The Biology of Paternal Care in Human and Nonhuman Primates

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Abstract

Among primates, intense paternal care is manifested in only a few distantly related species, including humans. Thus, neither purely phylogenetic nor socioecological hypotheses can explain its presence or the variability in the expression of paternal behaviors. Traditional theoretical models for the evolution of paternal care can now be reexamined, focusing on male-female interactions as a possible key to understanding parental strategies. At a proximate level, the existing evidence implies a common physiological substrate for both paternal behavior and pairbonds. Vasopressin, and perhaps prolactin and testosterone, apparently underlies the endocrinological bases of paternal care, and neuroanatomical reward pathways may be involved in the formation of attachment bonds. Understanding of the genetic structure of primate populations and the neurogenetics of social behavior is also emerging. A multidisciplinary approach that also considers epigenetic and transgenerational effects promises to open new avenues to explain the flexible nature of paternal care in primates.

INTRODUCTION

Few aspects of primate behavior are so intriguing, yet so poorly understood, as the expression of intense paternal care. Although rare, paternal care in a few primate species and some human societies includes providing protection from predators and other conspecifics, sharing food, playing, grooming, carrying infants, teaching hunting skills, and singing lullabies. All avian and mammalian males face the uncertainty of paternity because of internal fertilization. Participation of mammalian fathers in the most essential parental activities is further constrained by pregnancy and lactation. Yet, in spite of these limitations, some primate males display intense paternal care (Gubernick & Klopfer 1981, Kleiman 1985, Kleiman & Malcolm 1981, Smuts & Gubernick 1992, Whitten 1987, Wright 1990).

Field and laboratory data on primate paternal care have accumulated to the point where a synthesis of its expression is possible. Paternal care among primates, illustrated in its extreme form by our research on a few nonhuman primate species and some human societies, is varied (Di Fiore et al. 2007; Fernandez-Duque et al. 2008, 2009; Mendoza & Mason 1986a,b; Rotundo et al. 2005; Valeggia 2009; Wolovich et al. 2008). Using information from disciplines as disparate as evolutionary biology and neuroscience, we provide an initial attempt to understand this variation, ecological and social determinants, and common proximate mechanisms.

A TAXONOMY OF PATERNAL CARE

Paternal Care and Paternal Investment

Paternal/parental care, biparental care, paternal/parental investment, and alloparental care are terms regularly mentioned in the primate literature. Given the different ways in which they are used, it is important to state that our work has focused on paternal care, not paternal investment. Paternal care and paternal investment are frequently used interchangeably, and wrongly so (Sheldon 2002). Thus, we do not

attempt to relate the two terms or to use paternal care as proxy for paternal investment.

Paternal care is a suite of behaviors performed by a mature male (the putative/social father of the immature young), which would not be performed in the absence of the young. These behaviors are directed to the infant and have a positive effect on infant development, growth, well-being, or survival. They may include carrying, grooming, playing, sharing food, feeding, cleaning, retrieving, huddling, babysitting, defending, and teaching. Some of these behaviors may continue beyond the stage of development when they are necessary for infant survival. This is so because infant primates, unlike other mammals, experience a long period of dependency during which they require significant assistance.

Infants play an active role in directing their own development and have considerable skill in eliciting care behaviors. Generally the mother is the primary target of the infant's solicitation of care, but in many primate species other group members are also responsive to infants. Alloparental care, care provided by nonmothers, has received significant attention recently (Hrdy 2005, 2008; Ross & MacLarnon 2000; Tardif 1997), but here we are concerned with the relatively rare situation where alloparental care is provided by the putative father.

Paternal care, as defined above, is widespread among birds and fish and is occasionally present in amphibians, insects, and worms (Beltran & Boissier 2008, Clutton-Brock 1991, Trumbo 2006, Zeh & Smith 1985). On the other hand, paternal care is relatively rare in mammals. Among the mammalian orders, it is more frequent in carnivores, rodents, and primates (Kleiman & Malcolm 1981, Woodroffe & Vincent 1994).

Paternal Care in Nonhuman Primates

In most primates, males may be tolerant of infants, or they may occasionally interact affiliatively with them without any clear direct or indirect paternal care provided (Whitten 1987, Wright 1990). The most conclusive evidence

Paternal care: behaviors performed by putative/social fathers, which appear to have positive effects on infant development, growth, well-being, and/or survival

Paternal investment: behaviors performed by putative/social fathers, which increase the probability of the infant's survival

for the benefits that infants may accrue from these infrequent interactions with males comes from studies of wild savannah baboons (*Papio cynocephalus*). Adult males selectively support their offspring in agonistic disputes with a direct effect on the offspring fitness (Buchan et al. 2003, Charpentier et al. 2008). It is still not fully understood whether fathers can somehow recognize offspring likely to be their own or if it is a generalized response to all infants. Still, the putative father interacts affiliatively with infants only in very particular and restrictive circumstances.

It is only among a handful of primate genera that the relationship between males and infants takes on a qualitatively different form. Among siamangs, tamarins, marmosets, titi monkeys, owl monkeys, and some human societies, paternal care is direct, conspicuous, and sustained across time and circumstance. These taxa are only distantly related, suggesting that paternal care may result from evolutionary trajectories developing under different social and ecological conditions (**Figure 1**, see color insert; Di Fiore & Fernandez-Duque 2007).

Paternal care among siamangs is intriguing. All hylobatids (i.e., gibbons, lesser apes) show the traditional correlates of paternal care—social monogamy, territoriality, and reduced sexual dimorphism—but it is only the siamangs (*Symphalangus syndactylus*) that show paternal care. Female siamangs take exclusive care of the infants during the first year of life, but adult males and older juveniles carry infants beginning in the second year (Chivers 1974, Lappan 2008).

Generalized sharing of infant transport is also exhibited by the callitrichids of South America (**Figure 1**). Alloparental care (also called cooperative breeding) is the norm, and the mother, father, siblings, and other group members share in the care of the twins (or triplets) that are born twice a year (Bales et al. 2000, Tardif et al. 2002, Tardif & Garber 1994, Zahed et al. 2007, Ziegler 2000). The infants appear to be highly attractive to group members who often compete for the opportunity to carry dependent infants.

Nowhere is paternal care more extensive and more obligate than among titi monkeys (*Callicebus)* and owl monkeys (*Aotus*, **Figures 2** and **3**, see color insert). Both genera live in small groups consisting of an adult pair and 2–4 young (Fernandez-Duque 2007, Norconk 2007). Females give birth to a single infant each year and the male is the primary carrier for the infant, each assuming their roles soon after birth. Dependent infants may be carried as much as 90% of the time by their putative fathers and transfer to the mother for brief periods usually surrounding active nursing bouts (Dixson & Fleming 1981, Fernandez-Duque et al. 2009, Fragaszy et al. 1982, Mendoza & Mason 1986b, Wright 1984). Siblings very infrequently participate in transport of the infant (Fernandez-Duque et al. 2008). In titi monkeys, infants develop a preference for their fathers over their mothers (Mendoza & Mason 1986b), demonstrated via a strong pituitary-adrenal stress response when separated from their fathers but not from their mothers (Hoffman et al. 1995).

Paternal Care in Human Societies

Human societies vary in the expression of paternal care, from complete absence or aloofness to great intimacy and direct care. A range of variation manifested even within foraging societies. At one end, Aché fathers of the Paraguayian forests seldom hold or interact with infants and young children (Hill & Hurtado 1996). At the other end, male Aka Pygmies are heavily involved in paternal care, spending up to 22% of their time holding young infants (Hewlett 1991).

Societies in both developed and developing countries, with varying levels of industrialization fall within this broad spectrum of expression of paternal care. Intercultural variability in fathering seems to be associated with the local ecology and social environment. Household composition, availability of mating opportunities and resources, the extent of extrinsic mortality, and pathogen stress have all been identified as potential correlates of paternal care in

Alloparental care/Cooperative breeding: infant and young care provided by individuals other than the mother

humans (Hewlett 1991, 1992; Marlowe 1999; Quinlan 2007).

In addition to the great variability in paternal care among human groups, there is usually significant variation among men within societies known for their high levels of paternal care. In those societies, some men do not participate in child care, whereas others cannot do more (Hewlett 1991). Even though human mothers clearly need a considerable amount of help rearing their offspring, paternal care among humans is highly variable and far from a universal trait. This disconnect leads anthropologist Sarah Hrdy to talk about "the paradox of facultative fathering" in the human species (Hrdy 2005, 2008).

EVOLUTION OF PATERNAL CARE

The 1970s and 1980s brought a series of predominantly qualitative theoretical models that attempted to explain the evolution of parental investment or parental care (Dawkins & Carlisle 1976, Hamilton 1984, Kurland & Gualin 1984, Lancaster & Lancaster 1983, Maynard Smith 1977, Trivers 1972). The models emphasized primarily parental investment with a focus on cost-benefit analyses. Nonetheless, two hypotheses remain particularly relevant in attempting to explain the evolution of paternal care.

The first hypothesis is that paternal care evolved in response to the necessity of obligate biparental care to rear offspring successfully (Achenbach & Snowdon 2002; Fite et al. 2005; Hill & Hurtado 1996; Key & Aiello 2000; Miller et al. 2006; Smucny et al. 2004; Tardif 1997; Tardif et al. 2005; Van Schaik & Kappeler 1997; Wright 1984, 1990; Ziegler et al. 2006). This hypothesis seems particularly relevant for explaining the evolution of alloparental care in the callitrichids. The mother, whose body mass is often exceeded by the combined body mass of her infants is incapable of raising the offspring on her own and even a male-female pair have difficulty raising

twins successfully. Her situation is further compounded by a postpartum estrous that results in females being simultaneously and continuously pregnant and lactating. Most callitrichids have elaborate behavioral and physiological mechanisms that prevent nondominant group members from participating in reproduction and thereby facilitate paternity certainty. The care provided by the male (or other conspecifics) contribute to reducing the metabolic costs to the female of raising the offspring as illustrated by the fact that callitrichid males lose weight when they are providing most infant transport. The obligate biparental care hypothesis has less appeal for other species exhibiting intense paternal care, such as titi and owl monkeys.

The second hypothesis considers the affiliative interactions between males and infants as a mating strategy by males that helps them develop a relationship with a female and secure a position in the larger social network. The hypothesis has been useful to examine male-infant interactions in taxa where there is no conspicuous and direct care (Smuts & Gubernick 1992), and more recently in humans (Marlowe 2000). The relationship between paternal care and the development of emotional attachments (or pair-bonds) in humans has played a central role in evolutionary models of human behavior (Geary & Flinn 2001, Hawkes 2004; see sidebar, Attachment Bonds). Investigators have historically argued that pair-bonds evolved given the female need for paternal infant care and provisioning. For example, men in Xhosa (South Africa) invested the most (in terms of money and time) in their coresiding putatively biological children and the least in the step-offspring of a former partner (Anderson et al. 1999, 2007). However, biological children living with a former partner and stepchildren of current partners receive similar levels of investment. Among the Hazda of Tanzania, biological children receive more care (both direct and indirect) than do stepchildren (Marlowe 1999). Thus men provide care to their partner's offspring as a component of their mating

Attachment: an enduring form of emotional bond between two individuals

strategy, but they tend to provide more to their own offspring. This tendency suggests that paternity confidence plays an important role in shaping men's relationships with women and with their putative genetic children (Anderson 2006). These studies illustrate problems inherent in quantifying and differentiating parental investment and parental care. This is true particularly when men may be providing investment or care for children that will have benefits only in the very long term (e.g., college tuition, teaching hunting skills).

These early models were extremely influential and shaped the research on paternal care and parental investment during the next decades. Their impressive contributions notwithstanding, it cannot be overemphasized that they were developed and evaluated on very limited data. Bateman's and Triver's contributions have recently been reexamined with some fascinating new insights (Parker & Schwagmeyer 2005, Queller 1997, Wade & Shuster 2002). Wade & Shuster (2002, p. 291) proposed that "differences in initial parental investment between the sexes are likely to arise from rather than lead to sexual selection favoring increased mate numbers in males and emphasis on parental care by females." This effectively reverses the direction of causality between sexual selection and parental investment and would lead, if accepted, to a major reconsideration of sex differences in parental care (Kokko & Jennions 2003). Other authors continue to remind us of the need to abandon the now untenable traditional view of coy females and ardent males championed by Bateman and Trivers and followed dogmatically ever since (Snyder & Gowaty 2007, Tang-Martinez & Ryder 2005). We have enough evidence in a wide range of taxa, primates included, to show that the relative contributions of males and females in the shaping of social systems and in the provision of care are better understood as the outcome of a conflict between the sexes. A conflict during which females regularly exercise choice and control and during which female promiscuity is far from an exception (Gowaty 1996, 2004; Hrdy 2000).

ATTACHMENT BONDS

In many species, infants are highly motivated to form an emotional bond with their mothers (Bowlby 1969) and, in the absence of the mother, will direct filial attachment to the closest individual (Mason & Kenney 1974). Ainsworth (1969) elaborated the elements of attachment bonds to include the following: (*a*) individual recognition, (*b*) specific preference, and (*c*) separation distress (Mendoza et al. 1980). Infant monkeys will return to their attachment figure when distressed, suggesting that stress-buffering or secure base is also a component of attachment (Suomi 1999). Using these criteria it is possible to determine whether affiliative relationships qualify as attachment or something more akin to friendship (Mendoza et al. 1991). In titi monkeys, infants form a unidirectional attachment bond with their fathers, which persists into adulthood; mothers are less effective attachment figures in the absence of the father (Hoffman et al. 1995, Mendoza & Mason 1986b). Mothers and fathers do form attachment bonds with each other, but not with their offspring. Other nonattachment relationships among family members are amicable (including close following, play, food sharing, and passive contact). Thus it is not possible to distinguish attachment bonds on the basis of proximity or contact alone, as has been often incorrectly assumed.

ENDOCRINE, GENETIC, AND NEURAL SUBSTRATES OF PATERNAL CARE

Hormonal Substrates of Paternal Behavior

The hormonal correlates of paternal care in mammals have not been as extensively studied as those of maternal care (Bridges 2008). In females, mechanisms regulating maternal behavior may be derived from processes involved in birth or, for mammals, in the regulation of lactation. Sudden changes in progesterone, estrogen, oxytocin, and prolactin, all involved in birth or lactation, are also implicated in maternal behavior. Therefore, although it is reasonable to suppose there is overlap between mechanisms supporting maternal and paternal behavior, it is unlikely that they are the same ones related to birth and lactation, which obviously do not have male parallels. When

examining the hormonal basis of paternal care, we are compelled to signal the correlational nature of most of the evidence and the bidirectionality of hormone-behavior interactions (Almond et al. 2008, Schradin & Anzenberger 2002).

Prolactin, a peptide secreted by the anterior pituitary gland, has long been associated with maternal care in birds and mammals (Ziegler 2000). Prolactin also appears to be involved in paternal care in a variety of species (Schradin & Anzenberger 1999, Wynne-Edwards & Timonin 2007, Ziegler 2000). Among some of the neotropical primates that display intense paternal behavior, adult reproductive males show changes in prolactin levels associated with fatherhood (Schradin et al. 2003). The way prolactin changes are associated with paternal care widely varies, and this variation could reflect the different ways in which males experience and express infant care. In humans, the role of prolactin in paternal care is not straightforward. Parental experience affects men's prolactin responses, but recent contact with infants and individual differences in responses to infant cues may be responsible for the hormonal changes rather than the reverse (Delahunty et al. 2007, Fleming et al. 2002, Gray et al. 2007). No evidence as yet indicates that elevations in prolactin actually contribute to the expression of paternal behavior. Because prolactin is stress responsive and is regulated by each of the monoamine systems involved in emotion regulation, the prolactin changes attendant to interactions with the infant may be epiphenomenal.

Investigators have conclusively associated two other peptide hormones, oxytocin and vasopressin, with parental care. Oxytocin is implicated in maternal behavior and in female reproduction through its role in parturition, milk let down during lactation, sexual behavior, and sperm transport (Pedersen et al. 2006, Pedersen & Prange 1985). Although oxytocin may underlie the expression of paternal behaviors (Parker & Lee 2001), contradicting evidence indicates otherwise (Bales et al. 2004a). Vasopressin has been implicated in other sociosexual behaviors including courtship, male-male competition, and pair-bonding (Lim et al. 2004a, Moore 1992). Both sexes respond to both peptides, but oxytocin seems to be more relevant in females and vasopressin in males (Bales et al. 2004b, Carter 2007, Carter et al. 2008b). The sexually dimorphic physiological and behavioral effects of oxytocin and vasopressin appear to be conserved in humans as well (Feldman et al. 2007, Gray et al. 2007, Sanchez et al. 2009).

Testosterone is a steroid hormone strongly associated to reproduction and infant care. One seminal idea in behavioral endocrinology is that testosterone is antagonistic to infant care, and males may have to make trade-offs between mating effort and parental care (Ketterson & Nolan 1999, Wingfield et al. 1990). For example, marmoset males who carried infants the most had the lowest urinary testosterone levels (Nunes et al. 2001) and the most significant declines in gonadal steroids (Nunes et al. 2000). Male titi monkeys do not show changes in gonadal steroids with the birth of infants, but changes in adrenal steroids suggest that the animals become more stress responsive with the advent of new infants (Reeder 2001). Among humans, several cross-cultural studies indicate that married men with young children tend to have lower testosterone levels than single, unpaired men and married men with no children (Berg & Wynne-Edwards 2001; Gray et al. 2006, 2007; Muller et al. 2008; Storey & Walsh 2000). Although the evidence is not wholly in line with the idea that testosterone is inimical to paternal behavior, the evidence is strong that steroid hormones are involved in expression of paternal behavior.

Genetic Substrates of Paternal Behavior

Genetic studies are making significant contributions in at least two aspects relevant to understanding paternal care. First, they provide data on the biological relatedness between care providers and infants. The presentation of these data will be a most crucial contribution because theoretical formulations have

generally assumed that care providers will adjust their investment on the basis of paternity certainty, which may not always be true (Queller 1997, Sheldon 2002). Second, they are helping us understand the neurogenetic basis of social behavior.

Paternal care and paternity. Molecular genetic studies, combined with long-term behavioral and demographic data, are required to determine biological relatedness and reproductive success. Most primate studies of genetic structure have focused on polygynous species (Altmann et al. 1996, Di Fiore & Fleischer 2005, Gagneux et al. 1999, Keane et al. 1997). Genetic evidence has been used to suggest that some males in polygynous species intervene in agonistic disputes or defend infants from infanticidal males in a manner that directly favors the development and/or survival of their offspring (Borries et al. 1999, Buchan et al. 2003, Charpentier et al. 2008). That said, even if it is shown that males are somehow intervening in favor of their offspring, the nature of their interventions are qualitatively different from those observed in taxa in which there is direct and conspicuous care. Thus, the genetic substrates of the neurobiological mechanisms underlying a tendency to interfere in agonistic disputes would be expected to be different from the ones underlying behaviors such as infant retrieval, transport, and active food sharing.

Unfortunately, only a handful of studies have examined genetic paternity among taxa with direct paternal care. In at least one marmoset species (*Callithrix kuhlii*), genetic chimerism, mixing of two or more genomic lineages within an individual, changes the predicted pattern of 50% sharing of genetic information in siblings (Ross et al. 2007). The caregivers could apparently detect differences due to chimerism inasmuch as males carried chimeric infants more often than nonchimeric ones. Among mustached tamarins and common marmosets, most infants were sired by one male, but nonfathers participated in carrying infants (Huck et al. 2005, Nievergelt et al. 2000). Among fat-tailed dwarf lemurs, there is a high rate of extrapair

paternity and social fathers provide care to extra-pair young (Fietz & Dausmann 2003, Fietz et al. 2000).

No published studies have yet described the genetic structure of populations of titis and owl monkeys in which paternal care is most intense. Still, on the basis of their dispersal patterns, serial monogamy, and mtDNA population structure (Babb et al. 2008, Bossuyt 2002, Fernandez-Duque 2009, Rodman & Bossuyt 2007), it seems likely that the potential genetic benefits of providing paternal care will need to be considered at a community level as has been suggested for gibbons (Reichard 2003). Relatively short dispersal distances and a fast rate of adult replacement may result in males providing care to young who are not their offspring but who are still closely related kin.

Genetics, pair-bonding, and paternal care. Recent attempts to examine the genetics of pair-bonding and paternal care in primates are exciting, but correlational and preliminary. Thus far, they have focused on the potential role of the distribution and quantity of neural receptors for vasopressin (Donaldson & Young 2008, Walum et al. 2008). In voles, polymorphisms in the promoter region of vasopressin receptor 1a gene (*avpr1a*) apparently contribute to behavioral differences between monogamous and polygynous males by altering gene expression and ultimately the distribution and density of vasopressin receptors in brain tissue (Hammock & Young 2005). Primate mating and social behaviors may also be influenced by variation in the number of repeat sequences in the promoter region of the *avpr1a* gene (Rosso et al. 2008, Walum et al. 2008), but evidence on a large number of rodent species strongly indicates that it is extremely unlikely that similar mechanisms are regulating such complex behaviors in humans and nonhumans alike (Fink et al. 2007).

Neural Substrates of Paternal Behavior

At this point, we know very little about the neural substrates of primate paternal behavior. Because paternal behavior co-occurs with

Genetic chimerism: a mixing within an individual of two or more populations of genetically distinct cells that originated in different zygotes

Extra-pair paternity: a male sires an infant with an individual other than the pair-mate

Epigenetic effects:
heritable changes in
gene expression or
phenotype that occur
without changes in the
underlying genetic
sequence

pair-bonding, we can use studies of pair-bonding to supplement what is known, and in doing so, we must draw heavily from studies of monogamous prairie voles (Nair & Young 2006). Two components of the neural circuitry underlie pair-bonding and paternal behavior in voles: a cognitive component required for individual recognition and an emotional component that provides the reward for engaging with particular other individuals (Lim et al. 2004b; Liu et al. 2001; Young et al. 2001, 2005). These circuits did not evolve specifically to support paternal behavior; rather they are an elaboration of existing social recognition and reward circuits that function in a variety of behaviors.

Titi monkeys seem to have neurobiological mechanisms of pair-bonding that parallel the pathways identified in voles. Male titi monkeys that were in long-term pair-bonds (conflating pair-bonding and paternal experiences) showed differences in glucose uptake when compared with males living alone (Bales et al. 2007). The lone males in that study were subsequently paired and PET scans repeated. Then, males in new pairs (without paternal experience) showed some changes in neural activity in the direction of males in long-term relationships but overall were not as different from lone males as they were from males in long-term bonds.

The neurobiological mechanisms facilitating pair-bonding and paternal care may be elaborations of mechanisms that foster sociality more generally. Familiar conspecifics attenuate behavioral and physiological stress in rodents and primates (Gust et al. 1994, Kiyokawa et al. 2004, Mendoza & Mason 1986a, Ruis et al. 1999, Terranova et al. 1999). The pathway by which the social environment influences stress responsiveness has been partially identified and is believed to include activation of oxytocin and vasopressin pathways and ultimately the dopamine and opiate reward pathways in the brain (Carter et al. 1999). Monogamous voles, as compared with nonmonogamous voles, have a greater density of oxytocin receptors in neural structures involved in the reward pathway. Male voles also have a much higher level of vasopressin receptors in structures necessary for

both reward and social cognition (Lim & Young 2006). The evidence in primates is still limited, but fatherhood apparently increases the abundance of vasopressin receptors in the brains of male marmosets (Kozorovitskiy et al. 2006). In humans, a recent review of studies using functional neuroimaging indicates that responses to infant stimuli include the same circuitry identified in rodent and nonhuman primate studies and thus are highly conserved through evolution (Swain et al. 2007).

DEVELOPMENTAL PROGRAMMING AND TRANSGENERATIONAL INFLUENCES

The studies reviewed above give strong support to hypotheses that involve certain neural and endocrine pathways in the expression of paternal care. However, evidence is accumulating that shows epigenetic effects on parental behavior and an increasingly important role of early experience in shaping its development (Carter et al. 2008a, Champagne & Meaney 2007, Michel & Tyler 2007). Laboratory experiments with prairie voles have shown that relatively subtle changes in early experience (e.g., handling of pups, licking, sniffing) have long-term consequences for later social behavior of the offspring. A single handling event in the postnatal period was associated with increased future paternal care in male offspring (Carter et al. 2008a). In turn, these differences in early experiences were correlated with changes in oxytocin and vasopressin patterns in adulthood. Variation in early experiences, then, could be translated into endocrine signals that would influence certain behavioral patterns later in life. For example, epigenetic influences on early oxytocin modulation may be implicated in social aspects of personality and may be the underlying base for some psychiatric disorders such as autism, anxiety, and depression (Carter 2007, Swain et al. 2007). Along the same lines, it is not unreasonable to expect that a stable environment during early development may modulate the establishment of neuroendocrine pathways

that would promote certain types of parental behaviors, on the basis of that early experience, which would be differentially expressed in the adult.

Evidence of developmental programming of social behavior via epigenetic effects introduces the possibility of transgenerational influences in the development and expression of paternal care. Hypotheses of developmental programming of parental behavior, stemming mostly from studies with biparental rodents (Michel & Tyler 2007), are receiving considerable attention. Systematic research in primates, however, is still scarce. Preliminary data from titi monkeys indicate that males with lesions to a very small part of the prefrontal cortex were more tolerant of other group members and hence spent even more time in contact with mates and offspring than is typical. The offspring of lesioned males, in turn, were more likely to engage affiliatively with their siblings (S.P. Mendoza, W.A. Mason, J. Padberg, and K. Bales, unpublished data). Significantly, these males showed more extreme differences in brain regions associated with social recognition and reward when compared with lone or newly paired males than did the nonlesioned males in long-term bonds (Bales et al. 2007). In humans, several hypotheses propose a relationship between childhood experiences and an adult focus on mating or parenting effort (Belsky et al. 1991, Chisholm 1993, Geary 2000, Quinlan 2007). According to these views, local unstable environments (e.g., high mortality risks, low resource availability) during childhood would be associated with a higher focus by men on mating rather than on parenting. This focus on mating would lead to less-responsive paternal behaviors. Although the existing evidence is scant, there may be developmental influences modulating the degree of paternal involvement.

CONCLUSIONS

Among primates, paternal care is present in a wide range of body sizes, from the small callitrichids (0.5–0.7 kg) to siamangs (5–7 kg) and humans (50–70 kg). Paternal care is present with and without simultaneous sibling care. Sometimes, within the same genus, paternal care is present in extremely varied ecological settings. For example, the owl monkey species ranging evergreen tropical forests exhibit patterns of paternal care that are similar to the ones showed by owl monkeys in relatively dry subtropical forests. In some taxa, paternal care is omnipresent, whereas in others its frequency and intensity are more variable. It seems reasonable to conclude that paternal care has evolved independently at least a few times in the radiation of the primate order.

Long-term behavioral and demographic data strongly indicate that direct, conspicuous and frequent paternal care tends to occur simultaneously with the development of a pair-bond between the mother and the putative father providing care. An association between pair-bonds and paternal care is further supported by our understanding of the proximate mechanisms underlying these aspects of the social behavior of primates. There seems to be a common biological substrate with similar neuroanatomical and neuroendocrine processes regulating the manifestation of pair-bonds, monogamy, and paternal care. Following the lead of the rodent research, it is increasingly likely that neurobiological processes underlying paternal behavior are related to mechanisms that promote social behavior generally. Still, much more work is needed to identify the precise mechanisms that are altered to facilitate expression of paternal care. The most promising research is on vasopressin and its receptor quantity and distribution, which is closest to being linked to enhanced sociality. It is unlikely that vasopressin will fully explain the intriguing role that emotional bonds seem to play in the expression of the monogamous social system in titi monkeys, but it may act on them to facilitate expression of paternal care. We tend to think in human terms that something akin to love motivates fathers to provide care for their infants. This is not the case in titi monkeys in which the fathers are tolerant, nonrejecting, and nonaggressive to their infants but show no evidence of an emotional bond with them.

Perhaps, all that is needed to bring about the expression of paternal behavior is a relatively small change in mechanisms regulating social tolerance, rather than an elaborate mechanism specifically designed for that end. For example, vasopressin may be playing a prominent role in regulating paternal care because it reduces fear and hence enhances tolerance.

The ability to form social bonds, being those pair or parental bonds, may be influenced early during development in response to individual infant rearing styles or to extrinsic environmental variables (e.g., war, famine, pathogenic load). This proposal implies the existence of a high degree of phenotypic plasticity, which is a salient feature of primate adaptation in general and human adaptation in particular (Quinlan 2007). The incorporation of, possibly adaptive, developmental programming into models of paternal care may help explain the intra- and interpopulation variation in the expression of paternal behaviors. Studies of paternal care provide an ideal model to understand the epigenesis of complex behavioral traits in model systems that are characterized in the field and the laboratory.

FUTURE ISSUES

1. From a life-history approach, the energetic costs of providing paternal care should be reflected in the life history of the species. How does paternal care affect the developmental trajectory of offspring?

2. Given the broad taxonomic distribution of paternal care, different evolutionary trajectories may have resulted in the same outcome. Titis and owl monkeys may be excellent models for studying homoplasy in paternal care.

3. Developmental programming and transgenerational effects are particularly exciting areas of future research on parental behavior. Biocultural models of developmental histories may explain the variation in the expression of paternal behavior in human societies. If so, what does this tell us about the evolution of the human family?

4. Given the flexibility in primate behavioral patterns, more data are needed on variation within and among populations. To identify successfully subtle differences among individuals in a population or among populations, data collection procedures need to be better validated across field sites, species, and researchers.

5. Genetic studies of paternity need to examine the costs and benefits of care at a community level to incorporate possible kin selection effects.

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LITERATURE CITED

Achenbach GG, Snowdon CT. 2002. Costs of caregiving: weight loss in captive adult male cotton-top tamarins (*Saguinus oedipus*) following the birth of infants. *Int. J. Primatol.* 23:179–89

Ainsworth MDS. 1969. Object relations, dependency, and attachment: a theoretical review of the infant-mother relationship. *Child Dev.* 40:969–1025

Almond RE, Ziegler TE, Snowdon CT. 2008. Changes in prolactin and glucocorticoid levels in cotton-top tamarin fathers during their mate's pregnancy: the effect of infants and paternal experience. *Am. J. Primatol.* 70:560–65

Altmann J, Alberts SC, Haines SA, Dubach J, Muruthi P, et al. 1996. Behavior predicts genetic structure in a wild primate group. *Proc. Natl. Acad. Sci. USA* 93:5797–801

Anderson KG. 2006. How well does paternity confidence match actual paternity? Evidence from worldwide nonpaternity rates. *Curr. Anthropol.* 48:511–18

Anderson KG, Kaplan H, Lam D, Lancaster JB. 1999. Paternal care by genetic fathers and stepfathers II: reports by Xhosa High School students. *Evol. Hum. Behav.* 20:433–51

Anderson KG, Kaplan H, Lancaster JB. 2007. Confidence of paternity, divorce, and investment in children by Albuquerque men. *Evol. Hum. Behav.* 28:1–10

Babb P, Fernandez-Duque E, Gagneux P, Schurr TG. 2009. Phylogeography and population structure of mtDNA diversity in Azara's owl monkeys (*Aotus azarai azarai*) of the Argentinean Chaco. *Mol. Phylogenet. Evol.* Submitted

Bales KL, Dietz JM, Baker AJ, Miller KE, Tardif SD. 2000. Effects of allocare-givers on fitness of infants and parents in callitrichid primates. *Folia Primatol.* 71:27–38

Bales KL, Kim AJ, Lewis-Resse AD, Carter CS. 2004a. Both oxytocin and vasopressin may influence allo-parental behavior in male prairie voles. *Horm. Behav.* 45:354–61

Bales KL, Pfeifer LA, Carter CS. 2004b. Sex differences and developmental effects of manipulations of oxytocin on alloparenting and anxiety in prairie voles. *Dev. Psychobiol.* 44:123–31

Bales KL, Plotsky PM, Young LJ, Lim MM, Grotte N, et al. 2007. Neonatal oxytocin manipulations have long-lasting, sexually dimorphic effects on vasopressin receptors. *Neurosci.* 144:38–45

Bearder S, Campbell CJ, Fuentes A, MacKinnon KC, Panger M, eds. 2007. *Primates in Perspective.* Oxford, UK: Oxford Univ. Press

Belsky J, Steinberg L, Draper P. 1991. Childhood experience, interpersonal development, and reproductive strategy: an evolutionary theory of socialization. *Child Dev.* 62:647–70

Beltran S, Boissier J. 2008. Schistosome monogamy: who, how and why? *Trends Parasitol.* 24:386–91

Berg SJ, Wynne-Edwards KE. 2001. Changes in testosterone, cortisol, and estradiol levels in men becoming fathers. *Mayo Clin. Proc.* 76:582–92

Borries C, Launhardt K, Epplen C, Epplen JT, Winkler P. 1999. Males as infant protectors in Hanuman langurs (*Presbytis entellus*) living in multimale groups—defence pattern, paternity and sexual behaviour. *Behav. Ecol. Sociobiol.* 46:350–56

Bossuyt F. 2002. Natal dispersal of titi monkeys (*Callicebus moloch*) at Cocha Cashu, Manu National Park, Peru. *Am. J. Phys. Anthropol.* S34:47

Bowlby J. 1969. *Attachment and Loss. Volume I. Attachment.* New York: Basic Books

Bridges R. 2008. *Neurobiology of the Parental Brain.* Burlington, MA: Academic. 584 pp.

Buchan JC, Alberts SC, Silk JB, Altmann J. 2003. True paternal care in a multi-male primate society. *Nature* 425:179–81

Carter CS. 2007. Sex differences in oxytocin and vasopressin: implications for autism spectrum disorders? *Behav. Brain Res.* 176:170–86

Carter CS, Boone EM, Bales KL. 2008a. Early experience and the developmental programming of oxytocin and vasopressin. See Bridges 2008, pp. 417–34

Carter CS, Grippo AJ, Pournajafi-Nazarloo H, Ruscio MG, Porges SW. 2008b. Oxytocin, vasopressin and sociality. *Prog. Brain Res.* 170:331–36

Carter SC, Lederhendler II, Kirkpatrick B, eds. 1999. *The Integrative Neurobiology of Affiliation*. Cambridge, MA: MIT Press. 418 pp.

Champagne FA, Meaney MJ. 2007. Transgenerational effects of social environment on variations in maternal care and behavioral response to novelty. *Behav. Neurosci.* 121:1353–63

Charpentier MJE, Van Horn RC, Altmann J, Alberts SC. 2008. Paternal effects of offspring fitness in a multimale primate society. *Proc. R. Soc. London B Biol. Sci.* 105:1988–92

Chisholm JS. 1993. Death, hope, and sex: life-history theory and the development of reproductive strategies. *Curr. Anthropol.* 34:1–24

Chivers DJ. 1974. *The Siamang in Malaya. A Field Study of a Primate in Tropical Rain Forest.* Basel, Switz.: S. Karger AG. 335 pp.

Clutton-Brock TH. 1991. *The Evolution of Parental Care*. Princeton, NJ: Princeton Univ. Press

Dawkins R, Carlisle TR. 1976. Parental investment, mate desertion and a fallacy. *Nature* 262:131–33

Delahunty KM, McKay DW, Noseworthy DE, Storey AE. 2007. Prolactin responses to infant cues in men and women: effects of parental experience and recent infant contact. *Horm. Behav.* 51:213–20

Di Fiore A, Fernandez-Duque E. 2007. A comparison of paternal care in three socially-monogamous neotropical primates. *Am. J. Phys. Anthropol.* 132:99

Di Fiore A, Fernandez-Duque E, Hurst D. 2007. Adult male replacement in socially monogamous equatorial saki monkeys (*Pithecia aequatorialis*). *Folia Primatol.* 78:88–98

Di Fiore A, Fleischer RC. 2005. Social behavior, reproductive strategies, and population genetic structure of *Lagothrix poeppigii*. *Int. J. Primatol.* 26:1137–73

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

Donaldson ZR, Young LJ. 2008. Oxytocin, vasopressin, and the neurogenetics of sociality. *Science* 322:900–4

Feldman R, Weller A, Zagoory-Sharon O, Levine A. 2007. Evidence for a neuroendocrinological foundation of human affiliation: plasma oxytocin levels across pregnancy and the postpartum period predict mother-infant bonding. *Psychol. Sci.* 18:965–70

Fernandez-Duque E. 2007. The Aotinae: social monogamy in the only nocturnal haplorhines. See Campbell et al. 2007, pp. 139–54

Fernandez-Duque E. 2009. Natal dispersal in monogamous owl monkeys (*Aotus azarai*) of the Argentinean Chaco. *Behaviour* 146:583–606

Fernandez-Duque E, Di Fiore A, de Luna AG. 2009. Pair-mate relationships and parenting in ecuatorial saki monkeys (*Pithecia aequatorialis*) and red titi monkeys (*Callicebus discolor*) of Ecuador. In *Evolutionary Biology and Conservation of Titis, Sakis and Uacaris*, ed. LM Veiga, AA Barnett. Cambridge, UK: Cambridge Univ. Press. In press

Fernandez-Duque E, Juárez C, Di Fiore A. 2008. Adult male replacement and subsequent infant care by male and siblings in socially monogamous owl monkeys (*Aotus azarai*). *Primates* 49:81–84

Fietz J, Dausmann KH. 2003. Costs and potential benefits of parental care in the nocturnal fat-tailed dwarf lemur (*Cheirogaleus medius*). *Folia Primatol.* 74:246–58

Fietz J, Zischler H, Schwiegk C, Tomiuk J, Dausmann KH, Ganzhorn JU. 2000. High rates of extra-pair young in the pair-living fat-tailed dwarf lemur, *Cheirogaleus medius*. *Behav. Ecol. Sociobiol.* 49:8–17

Fink S, Excoffier L, Heckel G. 2007. Mammalian monogamy is not controlled by a single gene. *Proc. Natl. Acad. Sci. USA* 103:10956–60

Fite JE, Patera KJ, French JA, Rukstalis M, Hopkins EC, Ross CN. 2005. Opportunistic mothers: female marmosets (*Callithrix kuhlii*) reduce their investment in offspring when they have to, and when they can. *J. Hum. Evol.* 49:122–42

Fleming AS, Corter C, Stallings J, Steiner M. 2002. Testosterone and prolactin are associated with emotional responses to infant cries in new fathers. *Horm. Behav.* 42:399–413

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

A taxonomic-wide review of the neurobiology of social behavior and implications for our societies.

Gagneux P, Boesch C, Woodruff DS. 1999. Female reproductive strategies, paternity and community structure in wild West African chimpanzees. *Anim. Behav.* 57:19–32

Geary DC. 2000. Evolution and proximate expression of human paternal investment. *Psychol. Bull.* 126:55–77

Geary DC, Flinn MV. 2001. Evolution of human parental behavior and the human family. *Parent. Sci. Pract.* 1:5–61

Gowaty PA. 1996. Battles of the sexes and origins of monogamy. In *Partnerships in Birds: The Study of Monogamy*, ed. JM Black, pp. 21–52. Oxford: Oxford Univ. Press

Gowaty PA. 2004. Sex roles, contests for the control of reproduction and sexual selection. In *Sexual Selection in Primates*, ed. PM Kappeler, C Van Schaik, pp. 37–56. Cambridge, UK: Cambridge Univ. Press

Gray PB, Parkin JC, Samms-Vaughan ME. 2007. Hormonal correlates of human paternal interactions: a hospital-based investigation in urban Jamaica. *Horm. Behav.* 52:499–507

Gray PB, Yang C-FJ, Pope HGJ. 2006. Fathers have lower salivary testosterone levels than unmarried men and married non-fathers in Beijing, China. *Proc. R. Soc. London B* 273:333–39

Gubernick DG, Klopfer PH, eds. 1981. *Parental Care in Mammals*. New York: Plenum Press. 459 pp.

Gust DA, Gordon TP, Brodie AR, McClure HM. 1994. Effect of a preferred companion in modulating stress in adult female rhesus monkeys. *Physiol. Behav.* 55:681–84

Hamilton WJ III. 1984. Significance of paternal investment by primates to the evolution of adult male-female associations. See Taub 1984, pp. 309–35

Hammock EAD, Young LJ. 2005. Microsatellite instability generates diversity in brain and sociobehavioral traits. *Science* 308:1630–34

Hawkes K. 2004. Mating, parenting, and the evolution of human pair bonds. In *Kinship and Behavior in Primates*, ed. B Chapais, C Berman, pp. 443–73. Oxford: Oxford Univ. Press

Hewlett BS. 1991. *Intimate Fathers: The Nature and Context of Aka Pygmy Paternal Infant Care*. Ann Arbor: Univ. Mich. Press

Hewlett BS, ed. 1992. *Father-Child Relations*. New York: Aldine DeGruyter

Hill KR, Hurtado AM. 1996. *Ache Life History: The Ecology and Demography of a Foraging People*. New York: Aldine de Gruyter

Hoffman KA, Mendoza SP, Hennessy MB, Mason WA. 1995. Responses of infant titi monkeys, *Callicebus moloch*, to removal of one or both parents: evidence for paternal attachment. *Dev. Psychobiol.* 28:399–407

Hrdy S. 2000. The optimal number of fathers. Evolution, demography, and history in the shaping of female mate preferences. *Ann. N. Y. Acad. Sci.* 907:75–96

Hrdy SB. 2005. Evolutionary context of human development: the cooperative breeding model. In *Attachment and Bonding. A New Synthesis*, ed. SC Carter, L Ahnert, KE Grossmann, SB Hrdy, ME Lamb, et al., pp. 9–32. Cambridge, MA: MIT Press

Hrdy SB. 2008. Cooperative breeding and the paradox of facultative fathering. See Bridges 2008, pp. 407–16

Huck M, Lottker P, Bohle UR, Heymann EW. 2005. Paternity and kinship patterns in polyandrous moustached tamarins (*Saguinus mystax*). *Am. J. Phys. Anthropol.* 127:449–64

Keane B, Dittus WPJ, Melnick DJ. 1997. Paternity assessment in wild groups of toque macaques *Macaca sinica* at Polonnaruwa, Sri Lanka using molecular markers. *Mol. Ecol.* 6:267–82

Ketterson ED, Nolan VJ. 1999. Adaptation, exaptation, and constraint: a hormonal perspective. *Am. Nat.* 54: S4–25

Key C, Aiello LC. 2000. A prisoner's dilemma model of the evolution of paternal care. *Folia Primatol.* 71:77–92

Kiyokawa Y, Kikusui T, Takeuchi Y, Mori Y. 2004. Partner's stress status influences social buffering effects in rats. *Behav. Neurosci.* 118:798–804

Kleiman DG. 1985. Paternal care in New World primates. *Am. Zool.* 25:857–59

Kleiman DG, Malcolm JR. 1981. The evolution of male parental investment in mammals. In *Parental Care in Mammals*, ed. DG Gubernick, PH Klopfer, pp. 347–87. New York: Plenum Press

Kokko H, Jennions M. 2003. It takes two to tango. *Trends Ecol. Evol.* 18:103–4

Kozorovitskiy Y, Hughes M, Lee K, Gould E. 2006. Fatherhood affects dendritic spines and vasopressin V1a receptors in the primate prefrontal cortex. *Nat. Neurosci.* 9:1094–95

A study of fatherhood in foraging societies with an insightful discussion on the sources of variation in human paternal care among foraging societies.

The first and only evidence of attachment between mammal infant and father.

An extension of the cooperative breeding hypothesis with special reference to paternal care.

Kurland JA, Gualin SJC. 1984. The evolution of male parental investment: effects of genetic relatedness and feeding ecology on the allocation of reproductive effort. In *Primate Paternalism*, ed. DM Taub, pp. 259–306. New York: Van Nostrand Reinhold

Lancaster JB, Lancaster CS. 1983. Parental investment: the hominid adaptation. In *How Humans Adapt: A Biocultural Odyssey*, ed. DJ Ortner, pp. 33–69. Washington, DC: Smithson. Inst. Press

Lappan S. 2008. Male care of infants in a siamang (*Symphalangus syndactylus*) population including socially monogamous and polyandrous groups. *Behav. Ecol. Sociobiol.* 62:1307–17

Lim M, Young LJ. 2006. Neuropeptidergic regulation of affiliative behavior and social bonding in animals. *Horm. Behav.* 50:506–17

Lim MM, Hammock EA, Young LJ. 2004a. The role of vasopressin in the genetic and neural regulation of monogamy. *J. Neuroendocrinol.* 16:325–32

Lim MM, Wang Z, Olazabal DE, Ren X, Terwilliger EF, Young LJ. 2004b. Enhanced partner preference in a promiscuous species by manipulating the expression of a single gene. *Nature* 429:754–57

Liu Y, Curtis J, Wang ZX. 2001. Vasopressin in the lateral septum regulates pair bond formation of male prairie voles. *Behav. Neurosci.* 115:910–19

Marlowe F. 1999. Male care and mating effort among Hadza foragers. *Behav. Ecol. Sociobiol.* 46:57–64

Marlowe F. 2000. Paternal investment and the human mating system. *Behav. Processes* 51:45–61

Mason WA, Kenney MD. 1974. Redirection of filial attachments in rhesus monkeys: dogs as mother surrogates. *Science* 183:1209–11

Maynard Smith J. 1977. Parental investment: a prospective analysis. *Anim. Behav.* 25:1–9

Mendoza SP, Coe C, Smotherman W, Kaplan J, Levine S. 1980. Functional consequences of attachment: a comparison of two species. In *Maternal Influences and Early Behavior*, ed. R Bell, W Smotherman, pp. 235–52. New York: Spectrum

Mendoza SP, Lyons DM, Saltzman W. 1991. Sociophysiology of squirrel monkeys. *Am. J. Primatol.* 23:37–54

Mendoza SP, Mason WA. 1986a. Contrasting responses to intruders and to involuntary separation by monogamous and polygynous New World monkeys. *Physiol. Behav.* 38:795–801

Mendoza SP, Mason WA. 1986b. Parental division of labour and differentiation of attachments in a monogamous primate (*Callicebus moloch*). *Anim. Behav.* 34:1336–47

Michel GF, Tyler AN. 2007. Can knowledge of developmental processes illuminate the evolution of parental care? *Dev. Psychobiol.* 49:33–44

Miller KE, Bales KL, Ramos JH, Dietz JM. 2006. Energy intake, energy expenditure, and reproductive costs of female wild golden lion tamarins (*Leontopithecus rosalia*). *Am. J. Primatol.* 68:1037–53

Moore FL. 1992. Evolutionary precedents for behavioral actions of oxytocin and vasopressin. *Ann. N. Y. Acad. Sci.* 652:156–65

Muller MN, Marlowe FW, Bugumba R, Ellison PT. 2008. Testosterone and paternal care in East African foragers and pastoralists. *Proc. Biol. Sci.* 276(1655):347–54

Nair H, Young LJ. 2006. Vasopressin and pair-bond formation: genes to brain to behavior. *Physiology* 21:146–52

Nievergelt CM, Digby LJ, Ramakrishnan U, Woodruff DS. 2000. Genetic analysis of group composition and breeding system in a wild common marmoset (*Callithrix jacchus*) population. *Int. J. Primatol.* 21:1–20

Norconk MA. 2007. Sakis, uakaris and titi monkeys: behavioral diversity in a radiation of seed predators. See Campbell et al. 2007, pp. 123–38

Nunes S, Fite JE, French JA. 2000. Variation in steroid hormones associated with infant care behaviour and experience in male marmosets (*Callithrix kuhlii*). *Anim. Behav.* 60:857–65

Nunes S, Fite JE, Patera KJ, French JA. 2001. Interactions among paternal behavior, steroid hormones, and parental experience in male marmosets (*Callithrix kuhlii*). *Horm. Behav.* 39:70–82

Parker GA, Schwagmeyer PL. 2005. Male "mixed" reproductive strategies in biparental species: Trivers was probably right, but why? *Am. Nat.* 165:96–105

Parker KJ, Lee TM. 2001. Central vasopressin administration regulates the onset of facultative paternal behavior in *Microtus pennsylvanicus* (meadow voles). *Horm. Behav.* 39:285–94

Pedersen CA, Prange AJ Jr. 1985. Oxytocin and mothering behavior in the rat. *Pharmacol. Ther.* 28:287–302

Pedersen CA, Vadlamudi SV, Boccia ML, Amico JA. 2006. Maternal behavior deficits in nulliparous oxytocin knockout mice. *Genes Brain Behav.* 5:274–81

An elaboration of the interface between developmental biology and paternal care.

Queller DC. 1997. Why do females care more than males? *Proc. R. Soc. London B Biol. Sci.* Series B. 264:1555–57

Quinlan RJ. 2007. Human parental effort and environmental risk. *Proc. R. Soc. London B Biol. Sci.* 274:121–25

Reeder DM. 2001. *The biology of parenting in the monogamous titi monkey* (Callicebus moloch). PhD thesis. Univ. Calif., Davis
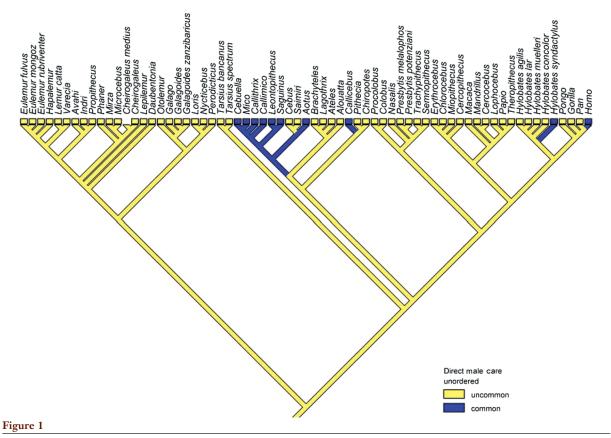
Reichard U. 2003. Social monogamy in gibbons: the male perspective. In *Monogamy. Mating Strategies and Partnerships in Birds, Humans and Other Mammals*, ed. UH Reichard, C Boesch, pp. 190–213. Cambridge, UK: Univ. Cambridge Press

Rodman PS, Bossuyt FJ. 2007. Fathers and stepfathers: familial relations of old and new males within groups of *Callicebus brunneus* in southeastern Perú. *Am. J. Phys. Anthropol.* 132(S44):201

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

Ross CN, French JA, Orte G. 2007. Germ-line chimerism and paternal care in marmosets (*Callithrix kuhlii*). *Proc. Natl. Acad. Sci. USA* 104:6278–82

Rosso L, Keller L, Kaessmann H, Hammond R. 2008. Mating system and avpr1a promoter variation in primates. *Biol. Lett.* 4(4):375–8

Rotundo M, Fernandez-Duque E, Dixson AF. 2005. Infant development and parental care in free-ranging *Aotus azarai azarai* in Argentina. *Int. J. Primatol.* 26:1459–73

Ruis MA, te Brake JH, Buwalda B, De Boer SF, Meerlo P, et al. 1999. Housing familiar male wildtype rats together reduces the long-term adverse behavioural and physiological effects of social defeat. *Psychoneuroendocrinology* 24:285–300

Sanchez R, Parkin JC, Chen JY, Gray PB. 2009. Oxytocin, vasopression, and human social behavior. In *Endocrinology of Social Relationships*, ed. PB Gray, PT Ellison, pp. 319–39. Cambridge, MA: Harvard Univ. Press

Schradin C, Anzenberger G. 1999. Prolactin, the hormone of paternity. *News Physiol. Sci.* 14:223–31

Schradin C, Anzenberger G. 2002. Why do new world monkey fathers have enhanced prolactin levels? *Evol. Anthropol.* 11:122–25

Schradin C, Reeder DM, Mendoza SP, Anzenberger G. 2003. Prolactin and paternal care: comparison of three species of monogamous new world monkeys (*Callicebus cupreus, Callithrix jacchus*, and *Callimico goeldii*). *J. Comp. Psychol.* 117:166–75

Sheldon BC. 2002. Relating paternity to paternal care. *Philos. Trans. R. Soc. London B Biol. Sci.* 357:341–50

Smucny DA, Abbott DH, Mansfield KG, Schultz-Darken NJ, Yamamoto ME, et al. 2004. Reproductive output, maternal age, and survivorship in captive common marmoset females (*Callithrix jacchus*). *Am. J. Primatol.* 64:107–21

Smuts BB, Gubernick DJ. 1992. Male-infant relationships in nonhuman primates: paternal investment or mating effort? In *Father-Child Relations. Cultural and Biosocial Contexts*, ed. BS Hewlett, pp. 1–30. New York: Aldine de Gruyter

Snyder BF, Gowaty PA. 2007. A reappraisal of Bateman's classic study of intrasexual selection. *Evolution* 61:2457–68

Storey AE, Walsh CJ. 2000. Hormonal correlates of paternal responsiveness in new and expectant fathers. *Evol. Human Behav.* 21:79–95

Suomi S. 1999. Attachment in rhesus monkeys. In *Handbook of Attachment: Theory, Research, and Clinical Applications*, ed. J Cassidy, PR Shaver, pp. 181–97. New York: Guilford

Swain JE, Lorberbaum JP, Kose S, Strathearn L. 2007. Brain basis of early parent-infant interactions: psychology, physiology, and in vivo functional neuroimaging studies. *J. Child Psychol. Psychiatry* 48:262–87

Tang-Martinez Z, Ryder TB. 2005. The problem with paradigms: Bateman's worldview as a case study. *Integr. Comp. Biol.* 45:821–30

Tardif SD. 1997. The bioenergetics of parental behavior and the evolution of alloparental care in marmosets and tamarins. In *Cooperative Breeding in Mammals*, ed. NG Solomon, JA French, pp. 11–33. Cambridge, UK: Cambridge Univ. Press

Tardif SD, Garber PA. 1994. Social and reproductive patterns in neotropical primates: relation to ecology, body size, and infant care. *Am. J. Primatol.* 34:111–14

A review of the neural basis of parental care from a psychobiological perspective.

Tardif SD, Santos CV, Baker AJ, Van Elsacker L, Ruiz-Miranda CR, et al. 2002. Infant care in lion tamarins. In *Lion Tamarins. Biology and Conservation*, ed. DG Kleiman, AB Rylands, pp. 213–32. Washington, DC: Smithson. Univ. Press

Tardif SD, Ziegler TE, Power M, Layne DG. 2005. Endocrine changes in full-term pregnancies and pregnancy loss due to energy restriction in the common marmoset (*Callithrix jacchus*). *J. Clin. Endocrinol. Metab.* 90:335–39

Taub DM, ed. 1984. *Primate Paternalism*. New York: Van Nostrand Reinhold

Terranova ML, Cirulli F, Laviola G. 1999. Behavioral and hormonal effects of partner familiarity in periadolescent rat pairs upon novelty exposure. *Psychoneuroendocrinology* 24:639–56

Trivers RL. 1972. Parental investment and sexual selection. In *Sexual Selection and The Descent of Man, 1871–1971*, ed. BG Campbell, pp. 136–79. Chicago: Aldine

Trumbo ST. 2006. Infanticide, sexual selection and task specialization in a biparental burying beetle. *Anim. Behav.* 72:1159–67

Valeggia CR. 2009. Flexible caretakers: responses of Toba families in transition. In *Substitute Parents: Biological and Social Perspectives on Alloparenting in Human Societies*, ed. G Bentley, R Mace. Oxford: Berghahn. In press

Van Schaik CP, Kappeler PM. 1997. Infanticide risk and the evolution of male-female association in primates. *Proc. R. Soc. London B Biol. Sci.* 264:1687–95

Wade MJ, Shuster SM. 2002. The evolution of parental care in the context of sexual selection: a critical reassessment of parental investment theory. *Am. Nat.* 160:289–92

Walum H, Westberg L, Henningsson S, Neiderhiser JM, Reiss D, et al. 2008. Genetic variation in the vasopressin receptor 1a gene (AVPR1A) associates with pair-bonding behavior in humans. *Proc. Natl. Acad. Sci. USA* 105:14153–56

Whitten PL. 1987. Infants and adult males. In *Primate Societies*, ed. BB Smuts, DL Cheney, RM Seyfarth, RW Wrangham, T Struhsaker, pp. 343–57. Chicago: Univ. Chicago Press

Wingfield JC, Hegner RE, Dufty AM, Ball GF. 1990. The Challenge Hypothesis: theoretical implications for patterns of testosterone secretion, mating systems, and breeding strategies. *Am. Nat.* 136:829–46

Wolovich CK, Perea-Rodriguez JP, Fernandez-Duque E. 2008. Food transfers to young and mates in wild owl monkeys (*Aotus azarai*). *Am. J. Primatol.* 70:211–21

Woodroffe R, Vincent A. 1994. Mother's little helpers: patterns of male care in mammals. *Trends Ecol. Evol.* 9:294–97

Wright PC. 1984. Biparental care in *Aotus trivirgatus* and *Callicebus moloch*. In *Female Primates: Studies by Women Primatologists*, ed. M Small, pp. 59–75. New York: Alan R. Liss

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

Wynne-Edwards KE, Timonin ME. 2007. Paternal care in rodents: weakening support for hormonal regulation of the transition to behavioral fatherhood in rodent animal models of biparental care. *Horm. Behav.* 52:114–21

Young L, Lim M, Gingrich B, Insel T. 2001. Cellular mechanisms of social attachment. *Horm. Behav.* 40:133–38

Young LJ, Murphy Young AZ, Hammock EAD. 2005. Anatomy and neurochemistry of the pairbond. *J. Comp. Neurol.* 493:51–57

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

Zeh DW, Smith RL. 1985. Paternal investment by terrestrial arthropods. *Am. Zool.* 25:785–805

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

Ziegler TE, Prudom SL, Schultz-Darken NJ, Kurian AV, Snowdon CT. 2006. Pregnancy weight gain: marmoset and tamarin dads show it too. *Biol. Lett.* 2:181–83

Probably the most provocative recent evaluation of the relationship between sexual selection and parental investment theories.

Figure 1

Primate phylogeny showing the taxa where paternal care is direct and conspicuous (*dark branches*).

Figure 2

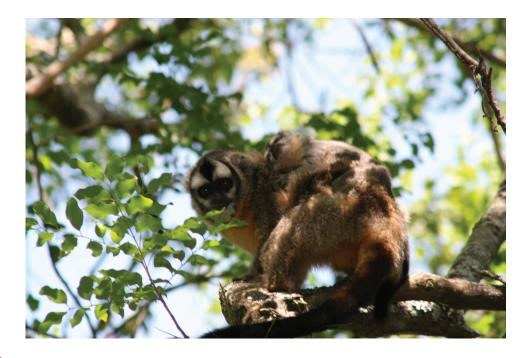A titi monkey infant (*Callicebus moloch*) sits in physical contact with his father.

Figure 3

An owl monkey infant (*Aotus azarai*) rides dorsally on the back of his father.