema* spent less time playing in Phase 3 than they did in Phases 1 and 2. Similarly, infant *L. catta* spent significantly less time playing independently past week 12, but continued to spend just under 10% of their time in social play (Gould 1990). In primates, independent, or presocial play, where infants explore their environment and manipulate objects, is important for developing the motor skills needed to forage and feed independently and to move through the environment effectively and efficiently (Poirier & Smith 1974; Gould 1990). Social play, involving infants playing with other group members is also important for developing the social skills to be assimilated into a group and to interact with other groups (Poirier & Smith 1974; Gould 1990; Antonacci et al. 2010; Norscia & Palagi 2011; Volampeno et al. 2011). In my study, juveniles frequently engaged in social play behaviour, and occasionally adults did as well, however they very rarely engaged in independent play (unpublished data). I suggest that while social play continues to be an important aspect of juvenile and perhaps adult behaviour, the main functions of independent play are to develop the motor skills required to acquire food and to move through the environment. As they aged, *P. diadema* infants spent less time in independent play and more time engaged in the important adult behaviours that they have developed through play, including independent feeding, grooming and independent locomotion.

Time spent grooming - *P. diadema* infants were first observed self-grooming and allogrooming in Phase 1, and were observed in both of these behaviours significantly more as they aged. Self-grooming in primates is important for removing ectoparasites and maintaining the condition of the fur and allogrooming is suspected to help in removing ectoparasites from places that are hard for the recipient to reach (Hutchins & Barash 1976). In addition to these hygenic functions, allogrooming in primates has been found to be connected to bond formation, rank acquisition and social integration (Dunbar 1991; Schino 2001; Lewis 2010). The relative importance of self and allogrooming behaviours in *P. diadema* infants increased as they got older, while grooming by the mother decreased (Chapter 5), shifting the responsibility of this hygienic and social behaviour to the infant.

Infant Survival for *P. diadema*

Sifaka tend to have high rates of infant mortality and corresponding low rates of infant survival through the first year relative to haplorhine primates (Wright 1995) and therefore, I predicted that *P. diadema* would exhibit low infant survivorship as well. However, although my study only spans field seasons that occurred in three consecutive years, I found that infant survival for *P. diadema* at Maromizaha was significantly higher than that reported for other species of sifaka and for smaller species of lemurs (for one exception see Tarnaud 2004). Infant mortality for *P. diadema* in my study was 12.5%, and consequently 87.5% of infants (7 of 8) survived past 12 months (and to at least 24 months). In *P. edwardsi* only 48 – 57% of infants survive to 12 months (Wright 1995; Pochron et al. 2004; Morelli et al. 2009) and in *P. verreauxi* only 52% of infants survive past 12 months (Richard et al. 2002). This high infant mortality has been suggested to be a product of the bet-hedging strategy employed by female sifaka living in the harsh and unpredictable environments of Madagascar (Wright 1995; Wright 1999; Richard et al. 2002). Under this hypothesis, a high percentage of infant deaths are expected to result from factors that could not be eliminated by higher levels of maternal care in the form of higher milk quality or a longer lactation period (Wright 1995). In other studies, the causes of infant mortality in lemurs include predation (Irwin et al. 2009) and infanticide events (Jolly et al. 2000; Richard et al. 2002; Littlefield 2010; Morelli et al. 2009), and environmental stress, punctuated in years with severe climatic events (ex. droughts or cyclones) (Gould et al. 1999; Richard et al. 2002; King et al. 2005; Lewis & Rakotondranaivo 2011), and these deaths are frequently unpreventable on the part of the mother (Wright 1995). Next, I will examine each of these causes of infant mortality and provide possible explanations for the high rate of infant survival observed in my study.

The main predator of sifaka is the fossa (*Cryptoprocta ferox*), a large bodied carnivore found throughout the dry forests and rainforests of Madagascar (Meyers & Wright 1993; Wright 1995; Powzyk 1997; Patel 2005; Goodman 2003; Irwin et al. 2009). Although rare, in two cases, *P. diadema* infants were reported to have been predated upon by aerial predators (Day et al. 2009), and anti-predator responses elicited by sifaka when potential aerial predators are detected suggests that they do prey on these sifaka (Karpanty & Grella 2001). In my study, while *C. ferox* were observed in the study area on two separate occasions and potential aerial predators were frequently observed during focal follow sessions of *P. diadema* infants, I did not witness any direct predation events or evidence for them having occurred. Irwin et al. (2009) suggested that the large home range of *C. ferox* relative to rainforest sifaka contributes towards a pattern of low average per capita predation on sifaka but high temporal variability. This predation strategy often results in most or all of the members of a small group of sifaka being preyed upon in a short period of time, while other groups are not targeted for several years (Irwin et al. 2009). There was no infant mortality of *P. diadema* resulting from predation in my study and I suggest that this may be due to a low density of *C. ferox* in my study area. More focused work into *C. ferox* in Maromizaha would allow us to better understand the relationship between these two species at this site.

Although rare, infanticide, or infant killing by conspecifics, has been documented in some species of lemurs (Jolly et al. 2000) including sifaka (Richard et al. 2002; Morelli et al. 2009; Day et al. 2009; Littlefield 2010). In a long-term study of *P. edwardsi*, researchers found that females came into estrus sooner if their infants were killed by immigrant males (Morelli et al. 2009). Conversely, females dispersed from their natal groups when their infants were killed by immigrant females (Morelli et al. 2009). The authors also reported that in almost all of the cases when a takeover happened, the infants that had been in the group disappeared immediately (Morelli et al. 2009). Three of seven infant *P. diadema* born to females who had been translocated to Analamazaotra Special Reserve (ASR) were killed by competing females (Day et al. 2009) suggesting that the high incidence of infanticide in this study could have been influenced by the sudden change in density as a result of the translocation. At both of these field sites, infanticide appears to be influenced by density and by dispersal. I did not witness any evidence of infanticide in my study of *P. diadema* at Maromizaha, reflecting a lower rate than what was observed for translocated *P. diadema* at ASR. In *L. catta*, infanticide tends to occur if home ranges are small and overlap and there is a low availability of resources (L. Gould, personal communication). By contrast, the home ranges of *P. diadema* at Maromizaha are relatively large, and there is very little overlap between the home ranges of neighbouring groups (Chapter 5). It could be that there are sufficient resources to support the number of groups currently inhabiting my study area, and that this reduces the potential for infanticide. However, more years of study would be needed to document if this behaviour occurs and what specific conditions influence the likelihood of it occurring.

Finally, sifaka infants tend to be born in the harshest time of the year (Wright 1999). While this strategy is predicted to time infant weaning to occur during the time of year with the most food available (Wright 1999), it also causes infant deaths in the early stages of lactation due to factors associated with environmental stress such as dehydration and hypothermia (Richard et al. 2002; King et al. 2005) particularly in infants with older mothers (Richard et al. 2002; King et al. 2005). In my study, one mother-infant pair disappeared from PD2 when the infant was 5 weeks old, in early August 2011. Later, in what would have been the infant's 7th week, the mother was observed alone, without her infant or her group, near our camp for close to 24 hours. She only rested, and appeared to be in poor health. In the weeks surrounding this event, there were high levels of rainfall and the lowest temperatures recorded relative to other times of the year (Appendix I). Just prior to the disappearance, the mother was observed spending most of her time resting in a huddle position and rarely feeding or engaging in social behaviours with other group members. Although I have no prior knowledge of the female's age (2011 was year we habituated this group), her body and fur condition were poor relative to other mothers in my study and I assumed she was in poor health. While I have no direct evidence, I suspect that environmental stress, and the factors associated with the mother's poor health could have led to the death of the one infant in this study.

What is particularly striking is that the remaining infants all survived intense tropical cyclone Giovanna, which struck Maromizaha in February of 2012 with winds of over 195 km/h. More than half of the trees in the forest were destroyed and most of the trees were completely defoliated by the cyclone (R.M. Randrianarison personal communication/ unpublished data). One lemur (*Avahi laniger*) was found dead and presumed to have died as a direct result of the storm, but no *P. diadema* infants from my study died as a direct or indirect result of this severe climatic event. In fact, all four infants that were alive before the cyclone have survived to at least two years old. In addition, infants born in the birth season a few months after cyclone Giovanna also survived past 12 months. This positive, yet puzzling outcome contrasts to what has been found for other lemur populations that experience severe climatic events (Gould et al. 1999; Richard et al. 2002). For example, at Beza-Mahafaly Special Reserve, 80% of *L. catta* infants died in the second year of a severe drought in contrast to 18% in non-drought years (Gould et al. 1999). However, the resilience of sifaka to intense cyclones has been documented in Kirindy (Lewis & Rakotondranaivo 2011) and more detailed investigation are required to better understand how some species of lemurs endure during these severe climatic events.

In this chapter, I presented the first data on the distinct phases of weaning, ontogeny of behaviours and infant survival in the critically endangered diademed sifaka (*P. diadema*). By using specific, pre-determined criteria for defining the beginning of each phase of weaning, I was able to expand upon this conceptual framework to further quantify and compare the proportion of time that infants spent suckling, feeding independently, resting, observing, playing, self-grooming and allogrooming in each of the three distinct phases of weaning. As predicted, *P. diadema* were slower to develop nutritional independence and locomotory independence than the smaller and more frugivorous lemurids. However, in contrast to what has been documented for other species of lemurs, infant survivorship of *P. diadema* was relatively high in my study. Future studies, including longer-term studies of maternal strategies and infant development in *P. diadema* could reveal how infant survival remained high in my study despite a severe cyclone. In addition, presenting data for other sifaka infants according to the phases outlined in this study would be valuable in future comparisons both between species and within species inhabiting different field sites.

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3 - DIET, COPROPHAGY AND PHASES OF FEEDING ONTOGENY OF INDRI (*INDRI INDRI*) INFANTS AT MAROMIZAHA FOREST

3.1 Introduction

In order to survive to maturity, young mammals must acquire the specific diet and feeding behaviours of their respective species. As they gradually obtain nutritional independence, infants are required to develop an awareness for when to feed, where to feed, which food items to select and which to avoid, how to obtain and process particular food items and for how much time they should spend feeding on particular food items (Galef & Giraldeau 2001). Initially, infants may develop this awareness in part through chemical cues in their mother's milk, on her breath, or by ingesting her fecal pellets (Galef & Giraldeau 2001). When infants first begin ingesting solid foods, social learning may also influence how diet and the specific food acquisition, processing, and feeding behaviours of adults are developed. Specific mechanisms for social learning of diet and feeding behaviours in primates, reviewed by Rapaport & Brown (2008), often include a combination of enhancement, observational conditioning, and imitation. Local or stimulus enhancement is commonly documented in mammals and is used to explain how most infants eventually acquire the diet of adults (Galef & Giraldeau 2001). For example, immature animals closely associating with experienced conspecifics during feeding, a behaviour termed co-feeding, likely affects the discovery of which food items to select and which to avoid (Rapaport & Brown 2008). Mountain gorilla (*Gorilla beringei*), baboon (*Papio* spp.), brown lemur (*Eulemur fulvus*) and orangutan (*Pongo pygmaeus wurmbii*) infants tend to feed at the same times, and on most or all of the same food items as their mothers (Watts 1985; King 1994; Tarnaud 2004; Jaeggi et al. 2010).

Immature primates may also learn species specific foraging techniques through imitation (Rapaport & Brown 2008). For example, brown capuchins (*Cebus apella*), aye-aye (*Daubentonia madagascarensis*) and orangutans (*Pongo pygmaeus wurmbii*), first observe and then match the detailed sequence of food extraction they observed in experienced conspecifics (Krakauer 2005; Gunst et al. 2007; Jaeggi et al. 2010). After finding that infants almost always observed the feeding behaviour of other individuals in the group before they began feeding on leaves, Whitehead (1986) suggested that howler monkeys (*Alouatta palliata*) use observational conditioning and imitation specifically, to learn how to select particular species that are lower in secondary compounds.

Infants may also rely on trial-and-error learning and individual exploration to acquire the diet and feeding behaviours of their respective species. For example, young ring-tailed lemurs (*Lemur catta*) in a gallery forest habitat rarely engaged in co-feeding and their diets were more diverse than those of adults (O'Mara & Hickey 2012). This suggests that young *L. catta* may rely more on individual rather than social learning for dietary development (O'Mara & Hickey 2012). Whether infants of a particular species employ more social learning behaviours or more individual learning behaviours to develop their diet is influenced by four variables. The first is the degree of dietary specialization of the species. Immatures of species with more generalized diets tend to rely more on individual learning whereas species with more specialized diets rely more on social learning (Rapaport & Fragazy 2008). The second variable is the type of social system and relative tolerance level of the group. Young primates living in more tolerant social groups with relatively low rates of agonism between group members tend to have more opportunities for social learning than those in less tolerant social groups, with higher rates of agonism between group members (Coussi-Korbel & Fragazy 1995). In these latter groups, individual learning is presumably less risky than social learning because it is less reliant on close contact with other group members, who could be potentially aggressive towards young individuals. The third variable is the amount of environmental change typically observed in the environment. Species inhabiting environments with lower levels of habitat change tend to exhibit more examples of social learning behaviours than those that inhabit environments that are highly changeable due to unpredictable climatic events (Boyd & Richerson 1988). The fourth variable is the relative length of the juvenile period and the overall pace of life history. Immatures with a prolonged period of dependency tend to have more opportunities for social learning over a longer period of time and engage in less independent exploration than those with shorter periods of time in close association their mothers (Jaeggi et al. 2010).

The results of O’Mara & Hickey (2012) support all four of these predictions and thus, the lack of complex social learning mechanisms observed in developing *L. catta* is likely because they: 1) eat a more generalized diet, primarily composed of fruits, leaves and occasionally supplemented by insects (Sauther 1998; Sauther et al. 1999; Jolly 2003; Gemmill & Gould 2008; Gould et al. 2009; Gould et al. 2011), 2) live in groups with intolerant dominance hierarchies and high agonistic rates relative to other female-dominant species (Erhart & Overdorff 2008), 3) inhabit environments that experience rapid and unpredictable changes in temperature and rainfall from climatic events (Gould et al. 1999; Dewar & Richard 2007; Lawler et al. 2009) and 4) develop independence relatively quickly compared to other similarly sized primates, resulting in a shorter period of time in close association with their mothers (Gould 1990; Meredith 2011; O’Mara

2012). Although *L. catta* tended to use more individual rather than social forms of learning, the above predictions have yet to be tested in other species of lemurs.

In this chapter, I examined the early ontogeny of diet and feeding behaviours in the indri (*Indri indri*), the largest folivorous strepsirhine primate. In contrast to *L. catta*, *I. indri*: 1) eat a specialized diet composed primarily of leaves (Britt et al. 2002; Powzyk & Mowry 2003), 2) live in tolerant groups with low agonistic rates compared to other lemur species (Erhart & Overdorff 2008), 3) inhabit the eastern rainforest, which experiences fewer fluctuations in temperature and rainfall (Powzyk 1997; Britt et al. 2002), 4) only produce offspring every two to three years and thus infants have a protracted period of time in close contact with their mothers (Pollock 1975a; Pollock 1975b). All of these characteristics predict that *I. indri* infants should rely more on complex social learning mechanisms than do *L. catta*.

In this chapter, I also compared feeding ontogeny and infant development of *I. indri* to that of *Propithecus diadema* using the same pre-determined definitions for the phases of weaning that I described in Chapter 2. These two species share several important traits that suggest they might exhibit similar periods of infant development. Specifically, *I. indri* and *P. diadema* are: 1) closely related phylogenetically, both belonging to the taxonomic family Indriidae (Mittermeier et al. 2008; Rumpler et al. 2004; Rumpler et al. 2011), 2) roughly the same weight as adults (Glander & Powzyk 1995; Britt et al. 2002; Gordon et al. 2013), 3) highly arboreal, employing vertical clinging and leaping (VCL) as their main form of locomotion (Napier & Walker 1967; Demes et al. 1996), and 4) often sympatric, both inhabiting the eastern rainforest of Madagascar (Powzyk 1997; Mittermeier et al. 2008). Because of these similarities, which reduce the variability inherent with differing phylogeny, body size, locomotion and habitat, these two species are ideal for comparison.

In the late 1990s, Powzyk conducted a comparative study of *I. indri* and *P. diadema* at Mantadia National Park and elucidated several key differences in the ecology of these two sympatric species including; i) *P. diadema* eat a more diverse diet of fruits, seeds, flowers and leaves, while *I. indri* eat a diet dominated by leaves, ii) *I. indri* spend more time resting, have shorter daily path lengths and have shorter active periods than do *P. diadema*, and iii) *I. indri* defend their territories using long-call vocalizations while *P. diadema* actively patrol their territories and scent-mark significantly more frequently than do *I. indri* (Powzyk 1997; Powzyk & Mowry 2003; Powzyk & Mowry 2006). To date, there have been three longer-term studies (at least 12 months in duration) of *I. indri* ecology and behaviour (Pollock 1975a; Powzyk 1997; Britt et al. 2002), and important attention to their distinctive loud calls (Pollock 1986b; Thalmann et al. 1993; Giacoma et al. 2010; Sorrentino et al. 2013; Torti et al. 2013), however no one has studied infant development in this enigmatic species.

In addition, no study has specifically questioned why female *I. indri* have evolved to have the longest inter-birth interval amongst the lemurs, giving birth in May or June to a single infant every two to three years (Pollock 1975a; Tecot et al. 2013; Chapter 5). Within primates, most life history variables are correlated with phylogeny (Stearns 1983; Kappeler 1996), body size (Kappeler 1996; Lee 1997), and occasionally habitat and food availability (ex. orangutans, van Noordwijk et al. 2009; gorillas, Stoinski et al. 2013). It is therefore puzzling that *I.indri* only give birth every two to three years while *P. diadema*, the similarly sized and often sympatric indriid, gives birth every one to two years. Why do *I.indri* require this protracted inter-birth interval? Here, I offer two, non-mutually exclusive explanations for why there is such a discrepancy between the inter-birth intervals for these two species.

The first explanation is that the difference in inter-birth interval between the two species is correlated to the differing social organizations of their respective groups. Rapaport & Brown (2008) theorized that when adult size and phylogeny are controlled for in analyses, that primate species that live in monogamous groups tend to have a faster pace of infant development than those living in other types of social groups. In these cases, paternal care (Wright 1990) is suggested as the proximate mechanism that allows for faster development in infancy in monogamous groups. For example, male red-bellied lemurs (*Eulemur rubriventer*) and siamangs (*Symphalangus syndactylus*) facilitate a faster pace of development in their infants by carrying them (Overdorff 1996; Lappan 2009), while male owl monkeys (*Aotus azarai*) carry (Rotundo et al. 2005) and transfer food items to their young (Wolovich et al. 2008) as do titi monkeys (*Callicebus torquatus*) (Starin 1978) . In callitrichids there is also extensive allocare and males frequently transport and share food with their infants (Leutenegger 1980; Garber 1997).

I. indri are also classified as monogamous (Pollock 1975b), although mating pairs do change (Pollock 1975b) and at least one instance of extra pair copulation (Bonadonna et al. 2013), and one instance of female takeover by infanticide (Ratolojanahary & Dolch 2013) have been documented. *I. indri* infants are born into territorial groups of two to five individuals composed of a breeding pair and their offspring (Pollock 1986a; Powzyk 1997; Glessner & Britt 2005) whereas *P. diadema* infants are born into groups of two to nine individuals that may be polygynous, polygynandrous, pairs or polyandrous (Pochron

& Wright 2003; Irwin 2006b). In both *I. indri* and *Propithecus* species, females are dominant and exhibit feeding priority over males (Pollock 1979; Erhart & Overdorff 2008). However, despite their social organization, *I. indri* do not exhibit paternal care via infant-carrying or food transfers as has been documented for these other socially monogamous species (Tecot et al. 2013; *this study*) and it is therefore unlikely that monogamy or paternal care facilitates faster infant development in *I. indri* as suggested by Rapaport & Brown (2008). In comparison, *P. diadema* very occasionally exhibit paternal care via infant-carrying (M. Irwin personal communication/unpublished data) and this might in part facilitate the shorter inter-birth interval observed in this species, relative to *I. indri*.

I. indri may also produce offspring less frequently than *P. diadema* due to energetic restrictions imposed by a diet dominated by leaves with little accessible energy. In order to digest cellulose, the structural carbohydrate found in the cell walls of plants, animals require the enzyme cellulase (Alexander 1993; Bauchop 1978; Eisenberg 1978; Lambert 1998). Since no vertebrates possess cellulase, folivorous animals must rely on microbes in their digestive tracts to break-down cellulose and produce volatile fatty acids (VFA) for energy (Bauchop 1978; Eisenberg 1978; Lambert 1998). This process is slow, and to aid in the effective digestion of leaves, primates have evolved several adaptions including specialized dentition and gut anatomy and the expression of particular behavioural traits (Lambert 1998; Fleagle 1999; Strier 2003; Godfrey et al. 2001).

I. indri are particularly folivorous, dedicating 71 – 82% of their feeding time to leaves (Pollock 1975a; Britt et al. 2002; Powzyk & Mowry 2003). Conversely, *P. diadema* only dedicate 44 – 53% of their feeding time to leaves and supplement their diet with more fruits, seeds and flowers than do *I. indri* (Powzyk & Mowry 2003; Irwin 2008; Irwin et al. 2013). While the African and Asian colobine monkeys possess specialized gut anatomy adapted for the challenges of folivory, *I. indri*, like howler monkeys (*Alouatta* spp.) must expend considerable physiological energy breaking down plant material including toxins and secondary compounds (Milton 1981; Langer 2003; Powzyk & Mowry 2006; Borries et al. 2011). To compensate for the amount of energy needed for digesting a diet dominated by leaves, *I. indri* spend a large amount (45 – 59 %) of their time resting (Powzyk 1997; Britt et al. 2002) as do other highly folivorous primates including *Alouatta palliata* (63%; Raguet-Schofield 2010) and *Lepilemur mustelinus* (80%; Hladik & Charles-Dominique 1974). In addition, *I. indri* rarely engage in energetically costly behaviours such as play or scent-marking (Powzyk 1997) and the daily distances they tend to travel are less than half that of *P. diadema* (Powzyk 1997). Overall rates of agonism are extremely low between group members (Erhart & Overdorff 2008) and aggressive interactions between groups are rare, particularly in pristine forests (Pollock 1975b; Powzyk & Mowry 2006).

In contrast to physical contests, *I. indri* defend their territories using a very conspicuous loud call that persists for 40–250 seconds and can be heard 3–4 km away from the source (Pollock 1986a; Torti et al. 2013). This call, or song, often elicits the same behaviour from neighboring groups. Adults and older offspring in a group all sing together, and information on group composition including the sex (Giacoma et al. 2010) and age (Sorrentino et al. 2013) of each individual singer is advertised by the type and number of notes used. In addition, the structure of these loud calls can contain context specific information and serve to maintain group cohesion when individuals are visually separated (Torti et al. 2013). Although highly effective, very little energy is required for these calls, compared to the territory defense behaviours of *P. diadema* which include active patrolling of territory borders, frequent scent-marking and aggressive intergroup encounters (Powzyk & Mowry 2006). These activity patterns led Powzyk & Mowry (2006) to suggest that *I. indri* are 'energetic minimizers', and I suggest that the long interval between births in this species is part of this overall strategy as well. The protracted period between births reduces energetic stress on the female, by allowing at least one extra year for females to recover from the energetic costs of lactation and infant-carrying and prepare for the following gestation period. In comparison, *P. diadema* females frequently conceive and commence their next gestations when their offspring are approximately seven months old. In addition, I hypothesize that this longer inter-birth interval allows more time for individual infants to develop the behavioural and physiological adaptations required for acquiring, processing and digesting the particularly folivorous diet of adults.

In this chapter, I explore this hypothesis by 1) examining opportunities for social learning mechanisms in *I. indri* and comparing my findings to what was observed in *L. catta* (O'Mara & Hickey 2012) and 2) describing and quantifying the pace of feeding ontogeny in *I. indri* infants and comparing this to what I reported for sympatric *P. diadema* in Chapter 2. If the longer inter-birth interval in *I. indri* allows more time for individual infants to develop the behavioural adaptations required for acquisition, processing and digesting the particularly highly folivorous diet of adults, then I expected that I would find evidence for social learning of diet and feeding behaviours in infancy. Specifically, I predicted that *I. indri* infants would spend a large proportion of their time observing their environment and other individuals in their respective groups. I also predicted that I would find a high level of dietary overlap between *I. indri* infants and their mothers. Since *I. indri* are more folivorous than *P. diadema*, and despite their monogamy show no paternal care, I also predicted that *I. indri* infants would develop more slowly than *P. diadema*. Specifically, I predicted that they would be slower to reach developmental markers than sympatric *P. diadema*. This is the first study to identify infant diet and describe the ontogeny of feeding behaviours in the critically endangered *I. indri* (IUCN 2013; Schwitzer et al. 2013).

3.2 Methods

Study Area

I studied the behaviours of *P. diadema* infants in Maromizaha forest (18°57'S, 48°36'E), a New Protected Area, located 140 km east of the nation's capital of Antananarivo, near the village of Anevoka. This montane rainforest is part of the Ankeniheny-Zahamena rainforest corridor conservation initiative (CAZ; Schwitzer et al. 2013) and includes a protected area encompassing approximately 1,600 ha, composed of 820 ha of intact hard wood forest and 360 ha of regenerated forest, with the remaining classified as degraded habitat. My study area is within mid-altitude rainforest and the *P. diadema* groups that I studied are found at elevations ranging from 970 – 1223m. The annual rainfall for 2012 was 3163 mm, with close to one third falling in January and February combined (Appendix I). February 2012 was also when cyclone Giovanna struck the area, leaving all trees defoliated and several large trees dying. The average temperature (at 7:30 am) during the study period was 16°C (min=12.6, max=19.1), and the overall maximum and minimum temperatures were 36.8°C and 7.6°C respectively

(Appendix I). The hottest months of the year were November – February and the coldest were July – September (Appendix I). This study took place in the cold (July – September) and hot (October – December) seasons of 2011 and 2012 and is part of my larger study comparing infant development and maternal strategies in *I. indri* and *P. diadema* inhabiting Maromizaha forest.

Study Subjects

With the help of five trained assistants (see Acknowledgements), I collected behavioural data for five *I. indri* infants and their mothers from June – December 2011 and June – December 2012. All five infants belonged to one of five focal groups ranging in size from 3 – 5 individuals and each group was habituated in the months preceding data collection (Table 3.1).

Table 3.1 Mother-infant dyads within five groups of *I. indri* over two successive birth seasons in Maromizaha forest

Dyad ID	Group	Group Size	Mother	Infant	Birthday
1	IN1	5	Bevolo	Berthe	June 4, 2012
2	IN2	3	Soa	Fanihy	May 2, 2012
3	IN3	5	Mena	Jo	June 6, 2012
4	IN4	4	Ava	Gebe	June 4, 2012
5	IN5	4	Fern	All Black	June 8, 2011

Each group was monitored at least once per week and therefore the dates of each birth are known to within one week. We often knew the actual day of an infant's birth, due to absence one day and presence the next, but in cases where there was a full week between observations of the group, we estimated the birthdate to be in the middle of the preceding week. Four of the five births occurred between June 4 and June 8, and one infant was born on May 2. The mother in Dyad ID 2 had lost an offspring (estimated at ~ 16 months old) to assumed predation in October of 2010 and had not reproduced in the previous three years. All five of the infants from this study have currently survived past two years, as of September 2013. Focal dyads were identifiable by distinguishing fur colouration and natural body markings to ears and/or tails. All five of the infants were the only infants in their groups that year.

Behavioural Sampling

I collected behavioural data on five infant *I. indri*, and their mothers in two consecutive birth seasons (2011 and 2012). Focal groups were located each day with the assistance of local guides and all-day follows of each infant were conducted for approximately two days each week. Continuous and instantaneous sampling methods (Altmann 1974) were used to sample suckling, independent feeding, resting, observing, playing, allogrooming, and self-grooming behaviours (see Table 3.2 for definitions). Time, to the nearest second, was recorded every time the behavioural state of the infant changed for longer than 10 seconds. When infants or their mothers were feeding, I recorded the plant name and part consumed as leaves, fruit, buds, flowers, shoots or bark). If possible, I counted the number of items consumed per minute of feeding time and recorded the sequence of feeding behaviours for particular food items.

Table 3.2 Ethogram describing the infant behaviours recorded for focal observations of *I. indri*

Behaviour	Definition
Suckling	Infant's face is in contact with the mother's nipple
Independent Feeding	Infant is harvesting with hands and/or mouth, and chewing or ingesting, a plant item
Resting	Infant is not moving, eyes are either closed, or, if open they are not focused on anything in the environment
Observing	Infant is not moving, eyes/gaze and attention are focused on something specific in the environment, including other group members, sounds/movement in the trees/air/ground, and the observer
Playing	Infant is moving/active but not engaged in other active behaviours (feeding, allo, or self-grooming). Play behaviour includes individual exploration and exaggerated movements, and rough and tumble play and chases, and approach/retreat play with other individuals (Poirier 1974). Play behaviour is often accompanied by play face (Jolly 1966; Chevalier-Skolnikoff 1974)
Allogrooming	Infant is using the mouth/toothcomb to pick through and clean the fur of another individual
Self-Grooming	Infant is using the mouth/toothcomb to pick through and clean/lick the fur on its own body

Data Analysis

Data were summarized as proportions of observed time that infants spent suckling, independent feeding, resting, observing, playing, allogrooming, and self-grooming behaviours per focal follow session. To determine the precise week when infants transitioned from one phase to the next, I plotted suckling and independent feeding data as proportions of consumption time, per age of the infants, per week. The end of Phase 1 was predetermined to be the last week that infants were consistently suckling for more than 50% of their consumption time (time spent suckling and independent feeding combined). I predetermined that Phase 2 would end when there were no longer any weeks when the proportion of consumption time that infants spent suckling exceeded the proportion of consumption time spent feeding independently. I defined Phase 3 as beginning when the infants were feeding independently for more than 50% of their consumption time, consistently, for the remainder of the study. After determining the three phases of development for *I. indri* infants by applying these preset criteria to the data, I categorized each focal follow session as being one of Phase 1, 2 or 3, depending on the age of the infant, in weeks at the time of the session. For these analyses, I only used focal follow sessions that included at least 30 minutes of the infant in-view. To statistically compare the behaviours of *I. indri* throughout these three phases of development, while accounting for overall observed time, I performed chi-square analyses of potential differences for proportions of time infants were engaged in each behavioural state, during each developmental phase. I quantified and compared the proportion of observed time that infants spent in each of the three main positions (ventral, dorsal and independent) by week and by phase. I also examined the proportion of observed time that infants spent in physical contact with either their mothers or another group member, and compared this to the proportion of time infants spent physically independent (no physical contact with another individual), by phase. I used Spearman's correlation test to examine whether there was a relationship between the infant's age and the proportion of time they spent independent and feeding independently. I estimated the dietary overlap of infants and mothers via the dietary overlap index (Pianka 1973). The formula is $R = \sum(pij \text{ x } pik)/\sqrt{((\sum pij)^2 \text{ x } (\sum pik)^2)}$, where pij and pik are the proportions of food item i in the diet of infant (j) and mother (k). R varies between 0 (no overlap) and 1 (total overlap between the proportions of items ingested). All statistical analyses were performed in R 3.0.2 (R Core Development Team 2013).

Research authorizations for this study were obtained from the Malagasy Direction Générale des Forêts (DGF) du Ministère de l'Environnement et des Forêts (MEF). This research was strictly observational and was in compliance with the Ethical Treatment of Non-Human Primates as described by the American Society of Primatologists. Furthermore, all research described in this manuscript complies with protocols approved by the University of Victoria's Animal Care Committee.

3.3 Results

I collected a total of 620 hours of behavioural data for five *I. indri* infants, aged 3 – 33 weeks old. For comparisons by phase, I used 159 focal follow sessions and a total of 540 hours of behavioural data.

Schedule of Development for *I. indri* infants

When first born, *I. indri* were completely black with dark green and then saphire blue eyes, compared with the yellow eyes and the variegated colour of adults. They gradually gained their colouration pattern as they aged, beginning with small amounts of grey, then white on their pygal region, and later at the top of their head for photographs of infants in each of the three phases of development). From visual approximations, infants were roughly 11% of the size of their mothers at 19 weeks. Infants at this age had the face and head shape of adults and white on their forearms, legs, gluteal region and tail. Infants were first observed ingesting solid foods (bites of leaves) at 6 weeks. Indri infants were first observed travelling in dorsal position at 8 weeks, and independent (no physical contact with another individual) at 6 weeks.

Defining Phases of Weaning for *I. indri*

In total, infants spent over 125 hours of *observed* time either suckling or feeding independently. Figure 3.1 displays the proportion of overall consumption time that infants were suckling and feeding independently by age, in weeks. For the first five weeks, infants received 100% of their nourishment from their mothers. Infants were suckling for a greater proportion of their consumption time consistently until week 9. This was therefore defined as the end of Phase 1. Between weeks 10 and 19, there were some weeks when the proportion of consumption time that infants spent suckling exceeded the proportion of consumption time spent feeding independently and vice versa. This period was defined as Phase 2. Beginning in week 20, infants were consistently feeding independently for a greater proportion of their consumption time through until the end of the study. This was therefore defined as Phase 3.

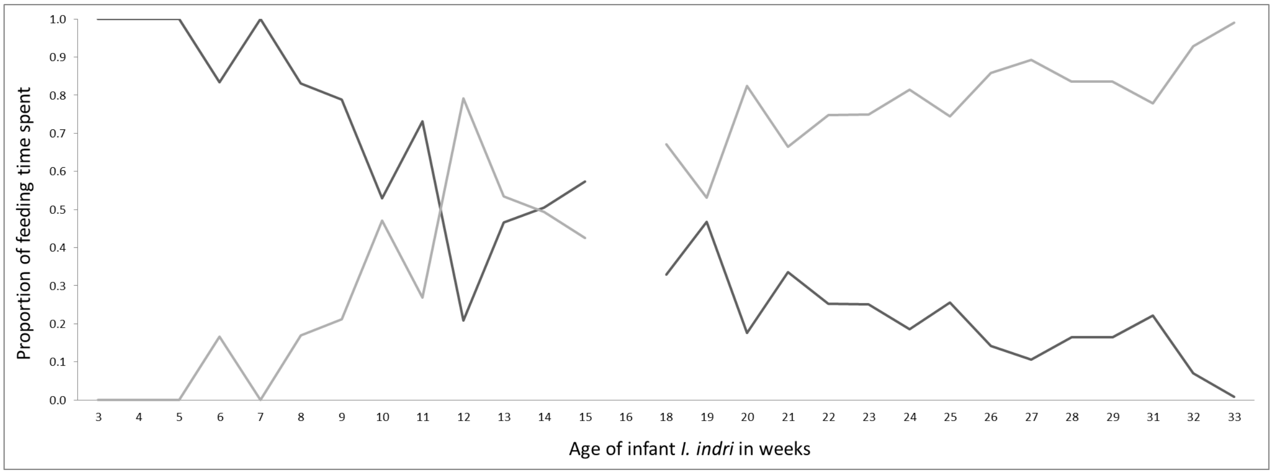

Figure 3.1 Proportion of observed feeding time that infant *I. indri* (N=5) spent suckling (black) and feeding independently (grey) by week, from 3 – 33 weeks. Week 16 was excluded from this figure due to the small sample size for infants at this age.

I found a strong positive correlation between *P. diadema* infant age in weeks and the proportion of consumption time dedicated to individual feeding (Spearman's rank correlation, $r = 0.92$, $N = 33$ weeks, $P < 0.001$; Figure 3.1).

Each focal follow session was subsequently categorized according to the weaning phase definitions as follows: Phase 1 included sessions when infants were 0 – 9 weeks old, Phase 2 included sessions when infants were 10 – 19 weeks old, and Phase 3 included sessions when infants were 20 – 33 weeks old. Figure 3.2 displays the proportion of consumption time (suckling + independent feeding) that infants suckled (grey) and fed independently (black), according to these phases.

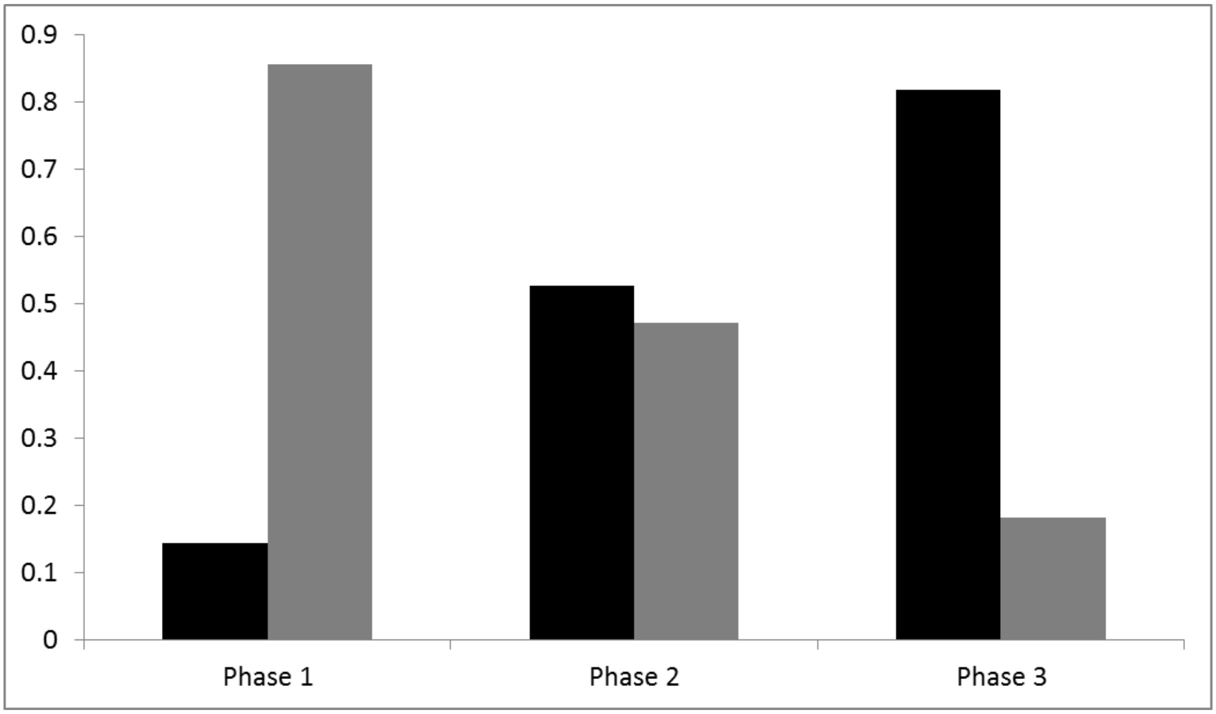

Figure 3.2 Phases of feeding ontogeny for *I. indri* infants at Maromizaha forest (N=5). Phase 1 includes weeks 3 – 9, Phase 2 includes weeks 10 – 19, and Phase 3 includes weeks 20 – 33.

In examining infant feeding behaviours as part of the overall activity budget (including all behaviours, not exclusively time spent feeding), *I. indri* infants spent a significantly greater proportion of time overall observed time consuming food (suckling + independent feeding) in Phase 2 than they did in Phase 1 ($\chi^2 = 146.23$, $P < 0.001$), and significantly more time consuming food (suckling + independent feeding) in Phase 3 than in Phase 2 ($\chi^2 = 1175.14$, $P < 0.001$; Figure 3.3). However, while infants spent a significantly greater proportion of time feeding independently in Phase 2 than they did in Phase 1 ($\chi^2 = 330.71$, $P < 0.001$) and in Phase 3 than they did in Phase 2 ($\chi^2 = 1511.14$, $P < 0.001$; Figure 3.4), suckling did not change significantly by phase (Figure 3.5).

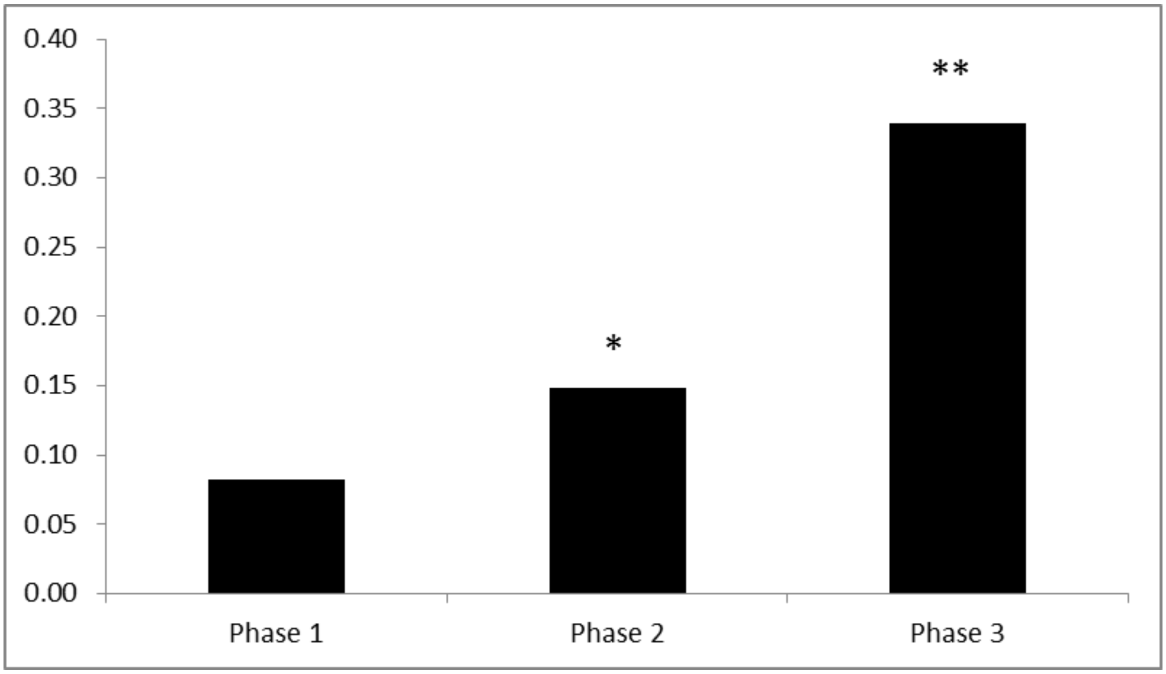

Figure 3.3 Total proportion of observed time that *I. indri* infants consumed food (suckling + independent feeding) during each of the three developmental phases. *I. indri* spent a significantly greater proportion of time consuming food in each phase. Asterisks denote a significant difference between that phase and the preceding phase.

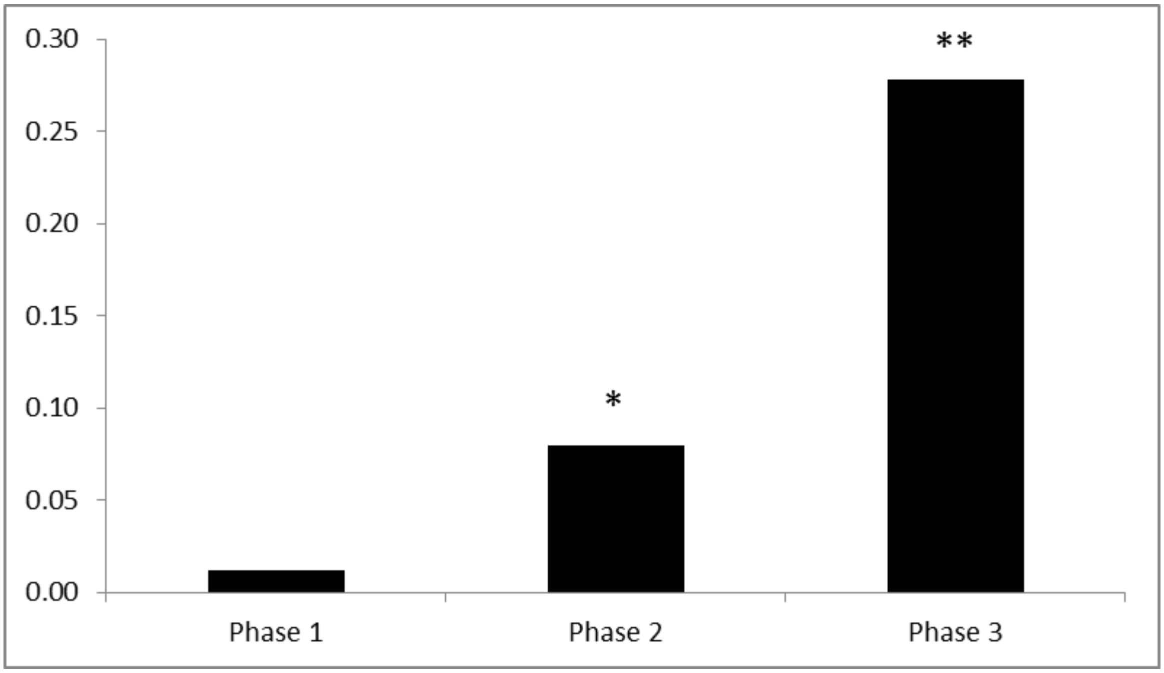

Figure 3.4 Total proportion of observed time that *I. indri* infants fed independently during each of the three developmental phases. *I. indri* infants spent a significantly greater proportion of time feeding independently in each phase. Asterisks denote a significant difference between that phase and the preceding phase.

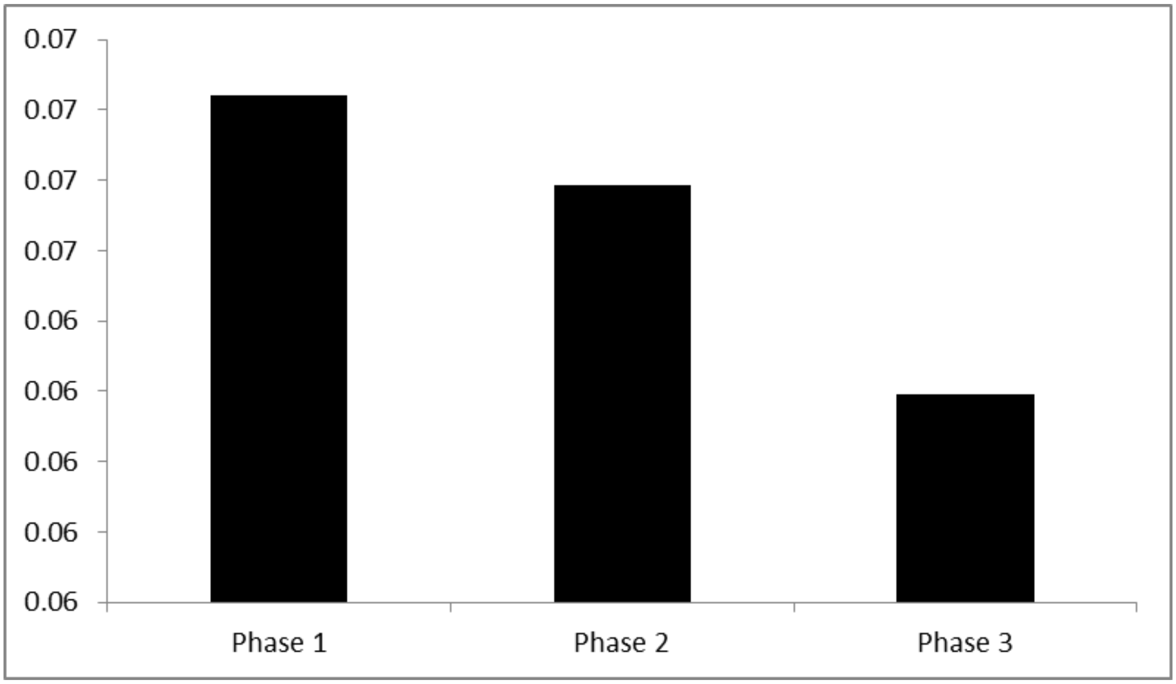

Figure 3.5 Total proportion of observed time that *I. indri* infants were suckling in each of the three developmental phases. There were no significant differences in the proportion of time *I. indri* spent suckling by phase.

Diet of Indri Infants

Indri infants were observed feeding on plants from 12 different plant families between July and December when they were 6 – 33 weeks old. Infants were observed feeding on the same plants as their mothers, although their order of preference, and plant parts consumed differed slightly (see Table 3.3). Both infants and mothers dedicated the largest proportion of their feeding time to *Uapaca* spp., followed by *Cryptocaria* spp. for infants and *Tambourissa* spp. for mothers. The only plant species consumed by mothers and not by infants was *Erythroxylum spaerantum*. All of the 22 most frequently consumed plants listed in Table 3.3 are endemic to Madagascar.

Table 3.3 The most frequently consumed plants by infant *I. indri* and their mothers between June and December in Maromizaha. Food items in bold are items that were only observed to be consumed by infants or by mothers. Abbreviations for plant parts eaten are as follows: bu-buds, fr-fruits, fw-flowers, lv-leaves, sh-shoots, bk-bark

Percent of feeding time (infants)	Percent of feeding time (mothers)	Plant Family	Plant Code	Scientific name	Parts eaten by infants	Parts eaten by mothers
21.36	16.51	EUPHORBIACEAE	VPK	*Uapaca spp.* *Uapaca thouarsii* *Uapaca densiflora*	bu fr fw lv sh	bu fr fw lv sh
13.78	14.56	LAURACEAE	TVL	*Cryptocaria spp.*	fr fw lv sh	**bk bu** fr fw lv sh
12.26	11.60	CLUSIACEAE	KGY	*Ochrocarpos madagascariensis*	fr lv **sh**	fr lv
11.51	15.23	MONIMIACEAE	ABA	*Tambourissa spp.*	lv sh	**bu fr** lv sh
9.07	8.45	LAURACEAE	VRG	*Ocotea spp.*	fr fw lv	fr fw lv **sh**
8.39	5.95	ANNONACEAE	HZA	*Xylopia flexuosa*	fr fw lv	**bu** fr fw lv
4.91	5.33	LAURACEAE	TVR	*Potamea obovata*	fr fw lv	fr fw lv **sh**
4.04	2.08	CLUSIACEAE	VTN	*Calophyllum chapelieri*	fr lv	fr lv
2.28	2.86	SAPINDACEAE	RMD	*Tina isoneura*	lv	**fr** lv **sh**
1.29	2.70	APOCYNACEAE	NNK	*Carissa spp.* *Carissa edulis*	fr lv	fr lv **sh**
1.14	2.30	SAPOTACEAE	NTO	*Faucherea spp.*	fr fw lv	**bu** fr fw lv
0.97	0.31	CLUSIACEAE	VGO	*Mammea spp.*	lv	lv
0.97	0.36	ANNONACEAE	ABV	*Polyalthia richardiana*	lv	lv
0.91	0.92	FABACEAE	VAB	*Dalbergia spp.*	bu lv sh	bu lv sh
0.65	0.50	LAURACEAE	VKM	*Beilschmiedia grandiflora*	lv	lv
0.44	1.80	SAPINDACEAE	ETG	*Tina striata*	lv	**fr fw** lv
0.36	0.54	ANACARDIACEAE	DTM	*Protorhus ditimena*	fr fw lv	fr fw lv
0.29	0.33	LORANTHACEAE	DGV	*Bakerella clavata*	fr **fw** lv	fr lv
0.27	0.15	EUPHORBIACEAE	HDT	*Antidesma petiolare*	lv	lv
0.26	0.42	ANACARDIACEAE	MVT	*Protorhus thouvenotii*	lv	**fr fw** lv
0.18	0.31	ARALIACEAE	VNS	*Cuphocarpus spp.*	lv	lv
0	**0.41**	ERYTHROXYLACEAE	MNH	*Erythroxylum spaerantum*		**lv**

Indri infants were primarily observed consuming leaves (85.24%), followed by fruit (9.14%), buds and flowers (1.58%) and shoots (0.82%; Figure 3.6). This was very similar to the diet of their mothers, who were also primarily observed to consume leaves (86.08%), followed by fruit (9.83%), buds and flowers (3.05%) and shoots (0.58%; Figure 3.6). The dietary overlap of infants and mothers (*R*) was 0.77 demonstrating a very high overlap between the proportions of plant items ingested over the infant's first 25 weeks of life. Indri mothers also ate a small amount of bark from *Cryptocarya* spp.

(<0.01% of feeding time) but such feeding behaviour was never observed in infants. Both infants and mothers were observed consuming soil for a small portion of their observed feeding time (infants: 0.21%, mothers: 0.18%). Geophagy was observed in all five infants, with the earliest observation at 20 weeks old.

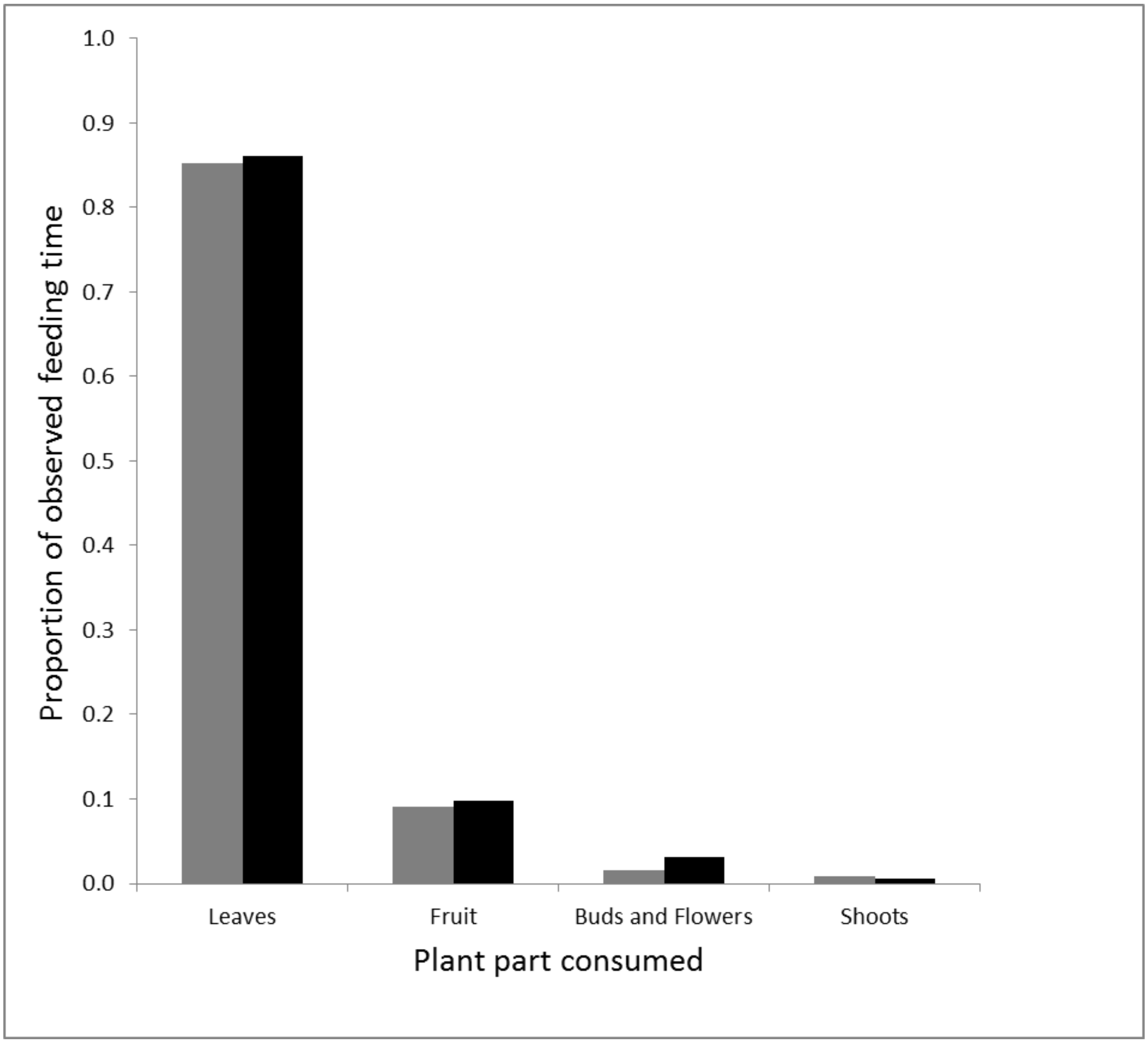

Figure 3.6 Total proportion of observed time that *I. indri* infants (grey) and mothers (black) consumed leaves, fruit, buds and flowers and shoots from 0 – 33 weeks.

Coprophagy by Indri Infants

All five indri infants were observed consuming the feces of their respective mothers. Infants were recorded watching the mother's feces fall to the forest floor and having their nose and mouth in contact with the mother's anus beginning in week six. The first confirmed observation of actual consumption of the mother's feces was in week 10, and this behaviour continued through until week 23. After this point, coprophagy was no longer observed. Infants were only ever observed consuming their *mother's* feces and this behaviour usually occurred between 8 and 10:00 am. Infants would crawl down to the mother's anus and grasp a fecal pellet in their teeth or with their hand as it was expelled by the mother. They would then usually return to the mother's ventral or dorsal position to eat the fecal pellet from their hands. On a few occasions infants ate three separate fecal pellets, however they usually only ate one or two pellets. This behaviour peaked when infants were 10–15 weeks old. Coprophagy was confirmed on 14 of 34 focal observation days (41%) with infants in this age bracket, which corresponds to Phase 2.

Development of Feeding Sequences and Consumption Rate for Indri infants

When feeding on leaves, the sequence of behaviours performed by mothers proceeded as follows: 1) reach for branch with arm and hand, 2) grasp branch with hand, 3) pull branch towards body, 4) bite off entire leaf, 5) ingest and chew leaf. Infants would begin by reaching for leaves with their mouth, then their hand. Eventually they would be able to grasp the branch however it took another 1–2 weeks before they were strong enough to pull the branch towards their bodies. I first observed infants completing the entire leaf feeding sequence of their mothers at 9 weeks old.

When feeding on fruit, the sequence of behaviours performed by mothers proceeded as follows: 1) reach for branch with arm and hand, 2) grasp branch with hand, 3) pull branch towards body, 4) bite off entire fruit, 5) transfer fruit to hand and 6) eat fruit from hand. Infants began reaching for fruits with their mouths, then with their hands. As was the case with leaves, infants initially lacked the strength to pull the branch towards their bodies and get the fruits to their mouths. They often grasped and pulled the fruit from the branch with their hand to eat before they developed the strength the pull the entire branch. I first observed infants completing the entire fruit feeding sequence of their mothers at 24 weeks old. Infant consumption rate for both leaves and fruit was significantly less than that of their mothers (see Table 3.4 for examples).

Table 3.4 Comparison of consumption rates for *I. indri* infants and mothers feeding on same food item, at the same time, in Maromizaha

Plant name	Plant part	Consumption rate for infants	Consumption rate for mothers	Age of infant
Uapaca sp.	leaves	0.23 leaves/min	9.29 leaves/min	10 weeks
Uapaca sp.	fruit	2 fruits/min	6 fruits/min	19 weeks
Cryptocaria sp.	fruit	1.67 fruits/min	2.67 fruits/min	24 weeks
Ocotea sp.	fruit	3 fruits/min	7 fruits/min	24 weeks

Physical Contact with Mother

I. indri infants spent 100% of their time in physical contact with their mothers in the first seven weeks and progressively spent less time in contact with her as they aged. Infants spent 0.5%, 13% and 51% of their time independent (not in physical contact with their mothers) in Phases 1, 2, and 3 respectively. Infants spent significantly more time independent in Phase 2 than they did in Phase 1 ($\chi^2 = 1188.68$, $P < 0.001$), and significantly more time independent in Phase 3 than they did in Phase 2 ($\chi^2 = 5709.27$, $P < 0.001$; Figure 3.7). I found a strong positive correlation between *I. indri* infant age in weeks and the proportion of observed time infants spent independent (Spearman rank correlation, r = 0.99, N = 33 weeks, P < 0.001).

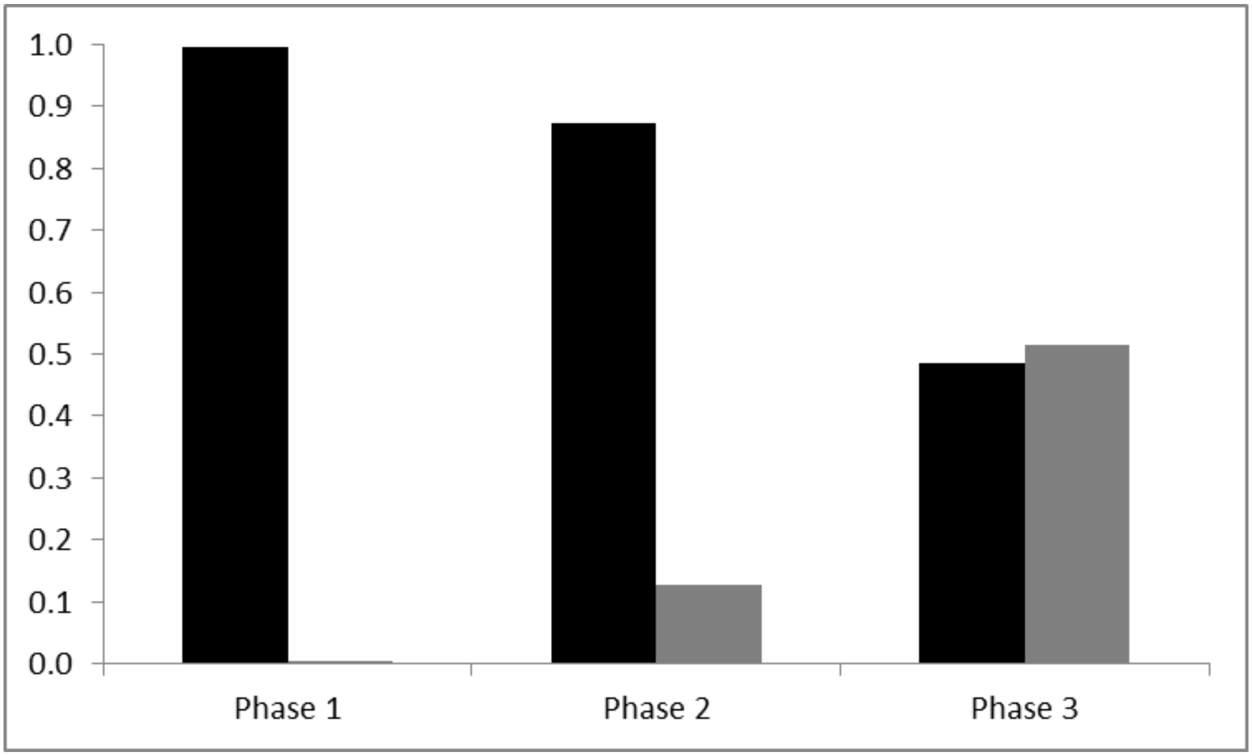

Figure 3.7 Proportion of observed time that *I. indri* infants (N=5) were in physical contact with their mothers (black) and independent (grey) during each of the three developmental phases.

Position of the Infant

I. indri infants were either in the mother's ventral position, dorsal position or independent throughout this study. Infants spent 99%, 83% and 31% of their time in the ventral position in Phases 1, 2, and 3 respectively. Infants spent significantly less time in ventral position in Phase 2 than they did in Phase 1 (χ^2 = 1620.34, $P < 0.001$), and significantly less time in ventral position in Phase 3 than they did in Phase 2 (χ^2 = 9126.83, $P < 0.001$; Figure 3.8). In Phase 2, infants spent 5% of their time in dorsal position, compared to only 0.5% in Phase 1 (χ^2 = 359.84, $P < 0.001$). In Phase 3, infants spent 17% of their time in dorsal position, which was significantly more than they did in Phase 2 (χ^2 = 1303.27, $P < 0.001$; Figure 3.8).

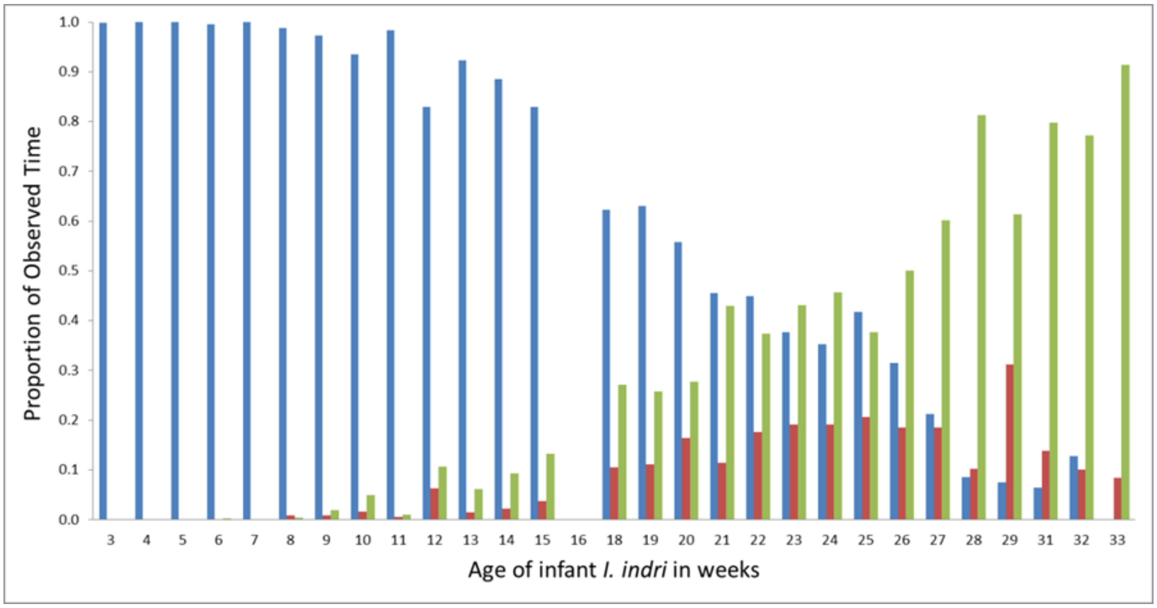

Figure 3.8 Proportion of observed time that *I. indri* infants (N=5) were in the ventral position (blue), the dorsal position (red) or independent (green) by week from 3 – 33 weeks. Week 16 was excluded from this figure due to the small sample size for infants at this age.

Behavioural Changes by Phase

I. indri infants spent a significantly smaller proportion of time observing in Phase 3 than they did in Phase 2 ($\chi^2 = 236.10$, $P < 0.001$; Figure 3.9). Infants were resting for a smaller proportion of their time in Phase 2 than they were in Phase 1 ($\chi^2 = 1020.32$, $P < 0.001$) and even less in Phase 3 than Phase 1 ($\chi^2 = 9.96$, $P < 0.002$; Figure 3.10). They spent a significantly greater proportion of time playing in Phase 2 than they did in Phase 1 ($\chi^2 = 263.42$, $P < 0.001$), but less time playing in Phase 3 than they did in Phase 2 ($\chi^2 = 544.27$, $P < 0.001$; Figure 3.11).

I. indri infants spent a significantly greater proportion of time self-grooming in Phase 2 than they did in Phase 1 ($\chi^2 = 69.20$, $P < 0.001$), and in Phase 3 than they did in Phase 2 ($\chi^2 = 218.03$, $P < 0.001$; Figure 3.12). They also spent a significantly greater proportion of time allogrooming with other group members in Phase 3 than they did in

Phase 2 ($\chi^2 = 14.33$, $P < 0.001$), but allogrooming was never observed in Phase 1 (Figure 3.13).

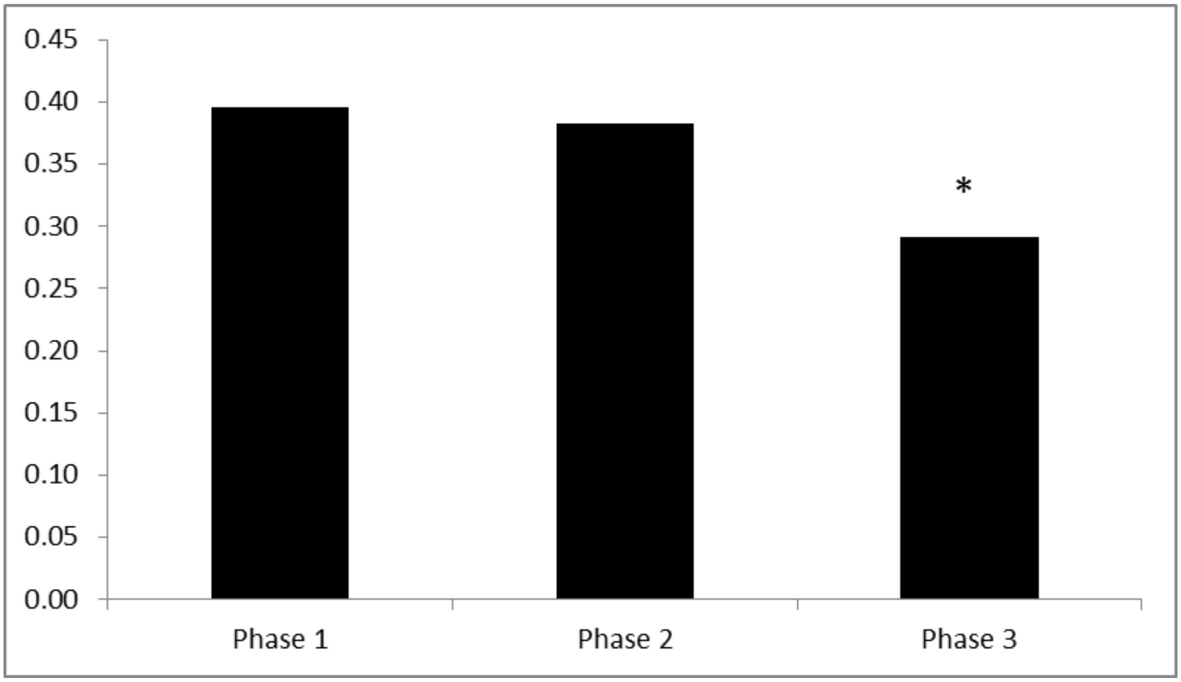

Figure 3.9 Total proportion of observed time that *I. indri* infants were observing during each of the three developmental phases. *I. indri* spent significantly less time observing in Phase 3. Asterisks denote a significant difference between that phase and the preceding phase.

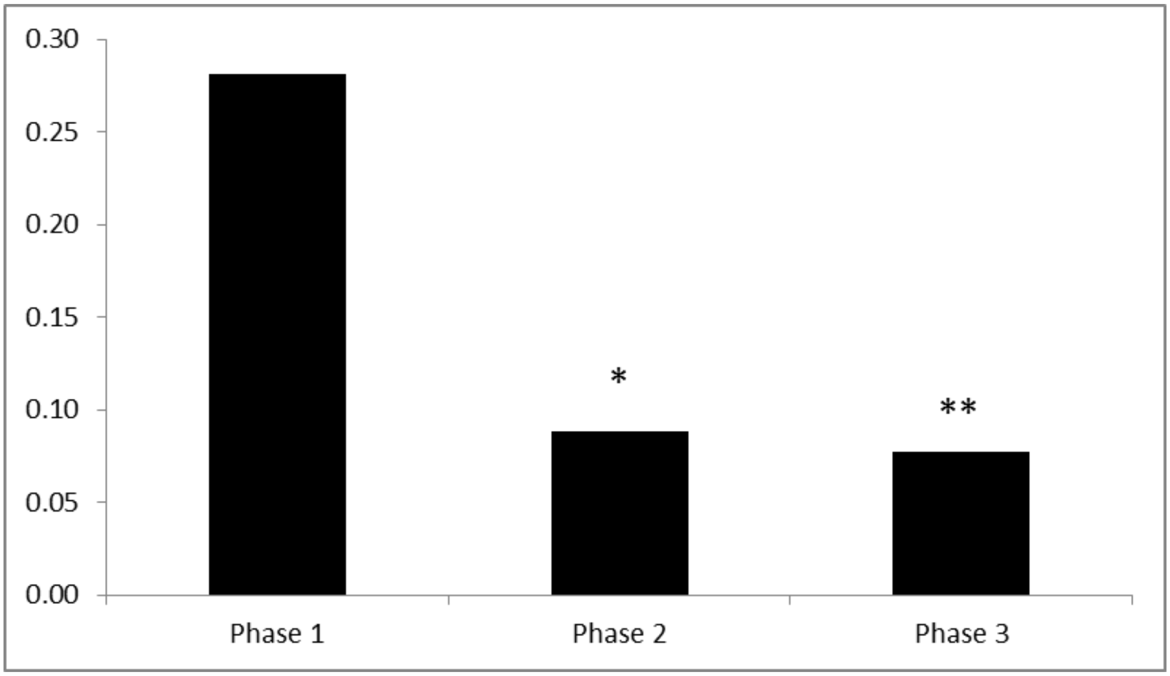

Figure 3.10 Total proportion of observed time that *I. indri* infants rested during each of the three developmental phases. *I. indri* spent significantly less time resting in each phase. Asterisks denote a significant difference between that phase and the preceding phase.

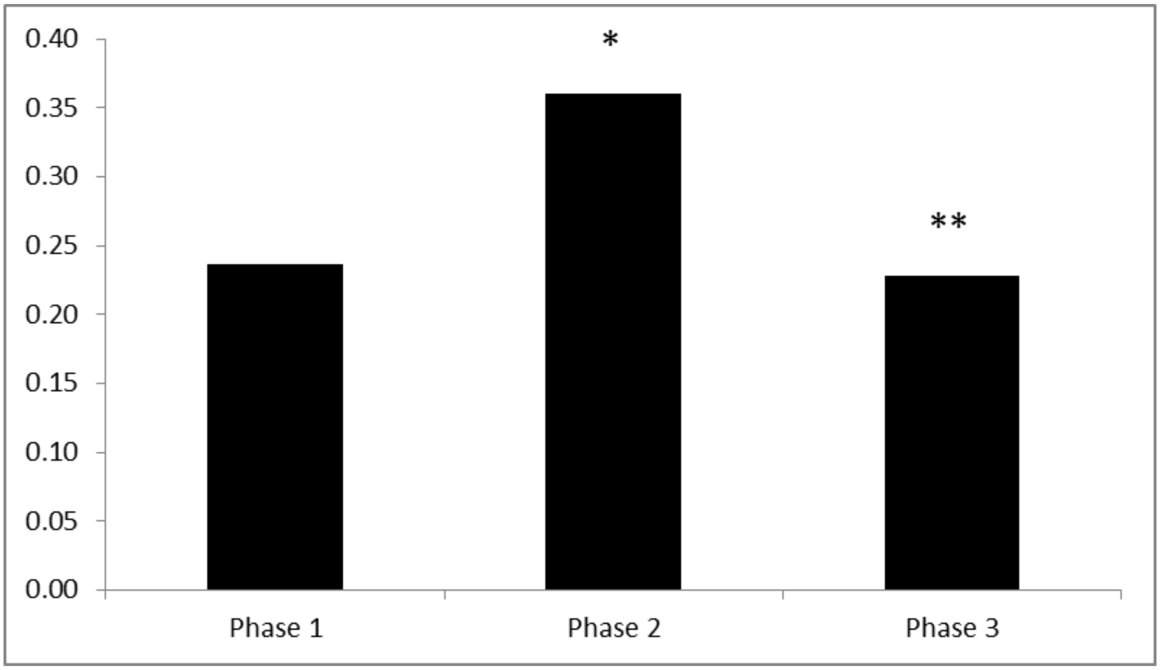

Figure 3.11 Total proportion of observed time that *I. indri* infants spent playing during each of the three developmental phases. *I. indri* spent a significantly greater proportion of time playing in Phase 2 than Phases 1 & 3. Asterisks denote a significant difference between that phase and the preceding phase.

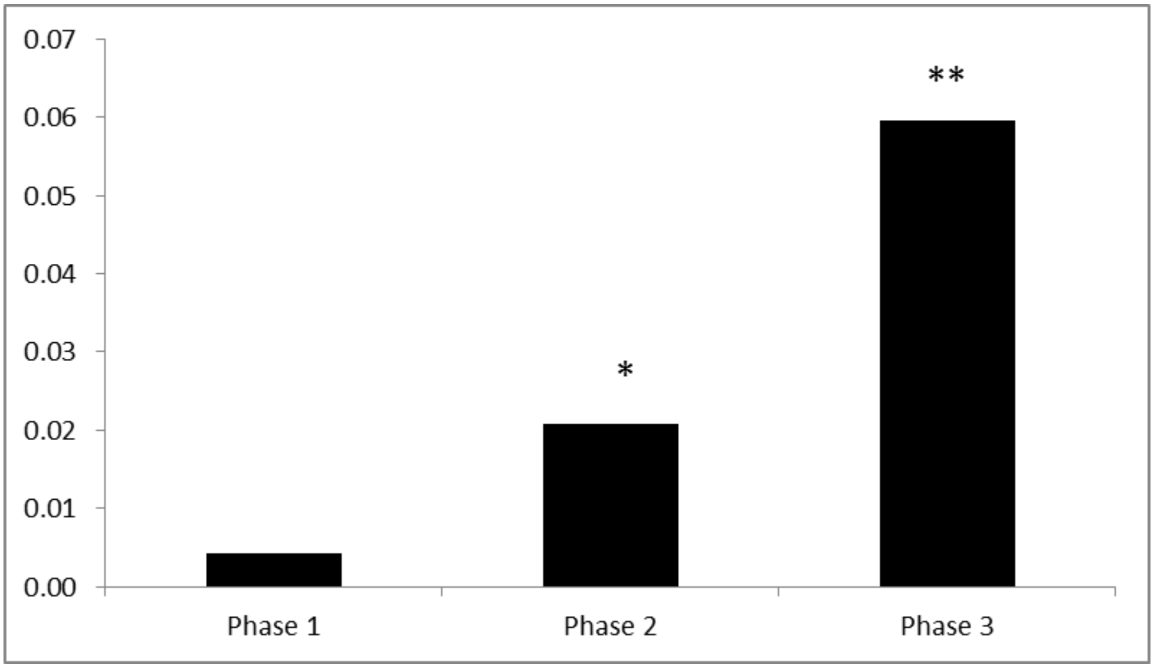

Figure 3.12 Total proportion of observed time that *I. indri* infants spent self-grooming during each of the three developmental phases. *I. indri* spent a significantly greater proportion of time self-grooming in each phase. Asterisks denote a significant difference between that phase and the preceding phase.

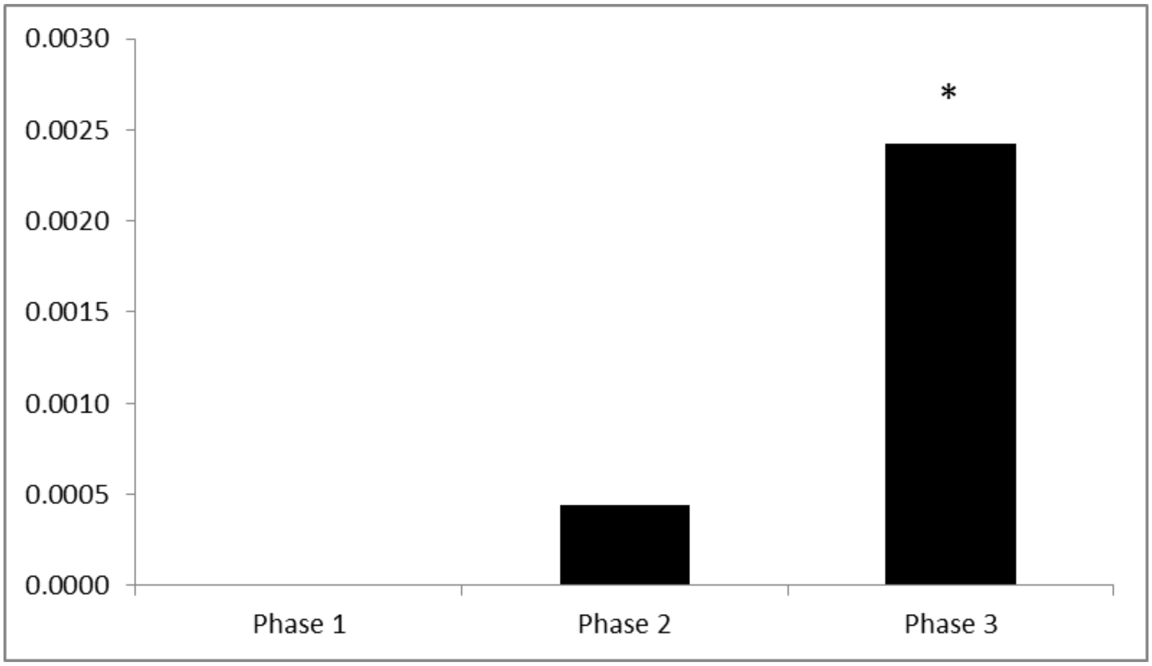

Figure 3.13 Total proportion of observed time that *I. indri* infants spent allogrooming during each of the three developmental phases. *I. indri* spent a significantly greater proportion of time allogrooming in Phase 3. Asterisks denote a significant difference between that phase and the preceding phase.

3.4 Discussion

The extended period between births for *I. indri*, is likely part of their overall strategy to minimize energy expenditure. Their highly folivorous diet requires considerable energy to digest and therefore a high proportion of their time must be spent resting (Powzyk & Mowry 2006). In addition, *I. indri* infrequently expend energy travelling for long distances, scent-marking their territory or engaging in physical contests (Powzyk 1997). Instead, *I. indri* rely on their long call vocalizations to defend their territories and these demand considerably less energy (Powzyk & Mowry 2006). By protracting the period of time between births, *I. indri* are able to spread out the costs of maternal investment over a longer amount of time and they also have more time to regain condition and prepare for the next gestation. In addition, the long inter-birth interval observed in *I. indri* likely allows infants more time in close contact with the mother, and this time may assist infants in developing the behavioural and physiological adaptations required for acquiring, processing and digesting the particularly folivorous diet of adults before the birth of the next sibling. This prolonged period of maternal care may also provide extra time to develop other behaviours, including proficient vertical clinging and leaping (VCL) and group long calls. Here I will discuss each of these findings and provide suggestions for how particular aspects of infant development in *I. indri* are reliant on a longer period of dependency than any other lemur.

Social Learning, Diet and Coprophagy

In accordance with my prediction, I found more evidence for complex social learning of diet and feeding behaviours than what has been reported for *L. catta* (O’Mara & Hickey 2012). The highly folivorous diet of *I. indri* is developed in the first six months of infancy. Similar to juvenile and adult *I. indri* at both Mantadia and Betampona (Britt et al. 2002; Powzyk & Mowry 2003), infants and their mothers in my study consumed leaves for over 85% of their feeding time. *I. indri* infants and their mothers had a very high level of dietary overlap and both dedicated over half of their feeding time to *Uapaca* spp., *Crypotocaria* spp., *Ochrocarpos madagascariensis*, and *Tambourissa* spp. Powzyk & Mowry (2003) also found that *I. indri* in Mantadia spent the largest proportion of their feeding time consuming *Uapaca* and *Crypotocaria* spp. Infant *I. indri* were first observed eating small amounts of soil when they were 20 weeks old. Soil ingestion may serve several functions in primates, including mineral supplementation, adsorption of toxins, and pH adjustment of the gut (Krishnamani & Mahaney 2000). De Sousa et al. (2002) hypothesized that the primary function of geophagy in folivorous howler monkeys is to aid in reducing harmful secondary compounds present in the leaves that they consume. However, Powzyk & Mowry (2003) found that *I. indri* at Mantadia tended to avoid potential toxins in their food choices and their diets contained little to no tannins or alkaloids. Although geophagy made up only 0.21% of infant *I. indri* feeding time, the early adoption of this behaviour suggests its importance to feeding ontogeny, although its specific function remains unclear. Short bouts of geophagy were also documented for adults and for juveniles at Maromizaha (*this study*), Betampona (Britt et al. 2002) and Mantadia (Powzyk 1997) indicating the importance of soil ingestion to the overall feeding ecology of this species.

Infants ate nearly all of the same plant species and plant items as their mothers, suggesting that enhancement, observational conditioning, and imitation of the mother's feeding behaviours may be important aspects of feeding ontogeny in this species

(Rapaport & Brown 2008). As predicted, *I. indri* infants spent more than one third of their time observing their environment and the individuals in their group during this study, and this possibly helped them to learn which plant parts to consume and which to avoid. Infants only fed while their mothers were feeding, and they fed almost exclusively on the same plants. On a few occasions I documented infants imitating their mother's meticulous selection of the few orange leaves on a tree with primarily green leaves. Whitehead (1986) also found that infant howler monkeys (*Alouatta palliata*) almost always observed the feeding behaviour of other individuals in the group before they began feeding themselves. He suggests that this observational conditioning may be how infants learn to select particular species that are lower in secondary compounds (Whitehead 1986). Since adult *I. indri* appear to avoid potentially toxic species as well (Powzyk & Mowry 2003), it is possible that infants are learning the important distinctions between species as part of their early feeding ontogeny. Furthering my analyses to examine the precise amount of synchronization between infants and their mothers would further illuminate how infants use social learning to develop the specific diet of adults.

Juvenile and adult *I. indri* use their hands to pull branches to their mouth and then bite off the food item (Britt et al. 2002; Rigamonti et al. 2005). I found that infants developed and imitated the leaf feeding sequence of adults approximately three months earlier than the fruit feeding sequence. In both cases, the strength needed by the infant to pull a branch towards their body was a limiting factor early on. For fruit, infants initially did not have the required strength to pull the fruit from the branch. Infant consumption rate for both leaves and fruit were lower than those of their mothers indicating that while infants and mothers spent a similar amount of time feeding in late infancy/lactation (Phase 3), infants were still ingesting a considerably lower amount of solid food than their mothers overall.

Perhaps the most surprising finding in my study was that all of the *I. indri* infants regularly consumed the feces of their respective mothers on an almost daily basis from 10 to 15 weeks. The term for this behaviour, ‘allocoprophagy’ literally means the ingestion of another individual’s feces, whereas ‘autocoprophagy’ refers to animals consuming their own feces (Hirakumi 2001). Autocoprophagy is a critical part of the hindgut fermentation and digestion process for several herbivorous and folivorous mammals although there has been little evidence for this behaviour in primates (Soave & Brand 1991; Hirakumi 2001). To date, the weasel sportive lemur (*Lepilemur mustelinus*) is the only primate species that has been reported to regularly reingest their own feces and little is known about the details of this process in *Lepilemur* spp. (Hladik et al. 1971; Hikarumi 2001). Similar to the *I. indri*, *Lepilemur* spp. are hindgut-fermenting folivores (caecal fermenters) consuming a diet heavily dominated by leaves (75%) and spending 80% of their time resting to aid in the digestion process (Hladik & Charles-Dominque 1974). As opposed to foregut fermenters such as ruminants and colobine monkeys (subfamily: Colobinae) which digest cellulose using multi-chambered and complex stomachs, hindgut fermenters such as elephants, horses, rhinoceros and indriids, all possess a single chambered stomach and rely instead on symbiotic bacteria and microbial fermentation in the large intestine and the cecum to digest cellulose (Campbell 2000). Leporids, pikas, possums and many rodent species including the capybara, regularly reingest their own feces immediately as it exits the anus (Hirakumi 2001; Hirakumi 2002). In leporids specifically, the reingestion of soft feces termed 'caecotrophy' is critical to the microbial fermentation process as these feces, that originate in the caecum, are rich in vitamins and microbial proteins that aid in digestion (Hikarumi 2001). Although untested, it is suspected that this behaviour has a similar function in *Lepilemur* spp. (Hladik et al. 1971; Hladik & Charles-Dominque 1974).

Since I observed *I. indri* infants eating the feces of other individuals, (specifically their mothers) this behaviour is more specifically classified as 'allocoprophagy'. Different variations of allocoprophagy have been documented in two other species of lemurs. Overdorff (1993) documented a few instances where *E. rufifrons* adults ate the feces of other group members, and Fish et al. (2007) reported that *L. catta* very occasionally consumed the feces of humans, cattle and feral dogs during the dry season when food resources are reduced. Fish et al. (2007) suggested that since the animals that engaged in this behaviour were older and/or dentally impaired, that coprophagy in this population of *L. catta* may be an adaptation that provides energy and nutrients to individuals that need to compensate for their lack of dental proficiency (Fish et al. 2007). Young indri infants lack the dental proficiency required for the complete seed mastication exhibited by adults (Powzyk & Mowry 2003; Godfrey et al. 2004). It is therefore possible that by ingesting their mother's feces, infants are gaining access to small amounts of these protein-rich seeds that have already been softened by the passage through her digestive system. This has been suggested as one reason why lowland gorillas (*Gorilla gorilla*) and bonobos (*Pan paniscus*) very occasionally eat feces of other group members, although in both of these cases, this behaviour is extremely rare (Rothman et al. 2006; Sakamaki 2010).

Although untested at this point in time, it is possible that the behaviour I observed in my study of *I. indri*, has an adaptive function similar to what has been documented in koalas, elephants and sloths. In these species, infants are not born with the gut microbiota required to digest their high fiber diet and it is suspected they eat their mother's feces to acquire these particular microbes (elephants, Guy 1977; koalas, Osawa et al. 1993; sloths, Sunquist 1978). The development of the complex and host-specific microbes needed for digestion requires several successions of microbial colonization until a stable, adult-like microbiome community is achieved in the gut (Bezirtzoglou 1997; Mackie 2002; Langer 2008). Many species are able to develop this gut community through microbes transferred during vaginal birth, through the mother's milk and with the commencement of solid foods (Langer 2003; Langer 2008). Certain species, however, including koalas, elephants, sloths, and now possibly indri, also require coprophagy to develop the specific microbiome community needed to effectively digest the specific plants and high amount of foliage in their respective diets.

Do *I.indri* infants develop more slowly than *P.diadema*?

As predicted, *Indri indri* infants were slower to reach most developmental markers than the sympatric and similarly sized indriid, *Propithecus diadema* (Table 3.5). *I. indri* infants began eating solid foods, riding in dorsal position and locomoting independently of their mothers considerable later than did *P. diadema* infants. *I. indri* spent a shorter amount of time in Phase 1, but a greater amount of time in Phase 2 than did *P. diadema*. This indicates that although *I. indri* began eating solid foods later than did *P. diadema*, they began feeding independently more, relative to the time they spent suckling, earlier than did *P. diadema*. *I. indri* spent more weeks alternating between more time suckling and more time feeding independently than did *P. diadema* (Phase 2), however both species were consistently feeding independently more than they were suckling at the same age (20 weeks/Phase 3).

Table 3.5 Infant development in two sympatric indriids at Maromizaha forest

Developmental Markers	*Indri indri*	*Propithecus diadema*
Birth season	May-June	June-July
Phase 1 ends	week 9	week 13
Phase 2 ends	week 19	week 19
Length of Phase 2	10 weeks	6 weeks
First solids foods	week 6	week 3
Feeding independently for over 50% of consumption time	week 20	week 20
First riding dorsal	week 8	week 5
First independent	week 8	week 5
Independent for over 50% of observed time	week 27	week 21

Both *I. indri* and *P. diadema* began feeding on solid foods relatively early and this is consistent with what had been observed in other indriids (Godfrey et al. 2004). Across primates, and in particular within the lemurs, folivores have a more rapid rate of dental development than similarly sized frugivores (Godfrey et al. 2001; Godfrey et al. 2004). In the indriids in particular, infants are "born with their milk teeth erupted, their first and second permanent molars in advanced states of crown calcification, the crypts for the third molars open, and the M_3 crown initiated teeth…Most, if not all of the deciduous teeth erupt before birth" (Godfrey et al. 2004, p.254). This early dental proficiency facilitates early mastication of solid foods.

In a meta-analysis of eutherian taxa, Langer (2008) referred to the period *before* the first ingestion of solid foods as the 'milk-only period' and the phase when infants are feeding on both solid foods *and* their mother's milk as the 'mixed-feeding' period. He found that taxa with relatively low quality diets, such as folivores and herbivores, tend to have short milk-only periods, and relatively long mixed-feeding periods and proposed that this strategy serves two important purposes (Langer 2003; Langer 2008). The first is to reduce the energetic stress on the mother. Langer (2003) postulated that as soon as infants can ingest solid foods, the nutritional stress on the mothers is lessened because her milk is no longer providing the only nutrition her infant needs to survive. Langer (2003) also proposed that by beginning to eat solid foods early, these taxa facilitate the early microbial colonization process, and have an overall longer period of time for establishing the microbial population in the digestive tract. He goes on to explain that the transition from milk to dedicated folivory requires a more extreme change in digestive anatomy and enzymes than a transition to a diet richer in protein and in fat (ex. fruit, seeds) because the latter example is more similar to the protein and fat composition of milk.

These theories are partially supported by my findings for *I. indri* and *P. diadema*. I found that both species *began* eating solid foods at an early age, and hence have relatively short milk-only period as defined by Langer (2003). However, *I. indri* were faster to reach Phase 2, and therefore started spending a greater proportion of their time feeding on solid foods rather than suckling, earlier than did *P. diadema* (10 weeks vs. 14 weeks; Table 3.5). While not defined in precisely the same way, I propose that overall, *I. indri* has a longer mixed-feeding period, that likely serves to reduce energetic stress on mothers while providing an extended period of time for infants to develop the digestive capacity to consume their more folivorous diet. During this extended mixed-feeding period, *I. indri* also ate their mother's feces. These two adaptations may assist *I. indri* reach Phase 3 (when infants spend more time feeding independently than suckling) at precisely the same age as *P. diadema* (20 weeks; Table 3.5).

Within study sites in Madagascar, lemur births within each species, are highly seasonal and timed so that infants are weaned in the season when there is the greatest availability of food resources (Wright 1999). The rapid dental development in indriids is expected to help infants process large amounts of leaves around the same time that they start relying more on solid foods for nourishment than on milk (Godfrey et al. 2001; Godfrey et al. 2004). In the eastern rainforests, the months with the most food available are usually October – February (Powzyk 1997; Wright 1999; Irwin 2008) and in my study both species reached Phase 3 in October (*I. indri*) and November (*P. diadema*). Although in many ways similar to *P. diadema*, *I. indri* eat significantly more leaves and the consequences of this evolutionary trait (namely that females must minimize energy and reduce reproductive effort) are reflected in the early adaptations for feeding ontogeny *I. indri*.

Other advantages of a long inter-birth interval

Langer (2003; 2008), suggested that an extended period of mixed-feeding (Phases 2 & 3 combined) as I documented for *I. indri*, may provide developing infants with more than just nutritional benefits, including protection from predators and opportunities for social learning of particular diets and behaviours. Above I discussed examples of social learning of diet, and here I will explore how the protracted period of dependency observed in *I. indri* might additionally benefit offspring in two distinct ways.

The first is the benefit of additional time to develop proficient vertical clinging and leaping behaviour (VCL). In *I. indri*, efficient VCL behaviour takes over one year to develop (Pollock 1986b). In my study, infants were not physically independent of their mothers for the majority of their time until they were 27 weeks old compared to 21 weeks old for *P. diadema*. While VCL is the primary form of locomotion for all indriids, including *P. diadema* (Napier & Walker 1967), *I. indri* are the only primate species to do so without a tail. Indriids primarily use their hips, thighs and forelimbs for VCL behaviour (Demes et al. 1996), however a tail is likely important is maintaining balance in vertical positions between leaps and while maintaining feeding postures. For example, in *Tarsius* sp. the tail was found to be critically important in providing force during vertical resting positions (Grand & Lorenz 1968). Falls are assumed to be a leading cause of infant mortality in highly arboreal lemurs (Morland 1990; Richard et al. 2002) and although no *I. indri* infants were observed to fall in my study, Pollock (1986b) noted that they do fall, and that mothers do not retrieve fallen infants. By prolonging the time spent being carried, the probability of injury or death due to falls is presumably reduced (Ross 2001; Ross 2003). For *I. indri* specifically, I suggest that infants may take longer to achieve independence than *P. diadema* in part due to their lack of a tail which assists other indriids with balance and support while developing the locomotory behaviours of adults. The longer inter-birth interval in *I. indri* allows for a longer period of dependency on mothers for travel and presumably reduces the likelihood of fall-related deaths in infants.

Another important skill that infant *I. indri* must learn, is how to effectively join the group long call. These long calls, that eventually need to persist for 40 – 250 seconds and travel distances of 3 – 4 km, are sex (Giacoma et al. 2010), age (Sorrentino et al. 2013), and context specific (Torti et al. 2013). Therefore, as adults, *I. indri* are thought to use these low cost group vocalizations for advertising the age and sex composition of their group to other groups in the forest and for defending their territories against these same groups (Pollock 1986; Thalmann et al. 1993; Giacoma et al. 2010; Torti et al. 2013). Unlike the more energetically costly forms of territory defence used by *P. diadema,* including actively patrolling territories and frequent scent-marking, vocal calls cost very little energetically (Powzyk & Mowry 2006). However, although this behaviour is energetically less costly, it takes significantly longer to develop. Indri do not begin to join in the group long call until they are at least two years old (Sorrentino et al. 2013), whereas *P. diadema* infants are travelling independently and scent-marking within a few months (*this study*). Although research into how young *I. indri* develop their song is still in the early stages, we know that gibbons, another monogamous primate species that uses similar long call vocalizations, take approximately six years to develop the basic acoustic structure of their calls (Brockelman & Schilling 1984; Merker & Cox 1999). Social learning, through mother-daughter co-singing interactions is suggested as one mechanism for vocal development in gibbons (Koda et al. 2013). Thus, another important adaptive advantage of the especially long inter-birth interval in *I. indri* may be to provide enough time for immature offspring to learn and develop their vocal repertoire.

In summary, *I. indri* have likely evolved to give birth only every two to three years as part of their overall strategy as “energetic minimizers” as suggested by Powzyk & Mowry (2006). The transition from milk to the adult diet is more complex for *I. indri* than for *P. diadema* and this could in part explain why *I. indri* infants developed more slowly than *P. diadema*. The specific microbiotic community that *I. indri* require for effective digestion of their leaf based diet is facilitated by the early ingestion of solid foods and by the routine ingestion of their mother’s feces. As this is the first time this behaviour has been observed in a primate, I believe that further studies that examine and characterize the fecal microbiome of adults (as has been conducted for *Colubus guereza*, *Piliocolobus tephrosceles*, and *Cercopithecus ascanius* by Yilderim et al. 2010) would be extremely valuable in our understanding of how infant *I. indri* develop the digestive capabilities of adults. This information, considered as part of the overall strategy of how infants develop and survive to maturity, would be highly beneficial to the development of captive breeding programs for this unique, enigmatic, and extremely endangered lemur (Mittermeier et al. 2012; Schwitzer et al. 2013).

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4 - VARIABLES AFFECTING INFANT DEVELOPMENT IN THE TWO LARGEST LEMURS

4.1 Introduction

The successful development of a mammalian infant is a critical yet complex behavioural process. Mammals take time to acquire the motor skills to forage and to feed independently and to move through their environment effectively and efficiently (Martin 1984; Bekoff & Daniels 1984; Lee 1997). They depend on their mother's milk for nourishment, and her energy to carry them, while they develop the necessary skills to feed and to locomote on their own (Altmann 1980; Altmann & Samuels 1992; Noren & Edwards 2011). Similarly, developing the social skills to be assimilated into a social group, takes observation, practice and experience (De Waal 2002; Fairbanks 2002). Mammalian infants are often protected by their mothers, while the infants acquire the necessary social and motor abilities to protect themselves, from predators, parasites and other dangers (Altmann 1980), and to function appropriately in intraspecific interactions (Chapais & Gauthier 2002; Pereira 2002). The process of infant development, from complete dependence to independence, thus includes a complex suite of behavioural changes, with different factors potentially influencing each of these developments.

Reproductive traits, such as length of gestation, age at first reproduction and inter-birth interval (IBI) tend to correlate primarily with phylogeny (Stearns 1983; Fleagle 1999; Kappeler 1996) and with the body size of adults (Charnov 1991; Kappeler 1996; Deaner et al. 2003). Specifically, animals with common ancestry tend to show similar traits that cannot be explained by their current ecology (Kappeler 1996), and within phylogenetic groups, taxa with larger bodies generally have longer gestation lengths, begin reproducing later, and have longer IBI than taxa with smaller bodies (Bekoff et al. 1984; Charnov 1991; Kappeler 1996; Lee 1997; Tecot et al. 2013).

In addition, the quality of resources consumed (diet) may correlate with certain reproductive traits, however the way in which diet affects these traits varies greatly between studies. While folivorous primates tend to acquire their dentition faster than more frugivorous species (Godfrey et al. 2001; Godfrey et al. 2004), there remains contradiction of how diet affects the overall growth of infants. For example, Leigh (1994) found that in a captive environment, folivorous haplorhine primates (ex. *Alouatta caraya*, *Colobus guereza*, and *Presbytis entellus*) reach adult body size and reproductive age faster than do the more frugivorous species (ex. *Cebus paella*, *Macaca mulatta*, and *Pan troglodytes*), and Leigh & Shea (1996) found that the highly folivorous *Gorilla* grow faster than the more frugivorous chimpanzees and bonobos. In contrast to these patterns, Borries et al. (2011) found no difference in the age at first reproduction or the inter-birth interval between the folivorous colobines and the more frugivorous macaques, however they did find a difference between animals that were provisioned, and those that were not.

Folivorous primates are notoriously difficult to keep in captivity due to their highly specialized diets and digestive systems (Hill 1964; Collins & Roberts 1978). Borries et al. (2011) suggested that certain types of specialized folivores (if they manage to survive in captivity) may be especially efficient at digesting the unusually nutritious food provided in captivity, and therefore Leigh's (1994) results may be more correlated to taxonomic variation in response to provisioning, rather than an overall difference between folivores and frugivores. Also in contrast to Leigh's (1994) patterns, Godfrey et al. (2004) found that within several lemur species examined, frugivores tend to grow faster, in overall body size than do similarly sized folivores. Again, most of the data used for these analyses came from captive studies, and as they have yet to survive in captivity, estimates of growth (and other reproductive parameters) for two of the most folivorous taxa, the indri (*Indri indri*) and the diademed sifaka (*Propithecus diadema*) were based on extrapolations from extremely small same sizes (ex. 1 indri neonate) and few anecdotal observations.

In this chapter, my aim was to improve our understanding of infant development in these two species, particularly in relation to one another. I explore the complexities of an important reproductive trait, and one that is relatively infrequently and inconsistently reported; the length of the period that infants are dependent on their mothers (often termed *weaning*) (Martin 1984; Harvey & Clutton-Brock 1985; Lee 1997; Lee & Kappeler 2003). In Chapter 2, I proposed a method for defining and for quantifying the gradual process of weaning in primates that could be used to evaluate and compare trends across studies. The lemuriformes are endemic to Madagascar and include 5 families, 15 genera, and 99 species and 103 subspecies of varying sizes, diets, types of locomotion, habitat and social organization (Schwitzer et al. 2013). Because of the great variation in ecology within the infraorder, lemurs are an ideal group for illuminating the adaptive patterns of infant development. While a small collection of studies have examined various aspects of infant development in the smaller and more frugivorous species of lemurs (ex. *L. catta*, Gould 1990; Meredith 2011; O'Mara 2012; *Eulemur* spp., Overdorff et al. 1996; Tarnaud 2004; Volampeno et al. 2011, *Varecia* spp., Morland 1990; Vasey 2007), I am the first to study infant development in either of the two largest bodied species: the indri (*Indri indri*) and the diademed sifaka (*Propithecus diadema*).

Among the lemurs, the indriids, along with *Hapalemur* and the *Lepilemurs* exhibit the most ecological and anatomical specializations for folivory (Godfrey et al. 2004). Within the indriids, *Avahi*, and the monotypic *Indri* have a greater proportion of their diet dedicated to leaves than do *Propithecus* (Godfrey et al. 2004; Irwin 2006b). Unlike the colobine monkeys which have a differentiated stomach and large intestine , that allows for foregut fermentation and digestion of their leaf-based diet (Chivers 1994; Cork 1996; Langer 2003), indriids have a larger surface area in their hindgut, and they rely on symbiotic gut flora to ferment and digest their leaf-based diet (Bauchop 1978; Hladik 1978; Parra 1978; Campbell et al. 2000). *I. indri* relies on more intensive foliage digestion than do *P. diadema* (Britt et al. 2002; Powzyk & Mowry 2003; Irwin 2008), yet these two species share several important characteristics that make them ideal candidates for a comparative study of infant development. In particular, they are closely related phylogenetically, both belonging to the lemur family Indriidae (Rumpler et al. 2004; Mittermeier et al. 2008; Rumpler et al. 2011), and as adults, they are roughly the same size, weighing approximately 6 – 7 kg (Glander & Powzyk 1995). These two species also occur in sympatry in some areas of Madagascar (Powzyk 1997; Mittermeier et al. 2008), including Maromizaha forest, where I conducted my field research. These similarities allow us to focus more precisely on how species-specific adaptations for folivory are reflected in early ontogeny, while reducing the confounding effects of phylogeny and body size.

In the 1990s, Powzyk (1997) conducted a comparative study at Mantadia National Park that clarified several key differences in the ecology of these two sympatric species including; i) *P. diadema* spend more time feeding, and eat a more diverse diet of fruits, seeds, flowers and leaves, while *I. indri* eat a diet dominated by leaves, ii) *I. indri* spend more time resting, have shorter daily path lengths and have shorter active periods than do *P. diadema*, and iii) *I. indri* defend their territories using long-call vocalizations while *P. diadema* actively patrol their territories and scent-mark significantly more frequently than do *I. indri* (Powzyk 1997; Powzyk & Mowry 2003; Powzyk & Mowry 2006). These differences led Powzyk & Mowry (2006) to suggest that the highly folivorous diet of *I. indri* requires that they minimize energy expenditure compared to the more frugivorous *P. diadema*.

By using the same criteria for phases of development for both *P. diadema* and *I. indri,* in Chapter 3 I was able to determine that *I. indri* are slower to pass most developmental markers, than *P. diadema*, and I proposed that this is another way that *I. indri* compensate for their more folivorous diet by minimizing the energy they expend in reproductive effort. Although the published inter-birth intervals for both *I. indri* and *P. diadema* are very roughly approximated from scant and anecdotal data, *I. indri* consistently have longer IBI than do *P. diadema*. For example, in a review of reproductive strategies within lemurs, Tecot et al. (2013) reported IBI of 30 months for *I. indri* and 25 months for *P. diadema*. In my study, IBI for *I. indri* and *P. diadema* are 28 months (24 – 36) and 21.8 months (12 – 36) respectively (Chapter 5). Most importantly, *P. diadema*, like other species of sifaka are capable of breeding in consecutive years, whereas *I. indri* have never been reported to give birth in consecutive years. This means that *I. indri* infants, upon reaching Phase 3 and subsequent nutritional independence, will always have another year, at least, before their mothers are potentially gestating again. Borries et al. (2011) found that the length of gestation was significantly longer in Asian colobines than macaques and these authors suggested that this could be related to the colobine adaptations for folivorory. Specifically, the teeth and gut anatomy of colobines are more complex, and perhaps require a longer time to develop in utero, than similarly sized macaques (Borries et al. 2011). In Chapter 3, I proposed that this extended period for postnatal development in *I. indri* also provided infants with more time to develop their complex digestive system, learn their specific diet and vocal repertoire, and how to move through their environment without the support and balanced provided by a tail.

While Chapter 2 focused on development from 0 – 25 weeks in *P. diadema* and Chapter 3 focused on development from 3 – 33 weeks in *I. indri*, this chapter directly compares the main behaviours (feeding, resting, observing, playing, allogrooming and self-grooming) of the two species across the same age period (3 – 25 weeks). In addition, I examined how the variables of group size, developmental phase of the infant, and species (whether the infant was *I. indri* or *P. diadema*) affected the proportion of time infants spent engaged in each of these six behaviours. I generated the following hypotheses and associated predictions based on previous discoveries within primatology.

Hypothesis 1: Group size affects how infants develop

Group size has been demonstrated to affect several aspects of reproduction including inter-birth intervals and developmental rates (Borries et al. 2008; Creel & MacDonald 1995; Mann et al. 2000) and probability of conception (Roberts & Cords 2013). These differences, namely that there are longer inter-birth intervals, slower developmental rates and lower probability of conception in larger groups (within the same species), are largely attributed to the increased foraging competition within these larger groups (Silk 2007; Clutton-Brock & Janson 2012) and corresponding behavioural differences have been discovered that support this hypothesis (Grove 2012; Roberts & Cords 2013). For example, red colobus monkeys (*Procolobus rufomitratus*) in larger groups spend less time feeding and socializing, and more time travelling than do those in smaller groups (Gogarten et al. 2014). In my study I examined whether infants in large groups (defined here as composed of five or more individuals) were slower to develop than infants in small groups (less than five individuals). If group size affects infant development, by increasing feeding competition, then I predicted that I would find that the infants in large groups develop more slowly than those in small groups.

Hypothesis 2: The weaning phase affects the proportion of time infants are engaged in active behaviours

Using the specific framework that I developed and implemented in Chapters 2 and 3, I was able to distinguish between the different phases of weaning in both *I. indri* and *P. diadema.* Specifically, infants in Phase 1 are suckling for more time, per week, than they are feeding independently. In Phase 2 infants are fluctuating between spending more time suckling, and more time feeding on solid foods, per week, and in Phase 3 infants are feeding on solid foods for more time, per week, than they are suckling. Although these phases were different lengths for the two species, I predict that other types of behavioural development will correlate with these phases of feeding ontogeny. Since active behaviours, including independent feeding, playing, self-grooming and allogrooming require more motor skills than more passive behaviours such as observing and resting, I predicted that in both species, infants would gradually spend a greater proportion of their time in each of these first four (active) behaviours as they aged. Specifically I predicted that the greatest proportion of these active behaviours would be observed in Phase 3.

Hypothesis 3: Infants develop species-specific behaviour patterns in the first six months

In Madagascar, births are highly seasonal within species inhabiting the same forest (Wright 1999). This timing is expected to have evolved so that infants are *weaned* during the months with the highest probability of resource availability (Wright 1999). Under this theory, regardless of IBI, or overall period of dependence, both *I. indri* and *P. diadema* are required to be nutritionally independent by approximately six months (Chapter 3). Here, I examined if infants also developed species-specific behavioural differences by this same age. Since Powzyk (1997) found that juvenile and adult *I. indri* spend a greater proportion of their time resting than do *P. diadema*, and that *P. diadema* spend a greater proportion of their time feeding, allogrooming and playing than do *I. indri*, I predicted that infants would follow this same pattern, and develop species-specific differences within their first six months of development. Specifically, I predicted that infant *I. indri* would spend a greater proportion of their time resting and observing, and that *P. diadema* would spend more time feeding, allogrooming, and playing.

4.2 Methods

Study Area

I studied the development of infant behaviour of *P. diadema* and *I. indri* in Maromizaha forest (18°57'S, 48°36'E), a New Protected Area, located 140 km east of the nation's capital of Antananarivo, near the village of Anevoka. This montane rainforest is part of the Ankeniheny-Zahamena rainforest corridor conservation initiative (CAZ; Schwitzer et al. 2013) and includes a protected area encompassing approximately 1,600 ha, composed of 820 ha of intact hard wood forest and 360 ha of regenerated forest, with the remaining classified as degraded habitat. My study area is within mid-altitude rainforest and the *P. diadema* groups that I studied are found at elevations ranging from

970-1223m. The annual rainfall for 2012 was 3163 mm, with close to one third falling in January and February combined (Appendix I). February 2012 was also when cyclone Giovanna struck the area, leaving all trees defoliated and several large trees dying. The average temperature (at 7:30 am) during the study period was 16°C (min=12.6, max=19.1), and the overall maximum and minimum temperatures were 36.8°C and 7.6°C respectively (Appendix I). The hottest months of the year were November – February and the coldest were July – September (Appendix I). This study took place in the cold (July – September) and hot (October – December) seasons of 2011 and 2012 and is part of my larger study comparing infant development and maternal strategies in *I. indri* and *P. diadema* inhabiting Maromizaha forest.

Study Subjects

With the help of five trained assistants (see Acknowledgements), I collected behavioural data for five *I. indri* infants and seven *P. diadema* infants from June – December 2011 and June – December 2012. All five *I. indri* infants belonged to one of five focal groups ranging in size from three to five individuals and the seven *P. diadema* infants belonged to one of four focal groups ranging in size from four to nine individuals. All nine groups were habituated in the months preceding data collection. Each group was monitored at least once per week and therefore the dates of each birth are known to within one week. We often knew the actual day of an infant's birth, due to absence one day and presence the next, but in cases where there was a full week between observations of the group, we estimated the birthdate to be in the middle of the preceding week.

Behavioural Sampling

I collected over 1350 hours of behavioural data on 12 infants, in two consecutive birth seasons (2011 and 2012). Focal groups were located each day with the assistance of local guides and all-day follows of each infant were conducted for approximately two days each week. Continuous and instantaneous sampling methods (Altmann 1974) were used to sample suckling, independent feeding, resting, observing, playing, allogrooming, and self-grooming behaviours (see Table 4.1 for definitions of infant behaviours). Time, to the nearest second, was recorded every time the behavioural state of the infant changed for longer than 10 seconds.

Table 4.1 Ethogram describing the infant behaviours recorded for this study focal observations of *P. diadema* and *I. indri* at Maromizaha

Behaviour	Definition
Suckling	Infant's face is in contact with the mother's nipple
Independent Feeding	Infant is harvesting with hands and/or mouth, and chewing or ingesting, a plant item
Resting	Infant is not moving, eyes are either closed, or, if open they are not focused on anything in the environment
Observing	Infant is not moving, eyes/gaze and attention are focused on something specific in the environment, including other group members, sounds/movement in the trees/air/ground, and the observer
Playing	Infant is moving/active but not engaged in other active behaviours (feeding, allo, or self-grooming). Play behaviour includes individual exploration and exaggerated movements, and rough and tumble play and chases, and approach/retreat play with other individuals (Poirier 1974). Play behaviour is often accompanied by play face (Jolly 1966; Chevalier-Skolnikoff 1974)
Allogrooming	Infant is using the mouth/toothcomb to pick through and clean the fur of another individual
Self-Grooming	Infant is using the mouth/toothcomb to pick through and clean/lick the fur on its own body

Data Analysis

Data were summarized as proportions of the total time-in-view time that infants spent feeding independently, resting, observing, playing, allogrooming and self-grooming per focal follow session. For these analyses, I only used focal follow sessions that included at least 30 minutes of the infant in-view. Also, since I had only *P. diadema* sessions for ages 0 – 2 weeks, and only *I. indri* sessions for weeks 26 – 33, I also limited the following comparative analyses to those that were collected when the infants were between 3 and 25 weeks of age. All analyses were performed in R 3.0.2 (R Core Development Team 2013) using the glmer function in the lme4 library (Bates et al. 2011). Since my response variables were proportions, and since I wished to correct for pseudoreplication (multiple sessions with the same infant), I used generalized linear mixed effect models (GLMMs) with binomial errors, including identity of the infant and a time factor (season) as random effects in all models considered. Including identity of the infant and season as random effects controls for the repeated sampling of the same individual within developmental phases (Carter et al. 2012; Hilborn et al. 2012; O'Mara & Hickey 2012). For each session, I calculated the response variables as the proportion of time infants spent feeding independently, resting, vigilant, playing, allogrooming and self-grooming. The untransformed proportional data were then modeled as functions of species, group size, developmental phase, and season. The median group size for the nine study groups over the two years was five and therefore group size for each session was classified as either small (<5 individuals) or large (5-9 individuals). Developmental phase was categorized as 1, 2, or 3 based on infant age and categories defined in Chapters 2 and 3. Season was either cold (July-September) or hot (October-December). I used an Akaike's Information Criterion (AIC) approach to model selection. This approach offers a relative estimate of the amount of information that is lost when a particular model is used to represent the process that generated the data. AIC is not used to specifically test hypotheses, or to show how well each particular model fits the data, but rather to provide a relative score representing the goodness of fit and the complexity of a model that can then be compared to the scores of other models. I compared AIC scores of candidate models and the model with the lowest score was considered the best model (Burnham & Anderson 2002; see Appendix III). Likelihood for each model within 2 AIC points of the best model was approximated by $e^{(-0.5^{*}\,\Delta AICi)}$, and the weight of evidence provided by each model was calculated by normalising the likelihoods to 1. To further compare the developmental patterns of infant *P. diadema* and *I. indri*, I subsequently performed chi-square analyses of potential differences for proportions of time infants of each species were consuming food (suckling + independent feeding), suckling, independent feeding, observing, resting, playing, self-grooming and allogrooming, during each developmental phase.

4.3 Results

I used 271 focal follow sessions in the total analysis of behavioural data, including 130 sessions with *I. indri* infants and 141 sessions with *P. diadema* infants, aged 3–25 weeks old. Infants of both species spent the greatest amount of their time observing, followed by playing (Table 4.2).

Table 4.2 Total percentage of observed time infants spent in each of the main behaviour categories from 0 – 25 weeks.

Behaviour	*P. diadema*	*I. indri*
Observing	29 %	36 %
Playing	26 %	30 %
Suckling	17 %	7 %
Independent Feeding	14 %	12 %
Resting	10 %	13 %
Self Grooming	0.2 %	0.2 %
Allogrooming	0.8 %	0.09 %

Models for Infant Development

The best models for infant behaviours all included different types and combinations of factors, highlighting the importance of considering each behaviour separately to elucidate how particular variables affect infant development in different ways (Table 4.3). Group size did not have a significant effect on any of the best models for infant behaviour, and was thus excluded from all models presented here. Species (whether the infant was *I. indri* or *P. diadema*) had an effect on the proportion of time infants spent independent feeding, observing and allogrooming, but not on the proportion of time they spent resting, playing and self-grooming. Season had a significant effect on independent feeding, resting and observing behaviours but not on playing or either of the two grooming behaviours. Predictably, infants fed independently more as they got older. They also allogroomed and self-groomed more, but played less.

P. diadema infants spent a greater proportion of their time feeding independently than did *I. indri* infants (estimate +SE=0.50+0.20, *Z*=2.49, *P*=0.01) and infants of both species fed independently more in the hot season (estimate +SE=0.58+0.25, *Z*=2.32, *P*=0.02). There was a correlation between Phase and Season in the model for independent feeding that was not detected in any of the other models (Appendix IV). Interestingly, resting and observing were the only behaviours that were not affected by the developmental phase of the infant (Table 4.3). Infants spent a greater proportion of time resting and observing in the cold season than they did in the hot season (resting: estimate +SE = -1.72 + 0.27, *Z* = -6.33, *P* = <0.001, observing: estimate +SE = -0.36 + 0.04, *Z* = -8.85, *P* = <0.001) and *I. indri* infants spent more time observing than did *P. diadema* infants (estimate +SE = -0.24 + 0.08, *Z* = -3.05, *P* = 0.002). The developmental phase was the only variable that an effect on the proportion of time infants spent playing, and most play was observed in Phase 2 (estimate +SE = 0.80 + 0.27, *Z* = -2.96, *P* = <0.001), and least in Phase 3 (Table 4.3). Both species allogroomed and self-groomed for a greater proportion of their time as they got older, and *P. diadema* infants spent more time allogrooming than did *I. indri* infants (estimate +SE = 2.77 + 0.50, *Z* = 5.53, *P* = <0.001).

Table 4.3 Effect size and significance of fixed effects included in the best models for behaviours of infant *P. diadema* and *I. indri* in Maromizaha

Model	Fixed effect	Estimate	SE	*Z*	*P*
Independent Feeding					
	Intercept	-1.9545	0.2608	-7.495	<0.001
	Species PD	0.4967	0.2002	2.481	0.013
	Phase 1	-2.3899	0.3075	-7.773	<0.001
	Phase 2	-0.9176	0.2156	-4.255	<0.001
	Hot Season	0.5818	0.2505	2.322	0.020
Resting					
	Intercept	-1.4599	0.2066	-7.068	<0.001
	Hot Season	-1.7176	0.2710	-6.338	<0.001
Observing					
	Intercept	-0.4026	0.0621	-6.480	<0.001
	Species PD	-0.2402	0.0788	-3.048	0.002
	Hot Season	-0.3612	0.0408	-8.847	<0.001
Playing					
	Intercept	-1.4291	0.2012	-7.103	<0.001
	Phase 1	0.4471	0.2788	1.604	*0.109
	Phase 2	0.7992	0.2705	2.955	<0.001
Allogrooming					
	Intercept	-7.0015	0.3960	-17.678	<0.001
	Species PD	2.7683	0.5007	5.529	<0.001
	Phase 1	-1.4587	0.4413	-3.305	<0.001
	Phase 2	-0.6376	0.1691	-3.770	<0.001
Self-Grooming					
	Intercept	-3.4008	0.1853	-18.350	<0.001
	Phase 1	-1.5490	0.2768	-5.595	<0.001
	Phase 2	-0.7171	0.2560	-2.801	0.005

Between Species Comparisons by Phase

Figures 1-8 illustrate and compare the proportions of *observed* time that infants of both species engaged in behaviours, by developmental phase. Overall, *P. diadema* infants spent a significantly greater proportion of time consuming food (suckling + independent feeding) than did *I. indri* (Figure 4.1) in Phase 1 ($\chi^2 = 216.60$, $P < 0.001$), Phase 2 ($\chi^2 = 1053.78$, $P < 0.001$) and Phase 3 ($\chi^2 = 524.32$, $P < 0.001$). When examined separately, *P. diadema* infants spent a significantly greater proportion of time both feeding independently (Figure 4.2) in Phase 1 ($\chi^2 = 70.54$, $P < 0.001$), Phase 2 ($\chi^2 = 288.21$, $P < 0.001$) and Phase 3 ($\chi^2 = 41.22$, $P < 0.001$) and suckling (Figure 4.3) in Phase 1 ($\chi^2 = 139.53$, $P < 0.001$), Phase 2 ($\chi^2 = 654.98$, $P < 0.001$) and Phase 3 ($\chi^2 = 609.13$, $P < 0.001$) than did *I. indri* infants.

I. indri infants spent a greater proportion of time observing (Phase 1: $\chi^2 = 178.36$, $P < 0.001$, Phase 2: $\chi^2 = 195.53$, $P < 0.001$, and Phase 3: $\chi^2 = 6.34$, $P < 0.02$; Figure 4.4) and resting (Phase 1: $\chi^2 = 158.07$, $P < 0.001$, Phase 2: $\chi^2 = 158.41$, $P < 0.001$, and Phase 3: $\chi^2 = 75.82$, $P < 0.001$; Figure 4.5) than did *P. diadema* infants in all three phases. *I. indri* infants spent a greater proportion of time playing (Figure 4.6) in Phase 2 ($\chi^2 = 102.29$, $P < 0.001$) and Phase 3 ($\chi^2 = 447.22$, $P < 0.001$), but not in Phase 1 ($\chi^2 = 138.61$, $P < 0.001$).

I. indri spent a significantly greater proportion of time self-grooming (Figure 4.7) than did *P. diadema* in Phase 3 ($\chi^2 = 21.65$, $P < 0.001$) but in Phase 1, the reverse was true ($\chi^2 = 35.62$, $P < 0.001$). In Phase 2 there was no significant difference in self-grooming between the two species ($\chi^2 = 0.67$, $P > 0.41$). Allogrooming by infant *I. indri* was rarely observed and *P. diadema* infants spent a greater proportion of time allogrooming in all phases (Phase 1: $\chi^2 = 27.81$, $P < 0.001$, Phase 2: $\chi^2 = 51.98$, $P < 0.001$, and Phase 3: $\chi^2 = 86.52$, $P < 0.001$; Figure 4.8).

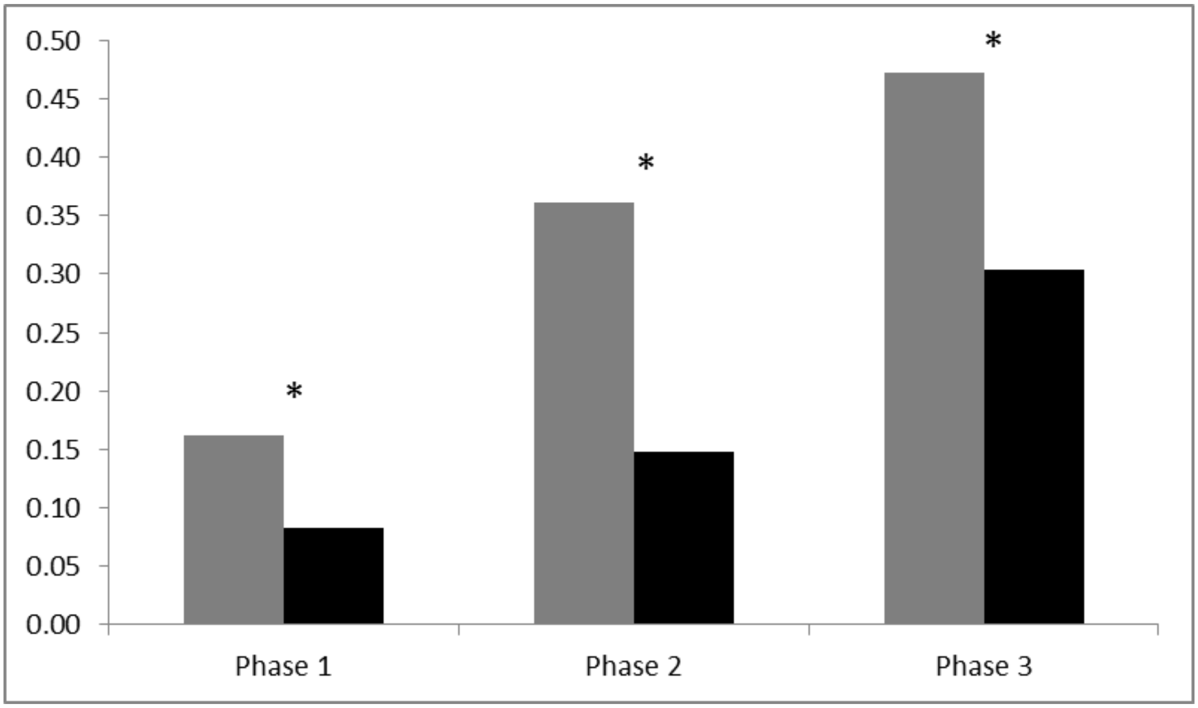

Figure 4.1 Total proportion of observed time that *P. diadema* infants (grey) and *I. indri* infants (black) consumed food (suckling + independent feeding) during each of the three developmental phases. An asterisk above a phase denotes a significant difference between the two species in that phase.

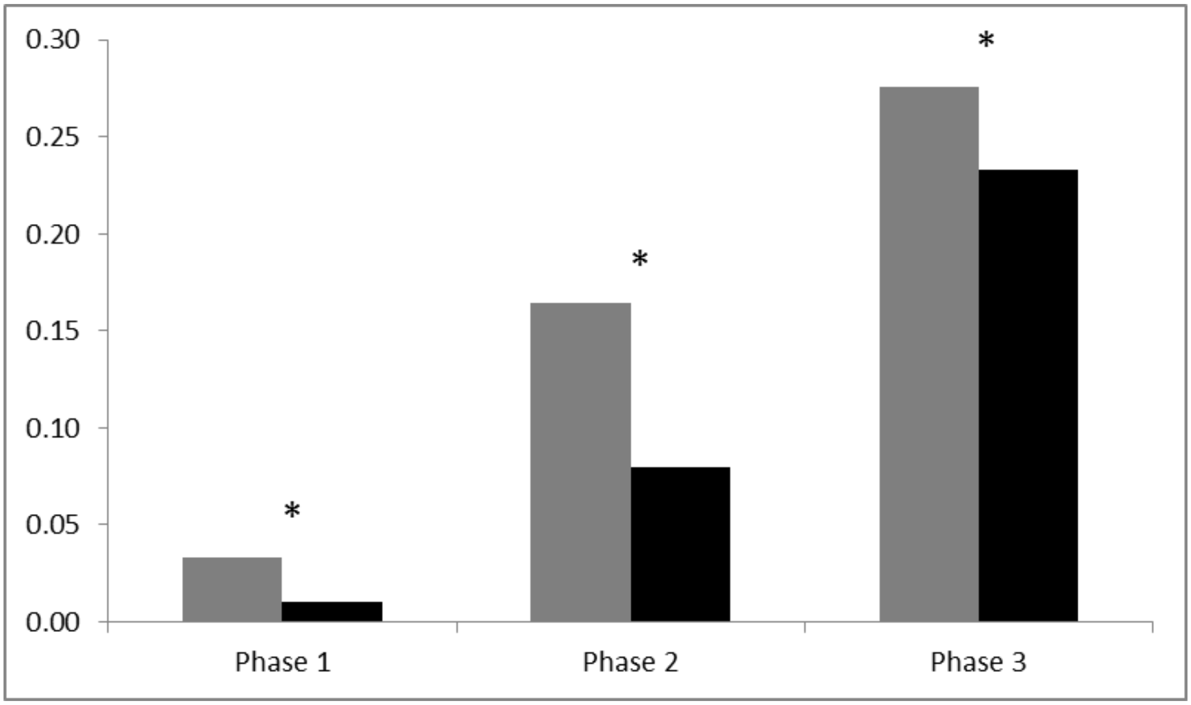

Figure 4.2 Total proportion of observed time that *P. diadema* infants (grey) and *I. indri* infants (black) fed independently during each of the three developmental phases. An asterisk above a phase denotes a significant difference between the two species in that phase.

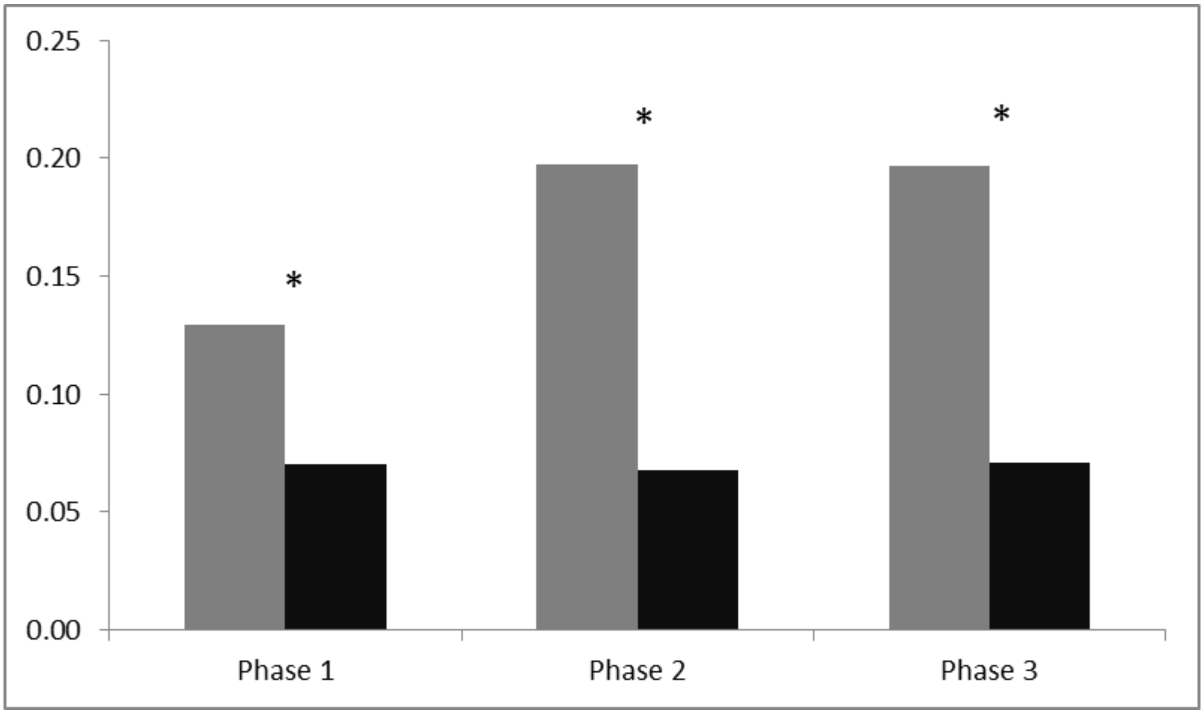

Figure 4.3 Total proportion of observed time that *P. diadema* infants (grey) and *I. indri* infants (black) suckled during each of the three developmental phases. An asterisk above a phase denotes a significant difference between the two species in that phase.

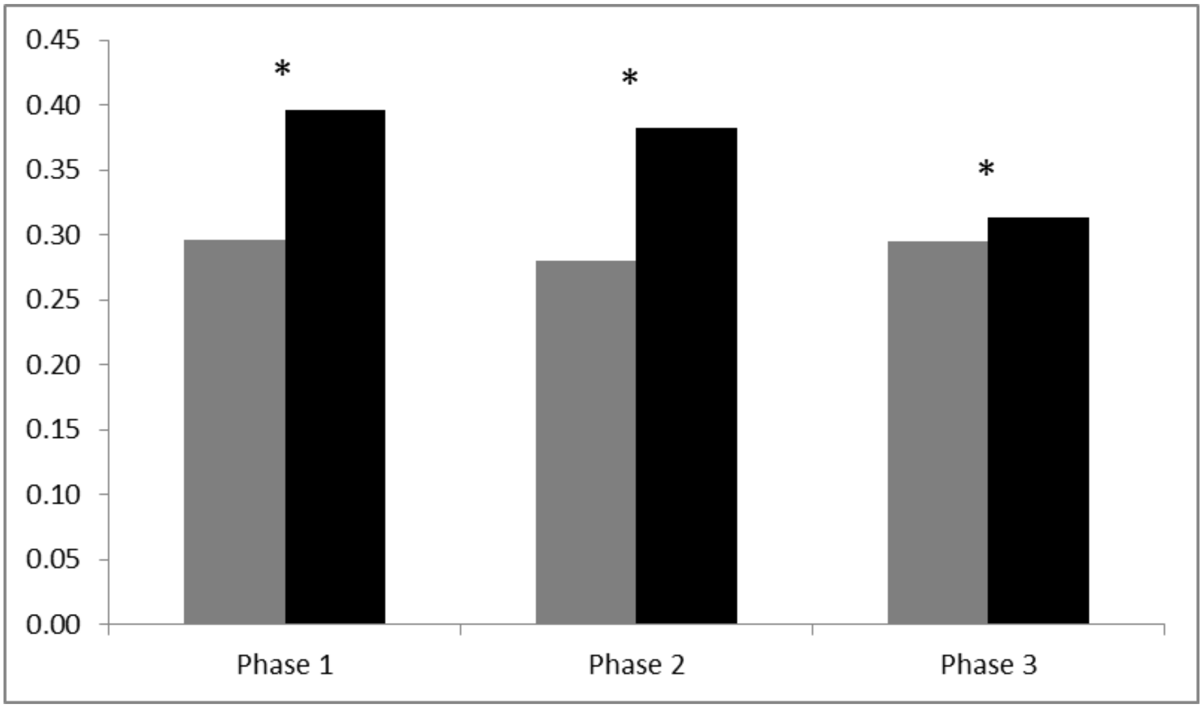

Figure 4.4 Total proportion of observed time that *P. diadema* infants (grey) and *I. indri* infants (black) were observing during each of the three developmental phases. An asterisk above a phase denotes a significant difference between the two species in that phase.

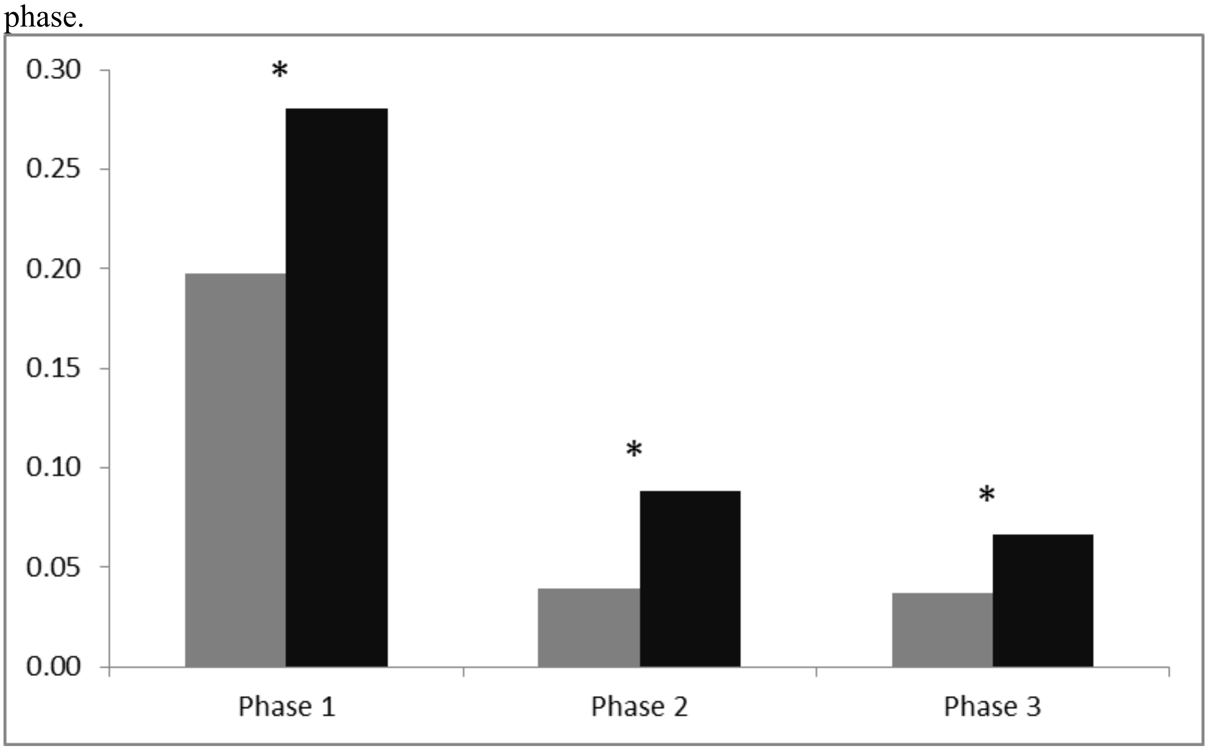

Figure 4.5 Total proportion of observed time that *P. diadema* infants (grey) and *I. indri* infants (black) rested during each of the three developmental phases. An asterisk above a phase denotes a significant difference between the two species in that phase.

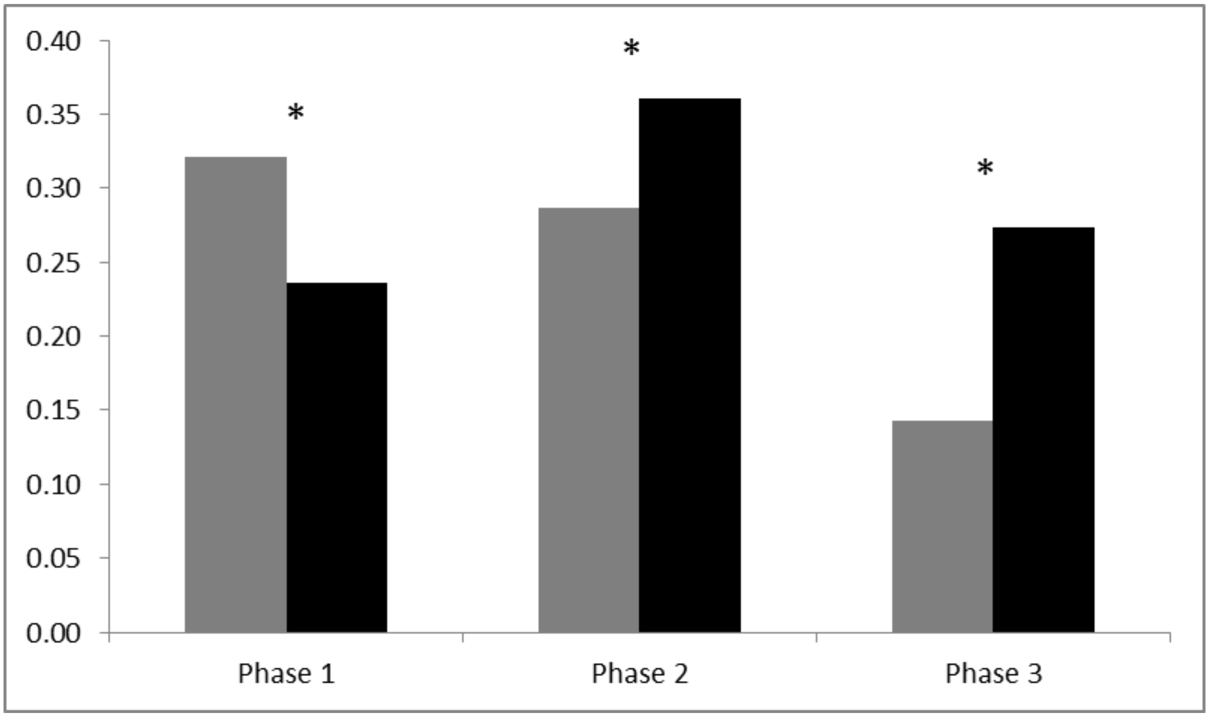

Figure 4.6 Total proportion of observed time that *P. diadema* infants (grey) and *I. indri* infants (black) played during each of the three developmental phases. An asterisk above a phase denotes a significant difference between the two species in that phase.

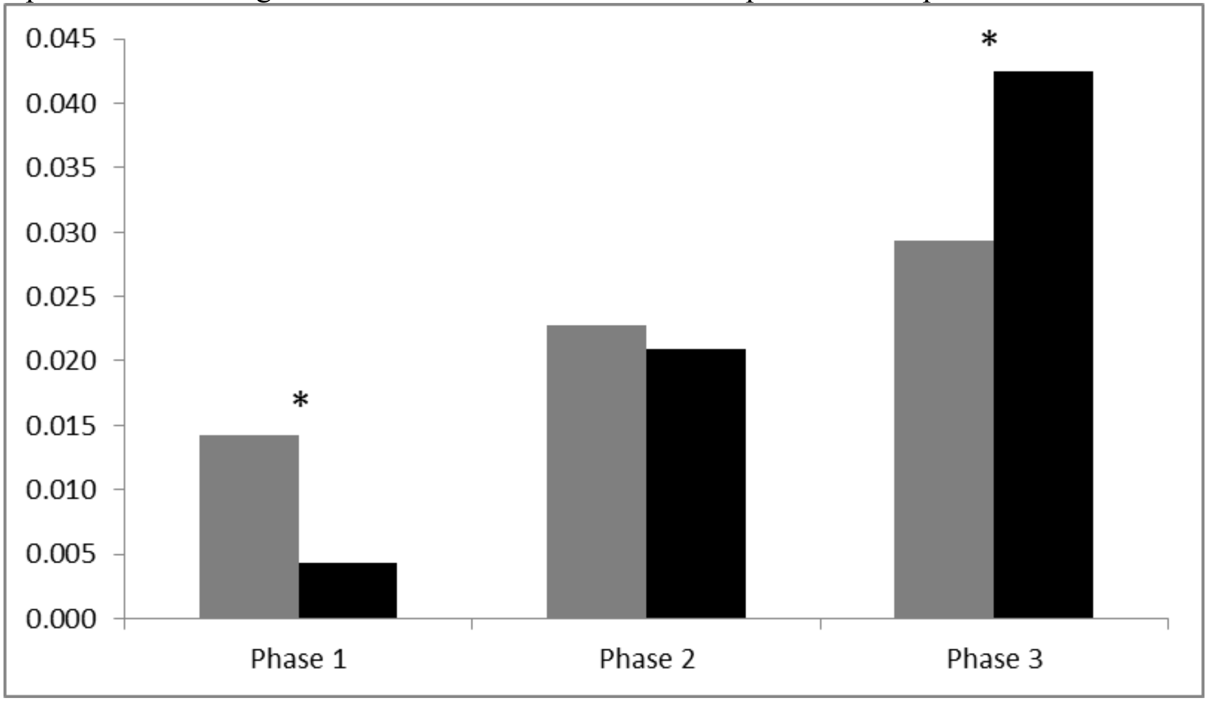

Figure 4.7 Total proportion of observed time that *P. diadema* infants (grey) and *I. indri* infants (black) self-groomed during each of the three developmental phases. An asterisk above a phase denotes a significant difference between the two species in that phase.

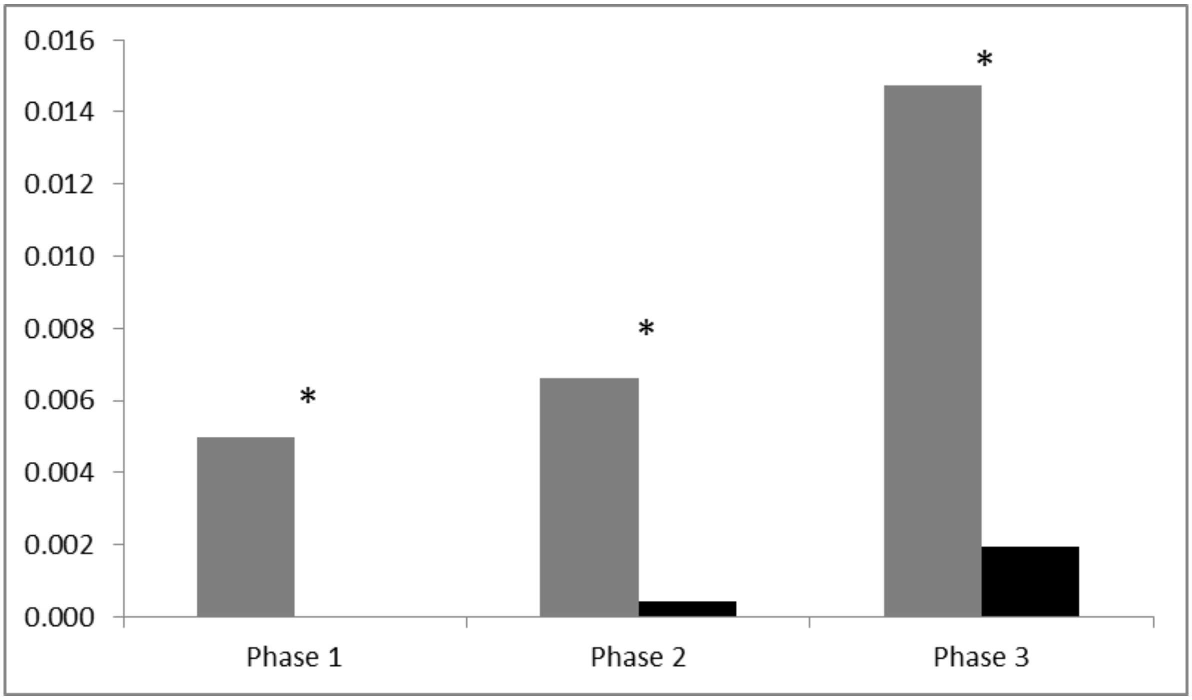

Figure 4.8 Total proportion of observed time that *P. diadema* infants (grey) and *I. indri* infants (black) were allogrooming during each of the three developmental phases. An asterisk above a phase denotes a significant difference between the two species in that phase.

4.4 Discussion

In this chapter I directly compared the ontogeny of six specific behaviours in indri *I.indri* and diademed sifaka (*P.diadema*) infants, aged 3 – 25 weeks old. I also examined how group size, weaning phase of the infant, and species (whether the infant was *I. indri* or *P. diadema*) influenced the proportion of time infants spent engaged in each behaviour. In the following sections I discuss my results in the context of my specific hypotheses and predictions.

Group size and infant development

By altering the level of potential feeding competition, group size may influence overall reproductive rates, as well as particular adult behaviours, including the proportion of time adults spend feeding, socializing, and travelling (Borries et al. 2008; Grove 2012; Gogarten et al. 2014). Group size has also been shown to affect stress levels and susceptibility to disease (Nunn & Heymann 2005; Pride 2005; Snaith et al. 2008) which may, in turn, influence reproductive effort. However, contrary to what I expected, group size, as categorized for this analysis, did not affect any of the six infant behaviours examined in my study. Specifically, I did not find any evidence that a large (defined here as five or more individuals) or a small (less than five individuals) group size had any effect on the proportion of time infants spent feeding independently, playing, resting, observing, allogrooming or self-grooming. This may be a reflection of the small sample size and/or the categories used to differentiate between group sizes. It is also possible that infants are not influenced by group size in the same ways that their mothers are. For example, Roberts & Cords (2013) found that probability of conception in blue monkeys (*Cercopithecus mitis stuhlmanni*) was highly correlated to group size with the optimal group size including approximately 31 members (group sized ranged from 7 – 70). It could be that in *I. indri* and *P. diadema*, if the group size is appropriate for conception and the subsequent birth of an infant (I only studied groups that had infants), that the young infants, whether in small or large groups, do not experience the same relative effects of feeding competition as their mothers. This could be due to their relatively minimal requirements in terms of the *amounts* of solid foods that they need to sustain themselves. In mammalian infants with a prolonged period of dependency, including primates, milk can serve as a ‘fallback’ food when other food resources as less readily available (Pond 1977; Pond 1984). For example in howler monkeys (*Alouatta palliate*), infants aged 6 – 12 months are consistently feeding on solid food but they also continue to suckle, and hence receive nourishment from their mothers as well (Raguet-Schofield 2010). Raguet-Schofield (2010) found that milk effectively serves as a fallback food for infants when food availability is limited or when adults are relying on tougher, harder food resources that infants are not yet able to process. Since the infants in my study were all suckling throughout the study period, it is possible that they had yet to experience the feeding competition potential within larger groups. In Chapter 5, I examine how group size affects the behaviours of mothers in groups of both *I. indri* and *P. diadema*.

Weaning phase and the proportion of time engaged in active behaviours

More active behaviours, that require a certain level of proficiency in motor skills, generally take longer to develop than do more passive behaviours such as resting or observing. For example, young cheetah (*Acinonyx jubatus*) are less effective hunters than mature individuals (Hilborn et al. 2012) and young aye-aye (*Daubentonia madagascariensis*) take several months to develop the coordinated series of tapping, gnawing and extraction behaviours needed to effectively locate and access wood-boring larvae, an important part of their diet (Krakauer 2005). Although young *I. indri* and *P. diadema* do not need to develop such complex foraging skills to survive, they do need to develop a certain level of motor skills to safely and effectively move between branches to feed or to play without falling. Similarly, infants are not born with the ability to groom themselves or other individuals and hence grooming behaviours presumably take time to develop. In my study, I found that in three of the four active behaviours that I examined, that my predictions were supported by my results. Specifically, infants of both species fed independently, self-groomed and allogroomed with other individuals, for increasingly greater proportions of their time as they aged from 3 – 25 weeks, and that infants engaged in these behaviours for the greatest proportion of observed time when they were in Phase 3 of development (at least 20 weeks old). By definition, this is also the phase when infants are feeding independently for a greater proportion of their time than they are suckling (Phase 3). Therefore, by the time infants are reaching nutritional independence, they are also grooming themselves and other individuals for a proportion of time similar to that observed in adults.

Playing (both independent and social play) was the second most commonly observed behaviour for infants of both species. However, contrary to my prediction infants did not play more as they aged. In most mammals, including primates, independent, or presocial play, in which infants explore their environment and manipulate objects, is important for developing the motor skills needed to forage and feed independently and to move through the environment effectively and efficiently (Poirier & Smith 1974; Fagen 2002). Social play, where infants interact with other group members is also important for developing the social skills to be assimilated into a group, and to interact with other groups (Poirier & Smith 1974; Antonacci et al. 2010; Norscia & Palagi 2011). Both types of play have been documented in all primate species including orangutans (*Pongo* sp., Gladikas 1985), bonobos (*Pan paniscus*, de Waal 1988), tarsiers (*Tarsius spectrum*, MacKinnon & MacKinnon 1980) and giant mouse lemurs (*Mirza* sp., Pages 1983). Unlike the other active behaviours, I observed less play by both species in Phase 3 compared with Phase 2. By comparison, ring-tailed lemurs (*Lemur catta*) are much more precocial and develop much more quickly than do either *Propithecus* sp. or *I. indri* (Chapters 2 and 3) and infant *L. catta* are feeding independently for a greater proportion of their time than they are suckling (Phase 3) by week 11 (Gould 1990), compared to week 20 (*this study*). However, in accordance with my results, Gould

(1990) also found that after week 12, at the time when they enter Phase 3, *L. catta* spend significantly less time in solitary play than they do in weeks 6 – 12.

Fagen (2002) reported that across nonhuman primates, both independent and social play, begin to decline with the onset of early juvenility, and then consistently decline through to adulthood. At this stage of development, it is suspected that other types of behaviours that are more typical of adults, such as independent feeding or aggressive interactions, gradually replace the high amounts of play exhibited in infancy (Fagen 2002). In both *P. diadema* and *I. indri*, as well as in *L. catta* (Gould 1990) the time when play decreased coincided with the time when independent feeding became more important than suckling. Therefore it is possible that energetically, infants must trade play for independent feeding in Phase 3, and that by this stage they have acquired the necessary motor skills to adequately feed themselves. According to Fagen (2002) this also indicates that Phase 3 could mark the overall end of infancy and the beginning of the juvenile period.

The ontogeny of species-specific behaviour patterns in the first six months

In accordance with my predictions, both *I. indri* and *P. diadema* developed species-specific behavioural differences in the first six months of life. As is typical of adults (Powzyk 1997; Powzyk & Mowry 2006), *I. indri* infants spent a greater proportion of their time in behaviours that require minimal energy (specifically resting and observing) and a smaller proportion of their time feeding independently than did *P. diadema* infants.

P. diadema infants also spent a greater proportion of their time allogrooming with other group members than did *I. indri*. Although mine is the first study to look specifically at allogrooming in these two species, Powzyk (1997) did report that her two *P. diadema* groups spent a greater percentage of their time each day engaged in social behaviours than did *I. indri*, and these presumably included allogrooming. Allogrooming is important for maintaining the condition of the fur and for removing ectoparasites that are hard for the recipient to reach (Hutchins & Barash 1976). In addition, allogrooming in primates, including *Propithecus* sp. and *L. catta* has been correlated to bond formation, rank acquisition and social integration (Dunbar 1991; Gould 1997; Schino 2001; Lewis 2010). Since *I. indri* live in monogamous groups of a breeding pair and their offspring, there is likely less need for these latter social benefits, whereas in *Propithecus* there tends to be more rank-based hierarchies and agonistic interactions between group members (Erhart & Overdorff 2008). This could in part explain why *P. diadema* began allogrooming very early in infancy and spent a greater proportion of their time allogrooming than did *I. indri* in all three phases. In addition, infants allogrooming with other group members could be viewed as a type of allocare, and if so, the faster development observed in *P. diadema* (Chapter 2 and 3) could in part be facilitated by this allocare, which reduces energetic restraints on the mother (Ross & McLarnon 2000). In Chapter 5, I examine the patterns of allogrooming in the mothers of my focal infants, and this reveals that infant *I. indri* and *P. diadema* in my study (*this chapter*) were actually allogrooming for the same proportion of time as mothers of their respective species in Phase 3.

The only species-specific difference that I predicted, but was not supported by my results, was the proportion of time infants of each species spent engaged in play. As part of their overall strategy to minimize energy expenditure, as adults and juveniles, *I. indri*, tend to play significantly less than do *P. diadema* (Powzyk 1997; Powzyk & Mowry 2006). However, I found that in infancy, while this pattern held true for Phase 1, in both Phase 2 and Phase 3, *I. indri* infants were playing for a greater proportion of their active time than were *P. diadema*. I suggest that this is another example of the prolonged period of time that *I. indri* have to transition from dependency to independence. Since *I. indri* mothers will not be gestating again for at least another year, infants are allowed a longer period in which to play and to develop their motor and social skills. By contrast, *P. diadema* infants must transition to juvenility earlier than *I.* indri, by reducing play and feeding independently more, since their mothers are likely to be preparing for their subsequent gestation. I did witness mother *P. diadema* rejecting their infants in Phase 3. Specifically, mothers would bite or nip at their infants when they attempted to suckle or to ride dorsal. I never witnessed these types of behaviours in *I. indri*. Maternal strategies and how these relate to her energetic investment throughout the lactation period will be examined in the following chapter.

In summary, both *I. indri* and *P. diadema* infants developed species-specific behaviours within their first six months of life. Active behaviours that require more developed motor skills gradually encompassed a greater proportion of time as the infants aged. By Phase 3, when infants of both species were feeding independently for a greater proportion of their time than they were suckling, they also reduced the amount of time they spent in play behaviours. As *I. indri* infants are afforded at least one more year before their mothers need to ingest energetically in the next offspring, they are not under the same selective pressure to feed independently and play less by Phase 3. Conversely, *P. diadema* infants are rejected earlier, and hence forced to feed independently more and play less, as their mothers are frequently preparing for their next gestation in Phase 3.

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5 - VARIABLES AFFECTING MATERNAL STRATEGIES IN THE TWO LARGEST LEMURS

5.1 Introduction

Newborn primates are completely dependent on their mothers for both nourishment and for transport in their first stages of infancy. A lactating female must therefore employ a strategy to meet the increasing requirements of her growing infant while not exceeding her own energetic capacity (Lee 1997). Both lactation and infant-carrying have a significant impact on maternal nutrient and energy requirements and are by far the two most energetically costly aspects of raising offspring (Oftedal 1984; Oftedal 1985; Altmann & Samuels 1992; Ross 2001; Dufour & Sauther 2002). Female tactics for balancing the costs of lactation may be observed in the frequency of nursing events, the duration of nursing events, the duration of the lactation period and variation in milk composition (Power 2006; Hinde & Milligan 2011). Similarly, tactics for balancing the costs of infant-carrying may be observed in the type of carrying, the frequency of carrying bouts, the duration of carrying bouts and the duration of the infant-carrying period. In addition, a lactating female may modify the time spent in other behaviours such as feeding, resting or social behaviours, to better adjust to the changing needs of her infant and the corresponding demands on her body. All of these tactics combine to reflect a behavioural pattern that is primarily constrained by phylogeny (Kappeler 1996), but may also be affected by additional factors including the quality of resources available, group size and the specific age or developmental phase of the infant. In this chapter I will explore how several different factors shape the maternal strategies employed by the two largest lemurs. This is the first study to examine the behavioural tactics and overall strategies utilized by lactating *P. diadema* and *I. indri*.

Lactation strategies of primates are characterized by an extended lactation period, frequent nursing events and poor milk quality overall (Hinde & Milligan 2011). For example, the milk of haplorhines is composed of 6.5-8% sugar, 1-16% fat, and 1.2-4.2% protein (Milligan et al. 2006). The milk composition in most strepsirhine primates is also very dilute and of poor quality (Tilden & Oftedal 1997). For example, female ring-tailed lemurs (*L. catta*) and *Eulemur*, produce dilute milk (9.9% dry matter) very low in energy, and composed of only 8.4% carbohydrates, 0.9% fat and 1.2% protein (Tilden & Oftedal 1997). Other strepsirhines however, where mothers frequently leave offspring unattended, including bushbabies (*Otolemur* sp.), lorises (*Nycticebus* sp.), and lemurs that belong to the genus *Varecia* produce relatively rich and high-energy milks (Tilden & Oftedal 1997). For example, ruffed lemurs, (*Varecia* spp.) produce milk containing 13.5% dry matter, 3.2% fat and 4.2% protein (Tilden & Oftedal 1997). These authors suggest that *Varecia* mothers are able to allocate more energy to producing higher quality milk because they nurse less frequently and do not expend as much energy constantly carrying their infants (Tilden & Oftedal 1997).

Infant-carrying, defined as “supporting the entire weight of an infant while standing or locomoting” (Altmann & Samuels 1992, p. 393) at times may require more energy from females than lactation and primate species that carry their infants tend to exhibit significant costs to reproduction including later weaning ages and later ages at first reproduction (Ross 2001). The prevalence of this costly behaviour within primates suggests benefits, including reduced mortality from predation and from infanticide (Ross 2001). Additionally, infants of highly arboreal species are at risk of death or injury from falls (Morland 1990; Richard et al. 2002) and a relatively long carrying period may be necessary for the infant to develop the motor skills and strength to safely locomote independently through the environment. The cost incurred by a female is expected to change according to both the weight and the nutritional needs of her growing infant.

Altmann & Samuels (1992) generated a model illustrating the immediate energetic costs of infant-carrying to mothers in yellow baboons, *Papio cynocephalus*, where newborn infants are carried continuously, but by eight months infants are rarely carried (Altmann & Samuels 1992). These authors calculated that an 11 kg baboon mother expends 3493 kJ/day for personal maintenance but with a young infant to care for, females expend an additional 21 kJ/g for the production of new tissue. Since the infants gained 4-5 g/day, lactating females also required an extra 100 kJ/day for growth (Altmann & Samuels 1992). These authors estimated that a mother who is lactating requires 5% more kJ/day for infant care during its first month and 12% more a day once the infant is actually locomoting independently, due to the added energy expenditure of an independently locomoting infant (Altmann & Samuels 1992). These authors suggest that the increased independent locomotion of an infant that is still not completely nutritionally independent increases the cost of lactation incurred by the mother at this stage (Altmann & Samuels 1992).

Since infants of different taxa develop at different rates and vary in the length of time they are dependent on their mother (Chapters 2 and 3), the stage or phase of greatest energetic cost to the female varies as well. In order to compensate for the energetic costs of lactating and infant-carrying, females may modify their feeding patterns, although the strategic timing of this behavioural change varies greatly between species. For instance, in many primates females increase the time they spend feeding in early lactation. For example, female brown lemurs (*E. fulvus*) increase their intake of food in the early lactation period when they are nursing most frequently (Tarnaud 2006) and female black howler monkeys (*Alouatta pigra*) females feed for a greater proportion of their time during early and mid-lactation than they do during late-lactation (Dias et al. 2011). Female orangutans continue to carry their infants constantly for three years and lactate for 6.5 years, but show an increase in their feeding time during the earliest phase of lactation, when infants are 0 - 6 months old (Jaeggi et al. 2010; van Noordwijk et al. 2013). Conversely, female siamangs (*Symphalangus syndactylus*) spend the greatest amount of time feeding when lactation has mostly ceased and infant-carrying had shifted to the male, suggesting that these females replenish energetic costs after the primary period of investment (Lappan 2009).

The particular type of habitat may also influence the type of strategy employed by females of the same species. For example, among ring-tailed lemurs (*L. catta*) inhabiting gallery forest habitat, females that are gestating or lactating have a higher intake of protein-rich foods than do males (Sauther 1998). In contrast, *L. catta* inhabiting spiny forest habitat did not exhibit any sex-based differences in time spent feeding or in protein consumption during the early to mid-lactation period (Gould et al. 2011). Similarly, Milne-Edwards sifaka (*Propithecus edwardsi*) did not exhibit any sex-based differences in the time they spent feeding, suggesting that these female sifaka do not satisfy the energetic demand of lactation by either increasing their feeding time or reducing activity during lactation (Hemingway 1999). The variation between results implies that strategies for balancing the costs of maternal investment are species-specific but may also depend on the environment or the particular climatic events surrounding the study (for example see LaFleur & Gould 2009). In this chapter, I will explore how the energetic costs of lactation and infant-carrying are reflected in the behaviours of lactating females of two sympatric lemur species.

The lemuriformes are endemic to Madagascar and include 5 families, 15 genera, and 99 species and 103 subspecies of varying sizes, diets, types of locomotion, habitat and social organization (Schwitzer et al. 2013). Because of the great variation in ecology within the lemurs, they are ideal for elucidating the adaptive patterns of maternal strategies for raising infants using comparative studies. My study examined the two extant species of lemurs with the largest body size; the diademed sifaka (*Propithecus diadema*) and the indri (*Indri indri*) (Glander & Powzyk 1995). These two species share several important traits that make them ideal candidates for comparison: 1) they are closely related phylogenetically, both belonging to the lemur family Indriidae (Rumpler et al. 2004; Rumpler et al. 2011), 2) they are approximately the same size as adults, weighing roughly 6 – 7 kg (Glander & Powzyk 1995), 3) they are both highly arboreal and exhibit the same kind of locomotion, known as vertical clinging and leaping (Napier & Walker 1967; Pollock 1986), 4) they are both highly folivorous, although the diet of *I. indri* includes more leaves than that of *P. diadema* (Pollock 1975b; Powzyk & Mowry 2003; Britt et al. 2002; Irwin 2008), and 5) they share the same habitat, occurring in sympatry in the eastern rainforests of Madagascar (Pollock 1975a; Powzyk 1997; Britt et al. 2002). While these similarities help to reduce confounding effects due to phylogeny, body size, type of locomotion, general feeding ecology and habitat, the differences in the behavioural ecology and the specific feeding ecology of *P. diadema* and *I. indri* allow for examination of the importance of these partially isolated factors on maternal strategies.

P. diadema live in multi-male, multi-female groups of three to nine individuals (Powzyk 1997; Powzyk & Mowry 2003; Irwin 2008; *this study*) and defend group territories using a combination of patrols, scent-marking and intergroup fighting (Powzyk 1997), while *I. indri* live in family groups composed of a monogamous pair and their offspring (Pollock 1975b; Powzyk & Mowry 2006) and primarily defend their territories through the use of long call vocalizations (Pollock 1975b; Pollock 1986a; Powzyk 1997; Powzyk & Mowry 2006). While both species are folivorous, the diet of *I. indri* is more biased towards leaves (Britt et al. 2002; Powzyk & Mowry 2003; Powzyk & Mowry 2006; Chapter 3) than *P. diadema* whose more varied diet includes a combination of leaves, fruits, seeds and flowers (Powzyk & Mowry 2003; Irwin, 2006; Irwin 2008; Irwin et al. 2013). Powzyk & Mowry (2006) suggested that the energy required for intensive foliage digestion by *I. indri* requires them to minimize their energy expenditures relative to *P. diadema*. In Chapter 3, I explained how *I. indri* mothers may also reduce their energetic costs, relative to *P. diadema* by prolonging their inter-birth interval. In this chapter, I examine my general hypothesis that *P. diadema* and *I. indri* also have species-specific behaviours that allow them to balance the costs of maternal investment over the first six months. In addition, I examine how other variables, that have been found to affect behaviour patterns in other primates, influence the behavioural budgets of lactating females in these two species. Specifically, I quantify the proportion of time females spend feeding, resting, observing, travelling, scent marking, travelling, long calling, self-grooming and allogrooming, and I evaluate the effects of species, season, group size and the stage of lactation (early, mid or late) on each of these behaviours. Below, I introduce each of these variables and provide hypotheses and predictions for what I expected, based on previously published findings for other primate species.

Seasonal Effects

Lemurs experience strict reproductive seasonality (Wright 1999). There is synchronization of births within sites and species, yet sometimes several months separate the births of different species within a site (Wright 1999; Richard et al. 2002; Lewis & Kappeler 2005). While factors of size and phylogeny tend to influence the respective gestation and lactation length of sympatric species (Kappeler 1996), within a particular site, all sympatric species tend to wean their infants during the same time of the year (Wright 1999). This 'weaning season' is also the season with the highest probability of abundant food resources and this timing is believed to aid in the survival of infants once they are no longer dependent on the mother (Wright 1999; Godfrey et al. 2004). Similarly, lactating females may rely on this season of abundance to rebuild energy stores depleted while lactating and infant-carrying throughout harsher times, with lower availability of food resources. For example, Verreaux's sifaka (*P. verreauxi*) in Kirindy Forest time the mid-late lactation period to coincide with the months with increasing food resources (Lewis & Kappeler 2005). The importance of this seasonal pattern has been theorized as one of the reasons that we see female feeding priority in several lemur species including *Lemur catta*, *Propithecus verreauxi* and *Indri indri* (Pollock 1979; Jolly 1984).

Hypothesis 1: Season affects the proportion of time females spend in territorial behaviours

Across different study sites in Madagascar, there tends to be less food available in the colder and drier months than in the hotter and wetter months (Wright 1999). While my study did not look at plant food availability, other studies of both *I. indri* and *P. diadema* have found that there is more preferred plant food available in October-December at Mantadia (Powzyk 1997), Tsinjoarivo (Irwin 2006) and Betampona (Britt et al. 2002) than in July-September. I assumed that patterns were similar at my study site and each session was categorized as either cold (June-September) or hot (October-December). Given the difference in temperature, rainfall, and preferred food availability between season (Powzyk 1997, Irwin 2006, Britt et al. 2002; Appendix A1), I expected that there would be more competition for food resources during the cold season. If this assumption holds true, and there is indeed more feeding competition during the cold season, then I predicted that females would spend a greater proportion of their time in territorial behaviours in this season as well. Specifically, I expected that *P. diadema* would scent mark and travel more in the cold season, and that *I. indri* would engage in more long-calling.

Group Size Effects

Group size has been demonstrated to affect several aspects of reproduction including probability of conception, developmental rates, and inter-birth intervals (Creel & MacDonald 1995; Mann et al. 2000; Roberts & Cords 2013). These differences, namely that there is a lower probability of conception, slower developmental rates and longer inter-birth intervals in larger groups (among the same species), are largely attributed to the increased foraging competition within these larger groups (Silk 2007; Clutton-Brock & Janson 2012) and corresponding behavioural differences have been discovered that support this hypothesis (Grove 2012; Roberts & Cords 2013). For example, red colobus monkeys (*Procolobus rufomitratus*) in larger groups spend less time feeding and socializing, and more time travelling than do those in smaller groups (Gogarten et al. 2014).

Hypothesis 2: Group size affects the proportion of time females spend feeding

Across different study sites, *P. diadema* tend to have larger group sizes than *I. indri*. However, there is overlap between the size of small groups of *P. diadema* and large groups of *I. indri*. Previously reported group sizes range from two to six for *I. indri* (Pollock 1975b; Powzyk & Mowry 2006) and three to nine for *P. diadema* (Powzyk 1997; Irwin 2008). In my study, *P. diadema* groups ranged in size from four to nine individuals, and *I. indri* groups ranged in size from three to five individuals. Therefore, I categorized each group as either small (less than five individuals) or large (five to nine individuals). If there is more feeding competition in larger groups, then I predicted that I would find that females in large groups spend less time feeding, and more time observing their environment and other individuals, than those in small groups.

Compared to the suspected costs of increased feeding competition in large groups, allocare, the caring of infants by non-mothers, is suggested as one way that mothers may actually benefit from living in larger groups with more potential care givers (Bekoff et al. 1984; Ross 2003). Allocare may facilitate an earlier weaning age, yet there is no clear relationship between the amount of allocare received and relative brain size, or time to reach sexual maturity, suggesting that mothers gain the most benefits from allocare in the form of infant-carrying (Ross 2003). If non-mothers aid in infant-carrying or other behaviours such as infant-grooming, this may reduce the energetic costs to the lactating female. The suggestion that allocare through infant-carrying by individuals other than the mother reduces the energetic cost of infant-carrying to the mother has, in turn, been used to explain why in some species that exhibit allocare, there is also a longer lactation period or denser concentration of milk. For example, *E. rufifrons* infants are slower to pass certain developmental markers than are *E. rubriventer* (Overdorff 1996). These two species are sympatric, closely related phylogenetically, similarly sized and have very similar diets, yet *E. rubriventer* males carry infants, while *E. rufifrons* males do not (Overdorff 1996). In this example, allocare appears to facilitate a longer lactation period in female *E. rubriventer* and a faster development of the infants (Overdorff 1996). In a similar comparison, *L. catta* infants are carried by females other than the mother by two weeks of age and develop much faster than sympatric *Eulemur* infants which are rarely ever carried by individuals other than the mother (Sussman 1977; Gould 1990; Gould 1992). In their review of infant care strategies in lemurs, Tecot et al. (2013) found that in contrast to haplorhine primates, allocare does not correlate with faster infant growth or shorter inter-birth intervals in lemurs. However, these authors restricted allocare to evidence of "nursing, carrying, or guarding infants by non-mothers" (Tecot et al. 2013 p. 327) and they report that thus far, there is no evidence for any of these specific allocare behaviours in either *P. diadema* or *I. indri*. In this chapter I search for evidence of allocare in both *I. indri* and *P. diadema* but I also include grooming of the infant, as has been used by Gould (1992) and Patel (2007) as an additional measure of allocare in these two species.

Hypothesis 3: Larger groups allow more opportunities for allocare

If larger groups allow more opportunities for allocare, including more time for non-mothers to groom infants, then I predicted that mothers in large groups would spend less time grooming their infants and more time grooming themselves, than those in small groups.

Lactation Phase Effects

Infant-carrying and lactating are the two most energetically costly behaviours for reproductive females (Oftedal 1984; Oftedal 1985; Altmann and Samuels 1992; Ross 2001; Dufour and Sauther 2002). As demonstrated by Altmann & Samuels (1992) the costs to a female are predicted to change throughout lactation depending on the relative weight of her infants and the amount of time her infant is locomoting independently. For example, newborn *P. edwardsi*, which are only slightly smaller than *I. indri* and *P. diadema*, weigh only 3% of their mother's mass at 165 g, but they grow to ~750 g by three months and 1.3 kg by six months (King et al. 2011). While the cost of infant care is relatively low when an infant is small and less active, and hence not expending and in turn not needing a large amount of calories, such costs are expected to increase as the infant develops. While the infant may not need to be carried as frequently, it is heavier and more active as it gets older, and therefore more energy is required to meet energetic demands as the infant develops. The costs to the female, and therefore the types of strategies employed, are likely to vary according to these changing energetic costs at each lactation phase. The main phases of feeding ontogeny (weaning) for infant *P. diadema* and *I. indri* were precisely identified in Chapters 2 and 3 and by the nature of how I defined them, correspond exactly to the early, mid and late lactation phases of mothers

(Martin 1984; Lee 1997; Tarnaud 2004). Both species go through each of these three lactation phases, however, the infant age at which transitions from one phase to the next occur, and therefore the length of time they spend in each phase, differs between them. For *P. diadema* Phase 1 lasts through until 13 weeks (Chapter 2), whereas *I. indri* transition after 9 weeks (Chapter 3). Both species transition to Phase 3 in week 20. *P. diadema* infants are usually entering Phase 3 in mid-November, whereas *I. indri*, who are born earlier than *P. diadema,* enter Phase 3 in mid-October (Chapters 2 and 3).

In examining relative maternal investment across early, mid and late lactation, certain trends are clarified (Table 5.1). For *P. diadema*, the time mothers spend nursing their infants nearly doubles during mid-lactation, but then stays constant throughout late lactation. From nursing data alone, I would expect that mid and late lactation are energetically more demanding than early lactation. However, when the added cost of infant-carrying is considered, I suspect that mid-lactation is the most costly of the three phases, given that infants are roughly five times the weight they were when they were first born (King et al. 2011) and still being carried by the mother for 70% of the time. In addition, although infants are feeding independently, and thus contributing to their own energy for a small portion of their time in mid-lactation, they are also expending a significant amount of their time actively playing during this phase (Table 5.2). *I. indri* exhibit a similar pattern, and thus I expect that mid-lactation is the most costly period for mothers of both species.

To illustrate the relative energetic costs to lactating females at each phase in *P. diadema* and *I. indri* living in sympatry at Maromizaha, I generalized the results from Chapters 2 and 3 to create Figure 5.1.

Table 5.1 Relative energetic investment by mothers throughout early, mid and late lactation represented by the percentage of time spent nursing and carrying her infant.

	Early Lactation		Mid Lactation		Late Lactation	
	Nursing	Carrying	Nursing	Carrying	Nursing	Carrying
P. diadema	13%	93%	20%	70%	20%	50%
I. indri	7%	99%	7%	87%	7%	49%

Table 5.2 Relative energy contribution and expenditure by infants throughout early, mid and late lactation represented by the percentage of time spent feeding independently and playing.

	Early Lactation		Mid Lactation		Late Lactation	
	Feeding	Playing	Feeding	Playing	Feeding	Playing
P. diadema	3%	32%	16%	29%	28%	14%
I. indri	1%	24%	8%	36%	23%	27%

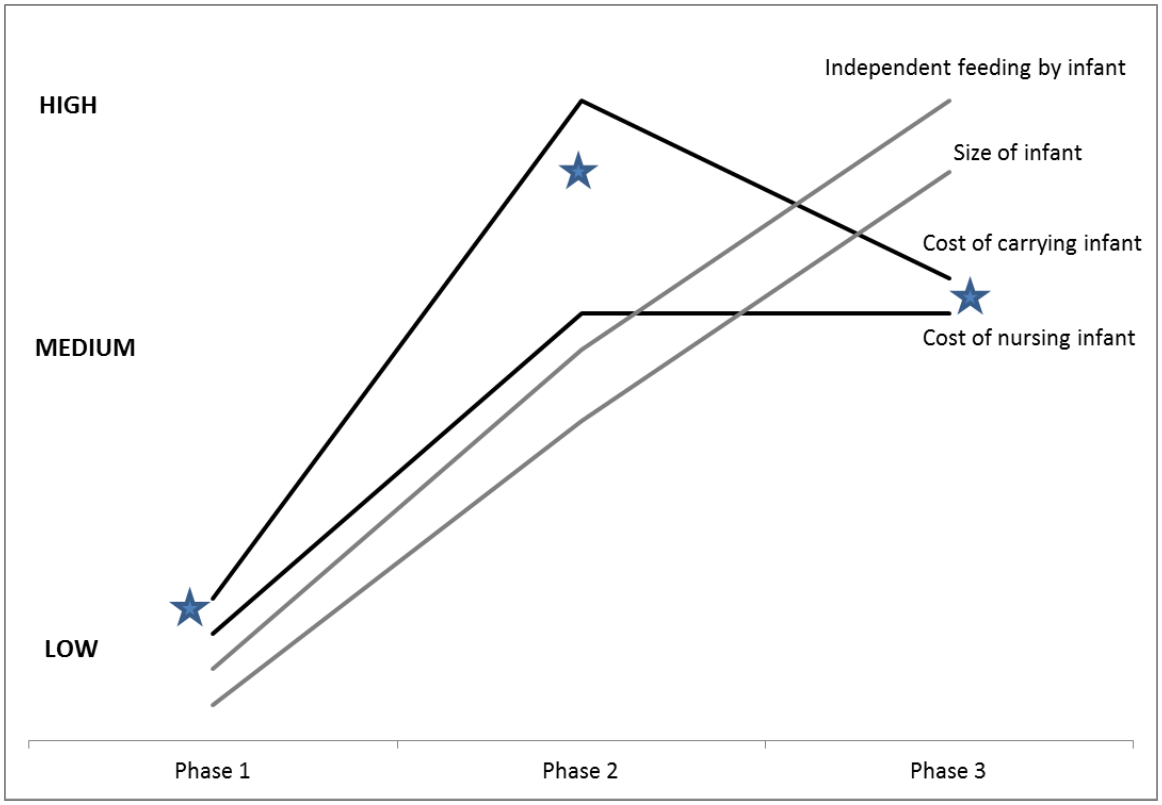

Figure 5.1 Relative costs to lactating females at each phase for *P. diadema* and *I. indri* living in sympatry at Maromizaha. Black lines represent costs of nursing and infant-carrying to the female and grey lines represent changes in infant size and proportion of time spent feeding independently. Blue stars approximate the relative overall energetic cost to the female in each of the three lactation phases.

Hypothesis 4: Females modify their behavioural budgets during the mid-lactation phase to compensate for the higher costs of maternal investment required during this period

If mid-lactation is the most energetically costly of the three phases for both *P. diadema* and *I. indri*, then I expected that females would modify their behaviour to meet the extra demands of this stage. Specifically, I predicted that females would spend more time feeding during mid-lactation compared to early and late lactation.

5.2 Methods

Study Area

I collected data on the social, feeding and infant care behaviours of *P. diadema* and *I. indri* mothers in Maromizaha forest (18°57'S, 48°36'E), a New Protected Area, located 140 km east of the nation's capital of Antananarivo, near the village of Anevoka. This montane rainforest is part of the Ankeniheny-Dazahamena rainforest corridor conservation initiative and includes a protected area encompassing approximately 1,600 ha, including 820 ha of intact hard wood forest and 360 ha of regenerated forest, with the remaining classified as degraded habitat. The study site is a mid-altitude rainforest with elevations ranging from 970-1223m. The annual rainfall for 2012 was 3163 mm, with close to one third falling in January and February combined. February 2012 is also when cyclone Giovanna struck the area, leaving all trees defoliated and several large trees dying. The average temperature (at 7:30 am) during the study period was 16°C (min=12.6, max=19.1), and the overall maximum and minimum temperatures were 36.8°C and 7.6°C respectively (Appendix I). The hottest months were November-February and the coldest were July-September. This study took place in the cold (July-September) and hot (October-December) seasons of 2011 and 2012. From a pilot study I conducted in 2010 and a follow up study in 2013, I was able to determine in which years the focal individuals gave birth.

Study Subjects

Both *P. diadema* and *I. indri* are endemic to the eastern rainforests of Madagascar. They have yet to breed in captivity and very little is known about reproductive strategies in these two species. With the help of trained assistants, I collected behavioural data for five *P. diadema* and five *I. indri* mothers from June-December, covering the first six months of their infant's development in 2011 and 2012. All 5 *P. diadema* belonged to one of four focal groups ranging in size from 4-9 individuals, and each of the five *I. indri* belonged to one of five focal groups ranging in size from 3-5 individuals. Focal groups were habituated in the three months preceding data collection. Each group was monitored at least once per week and therefore the infant's dates of birth are known to within one week. We often knew the actual day of an infant's birth, due to absence one day and presence the next, but in cases where there was a full week between observations of the group, we estimated the birthdate to be in the middle of the preceding week (Chapters 2 and 3).

Behavioural Sampling

With the help of five trained assistants (see Acknowledgements) I collected over 1470 hours of behavioural data on 10 mothers, over two consecutive birth seasons. We located focal groups each day with the assistance of local guides and conducted all-day follows of each infant for approximately two days each week. Continuous and instantaneous sampling methods (Altmann 1974) were used to sample feeding, resting, observing, allogrooming, infant-grooming, and self-grooming behaviours, as well as scent-marking, travelling and duet singing (see Table 5.3 for definitions). We recorded the time, to the nearest second, every time the mother's behavioural state changed for longer than 10 seconds.

Table 5.3 Ethogram describing the behaviours of lactating females recorded for *P. diadema* and *I. indri* at Maromizaha

Behaviour	Definition
Observing	Mother is not moving, eyes/gaze and attention are focused on something specific in the environment, including other group members, sounds/movement in the trees/air/ground, and the observer.
Feeding	Mother is harvesting with hands and/or mouth, and chewing or ingesting, a plant or food item
Resting	Mother is not moving, eyes are closed, or if open they are not focused on anything in the environment
Allogrooming	Mother is grooming, or being groomed by, another individual
Infant-Grooming	Mother is grooming her infant
Self-Grooming	Mother is grooming herself
Scent Marking	Mother is rubbing genitals on tree
Travelling	Mother is moving by vertical clinging and leaping in a specific direction
Long Calling	Mother is vocalizing in chorus with other group member(s)

Data Analysis

Data were summarized as proportions of the total time-in-view mothers spent feeding, resting, observing, allogrooming, infant-grooming, self-grooming, scent marking, travelling and long calling per focal follow session. For these analyses, I only used focal follow sessions that included at least 30 minutes of the mother in-view. Also, since I had only *P. diadema* sessions for infant ages 0 – 2 weeks, and only *I. indri* sessions for infant ages 26 – 33 weeks, I also limited the following comparative analyses to those that were collected when the infants were between 3 and 25 weeks of age. All analyses were performed in R 3.0.2 (R Core Development Team 2013) using the glmer function in the lme4 library (Bates et al. 2011). Since my response variables were proportions, and since I wished to correct for pseudoreplication (multiple sessions with the same mother), I used generalized linear mixed effect models (GLMMs) with binomial errors, including identity of the mother and a time factor (season) as random effects in all models considered. Including identity of the mother and season as random effects controls for the repeated sampling of the same individual within developmental phases (Carter et al. 2012; Hilborn et al. 2012; O'Mara & Hickey 2012). The untransformed proportional data for time mothers spent in each behavioural state were then modelled as functions of species, group size, developmental phase, and season. Group size was either small (<5 individuals) or large (5-9 individuals). Developmental phase was categorized as 1, 2, or 3 based on the age of their specific infant at the time of the session and as per phase definitions in Chapters 2 and 3. Season was either cold (July-September) or hot (October-December). I used an Akaike's Information Criterion (AIC) approach to model selection. AIC scores of candidate models were compared and the model with the lowest score was considered the best model (Burnham & Anderson 2002; see Appendix IV). To further compare behaviours of *P. diadema* and *I. indri* mothers both within and between species, I subsequently performed chi-square analyses of potential differences for proportions of time mothers were engaged in each behavioural state, during each developmental phase.

5.3 Results

Over four years of observation between 2010 and 2014 of 12 known females, I was able to calculate the inter-birth intervals and the birth season for *P. diadema* and *I. indri* at Maromizaha (Table 5.4). Most *P. diadema* infants were born in June or July, with only one born outside this time period, in October. The inter-birth intervals for *P.*

diadema ranged from 1 – 3 years. All *I. indri* infants were born in May or June and their inter-birth intervals ranged from 2 – 3 years. More specifically, the mean IBI for *P. diadema* was 21.8 months (range 12 – 36 months) and that for *I. indri* was 28 months (range 24 – 36 months). For one female *I. indri* we were able to determine that the gestation period was precisely 176 days, due to observations of conception on December 13, 2011 (Bonadonna et al. 2013) and appearance of the infant on June 6, 2012.

Table 5.4 Individual mothers in *P.diadema* and *I.indri* focal groups at Maromizaha from June 2010-September 2013. Each birth rate is calculated by dividing the number of births by the number of years when I knew that female. UK-Unknown, Y-Yes, N-No

Group ID	Reproductive Female	Infant 2010	Birthday 2010	Infant 2011	Birthday 2011	Infant 2012	Birthday 2012	Infant 2013	Birth Rate
PD1	Mavo	Y	Jun 10	Y	Jul 9	Y	Jun 24	N	0.75
PD1	Zoma	UK		Y	Oct 13	N		N	0.33
PD2	Rambo	UK		Y	Jun 27	*	*	N	*
PD2	Tandra	UK		Y	Jun 27	N		N	0.33
PD3	Orkide	Y	Jun	Y	Jul 1	Y	Jul 22	N	0.75
PD4	Volana	UK		Y	Jul 2	N		N	0.33
PD6	Havana	UK		Y	Jul	Y	Jul	N	0.66
IN1	Bevolo	Y	Jul	N		Y	Jun 4	N	0.50
IN2	Soa**	N		N		Y	May 2	N	0.40
IN3	Mena	Y	UK	N		Y	Jun 6	N	0.50
IN4	Eva	Y	UK	N		Y	Jun 4	N	0.50
IN5	Fern	UK		Y	Jun 8	N		N	0.33

* Mother and infant disappeared from group, last seen in group on July 17, 2011

** Soa gave birth in 2009 and her infant was killed by a fossa in October 2010, this birth is included in her IBI

I used 281 focal follow sessions in the total analysis of behavioural data, including 134 sessions with *I. indri* mothers and 147 sessions with *P. diadema* mothers, while their infants were aged 3–25 weeks old. Mothers of both species spent the greatest amount of their time feeding, followed by vigilant, resting, and self-grooming (Table 5.5).

Table 5.5 Percentage of observed time mothers spent in each of the main behaviour categories

Behaviour	*P. diadema*	*I. indri*
Feeding	45 %	49 %
Observing	35 %	36 %
Resting	13 %	11 %
Self-Grooming	3.1 %	2.8 %
Allogrooming	1.2 %	0.3 %
Infant Grooming	1 %	0.5 %
Travelling	2 %	0.07 %
Scent Marking	0.7 %	-
Long calling	-	0.5 %

Models for Behaviours of Lactating Females

The best models for behaviours of lactating females all included different types and numbers of factors, highlighting the importance of considering behaviours separately to elucidate complex maternal strategies for raising infants (Tables 5.6 – 5.8). Resting was the only behaviour that did not include species as a significant factor. Season had an effect on vigilance, infant-grooming, scent marking and duet singing, while group size had a significant effect on the proportions of time spent feeding, observing, and self-grooming. The lactation phase of the mother had a significant effect on the proportions of time spent feeding, resting, scent marking, and infant-grooming. Overall, *P. diadema* mothers spent a greater proportion of their time feeding (estimate +SE=0.44+0.21, Z=2.08, P>0.05; Table 5.6) than did *I. indri* mothers and mothers in large groups fed less than did mothers in large groups (estimate +SE=0.48+0.22, Z=2.2, P< 0.03; Table 5.6). The proportions of time mothers spent feeding (Phase 1: estimate +SE = -1.17 + 0.37, Z = -3.13, P = <0.002, Phase 2: estimate +SE = -1.05 + 0.38, Z = -2.76, P < 0.01) and resting (Phase 1: estimate +SE = 0.58 + 0.29, Z = -1.97, P = 0.049, Phase 2: estimate +SE = 0.44 + 0.28, Z = -1.57, P = 0.12; Table 5.6) were affected by the lactation phase of the mother. Both *I. indri* and *P. diadema* spent the most time feeding in Phase 2 (mid-lactation).

P. diadema mothers spent a greater proportion of their time infant-grooming (estimate +SE=0.71+0.35, *Z*=2.05, *P*= 0.04; Table 5.5) than did *I. indri* mothers, but self-groomed for a smaller proportion of time (estimate +SE=-1.20+0.49, *Z*=-2.46, *P*= 0.01; Table 5.6). Mothers in small groups were slightly, but not significantly, more likely to infant-groom (estimate +SE=0.59+0.35, *Z*=1.66, *P*= 0.09; Table 5.7) and spent a smaller proportion of time self-grooming than did mothers in large groups (estimate +SE=-1.14+0.51, *Z*=-2.24, *P*= 0.03; Table 5.6). Finally, in Phase 2 of lactation, mothers dedicated less time to infant-grooming than they did in other phases (Phase 1: estimate +SE = 0.76 + 0.35, *Z* = 2.16, *P* = <0.03; Table 5.7).

Overall, *P. diadema* mothers spent a greater proportion of their time allogrooming (estimate +SE=1.14+0.35, *Z*=3.23, *P*= 0.001; Table 5.8) than did *I. indri* mothers. *I. indri* mothers spent a greater proportion of time observing than did *P. diadema* mothers (estimate +SE=0.69+0.15, *Z*=-4.59, *P*= <0.001; Table 5.8) and mothers in large groups were more observant (estimate +SE=0.68+0.16, *Z*=-4.36, *P*= <0.001) than mothers in small groups. *P. diadema* mothers spent a greater proportion of their time scent marking (estimate +SE=6.81+1.24, *Z*=5.45, *P*= <0.001) and travelling (estimate +SE=3.44+0.40, *Z*=8.69, *P*= <0.001) than did *I. indri* mothers. Scent marking was observed more in the cold season (estimate +SE=-3.84+1.08, *Z*=-3.56, *P*= <0.001) and during Phase 1 (early lactation) (estimate +SE=3.15+1.13, *Z*=-2.79, *P*= 0.005), whereas long calling occurred more in the hot season (estimate +SE=1.13+0.21, *Z*=5.32, *P*= <0.001; Table 5.8).

Table 5.6 Effect size and significance of fixed effects included in the best models for self-care behaviours including feeding, resting and self-grooming for lactating *P. diadema* and *I. indri*

Model	Fixed effect	Estimate	SE	*Z*	*P*
Feeding					
	Intercept	0.4369	0.4127	1.059	0.290
	Species PD	0.4396	0.2110	2.083	0.037
	Small Group Size	0.4833	0.2191	2.206	0.027
	Phase 1	-1.1709	0.3744	-3.127	0.001
	Phase 2	-1.0484	0.3795	-2.763	0.005
	Hot Season	-1.0847	0.3710	-2.923	0.003
	Phase 1: Hot Season	0.8835	0.4526	1.952	0.051
	Phase 2: Hot Season	0.9157	0.4119	2.223	0.026
Resting					
	Intercept	-2.4549	0.2105	-11.663	<0.001
	Phase 1	0.5807	0.2948	1.970	0.049
	Phase 2	0.4369	0.2782	1.571	*0.116
Self-Grooming					
	Intercept	-2.5153	0.5372	-4.682	<0.001
	Species PD	-1.1975	0.4878	-2.455	0.014
	Small Group Size	-1.1381	0.5086	-2.238	0.025

Table 5.7 Effect size and significance of fixed effects included in the best models for infant-grooming by lactating *P. diadema* and *I. indri*

Model	Fixed effect	Estimate	SE	*Z*	*P*
Infant-Grooming					
	Intercept	-6.3193	0.4959	-12.744	<0.001
	Species PD	0.7117	0.3472	2.050	0.040
	Phase 1	0.7640	0.3538	2.159	0.031
	Phase 2	0.0383	0.2633	0.145	*0.884
	Hot Season	0.5820	0.2891	2.013	0.044
	Small Group Size	0.5898	0.3544	1.664	*0.096

Table 5.8 Effect size and significance of fixed effects included in the best models for social behaviours including allogrooming, travelling, observing, scent marking and long calling, of lactating *P. diadema* and *I. indri*.

Model	Fixed effect	Estimate	SE	*Z*	*P*
Allogrooming					
	Intercept	-6.0108	0.2483	-24.208	<0.001
	Species PD	1.1390	0.3528	3.229	0.001
Travelling					
	Intercept	-7.6773	0.3176	-24.174	<0.001
	Species PD	3.4399	0.3960	8.687	<0.001
Observing					
	Intercept	0.0511			
	Species PD	-0.6939	0.1512	-4.589	<0.001
	Hot Season	0.1891	0.0872	2.169	0.030
	Small Group Size	-0.6845	0.1571	-4.356	<0.001
Scent-Marking					
	Intercept	-8.2172	0.8946	-9.185	<0.001
	Species PD	6.8149	1.2496	5.454	<0.001
	Phase 1	-3.1523	1.1309	-2.787	0.005
	Phase 2	-0.7369	0.4651	-1.584	0.113
	Hot Season	-3.8367	1.0768	-3.563	<0.001
Long Calling					
	Intercept	-5.9595	0.2447	-24.354	<0.001
	Species PD	-18.9310	898.21	-0.021	0.983
	Hot Season	1.1329	0.2130	5.318	<0.001

Comparisons by Lactation Phase

Figures 5.2 – 5.10 and the following results illustrate the proportions of *observed* time that mothers of both species engaged in behaviours, as per the developmental phase of their respective infants and hence their own lactation phase. *I. indri* mothers spent the greatest proportion of time observing in Phase 3 ($\chi^2 = 56.14$, $P < 0.001$) while *P. diadema* mothers were most often observing in Phase 1 ($\chi^2 = 47.30$, $P < 0.001$). *I. indri* spent a greater proportion of time vigilant than did *P. diadema* in Phases 2 ($\chi^2 = 6.64$, $P < 0.01$) and 3 ($\chi^2 = 62.63$, $P < 0.001$; Figure 5.2). Overall, *I. indri* mothers spent a greater proportion of time feeding than did *P. diadema* in Phase 1 ($\chi^2 = 117.62$, $P < 0.001$), Phase 2 ($\chi^2 = 10.67$, $P < 0.001$) and Phase 3 ($\chi^2 = 2.74$, $P < 0.098$), but mothers of both species spent the greatest proportion of time feeding when their infants were in Phase 2 (*I. indri*: $\chi^2 = 20.85$, $P < 0.001$, *P. diadema*: $\chi^2 = 65.48$, $P < 0.001$; Figure 5.3). *P. diadema* spent a greater proportion of time resting than did *I. indri* in Phases 2 ($\chi^2 = 8.59$, $P < 0.01$) and 3 ($\chi^2 = 196.42$, $P < 0.01$) but in Phase 1, *I. indri* spent more time resting ($\chi^2 = 7.06$, $P < 0.001$). When considered separately, *I. indri* mothers spent the most time resting in Phase 1 ($\chi^2 = 72.48$, $P < 0.001$) while *P. diadema* mothers spent the most time resting in Phase 3 ($\chi^2 = 27.21$, $P < 0.001$; Figure 5.4).

P. diadema mothers spent a greater proportion of their time participating in allogrooming with other group members than did *I. indri* in all three phases (Phases 1: $\chi^2 = 140.64$, $P < 0.001$, Phase 2: $\chi^2 = 22.90$, $P < 0.001$, Phase 3: $\chi^2 = 1.50$, $P = 0.221$). Considered separately, *P. diadema* were allogrooming most often in Phase 1 ($\chi^2 = 80.80$, $P < 0.001$) while *I. indri* were allogrooming most often in Phase 3 ($\chi^2 = 11.66$, $P < 0.001$; Figure 5.5). *P. diadema* spent a greater proportion of time grooming their infants than did *I. indri* in the first 2 phases (Phase 1: $\chi^2 = 35.47$, $P < 0.001$, Phase 2: $\chi^2 = 5.94$, $P < 0.02$) with *P. diadema* allocating most time in Phase 1 ($\chi^2 = 35.09$, $P < 0.001$) and *I. indri* allocated most time in Phase 3 ($\chi^2 = 4.73$, $P < 0.05$; Figure 5.6). *P. diadema* spent the greatest proportion of time self-grooming in Phase 2 ($\chi^2 = 20.21$, $P < 0.001$), while *I. indri* spent the greatest proportion of time self-grooming in Phase 3 ($\chi^2 = 92.27$, $P < 0.001$). *P. diadema* also spent a greater proportion of time self-grooming than did *I. indri* in the first 2 phases (Phases 1: $\chi^2 = 23.39$, $P < 0.001$, Phase 2: $\chi^2 = 26.89$, $P < 0.001$) but *I. indri* spent more time self-grooming in Phase 3 ($\chi^2 = 18.40$, $P < 0.001$; Figure 5.7).

Overall, *P. diadema* mothers spent a far greater proportion of time scent marking ($\chi^2 = 250.93$, $P < 0.001$; Fig. 8) and travelling ($\chi^2 = 131.74$, $P < 0.001$; Figure 5.9) than did *I. indri*. They spent the greatest proportion of their time scent marking in Phase 1 ($\chi^2 = 21.16$, $P < 0.001$), and the least in Phase 2 ($\chi^2 = 26.00$, $P < 0.001$; Figure 5.8). They also spent the greatest proportion of time travelling in Phase 1 ($\chi^2 = 91.42$, $P < 0.001$), and the least in Phase 2 ($\chi^2 = 64.20$, $P < 0.001$; Figure 5.9). *I. indri* spent more time long calling in Phase 2 ($\chi^2 = 5.96$, $P < 0.02$), and the least in Phase 1 ($\chi^2 = 9.61$, $P < 0.01$; Figure 5.9). *P. diadema* never performed these species-specific long calls.

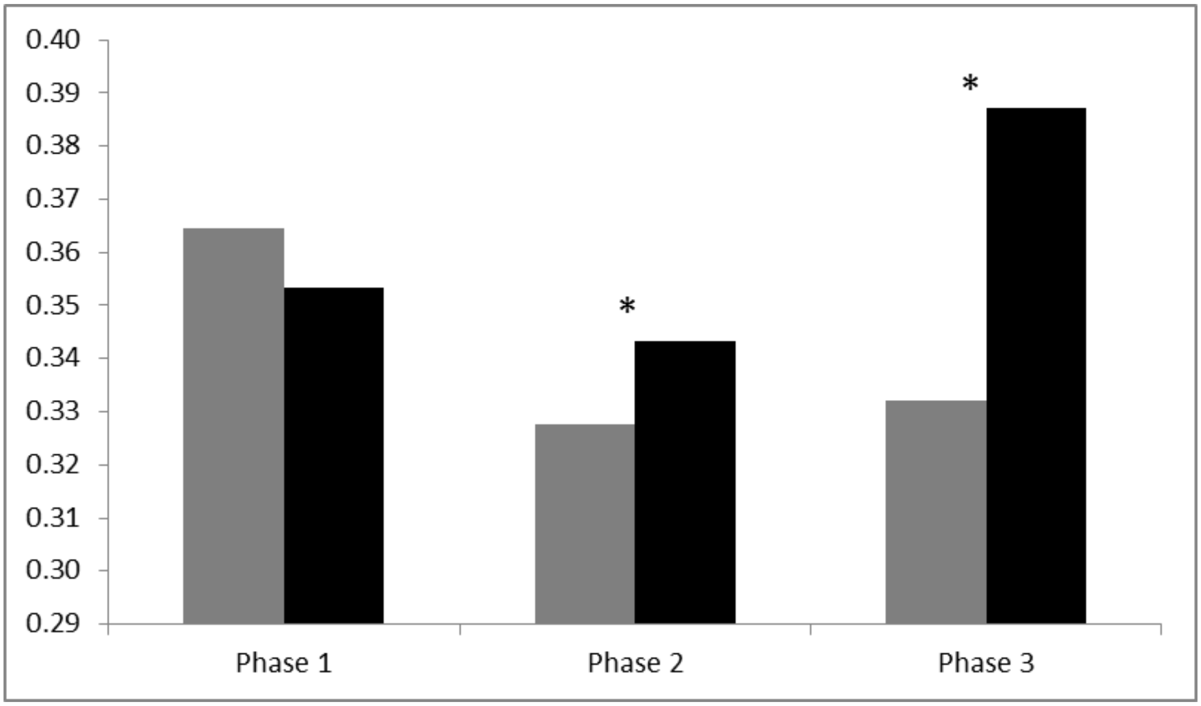

Figure 5.2 Total proportion of observed time that *P. diadema* mothers (grey) and *I. indri* mothers (black) were observing during each of the three developmental phases. An asterisk above a phase denotes a significant difference between the two species in that phase.

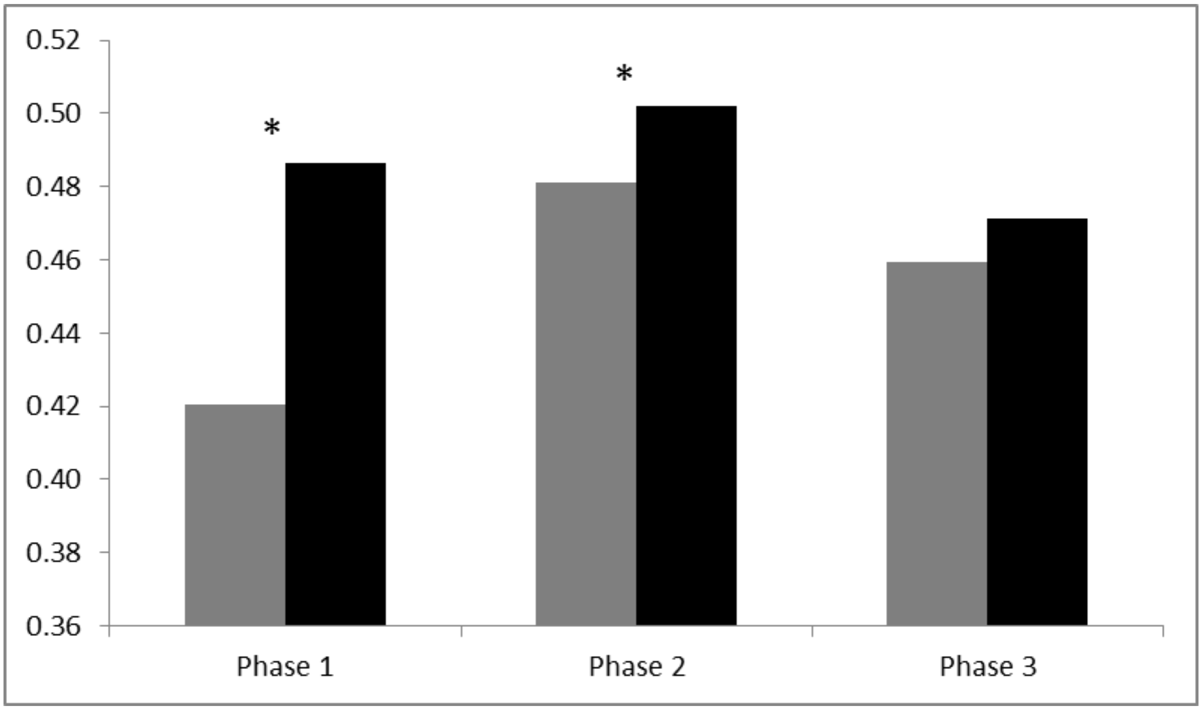

Figure 5.3 Total proportion of observed time that *P. diadema* mothers (grey) and *I. indri* mothers (black) were feeding during each of the three developmental phases. An asterisk above a phase denotes a significant difference between the two species in that phase.

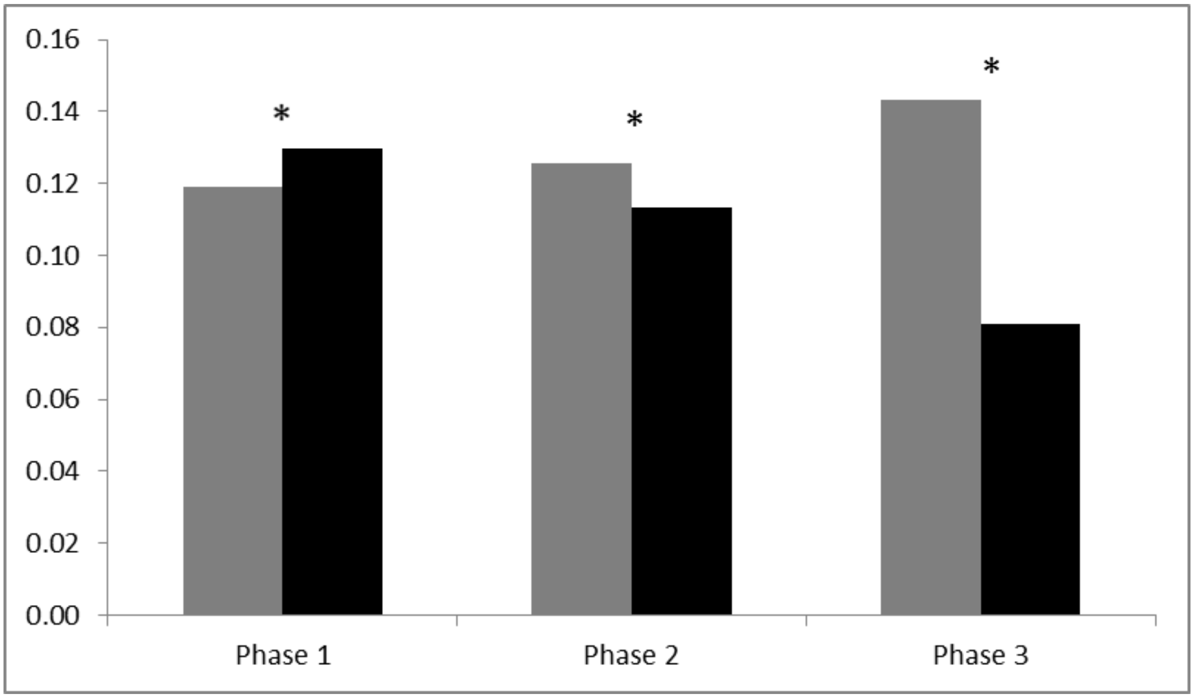

Figure 5.4 Total proportion of observed time that *P. diadema* mothers (grey) and *I. indri* mothers (black) rested during each of the three developmental phases. An asterisk above a phase denotes a significant difference between the two species in that phase.

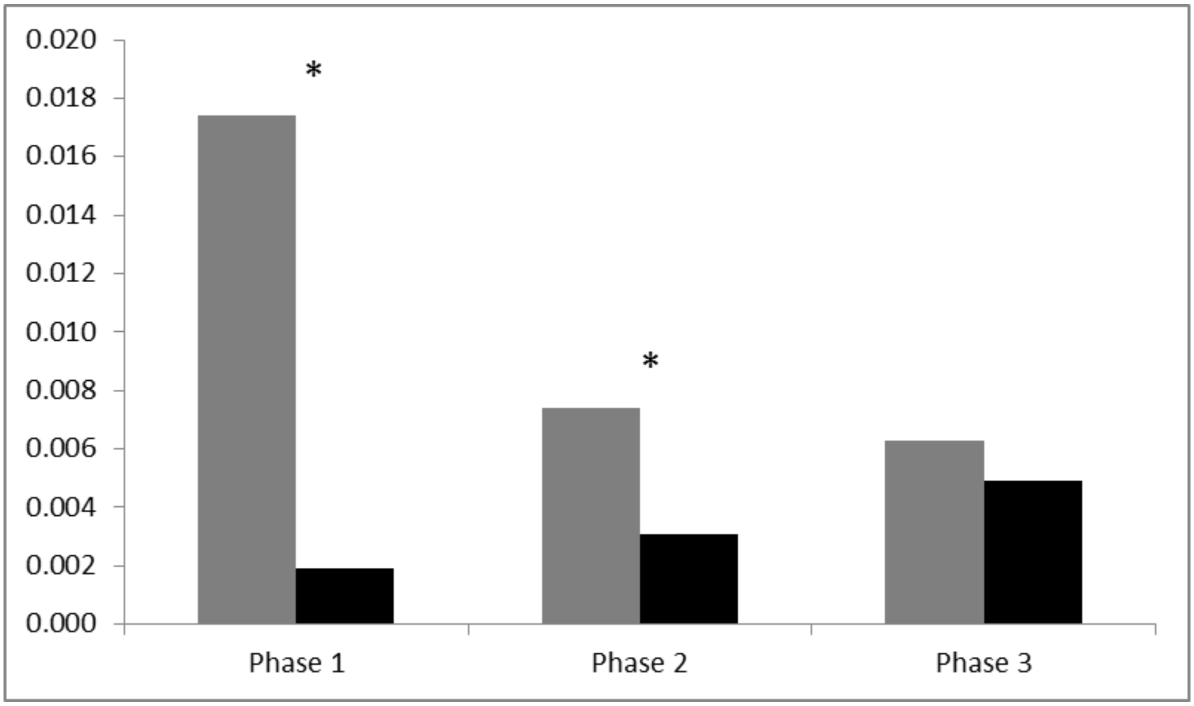

Figure 5.5 Total proportion of observed time that *P. diadema* mothers (grey) and *I. indri* mothers (black) spent allogrooming during each of the three developmental phases. An asterisk above a phase denotes a significant difference between the two species in that phase.

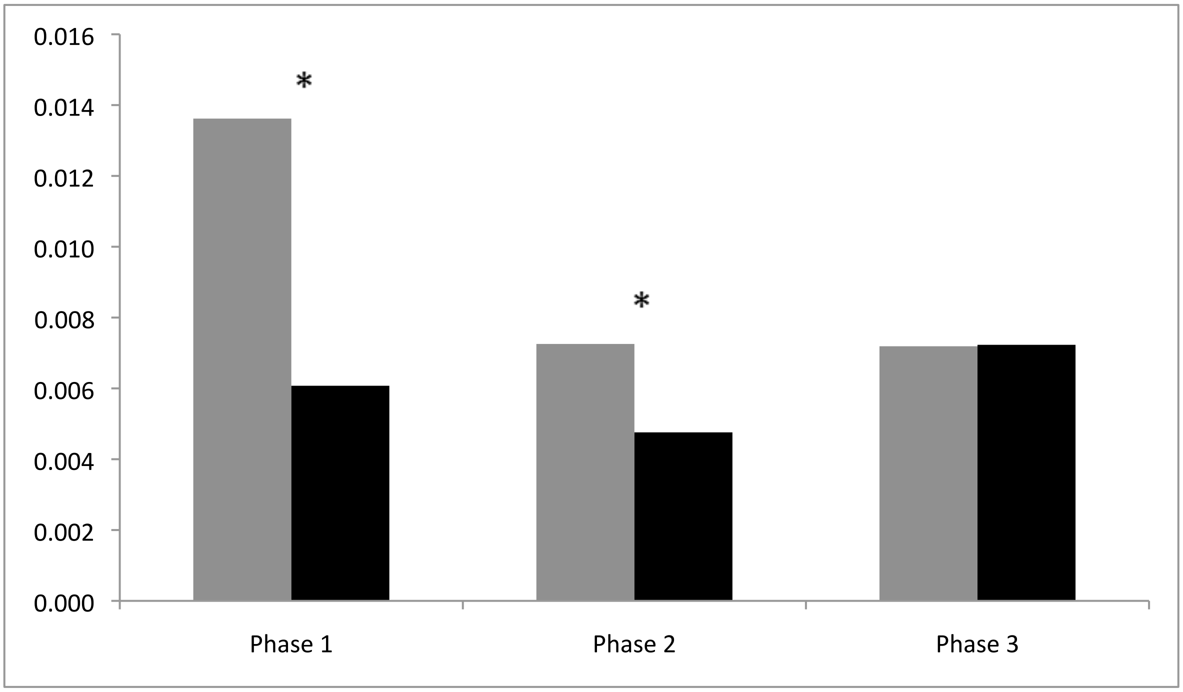

Figure 5.6 Total proportion of observed time that *P. diadema* mothers (grey) and *I. indri* mothers (black) groomed their infants during each of the three developmental phases. An asterisk above a phase denotes a significant difference between the two species in that phase.

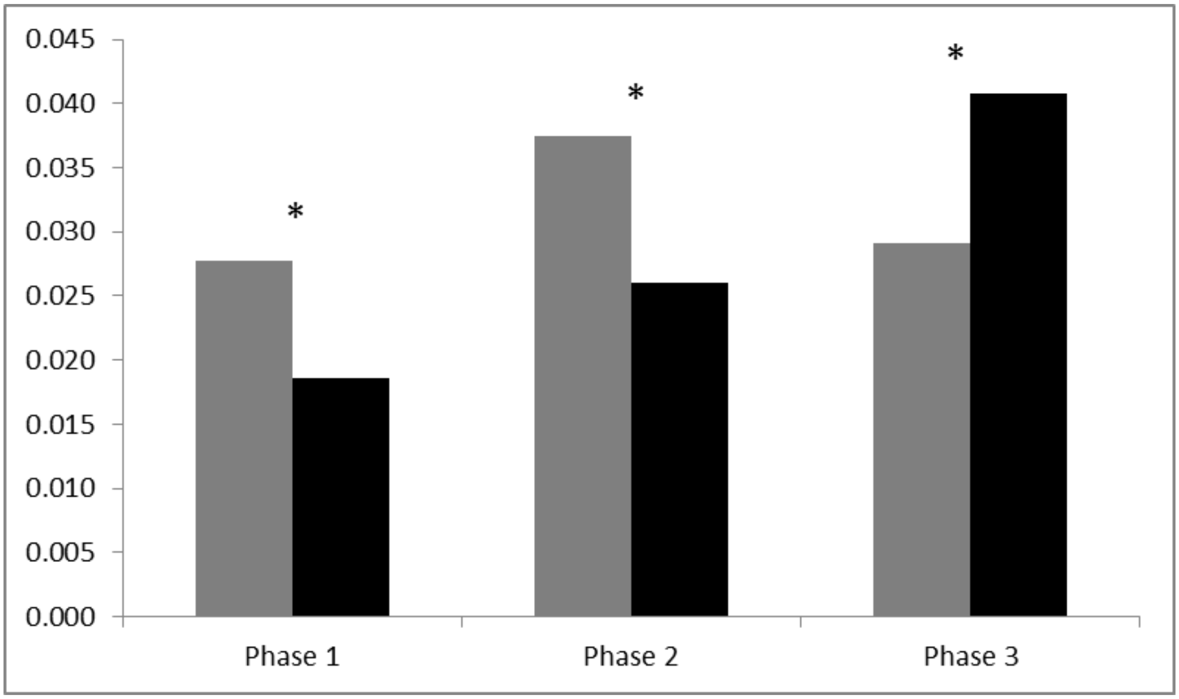

Figure 5.7 Total proportion of observed time that *P. diadema* mothers (grey) and *I. indri* mothers (black) self-groomed during each of the three developmental phases. An asterisk above a phase denotes a significant difference between the two species in that phase.

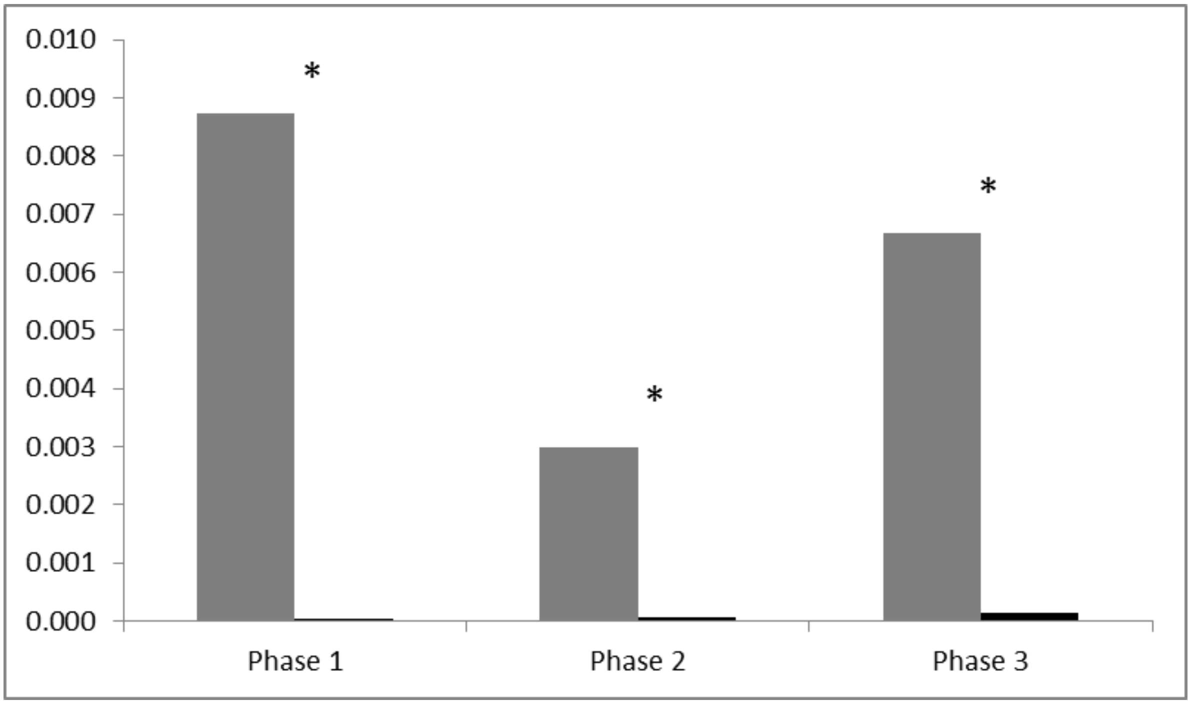

Figure 5.8 Total proportion of observed time that *P. diadema* mothers (grey) and *I. indri* mothers (black) scent marked during each of the three developmental phases. An asterisk above a phase denotes a significant difference between the two species in that phase.

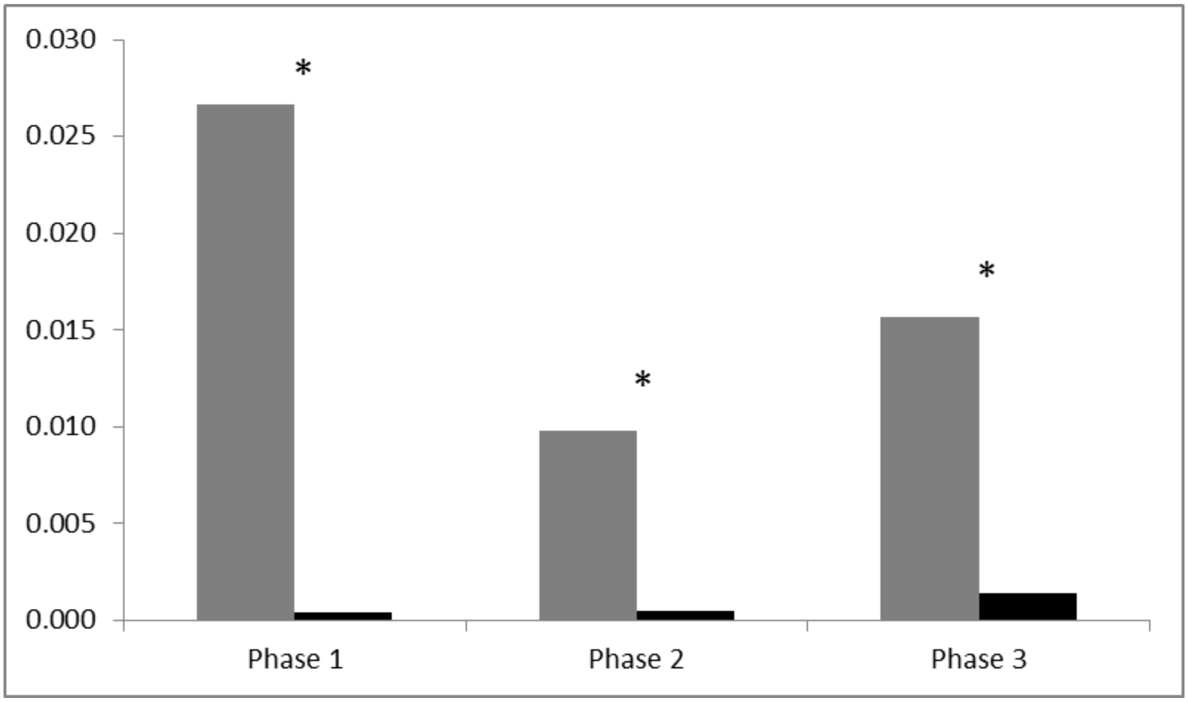

Figure 5.9 Total proportion of observed time that *P. diadema* mothers (grey) and *I. indri* mothers (black) travelled during each of the three developmental phases. An asterisk above a phase denotes a significant difference between the two species in that phase.

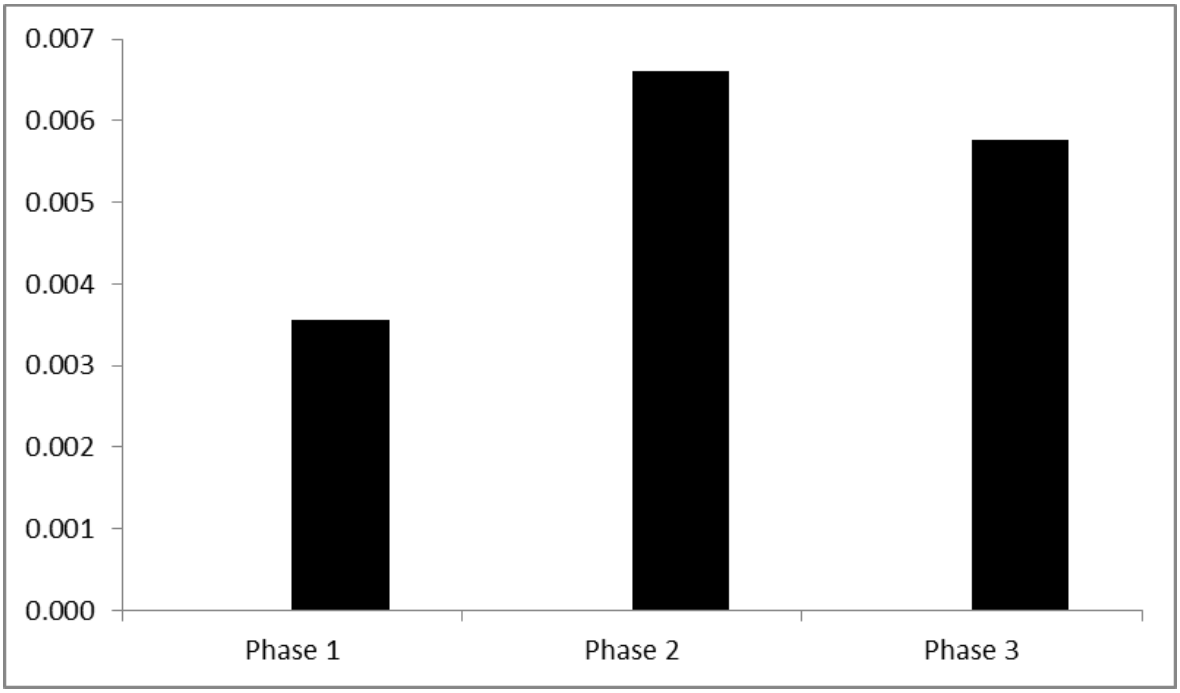

Figure 5.10 Total proportion of observed time that *P. diadema* mothers (grey) and *I. indri* mothers (black) long called during each of the three developmental phases. *P. diadema* never performed this species specific behaviour and therefore *I. indri* spent a greater proportion of time long calling in all three phases.

5.4 Discussion

My study is the first to specifically examine female reproductive traits and behavioural strategies in both indri (*Indri indri*) and diademed sifaka (*Propithecus diadema*). Therefore, I will begin with a comparison of my findings to those parameters currently reported in the published literature, and to those of similarly sized colobine monkeys and macaques. In my study, I found that both *P. diadema* and *I. indri* reproduced slightly more frequently than what has been previously reported. For example, in their review of reproductive strategies in lemurs, Tecot et al. (2013) reported that *P. diadema* and *I. indri* have inter-birth intervals of 25 and 30 months respectively. However, female *P. diadema* and *I. indri* in Maromizaha had mean inter-birth intervals of 21.8 and 28 months respectively. Similarly, the reported 153 day long gestation period for *I. indri* in Godfrey et al. (2004) is notably shorter than the 176 days precisely reported here. Although it is possible that another, later, copulation actually led to the conception of this infant, the very short period of estrus in lemurs (1–2 days) and the fact that these individuals were regularly monitored and no later copulation was observed, suggests that this longer gestation period is accurate. There is currently no published data for gestation length in *P. diadema*, and no mating was observed during the course of my study to correspond to known birth dates, however it is expected to be similar to that of *P. edwardsi* (179 days, Godfrey et al. 2004). If this is indeed the case, then both *I. indri* and *P. diadema* would have very similar gestation lengths. This is similar to the 171 days reported for southern pig-tailed macaques (*Macaca nemestrina*) and considerably shorter than the 205 days reported for Phayre's leaf monkeys (*Trachypithecus phayrei*) although both have similar adult weights to *I. indri* and *P. diadema* (Borries et al. 2011).

However, *M. nemestrina* have a much shorter IBI than both *I. indri* and *P. diadema*, at 13.3 months, while *T. phayrei* have an IBI of 22.3 months (Borries et al. 2011), which is quite similar to what I found for *P. diadema*.

My study is also the first to specifically examine the behaviours of *I. indri* and *P. diadema* females throughout the lactation period. In this chapter I directly compared the proportion of time that females spent in each of six specific behaviours throughout early, mid and late lactation. I also examined how season, group size, lactation phase, and species (whether the female was *I. indri* or *P. diadema*) influenced the proportion of time females spent engaged in each specific behaviour. In the following sections I discuss my results in the context of my specific hypotheses and predictions.

Seasonal effects on territorial behaviours

My results confirm strong seasonality in the breeding cycles for both *I. indri* and *P. diadema*. The birth season for *I. indri* and *P. diadema* at Maromizaha was May – June and June – July respectively, when it was relatively cold (Appendix I). *P. diadema* followed my prediction, and exhibited more territorial behaviours including scent marking and travelling in the cold season. Sifaka tend to have rich urinary scent signals and glandular secretions that carry information about the individual making the scent mark (Lewis 2005; Greene & Drea 2014). This energetically expensive behaviour is thought to serve multiple purposes, including defining territory boundaries, forming and reinforcing bonds between pairs, communicating relatedness and reproductive phase, and possibly as a way of conveying dominance to other group members (Lewis 2005; Greene & Drea 2014). In my study, I found that *P. diadema* scent marked and travelled for the greatest proportion of time in early lactation (Phase 1), when infant were less than 13 weeks old. It could be that reinforcing both pair and group bonds and forming new bonds with the newborn infant is particularly important during this early period. In contrast, *I. indri* rarely scent marked or travelled throughout the entire lactation period and this overall difference between the two species has also been documented across the yearly cycle at Mantadia (Powzyk 1997; Powzyk & Mowry 2006). These authors suggest that this difference is part of *I. indri*'s need to minimize energy expenditure, due to their greater reliance on the effective digestion of large amounts of leaves (Powzyk & Mowry 2006). Contrary to my prediction, *I. indri* spent the greatest proportion of time long calling in the hot season. This is likely due to a combination of factors. One reason why *I. indri* did not long call more in the cold season could be that there is not increased feeding competition between groups during that particular time of the year, and hence no reason to increase territorial behaviours. The other consideration is that *I. indri* song, like scent marking in sifaka, has a variety of different functions beyond defending territories. These long calls persist for 40 – 250 seconds and travel distances of 3 – 4 km, and are sex (Giacoma et al. 2010), age (Sorrentino et al. 2013), and context specific (Torti et al. 2013). Therefore, *I. indri* are thought to use these low cost group vocalizations for advertising the age and sex composition of their group to other groups in the forest (Pollock 1986; Thalmann et al. 1993; Giacoma et al. 2010; Torti et al. 2013) and it is possible that the hot season is when this particular form of communication is most pertinent.

Group size effects on female behaviours

Group size had a significant effect on certain female behaviours. As predicted, females in large groups (five or more individuals) spent less time feeding and more time observing their environment and other individuals than did those in small groups (less than five individuals). This could be the combined result of both increased feeding competition and increased dominance assertion required in large groups. In red colobus monkeys (*Procolobus rufomitratus*) all individuals in larger groups tended to spend less time feeding and more time travelling than did those in smaller groups (Gogarten et al. 2014). Borries et al. (2008) also suggested that nutritional stress affected lactating Phayre's leaf monkeys (*T. phayrei*) in larger groups and that this in turn led to the slower development of their infants, and longer periods of time between births.

In many lemur species, including *I. indri* and *P. diadema*, females exhibit dominance over males, and this dominance is shown in the feeding priority given to the dominant, usually reproductive, female leader of each group (Pollock 1979; Jolly 1984; Erhart & Overdorff 2008). With the exception of one mother (Zoma), who gave birth late, in a group with an older infant, all *P. diadema* and *I. indri* mothers in my study were dominant in their respective groups and had feeding priority. Frequently, while a group was feeding, the dominant female would displace other individuals from their feeding spots. Often, once obtaining the new feeding position, dominant females would not feed but would continue to be vigilant of the other individuals. Maintaining this dominance in a large group thus likely requires more vigilance of other group members and this could explain the higher levels of observing required by lactating females in large groups. Despite their dominance and feeding priority, the females in larger groups tended to feed for a smaller proportion of their time, suggesting an added cost to these lactating females.

Group size effects and allocare

I did not find evidence for allocare in the form of nursing, carrying or guarding of infants by non-mothers in either *P. diadema* or *I. indri*. I only saw non-mothers carry infants on two occasions and on both of these occasions, the infant was older, and the mother had left the infant to travel on its own when the infant jumped on the back of a non-mother and assumed dorsal riding position. In both of these cases, the non-mother carrier appeared surprised and confused by the infant on its back and effectively removed it within seconds. Both of these instances were observed in *P. diadema*. Although I did not observe actual infant-carrying by non-mothers, there have been some observations of *P. diadema* males carrying infants (M. Irwin, personal communication/unpublished data) and it is possible that this behaviour occurs in very specific situations. Although I did not see allocare as per defined by Tecot et al. (2013), I did frequently observe infants being groomed by non-mothers. Infant-grooming by non-mothers is observed frequently, beginning at an early age in *L. catta* (Gould 1990; Gould 1992). This behaviour, in conjunction with other forms of allocare exhibited in this species, is expected to provide mothers with more time to rest and to feed, thus enabling her to reduce maternal investment and increase her energy intake throughout lactation (Gould 1992). I suggest that in *I. indri* and *P. diadema* females are afforded more opportunities for allocare in the form of infant-grooming and monitoring, as opposed to other traditional forms of allocare. As predicted, mothers in large groups spent less time grooming their infants and more time grooming themselves, than did those in small groups. Therefore, if infant grooming by non-mothers is considered, my results provided support for my hypothesis that females in larger groups would have more opportunities for allocare.

Female behaviours during the mid-lactation phase

According to the relative proportions of time females nurse and carry their infants (Table 5.1), I predicted that mid-lactation (Phase 2) would be the most energetically costly of the three phases for both *P. diadema* and *I. indri* and that this would result in females feeding for a greater proportion of time during the mid-lactation period, compared to early and late lactation. In support of my hypothesis, both *P. diadema* and *I. indri* fed for the greatest proportion of time during mid-lactation. This is similar to what has been reported for howler monkeys. For example, female black howler monkeys (*Alouatta pigra*) spent more time feeding in the early and mid-lactation periods, when their infants were between one and ten months old, than during the late lactation period, when their infants were 10 – 14 months old (Dias et al. 2011). In comparison, female Bornean orangutans (*Pongo pygmaeus wurmbii*), continue to nurse their infants until they are 6.5 years and carry them constantly for the first three years (Jaeggi et al. 2010; van Noordwijk et al. 2013). Female orangutans increase their feeding time during the early lactation period when infants are less than six months, but then the time they spend feeding remains relatively constant and the subsequent variations in feeding time are not correlated with offspring age (van Noordwijk et al. 2013).

Hemingway (1999) did not find evidence that Milne-Edwards sifaka (*Propithecus edwardsi*) modified their feeding time during lactation when she examined the behaviours of both males and females across a complete year. I only observed lactating females, and so it is possible that the spike in feeding behaviours that I observed in *I. indri* and *P. diadema* females is mirrored in the males and therefore more likely to be a result of increased food availability during this time period. Both Pollock (1977) and

Powzyk (1997) found that female *I. indri* generally spent more time feeding on leaves than did males suggesting that there are indeed sex based differences in this species. A comparative sample from non-reproductive females and males could strengthen my findings.

In summary, both female *I. indri* and *P. diadema* exhibited the same characteristic species-specific behaviours throughout the lactation period as was documented by Powzyk (1997). *I. indri* tend to exhibit less energetically expensive behaviours, such as scent marking and travelling and instead rely on their long call vocalizations to communicate information pertaining to territory boundaries and group composition. Season, group size and lactation phase also influenced the behavioural budgets of lactating females and females of both species spent the greatest proportion of time feeding during mid-lactation (Phase 2), suggestion that these two species are in part 'income breeders', relying on energy and nutrients from food intake during lactation to sustain themselves and their infant, instead of 'capital breeders' who rely on energy and nutrients stored in the body stores of the female to sustain themselves and their infant throughout lactation (Gould et al. 2003; Houston et al. 2006; Lewis & Kappeler 2005; Gould et al. 2011). However, successful reproduction in other sifaka species has been found to depend in part on female body size and condition in the birth season, which suggests that they are 'capital breeders' in some aspects as well (Richard et al. 2002; Lewis & Kappeler 2005).

Overall, *P. diadema* and *I. indri* appear to have the longest gestation lengths and possibly the longest lactation periods of all of the lemurs where this data is available. These findings, in combination with the long inter-birth intervals that *I. indri* exhibit relatively to other lemurs and to similarly sized macaques and leaf-monkeys (Borries et al. 2011), suggests that these lemurs possibly have the slowest life-history patterns amongst similarly sized the primates.

5.5 References

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6 - CONCLUSION

6.1 Summary

As the global human population continues to grow exponentially and the suitable habitat remaining for wild species is rapidly reduced, an increasing number of species are threatened with extinction (Fahrig 2003; McKee et al. 2004; Woog et al. 2006; McKee et al. 2013). The relative vulnerability of each group of wild animals is both species and population specific and potentially influenced by several factors. Habitat type, diet and feeding ecology, size of required home range, and life-history traits including the age at first reproduction, the speed of infant development, infant survival rates and the number of offspring produced over the course of an individual's lifetime, may all affect extinction risk (Cardillo et al. 2006; Sax et al. 2013; Tomiya 2013). For instance, large bodied mammals with slow life-histories, such as Hector's dolphins (*Cephalorhynchus hectori*), Amur tigers (*Panthera tigris*) and black rhinoceros (*Diceros bicornis*) produce few offspring over their lifetime and this characteristic, coupled with anthropogenic sources of mortality has led to rapid population declines in these particular species (Jones 2011; IUCN 2014).

Compared with other similarly sized mammals, primates have especially slow life-history strategies (Harvey & Clutton-Brock 1985; Bielby et al. 2007). These slow life-histories combined with the rapid increase in human population density and growth in areas where non-human primates exist has heightened anthropogenic threats including habitat loss and direct hunting (McKee et al. 2004; McKee et al. 2013). Consequently, many primates inhabiting global 'hotspots' of biodiversity including Africa (ex. Chapman et al. 2012), Asia (ex. Srivastava et al. 2001) and Madagascar (Schwitzer et al. 2014) are now threatened with extinction.

Lemurs, the most imperilled group of mammals on the planet, are endemic to the island nation of Madagascar where 90% of 103 taxa are currently classified as threatened with extinction (IUCN 2013; Schwitzer et al. 2013). Large bodied species tend to be more vulnerable to anthropogenic impacts such as hunting and habitat loss and in the past 2,000 – 2,500 years that humans have inhabited Madagascar, at least 17 species of large-bodied, or "giant" lemurs have gone extinct (Godfrey & Jungers 2003; Muldoon 2010). These include *Archeoindris*, and other large bodied lemurs that ranged in size from 9 – 210 kg (Godfrey & Jungers 2003).

Weighing approximately 6.5 kg, *Indri indri* and *Propithecus diadema* are the two largest lemurs remaining alive today (Glander & Powzyk 1995; Britt et al. 2002) and yet prior to this study, we knew very little about how they grew and reproduced. Both face an extremely high risk of extinction in the near future (IUCN 2014) due to the illegal hunting of these animals for bushmeat (Jenkins et al. 2011) and the very rapid loss of their rainforest habitat from mining, slash and burn agriculture, illegal logging of rosewood and ebony, and illegal rum production (Irwin & Ravelomantsoa 2004; Irwin et al. 2010; Junge et al. 2011; Schwitzer et al. 2013). Neither species currently exists in captivity, and because of difficulties inherent in locating and observing these species within their very dense, steep and mountainous rainforest habitat (Irwin 2006b; Gordon et al. 2013) no prior study has focused on infants or lactating females in either species. Furthermore, within primatology there has previously been no standardized way of quantifying infant development (Harvey & Clutton-Brock 1985; Lee & Kappeler 2003) and thus no way to substantially evaluate and compare this critical life-history parameter between species or studies.

Understanding different patterns of infant development and how lactating females cope with the energetic demands of infant-care is important to our comprehension of how these particular life-history traits evolved under different sets of conditions. Furthermore, these studies are beneficial to the development of practical conservation programs for particular species. For example, these types of findings may be used to justify the creation of protected areas and the types of vegetation planted as part of reforestation projects. In addition, identifying the requirements for animals to survive in the wild, is highly beneficial to the development of species-specific breeding programs.

The results of this dissertation demonstrate an effective method for analyzing the gradual process of feeding ontogeny and for subsequently identifying three distinct phases, based on the relative energetic investment of infants and mothers over the course of the weaning period (Chapter 2). The pre-set definitions allow for clear and objective distinctions between the phases that can then be compared between species, populations, and studies. The three phases of weaning employed throughout this dissertation encompass and represent the total time that infants are receiving nourishment from their mothers relative to the time they are consuming solid foods. In contrast, most traditional definitions of weaning are based on one-off documentations of when a particular behaviour was first (ex. ingestion of solid foods) or last (ex. suckling) observed, and are therefore subjective to the schedule of the observer and likely highlight outlying events as opposed to overall patterns in the data. Given that weaning in primates is gradual and non-uniform and not in actuality demarcated by one-off events, the three phases provide set criteria that are significantly more biologically relevant to the overall process of feeding ontogeny. If this method is eventually used to quantify infant development in other species of primates, we will be able to further elucidate and compare the adaptive significance of particular schedules of infant development across a broader set of conditions and variables, and thus have a greater understanding of the infancy period in primates.

Indri indri and the nine species of sifaka, of which *Propithecus diadema* is the largest, all reproduce relatively slowly compared to haplorhine primates of similar size (Pochron et al. 2004). In particular, *I. indri* and *P. diadema* have the longest reported interbirth intervals amongst the lemurs (Tecot et al. 2013; Chapter 5), and this provides a protracted period for infants to be weaned and develop the diet and locomotory capacities of adults (Chapter 3). This adaptation accommodates the extended period of time required for infants to develop the complex digestive system needed to efficiently process the highly folivorous diet of adults (Langer 2003). It also likely reduces infant falls and subsequent mortality by allowing the infant more time reliant on the mother for locomotion before they become efficient at travelling by vertical clinging and leaping (Altmann 1980).

As predicted based on their larger body size, highly folivorous diet, and phylogeny, *P. diadema* infants achieve nutritional independence later than do the smaller and more frugivorous lemurs including *Eulemer* spp. and *L. catta* (Chapter 2). Also as predicted based on their high level of arboreality and their reliance on vertical clinging and leaping as their main form of locomotion, infants *P. diadema* are slower to achieve locomotory independence than are lemurs that do not use this kind of locomotion.

Although there were similarities to other rainforest sifaka, direct comparisons of the pace of infant development, and weaning specifically, in *P. diadema* to either *P. edwardsi* or to *P. candidus* were not possible at the time of writing due to the differences in how parameters of measurement were defined. A reorganization of other sifaka data to match the three phase criteria employed here, would be very useful to determining underlying trends and discrepancies between these closely related species and would provide a broader understanding of how infant development is influenced by particular sets of conditions.

I. indri only reproduce every 2–3 years, highlighting this monotypic species as unique in exhibiting the longest interbirth interval amongst the lemurs and similarly sized haplorhines (Borries et al. 2011; Tecot et al. 2013). This long period between births, relative to *P. diadema* and to other similarly sized species of primates (Borries et al. 2011) reflects their overall strategy as energy minimizers. A highly folivorous diet requires that a large proportion of their time be spent resting, and they infrequently expend energy travelling for long distances, scent-marking their territory or engaging in physical contests (Powzky 1997; Powzyk & Mowry 2006; Chapter 5). As with other species with long interbirth intervals, the protracted period of time between births, means that female *I. indri* are able to spread out the costs of maternal investment over a longer amount of time. This strategy allows *I. indri* more time to regain condition and to prepare for the next gestation compared with species that have shorter interbirth intervals (Langer 2008). As a consequence, infants are allocated a longer period of maternal care. This extra time may be necessary for infants to develop the behavioural and physiological adaptatations required for acquiring, processing and digesting the particularly folivorous diet of adults (Chapter 3). As predicted, based on their greater dedication to folivory, and their longer interbirth interval, *I. indri* were slower to pass most developmental markers than were *P. diadema*, however both species consistently ate solid foods for more time than they suckled at 20 weeks old, suggesting that both species are restricted by the seasonal availability of foods (Wright 1999).

One way that *I. indri* infants may facilitate their nutritional independence is by engaging in coprophagy. Infant *I. indri* regularly ingested their mother's fecal pellets from 10 – 15 weeks (Chapter 3). This behaviour may be a tactic used to establish a balanced microbial population for digesting their highly folivorous diet (Langer 2003; Yilderim et al. 2010). Infants may also be benefiting from this behaviour by accessing small amounts of protein-rich seeds that have already been softened by the passage through their mother's digestive system (Rothman et al. 2006; Fish et al. 2007; Sakamaki 2010). Although this specific behaviour has been observed in koalas, elephants and sloths (Guy 1977; Soave & Brand 1991; Osawa et al. 1993; Hirakumi 2001) the documentation of this behaviour in a primate suggests it could be a behaviour more widely adopted by other highly folivorous mammals. This information contributes to our collective understanding of how certain folivorous mammals have evolved to rely on a diet dominated by leaves.

Comparative studies are useful for illustrating similarities and differences between closely related species. Although *I. indri* and *P. diadema* have similar weights as adults, live in sympatry and are part of the same taxonomic family, there are several key differences in the ecology of these two species including; i) *P. diadema* eat a more diverse diet of fruits, seeds, flowers and leaves, while *I. indri* eat a diet dominated by leaves, ii) *I. indri* spend more time resting, have shorter daily path lengths and have shorter active periods than do *P. diadema*, and iii) *I. indri* defend their territories using long-call vocalizations while *P. diadema* actively patrol their territories and scent-mark significantly more frequently than do *I. indri* (Powzyk 1997; Powzyk & Mowry 2003; Powzyk & Mowry 2006). During infancy, infants develop the necessary skills to feed and to locomote on their own, the social skills to be assimilated into their social group and the social and motor abilities to protect themselves from predators, parasites and other dangers (Altmann 1990; Altmann & Samuels 1992; De Waal 2002; Pereira 2002). Many of these skills, including species-specific differences in behaviours patterns are developed during the infancy period (Chapter 4).

While their infants are developing the skills necessary for independence, lactating females must employ strategies to meet the changing requirements of their growing infants while not exceeding their own energetic capacity (Lee 1997). The time that primate mothers spend nursing and carrying her infant is most often correlated to the age of the infant and to the particular ecology of each species (Gould et al. 2011; van Noordwijk et al. 2013; Volampeno et al. 2011, Chapter 5). In addition, lactating females may modify the time they spend in other behaviours such as feeding, resting and social behaviours, to adjust to the changing needs of her infant and the corresponding demands on her body (e.g. black howler monkeys (*Alouatta pigra*) Dias et al. 2011). Group size may also influence the strategy adopted by individual mothers by affecting the level of feeding competition in the group (Silk 2007; Borries et al. 2008; Clutton-Brock & Janson 2012; Gogarten et al. 2014; Chapter 5).

Most lemur species exhibit low levels of infant survival due to predation (Irwin et al. 2009), infanticide events (Jolly et al. 2000; Richard et al. 2002; Morelli et al. 2009; Littlefield 2010) and environmental stress, especially in years with severe climatic events (ex. droughts or cyclones) (Gould et al. 1999; Richard et al. 2002; King et al. 2005; Lewis & Rakotondranaivo 2011). When combined with an overall long interbirth interval, certain species, including *P. diadema* and *I. indri* may be more severely impacted by anthropogenic sources of mortality. However, in contrast to what has been recorded for other species of lemurs, infant survivorship was relatively high at Maromizaha forest during the course of this study (2011–2014). This finding may illustrate a particular set of conditions at Maromizaha that is favourable to developing infants, relative to other study sites.

6.2 Future Directions

Amidst a global extinction crisis, much work remains to be done if we are to prevent the extinctions of the two largest-bodied lemurs remaining alive today. Efforts to eliminate hunting and prevent future habitat loss are essential, as are continuous long-term studies of wild populations. When examining different species and areas in Madagascar, Schwitzer et al. (2013) found that long-term researcher presence correlated with greater conservation success. I propose that Maromizaha forest merits a long-term research program that specifically focuses on infant development in this forest. Not only is this forest home to 13 species of lemur, 11 of which are currently threatened with extinction, Maromizaha also appears to have the set of conditions required for successful reproduction and infant survival for both *I. indri* and *P. diadema*. Ongoing monitoring might reveal if Maromizaha represents the ideal habitat for reproduction in both *I. indri* and *P. diadema* and is thus a critically important site for studying infant development, infant survival and maternal strategies and for the safeguarding of these particular species.

The information presented in this manuscript lends support to our growing understanding of infant development and maternal strategies, which is essential for the implementation of conservation schemes, including captive breeding programs. In a growing number of cases, these programs have successfully established insurance populations that could one-day provide reserves for the eventual restocking of wild populations (Conde et al. 2011; Lacy 2013; Schwitzer et al. 2013). Currently, within the three genera and 19 species in the lemur family Indriidae, there are only breeding programs for two species (*P. coquereli* and *P. coronatus*) and no other indriids exist in captivity (Schwitzer et al. 2013). From 1988 – 2008 there was a small colony of golden-crowned sifaka (*P. tattersalli*) at the Duke Lemur Center (DLC), however the last individual of that particular species, Titus, died in 2008. In 1993, a female diademed sifaka (*P. diadema*) and her infant were brought from Madagascar to the DLC. The female did not survive the journey, but her infant, Romeo, survived as the only diademed sifaka in captivity before he died in 2008, when he 19 years old. Of the world's 60 captive Coquerel's sifaka, all are owned by the Duke Lemur Center and roughly half of these are currently on loan to other facilities as part of the breeding program for this species (DLC 2014). The Parc Zoologique de Paris coordinates a breeding program for the crowned sifaka within European facilities and thus far, 42 infants have been born as part of this program, although 40% died a few days after they were born (Roullet 2013). As we now know a great deal more about the behavioural and feeding ecology of both *I.*

indri and *P. diadema*, including the work presented in this manuscript, it is possible that successful breeding programs may be established for these species in the near future (Schwitzer et al. 2013).

Through focused studies of infants and their mothers in the wild, we continue to develop a better understanding of the resources and conditions required by primates to reproduce successfully and for infants to survive to reproductive age (Custance et al. 2002; Britt & Iambana 2003; Britt et al. 2002). In addition to expanding our knowledge of infant development and maternal strategies, the results presented in this dissertation can contribute towards the development of breeding programs at regional lemur breeding facilities within Madagascar and eventually at international facilities (Schwitzer et al. 2013; King et al. 2013). Ultimately, these insurance populations could facilitate the eventual re-introduction and re-population of areas where these species could exist (fundamental niche; Sax et al. 2013), if hunting is eliminated and more suitable habitat is protected.

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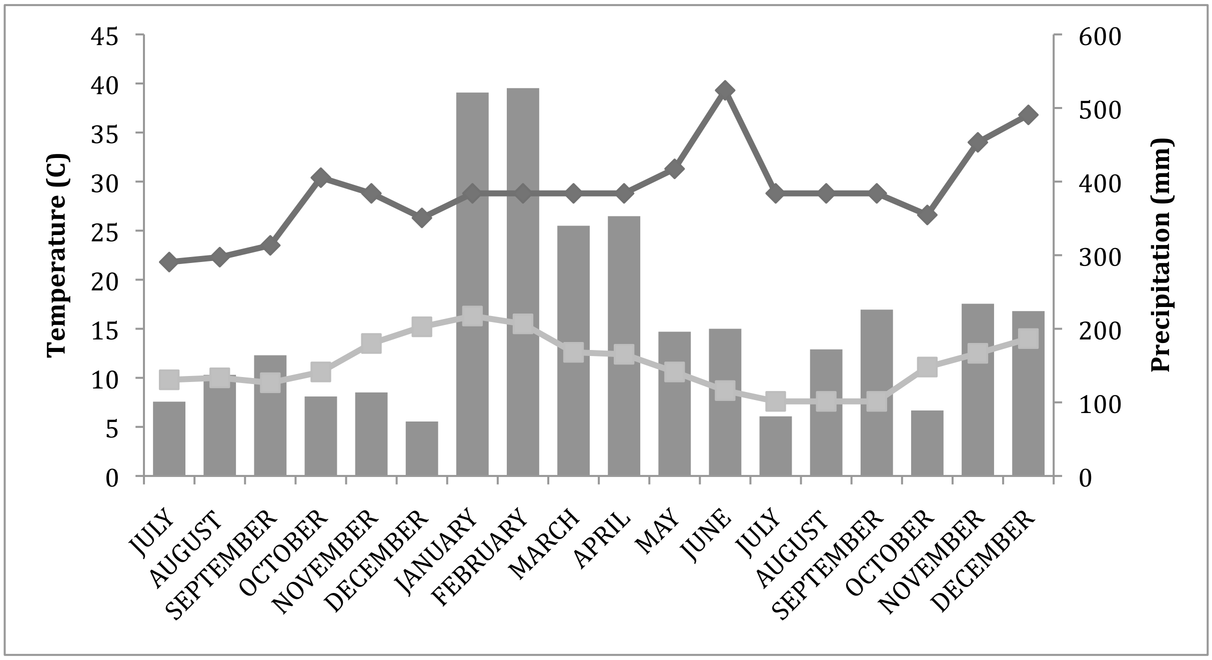
APPENDIX I

Climate at Maromizaha Forest between July 2011 and December 2012. Monthly maximum (diamonds) and minimum (squares) temperature as well as precipitation (bars) are displayed.



APPENDIX II

Species observed and birth months recorded for lemur species at Maromizaha during my study (June 2010-Dec 2012)

Species Reported in Maromizaha Forest	Diurnal (D) /Nocturnal (N)	Species Identified During This Study	Months Births Recorded
Propithecus diadema	D	Yes	June, July, October
Indri indri	D	Yes	May, June
Avahi laniger	N	Yes	September
Varecia variegata	D	Yes	October
Hapalemur griseus	D	Yes	November
Eulemur rubriventer	D	Yes	September
Eulemur fulvus	D	Yes	September
Lepilemur mustelinus	N	Yes	-
Cheirogaleus major	N	Yes	-
Microcebus rufus	N	Yes	-
Microcebus lehilahytsara	N	Yes	-
Allocebus trichotis	N	Yes	-
Daubentonia madagascariensis	N	No	-

APPENDIX III

Candidate models within two AIC points of the model with the lowest score for behaviours of infant *P. diadema* and *I. indri* in Maromizaha. Likelihood for a model given the data are approximated by $e^{(-0.5^{*}\,\Delta AICi)}$, and the weight of evidence provided by each model is calculated by normalising the likelihoods to 1.

Fixed Effects	Deviance	AIC	ΔAIC	Likelihood	Weight
Model: independent feeding					
Species + Phase + Season	3080.86	3096.86	0	1	0.72
Species + Phase + Season + Group Size	3080.74	3098.74	1.88	0.39	0.28
Model: resting					
Season	6742.04	6752.34	0	1	0.43
Phase + Season + Species	6736.60	6752.60	0.26	0.88	0.38
Phase + Season	6738.04	6754.04	1.7	0.43	0.19
Model: observing					
Species + Season	5190.75	5200.75	0	1	1
Model: playing					
Phase	6824.08	6840.08	0	1	0.39
Phase + Season	6823.35	6841.35	1.27	0.53	0.21
Phase + Species	6823.39	6841.39	1.31	0.52	0.20
Phase + Group Size	6823.48	6841.48	1.4	0.50	0.19
Model: allo-grooming					
Species + Phase	643.66	655.66	0	1	0.72
Species + Phase + Group Size	643.56	657.56	1.9	0.39	0.28
Model: self-grooming					
Phase	1708.04	1720.04	0	1	1

APPENDIX IV

Models with lowest AIC scores for behaviours of *P. diadema* and *I. indri* mothers in Maromizaha

Fixed Effects	Deviance	AIC
Model: feeding		
Species + Group Size + Phase * Season	5993.92	6015.92
Model: resting		
Phase	6773.72	6785.72
Model: observing		
Species + Season + Group Size	4611.07	4625.07
Model: allogrooming		
Species	1372.79	1382.79
Model: self -grooming		
Species + Group Size	3585.95	3597.95
Model: infant-grooming		
Species + Phase + Season + Group Size	1194.84	1212.84
Model: travelling		
Species	2035.28	2045.28
Model: scent marking		
Species + Phase + Season	900.63	914.63
Model: long calling		
Species + Season	533.01	543.01