Chapter 15
Reproductive Strategies and Infant Care in the Malagasy Primates

Stacey R. Tecot, Andrea L. Baden, Natalie Romine, and Jason M. Kamilar

Keywords Alloparental care • Malagasy primates • Lemurs • Infants • Investment • Meta-analysis

15.1 Introduction

The old African proverb, "It takes a village to raise a child," may extend well beyond the collective effort attributed to human child rearing strategies. In fact, allomaternal care is taxonomically widespread, particularly among mammalian taxa (e.g., rodents: Gubernick and Alberts 1987; Solomon and Getz 1997; chiroptera: O'Farrell and Studier 1973; canids: Moehlman and Hofer 1997; cetaceans: Gero et al. 2009; and primates: Hrdy 1976; Chism 2000). Allomaternal care includes infant care provided by the father (paternal care, Fernandez-Duque et al. 2009) or by conspecifics other than the parents (alloparental care, Wilson 1975). While well represented by a

---

S.R. Tecot (✉) • N. Romine
School of Anthropology, University of Arizona,
Emil W. Haury Building, P.O. Box 210030, Tucson, AZ 85721-0030, USA
e-mail: stecot@email.arizona.edu

A.L. Baden
Interdepartmental Program in Anthropological Sciences, Stony Brook University,
Stony Brook, NY 11794, USA

Department of Anthropology, Yale University, New Haven, CT 06511

J.M. Kamilar
Department of Anatomy, Midwestern University,
19555 N. 59th Avenue, Glendale, AZ 85308, USA

School of Human Evolution and Social Change, Arizona State University,
Phoenix, AZ 85287, USA

K.B.H. Clancy et al. (eds.), *Building Babies: Primate Development in Proximate and Ultimate Perspective*, Developments in Primatology: Progress and Prospects 37,
DOI 10.1007/978-1-4614-4060-4_15, © Springer Science+Business Media New York 2013

diversity of taxa, allomaternal care is not common among mammals (e.g., 9–10% of taxa display paternal care; Kleiman and Malcolm 1981; Huck and Fernandez-Duque 2012). However, allomaternal care has been recently noted to occur at relatively high frequencies in the Order Primates, particularly among many haplorhine (e.g., monkey and ape) species (Tardif 1997; Chism 2000; Ross and MacLarnon 2000; Hrdy 2009). While studies have examined the causes and consequences of allomaternal care among haplorhines, to our knowledge, there has yet to be a comprehensive analysis of allomaternal care across the entire primate order (e.g., including the primates of Madagascar, hereafter referred to as lemurs). This is in large part because studies of lemur allomaternal care have lagged behind those of their primate cousins. The most recent attempt at a synthesis of primate allomaternal care found that it was a haplorhine-biased phenomenon, finding no evidence of lemurs participating in allomaternal care-related behaviors (Ross 2003), and thus precluding any analysis of allomaternal care within that taxon. However, recent increases in attention to and sampling effort of lemur care behaviors have revealed that allomaternal care is more common in lemurs than originally thought (Mitchell 1969; Klopfer 1974; Pereira et al. 1987; Wright 1990; Patel 2007; Hrdy 2010; Rowe and Myers 2011; Tecot and Hrdy, unpublished data). Moreover, a number of studies in recent years have added to our understanding of this postnatal care strategy in lemurs, making it possible to include these species in broader taxonomic comparisons of primate reproductive strategies. In light of these recent discoveries, we aim to (1) describe the different types of allomaternal care observed in primates, including a discussion of how each type of care is expressed in monkeys and apes, and a summary of what is currently known for lemurs; (2) discuss the benefits of allomaternal caretaking and whether such behaviors benefit lemur mothers; and (3) outline important gaps in our knowledge of lemur allomaternal care, suggesting future avenues of research.

15.2 Primate Allomaternal Care

Investment in infants can take many forms (Ross 2003). In most mammalian species, mothers are their infants' primary care-providers; however, in some taxa, maternal care is supplemented by allomaternal care (Hrdy 1976; see Lewis and Pusey 1997 for review). Within the Order Primates, this phenomenon is taxonomically widespread (Hrdy 2009), though the form and frequency of allomaternal care among taxa are highly variable (Chism 2000; Ross and MacLarnon 2000). The variation in primate caregiving behaviors by mothers and/or allomaternal caregivers can be organized into nine categories that represent unique combinations of nesting, parking, carrying orally, carrying on fur, and allomaternal caring (Ross 2003). The variation in primate allomaternal care itself can be organized into three major categories: infant transport (Goldizen 1987a; b), babysitting (Stanford 1992), and energy transfer (i.e., food provisioning, Feistner and Price 1991; allomaternal nursing, Packer et al. 1992; Williams et al. 1994; Perry 1995) (see "Glossary" for definitions).

15.2.1 Infant Transport

Carrying infants long distances while foraging is rare among eutherian mammals, yet quite common among primates (Ross 2001). While some primates park their infants, the vast majority carries their infants (orally or with the infant clinging to the fur) or uses a combination of parking and carrying (Ross 2001). Infant transport is energetically expensive and may put the carrier at a disadvantage, particularly when foraging and avoiding predators (Schradin and Anzenberger 2001). For example, when carrying infants, maternal yellow baboons *(Papio cynocephalus)* are estimated to expend 5% more energy in the first month of carrying (Altmann and Samuels 1992), and leaping abilities in common marmosets *(Callithrix jacchus)* are compromised (Schradin and Anzenberger 2001). While individuals reduce their travel time when carrying infants, potentially balancing the additional energy required to carry (Tardif 1997), such adjustments may reduce necessary foraging time (Goldizen 1987a). Species whose infants ride dorsally or ventrally have smaller home ranges, and they begin reproduction at older ages, resulting in lower reproductive rates (Ross 2001). Thus, help with infant transport can be of great energetic benefit to mothers, particularly in energetically difficult habitats.

While carrying is ubiquitous across the Primate Order, taxa vary quite dramatically in the timing and intensity of nonmaternal infant transport. In siamangs (*Symphylangus syndactylus*), for example, females are exclusive care-providers during the infant's first year of life. It is only during the second year that adult males and older juveniles contribute to infant carrying (Chivers 1974; Lappan 2008), which can vary dramatically between individuals and group types (i.e., monogamous versus polyandrous) (Lappan 2008). In contrast, both titi monkeys (*Callicebus*) and owl monkeys (*Aotus*) are characterized by extensive and obligate paternal carrying (Fernandez-Duque et al. 2009). Soon after birth, males assume the role of primary care-provider, carrying infants for up to 90% of their total time carried (Dixson and Fleming 1981; Fragaszy et al. 1982; Wright 1984). Of course, infant transport can also extend beyond parental care, as is the case in the small new world monkeys, marmosets and tamarins (callitrichines) (Goldizen 1987a; b). In this taxon, all group members, including the mother, father, siblings, and other nonrelatives, share in infant transport (Bales et al. 2000; Tardif et al. 2002; Zahed et al. 2007). In fact, group members often compete for the opportunity to carry dependent infants (Fernandez-Duque et al. 2009).

Alternatively, as briefly stated above, some primates park and/or nest their offspring while foraging nearby (Ross 2001). In many cases, parking behaviors are biased toward litter-bearing taxa such as the cheirogaleids and *Varecia*; however, there are some non-litter bearing exceptions (e.g., lorises; Nekaris and Bearder 2011). While this strategy may help to reduce the energetic constraints on mothers by freeing females to travel and forage more efficiently away from infants, it also comes with added costs, including increased infant vulnerability to predators while mothers are away (see van Schaik and Kappeler 1997). One means by which parking/nesting mothers may reduce these costs is via allomaternal babysitting, whereby individuals other than the mother guard créched infants in their mothers' absence.

15.2.2 Babysitting and Infant Guarding

Babysitting has been described in a number of primate taxa, but is particularly prevalent in old world monkeys (i.e., cercopithecines and colobines; Stanford 1992; Chism 2000). The costs to babysitters have not been investigated extensively in primates. However, in the meerkat *(Suricata suricatta)*, a non-primate mammal with a cooperative breeding system, young are parked in burrows during the first month of life (Carlson et al. 2006) and parents rarely stay with them; babysitters are critical to this system, and lose weight in proportion to time spent babysitting (Clutton-Brock et al. 1998), indicating that the cost to babysitters can be great. Babysitting may also carry risks for mothers, as kidnaping and infant mistreatment (also known as "aunting to death"; Hrdy 1976; Hrdy 1977; Quiatt 1979; Altmann 1980; Silk 1980; Maestripieri 1994) have been observed in primates. But babysitting can be considered adaptive for a number of reasons (e.g., practice mothering by immature females: Lancaster 1971; Hrdy 1976; Quiatt 1979; increased likelihood of adoption: McKenna 1981; improved infant socialization: Hrdy 1976; McKenna 1981). The most commonly cited advantage conferred to mothers is that allomaternal care allows mothers to reduce their own energetic investment while simultaneously allowing the opportunity to maximize foraging efficiency (Vogel 1984; see also Poirier 1970; Lancaster 1971; Jolly 1972). Although initially examined from the perspective of the female helpers, these "aunting" behaviors are also common among males. Adult male baboons will commonly babysit "friends'" infants, and have been demonstrated to assist and protect infants during potential infanticidal attacks (Palombit et al. 1997; Smuts 1998).

15.2.3 Energy Transfer

The most extreme form of allomaternal care involves energy transfer, which includes allomaternal nursing (nonmaternal nursing of infant, Packer et al. 1992), a rare phenomenon among mammals (Packer et al. 1992), and food provisioning (Brown et al. 2004). For mothers, the energetic cost of infant transport is second only to lactation (Altmann and Samuels 1992), which far exceeds the costs of transport (Kirkwood and Underwood 1984; Tardif 1997) and can significantly increase female mortality rates (Packer et al. 1992). Thus, allomaternal nursing can be extremely costly to the caregiver if she nurses more than she would otherwise, and it can confer significant advantages to the mother whose energetic contribution may be lowered (König 2006). If allomaternal nursing is accompanied by babysitting, mothers may also benefit from increased time away from their infants, enabling them to spend more time foraging (facilitated by trading-off with other reproductive females, i.e., reciprocal allomaternal nursing). While reciprocal allomaternal nursing may not directly reduce the energetic burden to mothers or costs to helpers, reciprocal nursing may benefit all participating mothers by increasing foraging time relative to what they might otherwise experience in the absence of allomaternal contributions. Several hypotheses for why this behavior occurs have been discussed by Eberle and Kappeler (2006), and range from misdirected care due to an inability to discriminate offspring, to brood parasitism whereby non-offspring steal milk, to kin selection where allomaternal caregivers nurse only related infants. Food provisioning, the other form of energy transfer, occurs when infants approach individuals with food, so on some level the infant determines whether and from whom they receive provisions (Brown et al. 2004). In callitrichines this caregiving activity is performed by all group members (Feistner and McGrew 1989; Feistner and Price 1991), and may be a means by which dependence upon milk is reduced at an earlier stage while enabling infants to maintain growth rates, and allowing females to enter into estrus quickly (Garber and Leigh 1997). This behavior may also be necessary due to the complexity of extractive foraging (Brown et al. 2004).

Although relatively rare, some form of energy transfer has been observed in a handful of taxa in the form of either allomaternal nursing (e.g., squirrel monkeys: Williams et al. 1994; capuchins: Fragaszy et al. 2004; Baldovino and Di Bitetti 2008) or food provisioning (e.g., callitrichines: Huck et al. 2004; owl monkeys: Wright 1984; Wolovich et al. 2007; titi monkeys: Wright 1984; 1990). Energy transfer appears to be phylogenetically biased (Jaeggi and van Schaik 2011). For example, food provisioning is absent in Old World monkeys and present in one tarsier species (spectral tarsier, Gursky 2000), five ape species, and 21 New World species (including 13 callitrichines) (Brown et al. 2004). To our knowledge, only callitrichine infants rely entirely upon provisioning prior to independent feeding, and energy transfer is regularly observed only in this subfamily (see Feistner and Price 1991; Bales et al. 2000).

15.3 Benefits of Allomaternal Care

Allomaternal care is usually assumed to be adaptive, in that it is thought to benefit some or all of the individuals involved (Emlen 1991; Ligon and Stacey 1991; Mumme 1997; Tardif 1997; see Ross and MacLarnon 2000 Table 1 for a list of adaptive and nonadaptive causes of allomaternal care). However, as noted above, allomaternal care can also confer serious costs. Infants may be kidnapped or injured due to mishandling (Hrdy 1976; Quiatt 1979), they may receive reduced opportunities to nurse, and mothers may suffer reduced time foraging if vigilance is required when other individuals (such as inexperienced caretakers) handle infants (Chism 2000). Allomaternal caregivers are either nonbreeding individuals with delayed natal dispersal or reproductive suppression who sacrifice reproduction to care for offspring that are not theirs, or reproductive individuals who expend energy on offspring other than their own (Solomon and French 1997). Thus, with so many potential costs, the benefits of allomaternal care must be great in order for it to persist.

Traditionally, the evolution of allomaternal care has been addressed from the perspective of the helper (reviews in Hrdy 1976; Emlen 1991; Tardif 1997), with

Table 15.1 Lemur maternal and allomaternal care behavior

Care category	Care behavior[a]	Scientific name
1	Carry on fur	*Avahi laniger* *Eulemur fulvus* and sister taxa *Indri indri* *Prolemur simus* *Propithecus edwardsi*
2[b]	Carry on fur, park	*Hapalemur aureus*
3[b]	Carry on fur, carry orally, park, allomaternal care	*Hapalemur griseus*
4	Carry on fur, allomaternal care	*Eulemur collaris* *Eulemur macaco (flavifrons)* *Eulemur mongoz* *Eulemur rubriventer* *Lemur catta* *Propithecus candidus* *Propithecus coquereli* *Propithecus diadema* *Propithecus tattersalli* *Propithecus verreauxi*
5	Carry orally, park	*Lepilemur ruficaudatus*
6[b]	Carry orally, nest, allomaternal care	*Microcebus griseorufus* *Microcebus murinus*
7[b]	Carry orally, park, nest, allomaternal care	*Cheirogaleus medius* *Varecia rubra* *Varecia variegata*

[a] Characteristics of infant contact behaviors following Ross (2003), with numerically adjusted care categories. “Carry on fur” (infant clinging) and “carry orally” (carrying in the mouth) describe how individuals transport infants; “nest” indicates that infants are parked in nests or other protected shelters, and “park” indicates that infants are parked on tree branches or in vegetation; “allomaternal care” indicates that individuals other than the mother carry, babysit, or feed infants (only this category indicates the presence of care from individuals other than the mother). See “Glossary” for more information

[b] Previously undescribed categories

studies ranging from the proximate or physiological factors that affect alloparental care (e.g., Ziegler 2000; Ziegler et al. 2000; Numen and Insel 2003; Tecot 2007), to the functional roles of social and environmental factors and constraints (e.g., habitat saturation: Emlen 1984; queuing for breeding opportunities: Kokko and Johnstone 1999), as well as the possible adaptive explanations for the evolution and maintenance of nonparental care (e.g., learning to mother: Lancaster 1971; Hrdy 1977). It is much less common that allomaternal care is addressed from the perspective of the mother and/or infants (Mitani and Watts 1997; but see Bales et al. 2000; Ross and MacLarnon 1995; 2000; Ross 2003), though the benefits obtained are potentially great. For example, mothers receiving extensive help have been shown to benefit by shorter interbirth intervals (Fairbanks 1990), larger litters or faster infant growth (Leutenegger 1980; Goldizen 1987a; Wright 1990), and improved feeding time

(Stanford 1992), all of which may translate into higher lifetime reproductive success (Lemon and Barth 1992; Russell et al. 2002). Comparative analyses of allomaternal care in haplorhine primates controlling for phylogeny and body size found similar results to single-species investigations, in that allomaternal care is correlated with increased growth rates and decreased interbirth intervals overall (Mitani and Watts 1997; Ross and MacLarnon 1995; 2000). Moreover, infants can benefit from improved predator protection, thermoregulation, and improved competition later in life (König 1997).

15.4 Malagasy Primate Reproductive Strategies

Lemurs are glaringly absent from reviews of primate allomaternal care. While it is possible that this is in part due to lower frequencies of allomaternal care behavior in the taxon, it is certainly due to there being comparatively fewer studies. Several studies have focused on the unique reproductive strategies of Malagasy primates (e.g., Jolly 1984; Young et al. 1990; Pereira 1991; Richard and Dewar 1991; Whitten and Brockman 2001) and how these strategies reflect adaptations to an energetically poor and unpredictable environment (see below in “Malagasy Primates: An Unusual Case?”). Surprisingly, however, most such studies have focused primarily on these species’ strict breeding seasonality, particularly its timing and duration, the effects of photoperiod, and the associated physiological changes. More recently, some researchers have investigated pre-mating strategies such as changes in food intake and weight gain prior to conception (e.g., Lewis and Kappeler 2005). While these studies have made large strides in understanding lemur reproductive energetics, we know very little about postnatal strategies beyond milk quality (Buss et al. 1976; Tilden and Oftedal 1995; Hinde and Milligan 2011) and growth rates (e.g., Pereira 1993; Ravosa et al. 1993; Kappeler 1996; Godfrey et al. 2004), such as investment in infant care (but see Ross 2003), and thus how these strategies influence infant development, survivorship, and ultimately reproductive success.

To fill this gap in our understanding, we summarize the current state of knowledge of infant care in Malagasy primates, with emphasis on evidence of allomaternal care, its distribution, and expression. We first describe the types of infant care strategies used by lemur mothers and others (following Ross 2003) and then focus on one of those strategies: allomaternal care. Of those species in which allomaternal care was present, we describe the type of allomaternal care observed. Although some authors report the presence of allomaternal care in species on the basis of infant socialization through grooming, holding, or play by caregivers (e.g., Gould 1992; Bastian and Brockman 2007; Patel 2007), here we define allomaternal care as nursing, carrying, or babysitting/guarding infants by non-mothers, as these behaviors are exclusively performed by mothers in the majority of taxa, and thus it is notable when others perform such potentially costly behaviors (see Mitani and Watts 1997). Because few studies have quantified allomaternal care in lemurs, we were unable to use Ross’s (2003) definition of allomaternal care (when an individual other than the mother carries or protects the infant for more than 5% of the time). Based on published accounts or personal communications with researchers, we categorized care behaviors as present or absent (using similar methods to Mitani and Watts 1997), and only included taxa for which allomaternal care has been explicitly stated as being present or absent (with one exception, noted below). We used data on wild populations whenever possible, and supplemented these data with information from captive populations as indicated.

15.5 Infant Care in Malagasy Primates

Our review of the literature yielded data for 23 lemurs including taxa from four of the five lemur families (excluding Daubentoniidae). While our results include an additional eight taxa relative to those in Ross (2003), we could not confirm allomaternal care designations for two taxa included in her review (*Mirza, Cheirogaleus major*) in which allomaternal care was reportedly absent, a result that could be due to the fact that we did not consider allomaternal care absent unless it was explicitly noted as being absent in the literature or in personal communications (with the exception of one species, *Indri*, in which reports on maternal care were used to determine the absence of allomaternal care). We found that lemurs adopt seven combinations of infant caregiving behaviors, four of which include allomaternal care (Table 15.1). Three of these seven strategies were previously described by Ross (2003); four are described here for the first time (Table 15.1). Six additional strategies described by Ross (2003) were not present in lemurs, though one of those strategies was not assigned to any primate taxa in her review ("carry orally-carry on fur"), thus leaving five strategies present in haplorhine primates for which we found no evidence in lemurs. This result is in part due to new information included in our review. For example, four of the five strategies that we found to be absent in lemurs were reported by Ross (2003) to only occur in lemurs and other strepsirrhines. In her review, *Hapalemur griseus* was described as using a strategy of "carrying orally-carrying clinging to the fur-nesting-parking," whereas we identified *H. griseus* as having a strategy of "carrying orally-carrying clinging to the fur-parking-allomaternal care." One strategy reported to occur in the pygmy marmoset (*Cebuella pygmaea)* and humans ("carrying on fur-parking-allomaternal care") was not found in any lemur species.

Our findings are *contra* Ross (2003), in which allomaternal care was described as being absent in all lemur species, and in which allomaternal care was only present in primates who carried their infants clinging to the fur. Based on our results, allomaternal care was present in 16 of 23 species for which we could find explicit reports of either its presence or absence, and behaviors fell within each of the three major allomaternal care categories (Table 15.2).

Table 15.2 Allomaternal care behaviors and evidence of mishandling and abuse by caregivers observed in each species in the analysis

Scientific name	Allomaternal care	Infant transport	Babysit	Nurse	Details	Frequency of allomaternal care behaviors	Care-associated mishandling observed (or possible)?[a]	References
Avahi laniger	–	–	–	–	Only maternal care observed	Absent	No data	Ganzhorn et al. (1985)
Cheirogaleus medius	+	–	+	–	Paternal babysitting. Begins immediately after birth. Considered necessary for infant survival	Regular	No	Fietz (1999), (2003), P. Lahann, personal communication
Eulemur collaris	+	+	–	+	Carrying and nursing by an infant's grandmother	Unknown	No	Kesch (2009)
Eulemur fulvus and sister taxa	–	–	–	–	Only maternal care observed	Absent	No (kidnaping by female, infanticide by adult group male)	Barthold et al. (2009), Jolly et al. (2000), S. Johnson personal communication
Eulemur macaco (flavifrons)	+	+	–	–	Infant carrying by adult males, juvenile males, and siblings beginning at 5 weeks. Observed in one of two birth seasons. Allomaternal carrying 5% of the time. 67% by adult males	Regular	No (infanticide by extra-troop and troop males, troop females)	Andrews (1998), Volampeno et al. (2011)

(continued)

Table 15.2 (continued)

Scientific name	Allomaternal care	Infant transport	Babysit	Nurse	Details	Frequency of allomaternal care behaviors	Care-associated mishandling observed (or possible)?[a]	References
Eulemur mongoz	+	+	–	–	Infant carrying by father. Between weeks 2–5 on several occasions	Occasional-Regular	Unknown (infant wound, unknown source)	Curtis and Zaramody (1998), (1999)
Eulemur rubriventer	+	+	–	–	Infant carrying by father and siblings but not in all groups. Allomaternal carrying frequent with twins. Elevated cortisol levels in fathers and siblings follow mid-gestation maternal elevations	Occasional-Regular	No	Overdorff (1991), Overdorff and Tecot (2006), Tecot (2007), (2008), unpublished data
Hapalemur aureus	–	–	–	–	Only maternal care observed	Absent	No data	Tan (2000)
Hapalemur griseus	+	+	–	–	Infant carrying by fathers and siblings after 3 weeks in captivity. Fathers carried 20%, siblings 5%. Passive paternal food sharing and predation defense	Occasional	No	Wright (1990), Grassi (2001), Grassi, personal communication

Indri indri	–	–	–	–	Only maternal care observed	No data (designation based on reports of maternal care but no reports of allomaternal care)	No data	Pollock (1975)
Lemur catta	+	+	–	+	Infant carrying by other mothers and male and female juveniles. Nursing from females who lost own infants and mothers with infants. Reciprocal nursing between allomothers at 4-6 weeks. Adoption of dependent young after mother's death	Regular	Yes ("mothers often…kidnap infants" (Sussman 1977); infant wounding and killing by immigrant males, dominant females (during attack on mother), extra-troop individuals, and troop adult males)	Sussman (1977), Gould (1992), (2011), Jolly et al. (2000), A. Jolly, personal communication, T. O'Mara, personal communication, S.Meredith, personal communication, Mertl-Millhollen, personal communication
Lepilemur ruficaudatus	–	–	–	–	Only maternal care observed	Absent	No data	Hilgartner et al. (2008)
Microcebus griseorufus	+	–	?	+	Allomaternal nursing inferred	Unknown	No	Génin (2008)

(continued)

Table 15.2 (continued)

Scientific name	Allomaternal care	Infant transport	Babysit	Nurse	Details	Frequency of allomaternal care behaviors	Care-associated mishandling observed (or possible)?[a]	References
Microcebus murinus	+	+	+	+	Allomaternal nursing common among relatives. Adoption of related, dependent young after mother's death. Group nesting. Babysitting observed in Ampijoroa. Related females carry in captivity	Occasional-Regular	No	Martin (1972), Eberle and Kappeler (2006), E. Zimmerman, personal communication
Prolemur simus	–	–	–	–	Only maternal care observed	Absent	No data.	Tan (2000)
Propithecus candidus	+	–	–	+	Infant carrying by nursing allo-mother at 6 weeks and by adult male. Allomaternal nursing observed during months 4 and 5.	Occasional	Yes (2-year-old male took infant from male babysitter, returned without infant)	Patel (2007), personal communication
Propithecus coquereli	+	–	–	–	Infant carrying by juvenile males	Unknown	No (transfers between juveniles and infants rough: pulling, jerking, squirming, crying)	Bastian and Brockman (2007)

Propithecus diadema	–	–	–	–	Infant carrying by a nonmaternal dominant female	Rare	No data	Grieser (1992)
Propithecus edwardsi	–	–	–	–	Only maternal care observed	No data (based on ~24 years of consistent research)	No (infanticide by immigrant males)	Wright (1995), personal communication, Erhart and Overdorff (1998)
Propithecus tattersalli	+	+	–	–	Infant carrying by nonmaternal females. In one group occurred for “very large amounts of time.” However, “in most groups infant care was completely handled by the mother.”	Rare	No (one several-month-old infant left briefly with main male who “practically sat on the infant” (Meyers 1993). Infant emitted distress calls)	Meyers (1993)
Propithecus verreauxi	+	–	+	–	Infant carrying (2% of time)	Rare	No (kidnaping observed, H Rasamimanana, RJ Lewis, personal communication)	H. Rasamimanana, personal communication, R.J. Lewis, personal communication

(continued)

Table 15.2 (continued)

Scientific name	Allomaternal care	Infant transport	Babysit	Nurse	Details	Frequency of allomaternal care behaviors	Care-associated mishandling observed (or possible)?[a]	References
Varecia rubra	+	–	+	+	Infant carrying by non-maternal females ($n \geq 1$). Infant guarding by adult males and females. All males in study ($n=3$) guarded infants. Allomaternal nursing observed ($n=2$). Inferred adoption by an adult female. All reproductive males observed	Regular	No	Vasey (2007)
Varecia variegata	+	–	+	+	Allomaternal nursing inferred. Infant guarding by adults of both sexes and a male sibling. Group nesting ("kindergartens")	Regular	No	Morland (1990); White et al. (1992); Baden 2011; Baden et al. 2011; Baden et al. in revision; Balko, unpublished data

[a] Refers to any mention of mishandling within the context of allomaternal care, found in allomaternal care references. Other instances of mishandling outside of the allomaternal care context are noted parenthetically

15.5.1 Infant Transport

The ancestral primate pattern of infant care during travel is proposed to be non-riding (i.e., oral transport or parking of infants) (Kappeler 1998; Ross 2001). Transport by extant Malagasy primates takes two forms: the "ancestral" pattern, whereby infants are carried orally, and the "derived" pattern with the infant clinging to the fur. Ross (2001) proposed that transport of clinging infants evolved at least four times in the lemurs and their close relatives (e.g., galagos, lorises, and tarsiers). The transport of clinging infants occurs in the Lemuridae and Indriidae; infant parking and/or oral carrying occurs in *Phaner, Varecia*, *Daubentonia, Lepilemur,* and the Cheirogaleidae (e.g., *Microcebus* and *Cheirogaleus*; references within Ross 2001; Schülke 2005); and parking during the first 2–4 weeks, followed by carrying orally, and then carrying by clinging occurs in *Hapalemur* (Wright 1990; Tan 2000; C. Grassi, personal communication). In all cases, allomaternal carrying occurs.

Similar to *Callicebus* and *Aotus* (Dixson and Fleming 1981; Fragaszy et al. 1982; Wright 1984), frequent carrying by adult male and/or juvenile helpers has been reported in *Hapalemur griseus* in captivity (Wright 1990) and several *Eulemur* species in the wild or captivity (Curtis and Zaramody 1999; Tecot 2008; Duke Lemur Center Records), particularly when twins are present (Tecot, personal observation). *E. mongoz* adult males frequently carry pair-mates' infants before infants begin exploring independently, between their second and fifth weeks of life (Curtis and Zaramody 1999). *E. rubriventer* pair-mates carry infants any time after four days of life in captivity, and 20 days in the wild, and males and females do not differ in the amount of time spent caring for infants until day 55, when the infant either travels independently or is carried exclusively by the male (Overdorff 1991). While juvenile *E. rubriventer* carry infants as well (Tecot 2008), detailed data are lacking. Overdorff (1991) suggested that faster infant development in *E. rubriventer* compared with *E. rufifrons* (a species belonging to the brown lemur species complex) could be related to allomaternal care, as no allomaternal care has been observed in *E. rufifrons* (Overdorff 1996a).

While *Hapalemur* and *Eulemur* species with extensive allomaternal carrying tend to live in small, pair-bonded groups (e.g., Curtis and Zaramody 1999; Grassi 2001; Overdorff and Tecot 2006), males of non-pair-bonded species have also been reported to carry (and hold, groom, and play with) infants on occasion. *Propithecus coquereli* juvenile males (Bastian and Brockman 2007) and fathers (Grieser 1992) carried infants in captivity, and a juvenile male *Lemur catta* (Gould 1992), a male *P. candidus* (Patel 2007), and resident dominant male *P. verreauxi* (see Bastian and Brockman 2007) were observed briefly carrying infants in the wild. Non-maternal adult females have been observed carrying infants as well, although this behavior occurs only occasionally in the wild (*E. coronatus*: Kesch 2009; *Lemur catta*: Gould 1992; *P. diadema*: Grieser 1992; *P. tatersalli*: Meyers 1993; *P. candidus*: Patel 2007; *Varecia rubra*: Vasey 2007). In *L. catta,* infants may initiate such behavior, though it may be unwelcome by the designated carrier, as indicated by the carrier's acrobatics and nips seemingly meant to remove the infant from its back (T. O'Mara, personal communication). Such occasional infant transport by caregivers may not be important in terms of an evolved reproductive strategy to increase maternal reproductive success or inclusive fitness in these species, though it may be employed when environmental or social circumstances require. The benefits of allomaternal carrying have not been investigated in any of these species.

15.5.2 Babysitting and Infant Guarding

Babysitting and infant guarding are primarily found in nesting species that park their infants, particularly in *Varecia* (Morland 1990; Vasey 2007; Baden 2011; Baden et al. 2011; Baden et al. in revision) and some cheirogaleids (*Cheirogaleus medius*: Fietz 1999; *Microcebus murinus*: Eberle and Kappeler 2006; E. Zimmerman, personal communication), but perhaps also in some non-nesting *Propithecus* species (e.g., *P. coquereli*: Grieser 1992; Bastian and Brockman 2007) and *Lemur catta* (L. Gould, personal communication). As nesting species tend to have relatively large litters of rapidly growing, altricial (nonclinging) offspring (e.g., Table 15.3; Kappeler 1998; but see Ross 2001), mothers are required to leave their offspring at the nest, with or without babysitters, because they cannot transport the entire litter at once. Babysitting can therefore reduce the risk of infant mortality by such events as predation and accidental falls, and in the exceptional case of *Varecia,* perhaps infanticide (see van Schaik and Kappeler 1997). Babysitting may also reduce energetic stress on mothers spending time protecting vulnerable infants from predation or other mortality risks. For example, pair-living fat-tailed dwarf lemurs (*Cheirogaleus medius*) rely on fat stores for seasonal hibernation. Fietz and Dausmann (2003) found that reproductive females had lower fat stores and body condition than nonreproductive females, which is not unexpected after reproduction. However, there was also a trend for males who shared babysitting duties to have lower fat stores and body condition than nonreproductive males, suggesting that this care behavior is costly, but that it also benefits the mother by reducing the energetic burden that would otherwise be solely her responsibility (Fietz and Dausmann 2003). Another recent study found that such energetic benefits to mothers could result in higher infant survival. Maternal ruffed lemurs (*Varecia variegata)* suffered a significant reduction in feeding time following the birth of offspring (Baden 2011; Baden et al. 2011; Baden et al. in revision), a burden that was later mitigated by the onset of co-nesting and babysitting. Following the onset of communal nesting, an infant care strategy involving crèches of multiple litters parked together into a single nest, communal nesters fed significantly more and experienced higher infant survival than did singly nesting females (Baden 2011; Baden et al. 2011; Baden et al. in revision). In both *C. medius* and *Varecia* species, males, nonreproductive females, and other mothers took turns at babysitting their offspring (Morland 1990; Fietz 1999; Vasey 2007; Baden 2009; Baden 2011; Baden et al. 2011; Baden et al. in revision). In both taxa, females without allomaternal care were significantly less successful at raising their young.

Table 15.3 Lemur diet, interbirth interval (IBI), litter size, fetal growth rate, and postnatal growth rate

Scientific name	Common name	Diet[a]	IBI (mos)	Litter size	Fetal growth rate	Postnatal growth rate	Mean group size[f]	Mean home range size (ha)[f]	References
Avahi laniger	Eastern Woolly Lemur	Foliv	12	1	0.187	3.16	Adult pair and offspring	1–2	Tattersall (1982)[c,e], Godfrey et al. (2004)[d,e], Jones et al. (2009)[b,c], Catlett et al. (2010)[e], Mittermeier et al. (2010)[c,e]
Cheirogaleus medius	Fat-tailed dwarf lemur	Omni	18	2.5	0.594	3.75	Adult pair and offspring	4	Tattersall (1982)[c], Kappeler (1996)[d], Fietz (1999)[c], (2003)[b,c], Lindenfors (2002)[d], Jones et al. (2009)[b,c]
Eulemur collaris	Collared brown lemur	Frug	12	1.1	0.688	–	3–7	–	Rasmussen (1985)[c], Mittermeier et al. (2010)[b], Donati, personal communication[b], Duke Lemur Center Records[d]
E. fulvus and sister taxa	Brown lemur species complex	Frug	15	1.1	0.708	9.45	Range 6–12	Range 1–>20, up to 100 seasonally (Ranomafana Nat'l. Park)	Boskoff (1978)[c,e], Tattersall (1982)[c,e], Harvey and Clutton-Brock (1985)[e], Rasmussen (1985)[c,e], Duke Lemur Center Records in Wright (1990)[e], Kappeler (1996)[d], Overdorff et al. (1999)[b], Lindenfors (2002)[d], Kappeler and Pereira (2003)[e], Godfrey et al. (2004)[e], Brockman and van Schaik (2005)[e], Jones et al. (2009)[b,c]

(continued)

Table 15.3 (continued)

Scientific name	Common name	Diet[a]	IBI (mos)	Litter size	Fetal growth rate	Postnatal growth rate	Mean group size[f]	Mean home range size (ha)[f]	References
E. macaco (flavifrons)	Black lemur	Frug	12	1	0.588	6.76	10 (range 5–14)	3.5–7	Harrington (1978)[e], Tattersall (1982)[c,e], Harvey and Clutton-Brock (1985)[e], Harvey et al. (1987)[e], Kappeler (1996)[d], Godfrey et al. (2004)[e], Lindenfors (2002)[d], Kappeler and Pereira (2003)[e], Jones et al. (2009)[b,c], Catlett et al. (2010)[e], Mittermeier et al. (2010)[c,e], Volampeno et al. (2011)[b,e]
E. mongoz	Mongoose lemur	Frug	12	1	0.399	4.19	Range 3–8	2.8	Tattersall (1982)[c,e], Duke Lemur Center Records in Wright (1990)[e], Kappeler 1996[d], Curtis (1997)[b,e], Curtis and Zaramody (1999)[c,e], Lindenfors (2002)[d], Ross (2003)[e], Godfrey et al. (2004)[e], Jones et al. (2009)[c]
E. rubriventer	Red-bellied lemur	Frug	15	1.5	1.086	6.84	Adult pair and offspring	19	Kappeler (1996)[d], Tecot and Overdorff (2005)[c], Tecot (2010)[b,c]

Hapalemur aureus	Golden bamboo lemur	Foliv	12	1	–	–	Range 2–6	26–80	Tan (2000)[c]; (2006)[b]
H. griseus	Gentle bamboo lemur	Foliv	13	1.5	0.504	4.372	Range 1–9	0.6–26	Tattersall (1982)[c,e], Harvey and Clutton-Brock (1985)[e], Duke Lemur Center Records in Wright (1990)[e], Kappeler (1996)[d], Tan (2000)[c,e], Lindenfors (2002)[d], Kappeler and Pereira (2003)[e], Ross (2003)[e], Godfrey et al. (2004)[e], Jones et al. (2009)[b,c], Grassi, unpublished data[e]
Indri indri	Indri	Foliv	30	1	0.875	–	Adult pair and offspring	34–40	Pollock (1977)[b,c], Powzyk (1997)[c], Lindenfors (2002)[d]
Lemur catta	Ring-tailed lemur	Frug	15	1	0.616	8.235	11.5 and 16 (at two sites), range 3–27	6–35	Jolly (1966)[b], Tattersall (1982)[c,e], Sussman 1991[b,c], Kappeler (1996)[d], Lindenfors (2002)[d], Godfrey et al. (2004)[e], Jones et al. (2009)[b,c]
Lepilemur ruficaudatus	Red-tailed sportive lemur	Foliv	12	1	0.163	2.63	Solitary or male–female pairs	0.8	Martin (1972)[c], Tattersall (1982)[c,e], Godfrey et al. (2004)[d,e], Hilgartner et al. (2008)[b,c,e], Jones et al. (2009)[c], Mittermeier et al. (2010)[c,e]
Microcebus griseorufus	Gray-brown mouse lemur	Omni	14	2	–	–	–	–	Génin (2008)[b,c]

(continued)

Table 15.3 (continued)

Scientific name	Common name	Diet[a]	IBI (mos)	Litter size	Fetal growth rate	Postnatal growth rate	Mean group size[f]	Mean home range size (ha)[f]	References
M. murinus	Gray mouse lemur	Omni	12	2.5	0.195	1.92	Sleeps in groups of 1–15	0.22–3.2 (males); 0.24–1.8 (females)	Petter-Rousseaux (1964)[b], Tattersall (1982)[c], Harvey and Clutton-Brock (1985)[b], Kappeler (1996)[d], Lindenfors (2002)[d], Jones et al. (2009)[b,c], Mittermeier et al. (2010)[c]
Prolemur simus	Greater bamboo lemur	Foliv	12	1	–	–	Range 4–12	62	Tan (2000)[b,] (2006)
Propithecus candidus	Silky sifaka	Foliv	20	1	–	–	4.3, Range 3–7	–	Patel (2007)[b,c]
P. coquereli	Coquerel’s sifaka	Foliv	12	1	0.718	5.94	Range 3–10	4–8	Richard (1976)[c,e], Tattersall (1982)[c,e], Kappeler and Pereira (2003)[b,d,e], Godfrey et al. (2004)[d,e], Jones et al. (2009)[b,c,d]
P. diadema	Diademed sifaka	Foliv	25	1	0.846	5.05	4.83, Range 3–8	33–42	Tattersall (1982)[c,e], Powzyk (1997)[c,e], Godfrey et al. (2004)[d,e], Jones et al. (2009)[b,c,d]
P. edwardsi	Milne-Edwards’ sifaka	Foliv	19	1	0.922	6.305	5.3, Range 2–9	400	Wright (1995)[e], Pochron et al. (2004)[b], Arrigo-Nelson (2006)[c,e], Morelli et al. (2009)[b], King et al. (2011)[d,e]
P. tattersalli	Golden-crowned sifaka	Foliv		1	0.582	4.21	5, Range 3–10	9–12	Tattersall (1982)[e], Meyers and Wright (1993)[c,e], Kappeler and Pereira (2003)[d,e], Godfrey et al. (2004)[d,e], Jones et al. (2009)[d]

P. verreauxi	Verreaux's sifaka	Foliv	18	1	0.686	5.07	6, Range 2–14	3–10	Richard (1978)[b], Tattersall (1982)[c,e], Harvey and Clutton-Brock (1985)[e], Kappeler (1996)[d], Lindenfors (2002)[d], Richard et al. (2002)[b,c,e], Kappeler and Pereira (2003)[e], Godfrey et al. (2004)[e], Lewis and Kappeler (2005)[e], Jones et al. (2009)[b,c]
Varecia rubra	Red ruffed lemur	Frug	12	2.1	2.157	–	2–6, 18–31	25–58	Vasey (2007)[b,c], Zehr et al. (2011)[d]
V. variegata	Black-and-white ruffed lemur	Frug	12	2.2	2.14	50.09	Range 2–6 and 8–16	30–150	Tattersall (1982)[c,e], Harvey and Clutton-Brock (1985)[e], Harvey et al. (1987)[e], Morland (1990)[c,e], (1991)[c,e], White et al. (1992)[c,e], Kappeler (1996)[d], Balko (1998)[c,e], (2011)[e], Lindenfors (2002)[d], Kappeler and Pereira (2003)[e], Godfrey et al. (2004)[e], Jones et al. (2009)[b,c], Baden (2011)[c,e]

Values represent the midpoints when more than one source was available

[a] Foliv = folivore, Omni = omnivore, Frug = frugivore. Diet data from Muldoon and Goodman (2010)

[b] References for interbirth interval (IBI)

[c] References for litter size

[d] References for fetal growth rate or variables used to calculate fetal growth rate (litter mass and gestation length)

[e] References for postnatal growth rate or variables used to calculate postnatal growth rate (litter mass at weaning, litter mass at birth, age at weaning)

[f] See references in Gould et al. (2000) for mean group size and mean home range size

15.5.3 Allomaternal Nursing

Allomaternal nursing differs from the other categories of non-maternal infant care in that, as far as we know, it does not appear to be a strategy used consistently by any lemur species with the exception of one, or possibly two (see below). The rarity of this behavior in lemurs may be due in part to the relatively large number of species that are singular breeders, in which only one female breeds at a time (e.g., several *Eulemur* species, *Avahi*, *Cheirogaleus, Indri*, *Hapalemur aureus,* and occasionally *H. griseus* and *Propithecus* species) (Mittermeier et al. 2010), and thus opportunities for allomaternal nursing do not exist. In a clever study employing the use of infrared cameras in nests, litter-bearing (1–3 infants per birth) *Microcebus murinus* were observed nursing others' infants (9 of 12 females, 16.7% of their nursing time when other mothers were not present), though they exclusively carried their own offspring, and thus could likely discriminate kin (Eberle and Kappeler 2006). Wright (1990) noted that although small body size or high infant/maternal weight ratios are associated with extensive paternal care, this relationship is lacking in *Cheirogaleus* and *Microcebus*, the smallest Malagasy primate species. It might then be expected that future research with these genera will discover that allomaternal nursing occurs in more cheirogaleid species than presently known. Other plural breeding species (where several females breed per group) in which allomaternal nursing has been witnessed include *E. collaris* (Kesch 2009), *Lemur catta* (Klopfer 1974; Gould 1992; 2011; A. Jolly, T. O'Mara, S. Meredith, personal communication), *P. candidus* (Patel 2007), *Varecia rubra* (Vasey 2007), and *M. griseorufus* (inferred, Génin 2008) in the wild, and *V. variegata* in captivity (Pereira et al. 1987). Some of the best descriptions available are from recent work with *L. catta,* in which almost 55% (12 of 22) of all infants were nursed by allomothers (T. O'Mara, personal communication). The frequency of allomaternal nursing varied depending on the infant's age (peaking toward the end of weaning), and ranged from 10% to 90% of all nursing bouts (T. O'Mara, personal communication). Future work on the differential treatment of infants who are orphaned versus those who are not (S. Meredith, personal communication), and on the relatedness of helpers and mothers should help determine ultimate explanations for this behavior. Food sharing by caregivers, beyond passive tolerance of infants tasting foods, occurs in relatively few primate species (Brown et al. 2004), and has not been observed in any Malagasy primate.

15.6 Allomaternal Care and Life History Traits

To determine the benefits of allomaternal care in primates, we can look at the distribution of allomaternal care and life history traits such as growth rates and interbirth intervals. Cross-taxonomic analyses of life history traits and infant care in haplorhines (Mitani and Watts 1997; Ross and MacLarnon 2000), and haplorhines and strepsirhines (Ross 2003), found that increased levels of primate allomaternal care correlated with faster growth rate, younger age at weaning, and shorter interbirth interval. These studies suggest that allomaternal care benefits the mother by reducing the intensity and duration of her energetic contribution to infant rearing (e.g., carrying, babysitting, nursing) and increases her potential reproductive output. It is important to note that previous research treated all Malagasy primate species as non-allomaternal caregivers. Therefore, it is uncertain whether these benefits of allomaternal care also exist within Malagasy primates.

We recently tested the hypothesis that, like haplorhines, lemur mothers benefit from allomaternal care (Tecot et al., in revision). Based on earlier studies, we predicted that the presence and type of allomaternal care are associated with faster fetal and postnatal growth rates, as well as shorter interbirth intervals, when controlling for diet and body mass (Mitani and Watts 1997; Ross and MacLarnon 2000; Ross 2003). Using data collected from the literature and from personal communication with lemur researchers and the Duke Lemur Center (DLC) (Table 15.3), we scored five predictor variables as absent or present. The predictor variables were: (1) allomaternal care, (2) allomaternal nurse, (3) carry by caregiver, (4) nest, and (5) park. We conducted phylogenetic generalized least squares models (Pagel 1999). Controlling for body mass and dietary niche (as defined by Muldoon and Goodman 2010), we tested the relationship between our five predictor variables and three dependent variables: (1) postnatal growth rate, (2) fetal growth rate, and (3) interbirth interval (see Tecot et al., in revision).

Counter to our expectations, our hypothesis was not supported; contrary to what has been found in haplorhines (Mitani and Watts 1997; Ross and MacLarnon 2000), the presence of allomaternal care does not translate into more rapid infant growth, nor does it yield reduced interbirth intervals in lemurs (Tecot et al., in revision). This result may, in part, be due to Malagasy primates' adaptations to their unique ecology, as discussed in detail below. Unlike haplorhines, weaning in lemurs is timed with resource abundance (Wright 1999). Thus, increasing growth rates and decreasing the age at weaning may not be appropriate reproductive strategies, as weaning must coincide with sufficient resources for a mother recovering from lactation or an infant largely inexperienced in supporting itself nutritionally. Furthermore, faster growth rates and earlier weaning may not, in fact, increase reproductive rates at all, since lemurs tend to be highly seasonal breeders (Wright 1999; Tecot 2010). It is true however that interbirth intervals can range from 1 to 3 years (Table 15.3). Thus, one might expect mothers to benefit by reproducing in consecutive years, thereby shortening interbirth intervals, yet we did not find a relationship between allomaternal care and interbirth interval for lemurs overall (Tecot et al., in revision). Thus, the benefit to species that express allomaternal care behaviors remains to be determined.

Interestingly, while allomaternal care itself is unrelated to increased infant growth in lemurs, infant parking and nesting were associated with faster life histories. Parking and nesting were positively related to fetal and postnatal growth rates (*contra* Kappeler 1998), and nesting was further positively related to shorter interbirth intervals, when accounting for body mass and diet (Tecot et al. in revision). Ross (2003) found a similar relationship between nesting and postnatal growth rates, suggesting that parking and nesting may impact female reproductive energetics. Higher fetal growth rates have been argued to indicate higher maternal investment (Godfrey et al. 2004); thus our results indicate that parkers and nesters may actually invest more heavily (or efficiently) in offspring than mothers who carry their young. Since approximately half of the parking species included in our analysis also build nests, it was difficult to disentangle the individual effects that each of these behaviors has on infant growth. If, however, nesting can be used as a proxy for babysitting, as is the case in some taxa (e.g., *Varecia*: Morland 1990; Vasey 2007; Baden 2011; Baden et al. 2011; Baden et al. in revision), then this particular type of infant care may indeed reduce maternal energy expenditure in species with the highest maternal investment. These infants may also reach maturity faster. Although offspring of haplorhine species with allomaternal care and faster growth rates do not reach maturity sooner, likely due to the constraints of brain growth (Ross 2003), offspring of litter-bearing taxa may. Mothers of litters tend to have higher quality milk compensating for parking offspring for long periods without access to their mother's milk, and as a result infants tend to mature faster (wean and breed earlier) (Tilden and Oftedal 1995; 1997).

We currently lack data on babysitting in some nesters and parkers. Nevertheless, if nesting and parking are associated with babysitting or guarding, it remains to be determined whether allomaternal care, or just general relief from the energetic burden of transporting an infant, drives these relationships. There is some evidence that mothers who park and nest directly benefit from receiving help with their infants. In *Varecia variegata,* a taxon known for its exceptionally high prenatal and postnatal energetic investment (see references in Vasey 2007), energy intake post-parturition as measured by time spent feeding was higher in communal nesters compared with single nesters (Baden 2011; Baden et al. 2011; Baden et al. in revision). Furthermore, communally nested infants had higher survival rates (Baden 2011; Baden et al. 2011; Baden et al. in revision), indicating that infants directly benefit from allomaternal care, not just via inclusive fitness, as has been suggested for primates overall (Ross 2003), and not just from parking or nesting per se. Thus, nesting (and possibly babysitting) may be one strategy that saves the mother energy that she can then invest in future reproductive opportunities, and allows her to reproduce quickly with high prenatal and postnatal growth rates and relatively short interbirth intervals.

15.7 Comparisons with Haplorhines

We can observe gross phylogenetic patterns in the distribution of caregiving behaviors in lemurs: allomaternal nursing and parking or nesting occurs in fast-growing (Leigh and Terranova 1998), litter-bearing species (e.g., *Varecia* spp.*, Microcebus* spp.), and allomaternal carrying occurs in slow-growing (Leigh and Terranova 1998), frequently twinning or pairbonded species (e.g., *Eulemur* spp.). In her comparison of caregiving behaviors and life history traits, Ross (2003) found that the positive relationship between allomaternal care and litter weight in species where infants cling to fur was largely due to the high frequencies of allomaternal care and twinning in callitrichines. She noted that the presence of paternal care and the absence of twinning in Goeldi's monkeys support Dunbar's (1995) suggestion that twinning secondarily evolved after paternal care. The distribution of allomaternal care in form and frequency in lemur taxa support this hypothesis (as far as we can tell from the published literature and personal observations). *Eulemur* demonstrate the most habitual use of allomaternal carrying and perhaps allomaternal care, and frequently twin (though more data from more species are needed to confirm this assertion) (Tecot 2010). Fathers and siblings often carry offspring in several *Eulemur* species, though this behavior is not always employed in all groups (e.g., *E. macaco*: Volampeno et al. 2011; *E. rubriventer*: Overdorff 1991; Tecot, personal observation). *Varecia* may also fall within this framework, though infants are transported orally. *Varecia* bear litters and there is some indication that babysitters at the nest may be fathers (Baden 2009). However, litter-bearing species do appear to have very different strategies than twinning species, and *Varecia* in particular show a combination of caregiving behaviors (carry orally, park, nest, allomaternal care [babysitting]) not observed in any other primate species (Table 15.1). In particular, parking and nesting enable at least some independent movement on the mother's part, regardless of allomaternal care received. Nevertheless, in lemur species with relatively high variance in litter mass, a relationship between allomaternal care and litter mass may exist, and remains to be tested.

As predicted by inclusive fitness theory (Hamilton 1964; Trivers 1972), allomaternal care in vertebrates (excluding primates) is largely restricted to family groups, and where kin and nonkin are present, individuals preferentially help kin (Emlen 1997). Within primates, allomaternal care by males tends to be strongest in species where paternity is certain (Ross and MacLarnon 2000). Interactions between parents may stimulate male care of offspring (Storey et al. 2006). For example, changes in maternal hormones during gestation may be honest cues received by her pairmate that she is pregnant. Upon receiving this cue, male hormone levels (e.g., prolactin and cortisol) respond and may in effect prepare him for providing infant care (Ziegler et al. 2004). Within the genus *Eulemur*, the distribution of allomaternal care may be consistent with haplorhine trends. For instance, of all *Eulemur* species in this study, the brown lemur species complex (*E. fulvus* and sister taxa) live in the largest groups, consisting of multiple males and females (Richard 1987; Overdorff et al. 1999), and *E. mongoz* and *E. rubriventer* live in small pairbonded family groups (Curtis and Zaramody 1999; Overdorff and Tecot 2006). To date, allomaternal care has not been reported in the brown lemur species complex, whereas carrying by adult males (*E. mongoz, E. rubriventer)* and juveniles (*E. rubriventer*) is common in the pairbonded species (Curtis and Zaramody 1999; Overdorff 1996a; Overdorff and Tecot 2006; Tecot 2008). These patterns are also consistent with the hypothesis that paternal behaviors (but not necessarily allomaternal care) are more likely in smaller groups of a given species (Eaglen and Boskoff 1978; Bastian and Brockman 2007). Future work within *Eulemur* species measuring allomaternal care, group size, and paternity certainty would allow us to begin to test these hypotheses.

15.8 Malagasy Primates: An Unusual Case?

While allomaternal care is present in some form in each lemur taxon, its expression does not conform to the pattern evident in haplorhines, whereby allomaternal care is positively correlated with female reproductive output. We propose that this strategy may not equally benefit Malagasy primates because reproductive rates in this taxon appear to be less flexible. Further, the combination of rapid infant growth rates (Leigh and Terranova 1998), perhaps already at maximal, sustainable velocity, and concomitant shortened duration of infant dependence in lemurs compared with haplorhines, may reduce the need for allomaternal care at all. Alternatively, it is possible that we need to test a different set of predictions altogether in order to understand the distribution of allomaternal care in lemurs. Ross and MacLarnon (2000) tested several ecological hypotheses in haplorhines to investigate whether energetic stress might select for allomaternal care, none of which were supported. In contrast, Malagasy primates live in unique and challenging environments that are said to differ from those of other primate habitats (Wright et al. 2005; Dewar and Richard 2007) and are thought to have shaped them in ways that distinguish them from even their closest primate relatives. For example, the relationships between diet (folivory vs. frugivory), infant development, and maternal investment in Malagasy primates differ from haplorhines in that folivores (leaf eaters), rather than frugivores (fruit eaters), have higher maternal investment, develop more slowly, and reach reproductive maturity later (Godfrey et al. 2004). We might therefore expect to see relationships between allomaternal care and ecological factors, particularly those that impact energetic stress, such as the abundance and predictability of resources (Tecot in press).

Although many mammals time reproductive events with dynamic ecological processes such as temperature, rainfall, and food production (Negus and Berger 1972; Bronson and Heideman 1994; Brockman and van Schaik 2005), Madagascar's environmental challenges demand that the island's fauna adapt unusual strategies for coping with seasonal yet unpredictable environments (Tecot 2010). While other primate species may live in equally difficult habitats, lemurs as a whole exhibit a distinctive suite of traits that sets them apart from other primates (Wright 1999). For example, lemurs possess adaptations to seasonality such as strict seasonal breeding (Janson and Verdolin 2005) with short estrus periods cued by photoperiodicity (van Horn 1975; Rasmussen 1985; Pereira 1993), typically occurring once per year and resulting in high birth synchrony (Jolly 1967; Rasmussen 1985; Pereira 1991; Sauther 1998). Moreover, lemurs also exhibit adaptations to unpredictability that confer flexibility, as also observed in other primates. Recent evidence suggests that several species adopt a strategy whereby they time reproduction with the best environmental conditions in response to exogenous cues such as photoperiod, but there is some flexibility in the system. Some species may respond to endogenous cues such as fat stores (e.g., Lewis and Kappeler 2005), which enables them to make reproductive decisions based on internal and external states (Brockman and van Schaik 2005). Finally, Malagasy primates display adaptations to energy-poor environments. For instance, small group size allows individuals to exploit scarce, small resource patches (Ganzhorn et al. 1999), with little intra-group competition (Wright 1995; Overdorff 1996a; b), and for longer periods of time (Wright 1999). *Cheirogaleus* and *Microcebus* spp. in particular further reduce energy expenditure by entering torpor in the winter (see Geiser and Ruf 1995; Petter-Rousseaux 1980; Wright and Martin 1995; Schmid and Kappeler 1998; Sørg et al. 2003; Dausmann et al. 2004). While torpor can be considered an adaptation to seasonal environments, it is generally understood to be an adaptation to enable energy conservation in harsh environments (Schmid and Stephenson 2003). As a whole, these suites of traits observed in Malagasy primates, as well as others not discussed here, maximize energy intake and minimize energy expenditure (Wright 1999), preventing physiological stress and promoting reproduction in a harsh and unpredictable environment (Tilden and Oftedal 1995; Pereira et al. 1999; Tecot 2008; Tecot in press).

15.9 Avenues for Future Research

Ross (2003) points out that meta-analyses of allomaternal care across the order are difficult because of the paucity of high quality, detailed data from strepsirhine taxa, including, for example, quantifications of allomaternal care behaviors such as those employed by Ross and MacLarnon (2000). While broader taxonomic studies were able to categorize presence and absence relative to a threshold of percent allomaternal care (e.g., 5%, Ross and MacLarnon 2000), such methods precluded the inclusion of any lemur taxa as allomaternal caregivers. Differences between Ross's (2003) review and ours may be due to these differences in criteria for the presence of allomaternal care, leading to the exclusion of all accounts of allomaternal care in lemurs during her study. Differences between studies may also be due to the fact that such information is not often the subject of study, is only addressed in discussions, and is thus easily missed or left unquantified. Finally, our results may differ because of the availability of more recent data on lemur allomaternal care. While our method may overestimate the presence of allomaternal care in the species included in our analysis, we believe that the reality likely falls somewhere between Ross's (2003) study (no allomaternal care in lemurs) and ours. The absence of a relationship between growth rates and allomaternal care within lemur species in our study may be due to this inability to analyze percent allomaternal care. More conservative assessments of allomaternal care within these species might yield different results, and as a first step, we suggest that comparisons of relative time spent caring for infants by the mother and allomaternal caregivers be made. Until these data are available, we feel that it is premature to speculate as to the potential differences between haplorhine and lemur allomaternal care, if in fact they exist.

Lemur researchers do not often conduct field research with the goal of studying allomaternal care because allomaternal care is largely unexpected in these species (and non-haplorhine primates as a whole), and does not occur at high rates (to our knowledge). Moreover, our knowledge of life history traits in wild species is slim, as many species are rarely, if at all studied, and comparatively few long-term studies exist (see Wright et al. 2012). With more and more long-term studies initiated every year, we are hopeful that these data will soon be available, and current sample sizes will be boosted. We can then begin to ask questions such as whether allomaternal helpers are related and thus satisfy requirements for kin selection (Hamilton 1964; van Schaik and Paul 1996; see Buchan et al. 2003 for agonistic interventions by fathers on behalf of juveniles), or if helpers are unrelated and might help as a way to strengthen social ties (see Mumme 1997 and Ross and MacLarnon 2000). Are infants, mothers, or helpers responsible for transferring infants between caregivers and is this transfer met with resistance (Poirier 1968; Lessnau et al. 1993)? Can caregiving be a mechanism of "agonistic buffering" (Deag and Crook 1971), reducing aggression between adults? Are helpers juvenile and nulliparous females who might be learning to mother (Lancaster 1971; Hrdy 1977)? What are the costs to helpers? For example, do helpers delay dispersal (Koenig et al. 1992) or experience lower reproductive rates (as observed in siamangs, *Symphalangus syndactylus*, Lappan 2008)? However, in the meantime, we encourage researchers to report even anecdotal accounts of allomaternal care, as well as exclusive maternal care when they do not observe allomaternal care (e.g., Tan 2000). Studies of allomaternal care can be better developed with an understanding of which species express these behaviors, and many more species can be included in comparative analyses to provide a broader perspective, and help determine the selective pressures for non-maternal infant care in primates.

Finally, we suggest that future research should focus on ecological explanations for the presence of allomaternal care in Malagasy primates. Specifically, how do the type and frequency of allomaternal care vary with diet, day range, and food availability (or competition)? For instance, day range is known to affect life history traits across primates (e.g., Pontzer and Kamilar 2009). Yet, because there is such great variation in habitat quality (largely due to habitat degradation), certain data such as day range can be highly variable within species. While site-specific variation can be a cause for difficulty in broad-scale analyses, it is our belief that such variation can be especially informative. With more site-specific data, particularly for species in which allomaternal care exists but is not ever-present, investigations of these proximate relationships can lead us to ultimate explanations of the evolution of allomaternal care in Malagasy primates.

Acknowledgments We would like to thank Katie Hinde, Julienne Rutherford, and Kate Clancy for inviting us to contribute to this volume, and for their insightful comments. We are grateful to the three anonymous reviewers for their thoughtful feedback and suggestions, and the numerous lemur researchers who took the time to answer our questions. We appreciate access to unpublished data from the All the World's Primates database, generously contributed by several researchers and provided by Noel Rowe; the Duke Lemur Center, provided by Sarah Zehr and Julie Taylor; Teague O'Mara, and Erik Patel. SRT would like to thank Toni Ziegler, Pat Wright, Anita Ginther, and Sarah Hrdy for insight and discussions on allomaternal care.

Glossary

Allomaternal care Costly behaviors directed toward infants, which are provided by individuals other than the mother. This can include care by the genetic father, siblings, and other distantly related or unrelated group members.

Allomaternal nursing The behavior of females nursing offspring that are not genetically their own.

Carrying on fur Also known as infant riding; the infant clings to its mother's fur during movement between locations.

Carrying orally Care-providers transport young in their mouths, such as when moving between nests. Oral carrying typically occurs when infants are altricial and cannot cling to their mother's fur.

Cheirogaleidae A family within the infraorder Lemuriformes including the genera *Allocebus, Cheirogaleus, Microcebus, Mirza*, and *Phaner.*

Crèching A shared nest or centralized location where the young of several mothers are cared for in a communal fashion (i.e., by one or many individuals other than the mother).

Daubentoniidae A family within the infraorder Lemuriformes including the genus *Daubentonia.*

Energy transfer When group members provision infants with food resources to the energetic benefit of the infant. Includes food sharing and allomaternal nursing.

Food sharing Transfer of food resources from group members to infants, often due to infant solicitation.

Haplorhini A suborder of primates including catarrhines (Old World monkeys and apes), platyrrhines (New World monkeys), and tarsiers.

Helper Infant care-provider other than the mother.

Indriidae A family within the infraorder Lemuriformes including the genera *Avahi*, *Indri*, and *Propithecus.*

Infant guarding or "babysitting" When group members other than the mother remain with an infant while its mother is away. This can involve predator protection, protection against infanticide, and general supervision.

Infant transport When a care-provider moves an infant between locations (transport can be over short or long distances) and includes carrying on fur (i.e., infant clings) and/or oral carrying, as in cases where infants cannot cling.

Infant mistreatment/"Aunting to death" Exploitative cases of allomaternal care which result in the mishandling, injury, and sometimes death of infants receiving care.

Lemuridae A family within the infraorder Lemuriformes including the genera *Eulemur*, *Hapalemur*, *Lemur*, *Prolemur*, and *Varecia.*

Lemuriformes An infraorder of strepsirhini primates endemic to the island of Madagascar.

Lepilemuridae A family within the infraorder Lemuriformes including the genus *Lepilemur.*

Nesting When infants are left in actual nests that have been constructed from leaves, lianas, and other materials. Often occurs when infants are altricial and cannot cling, and is common among litter-bearing taxa.

Parking When infants are left hidden in a tree-hole, amongst lianas and tree tangles, or clinging to a branch while family members feed and forage. Often occurs when infants are altricial and cannot cling.

Strepsirrhini A suborder of primates including lemurs, lorises, and galagos.

References

Altmann J (1980) Baboon mothers and infants. Harvard University Press, Cambridge, p 272

Altmann J, Samuels A (1992) Costs of maternal care: infant-carrying in baboons. Behav Ecol Sociobiol 29:391–398

Andrews J (1998) Infanticide by a female black lemur, *Eulemur macaco*, in disturbed habitat on Nosy Be, North-Western Madagascar. Folia Primatol 69:14–17

Arrigo-Nelson SJ (2006) The impact of habitat disturbance on the feeding ecology of the Milne-Edwards' sifaka *(Propithecus edwardsi)* in Ranomafana National Park. Dissertation, Stony Brook University. 181 p

Baden AL (2009) It takes a village: communal infant care and socialization in wild ruffed lemurs (*Varecia variegata*) in Ranomafana National Park, Madagascar. Am J Primatol 71(S1):93

Baden AL (2011) Communal infant care in black-and-white ruffed lemurs (*Varecia variegata*). Dissertation, Stony Brook University, 252 p

Baden AL, Louis EE Jr, Bradley BJ (2011) Cooperation confers fitness benefits in a communally nesting primate. Am J Phys Anthropol 144(S52):79–80

Baden AL, Louis EE Jr, Bradley BJ (in revision) Communal infant care confers maternal success in a social primate

Baldovino M, Di Bitetti M (2008) Allonursing in tufted capuchin monkeys (*Cebus nigritus*): milk or pacifier? Folia Primatol 79:79–92

Bales K, Dietz J, Baker A, Miller K, Tardif SD (2000) Effects of allocare-givers on fitness of infants and parents in callitrichid primates. Folia Primatol 71:27–38

Balko EA (1998) A behaviorally plastic response to forest composition and logging disturbance by *Varecia variegata variegata* in Ranomafana National Park, Madagascar. Dissertation, SUNY-CESF. 245 p

Balko EA (2011) Black and white ruffed lemur, *Varecia variegata*. In: Rowe N (ed) All the world's primates. Pogonias, Charlestown

Barthold J, Kappeler P, Fichtel C (2009) What is it going to be? Pattern and potential function of natal coat change in sexually dichromatic redfronted lemurs (*Eulemur fulvus rufus*). Am J Phys Anthropol 138:1–10

Bastian ML, Brockman D (2007) Paternal care in *Propithecus verreauxi coquereli*. Int J Primatol 28:305–313

Boskoff K (1978) The oestrous cycle of the brown lemur, *Lemur fulvus*. J Reprod Fertil 54:313–318

Brockman DK, van Schaik CP (2005) Seasonality and reproductive function. In: Brockman DK, van Schaik CP (eds) Seasonality in primates: studies of living and extinct human and non-human primates. Cambridge University Press, New York, pp 269–305

Bronson FH, Heideman PD (1994) Seasonal regulation of reproduction in mammals. In: Knobil E, Neil JD (eds) The physiology of reproduction, 2nd edn. Raven, New York, pp 541–583

Brown GR, Almond REA, van Bergen Y (2004) Begging, stealing, and offering: food transfer in nonhuman primates. Adv Stud Behav 34:265–295

Buchan JC, Alberts SC, Silk JB, Altmann J (2003) True paternal care in a multi-male primate society. Nature 425:179–181

Buss DH, Cooper RW, Wallen K (1976) Composition of lemur milk. Folia Primatol 26:301–305

Carlson AA, Russell AF, Young AJ, Jordan NR, McNeilly AS, Parlow AF, Clutton-Brock T (2006) Elevated prolactin levels immediately precede decisions to babysit by male meerkat helpers. Horm Behav 50:94–100

Catlett KK, Schwartz GT, Godfrey LR, Jungers WL (2010) "Life history space": a multivariate analysis of life history variation in extant and extinct Malagasy lemurs. Yearb Phys Anthropol 142:391–404

Chism J (2000) Allocare patterns among cercopithecines. Folia Primatol 71:55–66

Chivers DJ (1974) The siamang in Malaya: a field study of a primate in tropical rain forest. Contrib Primatol 4:1–335

Clutton-Brock TH, Gaynor D, Kansky R, MacColl ADC, McIlrath G, Chadwick P, Brotherton PNM, O'Riain JM, Manswer M, Skinner JD (1998) Costs of cooperative behaviour in suricates *(Suricates suricatta)*. Proc R Soc Lond, B 265:185–190

Curtis DJ (1997) The mongoose lemur (Eulemur mongoz): a study in behaviour and ecology. Dissertation, University of Zurich

Curtis DJ, Zaramody A (1998) Group size, home range use, and seasonal variation in the ecology of *Eulemur mongoz*. Int J Primatol 19:811–837

Curtis DJ, Zaramody A (1999) Social structure and seasonal variation in the behaviour of *Eulemur mongoz*. Folia Primatol 70:79–96

Dausmann K, Glos J, Ganzhorn JU, Heldmaier G (2004) Hibernation in a tropical primate. Nature 429:825–826

Deag JM, Crook JH (1971) Social behaviour and "agonistic buffering" in the wild Barbary macaque *Macaca sylvana*. Folia Primatol 15:183–200

Dewar RE, Richard AF (2007) Evolution in the hypervariable environment of Madagascar. Proc Natl Acad Sci 104:13723–13727

Dixson AF, Fleming D (1981) Parental behaviour and infant development in owl monkeys (*Aotus trivirgatus griseimembra*). J Zool 194:25–39

Dunbar RIM (1995) The mating system of callitrichid primates II: the impact of helpers. Anim Behav 50:1071–1089

Eaglen RH, Boskoff KJ (1978) The birth and early development of a captive sifaka, *Propithecus verreauxi coquereli*. Folia Primatol 30:206–219

Eberle M, Kappeler PM (2006) Family insurance: kin selection and cooperative breeding in a solitary primate (*Microcebus murinus*). Behav Ecol Sociobiol 60:582–588

Emlen ST (1984) Cooperative breeding in birds and mammals. In: Krebs JR, Davies NB (eds) Behavioural ecology: an evolutionary approach. Blackwell, Oxford, pp 305–339

Emlen ST (1991) Evolution of cooperative breeding in birds and mammals. In: Krebs JR, Davies NB (eds) Behavioural ecology: an evolutionary approach, 3rd edn. Blackwell, London, pp 301–335

Emlen ST (1997) Predicting family dynamics in social vertebrates. In: Krebs JR, Davies NB (eds) Behavioural ecology, an evolutionary approach, 4th edn. Blackwell Publishing, Oxford, pp 228–253

Erhart EM, Overdorff DJ (1998) Infanticide in *Propithecus diadema edwardsi:* an evaluation of the sexual selection hypothesis. Int J Primatol 19:73–81

Fairbanks LA (1990) Reciprocal benefits of allomothering for female vervet monkeys. Anim Behav 40:553–562

Feistner ATC, McGrew WC (1989) Food-sharing in primates: a critical review. In: Seth PK, Seth S (eds) Perspectives in primate biology, vol 3. Today and Tomorrow's Printers and Publishers, New Delhi, pp 21–36

Feistner A, Price E (1991) Food offering in New World primates: two species added. Folia Primatol 57:165–168

Fernandez-Duque E, Valeggia CR, Mendoza SP (2009) The biology of paternal care in human and nonhuman primates. Annu Rev Anthropol 38:115–130

Fietz J (1999) Mating system of *Microcebus murinus*. Am J Primatol 48:127–133

Fietz J (2003) Pair living and mating strategies in the fat-tailed dwarf lemur (*Cheirogaleus medius*). In: Reichard UH, Boesch C (eds) Monogamy: mating strategies and partnerships in birds, humans and other mammals. Cambridge University Press, Cambridge, pp 214–231

Fietz J, Dausmann KH (2003) Costs and potential benefits of parental care in the nocturnal fat-tailed dwarf lemur *(Cheirogaleus medius)*. Folia Primatol 74:246–258

Fragaszy DM, Schwarz S, Shimosaka D (1982) Longitudinal observations of care and development of infant titi monkeys (*Callicebus moloch*). Am J Primatol 2:191–200

Fragaszy DM, Fedigan LM, Visalberghi E (2004) The complete capuchin: the biology of the genus Cebus. Cambridge Univ Press, New York, p 339

Ganzhorn JU, Abraham JP, Razanahoera-Rakotomalala M (1985) Some aspects of the natural history and food selection of *Avahi laniger*. Primates 26:452–463

Ganzhorn JU, Wright PC, Ratsimbazafy HJ (1999) Primate communities: Madagascar. In: Fleagle JG, Janson CH, Reed K (eds) Primate communities. Cambridge University Press, Cambridge, pp 75–89

Garber PA, Leigh SR (1997) Ontogenetic variation in small-bodied New World primates: implications for patterns of reproduction and infant care. Folia Primatol 68:1–22

Geiser F, Ruf T (1995) Hibernation versus daily torpor in mammals and birds: physiological variables and classification of torpor patterns. Physiol Zool 68:935–966

Génin F (2008) Life in unpredictable environments: first investigation of the natural history of *Microcebus griseorufus*. Int J Primatol 29:303–321

Gero S, Engelhaupt D, Rendell L, Whitehead H (2009) Who cares? Between-group variation in alloparental caregiving in sperm whales. Behav Ecol 20:838–843

Godfrey LR, Samonds KE, Jungers WL, Sutherland MR, Irwin MT (2004) Ontogenetic correlates of diet in Malagasy lemurs. Am J Phys Anthropol 123:250–276

Goldizen AW (1987a) Facultative polyandry and the role of infant-carrying in wild saddle-back tamarins (*Saguinus fuscicollis*). Behav Ecol Sociobiol 20:99–109

Goldizen AW (1987b) Tamarins and marmosets: Communal care of offspring. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT (eds) Primate societies. University of Chicago Press, Chicago, pp 34–43

Gould L (1992) Alloparental care in free-ranging *Lemur catta* at Berenty Reserve, Madagascar. Folia Primatol 58:72–83

Gould L (2011) The Lemuriformes. In: Campbell C, Fuentes CA, MacKinnon K, Bearder SK, Stumpf R (eds) Primates in perspective, 2nd edn. Oxford University Press, Oxford, pp 55–79

Gould L, Sauther ML, Cameron A (2000) Adoption of a wild orphaned ringtailed lemur infant by natal group members: adaptive explanations. Primates 41:413–419

Grassi C (2001) The behavioral ecology of *Hapalemur griseus griseus*: the influences of microhabitat and population density on this small-bodied prosimian folivore. Dissertation, University of Texas at Austin. 345 p. Available from: University Microfilms, Ann Arbor, MI; AADAA-I3032404

Grieser B (1992) Infant development and parental care in two species of sifakas. Primates 33:305–314

Gubernick DJ, Alberts JR (1987) The biparental care system of the California mouse, *Peromyscus californicus*. J Comp Psychol 101:169–177

Gursky S (2000) Allocare in a nocturnal primate: data on the spectral tarsier, *Tarsius spectrum*. Folia Primatol 71:39–54

Hamilton WD (1964) The genetical evolution of social behaviour. I, II. J Theor Biol 7:1–52

Harrington J (1978) Development of behavior in *Lemur macaco* in the first nineteen weeks. Folia Primatol 29:107–128

Harvey PH, Clutton-Brock TH (1985) Life history variation in primates. Evolution 39:559–581

Harvey PH, Martin RD, Clutton-Brock TH (1987) Life Histories in comparative perspective. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RS, Struhsaker TT (eds) Primate societies. Chicago University Press, Chicago, pp 181–196

Hilgartner R, Zinner D, Kappeler PM (2008) Life history traits and parental care in *Lepilemur ruficaudatus*. Am J Primatol 70:2–11

Hinde K, Milligan LA (2011) Primate milk: proximate mechanisms and ultimate perspectives. Evol Anthropol 20:9–23

Hrdy S (1976) Care and exploitation of nonhuman primate infants by conspecifics other than the mother. In: Rosenblatt J, Hinde R, Shaw E, Beer C (eds) Advances in the study of behavior. Academic, New York, pp 101–158

Hrdy SB (1977) The langurs of Abu: female and male strategies of reproduction. Harvard University Press, Cambridge, p 382

Hrdy S (2009) Mothers and others: the evolutionary origins of mutual understanding. The Belknap Press, Cambridge, p 432

Hrdy S (2010) Estimating the prevalence of shared care and cooperative breeding in the Order Primates, an appendix to mothers and others: the evolutionary origins of human understanding. http://www.citrona.com/hrdy/documents/AppendixI.pdf

Huck M, Fernandez-Duque E (2012) When dads help: male behavioral care during primate infant development. In: Clancy KBH, Hinde K, Rutherford JN (eds) Building babies: primate development in proximate and ultimate perspectives. Springer, New York

Huck M, Lottker P, Heymann EW (2004) The many faces of helping: Possible costs and benefits of infant carrying and food transfer in wild moustached tamarins (*Saguinus mystax*). Behaviour 141:915–934

Jaeggi AV, van Schaik CP (2011) The evolution of food sharing in primates. Behav Ecol Sociobiol 65:2125–2140

Janson C, Verdolin J (2005) Seasonality of primate births in relation to climate. In: Brockman DK, van Schaik CP (eds) Seasonality in primates: studies of living and extinct human and non-human primates. Cambridge University Press, New York, pp 307–350

Jolly A (1966) Lemur behavior: a Madagascar field study. University of Chicago Press, Chicago, p 187

Jolly A (1967) Breeding synchrony in wild *Lemur catta*. In: Altmann SA (ed) Social communication among primates. Chicago University Press, Chicago, pp 3–13

Jolly A (1972) The evolution of primate behavior. Macmillan Company, New York, p 397

Jolly A (1984) The puzzle of female feeding priority. In: Small M (ed) Female primates: studies by women primatologists. Alan R. Liss, New York, pp 197–215

Jolly A, Caless S, Cavigelli S, Gould L, Pereira ME, Pitts A, Pride RE, Rabenandrasana HD, Walkder JD, Zafison T (2000) Infant killing, wounding, and predation in *Eulemur* and *Lemur*. Int J Primatol 21:21–40

Jones KE, Bielby J, Cardillo M, Fritz SA, O'Dell J, Orme CDL, Safi K, Sechrest W, Boakes EH, Carbone C, Connolly C, Cutts MJ, Foster JK, Grenyer R, Habib M, Plaster CA, Price SA, Rigby EA, Rist J, Teacher A, Bininda-Emonds ORP, Gittleman JL, Mace GM, Purvis A, Michener WK (2009) Pantheria: a species-level database of life history, ecology, and geography of extant and recently extinct mammals. Ecology 90:2648

Kappeler PM (1996) Causes and consequences of life-history variation among strepsirrhine primates. Am Nat 148:868–891

Kappeler PM (1998) Nests, tree holes, and the evolution of primate life histories. Am J Primatol 46:7–33

Kappeler PM, Pereira ME (2003) A primate life history database. In: Kappeler PM, Pereira ME (eds) Primate life histories and socioecology. University of Chicago Press, Chicago, pp 313–330

Kesch K (2009) Allomothering and allonursing behavior in collared lemurs (*Eulemur collaris*). Lemur News 14:54–55

King SJ, Morelli TL, Arrigo-Nelson S, Ratelolahy FJ, Godfrey LR, Wyatt J, Tecot S, Jernvall J, Wright PC (2011) Morphometrics and pattern of growth in wild sifakas (*Propithecus edwardsi*) at Ranomafana National Park, Madagascar. Am J Primatol 73:155–172

Kirkwood JK, Underwood SJ (1984) Energy requirements of captive cotton-top tamarins, *Saguinus oedipus oedipus*. Folia Primatol 42:180–187

Kleiman DG, Malcolm JR (1981) The evolution of male parental investment in mammals. In: Gubernick DJ, Klopfer PH (eds) Parental care in mammals. Plenum, New York, pp 347–387

Klopfer PH (1974) Mother-young relations in lemurs. In: Martin RD, Doyle GA, Walker AC (eds) Prosimian biology. Duckworth, London, pp 273–292

Koenig WD, Pitelka FA, Carmen WJ, Mumme RL, Stanback MT (1992) The evolution of delayed dispersal in cooperative breeders. Q Rev Biol 67:111–150

Kokko H, Johnstone RA (1999) Social queuing in animal societies: a dynamic model of reproductive skew. Proc R Soc Lond B 266:571–578

König B (1997) Cooperative care of young in mammals. Naturwissenschaften 84:95–104

König B (2006) Non-offspring nursing in mammals: general implications from a case study on house mice. In: Kappeler PM, van Schaik CP (eds) Cooperation in primates and humans: mechanisms and evolution. Springer, Berlin, pp 191–205

Lancaster JB (1971) Play-mothering: the relations between juvenile females and young infants among free-ranging vervet monkeys (*Cercopithecus aethiops*). Folia Primatol 15:161–182

Lappan S (2008) Male care of infants in a siamang (*Symphalangus syndactylus*) population including socially monogamous and polyandrous groups. Behav Ecol Sociobiol 62:1307–1317

Leigh SR, Terranova CJ (1998) Comparative perspectives on bimaturism, ontogeny, and dimorphism in Lemurid primates. Int J Primatol 19:723–749

Lemon WC, Barth RH (1992) The effects of feeding rate on reproductive success in the zebra finch, *Taeniopygia guttata*. Anim Behav 44:851–857

Lessnau RG, Taylor LL, Thompson WL (1993) Infant transfer patterns in a captive group of ringtailed lemurs (Lemur catta) at the Detroit zoological park. AAZPA Regional Conference Proceedings 1993, pp 254–259

Leutenegger W (1980) Monogamy in callitrichids: a consequence of phyletic dwarfism? Int J Primatol 1:95–98

Lewis RJ, Kappeler PM (2005) Seasonality, body condition, and timing of reproduction in *Propithecus verreauxi verreauxi* in the Kirindy Forest. Am J Primatol 67:347–364

Lewis SE, Pusey AE (1997) Factors influencing the occurrence of communal care in plural breeding mammals. In: Solomon NG, French JA (eds) Cooperative breeding in mammals. Cambridge University Press, Cambridge, pp 335–363

Ligon JD, Stacey PB (1991) The origin and maintenance of helping behavior in birds. Am Nat 138:254–258

Lindenfors P (2002) Sexually antagonistic selection on primate size. J Evol Biol 15:595–607

Maestripieri D (1994) Social structure, infant handling, and mothering styles in group-living Old World monkeys. Int J Primatol 15:531–553

Martin RD (1972) A preliminary field-study of the lesser mouse lemur (*Microceuns murinus* J.F. Miller 1777). In: Michael RP, Crook JH (eds) Comparative ecology and behavior of primates. Academic, London

McKenna JJ (1981) Primate infant caregiving behavior: origins, consequences, and variability with emphasis on the common Indian langur monkey. In: Gubernick DJ, Klopfer PH (eds) Parental care in mammals. Plenum, New York, pp 389–416

Meyers DM (1993) The effects of resource seasonality on behavior and reproduction in the golden-crowned sifaka (*Propithecus tattersalli,* Simons, 1988) in three Malagasy forests. Dissertation, Duke University. 251 p. Available from: University Microfilms, Ann Arbor, MI; AADAA-I9508755

Meyers DM, Wright PC (1993) Resource tracking: food availability and *Propithecus* seasonal reproduction. In: Kappeler PM, Ganzhorn JU (eds) Lemur social systems and their ecological basis. Plenum Press, New York, pp 179–192

Mitani JC, Watts D (1997) The evolution of non-maternal caretaking among anthropoid primates: do helpers help? Behav Ecol Sociobiol 40:213–220

Mitchell GD (1969) Paternalistic behavior in primates. Psychol Bull 71:399–417

Mittermeier RA, Louis EE Jr, Richardson M, Schwitzer C, Langrand O, Rylands A, Hawkins F, Rajaobelina S, Ratsimbazafy J, Roos C, Kappeler PM, MacKinnon J (2010) Lemurs of Madagascar, 3rd edn. Conservation International, Washington, p 762

Moehlman PD, Hofer H (1997) Cooperative breeding, reproductive suppression, and body mass in canids. In: Solomon NG, French JA (eds) Cooperative breeding in mammals. Cambridge University Press, Cambridge, pp 76–127

Morelli TL, King SJ, Pochron ST, Wright PC (2009) The rules of disengagement: takeovers, infanticide, and dispersal in a rainforest lemur, *Propithecus edwardsi*. Behaviour 146:499–523

Morland HS (1990) Parental behavior and infant development in ruffed lemurs (*Varecia variegata*) in a northeast Madagascar rain forest. Am J Primatol 20:253–265

Morland HS (1991) Preliminary report on the social organization of ruffed lemurs (*Varecia variegata variegata*) in a northeast Madagascar rainforest. Folia Primatol 56:157–161

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

Mumme RL (1997) A bird's eye view of cooperative breeding. In: Solomon NG, French JA (eds) Cooperative breeding in mammals. University Press, Cambridge, pp 164–388

Negus NC, Berger PJ (1972) Environmental factors and reproductive processes in mammalian populations. In: Velardo JT, Kasprow BA (eds) Biology of reproduction: basic and clinical studies. Third Pan American Congress on Anatomy, New Orleans. Pan American Association of Anatomy, pp 89–98

Nekaris KAI, Bearder SK (2011) The Lorisiform primates of Asia and mainland Africa: diversity shrouded in darkness. In: Campbell C, Fuentes CA, MacKinnon K, Bearder SK, Stumpf R (eds) Primates in perspective, 2nd edn. Oxford University Press, Oxford, pp 34–54

Numen M, Insel TR (2003) Neurobiology of parental behavior. Springer, New York, p 418

O'Farrell MJ, Studier EH (1973) Reproduction, growth, and development in *Myotis Thysanodes* and *M. Lucifugus* (Chiroptera: Vespertilionidae). Ecology 54:18–30

Overdorff DJ (1991) Ecological correlates to social structure in two prosimian primates*: Eulemur fulvus rufous* and *Eulemur rubriventer* in Madagascar. Dissertation, Duke University. 313 p. Available from: University Microfilms, Ann Arbor, MI; AAD92-02491

Overdorff DJ (1996a) Ecological correlates to social structure in two Lemur species in Madagascar. Am J Phys Anthropol 100:487–506

Overdorff DJ (1996b) Ecological correlates to activity and habitat use of two prosimian primates: *Eulemur rubriventer* and *Eulemur fulvus rufus* in Madagascar. Am J Primatol 40:327–342

Overdorff DJ, Tecot SR (2006) Social pair-bonding and resource defense in wild red-bellied lemurs (*Eulemur rubriventer*). In: Gould L, Sauther ML (eds) Lemurs: ecology and adaptation. Springer, New York, pp 235–254

Overdorff DJ, Merenlender A, Talata P, Telo A, Forward Z (1999) Life history of *Eulemur fulvus rufus* from 1988-1998 in southeastern Madagascar. Am J Phys Anthropol 108:295–310

Packer C, Lewis S, Pusey A (1992) A comparative analysis of non-offspring nursing. Anim Behav 43:265–281

Pagel M (1999) Inferring the historical patterns of biological evolution. Nature 401:877–884

Palombit RA, Seyfarth RM, Cheney DL (1997) The adaptive value of 'friendships' to female baboons: experimental and observational evidence. Anim Behav 54:599–614

Patel ER (2007) Non-maternal infant care in wild silky sifakas (*Propithecus candidus*). Lemur News 12:39–42

Pereira ME (1991) Asynchrony within estrous synchrony among ringtailed lemurs (Primates: Lemuridae). Physiol Behav 49:47–52

Pereira M (1993) Seasonal adustment of growth rate and adult body weight in ringtailed lemurs. In: Kappeler PM, Ganzhorn JU (eds) Lemur social systems and their ecological basis. Plenum, New York, pp 205–221

Pereira ME, Klepper A, Simons EL (1987) Tactics of care for young infants by forest-living ruffed lemurs (*Varecia variegata variegata*): ground nests, parking, and biparental guarding. Am J Primatol 13:129–144

Pereira ME, Russ AS, Cavigelli SA, Hughes CL, Pearson DD (1999) Metabolic strategy and social behavior in Lemuridae. In: Rakotosamimanana B, Rasamimanana H, Ganzhorn JU, Goodman SM (eds) New directions in lemur studies. Plenum Publishers, New York, pp 93–118

Perry S (1995) Social relationships in wild white-faced capuchin monkeys, *Cebus capucinus.* Dissertation, University of Michigan. 326 p. Available from: University Microfilms, Ann Arbor, MI; AADAA-I9542933

Petter-Rousseaux A (1964) Reproductive physiology and behavior of the Lemuroidea. In: Buettner-Janusch J (ed) Evolutionary and genetic biology of Primates. Academic, New York, pp 92–132

Petter-Rousseaux A (1980) Seasonal activity rhythms, reproduction, and body weight variations in five sympatric nocturnal prosimians, in simulated light and climatic conditions. In: Charles-Dominique P, Cooper HM, Hladik A, Hladik CM, Pages E, Pariente GF, Petter-Rousseaux A, Petter J-J, Schilling A (eds) Nocturnal malagasy primates: ecology, physiology, and behavior. Academic, New York, pp 137–152

Pochron ST, Tucker WT, Wright PC (2004) Demography, life history and social structure in *Propithecus edwardsi* in Ranomafana National Park, Madagascar. Am J Phys Anthropol 125:61–72

Poirier FE (1968) The Nilgiri langur *(Presbytis johnii)* mother-infant dyad. Primates 9:45–68

Poirier FE (1970) The Nilgiri Langur (*Presbytis johnii*) of South India. In: Rosenblum LA (ed) Primate behavior, developments in field and laboratory research, vol I. Academic, New York, pp 251–383

Pollock JI (1975) Field observations on *Indri indri*: a preliminary report. In: Tattersall I, Sussman RW (eds) Lemur biology. Plenum, New York, pp 287–311

Pollock JI (1977) The ecology and sociology of feeding in *Indri indri*. In: Clutton-Brock TH (ed) Primate ecology: studies of feeding and ranging behaviour in lemurs, monkeys and apes. Academic, New York, pp 37–69

Pontzer H, Kamilar JM (2009) Great ranging associated with greater reproductive investment in mammals. Proc Natl Acad Sci U S A 106:192–196

Powzyk J (1997) The Socio-ecology of two sympatric indriids: *Propithecus diadema diadema* and *Indri indri*, a comparison of feeding strategies and their possible repercussions on species-specific behaviors. Dissertation, Duke University. 307 p

Quiatt D (1979) Aunts and mothers: adaptive implications of allomaternal behavior of nonhuman primates. Am Anthropol 81:310–319

Rasmussen D (1985) A comparative study of breeding seasonality and litter size in eleven taxa of captive lemurs (*Lemur* and *Varecia*). Int J Primatol 6:501–517

Ravosa MJ, Meyers DM, Glander KE (1993) Relative growth of the limbs and trunk in sifakas: heterochronic, ecological, and functional considerations. Am J Anthropol 92:499–520

Richard AF (1976) Preliminary observations on the birth and development of *Propithecus verreauxi* to the age of six months. Primates 17:357–366

Richard A (1978) Behavioral variation: case study of a Malagasy lemur. Bucknell University Press, Lewisburg

Richard AF (1987) Malagasy prosimians: female dominance. In: Smuts B, Cheney D, Seyfarth R, Wrangham R, Struhsaker T (eds) Primate Societies. University of Chicago Press, Chicago, pp 25–33

Richard AF, Dewar RE (1991) Lemur ecology. Annu Rev Ecol Syst 22:145–175

Richard AF, Dewar RE, Schwartz M, Ratsirarson J (2002) Life in the slow lane? Demography and life histories of male and female sifaka *(Propithecus verreauxi)*. J Zool, Lond 256:421–436

Ross C (2001) Park or ride? Evolution of infant carrying in primates. Int J Primatol 22:749–771

Ross C (2003) Life history, infant care strategies, and brain size in primates. In: Kappeler PM, Pereira ME (eds) Primate life histories and socioecology. University of Chicago Press, Chicago, pp 266–284

Ross C, MacLarnon A (1995) Ecological and social correlates of maternal expenditure on infant growth in haplorhine primates. In: Pryce C, Martin R, Skuse D (eds) Motherhood in human and nonhuman primates. Karger, Basel, pp 37–46

Ross C, MacLarnon A (2000) The evolution of non-maternal care in anthropoid primates: a test of the hypotheses. Folia Primatol 71:93–113

Rowe N, Myers M (eds) (2011) All the world's primates. Primate Conservation Inc, Charlestown, www.alltheworldsprimates.org

Russell AF, Clutton-Brock TH, Brotherton PNM, Sharpe LL, McIlrath GM, Dalerum FD, Cameron EZ, Barnard JA (2002) Factors affecting pup growth and survival in co-operatively breeding meerkats *Suricata suricata*. J Anim Ecol 71:700–709

Sauther ML (1998) The interplay of phenology and reproduction in ringtailed lemurs: implications for ringtailed lemur conservation. Folia Primatol 69:309–320

Schmid J, Kappeler PM (1998) Fluctuating sexual dimorphism and differential hibernation by sex in a primate, the gray mouse lemur *(Microcebus murinus)*. Behav Ecol Sociobiol 43:125–132

Schmid J, Stephenson PJ (2003) Physiological adaptations of Malagasy mammals: lemurs and tenrecs compared. In: Benstead J, Goodman SM (eds) The natural history of Madagascar. University of Chicago Press, Chicago, pp 1198–1203

Schradin C, Anzenberger G (2001) Costs of infant carrying in common marmosets, *Callithrix jacchus:* an experimental analysis. Anim Behav 62:289–295

Schülke O (2005) Evolution of pair-living in *Phaner furcifer*. Int J Primatol 26:903–919

Silk J (1980) Kidnapping and female competition among captive bonnet macaques. Primates 21:100–110

Smuts B (1998) What are friends for? In: Ciochon RL, Nisbett RA (eds) The primate anthology: essays on primate behavior, ecology, and conservation from Natural History. Prentice Hall, New York, pp 36–43

Solomon NG, French JA (1997) The study of mammalian cooperative breeding. In: Solomon NG, French JA (eds) Cooperative breeding in mammals. Cambridge University Press, Cambridge, pp 1–10

Solomon NG, Getz LL (1997) Examinations of alternative hypotheses for cooperative breeding in rodents. In: Solomon NG, French JA (eds) Cooperative breeding in mammals. Cambridge University Press, Cambridge, pp 335–363

Sørg J-P, Ganzhorn JU, Kappeler PM (2003) Forestry and research in the Kirindy Forest/Centre de Formation Professionnelle Forestiere. In: Benstead J, Goodman SM (eds) The natural history of Madagascar. University of Chicago Press, Chicago, pp 1512–1519

Stanford CB (1992) The costs and benefits of allomothering in wild capped langurs (*Presbytis pileata*). Behav Ecol Sociobiol 30:29–34

Storey AE, Delahunty KM, McKay DW, Walsh CJ, Wilhelm SI (2006) Social and hormonal bases of individual differences in the parental behaviour of birds and mammals. Can J Exp Psychol 60:237–245

Sussman RW (1977) Socialization, social structure, and ecology of two sympatric species of lemur. In: Chevalier-Skolnikoff S, Poirier FE (eds) Primate biosocial development: biological, social and ecological determinants. Garland Publishing, New York, pp 515–545

Sussman RW (1991) Demography and social organization of free-ranging *Lemur catta* in the Beza Mahafaly Reserve, Madagascar. Am J Phys Anthropol 84:43–58

Tan CL (2000) Behavior and ecology of three sympatric bamboo lemur species (genus *Hapalemur*) in Ranomafana National Park, Madagascar. Dissertation, State University of New York at Stony Brook. 242 p. Available from: University Microfilms, Ann Arbor, MI; AADAA-I3000799

Tan CL (2006) Behavior and ecology of gentle lemurs (Genus *Hapalemur*). In: Gould L, Sauther ML (eds) Lemurs: ecology and adaptation. Springer, New York, pp 369–381

Tardif SD (1997) The bioenergetics of parental behavior and the evolution of alloparental care in marmoset and tamarins. In: Solomon NG, French JA (eds) Cooperative breeding in mammals. Cambridge University Press, Cambridge, pp 11–32

Tardif SD, Santos CV, Baker AJ, Van Elsacker L, Ruiz-Miranda CR, Moura ACA, Passos FC, Price EC, Rapaport LG, de Vleeschouwer K (2002) Infant care in lion tamarins. In: Kleiman DG, Rylands AB (eds) Lion tamarins: biology and conservation. Smithsonian University Press, Washington, pp 213–232

Tattersall I (1982) The primates of Madagascar. Columbia University Press, New York

Tecot S (2007) Fecal cortisol levels and maintenance behaviors in wild groups of a cooperatively breeding species, the red-bellied lemur *(Eulemur rubriventer)*. Am J Primatol 69:127

Tecot S (2008) Seasonality and predictability: the hormonal and behavioral responses of *Eulemur rubriventer* in Southeastern Madagascar. Dissertation, University of Texas-Austin. 544 p. Available from: University of Texas Libraries

Tecot S (2010) It's all in the timing: out of season births and infant survival in *Eulemur rubriventer*. Int J Primatol 31:715–735

Tecot S (2012) Variable energetic strategies in disturbed and undisturbed rain forest habitats: fecal cortisol levels in southeastern Madagascar. In: Masters J, Gamba M, Génin F (eds) Leaping ahead: advances in prosimian biology. Developments in primatology series. Springer, New York (in press)

Tecot S and Overdorff DJ (2005) Aseasonal births and reproductive patterns in *Eulemur rubriventer* in southeastern Madagascar. Am J Primatol 66(S1):111–112

Tecot S, Baden A, Romine N, Kamilar J (In revision). Infant parking and nesting, not allomaternal care, influence Malagasy primate life histories

Tilden CD, Oftedal OT (1995) The bioenergetics of reproduction in prosimian primates: is it related to female dominance? In: Alterman L, Doyle GA, Izard MK (eds) Creatures of the dark: the nocturnal prosimians. Plenum, New York, pp 119–131

Tilden CD, Oftedal OT (1997) Milk composition reflects pattern of maternal care in prosimian primates. Am J Primatol 41:195–211

Trivers RL (1972) Parental investment and sexual selection. In: Campbell BG (ed) Sexual selection and the descent of man, 1871–1971. Aldine, Chicago, pp 136–179

van Horn RN (1975) Primate breeding season: photoperiodic regulation in captive *Lemur catta*. Folia Primatol 24:203–220

van Schaik CP, Kappeler PM (1997) Infanticide risk and the evolution of male-female association in primates. Proc Biol Sci 264:1687–1694

van Schaik CP, Paul A (1996) Male care in primates: does it ever reflect paternity? Evol Anthropol 5:152–156

Vasey N (2007) The breeding system of wild red ruffed lemurs (*Varecia rubra*): a preliminary report. Primates 48:41–54

Vogel C (1984) Patterns of infant-transfer within two troops of common langurs (*Presbytis entellus*) near Jodhpur. Testing hypotheses concerning the benefits and risks. In: Roonwal M, Mohnot S, Rathore N (eds) Current primate researches. University of Jodhpur, Jodhpur, pp 361–379

Volampeno MSN, Masters J, Downs C (2011) Life history traits, maternal behavior and infant development of blue-Eyed black lemurs (Eulemur flavifrons). Am J Primatol 73:474–484

White FJ, Burton AS, Buchholz S, Glander KE (1992) Social organization of free-ranging ruffed lemurs, *Varecia variegata variegata*: mother-adult daughter relationship. Am J Primatol 28:281–287

Whitten PL, Brockman DK (2001) Strepsirrhine reproductive ecology. In: Ellison PT (ed) Reproductive ecology and human evolution. Aldine de Gruyter, New York, pp 321–350

Williams L, Gibson S, McDaniel M, Bazzel J, Barnes S, Abee C (1994) Allomaternal interactions in the Bolivian squirrel monkey (*Saimiri boliviensis boliviensis*). Am J Primatol 34:145–156

Wilson EO (1975) Sociobiology. Harvard University Press, Cambridge

Wolovich CK, Perea-Rodriguez JP, Fernandez-Duque E (2007) Food transfers to young and mates in wild owl monkeys (*Aotus azarai*). Am J Primatol 69:1–16

Wright PC (1984) Biparental care in *Aotus trivirgatus* and *Callicebus moloch*. In: Small M (ed) Female primates: studies by women primatologists. Alan R. Liss, New York, pp 59–75

Wright PC (1990) Patterns of paternal care in primates. Int J Primatol 11:89–102

Wright PC (1995) Demography and life history of free-ranging *Propithecus diadema edwardsi* in Ranomafana National Park, Madagascar. Int J Primatol 16:835–854

Wright PC (1999) Lemur traits and Madagascar ecology: coping with an island environment. Yearb Phys Anthropol 42:31–72

Wright PC, Martin LB (1995) Predation, pollination and torpor in two nocturnal prosimians: *Cheirogaleus major* and *Microcebus rufus* in the rain forest of Madagascar. In: Alterman L, Doyle GA, Izard MK (eds) Creatures of the dark: the nocturnal prosimians. Plenum, New York, pp 45–60

Wright PC, Razafindratsita T, Pochron ST, Jernvall J (2005) The key to frugivory in Madagascar. In: Dew JL, Boubli JP (eds) Tropical fruits and frugivores: the search for strong interactors. Kluwer Academic/Plenum, New York, pp 118–128

Wright PC, Erhart EM, Tecot SR, Baden AL, Arrigo-Nelson S, Morelli TL, Deppe A, Ratelolahy F, Blanco M, Atsalis S, Johnson SE, Ratolahy F, Tan CLM, Zohdy S (2012) Long-term lemur research at Centre ValBio, Ranomafana National Park, Madagascar. In: Kappeler PM, Watts D (eds) Long-term research in Primates. Springer, Dordrecht (2012)

Young AL, Richard AF, Aiello LC (1990) Female dominance and maternal investment in Strepsirhine primates. Am Nat 135:473–488

Zahed SR, Prudom SL, Snowdon CT, Ziegler TE (2007) Male parenting and response to infant stimuli in the common marmoset (*Callithrix jacchus*). Am J Primatol 69:1–15

Zehr S, Haring D, Taylor J, Katz A, Williams C, Yoder A (2011) Everything you ever wanted to know about infant growth rates in prosimians but didn't have a large enough sample size to ask: analyses of infant weight data at the Duke Lemur Center (abstract). Am J Phys Anthropol 144((Suppl)):317

Ziegler TE (2000) Hormones associated with non-maternal infant care: a review of mammalian and avian studies. Folia Primatol 71:6–21

Ziegler TE, Wegner FH, Carlson AA, Lazaro-Perea C, Snowdon CT (2000) Prolactin levels during the periparturitional period in the biparental cotton-top tamarin *(Saguinus oedipus)*: Interactions with gender, androgen levels, and parenting. Horm Behav 38:111–122

Ziegler TE, Washabaugh KF, Snowdon CT (2004) Responsiveness of expectant male cotton-top tamarins, *Saguinus oedipus*, to mate's pregnancy. Horm Behav 45:84–92