

Chapter 18

Identifying Proximate and Ultimate Causation in the Development of Primate Sex-Typed Social Behavior

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18.1 Introduction

Much like adult body size dimorphism (Leigh 1992; Leigh and Terranova 1998; O'Mara et al. 2012), the diversity of sex differences in social behavior that characterize adult primates must develop during the postnatal period because primate infants are only subtly sexually differentiated in behavior at birth (e.g., *Chlorocebus aethiops*, Lee 1984; *Papio anubis*, Bentley-Condit 2003; *Papio cynocephalus*, Nguyen et al. 2010, 2012). To the extent that adult sex-typed social behaviors are an important element of adult behavioral competence and to the extent that adult behavioral competence translates into reproductive success, the proximate mechanisms underlying the development of sex-typed social behaviors will be targets of selection. Understanding how those proximate mechanisms function to produce sex-typed adult social behaviors will clarify the adaptive nature of adult sex roles by yielding insight into the factors that influence and/or constrain their development (Beaupre et al. 1998; Duvall and Beaupre 1998).

We know from experimental research that social, ecological, and endocrinological experience (and their interactions) may all be important for the development of sex-typed social behavior, but we don't know which of those elements *actually* shapes sex-typed behavioral development in naturally occurring populations and in

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what ways. Compared to our understanding of primate development in captivity, little is known about the developmental processes that drive sex-typed behavioral development in the wild. This chapter explores the available evidence for social, physiological, and ecological drivers of the development of sex-typed social behavior in wild-living primates and highlights areas in need of increased research, emphasizing the strengths of the comparative method in maximizing the incisiveness of individual studies. Throughout, an infant is defined as an unweaned individual; a juvenile is a prepubescent, weaned individual; an adolescent is a peripubescent or postpubescent individual who has not achieved full adult size or first reproduction; and an adult is a sexually mature individual (Altmann and Pereira 1985). The term subadult refers collectively to infants, juveniles, and adolescents.

18.2 Adult Sex Differences in Wild Primates

Numerous and varied sex differences have been documented in wild adult primates in social behavior, resource use, and endocrine profiles. Socially, adults of some species exhibit sex differences in aggressive behavior (*Cercopithecus mitis*, Cords et al. 2010), dominance, overt sociability (*Alouatta palliata*, Clarke 1990; *Brachyteles arachnoides*, Strier 2002; *C. mitis stuhlmanni*, Cords et al. 2010), social network diversity (*A. palliata*; Clarke 1990), and three-dimensional spacing (*Cebus olivaceus*, Robinson 1981; *C. mitis stuhlmanni*, Ekernas and Cords 2007). Ecologically, adults exhibit sex differences in reliance on certain shared food sources (*Cebus capucinus*, Rose 1994; *Cebus nigrinus*, Agostini and Visalberghi 2005; *Cercocebus atys*, McGraw et al. 2010; *C. aethiops*, Harrison 1983; *C. aethiops* and *Erythrocebus patas*, Nakagawa 2000; *Lemur catta*, O'Mara 2012; *Macaca fascicularis*, van Noordwijk et al. 1993), daily and/or annual time budgeting of foraging (*C. aethiops*, Baldellou and Adan 1997; Harrison 1983; Nakagawa 2000), three-dimensional spacing specifically during foraging, (*C. nigrinus*, Agostini and Visalberghi 2005; *C. olivaceus*, Robinson 1981; *L. catta*, O'Mara 2012), reliance on particular types of foraging behaviors (*C. capucinus*, O'Malley and Fedigan 2005; *Cebus libidinosus*, de A. Moura and Lee 2010; *L. catta*, O'Mara 2012; *Pan troglodytes*, McGrew 1979), and foraging efficiency (*P. troglodytes*; Boesch and Boesch 1981). Hormonally, adults are characterized by sexually differentiated patterns of circulating androgens and estrogens (*C. aethiops*, Whitten and Turner 2009; *Pan paniscus*, Dittami et al. 2008).

Sexually differentiated resource use and endocrine profiles both will influence social behavior. While sex-differential dietary activities may not represent sex-typed social behavior per se, some elements of sexually differentiated ecology (such as sex-segregated spacing during foraging) may induce or constrain the nature of sexually differentiated social behavior. Circulating testosterone has been linked to aggressive behavior involved in male mate guarding and territorial defense in some (*L. catta*, Gould and Ziegler 2007; *P. troglodytes*, Muller and Wrangham 2004) but not all primate species (*Eulemur fulvus rufus*, Ostner et al. 2008). In females of

some species, circulating levels of testosterone are correlated with individual rates of aggressive behavior and dominance rank (*P. anubis* × *hamadryas*; Beehner et al. 2005). And adult female circulating levels of estradiol and progesterone are reliably associated with behavioral estrus and gestational state (*E. fulvus rufus*, Ostner and Heistermann 2003; *P. cynocephalus*, Beehner et al. 2006; Stavisky et al. 1995; *Propithecus verreauxi*, Brockman and Whitten 1996).

By adolescence, some behavioral sex differences are most likely motivated and maintained by the activational effects of gonadal hormones (reviewed in Wallen 2005) and, in sexually dimorphic species, by sexually differentiated energetic costs (*C. capucinus*, Rose 1994), predation risk (*C. capucinus*, Rose 1994), substrate use (*C. capucinus*, Rose 1994; *C. nigritus*, Agostini and Visalberghi 2005), and food resource accessibility (*C. capucinus*; O'Malley and Fedigan 2005; Rose 1994) that result from sex differences in body size. Preadolescent behavioral sex differences, though, are not likely explained either by the activational actions of pubertal hormones or by sexually dimorphic nutritional demands resulting from body size dimorphism. Available data suggests that gonadal hormones are not in production until puberty (reviewed in Wallen 2005), and substantial sex differences in body size do not emerge until the beginning of the pubertal growth spurt (*P. cynocephalus*, Altmann and Alberts 1987; *Papio ursinus*, Johnson 2003; *P. troglodytes*, Pusey 1990). A number of sex differences in primate juvenile social behavior and feeding ecology do emerge prior to sex differences in body size and hormonal maturation, implicating proximate drivers other than body size dimorphism and gonadal hormone surges in the development of those behaviors.

Due to the interactions of social behavior, ecology, and individual endocrinology, any consideration of sex-typed social development must also consider sex-typed ecological and hormonal development. Fortunately, this endeavor is synergistic, as the mechanisms underlying development in other domains may also apply directly to social development. For example, infant primates must eventually acquire adult diets at some point in their behavioral development (Lonsdorf 2012; Mackinnon 2012), and the mechanisms by which they do so may lend clues as to how the development of social behavior is accomplished.

18.3 Evidence for Proximate Causes of Sex-Typed Development from Captivity

Studies of captive primates demonstrate that sexually differentiated behavioral trajectories emerge from and are maintained by complex, interactive systems of extrinsic and intrinsic proximate factors. Research in this area has mainly targeted the outcomes of manipulating specific elements of social and hormonal experience and has clinched the importance of each in shaping primate developmental trajectories (e.g., Bentley-Condit 2003; Brown and Dixson 1999; Capitano 1984; Chamove et al. 1967; Champoux et al. 1989; Deputte and Goy 1991; Eisler et al. 1993; Goldfoot 1977; Goy and Phoenix 1971; Harlow 1962; Herman et al. 2003;

Mondragón-Ceballos et al. 2010; Pasterski et al. 2005; Pomerantz et al. 1986; Thornton et al. 2009; Tomaszycycki et al. 2001; Wallen and Hassett 2009).

In addition to demonstrating the importance of the rearing environment in shaping developmental outcomes in general (*Macaca mulatta*, Capitanio 1984; Champoux et al. 1991; Harlow 1965; Maestripieri 2005; Mason 1978; McCormack et al. 2006; *Macaca radiata*, Andrews and Rosenblum 1991; Rosenblum and Paully 1984; *P. troglodytes*, Bard and Gardner 1996), captive work has shown that socially complex and/or less stressful environments result in more competent sexual behavior (*M. mulatta*, Capitanio 1984; Champoux et al. 1991; Goldfoot 1977; Goy and Wallen 1979; Mason 1978; Wallen 1996; Wallen et al. 1977, 1981) and more sex-typical play (*M. mulatta*; Wallen 1996, 2005). Some of these early environmental perturbations have been outside the range of variation that primates in wild-living populations are likely to experience (Schino et al. 2001). But even variation in social experience during captive rearing that mirrors variation expected or observed in the wild has short-term effects on important developmental behaviors related to environmental exploration (*M. mulatta*; Sackett 1972) and maintenance of mother–infant contact (*M. mulatta*; Suomi 1987), as well as long-term effects on fitness-related behaviors such as infant care (*M. mulatta*; Maestripieri 2005) and social dominance (*M. radiata*; Andrews and Rosenblum 1991). In sum, the early social environment plays an important role in structuring individuals' behavioral repertoires, and these effects can be lifelong (*P. troglodytes*; Bard and Gardner 1996; Meredith and Fritz 2005).

Endocrinological experience is a key driver of sex differentiation in social behavior through its organizational and activational effects (Becker 2009; Phoenix et al. 1959; Schulz et al. 2009). In primates, prenatal and neonatal androgenic hormones influence the development of sex-typed play behavior and sexual behavior in both males and females (Smith et al. 2012, *M. mulatta*; Thornton and Goy 1986; Wallen 1996, 2001; Wallen et al. 1991). Pubertal and postpubertal androgens and estrogens activate and shape the expression of sex-typed aggression, sexual behavior, and infant interest (*Callithrix jacchus*, Dixson 1993; *L. catta*, Cavigelli and Pereira 2000; *P. troglodytes*, Anestis 2006; *M. mulatta*, Dixson and Nevison 1997; Maestripieri and Zehr 1998; Wallen 2001).

Social and hormonal factors also interact to shape sex-typed behavioral outcomes (reviewed in Wallen 2005). Even behaviors that are largely organized and activated by hormones depend on the social environment to facilitate their expression by providing appropriate behavioral experience. For example, appropriate sex-typed mating behavior does not develop in physiologically normal individuals unless they are reared in a social environment that is appropriate for expressing and shaping it. Rhesus macaques (*M. mulatta*) gonadectomized at birth will develop sex-typed mounting behavior if raised in a social environment, whereas intact rhesus monkeys raised without access to peers will not (Goy and Wallen 1979; Harlow 1965; Wallen 1996, 2005; Wallen et al. 1981).

Although it is well established that social and physiological experience and their interactions shape the development of later sex-typed social behavior, it is still uncertain which particular elements of early social experience underlie the

development of specific adult sex-typed behaviors in natural developmental conditions. Additionally, it is unknown how the ecological developmental domain influences the social and hormonal, and vice versa.

18.4 Importance of Research on Proximate Causation on Wild-Living Primates

The captive experimental approach to disentangling primate developmental complexity has made great strides in elucidating the primate developmental system, but comparative study of development in wild populations has a substantial and largely untapped potential to yield insight into the processes that drive sex-typed development. The study of wild populations examines behavioral sex differentiation under conditions of species and sex-typical ecology and can consider its importance directly (Altmann and Alberts 1987). This advantage cannot be overstated—captive research has confirmed that ecological stress can affect the social milieu in ways that affect infants' attachment to their mothers (*M. radiata*; Andrews and Rosenblum 1991) and, later, their stress hormone profiles (*M. radiata*; Rosenblum et al. 1994), social competence, and dominance (*M. radiata*; Andrews and Rosenblum 1994). Intraspecific comparisons of males and females from natural populations produce results that are relevant to understanding developmental processes as they play out in complex socioecological environments that, hopefully, resemble the environments of selection that produced and/or maintain those developmental processes. Interspecific comparisons of male and female development in the wild and intraspecific comparisons of male and female development across captive and wild settings can leverage the knowledge gained by individual studies in the wild to further elucidate general patterns of proximate causation in primate sex-typed development. Additionally, interspecific comparative approaches are uniquely suited to revealing the evolutionary history of primate sex-typed behavioral development (Nunn 2011) and, therefore, to producing data relevant to evaluating hypotheses about the adaptive nature of particular processes and outcomes of sexual differentiation.

18.4.1 Social Behavior

Only a few infant sex differences in social behavior have been reported, despite having been at least a partial focus of a number of studies in the wild (Barthold et al. 2009; Cords et al. 2010; Förster and Cords 2002; Gould 1990; Meredith 2012; Nash 1978; O'Mara 2012). Both blue monkey (*C. mitis stuhlmanni*) and olive baboon (*P. anubis*) male infants play longer and rougher than their female peers (Förster and Cords 2005; Owens 1975). Female vervet monkey (*C. aethiops*) infants tend to

exhibit more independence from their mothers at earlier ages (Lee 1984). Female mantled howling monkey (*A. palliata*) infants react more positively to social interactions initiated by non-maternal group members than male infants do (Clarke 1990). And newborn male yellow baboon (*P. cynocephalus*) infants initiate more changes in contact with their mothers than female infants (Nguyen et al. 2012). However, sex differences have not been found in the social behavior of infant red-fronted brown lemurs (*E. fulvus rufus*; Barthold et al. 2009), ring-tailed lemurs (*L. catta*; Gould 1990; Meredith 2012), or young blue monkey infants under the age of 6 months (Förster and Cords 2005).

Like the pattern of sex differences in social behavior exhibited by infants, sex-differential treatment of infants by others is also subtle in wild populations. Among common marmosets (*C. jacchus*), female twin pairs are carried more by fathers than male or mixed-sex twin pairs (Yamamoto et al. 2008). Mantled howling monkey infant females are engaged in social interactions with more group members than are male infants (Clarke 1990). High-ranking vervet monkey mothers tend to reject their infant daughters more often than their infant sons (Lee 1984). And in yellow baboons, mothers with more experience seem to promote their sons' independence more strongly than their daughters' via reduced infant carrying (Samuels and Altmann 1992), and infant sons are buffered from the effects of maternal rank on suckling time that female infants experience (Nguyen et al. 2012).

Mothers (and sometimes fathers) may tailor the amount and nature of their investment to foster the sexually differentiated social and somatic developmental trajectories that will increase the likelihood of their offsprings' eventual reproductive success. Decreased rates of infant carrying and more changes in infant contact are thought to promote infant independence (Schino et al. 2001), which may in turn promote the earlier acquisition of social and ecological competence. This is an important potential impact—at least in female yellow baboons, foraging efficacy as a yearling (with respect to protein and energy intake) has been shown to reliably predict the probability of surviving to adulthood, fertility, and reproductive lifespan (Altmann 1991). The apparent maternal bias toward encouraging the independence of sons more than daughters in this species and the apparent maintenance of suckling rates for sons (despite mechanisms that reduce them in daughters when mothers are high ranking) could reflect the much greater potential impact that increased caloric intake has on subadult male growth rates and maturational schedules as compared to those of subadult females (Altmann and Alberts 2005). Alternatively, some of these sex-differential interactions could be initiated by the infants themselves—for example, other group members may find female howling monkey infants more attractive because they react more positively to social interactions initiated by others than do male infants (Clarke 1990).

In contrast to the early infant period, sex differences in social behavior during juvenility are fairly common and robust in the wild. Juvenile females show more interest in infants than their male peers in many species (*A. palliata*, Clarke et al. 1998; *Alouatta seniculus*, Crockett and Pope 2002; *C. mitis stuhlmanni*, Cords et al. 2010; Förster and Cords 2005; *L. catta*, Meredith 2012; *P. ursinus*, Cheney 1978). As with infants, when sex differences in play are found, males play more frequently and

more intensely than females (*C. mitis stuhlmanni*, Förster and Cords 2005; *P. anubis*, Nash 1978; Owens 1975). Juveniles of many species preferentially associate and interact with same-sex partners (*A. seniculus*, Crockett and Pope 2002; *Ateles geoffroyi*, Milton 2002; *L. catta*, Meredith 2012; *M. fascicularis*, Van Noordwijk et al. 1993; *P. cynocephalus*, Pereira 1988; *P. ursinus*, Cheney 1978), although the intensity of those social associations varies by species and the pattern is not ubiquitous. Muriqui (*B. arachnoides*) juveniles associate preferentially with opposite-sex individuals up until older juvenile males shift their association preferences toward adult males (Strier 2002), and blue monkey (*C. mitis stuhlmanni*) and Hanuman langur (*Semnopithecus entellus*) juveniles of both sexes prefer female grooming partners over males (Cords 2000; Nikolei and Borries 1997). Several species also exhibit sex differences in the diversity of their social partners that are adultlike in nature. For example, juvenile female blue monkeys and Hanuman langurs are more sociable than their male counterparts in a number of measures of sociality (Cords et al. 2010; Ekernas and Cords 2007; Nikolei and Borries 1997). Similarly, male juvenile chimpanzees (*P. troglodytes*) direct their grooming attention toward all age–sex classes, while juvenile females restrict their grooming attention to their mothers and siblings (Pusey 1983). In some species, though, juvenile sex differences remain subtle, as in mantled howling monkeys, which exhibit no detectable sex differences in social time budgets or proximity to other age/sex classes except that juvenile males spend more time in proximity to adult males than juvenile females do (Clarke et al. 2007).

Subadults (who have the most to gain from their successful development) are expected to be active participants in shaping their own developmental trajectories, and their choices of social partners are expected to maximize current and/or future benefit (Cords et al. 2010; Pereira 1988). For male yellow baboons, coalitionary support from other males is important for the acquisition and maintenance of male dominance and/or access to females (van Schaik et al. 2004), which is, in turn, closely tied to male reproductive success (Schülke et al. 2010). As might be expected, juvenile male yellow baboons put more effort into maintaining proximity to adult males than do juvenile females. For females, which are philopatric, resident females will be lifelong social partners, while males will come and go. Accordingly, juvenile females put more effort into maintaining proximity to unrelated adult females than do juvenile males. Among unrelated adult females, juvenile females prefer lactating females as social partners. Lactating individuals provide the possibility of interacting with their infants. Infants are attractive to females of most species probably because female primates have long been under selection to respond to infants because doing so makes them better mothers (Silk 1999). Additionally, for females, relationships with higher-ranking females are likely to be of more current and future benefit than relationships with lower-ranking ones; as expected, among unrelated females, juvenile females prefer adult females from high-ranking matrilineal lines as social partners. Males, though, rise above all females in dominance rank when they surpass females in physical size (Pereira 1995), so the rank of their female social partners is likely to be much less important than the reproductive status of those partners; juvenile males thus prefer cycling females and are indifferent to female rank.

Regardless of the motivation underlying juvenile sex differentiation in social space, when it occurs, it will almost certainly drive sex differentiation in other social behaviors. Preferential social association with same-sex behavioral role models will facilitate social learning of other sex-typed behaviors through mechanisms such as imitation or goal emulation (Hoppitt and Laland 2008; Lonsdorf 2005) and may also constrain the expression of particular behaviors in sex-typed ways.

18.4.2 Foraging Behavior and Diet

Studies focusing on the development of sex-typed foraging behavior in the wild are few, but they illustrate that some sex-typed foraging behaviors probably depend on social learning for their development, while others rely on some other proximate cause. Juvenile wedge-capped capuchins (*C. olivaceus*) (Robinson 1981) and long-tailed macaques (*M. fascicularis*) (Van Noordwijk et al. 1993) exhibit some elements of adult, sex-typed foraging behaviors, and they also associate preferentially with same-sex individuals. While particular types of social learning in these species have yet to be identified, social learning of any type (Lonsdorf 2005, 2012) would be facilitated by sex-segregated spacing during foraging. A number of sex differences in the foraging behavior of juvenile male tufted capuchins (*Cebus apella*) are correlated with social measures in ways that are consistent with their acquisition via social learning (Agostini and Visalberghi 2005). Juvenile males preferentially associate with and direct their attention toward the feeding of same-sex adults, and the amount of time juvenile males spend in association with adult males is positively correlated with their targeting of animal prey. The authors suggest that especially complex sex-typed foraging behaviors, such as the extractive foraging habits characteristic of male capuchins, may require some type of social learning and that the acquisition of complex sex-typed foraging behaviors may be facilitated by preferential association with and attention to same-sex adults. In the same vein, Lonsdorf (2012) demonstrated that juvenile female chimpanzees spend more time than males watching their mothers termite fish (Lonsdorf 2004) and ultimately imitate their mothers' termite fishing techniques, while juvenile males do not and ultimately become less proficient termite fishers than females (Lonsdorf 2005).

While some primate sex-typed foraging behaviors depend on social input for their development, not all do. The amount of time juvenile tufted capuchin males spend in association with adult males is not correlated with male-typical foraging characteristics other than their targeting of animal prey, such as microhabitat foraging preference. And juvenile females neither preferentially associate with nor direct attention toward the feeding of same-sex adults (Agostini and Visalberghi 2005). Agostini and Visalberghi (2005) suggest that simple foraging behaviors arise independently and do not rely on any kind of social learning for their development. As with sex-typed social behavior, Milton (2002) reports that black-handed spider monkeys (*A. geoffroyi*) who survived initial release onto Barro Colorado Island as

subadults went on to develop species-typical diets without adult role models. And in some species, such as vervet monkeys, the sex differences in adult diet and foraging schedules are not found in juveniles at all (Harrison 1983), suggesting that they are related to the constraints of adult activities, nutritional requirements, or social relationships and do not rely on learning for their development.

As this field of study progresses, intraspecific observational comparisons will continue to reveal the specific processes that canalize particular types of foraging behavior, generating clues about how sex differences in other domains might be motivated. Where different elements of foraging behavior are driven by different developmental mechanisms, they may have evolved in response to distinct selection pressures and are likely to have had different evolutionary histories. Data from wild primate populations are best suited to further elucidating these issues.

18.4.3 *Hormones*

Data on hormonal development in wild primates are still rare but are increasingly becoming a focus of investigation (Beehner et al. 2009; Gesquiere et al. 2005; Seraphin et al. 2008; Whitten and Turner 2009). In yellow baboons, late gestational maternal fecal estrogen and testosterone concentrations are significantly higher when carrying male fetuses than female fetuses (Altmann et al. 2004). Neonatal males and females are characterized by high and rapidly declining levels of fecal testosterone and estrogen, respectively, which remain low through juvenility and increase again during the months just before testicular enlargement and menarche (Gesquiere et al. 2005). As expected based on captive research on endocrinological development, testosterone levels increase as individuals approach sexual maturity in male chimpanzees (Seraphin et al. 2008), vervet monkeys (Whitten and Turner 2009), yellow baboons, chacma baboons (*P. ursinus*), and geladas (*Theropithecus gelada*) (Beehner et al. 2009).

Despite the relative rarity of information on hormonal development in wild primates, some studies have been able to draw inferences about social factors that may shape sexually differentiated hormonal development. Maternal dominance rank during pregnancy and shortly after birth may influence the development of offspring endocrine profiles in yellow baboons. Maternal rank at the time of a male's conception accounted for 42% of variance in adolescent male fecal glucocorticoid concentrations in the 20 months prior to their natal dispersal, when sons of high-ranking mothers had lower fecal glucocorticoid levels than sons of low-ranking mothers (Onyango et al. 2008). Onyango et al. (2008) suggest that this could be selectively important because chronically elevated levels of glucocorticoids are associated with stress-related disease pathology. However, maternal rank at conception was not associated with sons' fecal glucocorticoid concentrations during other times in the subadult period (Gesquiere et al. 2005). Perhaps maternal effects on sons' stress physiologies are only detectable during the developmental stage when sons are

gearing up for natal dispersal—which will likely be their most costly life history event (Alberts and Altmann 1995)—and, over the subadult period in general, underlying maternal effects on sons' stress physiology are attenuated by other factors.

If, among other social factors, mother–infant interactions are somehow involved in shaping the development of offspring endocrine profiles, maternal physiology may be involved in modulating those mother–infant interactions. Late gestational fecal glucocorticoids in yellow baboons are positively correlated with maternal responsiveness to infants (Nguyen et al. 2008), and prenatal fecal estrogen concentrations and maternal rank are negatively correlated with suckling time in infant daughters (Nguyen et al. 2010, 2012), suggesting that hormonal modulation of some characteristics of the mother–infant relationship does occur. Late gestational fecal estrogen and testosterone concentrations in multiparous females are significantly higher when the fetus is male versus when the fetus is female (Altmann et al. 2004), suggesting that fetal sex may shape maternal hormone profiles in different ways, which may in turn influence maternal behavior toward infants in ways that vary according to infant sex. In other words, sexually differentiated mother–infant interactions begin before birth and may be initiated by the fetus (Nguyen et al. 2010). In contrast to the patterns seen with daughters, suckling time for sons is not influenced by prenatal estrogen concentrations (Nguyen et al. 2010, 2012), indicating that the relationships among fetal sex, maternal gestational physiology, and maternal–infant interaction are not straightforward, much like the hormonal influences on the development of sexual behavior that have been studied in captivity.

18.4.4 Systematic Integration Is Needed

Intraspecific comparative work has documented in wild primate populations all of the factors we expect to shape sex-typed development—sex-typed treatment of subadults by others, sex-typed three-dimensional spacing during feeding and otherwise, sexually differentiated subadult diets, and sexually differentiated prenatal, neonatal, and pubertal hormone profiles. Due to the sample size constraints inherent in studies of subadults, large-scale, holistic attempts to pin down how these myriad factors actually function to shape the development of adult sex-typed behaviors within species are still largely absent. There is limited, but clear, evidence that the development of some sex-typed foraging behaviors depends on social modeling of adults by juveniles. Research on sexually differentiated development in yellow baboons at Amboseli has made impressive strides toward illuminating the workings of the complex and interactive system of social, ecological, and endocrinological factors that together underpin life histories and social development (at least in this species). Work from this site clearly illustrates the promise of naturalistic observational research that seeks to understand linkages between maternal physiology, offspring physiology, ecology, and behavior in naturally living primates.

The most thorough studies of sexually differentiated development beg a number of interesting questions about causation of the developmental patterns they document.

Some aspect of maternal rank ultimately shapes at least some aspects of offspring endocrine response in baboons, but are sons of high-ranking mothers less stressed because they enjoyed more social support or more access to resources? Or did sons simply inherit their reactivity to major stressors from their mothers? Or did mothers' stress levels during gestation shape their sons' eventual stress reactivity profiles, as occurs in snowshoe hares conceived in high- and low-predation environments (Sheriff et al. 2010)? Naturally occurring variation in the prenatal hormone environment may influence postnatal mother–infant interactions (Nguyen et al. 2010), but is variation in suckling time controlled by infants or mothers or both? Do juvenile female blue monkeys groom more partners (Cords et al. 2010) because they are more often in proximity to more individuals, or are they more often found in proximity to others because they are actively seeking out more grooming partners? And, do these patterns actually depend on social input to shape their development, or are they somehow “preprogrammed” to arise, *de novo*, as suites of correlated sex-typed behaviors in every generation? Milton (2002) reports that black-handed spider monkeys who survived initial release onto Barro Colorado Island as subadults went on to develop species-typical sex-typed behavior and association patterns in the absence of adult role models, suggesting that adult sex-typed social behavior does not rely on behavioral models or social interactions with adults for its development in this species. Fortunately, these studies are ongoing and are constantly making gains in their abilities to infer causation.

A few areas of research still await attention in the wild. The effects of neonatal and early postnatal hormones on later behavior have not yet been investigated. This is probably due to the challenges of collecting biological samples from infants, but gains in this area should help clarify the relationships among maternal and offspring physiology and behavior. Additionally, the effects of ecological variation on hormonal development have not yet been addressed. In general, hormonal development in the wild seems to correspond well with patterns seen in captive primates (*M. mulatta*, Brown and Dixson 1999; *P. cynocephalus*, Castracane et al. 1986; Muehlenbein et al. 2001; *Saguinus oedipus oedipus*, Ginther et al. 2002), but there are still important reasons why these data are needed from wild populations. In many species, adult steroid hormone concentrations of both sexes vary according to ecological and/or social conditions (*E. fulvus rufus*, Ostner et al. 2002, 2008; *L. catta*, Gould and Ziegler 2007; *P. anubis*, Sapolsky 1985, 1986, 1991; *P. anubis* × *hamadryas*, Beehner et al. 2005; *P. cynocephalus*, Gesquiere et al. 2005, 2008, 2010, 2011; *P. verreauxi*, Brockman et al. 2009; *Saguinus mystax*, Huck et al. 2005), and there is substantial and selectively important intra- and interpopulation endocrine variation (*C. aethiops*, Whitten and Turner 2009; *L. catta*, Gould and Ziegler 2007; *P. cynocephalus*, Altmann et al. 2004). It stands to reason that infant and juvenile hormone profiles are also subject to such influences. If so, appropriate interpretation of subadult hormonal development and its behavioral effects requires knowledge of adult and subadult endocrinological variation in the study population.

Although sex differences in infant behavior and treatment by others have rarely been found in wild populations and are not marked when present, their potential

impact on the developmental trajectories of infants should not be underestimated, and they merit continued attention. In captivity, even subtle differences in the social milieu can impact infant development in selectively important ways (*M. radiata*, Andrews and Rosenblum 1994), such that eventual adult behavioral sex differentiation may be rooted in these types of very early sex differences in interactions with mother and others (Nguyen et al. 2012). If subtle differences in social interactions at early ages are important in shaping the development of later sex-typed behavior, early infancy deserves continued research attention even in taxa for which no sex differences have been found (*E. fulvus rufus*, Barthold et al. 2009; *L. catta*, Gould 1990; Meredith 2012). As infant samples are often characterized by small sizes and high dropout due to infant mortality (e.g., Meredith 2012), single studies often lack the statistical power to detect the small effect sizes expected in infants.

18.5 Interspecific Comparison in the Wild

Interspecific developmental comparisons—either in closely related species with divergent adult sex-typed behavior or in distantly related species with striking social similarities—can strengthen the inferential power of single-species investigations. Pereira's (1995) comparison of the development of sex-typed dominance patterns in yellow baboons and ring-tailed lemurs exemplifies this type of analysis. Although it was not limited to wild populations, his detailed comparison of ring-tailed lemur dominance acquisition to that in cercopithecine monkeys raises the question of why ring-tailed lemurs do not intervene in agonistic interventions on behalf of their matrilineal relatives as cercopithecine monkeys reliably do. There is no obvious reason why ring-tailed lemurs would not benefit from “top-down” agonistic intervention” (Pereira 1995); yet, the lack of matrilineal agonistic intervention in lemurs does not seem enigmatic until lemur behavior is compared to the cercopithecine species with which it shares so many other features of social organization and behavior (multi-male, multi-female social structure, promiscuous mating, stable dominance relationships, and matrilocality) (Pereira 1993).

Examining the intraspecific comparative studies in social and foraging behavior outlined above with an eye toward interspecific comparison lends support to some of the conclusions already drawn from intraspecific comparisons. Sex-segregated social association among juvenile primates is a fairly robust interspecific pattern among wild primates. The acquisition of sex-typed behaviors may be facilitated by sex-differential spatial patterning of juveniles (Agostini and Visalberghi 2005; Pereira 1988), which seems to bear similarities to adult spatial patterning in many species. In cases where juveniles choose sex-typed social association patterns, whether sex-typed social behaviors are acquired by social learning or not can be determined by detailed studies such as those by Lonsdorf (2005) and Agostini and Visalberghi (2005).

The interspecific variation in the developmental schedules of sexually differentiated foraging behavior—for example, that it develops before puberty in tufted capuchins (Agostini and Visalberghi 2005) but not in vervets (Harrison 1983)—supports the

conclusion that not all foraging behaviors are canalized by the same proximate mechanisms and that the same foraging behaviors may not be canalized by the same mechanisms in all primate species. The similarities in the types of foraging behaviors that seem to rely on imitation or emulation for their development in both chimpanzees and tufted capuchins—complex, extractive foraging behaviors—support Agostini and Visalberghi's (2005) position that simple foraging behaviors are learned independently and that only complex foraging skills require social input for their acquisition.

There are few datasets yet available to make incisive interspecific comparisons of sex-differential social behavior in the wild. Given the relative completeness of the baboon work already, species that would make good comparative taxa for baboons are efficient research targets. For example, ring-tailed lemurs are a useful comparator for investigating the importance of social and hormonal mechanisms of behavioral development given their important similarities to (enumerated above) and differences from (body size monomorphism, female dominance, and phylogenetic distance) baboons. Furthermore, the Lemur Biology Project at Beza Mahafaly Special Reserve and its associates have been amassing a large dataset on ring-tailed lemur ecology (O'Mara 2012; Sauther et al. 1999), health (Sauther et al. 2002), life history (Gould et al. 2003), social behavior (Gould 1997), and endocrinology (Gould and Ziegler 2007; O'Mara 2008), which is well suited to comprehensive comparisons with the baboon work. An impressive collection of data on the social development of blue monkeys, which have more relaxed dominance hierarchies than baboons (Cords 2000; Cords et al. 2010; Ekernas and Cords 2007; Förster and Cords 2002, 2005), is also promising. Once a sufficient number of taxa are well represented in the literature, interspecific comparative analyses can reveal important correlations among aspects of sex-typed development, phylogeny, and ecology, as well as explicitly test evolutionary hypotheses about primate sex-typed development.

With regard to better understanding the learning mechanisms underlying the acquisition of sex-differential foraging behavior, more focused studies in the vein of Lonsdorf (2005) and Agostini and Visalberghi (2005) should be pursued in both chimpanzees and capuchins, at minimum, which have been shown to possess sex differences in their reliance on complex foraging behaviors. This area of research has promise for understanding the development of sexually differentiated behavior in general because mechanisms for the acquisition of complex foraging behavior may also apply to the acquisition of behavior in the social domain.

18.6 Intraspecific Comparisons Between Wild and Captive Settings

In cases where results from captivity do not accurately characterize wild populations, those differences themselves are another useful comparative dataset that can help to tease apart the proximate drivers of particular elements of behavioral development. For example, scent-marking is a sexually differentiated behavior in adult ring-tailed lemurs. Both sexes scent-mark substrates with secretions from their anogenital glands (Scordato and Drea 2007). But only males typically have

keratinous antebrachial spurs and brachial and antebrachial scent glands (Sauther and Cuozzo 2008), which they use to gouge and deposit brachial and antebrachial secretions onto small tree trunks and branches (Jolly 1966; Scordato and Drea 2007). The developmental timing of these behaviors has been documented in captivity by Palagi et al. (2002) and Pereira (1995, 2002) and in the wild by Meredith (2012) and O'Mara (unpublished data). As in other species (colobines and macaques, Borries et al. 2011; *P. cynocephalus*, Altmann and Alberts 1987; Altmann and Altmann 1981), growth and sexual maturation in ring-tailed lemurs are greatly accelerated in captivity compared to the wild. At the Duke Lemur Center, ring-tailed lemurs are sexually mature by around 18 months of age, and it is common for females to have their first offspring at the age of two (Pereira 1995). At Beza Mahafaly Special Reserve, Madagascar, sexual maturation appears to occur around 26–28 months of age (as assessed by behavioral markers in both sexes and the onset of testicular enlargement in males; Meredith, unpublished data; O'Mara, unpublished data; Pereira 1995), and females have their first offspring at the age of three, at the earliest (Gould et al. 2003).

The developmental trajectories of scent-marking behaviors in captive and wild ring-tailed lemurs are quite different (Fig. 18.1). In wild infants, there is first a period between 3.5 and 6 months of age in which male infants tail play, wrist mark (Gould 1990; Meredith 2012), and even brachial mark at low frequencies (Meredith 2012). Then, all three behaviors disappear from the behavioral repertoire and do not appear again until the age of 13 months, at which point they persist (Meredith 2012). In captive infants, the timing of wrist and brachial marking has not been reported. Tail play appears at 6 months of age and is observed every month thereafter (Palagi et al. 2002). Wrist marking and brachial marking appear at 13 months and continue thereafter (Palagi et al. 2002), coincident with the reappearance of those behaviors in the wild. Anogenital marking appears in both sexes at 16 months in captivity, coincident with sexual maturation (Palagi et al. 2002; Pereira 2002), but not in the wild until 26–28 months (Meredith 2012; O'Mara, unpublished data; Pereira 1995).

If the development of all scent-marking behaviors were driven by the same proximate factor, then they should all vary in the same way between the captive and wild settings—they should either all be accelerated or all be delayed. The observed pattern of variation suggests a more complex story. The fact that the timing of juvenile wrist and brachial marking is invariant across settings, despite drastically different ecological constraints and maturational schedules, suggests that they are not shaped by postnatal environmental cues. Perhaps instead, the juvenile onset of antebrachial and brachial marking is determined by individual prenatal and neonatal hormone physiology, as seems to be the case with the development of male-typical urinary behavior in domestic dogs (Ranson and Beach 1985). In contrast, the fact that the timing of the appearance of anogenital marking, which is coincident with gonadal maturation in captivity, is substantially delayed in the wild suggests that anogenital marking is directly caused by sexual maturation, as has been previously suggested (Pereira 1995, 2002). The early appearance and subsequent disappearance of the

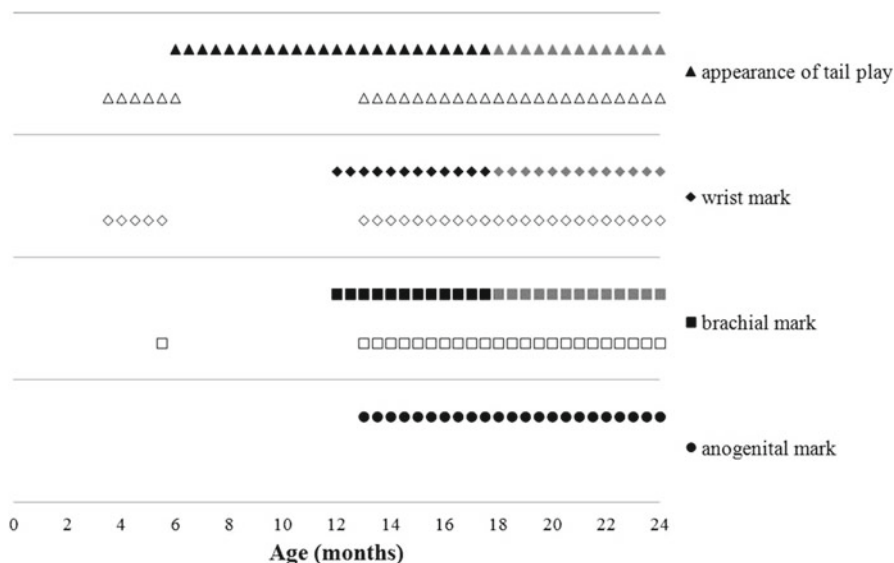


Fig. 18.1 Developmental timing of scent-marking behaviors in captivity (*solid symbols*) and in the wild (*open symbols*). Tail play, wrist mark, and brachial mark data are from Palagi et al. (2002), which observed individuals only through the age of 18 months. As these behaviors are unlikely to have ceased between the ages of 18 and 24 months in captivity, they are presented here in *gray*

suite of brachial and antebrachial marking and tail play in the wild is enigmatic. Perhaps the appearance of these behaviors in infants is socially mediated; if so, it should be correlated with increased rates of marking by adult males or with proximity of infant males to adult males. The initial disappearance of tail play occurs just after the transition from infancy to juvenility (Sauther et al. 1999). Perhaps the disappearance of tail play from the behavioral repertoire of infants is due to a decrease in all types of play due to ecological stress due to the seasonal decline in food availability during this time of the year (Sauther et al. 1999); if so, it should be correlated with increased levels of glucocorticoids in males of that age, decreased rates of play behavior, and/or actual changes in food availability. These hypotheses require additional data for testing and are variably appropriate for further testing in experimental and naturalistic settings, but one thing is clear—the development of anogenital marking is yoked to the pace of somatic growth, while the development of the other elements of scent-marking behavior is not.

The behavioral and well-known somatic developmental variation between wild and captive settings helps to tease apart, exclude, and generate reasonable testable hypotheses about the proximate factors that underlie the development of particular elements of scent-marking behavior in a way that an exclusive focus on either one or the other would not. Future research can easily incorporate more of this approach, which would extend the inferential reach of observational studies in the wild.

18.7 Conclusion

Sex-typed social and ecological behavior is not acquired as a single behavioral suite; instead, individual sex-typed behaviors depend on different causal factors for their development, suggesting that they may have resulted from different selective pressures. Studies of wild primates have identified several key causal relationships: social and ecological factors that shape individual hormonal profiles; social factors that drive ecological sex differentiation; and social, ecological, and hormonal factors that may drive sexual differentiation in social behavior. These studies also reveal that the relationships among social, ecological, and hormonal developmental factors vary across primate species. This complexity presents substantial challenges to research, but confirms the importance of studying these phenomena in natural populations, because substantial alteration of any system component will affect the relationships among all others in unknown ways, and no other method can definitively capture developmental processes as they occur in complex, evolutionarily relevant socioecological environments.

There are still large and important gaps in the dataset on wild primate development that need to be filled before we are positioned to understand the proximate and ultimate causes of primate sex-typed development from a holistic standpoint. We are just beginning to unravel the complex developmental processes that tie an individual primate's gestation, infancy, and juvenility to its adult behavioral outcomes and to discover how male and female subadults make choices that help them maximize the benefits and minimize the challenges of their circumstances. Once these processes are understood across a range of primate species, interspecific comparisons can be used to infer the polarity of primate sex-typed behavioral characters and of the proximate mechanisms that drive them, as well as to pinpoint processes and outcomes of sexual differentiation that are likely to represent adaptations to particular environmental and/or social circumstances.

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