Evolutionary developmental psychology: Contributions from comparative research with nonhuman primates ☆

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Abstract

Evolutionary developmental psychology is a discipline that has the potential to integrate conceptual approaches to the study of behavioral development derived from psychology and biology as well as empirical data from humans and animals. Comparative research with animals, and especially with nonhuman primates, can provide evidence of adaptation in human psychological and behavioral traits by highlighting possible analogies (i.e., similar function, but independent evolution) or homologies (i.e., inheritance from a common ancestor) between human traits and similar traits present in animals. Data from nonhuman primates have played a crucial role in our understanding of infant attachment to the caregiver as a developmental adaptation for survival. Primate and human data are also consistent in suggesting that female interest in infants during the juvenile years may be a developmental adaptation for reproduction that facilitates the acquisition of maternal skills prior to the onset of reproduction.
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There are two conceptually different views of organisms' development. In one view, development is a linear process of maturation whose endpoint is the adult individual; young and immature individuals are viewed as incomplete or miniaturized versions of the adult. Students of development who embrace this view typically emphasize continuities across stages of development, and the causal connections between earlier stages of development and subsequent ones. For example, they study adults retrospectively to identify developmental precursors of their traits, or they study young individuals prospectively to assess whether their early characteristics can predict their subsequent phenotype (see Kagan, 1996). This view often assumes that there is a normative development and that deviations from the norm are pathological.

In the other view, development is seen as a series of successive stages, each with its own problems requiring a specific solution, and without any endpoint to be reached. Individuals of different ages are seen as occupying different social and ecological niches and exhibiting adaptations to them similar to those of adult individuals living in different environments (e.g., Oppenheim, 1981). These developmental (or ontogenetic) adaptations may disappear and be replaced by new ones as the individual moves from one niche to the next. Students of development who embrace this view emphasize discontinuities across stages of development and the functional significance of particular developmental phenotypes rather than their causal connections with preceding or subsequent ones. They appreciate that variants of a particular phenotype may have meaningful functional significance, that is, be adaptive, instead of identifying one developmental pathway as normative and the others as pathological deviations from the norm. In other words, they appreciate the notion that alternative developmental pathways and the potential to express them may evolve as conditional life-history strategies (Stearns, 1992), that is, adaptive responses to the particular environments in which the individuals are situated.

These two views of development represent the opposite ends of a continuum. Generally speaking, developmental psychologists tend to be closer to the view of development as a process of maturation whereas evolutionary biologists tend to favor the view of development as a succession of age-specific adaptations. Evolutionary developmental psychology (EDP) is a discipline that has the potential to integrate psychological and biological approaches to the study of development and bridge the gap between different conceptual views of development. Researchers who follow the perspective of EDP have an appreciation for the view of development as maturation and for causal relationships between different stages of development but are conceptually driven by the notions that organisms display age-specific developmental adaptations and that natural selection may favor alternative life-history strategies (Bjorklund & Pellegrini, 2002; Geary & Bjorklund, 2000).

Developmental adaptations can arise as the result of selective pressures concerning survival or reproduction. Survival is a problem that is faced by any organism at any stage of its life span. Because threats to survival can take different forms for organisms of different ages, it is likely that organisms evolve multiple age-specific adaptations for survival during their life span. Therefore, the view that developing organisms may exhibit successive age-specific adaptations and that earlier adaptations may disappear and be replaced by new ones applies well to adaptations for survival. For example, young mammals are nutritionally dependent on other individuals, and especially on females who can breastfeed them, whereas adult mammals are not. Survival problems for young mammals involve finding females with milk who are willing to breastfeed them whereas survival problems for older mammals involve finding food and competing with others for access to it. These different problems are likely to select for very different sets of adaptations, which will be expressed at different points in the life span.

In species with a long life span, reproduction can begin many years after birth. Thus, from the standpoint of reproduction, a young individual is an incomplete version of the adult, and reproductive development is a process of maturation with puberty as its endpoint. In contrast to selection for survival, selection for reproduction does not maximize the chances of reproduction at any point in time, but rather the overall lifetime reproductive success of an individual. This implies that traits may be selected for at a particular age, which do not confer fitness benefits at that age but later on. Studying these developmental adaptations for reproduction requires an understanding of the causal relationships between events occurring at one stage of development and events occurring at later ages. Therefore, the view of development as a linear process with a specific endpoint applies well to reproductive maturation. Thus, it is clear that the two conceptual views of development described above are not incompatible but both of them are important and must be integrated for a comprehensive understanding of an organism's developmental adaptations across its life span.

Evolutionary developmental psychologists can be integrative not only with regard to the different conceptual views of development that are common in psychology and evolutionary biology but also with regard to the organisms that are the subject of study of these disciplines. Developmental psychologists focus on humans while evolutionary biologists typically work with nonhuman animals. Although evolutionary developmental psychologists and evolutionary psychologists extensively use theories and ideas imported from evolutionary biology, they rarely refer to empirical information from comparative studies of nonhuman animals (but see Bjorklund & Pellegrini, 2002; Geary, 2002, for exceptions) or conduct these studies themselves. In part this may be due to the fact that evolutionary developmental psychologists, and evolutionary psychologists in general, tend to have a background in psychology rather than in evolutionary biology, and in part to the fact that some evolutionary psychologists believe that comparative data are of limited use in the study of human psychological adaptations (see below).

In the first part of this article, we examine how evolutionary psychologists study adaptation in human behavioral and psychological traits and discuss how evidence from comparative research can contribute to the intellectual and research mission of evolutionary psychology. Although EDP has been more sensitive to the importance of comparative research than mainstream evolutionary psychology, there is significant theoretical and empirical overlap between these disciplines (Bjorklund & Pellegrini, 2002). Therefore, much of the discussion of the relation between comparative research and evolutionary psychology can apply to EDP as well. In the second part of this article, we discuss two developmental adaptations for survival and reproduction that humans share with nonhuman primates: specifically, infant attachment to the caregiver and female interest in infants during the juvenile period. We will use these two examples to illustrate the contribution that nonhuman primate studies can make to our understanding of human developmental adaptations, and therefore to the intellectual and research mission of EDP, and also to illustrate the notion that different conceptual views of development can apply to different kinds of ontogenetic adaptations.

How evolutionary psychologists look for evidence of adaptation in human psychological and behavioral traits

The goal of evolutionary psychology is to identify and study human psychological and behavioral adaptations, i.e., psychological and behavioral traits that evolved by natural or sexual selection (e.g., competition over mates) because they conferred fitness advantages to

individuals with these traits relative to individuals without them. A distinction can be made between traits that evolved by natural selection in the past and are currently under selective pressure for the same adaptive function, and traits that evolved by natural selection but are no longer under selective pressure. Although traits can be referred to as adaptive in both cases, in the latter case adaptation refers to the action of natural selection in the past. This distinction has implications for how adaptation is studied. The notion that adaptive traits are under current selective pressure implies that there should be observable differences in reproductive success associated with differences in the presence or absence of these traits. If the traits are no longer adaptive, they should no longer bring fitness benefits to the individuals who carry them. Instead, they may be neutral or even detrimental to an individual's fitness but be maintained in a population because they are linked to other advantageous traits or because there has not been enough time for selection to remove them.

One reason why traits that originally evolved by natural selection may no longer be under selective pressure is that the environment may have changed dramatically. This possibility should clearly be taken into consideration in the study of human adaptations. In fact, evolutionary psychologists often argue that modern humans live in an environment that is different in many ways from the environments in which their brain mechanisms evolved (e.g., Tooby & Cosmides, 1992). Therefore, there is no necessary expectation that adaptations will promote fitness in current environments and, accordingly, evolutionary psychologists do not typically cite the fitness benefits of traits in modern environments as evidence for adaptation (see Symons, 1992). Instead, evolutionary psychologists define adaptations historically, as traits that originated by natural selection, and they argue that the action of natural selection in the past can be identified from the design of adaptive traits. This argument from design maintains that only natural selection can produce complex functional design in biological organisms, and, as such, empirical evidence that a trait is well-engineered for the solution of a specific problem is evidence for the action of natural selection and therefore, evidence for adaptation.

A general objection to the argument from design is that special design in human behavioral and psychological traits may arise as a by-product of learning mechanisms that evolved for other purposes (Andrews, Gangestad, & Matthews, 2002). The argument from design, therefore, does not allow one to distinguish unequivocally behavioral and psychological adaptations from exaptations (i.e., traits that currently serve an adaptive function that is different from the function they were originally selected for; Gould & Vrba, 1982) as well as distinguish both adaptations and exaptations from "spandrels," i.e., traits that seemingly have complex design but serve no function and originated as by-products of other traits (Gould & Lewontin, 1979). These limitations of the argument from design argue for the importance of additional lines of empirical evidence for adaptation (see also Autumn, Ryan, & Wake, 2002). In the rest of this article, we argue that comparative research can provide such additional evidence.

The role of comparative research in the study of human behavioral and psychological adaptations

Although EDP recognizes the importance of comparative data, and especially of evidence from the nonhuman primates closest to us (e.g., Bjorklund & Pellegrini, 2002), mainstream evolutionary psychology has generally downplayed the importance of comparative research for the study of human psychological and behavioral adaptations. Animal

research is sometimes used by evolutionary psychologists to generate hypotheses, but not as a potential source of empirical evidence about adaptation. For example, some evolutionary psychologists dismiss the contributions made by phylogenetic analyses of animal behavior (Daly & Wilson, 1997, 1999), while others maintain that phylogenetic analyses are more likely to be useful for the analysis of neurobiological or physiological traits than for the understanding of behavior or cognition (Tooby & Cosmides, 1989). This position has recently been taken also by Gottlieb and Lickliter (2004), who "do not think that homologies can be readily documented with even our most closely related relatives' behavior and psychological functioning" (p. 311). In our view, this pessimism is not justified, and in the following sections, we will make the case that comparative research, and especially research with nonhuman primates, can play an important role in the study of human adaptations (see also Maestripieri, 2003a, 2005a; Roney & Maestripieri, 2002).

Comparative research can provide evidence of adaptation through analysis of convergent evolution

Similar morphological, physiological, behavioral, and psychological traits can evolve independently by natural selection in different species in response to similar environmental pressures. This phenomenon is called *convergent evolution*. These traits serve analogous functions in different species and are therefore called analogous. If particular human behavioral or psychological traits can be shown to serve a similar function as adaptive traits present in other animal species despite differences in terms of details of their structures or in their developmental precursors, one can argue that the human traits are likely to be adaptive as well and that they represent a case of convergent evolution.

This is an effective strategy for the study of human adaptations because demonstrating the adaptiveness of behavioral or psychological traits may be easier in animals than in humans for many reasons: many wild animals still live in environments that have not changed as much as the human environment, and many aspects of their behavior are currently under strong selective pressure; reproduction is unconstrained by cultural factors; in many cases life spans are shorter than in humans and life time reproductive success can be effectively quantified, therefore allowing for correlation between individual differences in phenotypic traits and differences in fitness; finally, behavioral traits can be experimentally manipulated and their effect on fitness can be assessed. Since functional approaches to animal behavior began to be systematically used in the 1970s, animal behavior researchers have provided empirical evidence for the adaptiveness of thousands of behavioral traits in virtually every animal taxon (e.g., Alcock, 2005). A great deal is also known about the adaptiveness of animal cognitive traits (e.g., Bekoff, Allen, & Burghardt, 2002).

Demonstration of similarities in the function and the design of behavioral and psychological traits between humans and other animals can be used as an argument that the human traits are unlikely to be the by-product of modern human environments. For example, the occurrence and adaptive function of pair bonding in other taxonomic groups strongly suggest that this social system may have independently evolved in humans and many other animal species (e.g., most species of birds) as an adaptive response to the need for bi-parental care of the young (Clutton-Brock, 1991; Geary, 2000). Humans and other pair-bonded animals also share some of the adaptive design features of pair bonding, e.g., emotional and behavioral responses to separation from a

social partner, although these responses may be regulated by different neurobiological or cognitive mechanisms (Carter, 1998; Insel & Young, 2000). The similarities in the function and basic design features of pair bonding in humans and other animals make it unlikely that human pair bonding is a product of modern culture. Therefore, in the case of pair bonding and potentially many other behavioral and psychological traits, comparative data can suggest convergent evolution in humans and other animals and be used, in addition to the argument from design, to make the case for adaptation.

Comparative research can provide evidence of adaptation through analyses of phylogenetic history

Morphological, physiological, behavioral, and psychological traits can be similar in different species because these species have inherited these traits from a common ancestor. These traits are called homologous. Therefore, homologous traits have, by definition, a common phylogenetic history and are produced by similar developmental processes (e.g., Sluys, 1996; Wagner, 1989). Homologies in behavior and its cognitive and neurobiological substrates can be assessed with the comparative approach, much like homologies in other traits (Atz, 1970; Heinroth, 1910, cited in Burkhardt, 2005; Lorenz, 1950; Wenzel, 1992). Phylogenetic analyses are one of fastest growing areas of comparative behavioral research; they have been successfully used in a wide range of animal species (e.g., Autumn et al., 2002; Cleaveland, Jager, Rossner, & Delius, 2003; Di Fiore & Rendall, 1994; Hale, Long, McHenry, & Westneat, 2002; Martins, 1996; Preuschoft & van Hooff, 1995; Stratton, Suter, & Miller, 2003; Thierry, Iwaniuk, & Pellis, 2000) and nothing prevents them from being extended to humans as well. For example, homologies between some human facial expressions of emotion and those of Old World monkeys and apes can be readily identified (Darwin, 1872; Preuschoft & van Hooff, 1995; van Hooff, 1972).

Homologous traits in different species may not necessarily serve the same adaptive function because the function of traits may change over time in response to changing social or ecological pressures. Demonstration that particular human behavioral or psychological traits are homologous to traits in other animals implies that these human traits are unlikely to be developmental by-products of modern human environments. To provide compelling evidence for adaptation, however, and exclude exaptation as a possible explanation for the origin of the trait, homologous traits must play the same functional roles in humans and in animals. Therefore, comparative phylogenetic analyses of traits must be complemented by functional analyses.

The use of phylogenetic continuity to support the hypothesis of adaptation may seem counterintuitive given that phylogenetic inertia and selection are often presented as competing explanations for the nature of phenotypes (Roney & Maestripieri, 2002). Darwin (1859), in fact, often used nonadaptive homologies as evidence for evolution and as an argument against special creation. For example, he argued that human facial expressions of emotion may be nonadaptive homologs of animal expressions (Darwin, 1872; see also Fridlund, 1994). Many functional traits, however, are preserved across taxa because of their adaptive consequences and many adaptations are likely to be homologous across species (e.g., Wagner & Altenberg, 1996). Therefore, phylogenetic analyses should be part of any comprehensive strategy for the empirical demonstration of human behavioral and psychological adaptations.

Usefulness of nonhuman primates

Many aspects of human behavior and cognition and their developmental trajectories were likely inherited from our mammalian ancestors. The probability that two species share similar behaviors due to common descent is higher the closer the phylogenetic relationship between the species. The great apes (chimpanzees, bonobos, gorillas, and orangutans) and the Old World monkeys (e.g., macaques and baboons) are, along with the lesser apes (gibbons and siamangs), the animals that are phylogenetically closest to humans. The great apes and the Old World monkeys share approximately 98 and 95% of their genetic material with humans, respectively (Marks, 2003). Therefore, human behavior is more likely to be homologous to the behavior of the great apes and the Old World monkeys than to the behavior of other animals.

In theory, analogies can exist between human behavioral and psychological traits and traits exhibited by animals in any taxonomic group. In reality, however, there are many constraints on the type of adaptations to the environment that organisms can evolve through natural selection. Therefore, similarities in genetic, anatomical, physiological, and cognitive constraints increase the probability that organisms will evolve similar adaptations to similar social or ecological contingencies (Maestripieri, 2003a).

In sum, because animals that are phylogenetically closer to humans are more likely to share with humans not only homologies but also analogies in their behavioral and psychological functioning, research with nonhuman primates, and especially with great apes and Old World monkeys can make an important contribution to research in evolutionary psychology and evolutionary developmental psychology. In the following two sections, we will illustrate and discuss two examples of developmental adaptations for survival and reproduction that humans appear to share with other primates. Many other examples could be provided with regard to early cognitive development, developmental sex differences in behavior and cognition, or behavioral and psychological changes associated with puberty and adolescence (e.g., see Bjorklund & Pellegrini, 2002).

Developmental adaptations for survival in nonhuman primates and humans: Attachment to the caregiver

According to the theory formulated by British psychiatrist John Bowlby, human infants and young children have a biological predisposition to become attached to a caregiver (Bowlby, 1969, 1973, 1980). Bowlby argued that the infant attachment system evolved in the Environment of Evolutionary Adaptedness as a set of psychological and behavioral adaptations that promoted infant survival by enhancing infant proximity and interaction with a caregiver. Comparative research made an important contribution to the formulation of attachment theory (e.g., Maestripieri, 2003b). Bowlby derived from ethology the notion that infant attachment should be explained in terms of causation, ontogeny, adaptive function, and evolution (Tinbergen, 1963). He also borrowed from ethology the concept of behavioral system viewed as a set of behavioral responses serving a particular biological end (Hinde, 1982). Finally, Bowlby gained important insights about the infant attachment system from observations of mother–infant interactions in rhesus macaques (e.g., Hinde & Spencer-Booth, 1967) and from experiments in the same species demonstrating the primary role of the caregiver as a source of contact/comfort and protection rather than nutrition (Harlow, 1959, 1974). Bowlby thus viewed the infant attachment system as a

developmental adaptation for survival with a phylogenetic history that could be traced back at least to the Old World monkeys.

The design features and development of the infant attachment system in humans

Bowlby argued that the infant attachment system has a specific set goal and multiple activating and terminating conditions. The set goal of the infant is the maintenance of contact or proximity to the mother. The system is activated when the infant is separated from the mother and is terminated when contact or proximity is established. The threshold of activation of the attachment system varies in relation to both exogenous (e.g., distance from the mother, natural clues to danger) and endogenous factors (e.g., illness, fatigue, or hunger). In Bowlby's view, the attachment system is composed of a set of design features with specific adaptive significance and emerges developmentally according to a four-stage sequence. In the first 8 to 12 weeks of life, there is no behavioral attachment to specific caregivers, although infants already show a preference for looking at the human face and listening to human voices, especially that of their mother (e.g., Kisilevsky et al., 2003). Infants behaviorally respond to stimuli in a manner that increases the likelihood of continued contact with other humans but behave the same way toward many people. This period is followed by a pre-attachment stage (between 8 and 12 weeks and 6 months of age), in which there is a restriction of the range of stimuli that can effectively activate and terminate the attachment responses. Infants also begin to discriminate their caregiver(s) from other people. Stage 3 (between 6 and 9 months and 2–3 years of age) is characterized by new attachment behaviors (e.g., following the caregiver) and changes in the organization of attachment behaviors under the infant's intentional control. The infant now has a cognitive representation of the attachment figure that is independent from perception, that is, it appears infants can either generate a mental representation of the caregiver even in his/her absence or such representation is automatically generated in some contexts (e.g., unfamiliar). As attachment is fully established, other motivational/behavioral systems such as the exploration and the fear systems become active as well.

According to Bowlby, the attachment system can be activated simultaneously with the fear/wariness system, and they both inhibit the exploration system. Thus, when the infant is frightened or anxious, he or she wants to be near the mother and does not explore the environment or play. When the infant feels secure, he or she will explore and play. Design features of the attachment system that appear at this stage include the use of the caregiver as a "safe haven" when the infant is frightened and a "secure base" for exploration; these features emerge concomitantly with the development of fear of strangers (∼6 months) and separation anxiety (∼9 months). In the last stage of attachment development (2–3 years and beyond), the caregiver is perceived as an individual with his or her own goals and the cognitive aspects of attachment become more prominent than the behavioral and emotional ones.

The infant attachment system in rhesus macaques

Similar to human infants, rhesus macaque infants initially direct attachment behaviors to a variety of individuals other than the mother, as well as to other animals or inanimate objects with the proper stimulus characteristics (e.g., Harlow, 1959; Mason & Capitanio, 1988). The range of stimuli capable of eliciting attachment responses, however, is gradually

restricted as infants grow older. Similar to the human attachment system, the main function of the monkey attachment system is to maintain proximity or contact with the caregiver, in this case the mother. When attachment is fully developed, this system interacts with the exploration and the fear system in a way similar to the human attachment system. This is clearly illustrated by developmental changes in the maintenance of contact and proximity between mother and infant. In the first few days after birth, rhesus macaque infants are in almost continuous contact with their mothers and if contact is broken, it is always re-established by the mother (Hinde & Spencer-Booth, 1967). Beginning from the second week of life, the infants' exploration of the surrounding environment takes the form of short radial trips from their mothers, which suggests that infants begin to use their mother as a secure base to explore the environment. Departure from the mother is inhibited or re-establishment of contact is accelerated if the infant is afraid or in distress, suggesting that the attachment, exploration, and fear systems begin to be mutually dependent (Hinde, 1984; Hinde & Spencer-Booth, 1967).

Distress calls and other signs of behavioral agitation shown by infants who have lost visual contact with their mothers or have been hurt by other group members cease almost immediately upon re-establishment of contact with the mother (Maestripieri & Call, 1996). This suggests the mother serves an important reassuring and soothing function equivalent to the caregiver's "safe haven" function in the human attachment system. As separation anxiety and fear of strangers emerge, rhesus macaque infants become primarily responsible for maintaining contact and proximity with their mothers (Hinde, 1984; Hinde & Spencer-Booth, 1967). Infant proximity to the mother is crucial for protection from predators and other members of the same species, and reduced maternal protection is associated with a variety of dangers (e.g., Maestripieri, 1995). Taken together, these observations suggest that rhesus monkey infants possess an attachment system whose design features, development, and adaptive function are very similar to those of human infant attachment (see also Suomi, 1999). Similar observations have also been made, though not as systematically as in rhesus macaques, also in other nonhuman primates (e.g., chimpanzees; Maestripieri, 2003b).

The phylogeny of infant attachment

The similarities in the infant attachment system in rhesus monkeys and humans raise the question of whether they evolved independently from one another (i.e., they are analogous), or whether they share a common evolutionary history (i.e., they are homologous). Bowlby appeared to believe that the basic features of attachment are homologous in rhesus monkey and human infants (see Suomi, 1999). In fact, a human-like attachment system is almost ubiquitous among the Old World monkeys and the apes (i.e., the primates phylogenetically closest to humans) and absent or rare among the prosimians (e.g., lemurs) and the New World monkeys (i.e., the primates phylogenetically more distant from humans; Maestripieri, 2003b; Mason & Mendoza, 1998). This suggests the attachment system is not the product of the modern human environment but instead is an adaptation the history of which can be tracked in the evolution of the Primate order.

Clearly some differences exist between the human and the nonhuman primate attachment system as well as among the attachment systems of different nonhuman primate species. Some of these differences involve whether attachment is to the mother, the father, or multiple caregivers, the specific behavioral expressions of attachment, the ontogenetic

sequence of attachment formation, the possible neurobiological mechanisms regulating attachment processes, and the relative importance of cognitive processes in attachment, especially at later stages of development. For example, the extent to which nonhuman primate infants develop a cognitive model of the caregiver in relation to the self and the external environment is not clear. In some cases, species differences in attachment can be related to the life-history characteristics of the species and its ecological, social, and reproductive adaptations (Maestripieri, 2003b). In other cases, they can be associated with species differences in cognitive or communicative skills.

According to some theorists, the attachment system continues to be active beyond the childhood period and to operate also in the context of relationships between peers in adolescence or in romantic relationships in adulthood (e.g., Hazan & Shaver, 1987). The hypothesis that the attachment relationship with the caregiver becomes a template for other relationships later in life, and especially for sexual and romantic relationships, suggests that attachment is an adaptation not only for survival but also for reproduction. It is possible that once the attachment system evolved as a developmental adaptation for survival in infancy, this system acquired new adaptive functions in humans (but see Kirkpatrick, 1998). The characteristics and the function of the infant attachment system in humans, however, are quite distinct from those of adult attachment and very similar to those of the infant attachment system in other nonhuman primates. Comparative research with nonhuman primates played an important role in the understanding of infant attachment and may contribute further to research on this and other early adaptations for survival.

Developmental adaptations for reproduction in nonhuman primates and humans: Early female interest in infants and the acquisition of mothering skills

Maternal care in primates and the role of experience in the acquisition of competent mothering skills

Female parental care is the rule among the over 300 species of nonhuman primates, the exceptions being a few socially monogamous species in which fathers carry and protect their infants. Social monogamy and paternal care are mostly concentrated among New World monkeys and associated with particular reproductive or ecological characteristics (e.g., the production of twins in marmosets and tamarins; Snowdon & Suomi, 1982). Among the Old World monkeys and the apes, females typically give birth to one infant at a time, feed their offspring with milk for one year or more, and in some cases continue investing in them for the rest of their lives with little or no contribution from males. During the period of infant dependence, maternal care manifests itself mainly as breastfeeding, carrying, and protecting the infant. Among great apes, mothers also play with their infants and share solid food with them. Primate maternal behavior is generally comparable, in terms of its basic characteristics, to that of many other mammalian species, although primate infants are generally carried more by their mothers than other mammalian young.

In mammalian species with a short life span (e.g., mice and rats), first-time mothers exhibit a full repertoire of maternal behavior from the moment their offspring are born and are generally successful in raising their litters in the absence of any prior experience with pups. In fact, in some of these species females without reproductive experience avoid any contact with other females' pups or kill them and cannibalize them (e.g.,

Fleming & Orpen, 1986). In rodents, maternal responsiveness and behavior are probably under relatively strong genetic control and are regulated by a combination of hormonal changes induced by pregnancy and lactation along with sensory stimuli from the offspring (e.g., Fleming & Orpen, 1986). Unlike rodents, Old World monkeys, apes, and humans have relatively long life spans, and in these species, many aspects of maternal behavior depend, in part, on experience acquired during development. For example, nonhuman primate mothers need this experience to learn how to carry their infants properly, to allow infants to maintain nipple contact long enough to obtain their necessary nourishment, to protect infants from unwanted attention from other conspecifics, and to encourage infant independence and weaning (e.g., Pryce, 1996).

Important experience for learning maternal behavior can be acquired by primate females during interactions with their own mothers in infancy, through observation of interactions between their mothers and younger siblings or between other females and their infants during the juvenile period, through direct interaction with younger siblings or other females' infants during the juvenile period, and through direct interactions with their own offspring. The importance of these forms of experience for the acquisition of competent maternal behavior is demonstrated by several lines of evidence. Monkey or ape females who are separated from their mothers after birth and are hand-reared in isolation or with surrogate mothers (e.g., toys, dogs, or other monkey infants) typically neglect or abandon their first-born infants or exhibit abnormal patterns of maternal care (e.g., Suomi, 1978). Females that are reared by their biological mothers but in socially impoverished environments in which opportunities to interact with infants and other conspecifics are limited also exhibit deficiencies in maternal behavior (Suomi, 1978).

Among female monkeys living in naturalistic social groups, first-time mothers are generally more likely than multiparous mothers to neglect and abandon their infants or to show clumsy maternal behavior such as carrying infants upside down (Maestripieri & Carroll, 1998; Schino & Troisi, 2005). The probability of infant abandonment is greatly reduced as females give birth to successive infants and the quality of maternal care typically increases as well (Maestripieri & Carroll, 1998; Schino & Troisi, 2005). Interactions with younger siblings or other females' infants during the juvenile period (collectively referred to as "infant handling"), however, can affect the quality of maternal care and the probability of infant survival of first-time mothers. In vervet monkeys, first-time mothers who had greater infant handling experience with infants as juveniles were more likely to be competent mothers and their infants had a higher probability of survival than females with less juvenile experience with infants (Fairbanks, 1990).

Although a female's experience with her own mother, with her siblings or other females' infants, and with her own offspring are all probably equally important for the acquisition of competent mothering skills, interest in infants in the juvenile years and motivation to engage in extensive social interactions with them probably represent a specific developmental adaptation shared by nonhuman primates and humans but not present in other mammals with shorter life spans such as rodents. In the next section, we will illustrate some of the evidence in favor of this hypothesis.

Sex differences in interest in infants in the juvenile period in human and nonhuman primates

Interactions between girls and infants or young children have been observed by anthropologists in virtually all human societies, whereas interactions between boys and infants or

young children are far less common (Edwards, 1993; Whiting & Whiting, 1975). A sex difference in interest in infants and involvement in caregiving interactions has also been demonstrated by developmental psychologists in a number of different contexts and with many different measures, including naturalistic observations of interactions with infants, responses to pictures of infants vs other individuals or objects, and preferences for playing with dolls vs other toys (e.g., Berman, 1980; Blakemore, 1983; Feldman, Nash, & Cutrona, 1977; Fullard & Reiling, 1976; Maestripieri & Pelka, 2002). Female responsiveness to infants is greatest in childhood and adolescence and declines in middle-aged and elderly women, whereas a similar pattern is not observed for males (Berman, 1980; Feldman et al., 1977; Frodi & Lamb, 1978; Fullard & Reiling, 1976; Maestripieri & Pelka, 2002).

Many socio-cultural anthropologists and psychologists interpret this sex difference as the result of socialization, i.e., parental and societal influences that encourage interest in infants and involvement in caregiving activities in young females but not in males (e.g., Whiting, 1980). A study, however, that specifically attempted to demonstrate the role of parental socialization in the origin of sex differences in interest in infants failed to do so (Blakemore, 1990). It has also been argued that the time course of sex differences in interest in infants is more consistent with the hypothesis that greater female interest in infants is an adaptation to facilitate the acquisition of parenting skills prior to puberty than a culturally driven preparation for adult sex roles (Maestripieri & Pelka, 2002). Finally, evidence that biological factors such as prenatal exposure to sex steroid hormones play a role in the development of interest in infants has been provided by studies of girls with congenital adrenal hyperplasia (CAH), a syndrome that involves exposure to excess androgen in utero. Girls with CAH exhibit several signs of morphological and behavioral masculinization including reduced interest in playing with dolls compared to normal girls (Berenbaum & Hines, 1992; Leveroni & Berenbaum, 1998). Therefore, although parental and cultural influences undoubtedly exist, it is possible that these influences exaggerate pre-existing (and biologically based) sex differences in psychological disposition towards infants and caregiving behavior (Geary, 1998; Roney & Maestripieri, 2003).

The hypothesis that early female interest in infants is a developmental adaptation rather than a product of human culture and socialization is supported by comparative evidence from nonhuman primates. In rhesus macaques, a strong sex difference in interest in infants (e.g., in rates of infant handling) emerges by the end of the first year of life and persists through the prepubertal years and beyond (Herman, Measday, & Wallen, 2003; Lovejoy & Wallen, 1988; Maestripieri, 2005b). In the first year of life, males and females are not treated any differently by their mothers or other group members (Fairbanks, 1996). Furthermore, male and female yearlings spend similar amounts of time in proximity to their mothers, and mothers do not encourage or discourage any social activities differentially in their sons and daughters (Fairbanks, 1996). Therefore, sex differences in interest in infants in rhesus macaques are more likely to result from biological factors including prenatal hormone exposure, than to be the product of socialization (Herman et al., 2003; Roney & Maestripieri, 2003). Parsimony would suggest that this may be the case in humans as well.

Interest in infants and female reproductive strategies

The hypothesis that early female interest in infants is a developmental adaptation to facilitate the acquisition of mothering skills and increase reproductive success predicts not only sex differences consistent with the prevalence of maternal vs paternal care but also

adaptive intra-individual variation in this trait. Specifically, because the developmental acquisition of mothering skills is crucial for the success of first reproduction, one would expect that adaptive intra-sex variation in the timing of the onset of reproduction should also affect the developmental time course of female interest in infants.

Life-history theory predicts that when food availability is scarce and offspring mortality is high, females should postpone the onset of reproduction and invest more in their own growth and maturation (Stearns, 1992). This is because food availability is crucial for lactation and offspring survival. Since food availability often fluctuates cyclically in the environment females are better off postponing reproduction until environmental conditions improve (Wasser & Barash, 1983). In contrast, if food is available and mortality is concentrated not in infancy but in adulthood, it would be advantageous to females to accelerate their reproductive maturation. This is because food is available for lactation and offspring survival but females have limited prospects for their own survival in adulthood. Therefore they should start reproducing as early as possible. Early reproduction would also predict early acquisition of parenting skills necessary to guarantee offspring survival, whereas when reproductive maturation is delayed, interest in infants may be delayed as well.

The association between low food availability and the delay or suppression of reproduction is well documented in female mammals (Wasser & Barash, 1983). Similarly, there is a large body of evidence in humans showing that nutritional stress and low body weight (or body fat) during adolescence can delay female reproductive maturation and result in later age of menarche (see Ellis, 2004, for review). Many studies, however, have shown that early physical or psychosocial stress (e.g., early family conflict or father absence from home) is associated with earlier menarche (see Ellis, 2004, for review). One possible interpretation of this association is that early physical or psychosocial stress is interpreted by the developing organism as a cue that risk of mortality will be elevated in adulthood due to social threats by conspecifics and lack of adequate protection by an adult male (Belsky, Steinberg, & Draper, 1991; Chisholm, 1999; Draper & Harpending, 1982).

Variation in the development of interest in infants among young girls has been poorly investigated. An early study by Goldberg, Blumberg, and Kriger (1982) reported that 12-year-old girls who had reached menarche were more attracted to pictures with infant faces than same-aged girls who had not yet reached menarche. The authors of this study suggested that possible neuroendocrine changes associated with the onset of menstruation may increase selective attention and responsiveness to infantile features, and that such attentional changes would function to increase opportunities to observe and respond to infants in the years between menarche and actual childbearing. Maestripieri, Roney, DeBias, Durante, and Spaepen (2004), however, offered a different interpretation of these findings; specifically, the possibility that girls with early menarche had greater interest in infants than girls with late menarche even before the onset of menstruation. Their interpretation argues that menarche per se does not affect female interest in infants but that the timing of menarche is the crucial variable because girls with early and late menarche may be on different developmental tracks that include early vs late reproduction and interest in infant. Maestripieri et al. (2004) presented data consistent with this interpretation. In a sample of 83 adolescent girls, there was no significant difference in interest in pictures of infant faces between premenarcheal and postmenarcheal girls. However, girls with early menarche showed greater preferences for infants than girls with late menarche. Early menarche, in turn, was significantly associated with father absence from home during childhood and adolescence. These findings suggest that the father-absent girls are on a fast

reproductive track and that by being more attracted to infant stimuli, or by expressing interest in infants earlier during development, these girls may acquire crucial parenting skills earlier in life and be better equipped for early reproduction and child-rearing.

It has been argued that the effects of early psychosocial stress on early female reproductive maturation may be mediated by the quality of parental care received at home (e.g., Belsky et al., 1991). In other words, lack of resources or high levels of conflict in the home environment would lead to harsh and inconsistent parenting behavior, and this in turn would affect the child's behavioral and reproductive development. Differences in the amount and quality of parental care between single-parent and two-parent households may also mediate the effects of father absence on early menarche and precocious sexual maturation (Belsky et al., 1991; Quinlan, 2003). However, early menarche and early interest in infants in girls who grow up in stressful environments or without a father may also be traits that are genetically inherited from the girls' mothers or fathers (see Figueredo et al., 2006).

A recent study of rhesus macaques used a cross-fostering procedure to examine the relative contribution of genes and early environment to the development of female interest in infants (Maestripieri, 2005b). Specifically, female infants were cross-fostered at birth between mothers with a history of harsh and inconsistent maternal care and mothers with a history of competent and nurturing maternal behavior. The females exposed to poor quality maternal care in infancy exhibited higher interest in other females' infants in the juvenile period, regardless of the identity of their biological mothers. These females also tended to have an earlier age at first conception than the other females. Therefore, the development of female interest in infants was influenced by the quality of early environment as predicted by life-history theory. Macaque females exposed to harsh and inconsistent maternal care in infancy tended to have higher cortisol responses to stress and to corticotropin-releasing-hormone (CRH) than controls in the first 3 years of life (see also Ellis, Jackson, & Boyce, 2006; Flinn, 2006). Furthermore, females with higher cortisol responses to stress exhibited higher interest in infants.

These findings suggest that some of the effects of early parental care on female reproductive maturation may be mediated by developmental changes in the activity of the hypothalamic–pituitary–adrenal axis. Similar effects of exposure to different patterns of maternal care on female reproductive maturation have also been reported in rats. Cameron et al. (2005) reported that females reared by mothers with low levels of licking, grooming, and arched-back nursing (LG-ABN) showed vaginal opening (an indicator of pubertal development in rats) earlier in life than the offspring of high LG-ABN mothers as well as higher sexual receptivity to males and higher probability of conception following mating interactions. As with the monkeys, these effects of early experience were demonstrated with cross-fostering studies and shown to be associated with alterations in neuroendocrine responsiveness to stress (Cameron et al., 2005).

Taken together, comparative evidence from humans, monkeys, and rats suggest that the quality of the early social environment, and especially the quality of maternal care received early in life, can result in adaptive programming of female reproductive maturation. In monkeys and humans, these maternal effects on reproductive maturation also include the development of interest in infants during the juvenile period. This finding, in addition to other comparative data on sex differences in interest in infants, the developmental time course of female interest in infants, and its function, is consistent with the hypothesis that early female interest in infants is a developmental adaptation that we share with other

primates that are phylogenetically close to us. Without the comparative data, however, socio-cultural explanations of early female interest in infants would be difficult to discard.

Conclusion

As illustrated by the examples of infant attachment to the caregiver and early female interest in infants, humans share with other primates age-specific behavioral and psychological adaptations for survival and reproduction. Some of these adaptive traits have immediate fitness benefits at the age at which they are expressed whereas others have delayed benefits. In some cases, similar developmental adaptations in humans and other primates are homologous whereas in other cases they are the result of convergent evolution. Evidence from comparative research can be used to argue against alternative, non-adaptive explanations for human behavioral and psychological traits and therefore can make a fundamental contribution to the intellectual and research mission of evolutionary developmental psychology.

References

Alcock, J. (2005). *Animal behavior: An evolutionary approach* (Eighth ed.). MA, Sunderland: Sinauer.

Andrews, P. W., Gangestad, S. W., & Matthews, D. (2002). How to carry out an exaptationist program. *Behavioral and Brain Sciences, 25*, 489–553.

Atz, J. W. (1970). The application of the idea of homology to behavior. In L. R. Aronson, E. Tobach, D. S. Lehrman, & J. S. Rosenblatt (Eds.), *Development and evolution of behavior* (pp. 53–74). San Francisco: W.H. Freeman.

Autumn, K., Ryan, M. J., & Wake, D. B. (2002). Integrating historical and mechanistic biology enhances the study of adaptation. *Quarterly Review of Biology, 77*, 383–408.

Bekoff, M., Allen, C., & Burghardt, G. (Eds.). (2002). *The cognitive animal: Empirical and theoretical perspectives on animal cognition*. Cambridge, MA: MIT Press.

Belsky, J., Steinberg, L., & Draper, P. (1991). Childhood experience, interpersonal development, and reproductive strategy: An evolutionary theory of socialization. *Child Development, 62*, 647–670.

Berenbaum, S. A., & Hines, M. (1992). Early androgens are related to childhood sex-typed toy preferences. *Psychological Science, 3*, 203–206.

Berman, P. W. (1980). Are women more responsive than men to the young? A review of developmental and situational variables. *Psychological Bulletin, 88*, 668–695.

Bjorklund, D. F., & Pellegrini, A. D. (2002). *The origins of human nature: Evolutionary developmental psychology*. Washington, DC: American Psychological Association Press.

Blakemore, J. E. O. (1983). Age and sex differences in interaction with a human infant. *Child Development, 52*, 386–388.

Blakemore, J. E. O. (1990). Children's nurturant interactions with their siblings: An exploration of gender differences and maternal socialization. *Sex Roles, 22*, 43–57.

Bowlby, J. (1969). *Attachment and loss. Attachment* (Vol. I). New York: Basic Books.

Bowlby, J. (1973). *Attachment and loss. Separation: Anxiety and anger* (Vol. II). New York: Basic Books.

Bowlby, J. (1980). *Attachment and loss. Loss: Sadness and depression* (Vol. III). New York: Basic Books.

Burkhardt, R. W. (2005). *Patterns of behavior. Konrad Lorenz, Niko Tinbergen, and the founding of ethology*. Chicago: University of Chicago Press.

Cameron, N. M., Champagne, F. A., Parent, C., Fish, E. W., Ozaki-Kuroda, K., & Meaney, M. J. (2005). The programming of individual differences in defensive responses and reproductive strategies in the rat through variations in maternal care. *Neuroscience and Biobehavioral Reviews, 29*, 843–865.

Carter, C. S. (1998). Neuroendocrine perspectives on social attachment and love. *Psychoneuroendocrinology, 23*, 779–818.

Chisholm, J. S. (1999). Attachment and time preference: Relations between early stress and sexual behavior in a sample of American university women. *Human Nature, 10*, 51–83.

Cleaveland, J. M., Jager, R., Rossner, P., & Delius, J. D. (2003). Ontogeny has a phylogeny: Background to adjunctive behaviors in pigeons and budgerigars. *Behavioural Processes, 61*, 143–158.

Clutton-Brock, T. H. (1991). *The evolution of parental care*. Princeton, NJ: Princeton University Press.

Daly, M., & Wilson, M. (1997). Evolutionary psychology: Adaptationist, selectionist, and comparative. *Psychological Inquiry, 8*, 34–38.

Daly, M., & Wilson, M. (1999). Human evolutionary psychology and animal behaviour. *Animal Behaviour, 57*, 509–519.

Darwin, C. (1859). *On the origin of species*. London: Murray.

Darwin, C. (1872). *The expression of the emotions in man and animals*. London: Murray.

Di Fiore, A., & Rendall, D. (1994). Evolution of social organization: A reappraisal for primates by using phylogenetic methods. *Proceedings of the National Academy of Sciences of the United States of America, 91*, 9941–9945.

Draper, P., & Harpending, H. (1982). Father absence and reproductive strategy: An evolutionary perspective. *Journal of Anthropological Research, 38*, 255–273.

Edwards, C. P. (1993). Behavioral sex differences in children of diverse cultures: The case of nurturance to infants. In M. E. Pereira & L. A. Fairbanks (Eds.), *Juvenile primates. Life history, development, and behavior* (pp. 327–338). New York: Oxford University Press.

Ellis, B. J. (2004). Timing of pubertal maturation in girls: An integrated life history approach. *Psychological Bulletin, 130*, 920–958.

Ellis, B. J., Jackson, J. J., & Boyce, W. T. (2006). The stress response systems: Universality and adaptive individual differences. *Developmental Review, 26*(2), 175–212.

Fairbanks, L. A. (1990). Reciprocal benefits of allomothering for female vervet monkeys. *Animal Behaviour, 40*, 553–562.

Fairbanks, L. A. (1996). Individual differences in maternal styles: Causes and consequences for mothers and offspring. *Advances in the Study of Behavior, 25*, 579–611.

Feldman, S. S., Nash, S. C., & Cutrona, C. (1977). The influence of age and sex on responsiveness to babies. *Developmental Psychology, 13*, 675–676.

Figueredo, A. J., Vasquez, G., Brumbach, B. H., Schneider, S. M. R., Sefcek, J. A., Tal, I. R., et al. (2006). Consilience and life history theory: From genes to brain to reproductive strategy. *Developmental Review, 26*(2), 243–275.

Fleming, A. S., & Orpen, G. (1986). Psychobiology of maternal behavior in rats, selected other species, and humans. In A. Fogel & G. Melson (Eds.), *Origins of nurturance* (pp. 141–208). Hillsdale, NJ: Erlbaum.

Flinn, M. V. (2006). Evolution and ontogeny of stress response to social challenges in the human child. *Developmental Review, 26*(2), 138–174.

Fridlund, A. J. (1994). *Human facial expression. An evolutionary view*. New York: Academic Press.

Frodi, A. M., & Lamb, M. E. (1978). Sex differences in responsiveness to infants: A developmental study of psychophysiological and behavioral responses. *Child Development, 49*, 1182–1188.

Fullard, W., & Reiling, A. M. (1976). An investigation of Lorenz's "babyness". *Child Development, 47*, 1191–1193.

Geary, D. C. (1998). *Male, female: The evolution of human sex differences*. Washington, DC: American Psychological Association Press.

Geary, D. C. (2000). Evolution and proximate expression of human paternal investment. *Psychological Bulletin, 126*, 55–77.

Geary, D. C. (2002). Sexual selection and human life history. *Advances in Child Development and Behavior, 30*, 41–101.

Geary, D. C., & Bjorklund, D. F. (2000). Evolutionary developmental psychology. *Child Development, 71*, 57–65.

Goldberg, S., Blumberg, S. L., & Kriger, A. (1982). Menarche and interest in infants: Biological and social influences. *Child Development, 53*, 1544–1550.

Gould, S. J., & Lewontin, R. C. (1979). The spandrels of San Marco and the Panglossian paradigm: A critique of the adaptationist program. *Proceedings of the Royal Society of London B, 205*, 581–598.

Gould, S. J., & Vrba, E. E. (1982). Exaptation: A missing term in the science of form. *Paleobiology, 8*, 4–15.

Gottlieb, G., & Lickliter, R. (2004). The various roles of animal models in understanding human development. *Social Development, 13*, 311–325.

Hale, M. E., Long, J. H., McHenry, M. J., & Westneat, M. W. (2002). Evolution of behavior and neural control of the fast-start escape response. *Evolution, 56*, 993–1007.

Harlow, H. F. (1959). Affectional response in the infant monkey. *Science, 130*, 421–432.

Harlow, H. F. (1974). *Learning to love*. New York: Jason Aronson Inc.

Hazan, C., & Shaver, P. R. (1987). Romantic love conceptualized as an attachment process. *Journal of Personality and Social Psychology, 52*, 511–524.

Herman, R. A., Measday, M. A., & Wallen, K. (2003). Sex differences in interest in infants in juvenile rhesus monkeys: Relationship to prenatal androgen. *Hormones and Behavior, 43*, 573–583.

Hinde, R. A. (1982). The uses and limitations of studies of nonhuman primates for the understanding of human social development. In L. W. Hoffman, R. Gandelman, & H. R. Schiffman (Eds.), *Parenting: Its causes and consequences* (pp. 5–17). Hillsdale, NJ: Erlbaum.

Hinde, R. A. (1984). Biological bases of the mother-child relationship. In J. D. Call, E. Galenson, & R. L. Tyson (Eds.), *Frontiers of infant psychiatry* (pp. 284–294). New York: Basic Books.

Hinde, R. A., & Spencer-Booth, Y. (1967). The behaviour of socially living rhesus monkeys in their first two and a half years. *Animal Behaviour, 15*, 169–196.

Insel, T. R., & Young, L. J. (2000). Neuropeptides and the evolution of social behavior. *Current Opinion in Neurobiology, 10*, 784–789.

Kagan, J. (1996). Three pleasing ideas. *American Psychologist, 51*, 901–908.

Kirkpatrick, L. A. (1998). Evolution, pair-bonding, and reproductive strategies: A reconceptualization of adult attachment. In J. A. Simpson & W. S. Rholes (Eds.), *Attachment theory and close relationships* (pp. 353–393). New York: Guilford Press.

Kisilevsky, B. S., Hains, S. M. J., Lee, K., Xie, X., Huang, H. F., Ye, H. H., et al. (2003). Effects of experience on fetal voice recognition. *Psychological Science, 14*, 220–224.

Leveroni, C. L., & Berenbaum, S. A. (1998). Early androgen effects on interest in infants: Evidence from children with congenital adrenal hyperplasia. *Developmental Neuropsychology, 14*, 321–340.

Lorenz, K. (1950). The comparative method in studying innate behaviour patterns. *Symposia of the Society for Experimental Biology, 4*, 221–268.

Lovejoy, J., & Wallen, K. (1988). Sexually dimorphic behavior in group-housed rhesus monkeys (*Macaca mulatta*) at 1 year of age. *Psychobiology, 16*, 348–356.

Maestripieri, D. (1995). Assessment of danger to themselves and their infants by rhesus macaque (*Macaca mulatta*) mothers. *Journal of Comparative Psychology, 109*, 416–420.

Maestripieri, D. (2003a). The past, present, and future of primate psychology. In D. Maestripieri (Ed.), *Primate Psychology* (pp. 1–16). Cambridge, MA: Harvard University Press.

Maestripieri, D. (2003b). Attachment. In D. Maestripieri (Ed.), *Primate Psychology* (pp. 108–143). Cambridge, MA: Harvard University Press.

Maestripieri, D. (2005a). On the importance of comparative research for the understanding of human behavior and development: A reply to Gottlieb & Lickliter (2004). *Social Development, 14*, 181–186.

Maestripieri, D. (2005b). Effects of early experience on female behavioural and reproductive development in rhesus macaques. *Proceedings of the Royal Society of London B, 272*, 1243–1248.

Maestripieri, D., & Call, J. (1996). Mother–infant communication in primates. *Advances in the Study of Behavior, 25*, 613–642.

Maestripieri, D., & Carroll, K. A. (1998). Risk factors for infant abuse and neglect in group-living rhesus monkeys. *Psychological Science, 9*, 143–145.

Maestripieri, D., & Pelka, S. (2002). Sex differences in interest in infants across the lifespan: A biological adaptation for parenting? *Human Nature, 13*, 327–344.

Maestripieri, D., Roney, J. R., DeBias, N., Durante, K. M., & Spaepen, G. M. (2004). Father absence, menarche, and interest in infants among adolescent girls. *Developmental Science, 7*, 560–566.

Marks, J. (2003). *What it means to be 98% chimpanzees: Apes, people, and their genes*. Berkeley, CA: University of California Press.

Martins, E. P. (1996). *Phylogenies and the comparative method in animal behavior*. New York: Oxford University Press.

Mason, W. A., & Capitanio, J. P. (1988). Formation and expression of filial attachment in rhesus monkeys raised with living and inanimate mother substitutes. *Developmental Psychobiology, 21*, 401–430.

Mason, W. A., & Mendoza, S. P. (1998). Generic aspects of primate attachments: Parents, offspring, and mates. *Psychoneuroendocrinology, 23*, 765–778.

Oppenheim, R. W. (1981). Ontogenetic adaptations and retrogressive processes in the development of the nervous system and behavior. In K. J. Connolly & H. F. R. Prechtl (Eds.), *Maturation and development: Biological and psychological perspectives* (pp. 73–108). Philadelphia: International Medical.

Preuschoft, S., & van Hooff, J. A. R. A. M. (1995). Homologizing primate facial displays: A critical review of methods. *Folia Primatologica, 65*, 121–137.

Pryce, C. R. (1996). Socialization, hormones, and the regulation of maternal behavior in nonhuman primates. *Advances in the Study of Behavior, 25*, 423–473.

Quinlan, R. J. (2003). Father absence, parental care, and female reproductive development. *Evolution and Human Behavior, 24*, 376–390.

Roney, J. R., & Maestripieri, D. (2002). The importance of comparative and phylogenetic analyses in the study of adaptation. *Behavioral and Brain Sciences, 25*, 525.

Roney, J. R., & Maestripieri, D. (2003). Social development and affiliation. In D. Maestripieri (Ed.), *Primate Psychology* (pp. 171–204). Cambridge, MA: Harvard University Press.

Schino, G., & Troisi, A. (2005). Neonatal abandonment in Japanese macaques. *American Journal of Physical Anthropology, 126*, 447–452.

Sluys, R. (1996). The notion of homology in current comparative biology. *Journal of Zoological Systematics and Evolutionary Research, 34*, 145–152.

Snowdon, C. T., & Suomi, S. J. (1982). Paternal behavior in primates. In H. E. Fitzgerald, J. A. Mullins, & P. Gage (Eds.), *Child nurturance: Psychobiological perspectives* (pp. 63–108). New York: Plenum Press.

Stearns, S. C. (1992). *The evolution of life histories*. Oxford: Oxford University Press.

Stratton, G. E., Suter, R. B., & Miller, P. R. (2003). Evolution of water surface locomotion by spiders: A comparative approach. *Biological Journal of the Linnean Society, 81*, 63–78.

Suomi, S. J. (1978). Maternal behavior by socially incompetent monkeys: Neglect and abuse of offspring. *Journal of Pediatric Psychology, 3*, 28–34.

Suomi, S. J. (1999). Attachment in rhesus monkeys. In J. Cassidy & P. R. Shaver (Eds.), *Handbook of attachment* (pp. 181–197). New York: Guilford Press.

Symons, D. (1992). The use and misuse of Darwinism in the study of human behavior. In J. H. Barkow, L. Cosmides, & J. Tooby (Eds.), *The adapted mind* (pp. 137–159). Oxford: Oxford University Press.

Thierry, B., Iwaniuk, A. N., & Pellis, S. M. (2000). The influence of phylogeny on the social behaviour of macaques (Primates: Cercopithecidae, genus *Macaca*). *Ethology, 106*, 713–728.

Tinbergen, N. (1963). On the aims and methods of ethology. *Zeitschrift fur Tierpsychologie, 20*, 410–433.

Tooby, J., & Cosmides, L. (1989). Adaptation versus phylogeny: The role of animal psychology in the study of human behavior. *International Journal of Comparative Psychology, 2*, 175–188.

Tooby, J., & Cosmides, L. (1992). The psychological foundations of culture. In J. H. Barkow, L. Cosmides, & J. Tooby (Eds.), *The adapted mind* (pp. 19–136). Oxford: Oxford University Press.

van Hooff, J. A. R. A. M. (1972). A comparative approach to the phylogeny of laughter and smile. In R. A. Hinde (Ed.), *Nonverbal communication* (pp. 209–241). Cambridge: Cambridge University Press.

Wagner, G. P. (1989). The biological homology concept. *Annual Review of Ecology and Systematics, 20*, 51–69.

Wagner, G. P., & Altenberg, L. (1996). Complex adaptations and the evolution of evolvability. *Evolution, 50*, 967–976.

Wasser, S. K., & Barash, D. P. (1983). Reproductive suppression among female mammals: Implications for biomedicine and sexual selection theory. *Quarterly Review of Biology, 58*, 513–538.

Wenzel, J. W. (1992). Behavioral homology and phylogeny. *Annual Review of Ecology and Systematics, 23*, 361–381.

Whiting, B. B. (1980). Culture and social behavior. A model for the development of social behavior. *Ethos, 8*, 95–116.

Whiting, B. B., & Whiting, J. W. M. (1975). *Children of six cultures: A psycho-cultural analysis*. Cambridge, MA: Harvard University Press.