



Review article

Primate paternal care: Interactions between biology and social experience

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ABSTRACT

This article is part of a Special Issue “Parental Care”.

We review recent research on the roles of hormones and social experiences on the development of paternal care in humans and non-human primates. Generally, lower concentrations of testosterone and higher concentrations of oxytocin are associated with greater paternal responsiveness. Hormonal changes prior to the birth appear to be important in preparation for fatherhood and changes after the birth are related to how much time fathers spend with offspring and whether they provide effective care. Prolactin may facilitate approach and the initiation of infant care, and in some biparental non-human primates, it affects body mass regulation. Glucocorticoids may be involved in coordinating reproductive and parental behavior between mates. New research involving intranasal oxytocin and neuropeptide receptor polymorphisms may help us understand individual variation in paternal responsiveness. This area of research, integrating both biological factors and the role of early and adult experience, has the potential to suggest individually designed interventions that can strengthen relationships between fathers and their partners and offspring.

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One of Jay Rosenblatt's most important research contributions was determining how hormones influence the onset of maternal behavior and how experience with pups maintained it (Rosenblatt and Seigel, 1981). The interplay between biology and experience in mammalian fathers provides further insight into hormonal influences and the critical role of social experience for the onset as well as maintenance of paternal behavior. In this regard, the transition to paternal responsiveness more closely resembles the sensitization response that Jay Rosenblatt (1967) discovered in virgin rats, wherein extensive pup exposure preceded any hormonal change. Recent research in the hormonal basis of paternal behavior indicates that the hormonal state of one individual influences its own behavior and then can affect the behavior and hormonal state of the dyad partner (mate or young), as with Danny Lehrman's (1965) work on the ring dove.

Mammalian fathers show considerable individual and interspecific variation in the extent to which they exhibit paternal responsiveness and in many species, contact with the pregnant partner, as well as the young, is important in the transition. Here we review the function and evolution of paternal behavior in primates, and then examine the interplay between social experience and each of the hormones implicated in parental behavior. Finally, we review recent findings about how hormones and social

experiences affect and reflect the paternal brain. The review is organized with non-human primates first in each section, then humans. The two sections cannot always be directly compared since experiments performed on non-human primates can often not be done on humans and the recent fMRI studies have been mainly conducted in humans.

Evolution, distribution and function of paternal care in primates*Evolution, distribution and function of paternal care in non-human primates*

Biparental care (care by both parents) has evolved repeatedly across vertebrate and invertebrate taxa (Dulac et al., 2014). While paternal care is quite rare in mammals, it is more common in primates than in other mammalian orders (Kleiman and Malcolm, 1981; Clutton-Brock, 1991; Opie et al., 2013). The sociality of primates may have led to an increase in co-operative care of infants (Hrdy, 2009) but there are other hypotheses concerning the repeated evolution of paternal care in primates. Lukas and Clutton-Brock (2013) suggest that social monogamy evolves in mammals when females occupy small and discrete ranges such that males cannot monopolize more than one female. Infanticide risk may have led to close attendance by resident males which in turn increased social monogamy and bi-parental care (van Schaik and Kappeler, 1997; Dunbar, 1995; Palombit, 1999; Opie et al., 2013; Fernandez-Duque et al., 2009).

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Primate species have flexible behavioral systems and with this comes high variability in social systems and in father–offspring parenting styles both between and within species. Biparental care allows the energetic demands to be shared between both parents, which can improve the number of surviving offspring a male produces (Satzman and Ziegler, 2014). Paternal care of infants has been observed in many of the general classifications of non-human primates: strepsirrhines, platyrrhines, cercopithecoids and apes. Infant care by fathers and non-breeding males is also currently associated with a range of mating systems including monogamy, polyandry, and cooperative breeding. The ways in which a father interacts with his offspring are usually classified as direct (e.g., feeding and carrying) or indirect (e.g., protection) care and there is considerable variation in what behaviors fathers display towards offspring. Only a few species of lemurs (such as the red-bellied lemur, *Eulemur rubriventer*; Overdorff and Tecot, 2006) and the New World marmosets, tamarins (*Saguinus oedipus*), titi monkeys (*Callicebus cupreus*), and owl monkeys show direct care of their offspring (Fernandez-Duque et al., 2009). In contrast, wild male savanna baboons (*Papio cynocephalus*) are known to protect their probable offspring from attacks by peers but show no direct offspring care (Buchan et al., 2003; Charpentier et al., 2008). Male Barbary macaques (*Macaca sylvana*) will assist in teaching behavioral skills to their developing offspring after they are weaned (Burton, 1972).

Infant carrying is the best-documented form of paternal care in non-human primates. Infant carrying by males reduces female energy expenditure. In addition to this advantage for females, infant carrying can benefit males by decreasing inter-birth intervals. There are, however, species differences in when and how much primate fathers carry their young. Similar to marmosets and tamarins, red-bellied lemurs often have twin births and fathers that carry as much as mothers (Overdorff and Tecot, 2006). Father titi monkeys carry infants almost exclusively from birth and they are the primary attachment figure for the developing infant (Hoffman et al., 1995). In contrast, Goeldii (*Callimico goeldii*) fathers carry infants only after 3 weeks of age (see Schradin et al., 2003). Common marmoset (*Callithrix jacchus*) fathers are the primary care giver but share the carrying with their mate (Schradin et al., 2003). In contrast, Hylobatids often display social monogamy and reduced sexual dimorphism, yet only in the siamangs (*Symphalangus syndactylus*) do fathers actually carry their young and then only starting in the second year of the infant's life (Chivers, 1974). One factor related to how much fathers carry offspring is whether females have early post-partum estrus. Fathers carry young more often in species where females can lactate and be pregnant simultaneously, and thus carrying by males results in a reduction in the mother's energy expenditure that benefits both parents.

Our information on the biological systems that facilitate paternal care behaviors is generally limited to a few species of monkeys, often using captive individuals. These species include titi monkeys, common marmoset, black tufted-ear marmoset (*Callithrix kuhlii*), geoffroyi marmoset (*Callithrix geoffroyi*), and the cotton-top tamarin. Data from these species indicate that fathers show similar physiological changes as their mates. Marmosets and tamarins are the most notable for their cooperative care of infants. This extra-maternal care allows females to offset the costs of high reproductive output by limiting maternal investment in each offspring (Garber and Leigh, 1997). Both common marmosets and the cotton-top tamarins have multiple infants per birth, with a post partum ovulation that occurs as early as 10 and 13 days respectively, following birth (marmosets: Lunn and McNeilly, 1982; tamarins: Ziegler et al., 1987). Post-partum conception rates are high, occurring in more than 80% of females (Ziegler et al., 1987) and thus, most mothers are lactating and pregnant at the same time. This high reproductive rate is energetically costly for mothers and so infant care support is required from the entire family. The ability to simultaneously lactate and conceive, as is seen for the callitrichid monkeys, is in part due to the lower frequency of nursing bouts allowed by mothers (Ziegler et al., 1990).

Evolution, distribution and function of paternal care in humans

Modern fathers contribute greatly to the emotional, cognitive and social development of their children (reviewed in Allen and Daly, 2007), as well as to long-established roles of providing resources, protecting, and teaching their children. A high degree of father involvement is not just a recent Western phenomenon: direct infant care by fathers has been documented in 40% of world societies (Barry and Paxson, 1971), with greater direct paternal care being associated with strong emotional bonds between parents (Whiting and Whiting, 1975; Broude, 1983; Belsky et al., 1991).

Paternal care in humans evolved independently from similar transitions in other primates. Paternal care is absent in our nearest relatives (chimpanzees, *Pan troglodytes*; bonobos, *Pan paniscus*; gorillas, *Gorilla gorilla*), making it difficult to determine how or why male care evolved and whether it preceded or followed increases in pair bond strength. Since our closest relatives are either promiscuous or polygynous, with males providing little parental care, it is difficult to infer whether paternal care co-evolved with pair bonding or whether it preceded or followed increased formation of long-term pair bonds. The Lukas and Clutton-Brock (2013) explanation for other mammals, that pair-bonding arose when females were so widely dispersed that males could only defend one mate, is unlikely to extend to humans, as we are the only mammalian species with a long history of both pair bonding and group living. Opie et al. (2013) argue that high levels of male infanticide led to pair bond formation and paternal care. They suggest that this factor was particularly important in species with long pre-weaning periods relative to pregnancy duration such that strange males could hasten ovulation by killing offspring sired by other males. Another model proposes that human paternal care arose as an alternative path to reproductive success for subordinate males in polygynous groups (Gavrilets, 2012). While dominant males could guard and mate with multiple females, subordinate males could potentially sire offspring by forming bonds, more or less exclusively, with females and providing paternal care. This paternal care could include provisioning, transport and protection from infanticidal males. An attractive feature of the Gavrilets (2012) model is that it addresses a possible source for the individual variation in paternal care we see in humans: some males provide extensive paternal care to the children of one woman while others pursue a more promiscuous mating strategy with less paternal investment (Marks and Palkovitz, 2004; Apicella and Marlowe, 2006). Cross-cultural analyses identify paternal care and reduction of male–male competition for mates as key factors in the evolution of human pair bonding (Marlowe, 2000; Quinlan and Quinlan, 2007).

Gangestad (2011) suggests that male provisioning from hunting can be viewed as mating effort, parental effort, or perhaps both. Provisioning is mating effort if females prefer to mate with successful hunters. Provisioning can also be viewed as parental effort if offspring that receive it have better survival prospects than those who do not (e.g., Alvergne et al., 2009). One important benefit of this paternal care is that inter-birth intervals are shorter in humans than in comparable-sized primates with only maternal care (Gangestad, 2011). This quicker return to fertility after birth may be due to hunting efforts that brought more high quality food to the family or, as Gettler (2010) suggests, it may in part be due to reduction of maternal energy expenditure in mobile groups if fathers carried offspring. Gettler (2010) suggests that we have overstated the sexual division of foraging labor in ancestral groups based on modern hunter gathering populations and he cites evidence that infant transport by fathers, as in some other primate species, was important for reducing maternal energy expenditure in mobile foraging groups.

One way we might determine whether human paternal care is adaptive is by examining the underlying hormonal mechanisms. Gangestad (2011) argues that the association of paternal care with decreased testosterone (as opposed to increased testosterone with

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