Mini–Review

Sex Differences In Nonhuman Primate Behavioral Development

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Sex differences in behavior and developmental trajectories in human children are of great interest to researchers in a variety of fields, and a persistent topic of discussion and debate is the relative contribution of biological vs. social influences to such differences. Given the potentially large effects of cultural and social influences on human child development, nonhuman primates are important model species for investigating the biological and evolutionary roots of sex differences in human development. This Mini-Review briefly summarizes the existing literature on sex-biased behavior toward infant nonhuman primates by mothers and other social partners, followed by a review of findings on sex differences (or lack thereof) in primate behavioral development from a variety of species in wild and naturalistic settings. These include differences in physical and social development, including play, grooming, and object manipulation patterns, as well as nursing and the development of foraging behavior. The Mini-Review concludes by providing potential avenues for future research.   © 2016 Wiley Periodicals, Inc.

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Sex differences in the behavioral development of human children are of great interest to researchers in a variety of fields. A persistent topic of discussion and debate is the relative contribution of biological (nature) vs. social (nurture) influences to such differences (for review see McIntyre and Edwards, 2009). However, it is clear that the nature vs. nurture debate is a false dichotomy and that human sex-typed behavior results from a dynamic blend of pre- and postnatal influences that combine somatic and physiological factors as well as the individual's particular social milieu (Alexander and Wilcox, 2012; Fausto-Sterling et al., 2012; Moore, 2012). The articles in this special issue highlight differing molecular, hormonal, neuroanatomical, and epigenetic effects according to biological sex as well as the downstream effects on behavior, pathology, and disease processes. The timing and interconnectedness of many of these processes remain unknown, so human sex differences remain an exciting and important area of study. In studies of child

development, it is quite difficult to disentangle biological from social drivers. Human children begin to gender self–identify by 27–30 months of age (Martin et al., 2002; Zosuls et al., 2009), and many studies report that parents and others treat male and female children differently (e.g., Fagot and Hagen, 1991; Ruble et al., 2006), but some do not (Lytton and Romney, 1991). The role that prenatal hormones and their neural substrates play in human gender development has been extensively studied, often focusing opportunistically on subjects with abnormal hormone profiles, such as girls with congenital adrenal hyperplasia (for a recent review see Berenbaum and Beltz, 2016). However, it remains ethically and logistically difficult to conduct most of the controlled experiments that would be required to investigate either biological (e.g., the precise timing and duration of hormonal influences) or social (e.g., the removal of one gender of parent) factors.

Given the potentially large effects of cultural and social influences on human child development,

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SIGNIFICANCE

Sex differences in human child behavioral development have long been of interest to both researchers and the general public. The "nature vs. nurture" debate has historically focused on the differing contributions of biological processes vs. social influences to these differences, yet we now know that nature and nurture interact in complex and varying ways. Many sex differences in behavioral development exist in nonhuman primates, despite a comparative lack of sex-biased treatment by mothers and other social partners. This Mini-Review briefly summarizes sex differences in infant behavioral development in nonhuman primates.

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nonhuman primates (hereafter "primates"), are important model species for investigating the biological and evolutionary roots of sex differences in human development. Experiments focusing on hormonal manipulations have been conducted in controlled settings in primates and have elucidated various physiological pathways for sex-typed behavioral development (for review see Meredith, 2015). However, such highly controlled studies raise questions about whether the processes found operate the same way in the natural environment. This contribution briefly reviews the published literature on sex differences in primate behavioral development but does not attempt to review all documented studies; rather it provides examples of key findings with regard to behaviors that are particularly important for developing primates. This Mini-Review also refers heavily, but not exclusively, to reports from subjects that are living either in wild settings or in species-typical social settings in captivity, given that these are arguably the most relevant for understanding the natural development of sex-typed behavior. Finally, studies of infants (defined below) are the focus here, to elucidate differences in behavioral development that occur well before the hormonal changes of puberty. Thus, the development of aggression and sexual behavior are outside the scope of this Mini-Review.

It is important to review briefly some fundamentals of primate natural history to set this Mini-Review in context. As in other mammals, adult primate behavior is shaped by sexual selection, such that females are expected to show more behaviors related to offspring care and males are expected to show more behaviors related to competition for mating opportunities. The manner in which early sex differences in behavior emerge is an intriguing question that is addressed below but must also be considered in light of social organization; infants of most nonhuman primate species grow up within a complex social environment that includes maternal and paternal kin and other relatives and nonrelatives. In addition, adult behavior in many primates is characterized by hierarchies of dominance rank in either or both sexes, which influences access to food, mates, and social partners. Many primate social systems are female philopatric (e.g., baboons; *Papio* spp.), wherein female offspring stay in their natal community and develop long-term social relationships and males disperse at sexual maturity. Fewer species are male philopatric (e.g., chimpanzees; *Pan troglodytes*) and show the opposite pattern of males staying in their natal community and females dispersing. In other species (e.g., gorillas; *Gorilla* spp.), both sexes may disperse and may change group membership more than once during their life. These sex-biased dispersal patterns can relate to sex differences in social development because relationships that are formed early in life can persist into adulthood.

The primary relationship for most infant primates is the mother. Following Periera and Altmann (1985), *infancy* is defined as the stage that begins at birth and continues while the offspring is nutritionally dependent on the mother. Juveniles are those individuals that are weaned (and can therefore physically survive the death of their mother) but have not yet entered puberty. Adolescence is harder to define, but encompasses the social and physical maturation associated with puberty and becoming a reproductively mature individual (Periera and Altmann, 1985; Setchell and Lee, 2004). Primates are unique among mammals in terms of the extended period of juvenility and adolescence, and several competing theories have been proposed to explain the prolonged period between weaning and sexual maturity (for review see Lonsdorf and Ross, 2012). For the purposes of this Mini-Review, the critical point is that mothers are of primary import throughout infancy, and for many species that primacy extends postweaning.

SEX-BIASED BEHAVIOR BY MOTHERS AND OTHERS

The Trivers–Willard (1973) hypothesis sets the theoretical groundwork for maternal investment to differ according to offspring sex. According to this hypothesis, mothers should invest more in the sex that has higher reproductive potential if they are in adequate physical condition themselves. That is, mothers in good condition should invest more in sons who will theoretically be in better condition and more successfully compete for mates. Mothers in poor condition should be biased toward daughters, who will likely be able to mate regardless, rather than sons who may not be able to compete. Trivers and Willard originally developed this hypothesis to apply to offspring birth sex ratios, but it was subsequently extended to postnatal maternal behavior as well (for review see Brown, 2001). However, the evidence for overt sex-differential behavior toward offspring by primate mothers is limited, and quantitative measures of maternal condition are rarely included. Most studies have shown few, or no, differences in the behavior of mothers toward sons or daughters (e.g., vervets [*Chlorocebus aethiops*]: Fairbanks, 1996; galagos [*Galago senegalensis braccatus*]: Nash, 2003), although such studies have simply not been conducted for most nonhuman primate species. Moreover, the existing research is heavily biased toward the cercopithecines (Old World monkeys such as baboons and macaques, *Macaca* spp.). In the rhesus macaque (*Macaca mulatta*), a particularly well-studied species, differences in maternal care according to infant sex exist in some dimensions but not others. Brown and Dixson (2000) found that mothers did not differ in their treatment of sons and daughters in the first 6 months of life, as measured by restraint, rejection, and grooming. However, Tomaszycki et al. (2001) found that mothers respond more readily to distress vocalizations of sons compared with daughters in the first 8 months of life. More recently, Dettmer et al. (2015) found that mothers engaged in more face-to-face mutual gazing and grooming with sons than with daughters during the first 3 months of life.

Other primates are understudied compared with rhesus macaques, but similar sex biases have been observed in other species. In Japanese macaques (*Macaca*

fuscata), mothers more often break contact and retrieve infant sons than infant daughters in the first year of life (Eaton et al., 1985). Similarly, Bentley-Condit (2003) found that olive baboon (*Papio anubis*) mothers initiated a break in contact with their sons earlier and were more often in contact with daughters in early infancy (up to 2 weeks of age). Bentley-Condit (2003) interpreted this as representing a higher level of attentiveness toward female infants and/or a "leniency" toward male infants. In patas monkeys (*Erythrocebus patas*), mothers both cradle and reject infant sons more than daughters, but no differences are found with regard to grooming, restraint, or retrieval (Rowell and Chism, 1986). In blue monkeys (*Cercopithecus mitis stuhlmanni*), such differences do not appear until later; mothers groom daughters more than sons (Forster and Cords, 2002) after 6 months of age.

None of the studies mentioned above explicitly incorporates a measure of maternal condition, which can be quite difficult to measure in natural settings but is a key component of the Trivers-Willard hypothesis. One proposed proxy for maternal condition is dominance rank, given that higher ranking females primates often have priority of access to better feeding areas (e.g., chimpanzees: Murray et al. 2006) and/or suffer less injury (e.g., baboons: Archie et al. 2014). Studies of yellow baboons (*Papio cynocephalus*) have shown that maternal dominance rank interacts with infant sex when it comes to differential treatment by mothers; high-ranking mothers showed reduced nursing (Nguyen et al., 2012) and carrying (Altmann and Samuels, 1992) of daughters relative to low-ranking mothers, but no such rank difference exists for mothers of sons. In this case, maternal treatment of daughters varied according to condition (as measured rank), but treatment of sons did not, which is counter to the predictions of the Trivers–Willard hypothesis. The authors proposed that low-ranking mothers may generally be less permissive of daughters, which, when coupled with sons being generally more exploratory (see below), could explain the observed differences.

In each of the above-mentioned studies it is difficult to separate differential maternal behavior from differential infant behavior, which presents a challenging "chicken or egg" problem for such studies. For example, if males are more independent or social than females, mothers may have more opportunities to retrieve them when they are interacting with others (Japanese macaques: Eaton et al., 1985) and/or more opportunities to groom daughters who stay in close proximity (blue monkeys: Forster and Cords, 2002). However, two studies have found convincing evidence of sex-biased maternal socialization of very young infants, who are arguably unable to actively influence maternal grouping patterns. For Barbary macaques (*Macaca sylvanus*), Timme (1995) found that mothers of female newborns interacted mostly with females of their own matriline, whereas mothers of sons interacted with nonmatriline females. Subsequently, at 5 months of age, daughters stayed closer to their mother than did sons. Timme (1995) suggests that these maternal social interactions during the newborn stage serve as a sex-specific

infant socialization process to integrate female infants into their matrilineal network and male infants into the larger social group, which foreshadows adult grouping patterns in this female philopatric species. In chimpanzees, a male philopatric species, Murray et al. (2014) found that mothers of sons spent more time in large groups and groups containing adult males than mothers of daughters. These differences were especially pronounced in the first 6 months of life, during which infants are in almost constant contact with the mother and therefore do not dictate grouping patterns. At the age of 2.5–3 years, when chimpanzee infants begin to spend more time out of maternal proximity, sons socialize with more individuals overall and with more adult males than daughters (Lonsdorf et al., 2014a). Together, these two case studies present the intriguing possibility that primate mothers are actively socializing their very young infants according to their future sex-specific social roles. Much work remains to determine the potential cognitive, hormonal, or other physiological mechanisms that may be involved in maternal socialization strategies.

Sex-differential treatment of infant primates by nonmothers is comparatively understudied both theoretically and empirically, and in the few studies that have been conducted the evidence is scant. No differences in behavior directed to infants by nonmothers according to sex were found in patas monkeys (Rowell and Chism, 1986) or blue monkeys (Forster and Cords, 2005). Similarly, in an investigation of nonmother infant handling in bonnet macaques (*Macaca radiata*), Silk (1999) found that male and female infants were handled at equal rates. However, in spider monkeys (*Ateles geoffroyi*), adult males were found preferentially to handle male infants (Evans et al. 2012), which was proposed to foster later social bonds in this male philopatric species. The most well-known example of differential treatment according to sex comes from Japanese macaques; nonmother group members show more punishing behavior toward infant females compared with infant males (Eaton et al., 1985), which continues through juvenility. The relative lack of sex-biased behavior by nonmothers stands in stark contrast to the case in humans, for whom societal and cultural gender socialization stems from a variety of nonparent sources (for review see Leaper and Friedman, 2007).

SEX DIFFERENCES IN INFANT DEVELOPMENT

Independence From Mother

For most primates, the mother is the safe "home base" from which infants begin to explore their physical and social environment (Hinde and Atkinson, 1970). As the infant matures, he or she begins moving away from the mother more often and has increased responsibility for maintaining proximity to the mother. Leaving the home base requires increasing degrees of physical and motor development, which is difficult to measure precisely in naturally living primates, although advances have been made in investigating skeletal remains (Zihlman

et al., 2004) and using photographic techniques (Smith et al., 2013). Mode of locomotion is often use as a proxy for motor development, because infant primates spend the earliest period of their lives being moved by their mothers, via clinging or riding, before travelling independently. The switch to independent locomotion is thus an important milestone but one that is relatively understudied in wild or naturally housed primates with regard to sex differences. In wild chimpanzees, male infants begin travelling independently earlier and spend more time traveling independently overall than female infants (Lonsdorf et al., 2014b). Although independent travel is a behavioral proxy for motor development, these results mirror those found in human children; infant boys have increased motor activity level compared with infant girls (Campbell and Eaton, 1999) and showed more leg activity both ante- and neonatally than girls (Almli et al., 2001).

In addition to representing physical development, independent travel may result in increasing distance from the mother, which has been proposed to represent a measure of social independence and/or riskier behavior. Among humans, boys spend more time away from their mothers than girls (Edwards, 1993) and engage in more risk-taking behaviors (Ginsburg and Miller, 1982). Similarly, independent travelling in chimpanzee infants is linked with being at increased distances from the mother, wherein male infants are at greater distance from their mother by age 3 and remain at greater distances than females for the rest of infancy (Lonsdorf et al., 2014b). These sex differences in proximity persist through the juvenile and adolescent stages of development, with male juveniles spending less time than females within 15 m of their mothers and also spending greater amounts of time "leading" their mothers during travel (Pusey, 1983). Bentley-Condit (2003) also found sex differences in proximity measures in newborn olive baboons; males average more time than females at 1-m distance from their mothers in the first 2 weeks of life. Similarly, Nguyen et al. (2012) found that newborn male yellow baboons initiated higher rates of changes in contact with mothers than did newborn females. In blue monkeys, such differences appear later in development but follow the same pattern; at 6 months, male infants initiated more changes in proximity from their mothers than did female infants (Forster and Cords, 2002).

Social Development

Among human children, girls have been found to excel in a variety of social measures, including higher rates of eye contact (Hall, 1985), social understanding (Hall et al., 2000), and prosocial behavior (Eisenberg et al., 2006). The degree to which these patterns are rooted in biology or encultured remains a somewhat open question because controlling for the influence of parents, teachers, peers, and social norms is exceedingly difficult. One study reduced these influences by examining neonates less than 2 days old, reporting that females prefer looking at pictures of a face, whereas males prefer looking at pictures of a mobile (Connellan et al., 2000), suggesting an innate sex difference in preferences for social vs. mechanical objects. An analogous study in rhesus macaques measured "social motivation" in newborns (under 5 weeks old) raised in a controlled postnatal environment and found that females looked more at conspecific computer-generated faces and engaged in more affiliative behavior with a human caregiver (Simpson et al., 2016). Given the relative lack of overt sex-specific socialization of primate infants, patterns of sex differences in sociability or social preferences may provide evidence of evolved biologically based processes that catalyze later sex-specific social development. Because the majority of socializing that a young primate does is through grooming or play, these are addressed in detail below.

Social grooming. Social grooming is a key behavior with regard to social development in primates; it is thought to serve primarily as a source of social bonding and relationship building (Henzi and Barrett, 1999). Although less well studied than in nonhuman primates, social grooming in an important relationship metric in humans as well (Nelson and Geher, 2007) and girls cross-culturally engage in more social grooming than boys (Edwards, 1993). Among nonhuman primates, the rhesus macaque is one of the most often studied primate models. These monkeys have a matrilineal social structure based around a stable groups of related females. As predicted by their adult social environment, female infants groom others more than males in the first year of life, and this grooming is targeted at female kin (Roney and Maestripieri, 2003; Kulik et al., 2015). Grooming continues to develop along sex-specific social lines through puberty and early adulthood. Similarly, Japanese macaque female infants under 1 year of age groomed others more (Eaton et al., 1985) and this difference continued through the juvenile phase in the second year of life (Eaton et al., 1986). In addition, in Sichuan snub-nosed monkeys (*Rhinopithecus roxellana*: Wang et al., 2007) and baboons (Young et al., 1982), female youngsters consistently groomed more than males. In chimpanzees, sex differences do not appear until juvenility (Nishida, 1988; Pusey, 1990), when female juveniles increase the amount of grooming directed at the mother and male juveniles groom more frequently outside the maternal unit. As detailed by Roney and Maestripieri (2003), sex differences in grooming by young primates are likely adapted to and reflect the particular social structure of the species. The mechanisms by which these differences arise remain an intriguing line of inquiry.

Play. As with grooming, play is a critical component of social development. Studies of human child play have documented several differences according to sex, but here again it is difficult to disentangle the dynamic influences of parents, other adults, and peers. Caregivers may encourage sex-typed activities (Lytton and Romney, 1991), but there may also be innate preferences or predispositions (Serbin et al., 2001) that caregivers reinforce. For example, researchers have found a male bias toward amount of time spent playing (Edwards, 1993), more

rough-and-tumble play (Maccoby, 1988), and play in larger groups (Maccoby and Jacklin, 1987); these sex differences continue to increase through juvenility and beyond. Human boys also engage in more object-oriented play than girls (Pellegrini and Bjorklund, 2004). In contrast, girls engage in more play parenting (Berman et al., 1977), but this difference becomes more marked in juvenility and beyond (Goldberg et al., 1982) and is highly likely to be influenced by parents, who more often assign child-care roles to girls (Whiting and Edwards, 1988).

Several of these patterns have also been found in primates for which there is scant evidence of reinforcement by other social group members. In general, juvenile male primates tend to play more than juvenile females (for review see Fagen, 1993; Meredith, 2013) but differences emerge early in life in several species. For example, male infants show more time spent playing in olive baboons (Owens, 1975), blue monkeys (Forster and Cords, 2005), Japanese macaques (Eaton et al., 1985), rhesus macaques (Kulik et al., 2015), and western lowland gorillas (*Gorilla gorilla gorilla*: Maestripieri and Ross, 2004). In chimpanzees, male infant social play peaks earlier than that for female infants (Lonsdorf et al., 2014b). As in humans, some studies have also found sex biases in play type among primates. Brown and Dixson (2000) studied infant rhesus macaques in the first 6 months of life and found that males initiated play and engaged in more rough-and-tumble and chasing play than females. The propensity for males to exhibit more rough-and-tumble play has also been found among blue monkeys (Forster and Cords, 2005), patas monkeys (Rowell and Chism, 1986), Japanese macaques, and olive baboons (for review see Brown and Dixson, 2000). In addition, male Japanese macaque infants under 1 year of age not only played more but played in larger groups than female infants (Eaton et al., 1985).

Sex differences in the realm of object manipulation and/or preference have also been found that are analogous to the human data. In a well-known study of captive vervet monkeys, Alexander and Hines (2002) found toy preferences among male and female vervets that paralleled human child toy preferences; males preferred toy cars and balls, whereas females preferred a doll and a pot. In a followup study of captive rhesus monkeys, Hassett et al. (2008) replicated the male preference for wheeled toys, but female preferences were more variable. Although intriguing, both of these studies should be interpreted with caution with regard to wild primate development given that a large proportion of individuals in both studies were fully adult. In addition, toys were presented in the social group, which makes true individual preferences difficult to detect because of social dynamics that may restrict access to objects. However, there is emerging evidence of such differences in the wild. Immature chimpanzee males were found to engage in more object-oriented play than females (Koops et al., 2015), but female youngsters at one study site perform a specific behavior called "stick carrying," in which a stick is cradled and carried in a form of play mothering, significantly more often than young males (Kahlenberg and Wrangham, 2010). Female biases in other forms of play parenting, such as interest in or attempting to interact with and carry other infants, are also widespread (e.g., western lowland gorillas, Meder, 1990; rhesus macaques: Lovejoy and Wallen, 1988; bonnet macaques: Silk, 1999; blue monkeys: Cords et al., 2010). Thus, there are diverse lines of evidence for sex differences in play behavior in many primate species. Indeed, these sex differences in play may represent evolved predispositions that reflect patterns of mating competition and parental investment that are shared by most mammalian species.

Development of Foraging and Complex Skills

Both human and nonhuman primates undergo a transition from an exclusive diet of mother's milk (or its substitute) to one of a variety of solid foods. This is an area in which it is particularly difficult to disentangle maternal influence from infant behavior, given that milk synthesis is a flexible and dynamic process of feedback between the mother and the infant (Hinde and Milligan, 2011). In humans, the evidence is equivocal on whether mothers produce different milk for sons vs. daughters. A study of well-nourished U.S. mothers found that mothers produced milk with higher caloric content for male infants compared with female infants (Powe et al., 2010). Similarly, Fujita et al. (2012) reported support for the Trivers-Willard hypothesis in a study of agropastoralists in northern Kenya: higher-economic-status mothers produced richer milk for sons, whereas poor mothers produced richer milk for daughters. However, in a study of Filipino mothers, no differences according to infant sex were found in milk composition, milk energy, or breast-feeding frequency (Quinn, 2013). Complicating the picture are the varied influences on the introduction of solid food. A recent study in the United Kingdom indicated that introduction of solid food is influenced by myriad maternal factors, including age, parity, and education level, but in addition sons were perceived as 'hungrier' and thus were introduced to solid food earlier (Brown and Rowan, 2016). In nonhuman primates, no sex differences were found in time spent nursing among wild chimpanzees (Hiraiwa-Hasegawa, 1990; Lonsdorf et al., 2014b) or galagos (Nash, 2003), whereas male patas monkeys were found to nurse more in late infancy (Rowell and Chism, 1986). However, studying primate nursing behavior in a naturalistic setting allows only crude measures, such as suckling time, to be observed. Suckling time is not an ideal measure for several reasons; it is hard to see, it may occur for comfort rather than nutritive purposes, and actual milk transfer amounts may not be correlated with suckling time. Additionally, recent experimental research demonstrates that milk synthesis in rhesus macaques may vary according to maternal rank, stress, parity, and offspring sex (Hinde and Milligan 2011) and that these differences predict infant temperament and behavior (Hinde et al., 2015). For example, macaque mothers of sons

produce milk with higher energy density but produce a lower total volume of milk (Hinde, 2009), whereas mothers of daughters produce milk with a higher mean calcium concentration (Hinde et al., 2013). Clearly, much more work remains in the area of primate milk synthesis as it relates to, among others topics, differential sex-biased maternal investment. The experimental techniques described above for macaques cannot be applied in a naturalistic setting, but advances in noninvasive assessment of stable isotope ratios (Reitsema, 2012) provide a promising avenue for future studies of primate nursing.

As the proportion of milk in the diet is reduced, a young primate's first interaction with solid food often occurs during cofeeding events in which the infant ingests a part of the food item being eaten by the primary caregiver (e.g., Japanese macaques: Ueno, 2005; mountain gorillas, *Gorilla beringei beringei*: Watts, 1985). Synchronicity between adult and offspring feeding suggests an important role for social learning in terms of which foods are edible and/or preferred as well as how to access food items that require more complex processing skills. Rapaport and Brown (2008) provide an excellent summary of the potential role of social learning in the development of foraging across the primate order, but sex differences in foraging development are relatively understudied. In tufted capuchins (*Sapajus nigritus*), youngsters exhibit sex differences in foraging development consistent with adult sex-typed foraging behavior. In particular, young males preferentially focused their attention on the feeding behavior of adult males and showed significantly more dietary overlap with adult males than with adult females (Agostini and Visalberghi, 2005). Similarly, for white-faced capuchins (*Cebus capucinus*), Perry (2009) found that, among two potential methods for processing a particular fruit to extract embedded seeds, female offspring were significantly more likely than males to adopt the maternal technique, although the underlying mechanism for the difference remains a mystery.

A few primate species habitually use tools for extracting embedded or difficult-to-access food sources. Chimpanzees use a larger variety of tools than any other nonhuman animal, and social learning is presumed to be of primary import for the ontogeny of these skills (Whiten et al., 1999). Several studies have now focused on offspring development of tool-assisted foraging techniques among chimpanzees, including studies of nut cracking (for review see Biro et al., 2003), termite fishing (Lonsdorf, 2005), and ant dipping (Humle et al., 2009). Distinct sex differences have been found with regard to the development of termite fishing. Female infants are more attentive to their mothers' termite fishing behavior and subsequently show shorter acquisition times and greater proficiency than male offspring. Daughters are also more likely than sons to match their mothers' precise technique (Lonsdorf et al., 2012; Lonsdorf, 2005). These differences occur despite no observable differences in the way in which mothers behaved toward male or female offspring during the task (Lonsdorf, 2006) and parallel findings in human children that females perform better on fine motor tasks (Thomas and French, 1985; Pahlevanian and Ahmadizadeh, 2014) and those requiring attention and planning (Warrick and Naglieri, 1993). Samples remain too small to investigate sex differences in nut cracking development (Biro et al., 2003), but no such differences were found with regard to ontogeny of ant dipping (Humle et al., 2009). Ant dipping is arguably a riskier foraging strategy than termite fishing because nonexpert individuals have a high likelihood of being subjected to swarming ants that deliver painful bites. Thus, it is possible that the lack of sex difference found here is related to either the need for youngsters of both sexes to pay careful attention to avoid injury or a higher likelihood of male youngsters to engage in high-risk behaviors, or both.

SUMMARY AND FUTURE DIRECTIONS

Despite a relative lack of overt sex-biased treatment by others, many species of primates show sex differences in behavioral development that echo differences found in infant humans. These include differences in physical and social development, including grooming and playing, and differences in more complex behaviors such as object manipulation and extractive foraging. Taken as a whole, these consistent and accumulating reports of sex differences in primate behavioral development suggest that, although gender socialization in humans plays a role in magnifying the differences between young males and females, these behavioral sex differences are rooted in our biological and evolutionary heritage. However, the studies described here are arguably just the tip of the proverbial iceberg, and much work remains. First and foremost, we need to investigate sex differences in behavioral development in a much broader taxonomic range of species. The studies presented here are largely biased toward cercopithecines and apes that live in complex social groups. Much less work has been done for the lemurs and New World monkeys and in solitary or monogamous species. Such studies would allow a better understanding not only of the phylogenetic distribution of sex differences but also whether and how such differences are taxonomically constrained. Once differences are identified, we can begin to examine how they arise, which would ideally be carried out in naturalistic settings so that the behavioral influences of the mother and others could be integrated with noninvasive measures of physiological processes (e.g., hormones). For example, a recent study of wild chimpanzees has linked grooming between strongly bonded individuals to increases in oxytocin levels (Crockford et al., 2013). Given the role of oxytocin in parental care and social bonding, a better understanding of how oxytocin relates to maternal–infant interactions and may influence sex differences in development is a fruitful area for future research, especially if it takes place in a species-typical social environment. Similarly, major advancements have been made in our understanding of primate milk synthesis and its flexibility through captive studies. Hopefully, such work will spur advancement in noninvasive measures of nursing and weaning behavior (such as fecal stable isotope

analysis; Reitsema 2012) so that we may better understand the proximate influences on sex differences in foraging development. Another potential area of focus should be the cognitive underpinnings of sex-biased behavior, which remain largely unaddressed. For example, with regard to the studies of sex-biased maternal socialization of infants, do mothers have a cognitive awareness of species–typical sex roles, or are more simple physiological mechanisms at work? This is an area in which controlled cognition studies in a laboratory environment could inform findings from wild populations. In summary, it is an exciting era for the study of sex differences in both human and nonhuman primate behavior, and an integrative approach across disciplines, species, and study settings provides much promise for understanding the dynamic blend of influences on developing primates.

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CONFLICT OF INTEREST STATEMENT

The author has no conflicts of interest.

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