Chapter 3

Fathering in Non-Human Primates

Karen L. Bales and Michael R. Jarcho

University of California, Davis and California National Primate Research Center

Human males display large amounts of variation in the quantity and quality of their contributions to infant care. Variation in these contributions is known to influence biological (Ellis, 2004; Ellis, Figueredo, Brumbach, & Schlomer, 2009; Tither & Ellis, 2010) and social development (Paschall, Ringwalt, & Flewelling, 2003; Pfiffner, McBurnett, & Rathouz, 2001) in offspring. An obvious place to examine the social and biological bases of this variation is in non-human primates, our closest evolutionary relatives.

Historical Overview and Theoretical Perspectives

Monogamy and the Evolution of Biparental Care

From a taxonomic perspective, the occurrence of male parenting behavior in non-human primates is closely associated, but not completely confounded, with the occurrence of social monogamy. Social monogamy in primates is characterized by group structure consisting of a mated male and female, sometimes with associated offspring (Fuentes, 1999; Kleiman, 1977). Although the male of the pair usually fathers a large proportion of the female’s offspring, mating exclusivity is not essential for this definition, and extra-pair copulations can occur. In addition to fathering, traits which may be found in monogamous species include alloparenting (in which older offspring care for younger offspring), delayed maturation or even suppression of young, and low sexual dimorphism (Kleiman, 1977); however, not all of these traits are found in all species considered monogamous. Sociobiological theory predicts that paternal behavior will evolve where parental certainty is high (Wilson, 1975). In certain species (e.g., hamadryas baboons) the mechanism driving this parental certainty is the fact that a single dominant male monopolizes the mating. This social structure, however, is clearly not monogamous. Another mechanism by which monogamy can evolve is in situations where females are unable to raise infants alone, but in which the habitat does not support the cohabitation of multiple females on the same territory (Kleiman, 1977). In this case, paternal care is obligate for the survival of his offspring (Westneat & Sherman, 1993). New World monkey species exhibiting paternal care
tend to have a very high offspring-maternal weight ratio, supporting this hypothesis (Kleiman, 1985). This increased offspring size is hypothesized to create a larger burden for a single parent which results in obligate biparental care.

In non-human primates, social monogamy primarily occurs in the New World monkeys, including owl monkeys (Aotus spp.), titi monkeys (Callicebus spp.), and saki monkeys (Pithecia spp.). These species contrast in the level to which males are involved in infant care, with owl and titi monkeys displaying high levels of care and saki males not displaying infant care. In contrast, New World marmoset and tamarins (family Callitrichidae), which display high levels of male care, exhibit flexible social systems which can be characterized as monogamy, polygyny (multiple females mating with a single male), or polyandry (multiple males mating with a single female) both within and across species (Albuquerque, Sousa, Santos, & Ziegler, 2001; Baker, Bales, & Dietz, 2002; Baker, Dietz, & Kleiman, 1993; Dietz & Baker, 1993; Goldizen, 1987, 1989; Goldizen, Mendelson, Van Vlaardingen, & Terborgh, 1996). No Old World monkeys display significant levels of fathering behavior, while the only apes to do so are the siamangs (Symphalangus syndactylus), which may display social monogamy or polyandry (Lappan, 2008; Palombit, 1995).

**Summary of Non-human Primate Taxa in Which Fathering Occurs**

**Titi monkeys.** Titi monkeys are small, arboreal New World monkeys that have been extensively studied as to their pair-bond relationships (Cubiciotti & Mason, 1975; Mason, 1966, 1974; Mendoza & Mason, 1997). Titi monkey fathers (Figure 3.1) are the primary infant-carriers, in most pairs carrying infants up to 90% of the time (Mendoza & Mason, 1986). As such, infants develop an emotional attachment to their father rather than their mother (Hoffman, Mendoza, Hennessy, & Mason, 1995), including an exaggerated stress response during separation from their father. Males, on the other hand, display their primary attachment to their pair-mate, and do not experience a rise in stress hormones if their infant is removed from the group (Mendoza, 1991; Mendoza & Mason, 1997).

Titi monkey fathers respond to distress calls from their infants (Mason & Mendoza, 1998) and are tolerant of infant contact, usually carrying the infant transversely across their necks. However, titi monkeys of any sex or age class do not appear to be attracted to infants (Mendoza & Mason, 1986; Welker, Jantschke, & Klaiber-Schuh, 1998) and become hyper-responsive to stressful stimuli when there are small infants in the group (Reeder, 2001). Many mothers are only motivated to retrieve infants from the father in order to nurse them (and thus relieve pressure from full mammarys). During early development, titi monkey infants must learn to navigate relatively independently between their father and mother; however, this navigation is facilitated by the large proportion of time that the adult pair-mates spend in contact with each other (Mendoza & Mason, 1986).

When titi infants begin to eat solid food, both parents share food with their offspring. There is no display of active food-sharing as has been demonstrated in some tamarin species (Addessi, Chiarotti, Visalberghi, & Anzenberger, 2007; Joyce & Snowdon, 2007; Ruiz-Miranda et al., 1999); however, infants take food both from their parents’ hands and through direct mouth-to-mouth contact, often without any resistance. Males also groom infants and juveniles; a report on one family of wild Callicebus torquatus found that the parents spent equal amounts of time grooming the two juveniles, and the juveniles received more grooming than they gave to the
parents (Kinsey & Wright, 1982). Most reports suggest that older offspring do not contribute significant amounts to infant care in titi monkeys, at least not on a regular basis (Mendoza & Mason, 1986); however, observations in an extant colony found large amounts of variability in this measure (Bales, Dietz, Baker, Mason, & Mendoza, 2007).

Owl monkeys. Owl monkeys closely resemble titi monkeys in many aspects of their social system, including maintenance of a common territory and the presence of older offspring in the group (Wright, 1994). Owl monkey fathers are also the primary carriers of their offspring, and the most attractive member of the group to other family members (Welker et al., 1998), although there are several significant differences in behavior between owl monkeys and titi monkeys. While titi monkey fathers often carry their infants from the first day of life, owl monkey fathers typically do not begin carrying until week three (Welker et al., 1998; Welker & Schafer-Witt, 1987). In addition, while titi monkey fathers carry infants transversely across the neck, owl monkey fathers usually carry infants ventrally in a way such that they are covered by the thigh. When carried on the back, the infants are carried longitudinally (Welker & Schafer-Witt, 1987).

Owl monkey siblings only rarely carry infants (Welker & Schafer-Witt, 1987). However, an infant owl monkey was reared without a father in a captive group (Jantschke, Welker, & Klaiber-Schuh, 1998). While the mother’s carrying did not decrease, the lack of the male was primarily made up by the increased involvement of an older female sibling. However, the infant was completely independent of carriers much earlier than normal (three months), probably due to lower tolerance of the sibling carrier when compared to the father. Infant care by older siblings was also observed during the replacement of an adult male in a wild owl monkey group.
(Fernandez-Duque, Juarez, & Di Fiore, 2008). After the new male was established in the group, he began to care for the infant as well; however, the infant disappeared at four months of age and was presumed dead, perhaps suggesting that its care was sub-optimal.

Another difference observed between owl monkeys and titi monkeys, in a colony which raised both species for decades, was that titi monkeys were more tolerant of their offspring and displayed aggressive behavior towards them much more rarely (Welker et al., 1998).

Owl monkeys also display food sharing both in captivity (Wolovich, Feged, Evans, & Green, 2006) and in the wild (Wolovich, Perea-Rodriguez, & Fernandez-Duque, 2008). In both captive and wild monkeys, the father is the primary sharer with offspring (Wolovich et al., 2008; Wolovich et al., 2006). In captive owl monkeys (Wolovich et al., 2006), at least some of the transfers from males to offspring are initiated by the male rather than the offspring.

**Marmosets and tamarins.** Marmosets and tamarins (family Callitrichidae) are small-bodied, arboreal Central and South American monkeys which produce twins approximately 80% of births in the wild (Bales, O’Herron, Baker, & Dietz, 2001; Savage et al., 1997) and even larger litter sizes in captivity (Jaquish, Gage, & Tardif, 1991; Jaquish, Cheverud, & Tardif, 1996; Tardif & Jaquish, 1997; Tardif, Layne, & Smucny, 2002). Because they experience a fertile post-partum estrus (Hearn, 1983), females can give birth to two litters per year, and are therefore sometimes lactating and pregnant simultaneously. This is presumably a rather large energy expenditure, and requires help from other family members to maintain the high reproductive rate.

Males contribute to infant care both by carrying infants and by sharing food (Eppe, 1975; Ruiz-Miranda et al., 1999; Tardif, 1994; Tardif, Carson, & Gangaware, 1990). In the wild, males contribute more care to infants which are more closely related, such as full siblings or those for which they have higher paternity certainty (Baker, 1991). The number of adult males predicts infant survivorship in wild golden lion tamarins, particularly in newly formed groups (Bales, Dietz, Baker, Miller, & Tardif, 2000). Alloparenting is very common in marmosets and tamarins (Tardif, 1997), and breeding males often reduce their contribution to infant care when helpers are available (Bales et al., 2000). In wild golden lion tamarins, breeding males which have more helpers also have longer reproductive tenures (the same is not true for females who have more helpers) (Bales et al., 2000).

Significant variations do exist between callitrichid species in the details of infant care behaviors; these are reviewed in detail elsewhere (Tardif, 1994; Tardif et al., 2002; Tardif & Garber, 1994; Tardif, Harrison, & Simek, 1987; Welker & Schafer-Witt, 1987). Perhaps one of the most interesting comparison species is *Callimico goeldii*, common name Goeldi’s monkey. While closely related to the marmosets and tamarins, Goeldi’s monkeys give birth only to one offspring per litter instead of twins. The father starts carrying the infant much later when compared to marmoset and tamarin species (Schradin & Anzenberger, 2001; Schradin & Anzenberger, 2003; Porter & Garber, 2009).

**Siamangs and gibbons.** Siamangs and gibbons are the only apes which demonstrate a monogamous social system (Fuentes, 1999), although it can also be polyandrous in some cases (Lappan, 2008). Despite the characterization of gibbons as monogamous, they have not been reported to display significant amounts of male care (Lappan, 2008). In contrast, male siamangs often carry infants (Chivers, 1974; Dielenthis, Zaiss, & Geissman, 1991; Lappan, 2008), particularly older infants in the second year of life (Chivers, 1974; Lappan, 2008, 2009). Juvenile males also sleep with the adult male after the birth of a new infant in the
group (Dielenithis et al., 1991; Lappan, 2008), while the mother and infant sleep together in a different place. Infants in monogamous groups received more care by adult males than infants in polyandrous groups, even when carrying by both males was summed (Lappan, 2008). Male care in polyandrous groups did not appear to be positively correlated with the male’s affiliative relationship with the mother (Lappan, 2008). Care by males did reduce the carrying by the mother (Lappan, 2008), and mothers providing more care had longer interbirth intervals, suggesting that male care may increase successful female reproduction. Care by juveniles is not common but was noted in a zoo in which twins were born (Dielenithis et al., 1991), where a juvenile male was sometimes noted to carry one of the twins.

**Summary**

Monogamy in primates is hypothesized to be an evolutionary solution to the problem of increasing infant to mother weight ratios, as exemplified by many New World callitrichid species. Indeed, several of the species that have the highest infant to mother weight ratios are the same species that engage in some degree of paternal care and exhibit a monogamous social system. Monogamy has been observed in titi monkeys (*Callicebus*), owl monkeys (*Aotus*), marmosets and tamarins (Family: Callitrichidae), and siamangs (*Symphalangus*). In most of these species, paternal care is common, and is usually expressed through paternal carrying of infants and food sharing. However, monogamy is not always the social system employed by all of these species, and even in those cases in which monogamy is employed, it is not always accompanied by paternal care.

**Current Research Questions**

**Factors Affecting Expression of Fathering in Non-human Primates**

How and why do we see variation in components of male parenting across species? Why do we see individual variation in components of male parenting within species? It is important to distinguish all of the factors which can impact the demonstration of male care. These include attraction to infants, motivation to interact with infants, tolerance of infants, and actual demonstration of male parenting behavior such as carrying or sharing food. These factors can vary between species with male care and within species according to other factors such as the age or prior experience of a male, either as a parent or as an alloparent.

**Hormonal Bases of Fathering in Non-human Primates**

What are the hormonal mechanisms for male parenting? Do male primate care-givers suppress testosterone during periods of care? If so, how do they suppress testosterone while (in some species) simultaneously mating with their pair-mate during her postpartum estrus? One of the most active areas of research on male care is the search for hormonal mechanisms. Testosterone, due to its well-known association with aggression, is usually hypothesized to be negatively associated with male care (Gray & Campbell, 2009; Wingfield, Hegner, Duffy Jr., & Ball, 1990). Hormones associated with female parenting, such as prolactin, estrogen, and oxytocin, have also been hypothesized to be positively associated with male care.
Neurobiological Bases of Fathering in Non-human Primates

What areas of the brain are involved in male parenting? Are these the same as the areas involved in female parenting? What neurotransmitters and receptor systems facilitate male care? While hormonal samples are relatively easy to obtain in saliva, blood, urine, or feces (see section 3b), the neurobiological study of male care is much more difficult to perform in non-invasive, non-terminal studies. Terminal studies of male parenting are relatively rare in non-human primates. The advent of imaging technologies such as positron emission tomography (PET) and functional magnetic resonance imaging (fMRI) have opened up this area of study.

Contributions of Fathers in Non-monogamous Species

What are the species and proximate circumstances in which this occurs? Although this chapter has focused on males of monogamous species that provide what (in some cases) may be care which is required for infant survival, males of other species may occasionally exhibit infant care.

Research Measures and Methodology

In studying paternal behavior, the starting point is observation and analysis of those behaviors performed by the father that are believed to be critical to the survival of his offspring. The exact behaviors that are performed may vary significantly depending on the species; as described earlier, infant care in male primates consists primarily of carrying and food-sharing with infants. In the following sections, we discuss the methodology of conducting observational research and both traditional and more recent methods of investigating the mechanisms driving behavior.

Behavioral Data Collection

Many considerations may affect behavioral data collection including whether data are from a captive colony or wild primates, what type of sampling is being done (focal, ad libitum, scan, etc.), and reliability of observers.

Captive vs. field. Researchers with captive colonies have extensive control over environmental factors including the temperature of their colony, the number of hours of light and dark each day, the timing of feeding, etc. They also have the convenience of always knowing where the subjects are located, and with daily health checks, they are immediately notified of any new births in the colony. All of these factors make observing any behavior, including paternal behaviors, more predictable and convenient. However, several behaviors exhibited in the wild are seemingly absent when animals are housed in captivity. For example, most primate species are highly social animals in their natural environments and maintain relationships with dozens of other conspecifics (Altmann, 1965). However, many nonhuman primate housing facilities have animals housed individually or in small groups (Schapiro, 2000). In many cases, this housing situation might limit the social behavior that a given animal encounters from other individuals and engages in itself. In addition, the physical dimensions might limit the types of behaviors that an individual can engage in. Therefore, capturing the full spectrum of a species’ behavioral repertoire often requires observation in the species’ natural environment.
**Behavioral sampling.** There are several possible behavioral sampling methods, each of which is ideal for addressing a certain type of research question. The type of behavioral sampling employed by a researcher should be chosen in order to optimize the ability of the observational data to address the research question. Potential sampling methods include *ad libitum* sampling, focal animal sampling, all occurrences sampling, one-zero sampling, and instantaneous or scan sampling (Altmann, 1974).

**Inter-observer reliability.** Most current behavioral research is conducted in a collaborative fashion, with multiple observers and multiple people scoring different behaviors of interest. Given this, some attention must be paid to consistency between observers. Inter-observer (a.k.a. inter-rater) reliability quantifies accuracy between observers. When working with discrete variables, inter-observer reliability can be calculated simply by dividing the number of observations that are agreed upon between observers by the total number of observations (Gwet, 2008).

**Hormonal Data Collection**

Peripheral and central hormones provide potential mechanisms affecting paternal behaviors. While central neurotransmitters are more directly tied to behavior, sampling these substances requires more invasive techniques and may not be possible in certain circumstances. Peripheral hormone concentrations can be measured through analysis of urine, fecal, or blood samples, but the relevance of these measures depends on the hormone being sampled. The benefits and consequences of the type of samples collected, and several other variables concerning hormonal sampling will be discussed further in the following sections.

**Sample type.** Different sample types can be useful in answering different questions, and can be more or less feasible to collect depending on several other factors. For example, as mentioned above, central measurements of neurotransmitter concentrations may not be feasible if a researcher is observing animals in their natural environments. Cerebrospinal fluid (CSF) may be used to measure neurotransmitters and/or their metabolites, but obtaining CSF is possible only after immobilizing the animal. It is an invasive technique and requires anesthesia. So while central concentrations are the most direct link to behavior, they are not always feasible.

Another measure is through the plasma component of peripheral blood. Many of the hormones that are thought to play critical roles in behavior are produced peripherally and have centrally located receptors. For example, anxiety-like traits are often correlated with glucocorticoids produced by the adrenal glands, which have receptors in the central nervous system (Capitanio, Mendoza, & Bentson, 2004). Feeding behaviors are influenced by insulin produced by the pancreas (Rodin, Wack, Ferrannini, & DeFronzo, 1985). Reproductive behaviors are influenced by concentrations of the steroid hormones testosterone (produced in the testes) (Crews, Traina, Wetzel, & Muller, 1978) and estrogen (produced in the ovaries) (Brawer, Naftolin, Martin, & Sonneschein, 1978). Blood samples represent internal conditions over a very short time period (i.e. seconds to minutes). Obtaining blood samples is a common technique for sampling hormone concentrations in both laboratory and wild studies of nonhuman primates (Coe, Mendoza, Smotherman, & Levine, 1978; Hennessy, Mendoza, & Kaplan, 1982; Sapolsky, 1985; Sapolsky & Krey, 1988). In order to reduce the stress of plasma
sampling, some nonhuman primate subjects have been trained to present an arm for obtaining a blood sample (Phillippi-Falkenstein & Clarke, 1992; Reinhardt, 1991).

Many hormones are excreted in the body’s waste. Importantly, the concentrations that are excreted are typically correlated to the concentrations of the active hormones in the blood. The benefit of sampling urine or feces is that they are the least invasive methods of obtaining hormonal information. For this reason, these methods are commonly used in field studies (Lynch, Ziegler, & Strier, 2002; Weingrill, Gray, Barrett, & Henzi, 2004). In addition, labs conducting long-term hormonal monitoring on many animals (Altmann, Gesquiere, Galbany, Onyango, & Alberts, 2010) often use one of these sampling methods because they allow a single researcher to collect samples from multiple animals in a relatively short time. Hormone concentrations from urine or fecal samples are summed over a relatively long time period (i.e., hours). For example, the hormone concentration in a morning urine sample represents the internal hormone state over the course of the previous night (Munro et al., 1991). For this reason, the types of questions that can be answered with urine samples are different than those that can be answered with blood samples.

A more recently developed method of obtaining estimates of hormone concentrations is through hair samples. Because hair grows at a fairly slow rate, the hormones estimated from hair samples represent concentrations averaged over the entire length that the hair was present on the animal’s body. One method that has been employed in order to narrow the temporal window represented in a given hair sample is shaving the area to be sampled ahead of time, then allowing a certain amount of time (weeks to months) to pass before collecting the hair that has grown in the shaved area (Davenport, Tiefenbacher, Lutz, Novak, & Meyer, 2006).

**Imaging**

With the advent of non-invasive imaging, it has become much easier to study brain activity in both humans and non-human primates. However, until now it has been little used to address the question of fathering in non-human primates, but more so actually in humans (Seifritz et al., 2003; Swain, 2008; Swain, Lorberbaum, Kose, & Strathearn, 2007). Most important is the choice of the proper imaging technology. While functional MRI provides superior temporal resolution, position emission tomography (PET) has the advantage of being able to image many different radio-tracers, as well as allowing the subject animal to be unconscious in the scanner (Bandettini, 2009; Otte & Halsband, 2006). The brain activity measured during the scan, however, reflects the uptake period for the radioactive ligand, during which the animal was unrestrained and freely behaving. This can remove the confounding effects of stress on brain metabolism.

**Summary of Research Measures and Methodology**

Several methods for studying monogamy and paternal behavior exist. Selection of a certain methodology by investigators should be done carefully in order to avoid using a method that is flawed, outdated, or inappropriate. The research measures should be selected so that they can appropriately answer the specific research question(s) being posed by the investigator. Once a methodology is selected, it is critical that the investigator becomes familiar with the inherent limitations of their methods in order to avoid making inaccurate conclusions.
Empirical Findings

Factors Affecting Expression of Fathering in Non-human Primates

As discussed previously, species may vary in how attractive infants are to males, males’ levels of responsiveness, and the full expression of male parental care (Pryce, 1996). For instance, male titi monkeys are only tolerant of, not attracted to infants (Mendoza & Mason, 1986), but carry infants extensively due to the intolerance of females. In contrast, male common marmosets (Zahed, Prudom, Snowdon, & Ziegler, 2007) are strongly attracted to infant cries and motivated to carry infants, whether the cry is coming from their own infant, a strange infant, or an iPod playing infant recordings.

Even within species in which paternal care is the norm, there is still substantial variation in male parenting, and there may be several factors that affect the likelihood that an individual will exhibit paternal care. Experience, either with his own infants or as an alloparent may contribute significantly to whether a male will exhibit paternal behaviors towards his offspring (Ziegler, 2009). Male common marmosets that had experience with their own infants responded with lower latencies to infant stimuli, whether familiar or unfamiliar (Zahed et al., 2007). In titi monkeys, infants born to parents with previous experience with their own infants had significantly higher survival; within experienced parents, it did not matter if they were wild-born or laboratory-born or how many previous litters they had raised (Reeder, 2001).

The effects of experience are often modulated hormonally (see the next section). While juvenile experience with siblings and adult experience as a father may explain some of the individual variation in behavior, it is notable that alloparenting itself is extremely variable both between and within species. In studies of marmosets and tamarins, sex differences in alloparenting are inconsistent, suggesting other sources of individual variation (Bales et al., 2000). It is possible that paternal style will turn out to be highly influenced by the style of fathering received as an infant, as has been shown for mothering in various species (Francis, Diorio, Liu, & Meaney, 1999) and for fathering in monogamous prairie voles, Microtus ochrogaster (Stone & Bales, 2010), and California mice, Peromyscus californicus (Bester-Meredith & Marler, 2003).

Hormonal Basis of Fathering in Non-human Primates

Prolactin (PRL) is a peptide hormone that in females is critical for milk production during lactation (Freeman, Kanyicksa, Lerant, & Nagy, 2000) and is involved in the onset and maintenance of maternal behavioral care of infants (Wynne-Edwards & Timonin, 2007). In males, PRL has been implicated in paternal behavior in taxa that are characterized by biparental care including rodents, non-human primates, and humans (Schradin, Reeder, Mendoza, & Anzenberger, 2003; Wynne-Edwards, 2001; Ziegler & Snowdon, 1997a), however the data linking PRL with paternal behavior remain somewhat equivocal. Essentially, species vary as to whether males experience rises in PRL around the birth of infants, and whether they experience acute rises when carrying infants.

Reduced testosterone has been associated with paternal care in two nonhuman primate species: cotton-top tamarins (Saguinus oedipus; Ziegler, Wegner, & Snowdon, 1996) and black tufted-ear marmosets (Callithrix kuhlii; Nunes, Fite, Patera, & French, 2001). In
the marmosets, high-carrying effort males showed not only reduced testosterone, but also reduced estradiol and reduced cortisol in comparison to non-father males of the same age and with similar numbers of previous litters. This suggests that something about the presence of new offspring is responsible for the reduced testosterone. In black-tufted-ear marmosets, the number of previous litters that a male had cared for (either as a sibling or as a father) significantly predicted his urinary testosterone concentrations (Nunes, Fite, & French, 2000). Perhaps most interesting is that experienced marmoset fathers show a reduction in testosterone when exposed to the scent of their own infant (Prudom et al., 2008).

Cortisol in some primate males also appears to respond to the birth of their own offspring. However, the direction of the response is not consistent. For example, cotton-top tamarin males with female partners at mid-gestation show increased cortisol concentrations (Almond, Ziegler, & Snowdon, 2008). However, Ziegler and colleagues (1996) showed that in the same species postpartum cortisol levels are lower in experienced males than they were in first-time fathers. In another biparental primate, the black tufted-ear marmoset fathers that were categorized as displaying “high carrying” effort had significantly lower cortisol than “low carrying” fathers during the first two weeks postpartum (Nunes et al., 2001).

**Neurobiological Bases of Fathering in Non-human Primates**

The neurobiology of male parenting has primarily been studied in monogamous rodents such as the prairie vole and the California mouse, and the neuropeptide arginine vasopressin has been implicated in both rodent species (Bester-Meredith & Marler, 2003; Wang, Liu, Young, & Insel, 2000; Wang, Young, De Vries, & Insel, 1998). However, one of the few primate studies to examine neural changes associated with paternal behavior (Kozorovitskiy, Hughes, Lee, & Gould, 2006) showed that male marmoset fathers had higher vasopressin V1a receptor binding in the prefrontal cortex compared to pair-bonded non-fathers. There were no changes in vasopressin V1b, oxytocin, or prolactin receptors. Within fathers, the receptor binding was negatively correlated with the age of the father’s youngest offspring, suggesting continued plasticity across the lifespan.

One window into the neurobiology of paternal behavior may be through the neurobiology of pair-bond formation. (For recent review, please see Fernandez-Duque, Valeggia, & Mendoza, 2009). Male titi monkeys that were in long-term pair-bonds showed differences in glucose uptake in many brain areas when compared with males living alone (Bales, Mason, Catana, Cherry, & Mendoza, 2007). The lone males in that study were subsequently paired, and PET scans showed changes in neural activity in the direction of males in long-term relationships.

**Contributions of Fathers in Non-monogamous Primate Species**

Many studies in polygynous species have used molecular genetic analysis to determine paternity (Altmann et al., 1996; Di Fiore & Fleischer, 2005; Gagneux, Boesch, & Woodruff, 1999; Keane, Dittus, & Melnick, 1997). Genetic evidence has then been used to suggest that some males in polygynous species intervene and defend their own offspring from infanticidal males. Importantly, offspring defense of infanticidal males does not appear to be universal, in that only genetically related infants are defended by a given male (Borries, Launhardt, Epplen, Epplen, & Winkler, 1999; Buchan, Alberts, Silk, & Altmann, 2003; Charpentier, Van Horn, Altmann, & Alberts, 2004). Although these interventions were shown to improve the survival
of offspring, the nature of this form of “care” is qualitatively different from that observed in monogamous species, in which infant carrying, infant retrieval, and food sharing are common.

**Summary of Empirical Findings**

Experiential and neurobiological factors are known to affect paternal care in nonhuman primates. In many species, whether the male has previously engaged in paternal behavior, either of his own offspring or of younger siblings, affects his future participation in paternal care. First time fathers behave differently than experienced fathers. Those individuals that were in their natal group when their younger siblings were born, and engaged in or observed parental care by their parents are more likely to behave appropriately when they become parents. Changes in prolactin, testosterone, and cortisol are all observed in male nonhuman primates around the time of parturition. Neurobiological changes in V1a receptor density in relationship to paternal care have also been observed in common marmosets.

**Bridges to Other Disciplines**

Research on non-human primate fathering is helpful in understanding the evolution of fathering and the circumstances under which it is displayed. For human fathering, it highlights the importance of considering differences in the motivation vs. the expression of fathering; the role of parenting experience; and also the role of alloparenting experience (exposure to babies as a child or teenager). Programs such as the Roots of Empathy (http://www.rootsofempathy.org) have even used interactions with infants as a treatment to increase pro-social behavior in schools.

In addition, the experimental control and higher level of invasiveness available in studies of non-human primates (as opposed to humans) allow examination of physiological and neurobiological mechanisms which would be difficult in humans. Many of the less invasive physiological techniques described here are now being applied to humans, particularly consideration of the role of testosterone in fathering (Gray, 2003; Gray & Campbell, 2009; Gray, Parkin, & Samms-Vaughan, 2007). Testosterone in human fathers appears to drop after the transition to fatherhood, similar to non-human primate fathers.

**Policy Implications**

Findings on fathering in non-human primates suggest that the role of positive experiences with infants (both own and others’) should be weighted heavily in programs to promote good fathering. Although it has been little studied to date, information on the consequences of “bad” fathering could be used to suggest treatment options for affected children. In addition, findings in non-human primates could help identify males that are at risk of poor fathering and suggest mechanisms for treatment. Finally, understanding the relationship between the mechanisms for pair-bonding and parenting may have relevance to understanding the relationships between these factors in humans.

**Future Directions**

Additional topics of interest in the physiology and neurobiology of male parental care are reviewed elsewhere (Bales, Maninger, & Hinde, 2011). In particular, in both human and
non-human primates, the neurobiology of male parenting is vastly under-studied. With use of new imaging technologies, these studies are now possible. Furthermore, the energetics of fatherhood (the changes in caloric demand and metabolism that are associated with the carrying of infants and other paternal behaviors), which have been studied some in non-human primates, are almost completely unstudied in human males.

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References


