Infant parking and nesting, not allomaternal care, influence Malagasy primate life histories

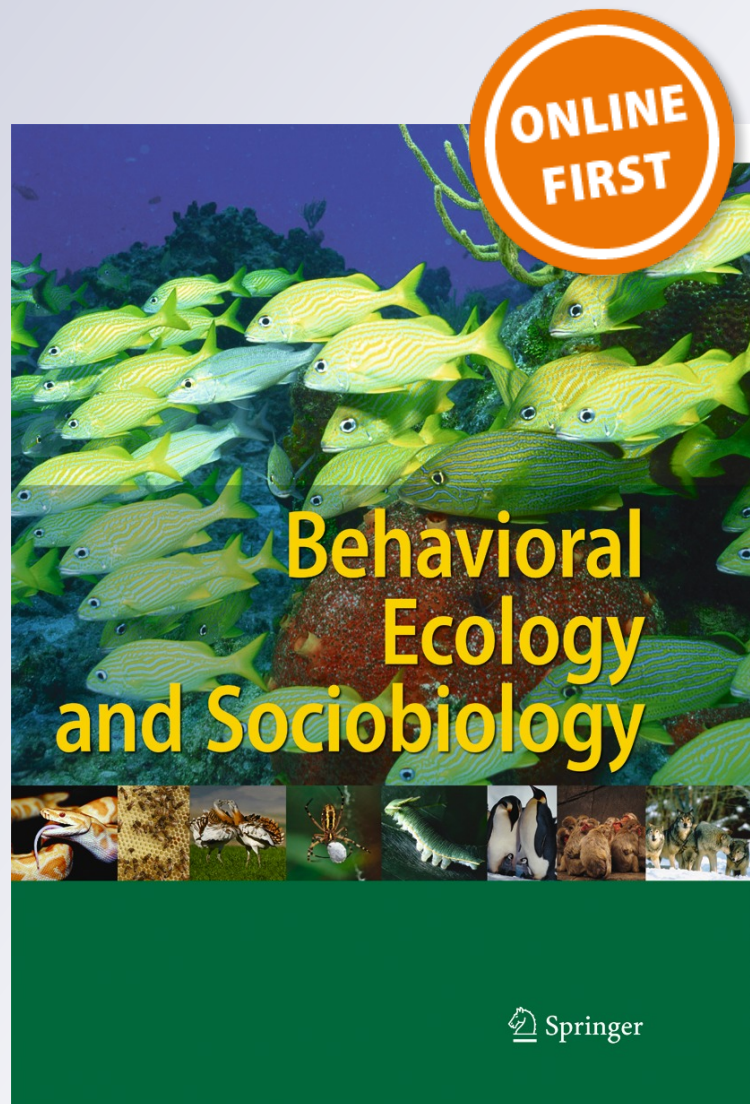## S. R. Tecot, A. L. Baden, N. K. Romine & J. M. Kamilar

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Infant parking and nesting, not allomaternal care, influence Malagasy primate life histories

S. R. Tecot · A. L. Baden · N. K. Romine · J. M. Kamilar

Abstract Allomaternal care is a rare, though phylogenetically widespread, mammalian infant care strategy. Among primates, the effects of allomaternal care are marked; its presence correlates with faster infant growth, younger age at weaning, and shorter interbirth intervals. Recent comparative research has found that such fertility benefits are absent in other mammals and are thus unique to primates. In large part because data describing lemur allomaternal care were lacking, the reproductive advantages of allomaternal care have never been demonstrated in Malagasy strepsirrhines. Using newly available data and rigorous phylogenetic methods, we extend this hypothesis to strepsirrhines and test whether allomaternal care in lemurs confers similar maternal reproductive benefits. Contrary to expectations, the presence of allomaternal care did not significantly impact lemur reproductive output; we did not find relationships between allomaternal care and either fetal or postnatal growth rates or interbirth intervals. Rather, infant parking and nesting, strategies employed primarily by litter-bearing species, were positively associated with faster fetal and postnatal infant growth, while nesting was negatively associated with interbirth interval. Thus, although each form of haplorrhine allomaternal care is also observed in Malagasy primates, the effects that these behaviors have on female reproductive output more closely resemble nonprimate mammals. We suggest that Malagasy strepsirrhines may not equally benefit from allomaternal care compared to haplorrhines because reproductive rates are less flexible and allomaternal care may instead increase infant survival in Madagascar's harsh and unpredictable environment. Our study has significant implications for understanding the evolution of infant care and developmental trajectories in mammals.

Keywords Life history · Energetics · Development · Malagasy strepsirrhines · Phylogenetic comparative methods

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Introduction

Raising dependent offspring can be an energetically expensive endeavor for primary caregivers, as it involves provisioning, transporting, and protecting young (Jennions and Macdonald 1994). Shared infant care can help to reduce this energetic burden. Alloparental care, often defined as care provided for conspecific young by individuals other than the genetic parents (e.g., siblings, aunts, uncles, or unrelated individuals, termed "helpers") (Wilson 1975; Riedman 1982), has been observed in a diverse array of species, including birds (Riedman 1982; Emlen 1984, 1991), social insects (Brockmann 1997; Salomon and Lubin 2007), and mammals (Emlen 1991; Jennions and Macdonald 1994).

The widespread occurrence of alloparental care is seemingly at odds with evolutionary theory: why invest in infants who are not your own?

While there has been a great deal of focus on the proximate and ultimate bases of alloparental care in birds (e.g., Stacey and Koenig 1990), understanding shared care in mammals requires that we first expand our definition of "helpers" to include fathers and instead use the term "allomaternal care" (care of infants by individuals other than the genetic mother, including nonmaternal carrying, babysitting, and nursing) (Hrdy 1976, 2010; Lewis and Pusey 1997; Burkart et al. 2009; Tecot et al. 2012). This is because, unlike birds, wherein both parents are often necessary for the successful growth and survival of young (Riedman 1982), only approximately 5–10 % of mammalian fathers provide care for their infants (Kleiman 1977; Kleiman and Malcolm 1981; Huck and Fernandez-Duque 2012). Mammalian mothers exclusively gestate and lactate and are thus tethered to their infants, while fathers are able to exploit other breeding opportunities (Trivers 1972). Therefore, it is likely that the expression and frequency of and pressures selecting for allomaternal care may differ in birds and mammals (see Jennions and Macdonald 1994; Mumme 1997; Solomon and French 1997).

In some cases, allomaternal care may be explained by kin selection (Hamilton 1964), in which caregivers increase their inclusive fitness by investing in related offspring. Habitat saturation, lack of mates, and/or scarce resources may also select for shared infant care when the costs of dispersal or finding one's own mate outweigh the cost of delaying dispersal and breeding (Riedman 1982; Kurland and Gaulin 1984). Alternatively, certain forms of allomaternal care are suggested to have no adaptive basis (Jamieson 1989; Boness 1990; Packer et al. 1992), while still other forms of alloparental infant handling may be better described as infant abuse (Hrdy 1976; Hrdy 1978) or parasitism (e.g., milk theft: Packer et al. 1992).

Though allomaternal care (excluding mishandling, kidnapping, milk theft, etc.) is relatively uncommon among mammals (e.g., Kleiman and Malcolm 1981; Clutton-Brock 1991; Huck and Fernandez-Duque 2012), it is phylogenetically widespread (Lukas and Clutton-Brock 2012). Several studies have investigated the benefits of allomaternal care to mammalian mothers and their infants and have yielded equivocal results. Single-species studies provide extensive support for a positive relationship between the number of helpers and infant survival (e.g., carnivores: see Silk 2007; Jennions and Macdonald 1994; callitrichines: Bales et al. 2000). In addition, primate species with allomaternal care have been found to have reduced interbirth intervals, faster prenatal and postnatal growth rates, and younger relative weaning ages (Mitani and Watts 1997; Ross and MacLarnon 2000; Ross 2003), suggesting that

additional energy devoted to offspring from sources external to the mother may have a profound impact on a species' life history, particularly during the earliest stage of infancy and during reproductive years. However, contrary to previous findings, a more recent comparative study of allomaternal care and fertility across mammals (445 species, 28 suborders) found a relationship between allomaternal care and increased brain size, but not faster reproduction (Isler and van Schaik 2012). In fact, while there was a trend for decreased weaning time in carnivores, primates alone showed a strong relationship between allomaternal care and fertility (number of offspring per year) (Isler and van Schaik 2012).

Within the Order Primates, allomaternal care occurs at a relatively high frequency (Hrdy 2009, 2010), particularly among the New World monkeys (Tardif 1997; Chism 2000; Ross and MacLarnon 2000). This behavior appears to benefit the mother by reducing both the duration and intensity of her energetic investment in infant rearing, while also increasing her potential reproductive output (Mitani and Watts 1997; Ross and MacLarnon 2000; Ross 2003; Isler and van Schaik 2012). However, these results in primates were largely due to the exceptional breeding patterns of the callitrichines (Isler and van Schaik 2012) in which infants are habitually provisioned by caregivers ("cooperative breeding"), a behavior that is suggested to require the evolution of particular psychological traits (Burkart et al. 2009). Moreover, all but one of these comparative studies (see Isler and van Schaik 2012) excluded strepsirrhine primates from their analyses or considered strepsirrhines as lacking allomaternal care (see Ross 2003), in large part because much of what had been known about strepsirrhine allomaternal care was limited to anecdotal evidence and brief reports of its presence or absence within a given taxon.

More recently, it has been observed that allomaternal care behaviors occur in an even wider range of primate species than previously recognized (Patel 2007; Hrdy 2010; Tecot et al. 2012), including several Malagasy strepsirrhines (lemurs), making it possible to include lemurs in broader taxonomic comparisons of reproductive and caregiving strategies. We previously found that allomaternal care was present in 16 of 23 species for which data exist on its presence or absence (Tecot et al. 2012). The patterns of infant care behaviors (including maternal care) exhibited by lemurs differ dramatically from those observed in haplorrhines; we identified five infant care strategies unique to Malagasy strepsirrhines (Tecot et al. 2012), four of which were previously undescribed in primates (see Ross 2003). Moreover, life history traits in Malagasy strepsirrhines differ substantially from those in haplorrhines, with strepsirrhines having faster growth rates and lower relative neonatal mass (Kappeler 1995). In contrast with apes and Old World monkeys (see Leigh and Blomquist 2007), juvenile strepsirrhine growth patterns do not

support the Risk Aversion Hypothesis (Janson and van Schaik 1993) whereby entry into the next life history stage is delayed due to feeding competition; instead, species with higher risk of feeding competition grow faster (during both infancy and juvenility), perhaps due to the energetic benefits of alloparental care, parking, or nesting (Godfrey et al. 2004). Thus, the relationships between lemur life histories and allomaternal care may differ from other primates and instead more closely resemble other nonprimate mammals, placing lemurs in a unique position to help us better understand the evolution of fertility benefits resulting from allomaternal care.

We currently have relatively little knowledge of whether allomaternal care benefits maternal fertility, infant survival, or caregivers (via inclusive fitness or preparation for parenting) in lemurs. While robust estimates of infant survival in natural populations and data on the relatedness of caregivers and infants are rare, we can begin to examine the ultimate benefits of allomaternal care by investigating maternal reproductive output. Here, we test the hypothesis that Malagasy strepsirrhine mothers benefit from allomaternal caretaking behavior, in that allomaternal care (consisting of allomaternal carrying, babysitting, or nursing; see the "Materials and methods" section) will be associated with faster fetal and postnatal growth rates and shorter interbirth intervals. As there are few quantitative data on the presence of babysitting in Malagasy strepsirrhines and a great deal more is known about the presence of parking and nesting (behaviors that may imply the presence of babysitting), we also analyze the relationship between these behaviors and growth rates and interbirth intervals to better understand the potential benefit of helpers (i.e., babysitters) to mothers.

Materials and methods

Data collection

We collected data (Online Resource 1) for three dependent variables that should reflect the energetic benefits of infant care: (1) postnatal growth rate, calculated as litter mass at weaning minus litter mass at birth divided by age at weaning (after Mitani and Watts 1997); (2) fetal growth rate, calculated as litter mass divided by gestation length (after Lindenfors 2002); and (3) interbirth interval. Wherever possible, data used in these analyses were collated from published studies of wild populations found in the primary literature. In order to increase sample size and fill gaps in the dataset, particularly regarding body mass and fetal and postnatal growth rates, we supplemented the dataset from captive studies and research from the Duke Lemur Center (Zehr et al. 2011, unpublished data). Because sample sizes were not always available, values represent midpoints of means when more than one source was available.

We used five independent variables to predict energetic benefits (Online Resource 1), based on care strategies used by mothers and allomaternal caregivers: (1) allomaternal care, (2) allomaternal nurse, (3) allomaternal carry, (4) nest (when infants are placed in nests constructed from leaves, lianas, and other materials, including tree holes) (Tecot et al. 2012), and (5) park (when infants are left in tree tangles, lianas, or nests) (Tecot et al. 2012). All nesting species park infants, and 62.5 % of parking species place their infants in nests (Online Resource 1). We defined allomaternal care as nursing, carrying, or babysitting/guarding another individual's infant(s) (see Tecot et al. 2012). While some authors report the presence of allomaternal care in species on the basis of infant socialization through grooming, holding, or playing 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 nonmothers. 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 detailed studies are unavailable for most Malagasy primate species, all predictor variables were scored as either present or absent on the basis of published reports and All the World's Primates Database (www.alltheworldsprimates.org), though we also noted whether allomaternal care was a regular component of the behavioral repertoire of the species (see Tecot et al. 2012). We separately quantified allomaternal nurse and allomaternal carry, two specific types of allomaternal care, and included whether species exhibited nesting and parking behaviors.

We obtained data for two additional variables, body mass and diet, that may influence life history characteristics (Online Resource 1) (Austad 1997; Wilkinson and South 2002; Pontzer and Kamilar 2009; Kamilar et al. 2010). Body mass data were obtained from Smith and Jungers (1997), Kappeler and Pereira (2003), and Gordon (2006), supplemented with data from the primary literature. The dietary niche of each species was defined as frugivore, folivore, or omnivore, according to Muldoon and Goodman (2010). For analysis, we recoded the three dietary niches as two dummy variables (Quinn and Keough 2002), following the approach used in Kamilar et al. (2012). Quantitative data were found for a total of 23 taxa from four of the five Malagasy strepsirrhine families (excluding Daubentoniidae), following the classifications from All the World's Primates Database (www.alltheworldsprimates.org).

Data analyses

We conducted phylogenetic generalized least squares models (PGLS) (Pagel 1999; Freckleton et al. 2002; Nunn 2011) to test the relationship between the predictor variables and

the three dependent variables: (1) postnatal growth rate, (2) fetal growth rate, and (3) interbirth interval. PGLS account for phylogenetic autocorrelation by weighing the error structure of the model according to the phylogeny of the species in the analysis. The strength of phylogenetic signal in the model, Pagel's lambda, ranges from 0 to 1 and is optimized via a maximum likelihood procedure (Pagel 1999; Freckleton et al. 2002). A value of 1 indicates that the error structure follows a perfect Brownian motion model, and a value of 0 indicates that the errors are completely independent of phylogeny, the latter scenario being identical to a linear model not accounting for phylogeny. We used a phylogeny based on a consensus tree generated from the 10kTrees Project (Arnold et al. 2010). We conducted all PGLS analyses with the caper package (Orme et al. 2011) for R (R Development Core Team 2009).

Ideally, we would analyze all of the predictor variables simultaneously to better understand the relative effect of each predictor on the dependent variable, yet this was not possible because of our relatively small samples sizes and the fact that not all species have data available for all variables (Quinn and Keough 2002). Instead, we performed five analyses with the same sample size for each dependent variable, with each model containing a different predictor variable. The models examining fetal growth rates contained 19 species, postnatal growth rates included 16 species, and interbirth interval comprised 21 species. In each of these analyses, we used body mass and diet as covariates. In addition, we performed a "null model" analysis for each dependent variable, which only contained body mass and diet as independent variables. This method allowed us to further asses the importance of our predictor variables of interest relative to other factors that may influence life history characteristics.

We used Akaike's Information Criterion with correction for small sample size (AICc) as the basis for judging the best models explaining each dependent variable (Burnham and Anderson 2002). AICc calculates the maximized log-likelihood of each model while penalizing more complex models (i.e., those with more predictor variables). Models with the lowest AICc value are considered the best. Equivalently, good models are those within two AICc values from the "best" model. This method of model selection is becoming increasingly popular in biology and biological anthropology (Kamilar and Paciulli 2008; Kamilar et al. 2010; Garamszegi 2011; Wheeler et al. 2011). All dependent variables were natural log-transformed to better meet the assumptions of the parametric statistical tests (Quinn and Keough 2002).

Results

We found that the presence or absence of allomaternal care in Malagasy strepsirrhines was a poor predictor of postnatal

and fetal growth rates, as well as interbirth interval (Tables 1, 2, and 3). We found similar results when we examined allomaternal nursing and allomaternal carrying; neither of these variables was a strong predictor of our dependent variables. Of the 23 species in our dataset, allomaternal care was present in 13 taxa, allomaternal nursing was found in six species, and allomaternal carrying was present in seven species (for details, see Online Resource 1).

In contrast, we found that species which park infants (Fig. 1) exhibited faster fetal growth rates (slope=0.591, p=0.003, n=19, lambda<0.001) and postnatal growth rates (slope=0.963, p=0.001, n=16, lambda<0.001), although parking infants was not significantly related to interbirth interval (slope=−0.110, p=0.302, n=21, lambda<0.001). Nest building had the strongest effect of any predictor variable. Species that build nests (Fig. 2) exhibited faster postnatal and fetal growth rates (respectively: slope=1.746, p<0.001, n=16, lambda<0.001; slope=0.771. p=0.009, n= 19, lambda<0.001). In addition, nest building was negatively correlated with interbirth interval (slope=−0.308, p= 0.046, n=21, lambda<0.001).

We used AICc to judge if more than one model best predicted each dependent variable. Lower AICc values indicate that the model better explains the variation in the dependent variable, and models within two AICc units are considered equally good (Burnham and Anderson 2002). For two of our three dependent variables, we found a single model that best explained the data. For the postnatal growth models (Table 1), the model including nest was the best with an AICc value of 5.348, and the model including park was the next best model (AICc=17.312). The null model performed relatively poorly, with an AICc of 27.968. For the fetal growth rate models (Table 2), the best model included park (AICc=14.848), and the model including nest was the next best model (AICc=16.910). These models were much better supported than the null model, which exhibited an AICc value of 22.137. Finally, for the interbirth intervals analyses (Table 3), the model including nest was the best model (AICc=−6.778), with the null model exhibiting an AICc value of −4.928. This latter model was within two units of the best model explaining interbirth interval, and therefore, should be considered equally as good. The importance of phylogeny in each model varied greatly, with several models displaying a Pagel's lambda of 0.000 and other models having lambda values of 0.998. The best models explaining the dependent variables always exhibited lambda values of < 0.001. This result indicated that phylogeny had no effect in these models. It is important to note that the Pagel's lambda values in regression models are measuring phylogenetic signal in the residuals only. Therefore, these values may or may not be similar to the amount of phylogenetic signal exhibited by any particular variable in the model (Revell 2010).

Table 1 Phylogenetic generalized linear model examining the relationship between infant care strategies and postnatal growth rates in lemuriformes

Model	Behavior	Estimate	p value	Mass		Frugivore		Folivore		Full model r^2	Full model intercept	Full model p value	Model AICc	Pagel's lambda
				Estimate	p value	Estimate	p value	Estimate	p value					
1	Allomaternal care	−0.006	0.982	0.647	0.044	1.383	0.192	0.774	0.519	0.539	0.383	0.049	32.331	0.907
2	Allomaternal nurse	0.559	0.126	0.545	0.021	1.030	0.221	0.376	0.626	0.706	0.599	0.006	30.236	<0.001
3	Carry by caregiver	−0.346	0.053	0.496	0.076	1.037	0.272	0.351	0.744	0.659	0.969	0.009	27.016	0.959
4	*Park*	*0.963*	*0.001*	*0.831*	*<0.001*	*2.498*	*0.001*	*1.541*	*0.016*	*0.869*	*−1.073*	*<0.001*	*17.312*	*<0.001*
5	**Nest**	**1.746**	**<0.001**	**0.403**	**0.001**	**−0.909**	**0.073**	**−1.439**	**0.006**	**0.941**	**2.549**	**<0.001**	**5.348**	**<0.001**
Null	–	–	–	0.648	0.031	1.383	0.172	0.776	0.498	0.539	0.378	0.016	27.968	0.906

Models in bold have a behavioral trait that is significant at the $p<0.05$ level and is the best model according to Akaike's Information Criterion. Models in italics have a behavioral trait that is significant at the $p<0.05$ level. All models include 16 species

Table 2 Phylogenetic generalized linear model examining the relationship between infant care strategies and fetal growth rates in lemuriformes

Model	Behavior	Estimate	p value	Mass		Frugivore		Folivore		Full model r^2	Full model intercept	Full model p value	Model AICc	Pagel's lambda
				Estimate	p value	Estimate	p value	Estimate	p value					
1	Allomaternal care	0.361	0.088	0.881	<0.001	2.389	<0.001	1.859	0.003	0.806	−3.590	<0.001	22.407	0.000
2	Allomaternal nurse	−0.074	0.735	0.810	0.001	2.278	0.017	2.075	0.044	0.571	−3.446	0.013	25.742	0.974
3	Carry by caregiver	−0.105	0.368	0.734	0.004	2.047	0.033	1.872	0.077	0.565	−3.17	0.011	25.021	0.998
4	**Park**	**0.591**	**0.003**	**0.982**	**<0.001**	**3.071**	**<0.001**	**2.382**	**<0.001**	**0.872**	**−4.191**	**<0.001**	**14.848**	**<0.001**
5	*Nest*	*0.771*	*0.009*	*0.760*	*<0.001*	*1.405*	*0.035*	*0.936*	*0.109*	*0.854*	*−2.378*	*<0.001*	*16.910*	*<0.001*
Null	–	–	–	0.803	0.001	2.219	0.014	2.067	0.038	0.566	−3.432	0.003	22.137	0.976

Models in bold have a behavioral trait that is significant at the $p<0.05$ level and is the best model according to Akaike's Information Criterion. Models in italics have a behavioral trait that is significant at the $p<0.05$ level. All models include 19 species

Table 3 Phylogenetic generalized linear model examining the relationship between infant care strategies and interbirth interval in lemuriformes

Model	Behavior	Allomaternal care Estimate	Allomaternal care p value	Mass Estimate	Mass p value	Frugivore Estimate	Frugivore p value	Folivore Estimate	Folivore p value	Full model r^2	Full model intercept	Full model p value	Model AICc	Pagel's lambda
1	Allomaternal care	−0.118	0.289	0.304	<0.001	1.073	0.002	1.154	0.001	0.597	1.341	0.003	−2.948	0.000
2	Allomaternal nurse	−0.154	0.184	0.314	<0.001	1.128	0.001	1.199	<0.001	0.613	1.251	0.003	−3.813	<0.001
3	Carry by caregiver	0.083	0.455	0.329	<0.001	1.059	0.002	1.250	0.001	0.582	1.178	0.004	−2.182	0.000
4	Park	−0.110	0.302	0.281	0.002	0.987	0.003	1.143	0.001	0.595	1.371	0.004	−2.871	<0.001
5	**Nest**	**−0.308**	**0.046**	**0.345**	**<0.001**	**1.444**	**<0.001**	**1.512**	**<0.001**	**0.664**	**0.908**	**0.001**	**−6.778**	**<0.001**
Null	–					1.001	0.002	1.150	<0.001	0.567	1.307	0.001	−4.928	0.000

Models in bold have a behavioral trait that is significant at the $p<0.05$ level and is the best model according to Akaike's Information Criterion. Models in italics have a behavioral trait that is significant at the $p<0.05$ level. All models include 21 species

Discussion

Allomaternal caretaking in mammals has long been considered adaptive, conferring fitness-related benefits to mothers and their infants, including faster postnatal growth rates and shorter interbirth intervals (Ross 1991; Ross and MacLarnon 1995, 2000; Mitani and Watts 1997). The energetic contribution of caretakers enables offspring to grow faster and mothers to reproduce sooner. Isler and van Schaik (2012) found that these effects of allomaternal care on life history modes are primate-specific. However, allomaternal infant care in Malagasy strepsirrhines does not influence infant growth rates and maternal interbirth intervals in the same manner as in haplorrhines (Mitani and Watts 1997; Ross and MacLarnon 2000). Rather, we found that infant parking and nesting were positively associated with both fetal and postnatal infant growth (contra Kappeler 1998) and that nesting was negatively associated with interbirth interval. Paired with our earlier work, these results demonstrate the stark difference in the importance of allomaternal care and infant care strategies in Malagasy strepsirrhines compared with other primate species. Regarding allomaternal care and life history modes, Malagasy strepsirrhines more closely resemble nonprimate mammals (cf. Isler and van Schaik 2012).

Nesting, parking, and life history traits

Our study clarifies earlier findings of the relationship between infant care strategies (nesting and parking) and life history traits, using a much larger sample of Malagasy strepsirrhines and a more rigorous analytical approach. Prior studies of infant care examining all primates (though a smaller sample of Malagasy primates) produced mixed results. Using phylogenetically independent contrasts, Ross (2001) found that nesting and parking species had slower fetal growth rates, yet faster postnatal growth rates, than non-nesting, non-parking species (Ross 2001). Later, Ross (2003) examined life history characteristics across primates with varying infant care strategies. She found that infant growth rates were high in primates with a particular combination of infant care behaviors, including nesting, parking, carrying the infant orally, and carrying clinging infants (i.e., nesting and parking, but not allomaternal care). Though this latter study did not account for confounding phylogenetic effects and did not examine the importance of each infant care behavior individually, our study supports her findings. More recent work incorporating a larger range of mammal species and using a similar analytical approach as reported here incorporated the category of nesting within a larger category of thermoregulation (including behaviors such as babysitting, communal nesting, and pup retrieval) (Isler and van Schaik 2012) and is thus not directly comparable to our results for parkers and nesters.
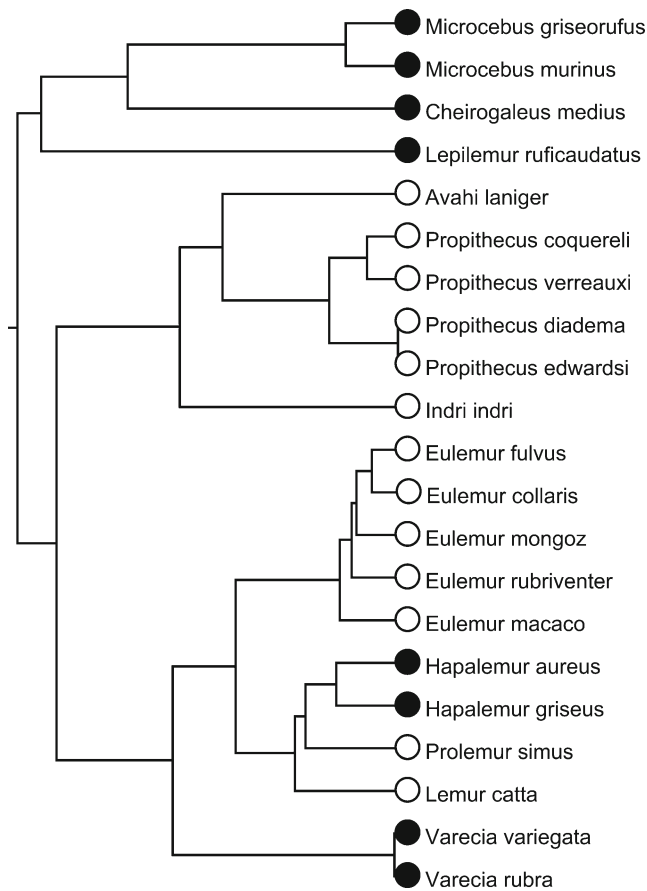
Fig. 1 The distribution of parking infants in tree tangles, lianas, or tree holes in a phylogenetic perspective. *Filled circles* indicate that the trait is present; *open circles* indicate that the trait is absent. MESQUITE (Maddison and Maddison 2007) and a phylogeny based on a consensus tree generated from the 10kTrees Project (Arnold et al. 2010) were used to produce this figure

Fig. 2 The distribution of nest building in a phylogenetic perspective. *Filled circles* indicate that the trait is present; *open circles* indicate that the trait is absent. MESQUITE (Maddison and Maddison 2007) and a phylogeny based on a consensus tree generated from the 10kTrees Project (Arnold et al. 2010) were used to produce this figure

Both nesting and parking behaviors occur most frequently in litter-bearing taxa that often give birth to rapidly growing, altricial infants (Kappeler 1998). In fact, litter-bearing taxa in our analysis (*Varecia* and the cheirogaleids) primarily drove the relationships between growth rates, nesting, and parking. Higher fetal growth rates have been argued to indicate higher maternal investment (Godfrey et al. 2004). Because nesting and parking infants eliminate the need to constantly carry offspring, the higher growth rates and shorter interbirth intervals observed in these species may be the result of reduced energetic constraints on mothers bearing litters. Thus, our results indicate that a strategy that enables mothers to travel and forage unencumbered, minimize energy expenditure, and increase energy intake may enable these species to invest more heavily or efficiently in offspring than mothers who exclusively carry their young.

Nesting, parking, and thermoregulation

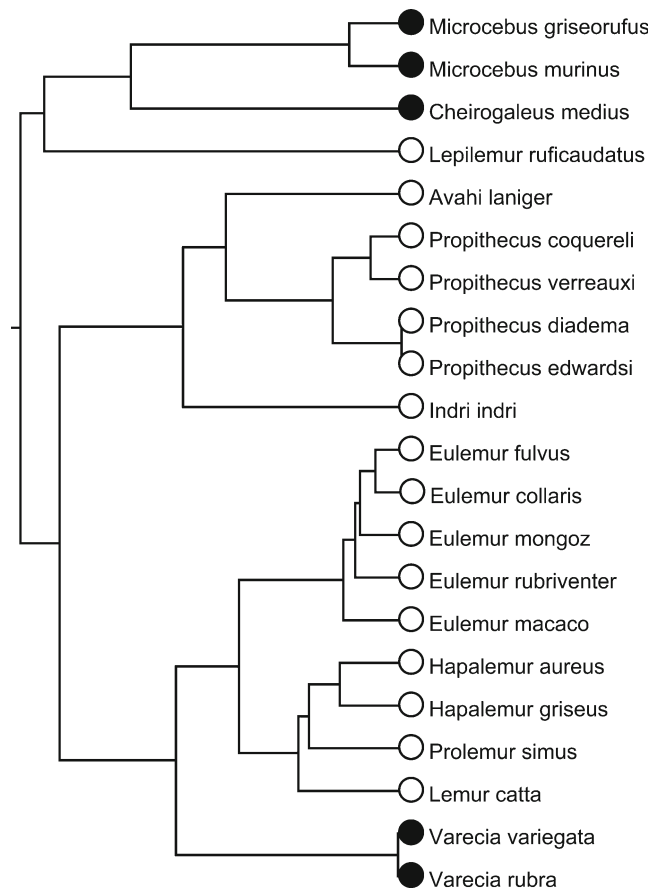Nesting and parking in litter-bearing species may additionally provide a thermoregulatory function whereby maintenance energy can be diverted to offspring growth. While altricial mammalian young are limited in their thermoregulatory abilities (Hull 1973), ambient temperature can be a particularly important influence on lemur energetics since they have low basal metabolic rates for their body sizes (Kleiber 1961; Young et al. 1990). Several researchers have suggested that lemurs are well adapted to avoid cold stress through behavioral modifications (Morland 1993; Curtis et al. 1999; Whitten and Brockman 2001; Kamilar et al. 2012). Indeed, during winter, small, litter-bearing cheirogaleids enter torpor (e.g., Petter-Rousseaux 1980; Wright and Martin 1995; Schmid and Stephenson 2003; Dausmann et al. 2004; Blanco and Rahalinarivo 2010), and several species reduce activity levels (e.g., Schmid and Ganzhorn 1996; Powzyk 1997; Tecot 2008), sun themselves, and/or huddle in groups while at rest (Richard and Dewar 1991; Morland 1993; Overdorff 1996a; Vasey 2005). Huddling has been shown to reduce heat loss and conserve energy in several birds and mammals (see Rödel et al. 2008). Such flexible thermoregulatory systems may reduce competition between energetic demands, thus allowing

the allocation of energy toward growth. This relationship has been demonstrated in tree swallows (*Tachycineta bicolor*), where warmer nests are associated with higher survival and faster infant growth (Dawson et al. 2005), and in European rabbits (*Oryctolagus cuniculus*), where thermoregulatory benefits are said to outweigh the costs of competition for milk among nest-mates (Rödel et al. 2008). In black-and-white ruffed lemurs (*Varecia variegata*), communally nested infants have higher survival (Baden 2011), and faster growth rates in this species (Pereira et al. 1987) are suggestive of a relationship between thermoregulation and growth. However, the impact of communal nesting vs. single nesting on infant thermoregulation, or temperature effects on nestling survival, has not yet been investigated in Malagasy primates.

Nesting, parking, and mortality risk

Life history theory predicts that high extrinsic mortality rates during particular life stages should result in shorter life history modes, including decreased longevity and increased reproductive and growth rates (Promislow and Harvey 1990). Therefore, increased growth rates may also be a function of increased infant mortality in species that build nests and/or park infants. Environmental unpredictability resulting in high mortality (e.g., due to high predation rates or starvation) at key life history stages may hasten or slow advancement to the next life history stage (Janson and van Schaik 1993; Leigh and Terranova 1998). In strepsirrhines and in contrast to Old World monkeys and apes (see Leigh and Blomquist 2007), advancement is hastened despite greater competition with conspecifics alongside growth in body size (Godfrey et al. 2004). Nested infants may be at greater risk of mortality due to increased parasitism through sustained periods of close physical contact in an environment that is conducive to parasite persistence (Hart 1990). In addition, a nest containing multiple infants may act as a greater target of predation due to its increased conspicuousness (Ebensperger and Blumstein 2006) and its greater energetic yield compared to a single infant. Alternatively, infants that are parked and left unattended may be less well defended if detected by a potential predator and suffer higher mortality rates (Ross 2001). Unfortunately, we currently lack field data to test this idea, though there is some indication that predation rates are notably high in litter-bearing *Microcebus murinus* (Goodman et al. 1993; Rasoloarison et al. 1995).

Allomaternal care and life history traits

Surprisingly, the presence of allomaternal care, and specifically allomaternal carrying and nursing, did not have a significant impact on lemur reproductive output. It should be noted that, while allomaternal nursing may in reality be milk theft by the infant, milk theft is most likely to occur in monotocous species living in large groups and was found to be absent in lemurs, including *Lemur catta* (Packer et al. 1992), who live in the largest groups of all strepsirrhines. It should be noted, however, that allomaternal nursing as a result of spontaneous lactation in one unrelated, nonreproducing female has been observed in captivity (Pereira and Izard 1998). Although each form of haplorrhine allomaternal care is also observed in Malagasy primates (Tecot et al. 2012), the effect that each of these has on female reproductive output is dissimilar to what has been found in haplorrhines (Mitani and Watts 1997; Ross and MacLarnon 2000; Isler and van Schaik 2012). The lack of an effect of allomaternal care on prenatal and postnatal growth rates and interbirth intervals may be due to our gross quantification of allomaternal care, combined with the fact that some species are understudied. However, using the same approach to analyze the effects of parking and nesting did produce a significant effect. We suggest that Malagasy strepsirrhines may not benefit from allomaternal care in the same way as haplorrhines because reproductive rates across the clade are less flexible. Breeding in these species is highly seasonal (Wright 1999; Janson and Verdolin 2005; Tecot 2010), and infant weaning is timed with resource abundance (Sauther et al. 1999; Wright 1999; Richard et al. 2000; Lewis and Kappeler 2005), presumably to ensure adequate nutritional intake for newly independent offspring and maternal recovery from the labors of lactation (Wright 1999). Tecot (2010) found that, when breeding is more flexible and infants are born out of peak season, infants do not survive, suggesting a strong selective force on strict seasonal breeding. Therefore, a strategy whereby growth rates are increased and infants are weaned more quickly is not likely to benefit mothers or infants. Decreasing interbirth intervals would be problematic for similar reasons, unless interbirth intervals are reduced by yearly increments. However, we did not find this to be the case. Finally, shifting the timing of conception to maintain weaning schedules while accommodating faster prenatal and postnatal growth rates should facilitate higher reproductive output. However, energetic need during conception may constrain such a strategy (Tecot 2010).

Alternative hypotheses for allomaternal care in lemurs

Alternatively, allomaternal care may benefit Malagasy strepsirrhines in ways that remain unexplored. Understanding the expression of these behaviors in lemur taxa may require that we test different, perhaps more ecologically driven, predictions. It has been proposed that Madagascar's unpredictable rainfall patterns (Dewar and Richard 2007) and slowly growing, low-quality resources with long periodicity (Overdorff 1993a, b, 1996a, b; Ganzhorn et al. 1999, 2009; Balko and Underwood 2005; Bollen and Donati

2005; Wright et al. 2005) present unique challenges compared with other primate habitats. As a result, Malagasy strepsirrhines possess a suite of traits that is distinctive (Wright 1999) and that is suggested to have shaped them in ways that set them apart from even their closest relatives. For example, in contrast to haplorrhines, folivorous, rather than frugivorous, species have faster infant development and higher maternal investment (Godfrey et al. 2004). Ross and MacLarnon (2000) tested several ecological hypotheses in haplorrhines to investigate whether energetic stress might select for allomaternal care. Though they did not find support for such ecological hypotheses, we might expect to see relationships between allomaternal care and ecological factors, particularly those that impact energetic stress (such as the abundance and predictability of resources), in Malagasy primates (Tecot 2012). Thus, we may find that, while allomaternal care does not increase reproductive output, it may improve reproductive success in other ways. In fact, the number of adult male alloparental caregivers is positively associated with infant survival in callitrichine primates (Bales et al. 2000), suggesting that the benefits of allomaternal care in haplorrhines extend further than increasing growth rates. In some litter-bearing lemur taxa, babysitting has been shown to reduce the vulnerability of infants to predators (see van Schaik and Kappeler 1997) and may result in higher maternal energetic intake and higher infant survival (Baden 2011). In frequently twinning species such as the red-bellied lemur, *Eulemur rubriventer*, infant survival may hinge upon allomaternal carrying since nesting is absent (Overdorff and Tecot 2006; Tecot, personal observation). As more long-term data on infant survival in wild lemur populations are collected, we will be better equipped to test the hypothesis that allomaternal care increases infant survival in Malagasy strepsirrhines.

Conclusions

Comparative studies of allomaternal care are critical to understand the evolution of the uniquely human form of cooperative breeding (allomaternal care including provisioning) in which prosocial motivation is combined with complex cognition. The "cooperative breeding hypothesis" suggests that the cognitive and psychological preconditions for human cooperative breeding evolved by common descent and convergent evolution, respectively (Burkart et al. 2009). Psychological traits associated with cooperative breeding in humans are also observed in other cooperatively breeding mammals and allow individuals to monitor, tolerate, and synchronize their movements (Burkart et al. 2009). By expanding our understanding of allomaternal care, we can broaden our perspective in investigating the evolution of this behavior that is seemingly, perplexingly at odds with evolutionary theory.

In conclusion, our study draws important contrasts between the infant care strategies and energetics of Malagasy strepsirrhines compared with other primates and finds similarities with nonprimate mammals. Our findings have significant implications for the evolution of infant care and developmental trajectories. Future studies quantifying the extrinsic risks of infant mortality and infant and adult energetics may provide more details regarding the mechanisms behind our findings. Finally, we encourage field researchers to collect quantitative data on infant care, including exclusive maternal care (e.g., Tan 2000). With high-quality, detailed data from a broader range of taxa, we can begin to conduct more fine-grain analyses that will contribute to our understanding of this relatively rare behavior.

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