

Chapter 16

When Dads Help: Male Behavioral Care During Primate Infant Development

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16.1 Introduction

In contrast to birds, male mammals rarely help to raise the offspring. Of all mammals, only among rodents, carnivores, and primates, males are sometimes intensively engaged in providing infant care (Kleiman and Malcolm 1981).¹ Male caretaking of infants has long been recognized in nonhuman primates (Itani 1959). Given that infant care behavior can have a positive effect on the infant's development, growth, well-being, or survival, why are male mammals not more frequently involved in

¹ Quantitative measures of male care in mammals, although occasionally cited, are problematic. Since Kleiman and Malcolm reviewed the then available data in 1981 much more and new information has become available, which sometimes lead to reclassifications, for example, of mating systems. Due to the lack of field data, their review mainly included data from captivity, which are not necessarily representative for patterns observed in the wild. Furthermore, the definitions of male care can vary substantially and thus the calculated proportions for different taxa.

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“building babies”? The Theory of Parental Investment originally provided an elegant explanation (Bateman 1948; Maynard Smith 1977; Parker et al. 1972; Trivers 1972) that has been recently modified with interesting implications (Houston and McNamara 2002, 2005; Kokko and Jennions 2008; Wade and Shuster 2002, 2005). Males may not necessarily have to trade-off mating opportunities and parental care, as suggested by classic theoretical formulations, but may instead benefit by direct involvement in infant care (Geary 2005).

We begin the chapter defining a few relevant terms and introducing the theory and hypotheses that have historically addressed the evolution of paternal care. We then review empirical findings on male care among primate taxa, before focusing, in the final section, on our own work on paternal care in South American owl monkeys (*Aotus* spp.). We conclude the chapter with some suggestions for future studies.

16.2 Parental Care Revisited

16.2.1 *Parental Investment and Male Care*

Male care, paternal care, and paternal investment are frequently, but incorrectly, used interchangeably (Sheldon 2002). First, we refer to “male care” instead of “paternal care” because genetic paternity is rarely known for most primate studies. Second, we make a distinction between “care” as a suite of behaviors that the male directs to the infant and “investment” which entails an increase or decrease in the present or future reproductive success of the male (Clutton-Brock and Vincent 1991; Trivers 1972). The investment made by the male can be in the form of direct care (e.g., transporting or feeding the infant) or indirect care. The latter might, for example, take the form of antipredator vigilance that frees time for the mother to forage or rest. Direct male care is a behavior directed to the infant that has a positive effect on its development, growth, well-being, or survival. It might consist in carrying, grooming, playing, food sharing, feeding, cleaning, retrieving, huddling, babysitting, or defending.

16.2.2 *The Theory of Parental Investment*

According to the classic formulation of the Theory of Parental Investment (Maynard Smith 1977; Parker et al. 1972; Trivers 1972), physiological sex differences in mammals have selected for females to provide significant infant care and males to compete for access to infant care providing females. This explanation is particularly relevant for mammalian females who make high energy and time contributions to gestation and lactation. Due to these high energetic demands, it is predicted that in most species the reproductive success of females will be mainly constrained by food intake, whereas male reproductive success will be primarily limited by access to

females. Several other factors favor the “typical” mammalian sex roles: strong intra-sexual selection on males, loss of paternity because of female promiscuity, or male mortality due to competition may all generate a female-biased adult sex ratio (Kokko and Jennions 2008). Any of these three factors will make it more beneficial for males to desert females since they all result in a higher proportion of females than males (i.e., a female-biased ratio). It follows from this that male care should be a rare phenomenon among mammals, and in fact it is.

In the last decade, however, several modifications to the theory have been proposed (Houston and McNamara 2002, 2005; Kokko and Jennions 2008; Wade and Shuster 2002, 2005) including the reevaluation of factors traditionally considered to favor the “typical” mammalian sex roles (Kokko and Jennions 2008). For example, the classic argument that females should invest more because they have invested more since the beginning (e.g., larger gametes) evokes the “Concorde Fallacy,” because it is not expected that optimal decisions are based on past investment, but instead on future payoffs (Dawkins and Carlisle 1976). With regards to males, a traditional assumption has been that a male-biased operational sex ratio will always lead to intra-male competition. In other words, it has been predicted that when there are more reproducing males than reproducing females in the population, this will quasi-automatically produce a trade-off between parental care and mating effort. But this is not necessarily true, since some of the earlier models neglected the “Fisher condition,” the fact that in sexually reproducing species each offspring has exactly one parent of each sex (Houston et al. 2005; Kokko and Jennions 2008). When the “Fisher condition” is properly considered, the theory predicts that when the operational sex ratio is male-biased (i.e., more reproductively active males than females at a given time), there will be more male competition which will result in increased parental investment by males. Finally, recent models have also shown that the operational sex ratio and the adult sex ratio might influence the evolution of patterns of parental care. If caring behavior is associated with increased mortality of the caregiving adult, this will change the operational sex ratio. The caring sex will be rarer due to the increased mortality and as a consequence the mating success of the less-caring sex will be diminished. This, in turn, will lead to more similar care behavior of both sexes (Kokko and Jennions 2008). An earlier analysis suggesting that caregiving is associated with lower mortality (Allman et al. 1998) was conducted on mortality data from captive individuals which may limit the generalizability of the findings. Furthermore, in particular with regards to monogamous species where male care is prevalent, this analysis suffered from lack of correction for phylogenetic effects, and an unjustified reliance on statistical significance and data of dubious origins.

16.2.3 Why Is Providing Care Beneficial to Males?

A male may derive benefits from infant care behavior in at least three ways: direct benefits through enhanced infant survival, reduction of the female’s reproductive burden, or as a mating strategy to enhance future mating success (Geary 2005).

First, providing care may enhance the survival or fitness of his own genetic offspring or highly related individuals like younger siblings or nephews and nieces (“genetic advantage” hypothesis, Table 16.1) (Charpentier et al. 2008; Gubernick and Teferi 2000; Kingma et al. 2010; Moreno et al. 1999; Wuensch 1985). Second, the male’s assistance may alleviate the reproductive burden of the female (“maternal relief” hypothesis) to an extent that she will be able to produce infants of better condition, or at a higher rate (Achenbach and Snowdon 2002; Austad and Rabenold 1986; Kingma et al. 2010; Morcillo et al. 2003; Price 1992a, b; Sánchez et al. 1999; Stallcup and Woolfenden 1978). Even if a female is able to successfully rear an offspring without male care, she may be energetically depleted and may not be able to reproduce again as quickly as she would with male assistance. In primates, allo-maternal care is correlated with relatively fast infant growth rates (Mitani and Watts 1997). Finally, providing infant care might also be a strategy to increase mating opportunities (“mating strategy” hypothesis) (e.g., Härdling and Kaitala 2004; Keddy Hector et al. 1989; Price 1990; Smuts and Gubernick 1992, but see Tardif and Bales 1997). In other words, males who provide infant care will receive benefits from the female, such as matings, in exchange for their caregiving behavior (Smuts and Gubernick 1992).

There are some predictions derived from these three hypotheses that might offer some insight into the mechanisms and evolution of parental care. The most basic adaptive explanation would be that *only* direct genetic benefits for the male are responsible for paternal care. In contrast, according to the “maternal relief” and “mating strategy” hypotheses, the benefits to the male should be independent of genetic relatedness to the current infant, and providing care would also benefit males who may be caring for non-offspring (Anderson 1992). If males only cared for their own genetic offspring, one would predict that the replacement of the biological father by another intruding male (“stepfather”) should have a negative impact on infant survival. We would also predict that subadults disperse at younger ages following the replacement of the biological father, given that the stepfather should be less tolerant of potential food and mate competitors. On the other hand, if male care served as “maternal relief” or as a “mating strategy,” we would predict that a stepfather should care for the offspring of his predecessor as well. Smuts and Gubernick (1992) suggested testing three predictions to set the “mating strategy” hypothesis apart from the “genetic benefits” hypothesis: (1) the infant benefits from the care provided by the male, (2) females are able to control important benefits like mating to males, and (3) females have opportunities to compare the behavior of different males, and based on this assessment and their own choice, they benefit some males, but not others. In the following sections, we will evaluate these predictions in view of the existing evidence in primates in general, and owl monkeys in particular.

16.2.4 Proximate Perspectives of Parental Care

In this chapter we primarily discuss ultimate approaches to the question of why male care is observed at all in mammals, even when there are other complementary

Table 16.1 Overview over patterns of paternal care in different primate taxa

	Example species	Relative contribution of allo-maternal care	Type of allo-care	Allo-maternal caretakers	Support for (+) or against (-) IS, MR, GEN, and FMS hypotheses	References
Strepsirrhines ^a	Ruffed lemurs; slender loris; sifakas	Low	Grooming, playing, babysitting, allo-nursing	Related and unrelated (?) males, other females	IS: na MR: - GEN: - (weak) FMS: na	[1-6]
Tarsiers ^a	Spectral tarsiers	Low	Grooming, playing, babysitting, allo-nursing	Related (?) males, sub-adults of both sexes	IS: na MR: - GEN: + (weak) FMS: na	[7]
Colobines	Hanuman langurs	Other females: frequent; males: very rare to absent	Babysitting, carrying, huddling, allo-nursing	Females	IS: - MR: - GEN: - FMS: -	[8]
Exception	Black-and-white snub nosed monkey	Moderate	Carrying and grooming	Related and unrelated (?) males	IS: na MR: + GEN: - FMS	[9]
Cercopithecines	Japanese macaques; chacma baboons, savannah baboons; vervet monkeys	Low	Playing, carrying	More likely potential fathers than unrelated males	IS: + MR: + GEN: + FMS: +	[10-12]
Exception	Barbary macaque	Moderate	Carrying, babysitting	Males and females of all age-classes	IS: na MR: na GEN: - FMS: na	[13, 14]
Hominoids (exceptions)	Siamang	Moderate	Carrying	More likely potential fathers than unrelated males	IS: na MR: ++ GEN: + FMS: na	[15]

(continued)

Table 16.1 (continued)

Example species	Relative contribution of allo-maternal care	Type of allo-care	Allo-maternal caretakers	Support for (+) or against (-) IS, MR, GEN, and FMS hypotheses	References
Human	Low to very high	Carrying, provisioning, playing, babysitting, allo-nursing	Fathers, other relatives, unrelated individuals	IS: -/+ MR: + GEN: + FMS: +	[16–24]
Platyrrhines	Very high	Carrying, food sharing, grooming, playing	All group members	IS: ++ MR: ++ GEN: - FMS: -/+	[25–37]
Titi monkey	Very high	Carrying	Adult males	IS: + MR: na GEN: (prob +) FMS: na	[38, 39]
Owl monkey	Very high	Carrying	Adult males	IS: ++ MR: + GEN: (prob +) FMS: + (weak)	[40, 41, 42, this study]

Note that this is a rough overview to depict a general pattern for several groups, and that specific proximate and ultimate mechanisms might differ between species of the same taxon

IS infant survival/fitness, MR maternal relief, GEN genetic advantage to male, FMS enhanced future mating success for males (“mating strategy”), na no data available

1. Morland (1990); 2. Nekaris (2003); 3. Whitten (1987); 4. Kappeler (in press); 5. Patel (2007); 6. Bastian et al. (2007); 7. Gursky (2000); 8. Ross and MacLarnon (2000); 9. Xiang et al. (2009); 10. Itani (1959); 11. Anderson (1992); 12. Buchan et al. (2003); 13. Small (1990); 14. Paul (1999); 15. Lappan (2008); 16. Geary (2005); 17. Marlowe (2000); 18. Geary (2000); 19. Hurtado and Hill (1992); 20. Hewlett (1989); 21. Marlowe (1999); 22. Anderson et al. (1999); 23. Hewlett (2004); 24. Gettler (2010); 25. Goldizen (1987a, b); 26. Huck et al. (2004); 27. Porter and Garber (2009); 28. Savage et al. (1996); 29. Yamamoto et al. (2009); 30. Sánchez et al. (1999); 31. Achenbach and Snowdon (2002); 32. Morcillo et al. (2003); 33. Tardif (1994); 34. Fite et al. (2005); 35. Bales et al. (2001); 36. Price (1990); 37. Tardif et al. (1997); 38. Frigaszy et al. (1982); 39. Mendoza and Mason (1986); 40. Fernandez-Duque (2011a); 41. Rotundo et al. (2005); 42. Wright (1984)

^aSpecies commonly show “infant-parking”

approaches that cannot be covered in detail here. For example, the influence of hormones like prolactin, vasopressin, oxytocin, and testosterone in relation to bonding and infant care, or behavioral trade-offs between care and mate-acquisition have been extensively studied, even if still not completely understood (Bales et al. 2004; Brockmann et al. 2001; Gettler et al. 2011; Goymann et al. 2007; Gray et al. 2007; Hirschenhauser and Oliveira 2006; Huck et al. 2005; Schradin and Anzenberger 2002; Schradin et al. 2003; Trainor and Marler 2001, 2002; Wingfield et al. 1990; Ziegler 2000; Ziegler et al. 1996, 2000). Differences in hormone production, responsiveness, or ontogenetic exposure may partly explain individual differences in caretaking behavior (Birnie et al. 2011; Drea 2007; Ziegler et al. 2009). Other influential factors include the rank, age and previous experience of the caretaker, sex of the infant, group size and composition, relatedness between caretaker and infant or mother, season of conception, or predation risk (Anderson 1992; Bercovitch 2002; Hoage 1977; McGrew 1988; O'Brien and Robinson 1991; Pryce 1988). Individual differences in caretaking behavior will necessarily be the outcome of a very complex mixture of directly genetic and environmental influences that manifest themselves during ontogeny, or sometimes in a shorter time frame due to seasonal or interannual fluctuations in environmental or social factors.

16.3 The Who, How, and When of Male Care in Primates

Primates are one of the orders of mammals with the highest prevalence of male care (Ross and MacLarnon 2000; Solomon and French 1997; Whitten 1987). The intensity of male care is variable, ranging from relatively little investment like occasional short rides or play bouts, to babysitting, to intense involvement in feeding and carrying of the offspring (Fernandez-Duque et al. 2009; Nicolson 1987; Whitten 1987; Wright 1990).

16.3.1 *Strepsirrhines and Tarsiers*

In many species of strepsirrhines and tarsiers, infants are not constantly carried, but rather left behind, outside the shelter, for up to several hours while the mother is foraging. When females “park” their infants (Kappeler 1998), like in ruffed lemurs (*Varecia variegata*, Morland 1990), slender loris (*Loris lydekkerianus*, Nekaris 2003), or spectral tarsiers (*Tarsius spectrum*, Gursky 2000), they save energy compared to females in anthropoid primates, where infants are carried much more frequently. This energy-saving behavior by the mothers might render strong male involvement unnecessary. Nevertheless, male care is shown in many strepsirrhines and tarsier species, albeit at relatively lower levels (reviews in Kappeler *in press*; Patel 2007; Tecot et al. 2012; Whitten 1987). Male care usually includes grooming or playing, and occasionally carrying (Bastian and Brockman 2007; Patel 2007).

For example, in slender lorises, males visit parked infants, groom and play with them, or just stay in proximity (Nekaris 2003). Slender lorises have a multi-male, multi-female social organization, and several males may show interest in a receptive female. At times, several males might interact with a particular infant, suggesting that infants may receive care not only from biological fathers (Nekaris 2003).

The spectral tarsier from Sulawesi Island (*T. spectrum*) is of special interest in comparison to owl monkeys and titi monkeys (see below), because it shares some of the features thought to have facilitated male care in these latter genera. Tarsiers are quite small primates (ca. 100 g) that produce single infants who weigh as much as 22% of the mother's body mass at birth (Gursky 2000). Like titi and owl monkeys, tarsiers are predominantly pair-living, though not as exclusively as the former two taxa. Care behavior is occasionally shown by subadults of both sexes and adult males, but it is the subadult females that are most involved (Gursky 2000). Care takes mainly the form of grooming, playing, and staying in proximity to the infant, but only rarely of carrying it, since infants are usually parked. Unfortunately, no genetic paternity analyses are available to evaluate whether male care is restricted to probable fathers. Yet, given that most groups consist of only one adult of each sex, this is a reasonable assumption.

Thus, in strepsirrhines and tarsiers, male care, albeit not uncommon, is usually of relatively low intensity and, at least occasionally, directed at unrelated infants. Since infants are often parked, it is not likely that male care will act as "maternal relief." However, there is not enough evidence to argue for or against the hypothesis that males provide care in order to obtain better mating opportunities.

16.3.2 *Catarrhines*

Among colobine monkeys, mothers often allow other females to interact with infants, but direct male care is rare (Ross and MacLarnon 2000). Male black-and-white snub nosed monkeys (*Rhinopithecus bieti*), however, provide direct care in the form of carrying and grooming, albeit of moderate contribution (Xiang et al. 2009). Genetic relationships are not available, but since groups of this species can contain as many as 200 individuals, paternity certainty is likely to be low, so that care is probably not exclusively directed to genetic offspring. Thus, male care might alleviate the female's burden, that is, likely to be quite high. Snub nosed monkeys inhabit an extremely cold environment with snow cover for half of the year making resources scarce and foraging effort substantial (Xiang et al. 2009).

In various cercopithecine monkeys (e.g., Japanese macaques, *Macaca fuscata* and chacma baboons, *Papio cynocephalus ursinus*), males are quite tolerant of infants, play with and carry them occasionally (Anderson 1992; Itani 1959). Chacma baboon males carry infants significantly more when they had a higher probability of being the father (Anderson 1992). Infants that are carried more frequently have higher survival probability, and mothers of these infants have shorter inter-birth intervals (Anderson 1992). Although these findings suggests some concrete direct

benefits to infants and mothers from male care, there are other possible underlying causes, like rank or condition of the mother that cannot be ruled out. In savannah baboons (*P. cynocephalus*) males selectively supported juveniles for which they had high paternity probability (Buchan et al. 2003). In vervet monkeys (*Chlorocebus pygerythrus*, formerly *Cercopithecus aethiops*) infant care might possibly serve as a mating strategy. Male vervet monkeys appear to modify their infant care behavior depending on their “audience.” In other words, they care more for infants when the mother is present; and females, in turn, are more affiliative toward males that have previously cared for an infant (Keddy Hector et al. 1989).

Thus, among cercopithecine monkeys, there is evidence for one or several of the potential benefits of male care: baboons care predominantly for their own offspring, and females seem to benefit by shorter inter-birth intervals, and vervet males might use infant care as a mating strategy. Nevertheless, we must reiterate that in all of these taxa male care is infrequent and most of the time indirect.

There are only three species among catarrhine primates that show more significant male care: humans, siamangs (*Symphalangus syndactylus*, Lappan 2008), and Barbary macaques (*Macaca sylvana*, Small 1990). In a population of semi-free-ranging Barbary macaques, infants were held or carried by non-mothers and adult males almost a fourth of the time (Small 1990). Since females mate with multiple males during estrous, paternity is equivocal, and male care is probably directed sometimes to unrelated infants. Infant handling was, however, not random, and adult males preferentially handled infants of high ranking mothers (Paul 1999); whether infant handling also results in preferential mating with these females is not known.

Among the hylobatids, pair-living is the prevalent, though not exclusive, social structure (Fuentes 2000; Lappan 2008; Reichard and Barelli 2008). Despite this, direct male care of infants has not been reported for most gibbon species in the wild, with the notable exception being the largest species of the family, the siamang. When siamang infants are approximately one-and-a-half-year old, they are frequently transported by males, but the care patterns seem to be variable: males in monogamous groups tended to carry infants more (27%) than males in socially polyandrous groups (12%, Lappan 2008). With male helpers, female siamangs were able to reduce their own carrying effort and had shorter inter-birth intervals than when males participated less (Lappan 2008).

In most human societies, mothers are not the sole caretakers of infants, and fathers, other relatives, and even unrelated individuals may participate in infant care (Geary 2005; Hewlett 1989; Hrdy 2008; Kramer 2010; Marlowe 2000). Direct male care is facultative for our species and can range from being virtually absent to providing a substantial contribution to a child’s upbringing. The amount of care provided by men varies between individuals and peoples, and is related to, among others, the subsistence type (forager men caring most) and marriage system, with decreasing father–infant interaction with increasing degree of polygamy (Geary 2000; Hewlett 2004; Marlowe 2000). Men’s contributions, whether direct or indirect, can have a profound influence on the survival rate and physical well-being of children. In the traditional hunter-gather society of the Paraguayan Ache, mortality rates of children without father are higher compared to children with the father

present (Hurtado and Hill 1992). In industrial societies, social competitiveness of children is also positively influenced by the father's investment (Geary 2005). Additionally, male care and investment by provisioning are likely to relieve the mother's burden and may explain the comparatively short inter-birth intervals of women compared to other apes (Gettler 2010). Childcare and investment by men are often primarily directed to genetic offspring, but can be viewed at least partly also as a mating strategy, if some care is provided to stepchildren as long as the mother still lives together with the caring man (Anderson et al. 1999; Hewlett 2004; Marlowe 1999).

16.3.3 *Platyrrhines*

Within the nonhuman primates, the highest levels of male care are found in several taxa of New World monkeys, particularly in the callitrichines, titi monkeys, and owl monkeys. For example, males are the primary caregivers among socially monogamous titi monkeys (Fragaszy et al. 1982; Mendoza and Mason 1986; Welker and Schäfer-Witt 1986). When infant titi monkeys are separated from their fathers, they show a strong pituitary-adrenal stress response and vocalize intensely, whereas the response is much weaker when the mother is removed. This indicates that infants are more strongly bonded to their fathers than their mothers (Hoffman et al. 1995). Likewise, in threat situations captive cotton-top tamarin infants run to the individual that carries them the most, which is usually the father or older sibling, but never the mother (Kostan and Snowdon 2002).

In the callitrichines, infants are usually born as twins and their combined weight might be as much as 15–20% of the mother's body mass (Garber 1994; Goldizen 1990; Leutenegger 1973). All group members participate in helping, including offspring from previous litters (Goldizen 1987b; Huck et al. 2004; Porter and Garber 2009; Savage et al. 1996; Yamamoto et al. 2009). The callitrichines show a highly variable mating system, but often live in polyandrous or polygynandrous groups (Garber 1997; Goldizen et al. 1996; Goldizen 1987a; Heymann 2000; Nievergelt et al. 2000; Porter 2001). Although males are often related to each other, helpers are not always related to the infants they care for, and in mustached tamarins (*Saguinus mystax*) fathers carry infants less than any other helper (Huck et al. 2004).

Carrying infants is an energetically costly behavior. Even in captivity, cotton-top tamarin (*Saguinus oedipus*) helpers lose weight during the carrying period, while mothers, who carry less frequently, gain weight (Achenbach and Snowdon 2002; Morcillo et al. 2003; Sánchez et al. 1999). Thus, the care provided by males seems to reduce the metabolic costs of the females, and females reduce their own efforts in the presence of helpers (Fite et al. 2005; Tardif 1994). In wild golden lion tamarins (*Leontopithecus rosalia*) the number of infants born is positively correlated with the number of helpers in the previous season (Bales et al. 2001). It is therefore likely that female future reproductive success is dependent on the amount of help she receives (Price 1992b).

It is less clear whether male care could also function as a mating strategy in this taxonomic group. One study suggested that female cotton-top tamarins mount preferentially with males carrying infants (Price 1990). However, in another study female cotton-top tamarins and common marmosets (*Callithrix jacchus*) did not preferentially copulate with males that had provided more infant care (Tardif and Bales 1997).

In summary, interactions between non-mothers and infants are common among primates, not only with other females, but also with males who are often quite tolerant toward infants (Nicolson 1987; Whitten 1987). Moreover, in some primate genera the interactions take on a qualitatively different form. In the three Neotropical taxa of titi monkeys, owl monkeys, and callitrichines, as well as in the old world siamangs, and some human societies, male care is much more direct and obligatory (Fernandez-Duque et al. 2009; Geary 2005; Hewlett 1989; Marlowe 2000). Male care seems to be linked to paternity certainty in many, albeit not all species, but it is not confined to monogamous taxa. Particularly in some taxa with obligate allo-maternal care, females seem to benefit from male care through shorter inter-birth intervals or in some cases through preferential interaction with males who provide infant care.

16.4 Parental Care in Owl Monkeys

16.4.1 General Biology

The owl monkeys of the Neotropics are among the few socially monogamous² mammal species (Fernandez-Duque 2011a), and as already noted, they show intense male care (Fernandez-Duque 2011a; Rotundo et al. 2005; Wright 1984; Fig. 16.1). Owl monkeys are the only anthropoid primate with primarily nocturnal activity (Wright 1989). However, one species, the Azara's owl monkey (*Aotus azarae*) from Paraguay and northern Argentina, shows cathemeral activity, being also active during the day (Erkert and Cramer 2006; Fernandez-Duque 2003, 2011a; Fernandez-Duque et al. 2010; Wright 1989). Wild owl monkeys live in small groups, normally composed of an adult heterosexual pair, one infant, and one or two juvenile or sub-adult individuals (Fernandez-Duque 2011a). The sex ratio, both adult and operational, is apparently even, as indicated by our capturing of similar numbers of females ($N=82$) and males ($N=76$; G-test, $G=0.2$, $p=0.63$). In our study population, males and females are replaced equally often. Between 2001 and 2010, we observed 25 female and 21 male replacements in a total of 142 group years in 18 groups (Fernandez-Duque et al. 2008; Huck and Fernandez-Duque 2012). Likewise,

² We define social monogamy as a social system in which a single adult female and adult male each have only one social adult partner of the opposite sex for at least one, but usually several, breeding seasons. Such pairs will share and often defend a common home-range and may or may not develop a special pair-bond (Kappeler and van Schaik 2002; Martin et al. 2007; Wickler and Seibt 1983).

both sexes seem to have similar survival rates (survival analysis for 53 females and 52 males over 2 years of age, accounting for censored data and using a Weibull distribution, $\chi^2=0.06$, $p=0.81$).

16.4.2 *Development and Parental Care*

Our understanding of infant care and development in owl monkeys comes from both studies of captive individuals and free-ranging ones. In captivity, a few studies have examined parental behavior and infant development in different owl monkey species (Dixson and Fleming 1981; Jantschke et al. 1998; Wolovich et al. 2007, 2008; Wright 1984). Birth seasonality has been reported in wild, as well as in some captive owl monkey populations (Fernandez-Duque 2002, 2011a; Gozalo and Montoya 1990). In the Argentinean Chaco, long-term pairs of Azara's owl monkeys often have one infant every year between September and December (Fernandez-Duque 2002). Both adults groom and clean the infant frequently with the mouth in captivity (on average 0.65 bouts/h, Dixson and Fleming 1981), but grooming seems to be less frequent in the wild (Fernandez-Duque et al. unpublished data; Wright 1984). During the first month of life, infants are almost constantly carried by their parents. By the third month of life, they spend half the time off their parents, and by the fourth month they move independently more than 90% of their time (Dixson and Fleming 1981; Rotundo et al. 2005; Wright 1984, dashed line in Fig. 16.1a). The first few days after birth the infant is carried mainly by the mother, but soon afterwards, the male becomes the main caretaker (Dixson and Fleming 1981, this study, Fig. 16.1). Males carry infants much more often than females, and they also play more with them (Fernandez-Duque et al. unpublished data; Wright 1984, this study). Older siblings hardly ever participate in infant carrying, in contrast to callitrichines (e.g., Huck et al. 2004; Tardif et al. 1992). In captivity, adults actively help the infant to transfer from one parent to the other (Dixson and Fleming 1981). Many transfers are triggered by the rejection of one parent, and mothers reject more often than fathers, who rarely induce infants younger than 2 months of age to leave their back. As with so many other traits, the pattern of infant-carrying in owl monkeys resembles closely that of titi monkeys (Welker and Schäfer-Witt 1986).

In the wild, the long process of weaning starts around the end of the third month, when mothers are seen for the first time to reject infants. Nursing continues, however, at least until the fifth month, and nipple contact may be observed, albeit rarely, as late as 8 months of age (Rotundo et al. 2005). These results are similar to those reported for captive individuals; nursing frequency in captivity is very low by the 18th week of life (Dixson and Fleming 1981). Infants start to explore, manipulate, and finally consume solid food during their second month of life in both captive and wild populations. Food sharing with infants, in both captive and wild owl monkeys (Rotundo et al. 2005; Wolovich et al. 2006, 2007, 2008), is not as frequent as it is among the callitrichines (Feistner and Price 2000; Huck et al. 2004; Porter 2001; Price and Feistner 2001). It also appears to be less frequent than in wild titi monkeys (*Callicebus torquatus*), where it was observed with a frequency of 0.08 begging

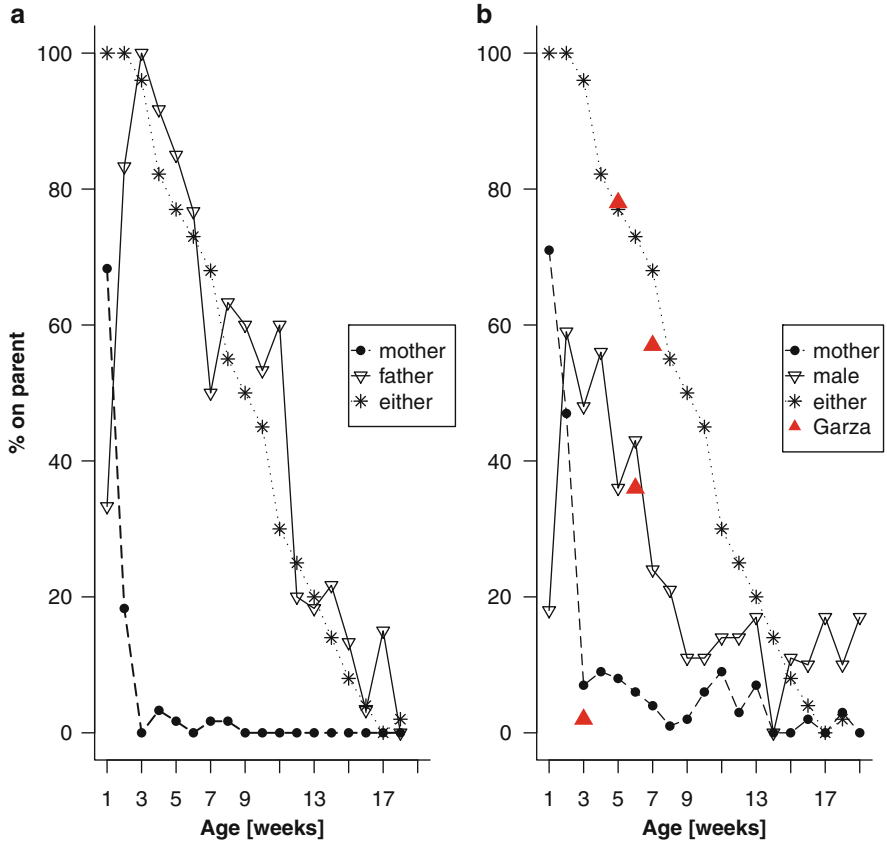


Fig. 16.1 Infant carrying. **(a)** Percentage of sampling points (“time”) that infants are carried by their mother or father (data from captivity after Dixson and Fleming 1981), or either parent (data from the wild after Rotundo et al. 2005). The data are in some cases interpolated. **(b)** Percentage of sampling points that infants are carried or nursed by their mother, the group’s adult male (this study), or either parent [after Rotundo et al. 2005, same as in **(a)**]. Note that the data for males and females were obtained in a slightly different manner than in Rotundo et al. (2005), where data were obtained by focal samples exclusively on infants. Here, we collected data in 20-min focal protocols on any group member, and every 4 min the carrier of the infant was noted. Since the focal animal was often not the infant, there are occasions when the carrier, if it was not the focal animal, might have been out of sight, thus resulting in lower total values for males and females. Likewise, we were occasionally not able to identify the carrier. The filled (or: upright) triangles give the weekly percentage of carrying effort by the female “Garza” before she was ousted from her group in week 4 and while she was caring for the infant on her own until the death of the infant in week 7 (see text for details). The numbers of focal samples of Garza per week were 15, 17, 16, and 2 for weeks 3, 5, 6, and 7, respectively

events/h, mainly directed toward the male and less often to an older juvenile or the mother (Starin 1978).

In the wild, the process of development differs little between the sexes (Huck et al. 2011, Fig. 16.2). Although no hormonal analyses have been conducted on any wild owl monkey population to characterize sexual maturity, based on testes size

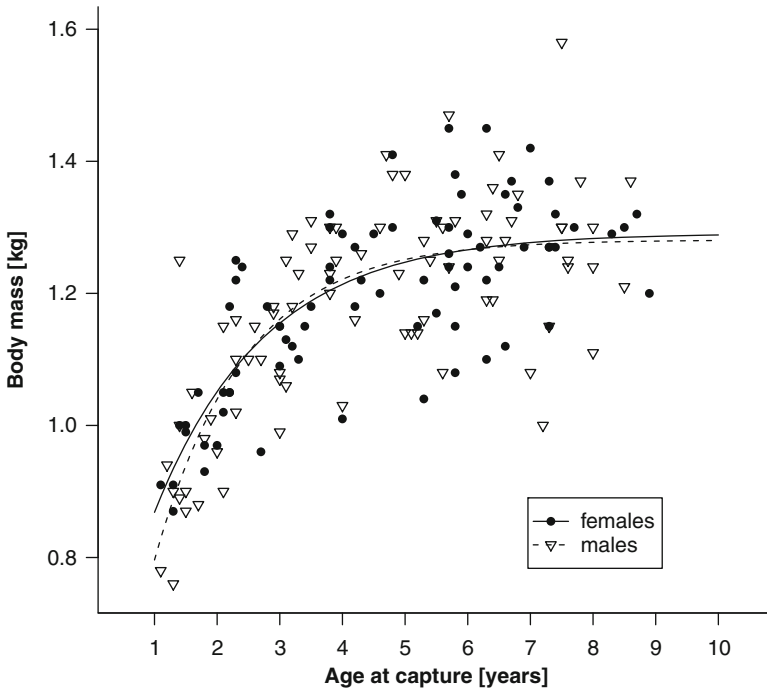


Fig. 16.2 Correlation between age and body mass in female and male owl monkeys. Von Bertalanffy curves are fitted through scatter plots (after Huck et al. 2011).

and the development of the sub-caudal gland, wild Azara’s owl monkeys seem to start puberty around 2 years of age and to reach sexual maturity toward the end of their fourth year (Huck et al. 2011). A study of a smaller owl monkey species in captivity estimated an earlier onset of puberty and found that the testes reached adult size by 2 years (Dixson et al. 1980). In captivity, owl monkeys from Peru (*Aotus nancimae*) usually had offspring when they were 3.5 years old, but sometimes when they were as young as 2 years old (Gozalo and Montoya 1990). In our population, individuals never had infants before they were 2 years old (Huck et al. 2011). Apart from the potentially younger ages at first reproduction in captivity, the postnatal development appears to be similar for different owl monkey species, both reared in captivity and in the wild.

16.4.3 Caring Dads

The described pattern of development in young owl monkeys shows that males strongly contribute to the upbringing of infants (see Fig. 16.1); but how do the males benefit from their involvement? In order to identify support for the “genetic advantage”

hypothesis, two things need to be established: the genetic relationship between the male and the infant, and a comparison of infant survival in groups with and without male caretakers. Genetic analyses suggest that the male present in the group when an infant is conceived is the genetic father of that infant (unpublished results). However, due to the replacements of adults described above, adult males may also be unrelated to infants in their group. When this happens, some evidence indicates that they still provide care in much the same way as genetic fathers (Fernandez-Duque et al. 2008). Regarding the second point, it is virtually impossible to estimate infant survival for groups without any male caretaker in the wild, because breeding vacancies that are due to the death or disappearance of one parent are usually filled up immediately by new incoming adults (Huck and Fernandez-Duque 2012).

Although the lack of groups without male care hinders an evaluation of the “maternal relief” hypothesis, there is some limited evidence to evaluate it. After the death of her mate, a captive owl monkey female had to bring up her infant with only the assistance of an older daughter (Jantschke et al. 1998). The older sibling provided substantial infant care, similar to the situation described for one wild group where the adult male died soon after the birth of the infant (Fernandez-Duque et al. 2008). In both cases, the carrying effort of the mother was essentially not higher than in groups with two adults, and in captivity the orphan infant was completely independent after 3 months, sooner than infants in groups with male caretakers (Jantschke et al. 1998, compare with Fig. 16.1). This evidence suggests that female owl monkeys may not be capable or willing to invest more in their current offspring, at least as long as adult males or older siblings are available. Siblings, however, might be not strong enough physically or too inexperienced to fully replace adult males, forcing the infant to become independent sooner. In the wild, earlier independence could lead to a higher energetic need for the infant, due to increased mobility, as well as increased predation risk. It is often in dangerous situations (e.g., an alarm call by a group member, a wide gap between tree branches) that even relatively old infants or young juveniles seek transport by the adult male (Rotundo et al. 2005). Therefore, enforced earlier independence might lower the overall fitness of young owl monkeys.

What would happen if a female had to raise an infant completely on her own? We predict that the female would increase her carrying effort, with the subsequent additional energetic cost that may result in a loss of body mass and a reduced probability of reproduction in the following year. Apparently, wild females do not lose body mass during the infant-rearing period when the male cares for the infant (Fernandez-Duque 2007, AAPA published abstract). On one occasion, a female with a dependent 1-month-old infant was replaced by a female intruder shortly after the group’s male had been replaced. During 8 months we occasionally saw the mother, ranging solitarily and in the first month with the infant, until eventually we found her radio-collar on the ground strongly suggesting she had died. Before she was ousted from the group, the mother carried the infant as infrequently as is typical for mothers (2% of time), while afterwards she carried it on average 58% of the time (Fig. 16.1b, filled (or: upright) triangles). During the first week as a “single mother” (week 5 in the life of the infant), she compensated nearly completely, and the infant was carried

as much as it would have been normally transported by the male. Yet, in the following week, the infant was carried much less than usual for that age. This natural experiment provides some data indicating that the female was not capable of completely compensating for the absence of the male's care, and the infant did not survive. Together, these two single-case observations provide some support for the "maternal relief" hypothesis, even when acknowledging that better data on energy budgets of males and females are still much needed.

As explained in the first section, we expect qualitatively different adult–infant interactions under the "genetic advantage" hypothesis than under the "mating strategy" or "maternal relief" ones. Following the replacement of the putative father by a new male, half of the immatures (0–24 months) disappeared (i.e., they probably died) before they reached 2 years of age. A similar proportion of immatures disappeared in stable groups or in groups where the mother has been replaced (Huck and Fernandez-Duque 2012). In other words, infant survival/disappearance, as a proxy for male–infant relationship, was similar in groups with the putative father and groups where the father had been replaced. Likewise, the age of natal dispersal, which can also be constructed as indicative of the relationship between young and adult male, did not differ between subadults from stable groups or those with male or female replacement (Fernandez-Duque 2009; Huck and Fernandez-Duque 2012). Finally, the spatial relationships between the infant and the adult males can also be used as a proxy for the quality of a relationship (Mitani et al. 2000; Palombit et al. 1997; Perry 1998). Intruding males are found in close proximity to the offspring of their predecessors as often as the fathers themselves before being replaced (Fig. 16.3). In conclusion, although these demographic and behavioral data provide some support for the "mating strategy" hypothesis, it is still difficult to distinguish between the hypotheses that male care relieves the female's energetic burden and that male help makes him attractive to the female.

16.5 Conclusions: Why Do Male Owl Monkeys Care to Care?

Despite some significant advances recently, we are just beginning to find answers to the question of why male owl monkeys invest so much in their offspring. Titi and owl monkeys are monogamous, but, as we have seen, not all monogamous species show extensive male care. For example, in saki monkeys (*Pithecia* spp., Norconk 2007) and gibbons with the exception of the siamang (Lappan 2008; Rafacz et al. 2012), mothers do most of the work, some occasional observations of infant carrying or babysitting notwithstanding (Schmitt et al. 2005). So it is obviously not the monogamous social system per se that makes dads help (see also Komers and Brotherton 1997; Smuts and Gubernick 1992; Whitten 1987). Rather, in several species where females mate with multiple males, males and even unrelated individuals might engage in infant care behavior, most prominently in the callictrichines (Garber 1997; Goldizen et al. 1996; Goldizen 1987a; Heymann 2000; Huck et al. 2004; Nievergelt et al. 2000; Porter 2001).

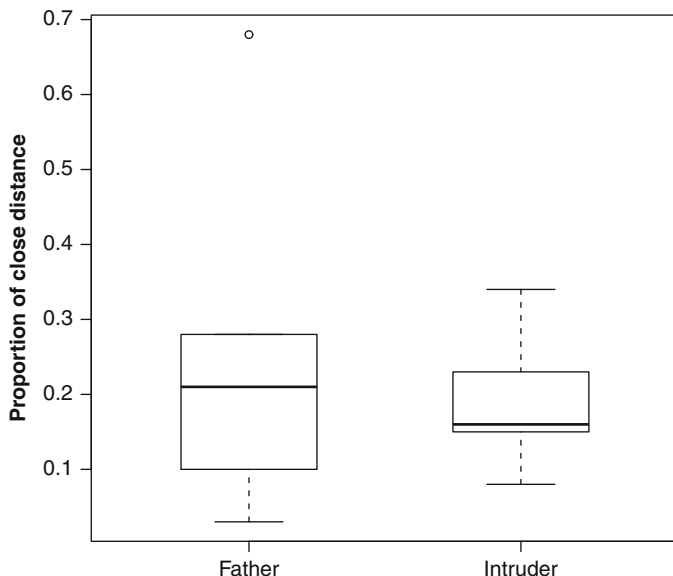


Fig. 16.3 Proportion of close distances (body contact to 1 m) between an immature and an intruding male ($N=5$ infants), or putative fathers ($N=6$). Data were collected in 20-min focal protocols, noting the distance to all other group members every 4 min. For more detailed description of the methods see Huck et al. (2011). Medians do not differ between the groups (Wilcoxon signed rank test, $W=12.5$, $p=0.71$), even if “repeated measures” for the same male are taken into account (results of mixed-effect models not presented)

We have shown that owl monkey infants rely on male care, and that the female is also likely to benefit from the male’s help (Jantschke et al. 1998, this study). Yet, rigorous analyses of energy budgets of males and females of wild owl monkeys still need to be conducted. The predictions of the “mating strategy” hypothesis are partly supported. As demonstrated above, owl monkey infants are likely to benefit by the care provided by the male. Second, given that female owl monkeys are the same size as males (Fernandez-Duque 2011b), females can probably exercise control via the offering or withholding of matings. The final prediction about the females’ ability to assess and compare males is more difficult to test in a pair-living species, because there is no day-to-day choice between several males. Studies on mate selection previous to pair formation have not been conducted, but since males care for unrelated offspring when they enter new groups (Fernandez-Duque et al. 2008), infant care as a mating strategy cannot be refuted either. Thus, from the individual male’s perspective, he might benefit in all three broad ways from providing paternal behavior.

What do our data indicate regarding the population modeling approach that considers how other individuals are behaving (Kokko and Jennions 2008)? At least two of the three conditions that are postulated to favor the traditional, female-biased, infant care pattern are not found in owl monkeys: biased sex ratio, uncertainty of

paternity, and sex differences in strength of sexual selection. In our study population, the sex ratio of captured individuals has been approximately even, and paternity certainty seems to be high. Even if future genetic studies should reveal some low levels of extra-pair paternity, there is apparently little incentive for a male to leave his mate to seek other mating partners. Finally, whereas strong sexual selection might reduce paternal behavior because it changes the operational sex ratio, it seems unlikely that sexual selection may be operating more strongly on males than on females. The species is not only monogamous, but remarkably monomorphic (Fernandez-Duque 2011a, b). This of course raises the question of why owl monkeys are monomorphic and monogamous, and leaves us with a hen-egg problem, though the evolution of monogamy before the evolution of paternal care, or even non-parental helping, seems the most likely scenario (Dunbar 1995; Goldizen 1990).

The model of Kokko and Jennions (2008) also indicates that the sex with the higher mortality rate due to caretaking behavior will be selected to provide more care due to the mortality-induced changes in the adult sex ratio. However, given the apparently even sex ratio and no significant differences in the rate of adult replacement (i.e., a possible proxy for mortality) or survival, it is unlikely that adults face different mortality rates due to either intrasexual competition or caretaking behavior. Although there might be still undetected differences in mortality, if owl monkeys have currently reached a stable equilibrium, historical differences in mortality rates might not be apparent any longer.

It is difficult to assess whether any of the sexes invests more than the other when lacking estimates of the specific energy costs of different caretaking behaviors. How many milliliters of milk equal how many minutes of carrying the infant? In mustached tamarins there seems to be a trend for an inverse relationship between the carrying effort and the amount of food shared with infants (Huck et al. 2004). Although female owl monkeys do not carry infants much, the whole energetic costs of gestation and lactation still rest with them.

A final puzzling aspect in the caretaking system of owl monkeys, like in titi monkeys, is that older siblings do not participate in the upbringing of the infants (Fernandez-Duque et al. 2009), which is in stark contrast to the callitrichines. We might speculate that it has to do with stronger intra-sexual competition in callitrichines, where dominant females often monopolize breeding positions (Löttker et al. 2004; Snowdon and Soini 1988). Additionally, it might be more disadvantageous for the smaller callitrichines to disperse at a young age and roam solitarily because of potentially higher predation pressure.

In summary, both new theoretical developments and our own data on owl monkeys suggest that when there are few differences in the strength of sexual selection between the sexes and no multiple matings, this could result in the evolution of egalitarian sex roles with regards to infant care, in a similar process as described for the evolution of equal sex ratios (Fisher 1930; Kokko and Jennions 2008). Under this light, the question might not be why monogamous and sexually monomorphic owl monkey or titi monkey males are “good dads,” but rather, why they became monogamous and sexually monomorphic. Did monogamy precede or follow from more egalitarian infant care behavior? Why do older siblings not participate in the

rearing of their brothers and sisters? And why do males in some presumably monogamous primates (like sakis and most gibbons) NOT help?

In order to answer these questions, we need comparative studies. Studies using similar methodology should be conducted on primate species living in pairs, one-male multiple-female groups, and multi-male groups. A particular focus should be on the energetics of infant care, male–infant interactions, male–female interactions, and pace of infant development. For example, analyses of C-peptide levels in captivity under varying food and activity schemes might help to determine the energetic burden of gestation, lactation, and infant carrying (e.g., Harris et al. 2010; Sherry and Ellison 2007), although this is unfortunately not feasible in the wild with such a small, arboreal species. Such studies should shed further light on the evolution of male participation in infant care, including our own species.

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