The Evolution and Function of Adult Attachment: A Comparative and Phylogenetic Analysis

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Although the evolutionary functions of attachment in infant–caregiver relationships are undisputed, it is unclear what functions—if any—attachment serves in adult romantic relationships. The objective of this research was to examine the evolution and function of adult attachment (i.e., pair bonding) by applying comparative and phylogenetic methods to archival data collected on 2 diverse samples of mammalian species. The authors found that species exhibiting adult attachment were more likely than others to be characterized by paternal care, developmental immaturity or neoteny, small social groups, and small body sizes. The authors also used phylogenetic techniques to reconstruct the evolution of adult attachment and test alternative evolutionary models of the comparative correlates of pair bonding. Phylogenetic analyses suggested that the relationship between paternal care and adult attachment may be a functional one (i.e., due to convergent evolution) but that the relationship between neoteny and adult attachment may be due to homology (i.e., shared ancestry). Discussion focuses on the potential of comparative and phylogenetic methods for advancing the science of social and personality psychology.

Keywords: adult attachment, close relationships, evolution, comparative methods, phylogeny

Observers of human nature have long noted the similarities between the behavioral patterns exhibited in infant–caregiver relationships and romantic relationships (Bowlby, 1969; Eibl-Eibesfeldt, 1971; Freud, 1964). Shaver, Hazan, and Bradshaw (1988), for example, noted that in both infant–caregiver and adult romantic relationships people (a) feel safer when the other person is nearby and responsive; (b) engage in a unique degree of intimate, bodily contact; (c) feel insecure when the other person is inaccessible and yearn for that individual; (d) exhibit a mutual fascination and preoccupation with one another; and (e) may communicate with one another using “motherese” or “baby talk.” According to adult attachment theory, these similarities exist because the same motivational system that underlies infants’ attachment to their caregivers also underlies the emotional bond that develops between romantic partners (Bowlby, 1969; Fraley & Shaver, 2000; Shaver et al., 1988). One of the primary objectives of contemporary research on adult attachment has been to document the ways in which this motivational system, which Bowlby (1969) called the attachment behavioral system, manifests itself and the role that it plays in the development, maintenance, and dissolution of romantic relationships.

Although an increasing amount of data indicates that the attachment behavioral system contributes to the dynamics observed in adult romantic relationships (see Hazan & Zeifman, 1999), it is unclear why the attachment system plays a role in adult relationships. From an evolutionary perspective, one of the critical adaptive problems solved by intimate relationships is reproduction (see Kirkpatrick, 1998; Simpson, 1999). However, as reviews of the literature on animal behavior reveal, many animals reproduce without developing emotional attachments to their mates (Barash & Lipton, 2001; Kleiman, 1977). In light of such observations, one of the greatest challenges for adult attachment theorists is to explain why the attachment system is active in human relationships, what functions it serves, and why it was co-opted by natural selection over the course of evolution (Fraley & Shaver, 2000).

The objective of the present article is to explore the evolution and function of attachment in adult romantic relationships. Although we are primarily interested in the evolution of attachments or pair bonds in human relationships, we believe that understanding attachment in humans requires a broader understanding of the evolutionary processes that may have shaped pair bonding across a variety of species. Accordingly, in this article we adopt a comparative psychological approach to examine hypotheses about the function of adult attachment. Using archival data, we investigate between-species covariation between pair bonding and a variety of morphological, social, and developmental characteristics in a broad sample of mammals (Study 1) and primates (Study 2). In addition to documenting the associations between these variables and pair bonding, we also use phylogenetic methods to reconstruct the evolution of pair bonding across time and to test alternative evolutionary models of the correlates of adult attachment.
Although our primary objective is to elucidate some of the evolutionary mechanisms that may have promoted pair bonding in humans and other species, we also hope that our article will serve as an introduction to the ways in which comparative and phylogenetic methods can be used to investigate broader issues in contemporary social and personality psychology (see Gosling, 2001, and Simpson & Gangestad, 2001, for further discussion). Over 40 years ago, Tinbergen (1963), one of the pioneers of the ethological approach to behavior, argued that it is necessary to answer four questions when trying to explain behavioral or psychological phenomena: those concerning causation (i.e., what contextual and physiological mechanisms control behavior?), ontogeny (i.e., how does the behavior develop?), function (i.e., how does the behavior contribute to fitness and what kinds of adaptive problems does it solve?), and evolution or phylogeny (i.e., how did the behavior evolve over evolutionary history?). Although contemporary social–personality psychologists have made progress toward answering proximate and developmental questions for a variety of social phenomena, less attention has been devoted to questions concerning function and even less to questions concerning phylogeny. It is our hope that this article will help raise an awareness of these issues and stimulate a broader ethological agenda in social and personality psychology.

The Function of Attachment Behavior

One of Bowlby’s objectives in the first volume of his Attachment and Loss series was to document and explain the intense distress exhibited by children who had been separated from their caregivers (Bowlby, 1969). He and his colleagues noticed that children who had been separated from their parents frequently expressed intense distress, often vigorously trying to regain their missing caregivers by crying, clinging, and searching (Bowlby, Robertson, & Rosenbluth, 1952; Heinicke & Westheimer, 1966). Bowlby (1969) argued that these attachment behaviors were regulated by an innate motivational system, the attachment behavioral system. According to Bowlby, the internal dynamics of the attachment system are similar to those of a homeostatic control system, in which a “set goal” is maintained by the constant monitoring of endogenous or exogenous signals and continuous behavioral adjustment. In the case of the attachment system, the set goal is physical or psychological proximity. When the child perceives the attachment figure to be nearby and responsive, he or she feels secure, and behaviorally, is likely to be playful and sociable. However, when he or she perceives a threat to the relationship or his or her well-being, the child feels insecure and seeks the attention and comfort of the primary caregiver. According to Bowlby (1969), these emotional and behavioral dynamics serve an important evolutionary function. Specifically, they promote proximity between child and caregiver, which helps to ensure the child’s safety and protection and, ultimately, his or her inclusive fitness.

Bowlby (1969, 1980) was primarily focused on understanding the nature of the infant–caregiver relationship and its implications for socioemotional development. Nonetheless, he also believed that the attachment system was relevant for understanding other kinds of intimate relationships. Hazan and Shaver (1987) observed, for example, that romantic love involves many of the same behavioral patterns that characterize the bond between infants and their caregivers. As discussed previously, adults, like infants, feel safe and secure when the other person is present, distressed or restless in the absence of the other and, at least in the early stages of the bonding process, deeply fascinated by the other individual (see Feeney, 1999).

Although the attachment behavioral system appears to influence the dynamics of adult romantic relationships (see Hazan & Zeifman, 1999), it is unclear why this should be the case. Pair bonding is a relatively rare phenomenon in mammalian species (Kleiman, 1977). For example, the reproductive and social behavior of our closest evolutionary ancestor, the common chimpanzee (Pan troglodytes), differs in a number of ways from our own. Chimpanzees frequently and freely mate with more than one male, there are clear signs of ovulation (e.g., sexual swellings), and males play little direct role in the rearing of their offspring. In light of such observations, it is necessary to explain why the attachment system—a system originally adapted to the ecology of infancy—has been coopted to play a role in mating for some species but not others. In this article we consider two nonmutually exclusive hypotheses that have been advanced in the social psychological literature on adult attachment. The first, the paternal care hypothesis, posits that attachment or pair bonding may enhance inclusive fitness by providing an additional means of protection and care for offspring (Belsky, 1999; Fraley & Shaver, 2000; Gubernick, 1994; Hazan & Zeifman, 1999). Consistent with this hypothesis, there is within-species evidence that offspring are more likely to survive to a reproductive age if they are reared in families in which the mother and father are pair bonded. As Wilson and Daly (1994) noted, unpaired women may at times abdicate their care of their offspring because of an inability to raise the child alone (see also Hrdy, 1992). There is also evidence that the presence of an invested primate male can deter potential threats by other members of the group (van Schaik & Dunbar, 1990). In short, if infants are at greater risk in the absence of the care and protection of both parents, there may have been selection pressures that facilitated pair bonding on the part of mates and a greater degree of parental investment on the father’s part.

A second hypothesis is that attachment among human adults may be a by-product of humans’ prolonged neotenous state (Bjorklund, 1997; Fraley & Shaver, 2000). According to the developmental immaturity or neoteny hypothesis, humans are unique in that juvenile characteristics are retained for an extended period of time. Compared with other primates, the human brain takes longer to develop, we remain relatively hairless, our teeth erupt at a late age, and our sexual maturation is delayed—taking twice as long as __________

1 Recent theory and evidence suggests that it is difficult to separate the role of attachment and caregiving in adult romantic relationships, despite the fact that the relative roles of the two behavioral systems are unequally distributed in infant–caregiver relationships (see Kirkpatrick, 1998). Although we discuss attachment per se in this article, in our thinking we draw no sharp distinction between attachment and caregiving in adult relationships. We suspect that these behaviors are actually part of the same behavioral system but that the caregiving component is less well developed in early infancy (see George & Solomon, 1999, for further discussion of the caregiving system in attachment theory and research).
that of chimpanzees, our closest biological relatives (Montagu, 1989; Poirier & Smith, 1974). According to some writers, change in the timing of developmental processes (i.e., heterochrony) is one of the major mechanisms of evolutionary change (deBeer, 1958) and may help account for some of the unique features of human behavior. Bjorklund (1997), for example, has observed that adult play is common to many mammalian species but tends to be limited to courtship contexts in nonhumans. Only in humans, he argues, is adult play manifested in such a diverse range of contexts. Perhaps attachment, like other infantile traits, is prolonged into early adolescence and adulthood because of the relative retardation of maturational processes in humans. If so, then the attachment system will not become dormant as children become sexually mature, as appears to occur in many other mammalian species. Instead, the system may continue to be sensitive to certain cues and signals and readily activated in contexts that resemble the infant–parent relationship (e.g., caring, safe, or physically intimate interactions) or elicit similar feelings or behaviors.

A Comparative Approach to Studying Adult Attachment

Although these hypotheses may seem compelling from an evolutionary perspective, they have not been tested systematically in a comparative sample of mammalian species. In fact, most of the evidence cited to support these conjectures is based on a highly selective sampling of information about a single species (e.g., humans) or comparisons that are limited to only a handful of species (see Garland & Adolph, 1994, for a review of the limitations of this approach). We believe that a more systematic way to examine these hypotheses is by quantifying the variables in question (i.e., pair bonding, parental care, developmental immaturity) and studying their covariation across multiple species (i.e., species that, a priori, may or may not exhibit patterns consistent with these hypotheses).

In recent years an increasing number of psychologists have begun to explore the benefits of using comparative methods (i.e., methods used to quantify the similarities and differences between species) to investigate issues in the study of social, developmental, and personality psychology (Gosling & John, 1999). Gosling (2001), for example, surveyed the animal behavior literature on individual differences and temperament to determine how common the Big Five personality traits are across species. His analyses suggested that variation in certain characteristics, such as sociability or extraversion, is quite common across a variety of taxa, whereas variation in other characteristics, such as openness to experience, is not. We believe that this general approach holds great promise for addressing evolutionary questions in the study of adult attachment. By comparing behavioral variation across a variety of species, it should be possible to identify some of the factors that differentiate species that exhibit pair bonding from those that do not, and, in the process, take a novel step toward evaluating hypotheses concerning the function and evolution of adult attachment.

In the studies presented here, we used archival methods to quantify several morphological, social, and developmental variables for a broad range of mammalian species. Our objective was to determine how these various factors are related to one another across species, and, most importantly, to determine which characteristics are associated with pair bonding. We used this information to evaluate hypotheses about the evolution and function of pair bonding. For instance, if pair bonding facilitates the care and protection of offspring, we should observe a positive association between pair bonding and paternal involvement in child rearing across species. In addition, if neoteny is one of the factors that leads to attachment in adult relationships, we should observe a positive association between pair bonding and developmental immaturity as quantified, for example, by the proportion of the life span spent in the family of origin or gestation time.

**Phylogenetic Considerations in Evolutionary Social Psychology**

By studying the between-species correlates of pair bonding, it should be possible to bring novel empirical data to bear on questions about the functional significance of adult attachment. Nonetheless, establishing the correlates of pair bonding is only a first step in evaluating adaptive hypotheses. Over the past two decades, evolutionary biologists have begun to recognize that two traits can covary with one another for functional or nonfunctional reasons (Brooks & McLennan, 1991; Felsenstein, 1985; Harvey & Pagel, 1991; Ridley, 1983). Observing a correlation between pair bonding and paternal care, for example, does not necessarily mean that these two traits have evolved together across repeated, independent occasions.

In order to evaluate the adaptive nature of the relationship between traits, it is necessary to account for the phylogenetic relationships among species (Garland & Adolph, 1994). The term *phylogenetic relationships* refers to the evolutionary relationships among species—the patterns of descent and ancestry across expansive time scales. These relationships are often summarized heuristically with phylogenetic trees. The phylogenetic tree illustrated in Figure 1 depicts the evolutionary relationships among eight hypothetical species. Evolutionary time is represented in this diagram by the vertical axis, and the phylogenetic relationships among species are characterized by the structure or patterning of the branches. According to this tree, Species C and D are closely related (i.e., they descended from a common ancestor relatively recently) as are Species G and H. Relatively speaking, however, the first two species are not closely related to the latter two. The ancestor shared by Species C and G, for example, is much more distant than that shared by Species C and D.

**Figure 1.** A phylogenetic tree characterizing the evolutionary relationships among 8 hypothetical species.
It is useful to consider phylogenetic relationships in comparative research because species that are phylogenetically related to one another tend to be similar with respect to a variety of traits (Blomberg, Garland, & Ives, 2003; Felsenstein, 1985). As a consequence, species may be similar to one another in their morphology and behavior because they evolved from a common ancestor, not necessarily because similar selection pressures led to the independent evolution of those traits. The upper row of Figure 2 helps to illustrate this distinction. Notice in the upper-left panel that Species A–D all possess a specific trait (denoted by the solid squares), whereas Species E–H do not (denoted by the empty squares). Species A–D are similar to one another because they evolved from an ancestor that also possessed the trait. The maintenance of this trait across time is represented by the solid branches in the segments of the tree that are ancestral to species A–D. In this situation, the similarities among species are due to **homology**—shared ancestry. The upper-right panel of Figure 2 depicts a different situation. In this case, Species A, C, E, and G all possess the trait, but not because they share a common ancestor that possessed the trait. In this scenario, the similarity among these species is due to **analogy**—the independent evolution of the trait across different branches of the phylogenetic tree. Evolutionary biologists often refer to this scenario as an example of **convergent evolution**.

We can easily extend this univariate example to illustrate the necessity of considering phylogenetic relationships when making inferences about the functional associations between traits. In the lower-left corner of Figure 2 we have depicted the values for two traits: X and Y. If a researcher were to examine the correlation between the two traits represented at the tips of the tree (i.e., among living species), he or she would observe that traits X and Y are perfectly correlated (i.e., the phi correlation for the 2 × 2 table is 1.00). Specifically, the presence of trait X (coded as the dark square in Figure 2) co-occurs with the presence of trait Y, and the absence of trait X (coded as the light square) co-occurs with the absence of trait Y. Moreover, there are no species in which X is present but Y is not (or vice versa). The correlation in this example is largely due to homology—both traits are shared (or not shared) by the ancestral species from which these living species evolved. Although the two traits may have originally emerged together for functional reasons, there is no evidence that the two traits have coevolved across repeated, independent occasions.

In contrast, if the two traits had evolved together on many separate occasions, there would be multiple instances in which changes in one trait are coupled with those in the other. The lower-right panel of Figure 2 illustrates this scenario with the same phylogenetic tree but in a situation in which the traits evolved independently on more than one occasion. As before, the two traits are perfectly correlated. However, both traits have emerged independently in several distinct lineages and, more importantly, the changes in the two traits tend to be coupled: When trait X changes, trait Y also changes. In short, the correlation between the traits across species reflects the repeated co-evolution of those traits, strongly suggesting a functional relationship.

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**Figure 2.** Phylogenies illustrating homologous (left-hand panel) and convergent (right-hand panel) evolution.
A variety of comparative methods have been developed to distinguish among these alternative models of trait covariation—what we refer to as models of homologous and correlated evolution, respectively (see Garland, Harvey, & Ives, 1992, and Harvey & Pagel, 1991, for reviews). In the present article, we apply these comparative methods to data from a broad sample of mammals (Study 1) and primates (Study 2) for which the phylogenetic relationships have been established previously. By studying the covariation of pair bonding with other variables (e.g., developmental immaturity, paternal care) while accounting for the phylogenetic relationships among species, it should be possible to determine whether the correlates of pair bonding are functional (i.e., due to correlated or convergent evolution) or better accounted for by homology (i.e., shared ancestry).

Study 1: The Evolution of Pair Bonding in Mammalia

In this study we examined a sample of mammals for which the phylogenetic relationships had been well established in the biological literature. Specifically, we studied the 44 families included in a phylogenetic analysis previously published by Murphy et al. (2001). In our investigation, we first sought to establish the pattern of correlations among pair bonding and other variables and then used the phylogenetic information reported by Murphy et al. to determine whether the correlates of pair bonding were more consistent with a model of homologous or correlated evolution.

Method

Sources

For each of the 44 mammalian families, we collected information from archival sources on social, developmental, and morphological variables (see below). The data were drawn mainly from the published literature and were supplemented by information obtained from the Internet. The Systematic Dictionary of Mammals of the World (Burton, 1962), Walker’s Mammals of the World (Nowak, 1999), and The New Encyclopedia of Mammals (Macdonald, 2001) were used to obtain approximately 30% of the data. It was not possible to obtain information for all variables for all families, so the bivariate analyses that follow are based on pairwise sample sizes that range from 28 to 32.

Variables

For each family we recorded information falling into five broad classes: pair bonding, paternal involvement, developmental immaturity, social characteristics, and body size.

Pair bonding. We classified a group as exhibiting pair bonding if the group was considered socially monogamous. It is important to note that it was not necessary that the group be considered sexually monogamous. As many biologists have demonstrated, very few species are sexually monogamous. The group is conspecific, the group mates only with one individual over an extended period of time (Barash & Lipton, 2001; Dewsbury, 1987). Animals are typically classified as being socially monogamous if mates spend a large amount of time together and if there are signs of mate guarding, extensive physical contact, and separation distress (e.g., see Carter, DeVries, & Getz, 1995). These kinds of features are central to the definition of adult attachment in the social psychological literature on close relationships (see Fraley & Davis, 1997; Hazan & Zeifman, 1999).

Paternal involvement. Each group was classified as exhibiting paternal involvement or not. If the father was considered to be involved in any aspect of rearing the offspring after birth, the group was considered to have paternal involvement. "Involved" behaviors included (but were not limited to) providing food for offspring, building a nest or den, protecting the young, and providing food for the mate while she tends to the young.

Developmental immaturity or neoteny. We quantified developmental immaturity or neoteny in several distinct ways: (a) the average life span of the group, (b) the gestation time for the group (days), (c) the age (months) at which offspring leave their families of origin or are able to care for themselves, and (d) the average age at which animals reach puberty. We examined the latter three variables both in their original metric and relative to the life span of the species; the results we report are the same across different scaling methods. Because these four variables were positively correlated with one another (average r = .52), we also examined a composite of these variables in the analyses that follow (α = .79). The composite was created by averaging the standardized scores across the four variables. Although we report analyses based on each of these four variables and their composite, it is probably the case that the time to leave the family of origin represents the most direct indicator of neoteny for the present purposes.

Social characteristics. The size of the social group was coded in an ordinal manner as solitary (living alone), a family unit (parents and offspring), a small colony (fewer than 30 individuals), or a large colony (30 or more individuals). We also coded the average number of offspring for the species as an indicator of sibling group size.

Body size. We recorded information about the average length and weight of each species.

Phylogenetic Information

Murphy et al.’s (2001) mammalian phylogeny was derived from a data set containing 16,397 molecular base pairs, comprising 18 nuclear and 3 mitochondrial gene sequences. Two marsupial outgroups (opossum and diprotodontian) were used to root the phylogenetic tree (i.e., to provide an origin for inferring the patterns of evolution among taxa). All of the remaining 42 mammals were placental, representing all of the major lineages. Murphy et al. used a general-time-reversible + gamma + invariants (GTR + I + I) model of sequence evolution (see Felsenstein, 2003, and Page & Holmes, 1998, for discussions of this and alternative models of molecular evolution). Both maximum likelihood and Bayesian methods of estimation yielded trees with identical structures. Furthermore, with the exception of two nodes, the posterior probabilities obtained through the Bayesian analysis were all above .95, suggesting that the final tree was resolved with few ambiguities. In other words, the resulting phylogenetic tree, illustrated in Figure 3, is highly compatible with the molecular evidence and provides one of the most rigorous reconstructions of the phylogenetic relationships among mammalian lineages available to date.

Data Analyses

We do not report significance tests in the present article for four reasons. First, the sampling conditions used in this research violate the assumption that cases are selected at random from a population. The sample that we are using here (and in Study 2) is based on taxa chosen by other researchers who were interested in phylogenetic issues. Second, the population itself is not static or finite. Thus, some of the population values that are estimated in this research (e.g., the average body weights of species) only exist as abstractions at one arbitrary point in time. Third, as we explain in more depth in the sections that follow, the observations are not statistically independent because of the phylogenetic relationships among taxa. Finally, because we studied all known taxa for which information was available and the phylogenetic relationships were known, in many respects our sample constitutes the population of interest, at least at this point in time (see

The data used in this study, as well as the data used in the study that follows, are available from the first author upon request.
Meehl, 1990; Schmidt & Hunter, 1997; Simonton, 1999, for further discussion of these issues in a psychological context).

Although we view all of the correlations reported as bearing on the issues at hand, we focus mostly on correlations that exceed an absolute magnitude of .10. We have chosen a relatively low threshold value for two reasons. First, point-biserial and phi correlations (i.e., correlations based on one or two discrete variables, respectively) tend to be smaller in magnitude than correlations based on multivariate normal data unless the base rates of the variables in question are 50–50. Because we are dealing with a relatively low base-rate phenomenon (i.e., pair bonding), the psychometric ceiling for these correlations is much lower than 1.00. Second, there are probably many factors, some systematic and others more unpredictable, that contribute to variation in pair bonding. To the extent to which pair bonding is multidetermined, the correlation between pair bonding and any single variable will not be large (see Ahadi & Diener, 1989).

Results
What Are the Correlates of Pair Bonding?

Table 1 reports the correlations between pair bonding and the other measured variables. Animals that were considered monogamous or pair bonded were more likely to have fathers who play a role in child rearing ($r = .10$). Pair-bonded animals also tended to have longer life spans ($r = .16$) and gestation times ($r = .12$), take

<table>
<thead>
<tr>
<th>Variable</th>
<th>Study 1</th>
<th>Study 2</th>
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</thead>
<tbody>
<tr>
<td>Father involvement</td>
<td>.10</td>
<td>.22</td>
</tr>
<tr>
<td>Life span</td>
<td>.16</td>
<td>.16</td>
</tr>
<tr>
<td>Gestation</td>
<td>.12</td>
<td>.21</td>
</tr>
<tr>
<td>Time to leave family of origin</td>
<td>.19</td>
<td>.51</td>
</tr>
<tr>
<td>Puberty</td>
<td>.26</td>
<td>.11</td>
</tr>
<tr>
<td>Composite</td>
<td>.21</td>
<td>.20</td>
</tr>
<tr>
<td>Number of siblings</td>
<td>−.20</td>
<td>.11</td>
</tr>
<tr>
<td>Group size</td>
<td>−.23</td>
<td>−.11</td>
</tr>
<tr>
<td>Body length</td>
<td>−.10</td>
<td>−.11</td>
</tr>
<tr>
<td>Body weight</td>
<td>−.10</td>
<td>−.11</td>
</tr>
</tbody>
</table>

Note. $r$ refers to the correlation between pair-bonding and the variable in question based on phylogenetically independent contrasts and correlation through the origin.
in small social groups, and, on average, they are smaller in size.

developmentally immature or neotenous, they are more likely to live playing an active role in child rearing, they are more likely to be ized by the following profile: They are more likely to have fathers

Homologous or a Correlated Model of Evolution?

Are the Correlates of Pair Bonding Best Explained by a Homologous or a Correlated Model of Evolution?

As discussed previously, it is possible for two variables to correlate with one another even if the two variables did not evolve together across repeated, independent occasions. To examine this possibility, it is necessary to take into account the phylogenetic relationships among species. A variety of methods have been developed for this purpose (see Harvey & Pagel, 1991, for a review), the basic logic of which is best illustrated with Felsenstein’s (1985) independent contrasts method. Felsenstein’s method takes advantage of the fact that any two species at adjacent tips of a phylogenetic tree uniquely share a common ancestor (e.g., species A and B in Figure 4). As such, the difference between those two species with respect to a trait represents change that has taken place since those species diverged from their most recent common ancestor. Thus, the difference between adjacent species is independent of phylogeny.

As an illustration, consider the phylogeny depicted in Figure 4. The left-hand panel illustrates the evolution of a binary trait, Trait X, across the tree; the right-hand panel illustrates the evolution of a continuous trait, Trait Y, across the same tree. The trait values for both living and ancestral species are given in Table 2. Because Species A and B share a common ancestor, the difference between them with respect to any measured trait is independent of phylogeny. For the discrete trait, X, the difference between these two species is 0 because both species possess the trait (i.e., there has been no evolutionary change within that portion of the tree). For the continuously valued trait, Y, the difference is 1.41 because Species A has a higher trait value (4.74) than Species B (3.33).

To study the association between two traits in a way that is not dependent on phylogeny, it is necessary to compute these differences, or contrasts, for all adjacent pairs of species—both living and ancestral. For k species, there are k – 1 contrasts that can be constructed for a trait. Table 3 illustrates the phylogenetically independent contrasts for the data presented in Table 2 and Figure 4. These contrasts capture evolutionary change in each trait, but in a way that is independent of evolutionary relationships. As such, they are referred to as phylogenetically independent contrasts (PICs). By computing the correlation between these two sets of contrasts through the origin, it is possible to estimate the correlation between the traits in a way that takes phylogenetic relationships into account (see Garland et al., 1992).

This general method of computing PICs is valuable because it allows researchers to test alternative hypotheses about the correlates of pair bonding. If, for example, the correlation between pair bonding and neoteny is due to homologous evolutionary processes,
Table 2  
*Observed and Estimated Trait Values for Species in Figure 4*  

<table>
<thead>
<tr>
<th>Species</th>
<th>Traits</th>
<th>X</th>
<th>Y</th>
</tr>
</thead>
<tbody>
<tr>
<td>Living</td>
<td>A</td>
<td>1</td>
<td>4.74</td>
</tr>
<tr>
<td></td>
<td>B</td>
<td>1</td>
<td>3.33</td>
</tr>
<tr>
<td></td>
<td>C</td>
<td>1</td>
<td>3.37</td>
</tr>
<tr>
<td></td>
<td>D</td>
<td>0</td>
<td>2.89</td>
</tr>
<tr>
<td></td>
<td>E</td>
<td>0</td>
<td>2.30</td>
</tr>
<tr>
<td>Ancestral</td>
<td>F</td>
<td>1</td>
<td>4.04</td>
</tr>
<tr>
<td></td>
<td>G</td>
<td>1</td>
<td>3.74</td>
</tr>
<tr>
<td></td>
<td>H</td>
<td>0</td>
<td>3.43</td>
</tr>
<tr>
<td></td>
<td>I</td>
<td>0</td>
<td>3.01</td>
</tr>
</tbody>
</table>

*Note.* The correlation between traits X and Y among living species is .74.

The correlation between the phylogenetically independent contrasts constructed for those traits should be close to zero. In other words, if the relationship is due to homology, there should no longer be a correlation between these two variables once phylogenetic information is taken into account. However, if the correlation between pair bonding and neonity is due to correlated evolution, the correlation between these two variables should be positive. This indicates that a relationship exists between the traits above and beyond what can be accounted for by homology alone. In the example presented in Tables 2 and 3, the correlation through the information is taken into account. However, if the correlation between these two variables once phylogenetic information is taken into account. Therefore, there were very few cases in which pair bonding appeared to characterize ancestral species (i.e., nodes below the tips of the tree). Second, pair bonding appears to be a relatively recent “invention” in the evolutionary landscape of mammals. Specifically, it was not possible to construct evolutionary pathways that placed pair bonding early in the tree without sacrificing parsimony. For example, if we assigned the root of the tree to represent a pair-bonded ancestral species, the number of evolutionary events necessary to reproduce the pattern of pair bonding that exists among living species would have far exceeded those necessary for the illustrated reconstruction. This suggests that, to the extent to which pair bonding may help solve certain adaptive problems, it is a solution that is relatively recent within the broader scope of mammalian evolution. Finally, there are cases in which pair bonding seems to have evolved independently (i.e., not descending from a common ancestor) and other cases in which pair bonding has homologous qualities (i.e., it is shared among closely related taxa).

The correlations based on the PICs are presented in Table 1. The correlation between paternal care and pair bonding remained positive \((r = .61)\), suggesting that pair bonding and paternal care may have coevolved across evolutionary history.\(^5\) The phylogenetic correlations between pair bonding and the neonity variables did not conform to a coherent pattern. In fact, the correlation between pair bonding and the neonity composite was only .05, suggesting that the positive zero-

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\(^4\) Both APE and R can be downloaded for free from the following websites: [http://www.maths.lth.se/help/R/](http://www.maths.lth.se/help/R/) and [http://cran.r-project.org/](http://cran.r-project.org/)

\(^5\) We used Ridley’s (1983) method for computing the phylogenetically independent correlation between pair bonding and paternal care because we treated both of these variables as binary. The Ridley method involves computing the correlation between two binary variables in segments of the tree in which a transition in either variable has taken place. As such, the cases are phylogenetically independent because they are based only on instances of evolutionary change. We should note that the Ridley (1983) approach is not the only phylogenetically informed way to examine the relationship between binary traits. For example, Pagel (1994) has developed an approach that involves comparing two log-likelihoods, one based on a model of independent evolution and the other based on a model of correlated evolution. Similarly, Maddison (1990) has developed a test called the concentrated changes test that can be used to calculate the probability that changes in a binary trait are distributed randomly on the branches of a tree. Of the various approaches that exist for studying the relationship between binary traits, the Ridley (1983) method is the only one of which we are aware that allows the relationship between those traits to be expressed in the metric of correlation—a metric commonly used in social and personality psychology. A detailed overview of the Ridley (1983) approach can be found in Harvey and Pagel (1991).

Table 3  
*Phylogenetically Independent Contrasts (PICs) for the Example in Figure 4*  

<table>
<thead>
<tr>
<th>Contrasts</th>
<th>PICs for Trait X</th>
<th>PICs for Trait Y</th>
</tr>
</thead>
<tbody>
<tr>
<td>A–B</td>
<td>0</td>
<td>1.11</td>
</tr>
<tr>
<td>F–C</td>
<td>0</td>
<td>0.67</td>
</tr>
<tr>
<td>G–D</td>
<td>1</td>
<td>0.85</td>
</tr>
<tr>
<td>H–E</td>
<td>0</td>
<td>1.14</td>
</tr>
</tbody>
</table>
order correlations between the neoteny variables and pair bonding were probably artifacts of homology. It is also noteworthy that the social variables were positively related to pair bonding, despite the fact that the zero-order correlations were negative. This raises the possibility that social group size promotes pair bonding in a way that is only clear once phylogeny has been taken into account. Finally, we found that the morphological variables remained negatively correlated with pair bonding, although weakening a bit in magnitude.6

To clarify the relationship between pair bonding and paternal care, we have illustrated the reconstructed phylogeny for paternal care in Figure 6. It is noteworthy that paternal care appears to have earlier evolutionary origins than pair bonding.7 This suggests that if there is a causal relationship between pair bonding and paternal care, it is most likely the case that pair bonding emerged following the evolution of paternal care rather than the other way around. It is also worth noting that the prevalence of paternal care is much more common in mammalian species than pair bonding.

Study 2: Homing in on Our Neck of the Woods

In Study 2 we examined 66 anthropoid primates for which the phylogenetic relationships had been previously compiled by Sillén-Tullberg and Möller (1993). We again examined the associations between pair bonding and various social, developmental, and morphological variables. In addition, we used the information about the phylogenetic relationships among species to take into account phylogenetic dependence.

Method

Phylogenetic Information

Sillén-Tullberg and Möller’s (1993) phylogeny of Anthropoidea was based primarily on cladistic methods for analyzing morphological data, but molecular evidence was used to fine-tune some aspects of the tree. The full phylogeny was composed of trees from four phylogenetic studies on smaller primate samples. Tarsioida was used as the outgroup for rooting the tree; thus, primate groups that are thought to have diverged from the ancestral line prior to Tarsioida (e.g., Strepsirrhini) were not included in the phylogeny.

6 Evolutionary biologists and ecologists have observed that a number of traits (e.g., home range area, brain size, age of puberty) tend to vary as a function of body size (e.g., weight, mass, height). Accordingly, some researchers construct allometric regression equations to model these relationships and to compute residuals that are uncorrelated with body size (see Garland et al., 1992). We used the method described by Garland et al. (1992, pp. 28-29) to examine allometric residuals. Controlling for body size in this fashion did not qualify any of the analyses we report.

7 There were several reconstructions of the evolution of paternal care that provided equally parsimonious accounts of evolutionary change. The ambiguous pathways are illustrated by the hatched branches in Figure 6. The associations we report are similar to those generated under alternative resolutions of the tree.
Sources

We collected data on morphology, development, social organization, and pair bonding from the published literature and Internet-based resources (see the Method section for Study 1). The four developmental variables were positively correlated again (average $r = .65$); thus, we created a composite of these variables as an index of neoteny ($\alpha = .94$).

Results

What Are the Correlates of Pair Bonding?

Table 1 reports the correlations between pair bonding and the other variables of interest. Primates that were considered monogamous or pair bonded were more likely to have fathers who play a role in child rearing ($r = .22$). They also tended to have longer life spans ($r = .16$) and longer gestation times ($r = .21$), take longer to leave the home or nest ($r = .51$), and reach puberty at a later age ($r = .11$). The correlation between pair bonding and the neoteny composite was $r = .20$. Although pair-bonded primates tended to have a social structure characterized by smaller social groups ($r = .11$), they actually had more siblings or offspring ($r = .11$). Overall, monogamous primates tended to be smaller than other primates in length ($r = -.11$) but not necessarily in weight ($r = .03$).

The general pattern of results was highly similar to that found in the first study. The only noteworthy exception was that the monogamous primates in this study tended to have larger family groups, whereas the monogamous mammals in Study 1 tended to have smaller family groups. If we exclude consideration of family size, it appears that pair-bonded animals from both samples can be characterized by the following profile: They are more likely to have fathers playing an active role in child rearing, to be developmentally immature or neotenous, and to live in small social groups, and, on average, they are smaller in size.

Are the Correlates of Pair Bonding Best Explained by a Homologous or a Correlated Model of Evolution?

Our reconstruction of the evolution of pair bonding is illustrated in Figure 7. As with our broader sample of mammals from Study 1, pair bonding was a relatively rare phenomenon in the primate sample. Nineteen percent of the species studied showed signs of pair bonding, and the phylogenetic roots of pair bonding did not extend very far back in evolutionary time.\(^8\)

The correlations based on the PICs are presented in Table 1. The correlation between paternal care and pair bonding remained pos-

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\(^8\) It should be noted that the reconstruction of the evolution of pair bonding in the primate clade of Study 1’s tree and the primates in Study 2 differ. Although pair bonding is relatively rare among primates, the reconstruction provided in Study 1 suggests that primates are characterized by pair bonds. This discrepancy exists because there were few primates sampled in Study 1, and those that were studied appear to overrepresent pair bonding primate species.
itive \( r = .49 \), suggesting that pair bonding and paternal care may have coevolved across evolutionary history. Body length continued to be negatively associated with pair bonding once phylogeny was considered. Many of the other correlations, however, were reduced considerably. For example, the positive association between pair bonding and time to leave the family of origin changed from \( .51 \) to \( -.01 \) when phylogeny was taken into account. Some of the associations reversed sign. For example, in both samples, pair bonding and group size were originally negatively correlated, but the phylogenetically independent correlation was positive \( (.14 \) in Study 1 and \( .33 \) in Study 2). This raises the possibility that group size promotes pair bonding but that this association is masked by artifacts of homology. It is also noteworthy that the PIC correlations for the neotenous variables tended to be negative and close to zero, suggesting that there is no compelling evidence for a functional relationship between pair bonding and variables indicative of neoteny.

To clarify the relationship between pair bonding and paternal care, we have illustrated the reconstructed phylogeny for paternal care in Figure 8. As in Study 1, paternal care appears to have earlier evolutionary origins than pair bonding, suggesting that pair bonding emerged following the evolution of paternal care rather than the other way around. It is also worth noting that the prevalence of paternal care is much more common in primate species than pair bonding.

General Discussion

Although the evolutionary functions of attachment are relatively clear in infant–caregiver relationships, it has been unclear what functions—if any—attachment serves in the context of adult mating relationships. One of the primary objectives of the research reported here was to investigate, using comparative and phylogenetic methods, the functional correlates of adult romantic attachment. Our comparative analyses suggest that there are a number of social, developmental, and morphological traits that distinguish pair-bonded species from those that do not exhibit pair bonding. Consistent with the paternal care hypothesis, for example, we found that pair-bonded species were more likely to have fathers who played a direct role in child rearing than were nonpairing species. In addition, we found that species that were more developmentally immature were more likely to exhibit pair bonding, as expected under the neoteny hypothesis.

Although these associations are consistent with hypotheses that previous researchers have put forward on the role of paternal care and neoteny in the evolution of close relationships (see Fraley & Shaver, 2000), documenting these associations is only a first step in evaluating functional hypotheses. If two traits, such as pair bonding and paternal care, have evolved together (as would be expected if they are functionally related), then not only should those traits covary across species, but the evolutionary changes in one trait should be related to those of the other. It is necessary to evaluate this assumption carefully because it is possible for two traits to covary across species even if they are not functionally related. For example, two traits may covary with one another simply because species that possessed both traits descended from a common ancestor who also possessed those traits (i.e., correlation due to homology). To provide a more rigorous evaluation of the paternal care and neoteny hypotheses, we computed phyloge-
netically independent contrasts—contrasts that essentially “con-
trol” for the phylogenetic relationships among species, allowing
hypotheses about homologous versus functional associations to be
examined. Our analyses suggested that paternal care may have
coevolved with pair bonding (i.e., these two variables may be
functionally related), but the association between pair bonding and
developmental neoteny may be due to homology (i.e., it is not
necessarily functional).

Why have paternal care and adult attachment evolved together
over the course of mammalian and primate evolution? This is not
a question that can be answered definitively, but we offer some
possibilities based on research and theory. We first note that our
analyses indicate that pair bonding emerged after paternal care in
mammalian evolution. This suggests that, if there is a causal
relationship between these two variables, it is probably the case
that the presence of paternal care set the stage for pair bonding
rather than the other way around. It is possible, for example, that
some fathers began playing a greater role in child care in situations
in which paternal investment was an advantageous strategy (see
Clutton-Brock, 1991, for a detailed discussion of the conditions
that influence paternal investment). Once the father was present
and available, it may have been the case that this contact facilitated
the development of a partnership or bond between mates.

We are obviously being speculative, but we should note that
research on the proximate mechanisms underlying pair bonding
has suggested that this kind of scenario is not implausible. For
example, in their review of research on adult attachment, Hazan
and Zeifman (1999) observed that one of the strongest predictors
of attraction is simple proximity and, moreover, that when two
individuals work toward a common goal, the intimacy between
those people increases. In addition, research on the psychophysi-
ology of attachment suggests that many of the neuroendocrine
systems involved in attachment are also relevant to caregiving. For
example, using prairie voles as a biological model for the study of
pair bonding, Carter et al. (1995) have found that oxytocin is
released both during mating and during the care of offspring. This
raises the possibility that once fathers began investing more in
their offspring, the same neuroendocrine systems that facilitated
paternal care had the consequence of strengthening the bond
between mates.

Notably, our analyses also suggested that, although develop-
mental neoteny tends to covary with pair bonding across species,
there is little evidence that these two traits have coevolved together
across evolutionary history. In other words, neoteny tends to be a
developmental feature of pair-bonded species, but the phylogenetic
evidence suggests that neoteny did not play a role in the evolution
of pair bonding or vice versa. This observation poses serious
problems for the neoteny hypothesis, as proposed by Fraley and
Shaver (2000).

Another noteworthy finding was that body size was related to
pair bonding, although this observation was not hypothesized a
priori. There are several possible explanations for this finding that
could be examined in future research. It is possible, for example,
that species that are of a smaller size are more subject to predation
than larger species. If this is the case, then it is possible that
pair-bonded relationships would allow for greater solidarity, in-
creased protection, and, ultimately, better rates of survival and
reproduction. We also found positive associations between social
group size and pair bonding. It might be the case that in larger
social groups, there are more opportunities for individuals to mate.
Between- Versus Within-Species Variation

In contemporary attachment research a distinction has been drawn between the study of attachment as a normative phenomenon (i.e., a species-typical behavioral system that exists in all humans; Belsky, 1999; Fraley & Davis, 1997; Mikulincer, Birnbaum, Woddis, & Nachmias, 2000; Miller & Fishkin, 1997; Simpson, 1999) and as an individual differences phenomenon (i.e., between-persons variation in the organization of the normative system, as exemplified by research on attachment styles). In the present research we have adopted a normative perspective on attachment, emphasizing adult attachment as a phenomenon that characterizes humans (and some other species) and studying the way in which the presence of the attachment system varies from one species to the next. Although we believe these kinds of cross-species comparisons are useful for evaluating evolutionary hypotheses, we should note that our emphasis on between-species differences should not be taken to imply that within-species comparisons are unimportant or nonexistent. Ultimately, we believe that the study of evolution and function will be enriched by investigating both between- and within-species differences. In fact, by studying both forms of variation simultaneously (as opposed to focusing only on variation within species or between species), it should be possible to determine whether patterns of trait covariation are similar across distinct taxonomic groups. It may be the case, for example, that two traits evolved together (e.g., neoteny and group size) in specific lineages, but that those traits are not functionally related in other branches of the phylogenetic tree. Phylogenetic methods for modeling between- and within-species variation simultaneously are still in their infancy (see Felsenstein, 2003, for a review of some models with potential). As these methods mature, we hope that attachment researchers, as well as psychologists more generally, will begin to explore their utility.

In the meantime, it should be possible to address questions about the evolution and function of individual differences in attachment patterns by bridging within- and between-species approaches. As an interesting example that highlights the potential of this kind of research, Topal, Miklosi, Csanyi, and Doka (1998) found that the same kinds of differences that characterize infants in the strange situation and adults in romantic relationships also characterize the differences observed among dogs who had been separated from their owners in a laboratory session. Specifically, Topal et al. discovered that the separation and reunion behavior of dogs could be organized with respect to several dimensions, including dimensions pertaining to anxiety and distress as well as the ability to use the owner as a secure base (see Brennan, Clark, & Shaver, 1998, and Fraley & Spieker, 2003, for a discussion of how these kinds of dimensions manifest in humans). This kind of comparative research is valuable because it underscores some of the similarities and differences in the ways in which attachment behavior is patterned within and across species and has the potential to inform our understanding of the evolutionary history of the attachment behavioral system. By broadening the scope of species sampled, it should be possible, for example, to determine whether patterns of attachment are the same across species, and, in cases in which they differ (either in number or function), to reconstruct the evolution of those differences. It could be the case, for example, that a single continuum of security allows attachment behavior to be appropriately modeled in some species, but that a continuum of activating versus deactivating strategies is also required to model variation in other species. It is also possible that some forms of attachment behavior have deeper evolutionary roots than others, and that by reconstructing the evolution of these behavioral patterns across known phylogenies, it would be possible to establish temporal precedence and evaluate some novel hypotheses about the evolution of attachment strategies. This kind of phylogenetic–comparative work could prove valuable in resolving contemporary debates about whether insecure attachment patterns represent secondary strategies (i.e., strategies that result from the breakdown of an ontologically prior, secure strategy) or whether they are adaptations that are activated under specific contexts (see Belsky, 1999, for a review of this debate). If insecure strategies are secondary, then it is possible that they have emerged after secure strategies throughout evolutionary history.\(^9\) In summary, by considering individual differences in attachment organization within a broader phylogenetic framework, it should be possible to advance our understanding of attachment in ways that many researchers have yet to envision.

Broader Implications for the Study of Social and Personality Psychology

Although our primary objective in this research was to tackle some theoretical questions about adult attachment phenomena, our secondary aim was to illustrate some of the ways in which comparative and phylogenetic methods can be applied to questions about social behavior and close relationships more generally. We believe such an illustration has the potential to be valuable because there is surprisingly little research on evolution per se in psychology, despite the fact that “evolutionary psychology” has become increasingly visible over the past decade. The use of comparative and phylogenetic methods has the potential to advance the science of evolutionary psychology by allowing researchers to reconstruct the evolution of behavioral traits and evaluate the extent to which the covariation among traits reflects different evolutionary processes. We hope the present research will provide a useful example of how phylogenetic methods can be used to address questions regarding evolution as well as how those methods can be used to study the adaptive functions served by a variety of phenomena of interest to social and personality psychologists.

Another implication of this research is that it may be advantageous for evolutionary psychologists to reach more deeply into the phylogenetic past. There is a tendency for psychologists to theorize about the evolution of human behavior by referencing the Pleistocene—an epoch in history that began approximately two million years ago. This hypothesis assumes that ontogeny (i.e., development) recapitulates phylogeny (i.e., evolution). Although this idea has been critiqued by many developmental biologists as being incomplete (see Gottlieb, 1992, and Gould, 1977, for reviews), the basic pattern holds in many situations and might prove to be a useful theoretical bridge for extending hypotheses of developmental relevance to the study of evolution.

\(^9\) This hypothesis assumes that ontogeny (i.e., development) recapitulates phylogeny (i.e., evolution). Although this idea has been critiqued by many developmental biologists as being incomplete (see Gottlieb, 1992, and Gould, 1977, for reviews), the basic pattern holds in many situations and might prove to be a useful theoretical bridge for extending hypotheses of developmental relevance to the study of evolution.
years ago, in which significant features of humanity were thought

to emerge. However, many of the motives, behaviors, and feelings
that characterize the human condition (e.g., love, hate, sex, work,
power) probably have their origins prior to the Pleistocene given
their commonality across phylogenetically unrelated species. By
sampling phylogenetically diverse species, it might be possible to
provide a more comprehensive account of the evolution and func-
tion of many psychological phenomena—an account that is not
limited to a specific (and relatively recent) epoch in the history of
life.

Limitations and Caveats

The present studies help to advance the study of adult attach-
ment in two significant ways. First, to the best of our knowledge,
this is the only investigation of the evolution of adult attachment
inspired directly by Bowlby’s (1969) theory that has used both
comparative and phylogenetic methods.10 Although this is not the
first attempt to address questions concerning evolution and attach-
ment in the social psychological literature, previous attempts have
relied primarily on anecdotal evidence or data from a small hand-
ful of species. A second significant contribution of this work is
that, in addition to systematically mapping the between-species
correlates of adult attachment, we have attempted to do so in a
manner that takes the phylogenetic relationships among species
into account. This is a critical step in evolutionary research be-
cause species are not independent of one another (see Garland &
Adolph, 1994, and Felsenstein, 1985). This phylogenetic depend-
ence makes it possible for two species to be quite similar with
respect to a variety of traits even if those traits did not co-evolve
with one another across evolutionary history.

Despite these strengths, there are a number of caveats that
should be considered when interpreting the results of these studies.
Most significantly, questions about evolution are rarely answered
definitively. The process of reconstructing the evolution of a
specific trait, for example, involves methods of phylogenetic in-
ference, and those methods, even when defensible on theoretical
grounds, simply cannot yield definitive answers (see Losos, 1999).
Like any historical enterprise, the study of evolution is constrained
by the absence of complete historical data, and the data that exist
are sometimes open to alternative interpretations.

A second caveat is that we have deliberately tried not to conflate
adult attachment with specific kinds of mating systems or mating
strategies. This is important to note because there is a tendency for
researchers to assume that pair bonding implies mating exclusivity.
In recent years, however, many biologists have observed that
members of pair-bonded species may have multiple mates at some
point during their lives or, even when pair bonded, selectively
engage in extra-pair copulations. These kinds of observations on
sexual infidelity have led some writers to question whether hu-
mans can be viewed properly as a pair-bonding species (e.g.,
Barash & Lipton, 2001). In considering this issue, we find it useful
to distinguish between sexuality and affectional bonds. Diamond
(2003), for example, has recently made a compelling case for the
functional independence of the behavioral systems mediating sex-
ual desire and the experience of love (see also Fisher, 1998). We
believe her distinction is an important one because it is quite
possible for individuals within a broad taxonomic group to exhibit
variation in the sexual strategies that they use (e.g., short-term vs.
long-term mating strategies; see Buss & Schmitt, 1993, and Simp-
son & Gangestad, 1991) or in the kind of mating system they adopt
(e.g., monogamous vs. polygamous; see Borgerhoff Mulder, 1992)
while still having the capacity for developing a strong and endur-
ing attachment to a specific individual. In short, readers should be
aware that our assumption that human adults exhibit attachment
does not mean that we are assuming that humans do not exhibit
variation in mating strategies nor that humans are always sexually
faithful. As research and theory on these issues progresses, we
suspect that evolutionary explanations for sexual desire and attach-
ment will diverge in some crucial ways.

It is also important to keep in mind that although we have
focused on two salient hypotheses regarding the evolution of
attachment, we have not exhausted all of the possible factors that
may have led to the evolution of pair bonding. Several writers have
suggested that concealed ovulation may have played a role in the
evolution of pair bonding (e.g., Alexander & Noonan, 1979; Hrdy,
1988; Sillén-Tullberg & Möller, 1993). Sillén-Tullberg and Möller
(1993) found that monogamous mating systems were more com-
mon in taxa with concealed ovulation than in taxa with visible
signs of ovulation. According to these authors’ phylogenetic anal-
yses, the lack of ovulatory signals is likely to have preceded the
development of monogamy during evolutionary history, suggest-
ing that concealed ovulation may have created confusion on the
part of males concerning paternal certainty, thereby indirectly
facilitating pair bonding.

Beyond these broad caveats, we should highlight some specific
limitations of our data, sampling methods, and analytic tools. First,
we were not always able to obtain complete social, developmental,
and morphological data for all of the species we studied. One
reason for this is that some of the information we sought was
simply not available in the literature. As biologists learn more
about the diversity of life, it should be possible to fill in some of
the gaps in the database. Fortunately, the basic pattern of correla-
tions among variables was replicated across two samples, making
us fairly confident in the patterns we have reported.

Another potential limitation of this research is that we restricted
the scope of our investigation to the class of mammals. This focus
reflects a compromise between two competing objectives on our
part. On one hand, we recognized that attachment is not unique to
humans and that it could be useful to sample a wide range of
species to understand attachment in a broader context. On the other
hand, as researchers who primarily study human attachment, we
did not want to sample species that were too distantly related to
humans. The potential disadvantage of restricting our investigation
in this manner is that it rules out the study of birds—species well
known for their pair-bonding behavior.

Finally, we note that, although the comparative methods we
used in this research are commonly used in research on evolution

10 Although this is the first study on evolution and attachment inspired
by the social–psychological literature on adult attachment, this is not the
only study to address the evolution of attachment among mammals. One
noteworthy study was published by Komers and Brotherton (1997) on the
evolution of mammalian monogamy. Komers and Brotherton (1997) de-
defined monogamy as “a social bond implying mating exclusivity” (p. 1261).
These authors found that one of the most salient features of mammalian
monogamy was that it evolved in conditions in which females were solitary
and occupied small ranges.
and ecology, they represent only a small sample of the many methods that are available in the evolutionary tool kit. For example, Blomberg et al. (2003) have developed a set of methods for quantifying the amount of "phylogenetic signal" that exists in a trait. This method has the potential to be valuable for examining the extent to which phenotypic similarities among species can be understood with respect to homology. When there is a high degree of phylogenetic signal in a trait, the need for methods that take phylogeny into account is especially warranted.

In closing, Bowlby originally conceived of the study of attachment as an ethological enterprise—one that seeks to elucidate the development, evolution, function, and proximate mechanisms of attachment relationships (Bowlby, 1969; Hinde, 1982). Researchers have made extraordinary progress in clarifying the developmental processes underlying attachment across the life span as well as the proximate mechanisms underlying attachment-related thought, feeling, and behavior. The objective of this article was to begin filling in some of the gaps that exist in our knowledge concerning the evolution and function of attachment in adult romantic relationships. We hope that this research will be viewed as a useful first step toward answering what we consider to be some of the most challenging questions in the study of adult attachment: Why does attachment exist in adult relationships? What functions does it serve? and How did attachment evolve over the course of mammalian evolution?

References


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