

Evolution and Proximate Expression of Human Paternal Investment

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In more than 95% of mammalian species, males provide little direct investment in the well-being of their offspring. Humans are one notable exception to this pattern and, to date, the factors that contributed to the evolution and the proximate expression of human paternal care are unexplained (T. H. Clutton-Brock, 1989). The nature, extent, and influence of human paternal investment on the physical and social well-being of children are reviewed in light of the social and ecological factors that are associated with paternal investment in other species. On the basis of this review, discussion of the evolution and proximate expression of human paternal investment is provided.

Issues centered on the nature and extent of parental investment of time and resources in children are socially and scientifically contentious (Silverstein & Auerbach, 1999; Travis & Yeager, 1991). Scientifically, assumptions about the mother–infant relationship influence the types of child-development research questions that are asked and the types of studies that are conducted (Silverstein, 1991). Socially, differences in the nature and extent of maternal and paternal care are often a source of marital conflict (Eibl-Eibesfeldt, 1989; Kluwer, Heesink, & Vandevliert, 1996; Parke, 1995; Scarr, Phillips, & McCartney, 1989). Social and scientific debate often centers on differences in the level of maternal and paternal care. In the vast majority of families, mothers provide more direct care to their children than fathers do (see, e.g., Whiting & Edwards, 1988). Points of contention arise when this pattern is contrasted with the social ideology of equality, namely, that mothers and fathers should contribute equally to the well-being of their children. However, the social ideology of equality is not the only vantage point from which the study of parental investment can be viewed.

A comprehensive understanding of human parental investment and any associated sex differences also requires consideration of the patterns of parental investment across mammalian and other species (Emlen, 1995). When considered in terms of mammalian parental investment, the most remarkable feature of human reproduction is the high degree of paternal care found in many human populations. For 95% to 97% of mammalian species, males provide little direct investment (e.g., provisioning) in their offspring (Clutton-Brock, 1989, 1991). For the two species most closely related to humans—chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*)—males typically provide no parental investment and, in fact, only rarely affiliate with juveniles (de Waal & Lant-

ing, 1997; Goodall, 1986; Whitten, 1987). On the basis of these patterns, the question then becomes, Why do men contribute to the care of their children at all (Clutton-Brock, 1989)?, as contrasted with the question Why don't men and women contribute equally to the care of their children (Silverstein, 1991)?

The questions of the origin and nature of human paternal investment are the foci of this article. The first section below focuses on nonhuman species and provides a brief overview of the relation between parental investment and offspring survival, as well as consideration of the correlates of paternal care in these species. When parental investment (by either parent) is a feature of the species' life history, it is inextricably tied to the dynamics of reproduction, that is, to sexual selection (Darwin, 1871). Thus, the second section provides an overview of the relations among sexual selection, reproductive strategies, and parental investment, again focusing on nonhuman species. The discussion of human paternal investment begins in the third section, with a consideration of the influence of fathers on the well-being of children. The fourth section provides discussion of the relations among paternity certainty, female sexuality, and human paternal investment, whereas the fifth provides a comparison of the cross-cultural pattern of paternal and maternal care. The penultimate section focuses on the correlates of the proximate expression of human paternal investment, and the final section provides discussion of the factors that may have influenced the evolution of human paternal investment.

Why Parental Investment?

A comprehensive treatment of human paternal investment first requires an understanding of parental and paternal investment in other species (Emlen, 1995). The study of parental investment in nonhuman species provides insights into the biological, ecological, and social conditions that influence the proximate expression of parental care and enables inferences to be drawn about the evolution of this care (Clutton-Brock, 1991). For instance, internal gestation and obligatory postpartum suckling result in features of parental care that are common to nearly all mammals, such as more maternal than paternal care (Clutton-Brock, 1989). Similar patterns of parenting can also emerge in unrelated species and are often associated with similar ecological or social conditions, a process termed convergent evolution (Emlen, 1995; Larson & Losos, 1996). For all species, the basic issues center on the costs

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and benefits of parental investment, maternal and paternal, and the ecological and social conditions that are associated with its proximate expression and apparent evolution (Clutton-Brock, 1991; Krebs & Davies, 1993; Westneat & Sherman, 1993).

In many species, neither the female nor the male invest in the growth and well-being of their offspring beyond the development of ova and sperm (Clutton-Brock, 1991). In those species in which females, males, or both invest in offspring, it is often at a considerable cost, such as a reduced lifespan (McNamara & Houston, 1996). Given this, the question of why parents—males, females, or both—invest in the development and well-being of their offspring is an important issue in and of itself (Clutton-Brock, 1991; Perrone & Zaret, 1979; Thornhill, 1976; Williams, 1966a; Wolf, Ketterson, & Nolan, 1988). Although the effect of parental investment on offspring survival can vary across ecological conditions and breeding season, in

virtually all species where young are fed by their parents, they do not survive if parents are removed, though where both parents are involved the removal of one is not necessarily fatal. . . . Both across and within species, there is usually a close relationship between feeding rate and the growth rate and survival of young. . . . Early growth may also affect reproductive success in adulthood. In mammals, for example, adult size is commonly related to breeding success and is usually well correlated with early growth, which is affected by birth weight and the mother's milk yield. (Clutton-Brock, 1991, p. 25).

Although uncommon in mammals, paternal investment—which typically involves provisioning or protecting young, or both—is found in many species of bird and fish and in some species of insect (Perrone & Zaret, 1979; Thornhill, 1976; Wolf et al., 1988). For these and other species, theoretical and mathematical models suggest that the evolution and proximate expression of paternal investment involve tradeoffs between reproductive and survival-related costs and benefits (Trivers, 1972; Westneat & Sherman, 1993). In some species, paternal investment may be obligate, that is, male care is necessary for the survival of his offspring. In such species, selection pressures strongly favor males who invest in offspring and could eventually result in nearly all males showing high levels of paternal investment, independent of proximate social and ecological conditions (Westneat & Sherman, 1993); an example might be the purple sandpiper (*Calidris maritima*; Pierce & Lifjeld, 1998).

In other species, including humans (described later), paternal investment is facultatively expressed, that is, the level and nature of this investment varies with proximate social and ecological conditions (Clutton-Brock, 1991; Westneat & Sherman, 1993). Although the conditions that influence the proximate expression of paternal investment can vary from one species to the next, there appear to be similar social and ecological conditions associated with paternal care in many of these species, suggesting convergent evolution. Across these species, the facultative expression of paternal investment is typically associated with paternity certainty and alternative mating opportunities and by the strength of the relation between paternal care and offspring survival (Clutton-Brock, 1991; Krebs & Davies, 1993). Paternal investment is often, but not always, found under conditions where there is a high degree of paternity certainty, where paternal investment improves offspring survival rates, and where paternal investment does not

severely restrict opportunities to mate with other females (Birkhead & Møller, 1996; Perrone & Zaret, 1979).

Paternal investment in fish, for instance, is typically found in species with external fertilization of eggs and where males defend territory and, thus, exclude competitors (Perrone & Zaret, 1979). Under these conditions, the paternity of the zygotes is relatively certain. Moreover, males are typically able to fertilize the eggs of more than one female, and thus, paternal investment does not reduce the males' mating opportunities. In contrast, paternal investment is uncommon in fish species with internal fertilization, presumably because paternity is not certain and because males can easily abandon females after fertilization and thereby avoid the cost of parental investment (Perrone & Zaret, 1979; Reynolds, 1996).

Nonetheless, paternal investment sometimes does occur in species with internal fertilization, including most species of bird and a few mammals, most notably carnivores and some primates (Clutton-Brock, 1991; Dunbar, 1995; Mock & Fujioka, 1990). Again, the degree of paternal investment in these species appears to vary with paternity certainty, the availability of other mates, and the extent to which such investment benefits offspring. In many species of socially monogamous bird, for instance, paternal investment usually improves offspring survival rate, but males appear to vary their level of investment with the likelihood of paternity. As the risk of cuckoldry (i.e., investing in the offspring of another male) increases, paternal investment generally decreases (Birkhead & Møller, 1996). This relation is most evident in comparative, or cross-species, comparisons: In species with lower levels of paternity certainty, the average level of male provisioning is lower than in species with higher levels of paternity certainty. Although informative, comparative studies cannot provide a definitive examination of the facultative expression of paternal investment.

Within-species studies of the relation between paternal investment and paternity certainty provide less definitive results than do comparative studies (Dixon, Ross, O'Malley, & Burke, 1994; Kempenaers, Lanctot, & Robertson, 1998; Møller & Tegelström, 1997; Sheldon, Räsänen, & Dias, 1997; Whittingham & Lifjeld, 1995). In one study of male barn swallows (*Hirundo rustica*), Møller and Tegelström (1997) compared the level of male provisioning when all of the nestlings were sired by the male (as determined by DNA fingerprinting) with provisioning when all or a portion of the nestlings were sired by another male. When the male was provisioning a brood in which all of the nestlings were his offspring, he provided, on average, 46% of the nestlings' food (the female provided the rest). When all or a proportion of the nestlings were sired by another male, the same male provided 34% of the nestlings' food. In this study, a 43% reduction, on average, in the number of offspring sired by the provisioning male was associated with a 26% reduction, on average, in the level of investment (i.e., amount of food provided) in the brood.

A similar pattern was found for two other species of bird, the reed bunting (*Emberiza schoeniclus*; Dixon et al., 1994) and the collared flycatcher (*Ficedula albicollis*; Sheldon et al., 1997). However, no relation between paternity certainty and paternal investment was found for three other species of bird, the house martin (*Delichon urbica*; Whittingham & Lifjeld, 1995), the eastern bluebird (*Sialia sialis*), and the tree swallow (*Tachycineta bicolor*; Kempenaers et al., 1998). At this point, all of these studies are difficult to interpret, because the degree to which males vary

their investment in response to social and ecological conditions is not known in these, or other, species. In other words, the degree to which paternal investment is facultatively responsive to proximate conditions (e.g., paternity certainty) is not well understood for individual species (Westneat & Sherman, 1993). For instance, in species with a long evolutionary history of obligate paternal investment, little or no relation would be expected between paternal investment and paternity certainty in current generations.

Although a definitive conclusion cannot be drawn at this point, the evidence suggests that, in at least some species, males are sensitive to paternity certainty (the mechanisms for determining paternity are not well understood) and adjust their level of investment in offspring accordingly. Even with paternal provisioning, it cannot be assumed that this always represents parental investment. In some species, paternal provisioning of offspring is more strongly related to mating effort (e.g., providing resources to infants who are not his biological offspring to obtain sexual access to the infants' mother) than to parental effort (Freeman-Gallant, 1998; Smuts & Gubernick, 1992). In any case, paternity certainty and an improvement in the survival rate of a male's offspring do not appear to be sufficient for the evolution or proximate expression of paternal investment.

For social monogamy and paternal investment to evolve, the benefits a male might accrue through paternal investment must, on balance, be greater than the benefits of siring offspring with more than one female (Dunbar, 1995). For instance, social monogamy and high levels of paternal investment are common in canids (e.g., coyotes, *Canis latrans*), who tend to have unusually large litters for a large mammal (Asa & Valdespino, 1998; Mock & Fujioka, 1990). Large litter sizes, prolonged offspring dependency, and the ability of the male to provide food during this dependency result in canid males being able to sire more offspring with a monogamous, high-investment mating strategy than with a polygynous mating strategy: For polygynous mammals, females tend to give birth to one offspring at a time (Clutton-Brock, 1991).

Social monogamy and high levels of paternal investment might also evolve if females are ecologically dispersed and males thus do not have the opportunity to pursue multiple mating partners, as appears to be the case with callitrichid monkeys (e.g., marmosets, *Callithrix*; Dunbar, 1995), although social monogamy and little or no paternal investment is sometimes found as well (e.g., most species of gibbon, *Hylobates*; Leighton, 1987). The evolution of social monogamy and paternal investment in callitrichid monkeys is not fully understood but appears to have involved several social and ecological factors (Dunbar, 1995; Rutberg, 1983). First, male-female pairs share in the joint defense of a defined territory, which, in turn, limits the male's ability to expand his territory to include that of more than one female. This is because males cannot effectively defend a large territory by themselves and because female-on-female aggression prevents males from forming harems on the territory that they can defend. Second, concealed ovulation increases the cost of male abandonment, because males must maintain a longer relationship with their mate to ensure conception. Finally, females often have twins, which increases the benefits of paternal care, as with canids (see Dunbar, 1995, and Rutberg, 1983, for further discussion), and increases the costs (i.e., survival risks for two offspring) of abandonment to pursue additional mates.

Even in species where paternal investment is common, the dynamics of reproduction are complex and can vary from one male (or female) to the next and from one season to the next (Reynolds, 1996). To more fully understand these dynamics and to better understand the relation between parental investment and reproduction in general, such as why paternal investment is so rare in mammals, it is necessary to explore the relation between sexual selection and reproductive strategies.

Sexual Selection and Reproductive Strategies

Darwin's (1871) principles of sexual selection capture the dynamics of sexual reproduction across all species in which these dynamics have been studied (Andersson, 1994; Geary, 1998). Unlike natural selection (Darwin, 1859), sexual selection is not a struggle for existence per se, but rather "depends on the advantage which certain individuals have over other individuals of the same sex and species, in exclusive relation to reproduction" (Darwin, 1871, Vol. I, p. 256). Sexual selection is thus restricted to characteristics that are directly related to and influence mate choice and competition for mates, most typically male-male competition and female choice of mating partners (see Andersson, 1994). The first section below provides a description of the general relation between sexual selection and parental investment, and the second focuses specifically on male-male competition and female choice as related to the issue of paternal investment.

Sexual Selection and Parental Investment

Sex differences in the relative costs and benefits of producing offspring appear to be the key to understanding the evolution of sex differences in reproductive strategies and in parental investment (Trivers, 1972; Williams, 1966b). Each individual's overall reproductive effort is a combination of mating effort (e.g., time spent searching for mates) and parental effort, or parental investment. Parental investment is any cost (e.g., time, energy) associated with raising offspring that reduces the parent's ability to produce or invest in other offspring. Given that some level of parental investment is necessary for the reproductive success—of both parents, the nature of the parental investment by females and males creates the basic dynamics of sexual reproduction and sexual selection.

If one sex provides more parental investment than the other sex, then members of the higher investing sex become an important reproductive resource for members of the opposite sex (Dawkins, 1989; Trivers, 1972). Basically, the reproductive success of members of the lower investing sex is more strongly influenced by the number of mates that can be found than by investing in the well-being of individual offspring, whereas the reproductive success of members of the higher investing sex is more strongly influenced, in most cases, by investment in offspring than in finding mates. In this view, the dynamics of sexual selection are influenced by the way in which each sex distributes its reproductive effort across mating and parenting (Clutton-Brock, 1991), which, in turn, is influenced by a variety of factors, including the potential reproductive rates of males and females and the operational sex ratio (OSR), among other things (Emlen & Oring, 1977).

These factors are interrelated but are discussed in separate sections below.

Reproductive rates. Any sex difference in the potential rate of reproduction can create a sex difference in the relative mix of mating and parenting. The sex with the higher potential rate of reproduction typically invests more in mating effort than in parental effort, whereas the sex with the lower rate of reproduction invests more in parental effort than in mating effort (Clutton-Brock & Vincent, 1991). This is because, following mating, members of the sex with the higher potential rate of reproduction can rejoin the mating pool more quickly than can members of the opposite sex, and it is often in their reproductive best interest to do so (Parker & Simmons, 1996), particularly when biparental care is not necessary for the viability of offspring (Clutton-Brock, 1991; Maynard Smith, 1977). In most species, males have a higher potential rate of reproduction than females do (Clutton-Brock, 1991; Parker & Simmons, 1996; Williams, 1966b; Trivers, 1972).

For species with internal gestation and obligatory postpartum female care (e.g., suckling in mammalian species), the rate with which females can produce offspring is considerably lower than the potential rate of reproduction of conspecific males (Clutton-Brock, 1991). At the same time, internal gestation and the need for postnatal care creates a female bias toward parental investment and creates a sex difference in the benefits of seeking additional mates (Trivers, 1972; but see Dawkins, 1989). Males can benefit reproductively from seeking and obtaining additional mates, whereas females cannot (Maynard Smith, 1977). Thus, a sex difference in reproductive rates, combined with offspring that can be effectively raised by the female, creates the potential for large female-male differences in the mix of mating and parenting.

The ability of females to effectively rear offspring is especially important if this potential sex difference is to be realized. This is because when biparental care is necessary for offspring survival, as is found in many species of bird (Black, 1996), selection favors the evolution of social monogamy and paternal investment, regardless of any physiologically based sex difference (e.g., internal fertilization) in the potential rate of reproduction. In 95% to 97% of mammalian species, however, females can effectively provide the majority of parental care and do so (Clutton-Brock, 1991). Female care, in turn, frees males to invest in mating effort, which typically takes the form of male-male competition over access to mates or for control of the resources (e.g., territory) that females need to raise their offspring.

Operational sex ratio. The OSR is defined as the ratio of sexually active males to sexually active females in any given breeding area at a given point in time and is related to the rate of reproduction (Emlen & Oring, 1977). For instance, in a population where there are as many sexually mature females as there are sexually mature males—an actual sex ratio of 1:1—any sex difference in the rate of reproduction will skew the OSR. For mammalian species, males necessarily have a faster potential rate of reproduction—due to the biology of internal gestation—and thus, there are typically more sexually receptive males than sexually receptive females in most populations. This biased OSR creates the conditions that lead to intense male-male competition over access to a limited number of potential mates. Although these patterns are most evident in mammals, they are also found in many species of bird, fish, and reptile (Andersson, 1994).

As an example of the relations between the potential rate of reproduction, the OSR, and mating strategies, consider the mating system of the red-necked phalarope (*Phalaropus lobatus*), a polyandrous shorebird (i.e., females potentially have more than one mate; Reynolds, 1987; Reynolds & Székely, 1997). In this species, males provide most or all of the parental care, specifically, the building of the nest and the incubation of the eggs; the fledglings fend for themselves once hatched (i.e., they are precocial). The high level of paternal care makes it possible for the female to pursue other mating opportunities, and she typically does: Once the clutch is laid, the female often leaves in search of another male. The crucial feature of this mating system is that females are ready to produce another clutch about 1 week after laying their first clutch, whereas the incubation time for males is close to 3 weeks. The result is that the effective rate of reproduction is potentially higher in females than in males, and the OSR is skewed such that there are typically more sexually receptive females than males at any given point in time. The limiting factor in the number of offspring that can be produced by any given female is thus the number of unmatched males (i.e., males available to incubate her eggs).

In theory then, the females of this species should show many of the characteristics that are typically associated with the males of species in which males compete for mates (Trivers, 1972). In fact, this “sex-role reversal” is found. Red-necked phalarope females are slightly larger than conspecific males, have a brighter plumage, fight with other females for access to males, and, once paired, guard their mates against competitors (Reynolds, 1987). Males, in contrast, rarely threaten or attack one another, although they do guard their mate until the eggs are laid; presumably, this mate guarding functions to ensure that any offspring are indeed his, that is, it ensures paternity certainty.

Not only are the behavioral sex differences in red-necked phalaropes similar, though reversed, to those found in species where male-male competition is prevalent, the consequences of this competition are also similar. The most important of these consequences—and the principal force governing the evolution of female-female competition in this species—is that the reproductive success of females is more variable than the reproductive success of males. Some females produce two clutches per breeding season, each with a different male, and many other females go unmated; unmated males, in comparison, are rare. In short, females who capitalize on the high level of paternal care produce more offspring than females who assist the male in clutch incubation. As long as the male can effectively incubate the eggs himself, selection—through differential reproduction—favors females who pursue and are successful in gaining additional mates, that is, females who invest more in mating effort than in parental effort.

It appears that the same basic mechanism (i.e., a sex difference in potential reproductive rates) is the ultimate source of the male focus on mating effort and the female focus on parental effort in the vast majority of mammalian species (Emlen & Oring, 1977; Parker & Simmons, 1996). However, the biology of internal fertilization and gestation are not the only factors that influence the potential rate of reproduction and the OSR in mammals; social and ecological factors are sometimes important as well. The earlier noted example of paternal investment in callitrichid monkeys illustrates this point. Callitrichid males have a higher potential rate of reproduction than females do, but shared territorial defense,

concealed ovulation, female-on-female aggression, twinning, and perhaps other yet unknown factors negate this physiologically based sex difference and appear to result in a more balanced OSR, monogamy, and high levels of paternal investment (Dunbar, 1995).

Male-Male Competition, Female Choice, and Paternal Investment

Male-male competition and paternal investment in primates. As is true for mammals in general, the males of most primate species invest more in mating than in parenting. Mating effort involves physical competition for the establishment of social dominance and, through this, access to multiple mating partners. Recent DNA fingerprinting studies indicate that in natural and semi-natural settings, the establishment and maintenance of social dominance have important reproductive consequences. In these settings, dominant males sire more, sometimes considerably more, offspring than do their less dominant peers (see, e.g., Altmann et al., 1996; Dixson, Bossi, & Wickings, 1993). One evolutionary result of this male-male competition is that males are physically larger than females in all primate species in which social dominance is established through physical contest (Clutton-Brock, Harvey, & Rudder, 1977; Plavcan & van Schaik, 1997).

In the roughly 15% of primate species where males do not intensely compete for social dominance, monogamy and sometimes intensive caregiving on the part of males are common (Clutton-Brock, 1991; Leighton, 1987; Rutberg, 1983; Whitten, 1987). These species are also characterized by a lack of sex differences in physical size and in the pattern of physical development (Leigh, 1996). The cross-species pattern suggests that intense male-male competition over access to mates and paternal investment are inversely related, although, in many species, some males use alternative, noncombative, reproductive strategies (e.g., courting females; Smuts, 1985). Even with alternative mating strategies, one general indicator of the intensity of male-male competition, and by inference the level of paternal care, is a sex difference in physical size (Clutton-Brock et al., 1977; Plavcan & van Schaik, 1997).

The use of these patterns to interpret the hominid fossil record suggests that physical male-male competition has been an important feature of sexual selection during human evolution (Wrangham & Peterson, 1996). Studies of one of the earliest identified and more extensively studied hominid species—*Australopithecus afarensis*—suggest an important sex difference in the physical size of males and females (Aiello, 1994; Frayer & Wolpoff, 1985; McHenry, 1991, 1992; Richmond & Jungers, 1995). Estimates of the degree to which males were larger than females range from about 50% (McHenry, 1991, 1992) to 100% (Frayer & Wolpoff, 1985). Although there is general agreement that this sexual dimorphism suggests a polygynous mating system and, by inference, lower levels of paternal than maternal investment, the exact nature and intensity of the associated male-male competition is debated (Plavcan & van Schaik, 1997; McHenry, 1992; Wrangham & Peterson, 1996). Even so, recent studies suggest that the predecessor of *A. afarensis*, that is, *A. anamensis*, showed the same sexual dimorphism, further supporting the position that there has been a long—at least 4,000,000 years—evolutionary history of physical male-male competition in hominids (Leakey, Feibel, McDougall,

& Walker, 1995; Leakey, Feibel, McDougall, Ward, & Walker, 1998).

The sexual dimorphisms found in our ancestors and in all extant great apes are, of course, the same sexual dimorphisms found in modern humans, that is, men are physically larger and stronger than women and have a longer maturational period (Leigh, 1996; Tanner, 1990). At the same time, there appears to have been a substantive reduction in the male advantage in physical size from *A. afarensis* to modern humans. The reduced sexual dimorphism suggests a change in the nature of male-male competition (e.g., from one-on-one to coalition-based competition), a decrease in polygynous matings and less intense male-male competition, and a corresponding increase in paternal investment, or some combination: Both coalition-based competition and decreased polygyny (and, by definition, a greater tendency toward monogamy) are associated with smaller sexual dimorphisms, in comparison with species with one-on-one competition and a highly polygynous mating system (Plavcan & van Schaik, 1997).

Female choice and paternity certainty. With a few exceptions, such as the red-necked phalarope, females do not typically compete with one another over access to mates, although they often compete over access to food (Wrangham, 1980). More typically, females influence the dynamics of reproduction through their choice of mating partners. Clear examples of female choice are found for most species of bird (see, e.g., Møller, 1994), although female choice is also evident in many species of primate, including humans (Buss, 1994; Geary, 1998; Smuts, 1985). For species in which females need male provisioning to successfully raise their offspring, female reproductive decisions are complicated by the trade-off associated with the need to secure such provisioning from their social partner and the benefits associated with having their offspring sired by the most fit male in the local population. For birds, the physical and genetic fitness (e.g., resistance to local parasites) of males is signaled through plumage coloration and symmetry, or complexity of song (see, e.g., Hamilton & Zuk, 1982). Offspring sired by these males have higher survival rates than do offspring sired by less colorful males, and thus, it is often in the females' best interest to mate with these males (Møller, 1994).

By definition, these males are in short supply. As a result, most females are paired with males who provision their offspring but are not the most genetically fit males in the breeding population. In many of these socially monogamous species, a female thus seeks extra-pair copulations with these genetically fit males, which, in turn, results in some of her offspring being sired by her social partner and her remaining offspring being sired by the extra-pair male (Birkhead & Møller, 1996; Møller & Tegelström, 1997). Thus, in many socially monogamous species, paternity is less than certain because it is sometimes in the females' best interest to deceive her social partner (who provisions her offspring) and mate with a healthier male. Although the empirical evidence is mixed, as described earlier, the predicted male counterstrategy is to reduce the level of paternal investment as cuckoldry risks increase. In theory, similar mating dynamics would likely evolve (through convergent evolution) in any species, including humans, where females must implicitly weigh the costs and benefits of obtaining provisioning from one male and genetic benefits from another (Bellis & Baker, 1990; Emlen, 1995).

Table 1
Factors Associated With the Evolution of Paternal Investment in Species With Internal Fertilization

Offspring survival
<ol style="list-style-type: none"> 1. If paternal investment is necessary for offspring survival, then it is obligate, that is, selection favors males who invest in offspring (Clutton-Brock, 1991). 2. If paternal investment has little or no effect on offspring survival rate or quality (e.g., size, which is often related to the offspring's reproductive success in adulthood), then selection favors male abandonment, if additional mates can be found (Maynard Smith, 1977; Trivers, 1972; Westneat & Sherman, 1993; Williams, 1966a, 1966b; Wolf et al., 1988). 3. If paternal investment results in a relative, but not an absolute, improvement in offspring survival rate or quality, then selection favors males who show a mixed reproductive strategy. Here, within-species variation is expected, with individual males varying their degree of emphasis on mating effort and parental effort, contingent on social (e.g., male status, availability of mates) and ecological (e.g., food availability, predator risks) conditions (Maynard Smith, 1977; Westneat & Sherman, 1993; Wolf et al., 1988).
Mating opportunities
<ol style="list-style-type: none"> 1. If paternal investment is not obligate and mates are available, then selection favors: <ol style="list-style-type: none"> A. Male abandonment, if paternal investment has little effect on offspring survival rate and quality (Clutton-Brock, 1991; Dunbar, 1995; Maynard Smith, 1977; Westneat & Sherman, 1993); or B. A mixed male reproductive strategy, if paternal investment improves offspring survival rate and quality, that is, variation in degree of emphasis on mating effort and parental effort contingent on social and ecological conditions (Clutton-Brock, 1991; Perrone & Zaret, 1979; Wolf et al., 1988). 2. Social and ecological factors that reduce the mating opportunities of males, such as dispersed females or concealed (or synchronized) ovulation, reduce the opportunity cost of paternal investment. Under these conditions, selection favors paternal investment, if this investment improves offspring survival rate or quality or does not otherwise induce heavy costs on the male (Clutton-Brock, 1991; Dunbar, 1995; Perrone & Zaret, 1979; Rutberg, 1983; Thornhill, 1976; Westneat & Sherman, 1993).
Paternity certainty
<ol style="list-style-type: none"> 1. If the certainty of paternity is low, then selection favors male abandonment. Given that any level of parental investment is likely to be costly (e.g., in terms of reduced foraging time), indiscriminant paternal investment is not likely to evolve (Clutton-Brock, 1991; Westneat & Sherman, 1993). 2. If the certainty of paternity is high, then selection favors paternal investment, if: <ol style="list-style-type: none"> A. Such investment improves offspring survival or quality, and B. The opportunity costs of investment (i.e., reduced mating opportunities) are lower than the benefits associated with investment (Clutton-Brock, 1991; Dunbar, 1995; Maynard Smith, 1977; Rutberg, 1983; Thornhill, 1976; Westneat & Sherman, 1993). 3. If the certainty of paternity is high and the opportunity costs, in terms of lost mating opportunities, are high, then selection favors males with a mixed reproductive strategy, that is, the facultative expression of paternal investment, contingent on social and ecological conditions (Dunbar, 1995; Westneat & Sherman, 1993).

Summary and Conclusion

Internal gestation and obligatory postpartum suckling create an important sex difference, favoring males, in the rate at which male and female mammals can reproduce (Clutton-Brock & Vincent, 1991; Trivers, 1972). When combined with the ability of females to effectively care for offspring, this sex difference results in a male focus on mating effort, through male-male competition, and a female focus on parental effort in 95% to 97% of mammalian species. On the basis of these patterns, it is almost certain that, in mammals, the ancestral state involved little if any paternal care. Nonetheless, paternal care is found in a small percentage of mammalian species, including humans, and the central question with these species is, What are the social and ecological conditions that resulted in the evolution of this care and its proximate expression?

One way to approach this question is to examine the ecological and social correlates of paternal care across mammalian and other species. Although the dynamics of paternal care in these species are not fully understood and can vary from one species to the next

(Clutton-Brock, 1989; Westneat & Sherman, 1993), a few general patterns have emerged and are described in Table 1. These patterns are based largely on cross-species comparisons and must thus be interpreted with some caution: More definitive conclusions must await within-species studies, as described with the relation between paternal investment and paternity certainty in various species of bird. Moreover, the patterns described in Table 1 assume that paternal investment is facultatively expressed, and thus might not apply to species in which the level of paternal investment has been fixed by strong selection for paternal care (i.e., for species with a long evolutionary history of obligate paternal investment). With these caveats in mind, it appears that, across many different species, some combination of improved offspring survival rate and quality, alternative mating opportunities, and paternity certainty is the central social and ecological correlate of the evolution and proximate expression of paternal investment (Clutton-Brock, 1991; Dunbar, 1995; Perrone & Zaret, 1979; Thornhill, 1976; Williams, 1966a; Wolf et al., 1988).

As described in Table 1, the reproductive behavior of males is especially complicated when paternal investment improves offspring survival rate and offspring quality but is not essential, and when the reproductive benefits of seeking additional mates do not always outweigh the reproductive benefits of paternal investment. As described in the following sections, these dynamics appear parallel to those found in humans. Under these conditions, selection favors a mixed male reproductive strategy, with different males varying in the degree of emphasis on mating effort and parental effort, as well as individual males varying in emphasis on mating and parenting at different points in their life span and in their relationships with different females (Draper & Harpending, 1988). Individual differences in paternal investment, in turn, are likely to be related to male condition (e.g., social status), ecological factors (e.g., OSR), female strategies to induce paternal investment, female quality (e.g., attractiveness, parenting skills), and genetically based differences in male reproductive strategy (Krebs & Davies, 1993; MacDonald, 1997).

Paternal Investment and the Physical and Social Well-Being of Children

As noted in Table 1, the theoretical expectation is that men show little paternal investment unless this investment has substantively reduced child mortality rates in ancestral environments or otherwise provided children with a competitive, and thereby a reproductive, advantage over their father-absent peers. The fossil record does not allow for a direct assessment of the relation between paternal investment and childhood mortality or competitiveness in ancestral environments. However, the relation between paternal investment and the well-being of children in extant populations and throughout the history of Western culture allows inferences to be drawn about the likely relation between these factors during human evolution. For instance, it is almost certain that many of the sources of childhood mortality—infectious disease, parasites, and malnutrition—in extant preindustrial societies and up through the demographic shift in Western nations are the same as those that confronted human beings throughout evolutionary history (Hed, 1987; Hill & Hurtado, 1996; Schultz, 1991).¹

Physical Well-Being

Information bearing on the issue of whether paternal investment reduces mortality rates in infancy and childhood is scant in comparison with the literature on the psychological correlates of paternal investment. The difficulty stems in part from the very low infant and child mortality rates in modern industrial societies, those societies in which most of the research on paternal influence is conducted. However, some information is available on the relation between paternal factors (e.g., occupation) and childhood mortality rates in preindustrial Europe and the United States and in a few extant preindustrial and developing societies. Across these contexts, there is a consistent relation between paternal investment (e.g., provisioning) and infant and child mortality rates.

Nonetheless, a strong causal relation between paternal investment and mortality risks cannot be drawn from existing data. This is because in species where males invest in offspring, including humans, assortative mating results in higher quality males pairing with higher quality females (see, e.g., Geary, 1998; Parker &

Simmons, 1996). As a result, the typically higher survival rates of the offspring of these pairs cannot be attributed solely to paternal investment but rather is a function of the qualities of both parents. Regardless, some results do suggest that paternal investment does lower infant and child mortality risks in many contexts, although the magnitude of this effect cannot be determined at this point.

Hill and Hurtado's (1996) extensive ethnography and demography of the Ache—a hunter-gatherer society in Paraguay—provide the most extensive assessment available of the relation between paternal investment and child mortality rates in an extant preindustrial society. For forest-dwelling Ache, about one out of three children die before reaching the age of 15 years, with highly significant differences in mortality rates for father-present and father-absent children. Father absence—due to death or divorce—triples the probability of child death due to illness and doubles the risk of being killed by other Ache or being kidnapped—and presumably killed or sold into slavery—by other groups (Hurtado & Hill, 1992). Overall, father absence at any point prior to the child's 15th birthday is associated with a mortality rate of more than 45%, as compared with a mortality rate of about 20% for children whose father resides with them until their 15th birthday.

Death due to sickness is related, in part, to the adequacy of the child's diet, and in many preindustrial societies, including the Ache, paternal provisioning provides an important component of this diet. Even though the Ache share the proceeds from hunts among all members of the group and thus, fathers do not directly provision their children, the children of skilled hunters have lower mortality rates than the children of less skilled hunters (Hill & Kaplan, 1988; see also Symons, 1979). It appears that children of skilled hunters are better treated than are children of less skilled hunters. According to Hill and Kaplan, better treatment involves a greater tolerance "of food begging by the children of good hunters" (Hill & Kaplan, 1988, p. 283), a greater willingness of band members to stay in one location to nurse the ill child of a good hunter, and greater alloparenting (e.g., baby-sitting) of these children. The Ache, however, are not generally willing to invest in the well-being of genetically unrelated children and, as noted above, often kill children whose father has died or left the group following divorce (see Hill & Hurtado, 1996).

There is evidence that a father's skill at provisioning his family is related to child mortality risks in other preindustrial societies, but the interpretation of this relation is confounded by other variables (Blurton Jones, Hawkes, & O'Connell, 1997; Borgerhoff Mulder, 1990; Griffin & Griffin, 1992; Irons, 1979). As noted above, the expectation is that culturally successful men will marry women who have qualities that improve the well-being of their children. Although this has not been explicitly assessed, there is evidence for such an effect: As an example, for the Hadza—a hunter-gatherer group in Tanzania—successful hunters have more

¹ The first phase of the demographic shift began in 19th-century Europe and involved a steady reduction in infant and child mortality rates (see, e.g., Hed, 1987; Schofield, Reher, & Bideau, 1991). The reduction in mortality rate was largely due to improved hygiene (e.g., closed sewers), nutrition, and medical care (e.g., vaccinations). The second phase of the demographic shift involved a steady reduction in the number of children per family, due largely to improvements in birth control. The third phase began after World War II and involved a further reduction in child mortality rates, due largely to antibiotics.

surviving children than less successful hunters do, but "successful hunters tend to have wives who are more efficient foragers than other women" (Blurton Jones et al., 1997, p. 301).

As with the Ache, in developing countries in South American, Africa, and Asia, there is a consistent relation between marital status and infant and child mortality rates (United Nations, 1985):

Both univariate and multivariate results show that mortality of children is raised if the women is not currently married, if she has married more than once or if she is in a polygamous union. . . . Overall, it appears that there is a strong, direct association between stable family relationships and low levels of child mortality, although the direction of causation cannot be inferred from the data. (p. 227)

For example, Indonesian children of divorced parents have a 12% higher mortality rate than children of monogamously married couples. The same pattern was found in 11 of the 14 developing nations surveyed, but it is possible that the death of a child increases divorce rates rather than paternal absence increasing mortality risks. However, death of the father is generally associated with higher infant and child mortality rates than is divorce, suggesting that father absence directly contributes to these risks.

The same pattern has been found for preindustrial Europe. In 19th-century Sweden, for instance, infant mortality rates were 1½ to 3 times higher for children born to unmarried mothers than for children born to married couples (Brändström, 1997). The same pattern was reported during the period 1885–1940 in the Netherlands (Kok, van Poppel, & Kruse, 1997). Moreover, the mortality risks of these "illegitimate" children were reduced if the father provided some economic support to the child and its mother, and the mortality rates of "legitimate" children increased if the father died, as is found in developing nations today. A relation between paternal provisioning and infant and child mortality risks has in fact been reported throughout preindustrial and industrializing Europe and the United States (Hed, 1987; Herlihy, 1965; Klindworth & Volland, 1995; Morrison, Kirshner, & Molho, 1977; Schultz, 1991; Vallin, 1991; Volland, 1988).

A. Reid's (1997) analysis of mortality risks in early 20th-century England and Wales suggested that "a child's chance of survival was strongly conditioned by who its parents were, or more precisely, by what job its father did" (p. 151). This conclusion was based on the finding of a strong relation between socioeconomic status (SES)—defined entirely by paternal occupation in this study—and mortality risks. In comparison with children whose fathers were unskilled laborers, the children of professional fathers had a 54% lower mortality rate during infancy. The children of unemployed fathers, in contrast, had a 38% higher mortality rate than did children whose fathers were unskilled laborers. Even when SES, environment (e.g., urban vs. agricultural setting), maternal age, and other factors were controlled, children (less than 3 years of age) of working mothers had a 34% higher mortality rate than did children whose mothers did not work. If care was provided to these children while the mother worked (e.g., through kin), the children had a 17% higher mortality rate than did children whose mothers did not work. These effects appear to have been related, in part, to whether (mother stayed at home) or not (mother worked) the infant was consistently breast-fed, with the likelihood of maternal breast-feeding being directly linked to paternal income.

As another example, in an extensive analysis of birth, death, and demographic records from 18th-century Berlin, Schultz (1991) found a strong correlation ($r = .735$) between SES and infant and child mortality rates; SES was defined, at least in part, by paternal occupation. Infant (birth to 1 year) mortality rates were about 10% for aristocrats but more than 40% for laborers and unskilled technicians. "A senior official of the welfare authorities (*Armenbehörde*) observed in 1769 that among the poor weavers of Friedrichstadt 75 out of every 100 children borne died before they reached [adulthood]" (Schultz, 1991, p. 243). During the 1437–1438 and 1449–1450 epidemics in Florence, Italy, child mortality rates increased five- to tenfold, and these mortality rates varied inversely with SES even at the high end of the continuum (Morrison et al., 1977).

In contexts where food and health care are more or less readily available, child mortality rates are very low, in comparison with extant preindustrial societies, developing nations, and Western nations prior to the demographic shift (Hill & Hurtado, 1996; Post, 1985; United Nations, 1985). As an example, Ache living on reservations have much lower child mortality rates than do forest-living Ache (except during the initial contact period). Health care is available on the reservation, and families are able to engage in small-scale gardening, to work for wages, and to accumulate material resources. Even with lower overall mortality rates, paternal investment is still correlated with the survival rate of children, especially infants. Over the course of about 25 years, considerable—fivefold—variation has emerged in the net worth (i.e., value of all personal property) of families living on the reservation, and Hill and Hurtado (1996) have found that "a man's SES is a strong predictor of his offspring's survival to adulthood" (p. 303).

The relation between SES and the physical well-being of children is still found in industrial nations today (see, e.g., I. Reid, 1998). In a review of the literature on the relation between SES—defined as a composite of income, educational level, and occupational status in industrial societies—Adler et al. (1994) concluded that

individuals in lower social status groups have the highest rates of morbidity and mortality within most human populations. Moreover, studies of the entire SES hierarchy show that differences in social position relate to morbidity and mortality even at the upper levels of the hierarchy. (p. 22)

The relation between SES and health holds for all members of the family, not just the primary wage earner, and is not simply related to access to health care or to differences in health-related behaviors (e.g., smoking). In addition, SES appears to influence how well one is treated by other individuals and the degree to which one can control the activities of everyday life, which, in turn, appear to influence physical health (see, e.g., Ray & Sapolsky, 1992). Across industrial societies today, paternal income and occupational status are an important, and sometimes the sole, determinant of the family's SES, and, given this, paternal investment in the family is correlated with the physical well-being of children, even in contexts with low infant and child mortality rates.

A recent study by Flinn and his colleagues provides some clues as to the potential relation between paternal investment and the physical health of children (Flinn & England, 1995, 1997; Flinn, Quinlan, Decker, Turner, & England, 1996), although causal relations cannot be drawn from these data. In this 8-year study, the

family environment, along with cortisol (the primary stress hormone in primates) and testosterone profiles, was assessed for children and adults in a rural village in Dominica, in the West Indies. It was found that the presence or absence of a father was related to the cortisol and testosterone levels of boys but not girls. In comparison with boys residing with their biological father, father-absent boys and boys living with a stepfather had either unusually low or highly variable cortisol levels and weighed less. An analysis of adults who grew up in father-present or father-absent households also revealed significant differences: As adults, father-absent men had higher cortisol levels and lower testosterone levels than did their father-present peers. The endocrine profile of father-absent men suggests chronically high stress levels, which can significantly increase the risk for a number of physical disorders (see, e.g., Sapolsky, 1986).

Across all of these different contexts there is a clear and consistent relation between paternal investment (e.g., provisioning) and infant and child physical health and mortality risks. It cannot be concluded, however, that paternal investment is the sole cause of these reduced risks. In modern society, SES is often influenced by maternal employment, and in preindustrial and industrializing Europe, SES was influenced, in some cases, by any dowry provided by the wife's family. Moreover, infant and child mortality rates are also related to maternal and paternal educational levels, even when SES is statistically controlled, in developing nations today and in preindustrial Europe (Herlihy, 1965; United Nations, 1985). It appears that better educated parents, especially mothers, are more likely to seek medical services, as contrasted with folk remedies, and to implement new health-related advances (e.g., hygiene in industrializing Europe), which often reduce infant and child mortality risks. In short, high SES fathers provide more resources to their children than do lower SES fathers, and these resource differentials are correlated with infant and child mortality risks. At the same time, high SES fathers are more likely to marry women who have qualities (e.g., better educated) that are also associated with reduced infant and child mortality rates (United Nations, 1985). Thus, the reduced mortality risks associated with paternal investment cannot be uncritically attributed to this investment.

Nevertheless, there are several patterns that suggest that paternal investment directly lowered infant and child mortality risks in preindustrial and industrializing Europe and the United States, as well as in developing nations today. As noted above, before sterilized milk was widely available, breast-fed infants had significantly lower—for example, 7% versus 37% in 1900 France (Rollet, 1997)—mortality rates than did bottle-fed infants. Paternal employment often increased breast-feeding rates by allowing the mother to stay at home with the child (A. Reid, 1997), although many wealthy parents choose to employ wet nurses (which increased infant mortality rates). The additional resources provided by fathers also allowed the family to live in healthier environments, provide a more stable food supply, and sometimes hire servants, all of which appeared to contribute to the relation between SES and infant and child mortality rates in industrializing Europe (A. Reid, 1997). Finally, prospective within-family studies—which control for maternal characteristics—indicate increased infant and child mortality rates following paternal death in developing nations today and in preindustrial Europe (Klindworth & Voland, 1995; Kok et al., 1997; United Nations, 1985; Voland,

1988). Although not definitive, the results are consistent with the view that children living in stable social and home environments and with both biological parents are in better health and in many contexts have reduced mortality risks in infancy and childhood than children living in other situations.

Social Well-Being

The research just described suggests that paternal investment reduces infant and child mortality risks but is not obligate, that is, many children survive without such investment. When investment is not obligate, men have the option of focusing their reproductive energies on mating or on parenting; given the biology of mammalian reproduction, women do not have this “freedom of choice” to the same degree. Given that some level of paternal investment is found in most human societies (described below), it is almost certain that under some conditions and at some point in our evolutionary past, men benefited reproductively by shifting some portion of their reproductive effort from mating to parenting (Lovejoy, 1981; E. M. Miller, 1994). Otherwise, the same pattern found in nearly all other mammals including our two closest relatives (i.e., chimpanzees and bonobos)—males exclusively focused on mating effort—would be found in humans. Human paternal investment is, nonetheless, puzzling when it is found in contexts with low infant and child mortality rates (Clutton-Brock, 1989). Under these conditions, selection would favor men who reduced or eliminated parental effort in favor of mating effort. However, many men still invest in their children in these contexts. The question is why?

One possibility is that paternal investment in such environments is an evolutionary by-product of selection for such investment in harsher environments. In this view, there are likely to be genetically based individual differences in the degree to which different men are biased toward paternal investment (see below) or mating effort. Although men with a bias toward paternal investment may have been favored or may have reproduced just as effectively as low-investment men during earlier historical periods, such men may no longer experience reproductive benefits from paternal investment. In fact, all other things being equal, culturally successful high-investment men may be disadvantaged, in terms of lost mating opportunities, by this investment; of course, their wives and children may benefit from this investment.

Another possibility is that paternal investment in low-risk environments provides social-competitive advantages to children, that is, investment designed to improve the “quality” of offspring (Davis & Daly, 1997). If so, then there are two issues to be addressed. First, does paternal investment improve social competitiveness? If so, under what conditions are a smaller number of socially competitive children reproductively advantageous as opposed to a larger number of less competitive children? These issues are addressed in the two respective sections below.

Paternal investment and social competitiveness. High levels of paternal investment—such as income, play time, and so forth—are typically correlated with better child outcomes (e.g., improved social and academic skills), including higher SES in adulthood (see, e.g., Kaplan, Lancaster, & Anderson, 1998; Pleck, 1997). However, a causal relation between such investment and child outcomes has not been firmly established (Amato, 1998; Parke & Buriel, 1998). As described for the relation between paternal

investment and infant and child mortality rates, assortative mating confounds the interpretation of these correlations. As with other species with paternal investment (Parker & Simmons, 1996), assortative mating results in high-investing men tending to marry women who are more socially competent, intelligent, and better educated and thus more effective parents than are women married to lower investing men (Luster & Okagaki, 1993). The relation between paternal investment and child outcomes might then simply reflect maternal and not paternal effects.

Indeed, the strength of the relation between paternal characteristics (e.g., income) and child outcomes is reduced considerably once maternal characteristics are statistically controlled (Amato, 1998). There are however unique relations between paternal investment (e.g., time and income) and some child outcomes. Kaplan and his colleagues found that paternal investment of time (e.g., helping with homework) and income (e.g., paying for tutoring or college) was associated with the upward social mobility of children even when maternal characteristics (e.g., years of education) were controlled (Kaplan et al., 1998; Kaplan, Lancaster, Bock, & Johnson, 1995). Amato (1998) found a similar pattern, with paternal investment being strongly related to educational outcomes. In fact, paternal investment explained 4 times more variance in educational outcomes than did maternal investment.

In keeping with these results is the finding that the withdrawal of paternal investment is associated with decrements in children's later social and cultural success. In industrial societies, paternal investment is typically reduced or withdrawn following divorce, and there are consistent differences in the social and educational competencies of children from divorced as compared with intact families, favoring the latter. However, causal relations are again difficult to determine. Many of the differences between children from divorced and intact families can be traced to differences in family functioning before any such divorce (Cherlin et al., 1991; Furstenberg & Teitler, 1994). Nonetheless, some differences between children from intact and divorced families are found after controlling for predivorce levels of family conflict and other potentially confounding variables. It appears that divorce results in small to moderate increases in aggressive and noncompliant behaviors, particularly in boys, and an early onset of sexual activity and lowered educational achievement for adolescents and young adults (both men and women), respectively (see also Amato & Keith, 1991; Belsky, Steinberg, & Draper, 1991; Florsheim, Tolan, & Gorman-Smith, 1998; Stevenson & Black, 1988). These findings are consistent with the view that paternal investment can improve children's later social competitiveness, given the strong relation between paternal investment and delayed sexual activity, educational outcomes, and later SES in industrial societies (Belsky et al., 1991; Parke & Buriel, 1998).

There is also evidence for more direct paternal effects on the social and psychological well-being of children (Parke, 1995; Parke & Buriel, 1998; Pleck, 1997). Paternal involvement in play, especially rough-and-tumble play and play where the child is able to control or influence the dynamics of the episode, is associated with children's skill at regulating their emotional states and their later social competence. For instance, children who have fathers who regularly engage them in physical play are more likely to be socially popular—that is, chosen as preferred playmates by their peers—than are children who do not regularly engage in this type of play (Carson, Burks, & Parke, 1993; Parke, 1995). Qualitative

features of fathers' relationships with their children, such as positive emotional tone of the interactions and affection, are also associated with greater social and academic competencies in children (Parke & Buriel, 1998) and with fewer behavioral (e.g., aggression) and psychological (e.g., depression) difficulties (Florsheim et al., 1998; Pleck, 1997; Rohner, 1998).

All of the relations between paternal investment and child outcomes are, however, confounded by genetic and child evocative effects, as well as the earlier mentioned maternal effects (Park & Buriel, 1998; Scarr & McCarthy, 1983). Motivated and intelligent children are more likely to receive education-related paternal investment than other children are (Kaplan et al., 1998), and even these effects might simply be related to shared genes (e.g., for intelligence). Studies that incorporate genetic influences, as well as simultaneously assessing maternal and paternal effects, are needed to more firmly establish a causal relation between paternal investment and child outcomes (Parke & Buriel, 1998; Reiss, 1995). At this point, it seems likely that paternal investment does improve children's social competencies and their later cultural success in contexts with low infant and child mortality rates. In fact, it is likely that paternal investment improves the cultural success of children in many contexts, through payment of dowry and bride price and inheritance of wealth and social title (Hartung, 1982; Irons, 1979; Morrison et al., 1977). But the magnitude of this effect is not known, nor is it known whether these effects vary in magnitude across cultures, families, or individual children.

Selection and social competitiveness. The finding of little relation between SES—an indicator of social competitiveness—and reproductive outcomes in industrial societies suggests that paternal investment that improves the competitiveness of children does not result in reproductive advantages for men (Kaplan et al., 1995; MacDonald, 1997; Vining, 1986). In fact, under these conditions, high levels of paternal investment might be associated with reproductive disadvantages, due to the costs of investment (e.g., lost mating opportunities). However, prior to the demographic shift and in extant developing and preindustrial societies, higher SES and cultural success are consistently related to lower infant and child mortality rates (Brändström, 1997; Hartung, 1982; Hed, 1987; Irons, 1979; United Nations, 1985).

Under conditions in which improvements in SES and social competitiveness reduce child mortality risks, paternal investment might be a viable reproductive strategy if it enabled children to maintain or improve their SES or cultural success in adulthood. More precisely, improved social competitiveness would enhance children's ability to acquire socially and culturally important resources in adulthood, such as marrying a competent spouse or generating wealth, which in turn would reduce the mortality risks of their children and the investor's grandchildren. Such investment might have been particularly advantageous in populations subject to frequent but unpredictable population crashes, if mortality varied inversely and strongly with SES, as it often did in preindustrial Europe and apparently throughout much of human evolution (Perrenoud, 1991; Post, 1985; Rouhani & Jones, 1992). Because fluctuating mortality risks were unpredictable and disproportionately affected low SES children, selection would have favored men who provided investment that facilitated the ability of their children to maintain or improve their later SES and men who maintained a high investment strategy even when current mortality risks were low.

Although not certain, the proposal here—and that of Kaplan et al. (1995, 1998), Lancaster and Lancaster (1987), and MacDonald (1997)—is that paternal investment reflects an evolved reproductive strategy that results in investment in the physical well-being of children and in their social competitiveness. In environments with intense competition over scarce resources and with fluctuating and therefore unpredictable mortality risks, paternal investment in children's social competitiveness is, in a sense, insurance against unforeseen future risks. Of course, given the uneven distribution of social capital (e.g., intelligence, social title, and so forth) and wealth in many human societies, not all men would have had the means to improve the social competitiveness of their children. Selection would favor a short-term quantity strategy (with one or many wives) for these men.

Paternity Certainty and Female Sexuality

Human paternal investment appears to reduce infant and child mortality rates and improve children's social competitiveness, but these outcomes are not likely to be sufficient for the evolution of paternal investment. As described in Table 1, the evolution and proximate expression of paternal investment is also related, at least in some species, to paternity certainty and alternative mating opportunities. These issues, as related to human paternal investment, are addressed in the two respective sections below.

Paternity Certainty

For many species, the level of paternal care appears to decrease as the risk of cuckoldry increases (Møller & Tegelström, 1997). Although the relations are not yet completely understood, as described earlier, it appears that in species in which male investment is obligate, that is, necessary to keep offspring alive, cuckoldry rates are very low (Birkhead & Møller, 1996; Pierce & Lifjeld, 1998). For these species, it is presumed that losing male investment is too costly for females to risk extra-pair copulations. For species in which male investment reduces mortality risks but is not obligate—as with humans—cuckoldry rates appear to vary with male quality, with females risking loss of male investment and copulating with healthier males if they are paired with low-quality males (Møller & Tegelström, 1997). Birkhead and Møller found that across 20 such species of bird, the rate of extra-pair paternity was about 15%.

Given that human paternal investment is beneficial but not obligate in many contexts, the theoretical expectation is that some women attempt to cuckold their social partners. The benefits of cuckoldry include additional social and material support from the extra-pair man and perhaps higher quality genes for her children. The costs are the same as those found in other species, male aggression and abandonment (Betzig, 1989; Daly & Wilson, 1988; Davis & Daly, 1997). The definitive study of human cuckoldry has not been conducted, and thus, no firm conclusions can be drawn about the overall cuckoldry rate or the social correlates of cuckoldry (e.g., whether men with low cultural success are more likely to be cuckolded than other men). Nonetheless, it is clear that many women are socially but not sexually monogamous (Baker, 1996; Bellis & Baker, 1990; Potthoff & Whittinghill, 1965). In fact, men's sexual jealousy and the social controls on women's sexual behavior found in many societies suggest that the sexual prefer-

ences of women are often in conflict with the best interests of their social partners (Buss, 1994; Daly, Wilson, & Weghorst, 1982; Dickemann, 1981; Lancaster & Lancaster, 1987).

In one random sample of 35- to 45-year-old American women, it was found that about 1 in 5 of these women reported engaging in at least one extramarital affair and that some of these affairs resulted in pregnancy (Essock-Vitale & McGuire, 1988). Bellis and Baker (1990) found that women who initiated extramarital affairs often did so around the time of ovulation and within a few days of a sexual relationship with the husband or boyfriend. These extra-pair copulations were less likely to involve the use of contraceptives than the copulations with the main partner were, indicating a greater than 50% chance of any resulting child being sired by the extra-pair partner. "Our study thus predicts a level of paternity discrepancy (i.e., offspring sired by males other than their putative father) of between 6.9 and 13.8%. Blood group studies in Britain indicate levels of paternity discrepancy of from 5.7% [to] . . . 30%" (Bellis & Baker, 1990, p. 998). Other studies suggest cuckoldry rates of between 10% and 15% (Flinn, 1988; Gaulin, McBurney, & Brakeman-Wartell, 1997), although all of these findings must be considered preliminary. Moreover, although not 100%, paternity certainty in humans is much higher than in our two closest relatives (chimpanzees and bonobos), suggesting that most women do not cuckold their social partners, presumably in return for social support and paternal investment.

Female Sexuality

As described earlier, the biology of mammalian reproduction results in a faster potential rate of reproduction for males than females (Clutton-Brock & Vincent, 1991). The sex difference in the potential rate of reproduction contributes greatly to the focus of mammalian males on mating effort and of mammalian females on parental effort. Exceptions are sometimes found in species where males can successfully raise more offspring with a single female than by mating with multiple females, as with canids, or in species where the opportunity cost of paternal investment is reduced (Mock & Fujioka, 1990). The former does not apply to humans to the same degree as it does with canids, given that most women give birth to one child at a time. Although paternal investment does allow women to raise more than one dependent child at a time (Lancaster & Lancaster, 1987), it is not likely that the number of "additional" children raised in this manner is sufficient to offset the reproductive benefits of polygyny. However, the latter, that is, reduced opportunity costs (e.g., reduced mating opportunities), probably does apply to humans.

The point is, given that women generally benefit from paternal investment, selection favors women who develop strategies (though these are not necessarily conscious) that increase the likelihood that men will invest in their children. One associated mechanism is increased paternity certainty, relative to that found in species with no paternal investment. Other mechanisms are likely to focus on reducing the opportunity costs of such investment. For other species, the primary opportunity cost of paternal investment is lost mating opportunities (Dunbar, 1995; Perrone & Zaret, 1979; Thornhill, 1976; Williams, 1966a; Wolf et al., 1988), and given this, women's strategies that reduce the mating opportunities of men might be expected.

Indeed, several features of women's sexuality might be considered strategies, at least in part, that reduce the mating opportunities of men, including concealed ovulation, women's aversion to casual sex, and female-female competition (Geary, 1998; Oliver & Hyde, 1993). Concealed ovulation requires men to maintain a longer relationship with women to ensure conception than is necessary for the males of most other primate species (Dunbar, 1995), but this in and of itself is not sufficient to ensure paternal investment. If other proximate mechanisms, such as pair-bonding (L. C. Miller & Fishkin, 1997), were not operating, then once physical signs of pregnancy were evident, men could easily abandon women. Concealed ovulation and the associated period of extended sexual activity may in fact be one mechanism that fosters pair-bonding and later paternal investment (discussed later; MacDonald, 1992).

Women's aversion to casual sex greatly restricts men's mating opportunities (Buss & Schmitt, 1993) and through this lowers the opportunity cost of paternal investment. It is not that women have somehow colluded to restrict men's mating opportunities. Rather, female choosiness is found in all species in which females invest more in parenting than males do (Andersson, 1994; Darwin, 1871), and one result is that many males have fewer mating opportunities than they would prefer. Men are, however, highly variable in this regard, with many men biased toward monogamous relationships and others toward polygynous relationships (L. C. Miller & Fishkin, 1997). Nonetheless, any evolved tendency toward monogamy on the part of men was potentially predated by restricted mating opportunities, as appears to be the case in monogamous primates (Dunbar, 1995).

One feature of female-female competition is relational aggression, which involves gossiping about and attempting to socially manipulate other girls and women (see, e.g., Crick, Casas, & Mosher, 1997). One function of this form of competition appears to be to exclude potential competitors (over mates) from the social group (Geary, 1998). When effective, this social strategy would reduce the mating opportunities of men and thus lower the opportunity cost of paternal investment.

Cross-Cultural Pattern of Paternal and Maternal Investment

For species where paternal investment is not obligate but can result in reproductive benefits for males—as with humans—theoretical and mathematical models of the coevolution of male and female reproductive strategies predict conflict and compromise (Clutton-Brock, 1991). Conflict results as females attempt to obtain more paternal investment than males prefer to give, whereas males attempt to reduce paternal investment and focus more resources on mating effort. Compromise would result in a level of paternal investment higher than males would prefer (i.e., no investment) but lower than females would prefer. For mammals, a female preference of at least 50% of parental investment provided by males might be expected. Internal gestation and postpartum suckling obligate female investment; thus, a preference for 100% paternal investment is not likely to evolve, and paternal investment is not likely to evolve at all—regardless of female preferences—unless other conditions are met (e.g., reduced mating opportunities).

When applied to humans, the prediction is that paternal investment is greater than zero but lower than maternal investment. This prediction, of course, refers to mean levels of paternal and maternal investment. A corollary prediction is greater variability in parental investment for groups of men than for groups of women. This is because when paternal investment results in reproductive benefits but is not obligate, both high-investment, low-fertility (tending toward monogamy) and low-investment, high-fertility (tending toward polygyny) reproductive strategies are viable options for men (Draper & Harpending, 1988; MacDonald, 1997).

In keeping with these models, there is considerable variability in men's focus on mating effort or parental effort (L. C. Miller & Fishkin, 1997; Parke & Buriel, 1998), as well as greater mean levels of maternal than paternal availability for and engagement with their children. The latter sex difference is found in all human cultures that have been studied (Belsky, Rovine, & Fish, 1989; Eibl-Eibesfeldt, 1989; Hewlett, 1992a; West & Konner, 1976; Whiting & Edwards, 1988; Whiting & Whiting, 1975). Whiting and her colleagues' extensive cross-cultural studies of children's social behavior and development provide numerous examples of this sex difference. In one study of the social behavior of 3- to 6-year-olds in Kenya, India, Mexico, the Philippines, Japan, and the United States, it was found that children of this age were in the proximity of or in contact with their mother 32% to 47% of the time in five of the six cultures and 9% of the time in the sixth (a rural village in Japan); the estimate for the latter is biased, however, because observations were not taken in the household (Whiting & Whiting, 1975). In these same communities, children were in the proximity of or in contact with their father between 3% and 14% of the time. Across these cultures, children were in the presence of their mother 3 to 12 times more frequently than in the presence of their father (see Whiting & Whiting, 1975). A similar pattern was found for 4- to 10-year-olds in studies of communities in Africa, South Asia, South America, Central America, and North America (Whiting & Edwards, 1988).

The sex difference in parental care is even more pronounced for infants and toddlers (i.e., the first 3 years of life; Crano & Aronoff, 1978). Breast-feeding is, of course, the domain of mothers and in many preindustrial and developing societies continues until the child is 3 to 4 years old (Eibl-Eibesfeldt, 1989). Mothers not only breast-feed infants and young children, they also provide most of the child's daily care, such as bathing. In observational studies of families in Liberia, Kenya, India, Guatemala, and Peru, it was found that fathers were rarely or never engaged in the care of infants (i.e., children younger than 1 year of age; Whiting & Edwards, 1988). In the United States, it was found that fathers provided more care to their infants than did fathers in these other settings, although American fathers still provided considerably less care than the infants' mothers (see also Belsky et al., 1989; Harkness & Super, 1992).

The sex difference in the extent to which mothers and fathers provide care to their offspring cannot be attributed to a general inability of men to care for infants and young children. When fathers do interact with infants and young children, they show many of the same characteristics as mothers (e.g., they switch to baby talk) and can provide competent routine care (Belsky et al., 1989; Eibl-Eibesfeldt, 1989; Lamb, 1981; Parke, 1995; Pleck, 1997), although there is some indication that custodial fathers—following divorce—monitor the activities of their children less

diligently, on average, than do custodial mothers (Buchanan, MacCoby, & Dornbusch, 1992). Nor can this sex difference be attributed to father absence, for instance, because he is away hunting or working outside of the home. Belsky and his colleagues found that when both parents were present, American mothers spontaneously engaged their infant 1½ to 2 times more frequently and provided routine care 3 to 4 times more frequently than their husbands did (Belsky, Gilstrap, & Rovine, 1984); these differences may have narrowed somewhat in recent years, at least for some men (Pleck, 1997).

The same result was found in similar studies conducted in Australia, Belgium, France, Great Britain, Israel, and Sweden, (Lamb, Prodi, Hwang, & Prodi, 1982; Lampert & Friedman, 1992; Parke & Buriel, 1998). In the Swedish study, home observations of maternal and paternal interactions with their infant were conducted for traditional and nontraditional families (Lamb et al., 1982). Nontraditional families were those in which the father had taken leave from work in order to care for the infant and had expressed a desire to be the primary caregiver of the infant. Indeed, on a self-report measure, nontraditional fathers rated parenthood more highly than nontraditional mothers did; the opposite pattern was found for traditional families. Despite differences in expressed attitudes toward child care, the mother was the primary caretaker in all of the traditional and nontraditional families. In fact, traditional and nontraditional fathers differed little in the ways in which they interacted with their infants, the primary difference being that traditional fathers were more likely to play with their infants than were nontraditional fathers. In keeping with this finding, Pleck (1997) reported no consistent relation between gender roles (e.g., androgyny) and paternal care.

Observation of parental care in preindustrial societies, such as the !Kung San (Botswana), reveals the same pattern found in Western nations (Flinn, 1992; Griffin & Griffin, 1992; West & Konner, 1976). Studies of the !Kung San are particularly interesting because their social customs center on equality among group members and because they have sometimes been described as being representative of the type of social structure in which human beings evolved (Eibl-Eibesfeldt, 1989). Despite the social norm of equality, observation of caregiving activities—for children younger than 2 years of age—indicates !Kung San fathers provide less than 7% of this care, with the majority of the remaining care provided by the mother (see Katz & Konner, 1981; West & Konner, 1976). In another hunter-gatherer society—the Aka pygmies (Central Africa)—fathers provide more direct care to their infants and children than do fathers in any other society that has been studied (Hewlett, 1988, 1992b). One observational study indicated that Aka fathers held their 1- to 4-month-old infants 22% of the time, on average, in which the fathers were in camp. Nevertheless, during the course of the day, “the father would on average hold his infant for a total of 57 minutes while the mother would hold the infant 490 minutes” (Hewlett, 1988, p. 268).

The sex difference in the level of parental investment is also reflected in the frequency with which mothers and fathers abandon their children, such as following a divorce (Betzig, 1989; Fisher, 1989). Although divorced fathers might not be representative of fathers in general, these studies reveal a great deal about the level of paternal investment in a significant portion of men. Studies conducted in industrial societies indicate that the majority of noncustodial fathers are not actively involved in the day-to-day

raising of their children (Amato & Booth, 1996; Fox, 1995; Furstenberg, 1990; Furstenberg & Nord, 1985). In one large-scale nationally (United States) representative study, it was found that about three out of five children had not seen their noncustodial father during the past year, four out of five had never slept at his house, and the majority of these fathers exerted little effort to maintain any type of contact—such as through phone calls—with their children (Furstenberg & Nord, 1985). In all, it was found that only one out of six children had any type of regular contact with their biological father. The same pattern was found in a more recent national (United States) longitudinal study of parent-child relationships (Amato & Booth, 1996). These findings cannot be attributed to the fact that fathers are much more likely to be the noncustodial parent (>85% of the time; Emery, 1988; Furstenberg, Peterson, Nord, & Zill, 1983) than mothers are.

Furstenberg and Nord (1985) noted that in comparison with noncustodial fathers, noncustodial mothers “tend to maintain a much more active role in childrearing . . . are distinctively more likely to visit with their child on a regular basis, have overnight visits, and have more indirect contact by phone and letter” (p. 896). Amato and Booth (1996) concluded that “divorce does not appear to weaken mothers’ affection for their children” but does lead to a deterioration in the relationship between fathers and their children (p. 364). The pattern of relatively less paternal than maternal investment in children is often more evident for children who are born to unmarried couples (Fox, 1995), although many of these fathers do remain in periodic contact with their children (Parke, 1995; Pleck, 1997). In addition to relatively little direct involvement with their children, about one half of the biological fathers who are not living with the mother (due to divorce or lack of marriage) fail to monetarily support their children, and those who do provide support often invest relatively little in their children, in comparison with the mother and with fathers in intact families (Fox, 1995; Furstenberg, Morgan, & Allison, 1987; Maccoby, Buchanan, Mnookin, & Dornbusch, 1993).

Although these patterns are more prevalent in the United States than in most other industrial nations—due to national differences in the rate of divorce—the pattern of reduced paternal involvement with children following separation from the children’s mother is found in other societies as well, including preindustrial societies. Basically, many fathers invest more in their children when they are residing with their children and the children’s mother (Brunelli, Wasserman, Rauh, Alvarado, & Caraballo, 1995; Draper, 1989; Flinn, 1992; Furstenberg et al., 1983; Hewlett, 1992b; Hill & Hurtado, 1996; West & Konner, 1976). For instance, in an observational study of parent-child social interactions in a Caribbean village, Flinn (1992) found that resident fathers were much more likely to provide some level of care to their children than were nonresident fathers, especially after the nonresident father or the mother remarried (see also Draper, 1989; Furstenberg et al., 1983). A similar pattern of paternal disengagement following remarriage is evident in industrial societies (Emery, 1988) and indicates that the level of paternal investment following divorce is influenced by a number of social factors—remarriage, nature of the relationship with his ex-spouse, and so on—above and beyond the inherent differences in maternal and paternal investment.

Despite the earlier described costs to their children (i.e., increased mortality risks and reduced social competitiveness), many men initiate divorce or reduce their level of investment in the

marriage and their children and thus contribute to the likelihood that their wives will initiate divorce. From the man's perspective, divorce or activities that prompt a spouse to initiate divorce (e.g., an affair) can be viewed as an implicit reproductive decision, that is, a reflection of the potential benefits associated with pursuing a new mate balanced against the costs to the current family. Several studies of divorce, remarriage, and reproduction in extant industrial populations and prior to the demographic shift in Western nations support this position (Johanna, Forsberg, & Tullberg, 1995; Käär, Jokela, Merilä, Helle, & Kojola, 1998). Following a divorce, men are more likely to remarry than women are. When men remarry, they typically marry women younger than their just-divorced wife and are more likely to have children with the new spouse than women are (Buckle, Gallup, & Rodd, 1996). Moreover, twice- (or thrice-) married men, but not women, sire more children, on average, than their monogamous same-sex peers in extant industrial societies, in Western nations prior to the demographic shift, and typically in preindustrial societies (Hill & Hurtado, 1996; Johanna et al., 1995; Käär et al., 1998). The pattern indicates that a reduction in paternal investment in favor of mating effort, that is, to pursue additional mates, is a viable reproductive strategy for some men but not for most women. One evolutionary result would be the maintenance of a greater focus of men, as a group, on mating effort than women and greater overall levels of maternal than paternal investment.

In sum, in all regions of the world, across subsistence activities and social ideologies, observational studies indicate more maternal than paternal investment; however, self-report measures sometimes show a more equal participation of men and women in "domestic labor" (see, e.g., Greenstein, 1996; Russell, 1982). On the basis of the mammalian pattern, the sex difference in physical size and development (indicating male-male competition and a focus on mating effort), and hormonal influences on parenting (Geary, 1998), a mean difference in maternal and paternal investment is not surprising. More important, the patterns described in this section are consistent with the theoretical prediction that when paternal investment is not obligate but otherwise results in reproductive benefits to males, given other conditions (e.g., paternity certainty), then paternal investment will be evident but less than maternal investment (Clutton-Brock, 1991).

The cross-national patterns also indicate that there is considerable variability in individual men's emphasis on mating effort or parental effort. The latter are illustrated by the large differences in the paternal investment of divorced men and men who remain married (MacDonald, 1997; Miller & Fishkin, 1997; Parke & Buriel, 1998; Pleck, 1997). It appears that some men tend toward monogamy and high levels of direct or indirect paternal investment and other men tend toward polygyny (i.e., focus on mating effort) and little or no paternal investment. What is not known is the degree to which this variability is related to genetic factors, responses to different social and ecological conditions, or some combination, issues addressed in the next section.

Correlates of the Proximate Expression of Human Paternal Investment

The first section reviews genetic, social, and developmental correlates of paternal investment, and the second focuses on wider social and ecological correlates.

Genetic, Social, and Development Correlates

Genetic correlates. Based on a parenting survey administered to twins, Pérusse and his colleagues found evidence for modest genetic contributions to two features of parental investment, care (e.g., sensitivity to the child's emotional state) and protection (e.g., keeping the child in close proximity; Pérusse, Neale, Heath, & Eaves, 1994). For fathers, genetic models explained between 18% and 25% of the individual differences on these dimensions of parental investment and between 23% and 39% of the individual differences in maternal investment. These same models suggested that unique environmental effects account for the majority of the individual differences in both paternal and maternal care and protection. The results are, however, very preliminary and in need of replication with more direct measures of parental investment.

Moreover, it is possible that the reported genetic effects do not reflect genetic influences on parental investment per se but rather reflect heritable personality factors that are not directly related to the evolution of parental care but nonetheless affect parenting. Of particular importance would be heritable personality factors, such as empathy and cooperativeness, associated with the stability of long-term relationships, especially with one's spouse, and factors, such as irritability, that would affect responsiveness to children (Graziano & Eisenberg, 1997; Luster & Okagaki, 1993). At this point, it is likely that individual differences in both paternal and maternal investment reflect some degree of heritable variability as well as responses to social and ecological conditions (MacDonald, 1997), although the relative influence of these factors cannot be determined from existing studies.

Social correlates. One apparent social influence on parental investment and parenting style is the nature of the spousal relationship (Belsky, 1993; Belsky et al., 1984; Brunelli et al., 1995; Feldman, Nash, & Aschenbrenner, 1983; Lamb, Pleck, & Levine, 1986; Scher & Maysel, 1994; Simons & Johnson, 1996). Although quality of the spousal relationship—for instance, degree of confidential communication, level of conflict, and so on—has been shown to be related to the ways in which both mothers and fathers interact with their children (Amato & Keith, 1991; Belsky, 1993; Cox, Owen, Lewis, & Henderson, 1989; Davies & Cummings, 1994; Howes & Markman, 1989), "paternal parenting is more dependent on a supportive marital relationship than maternal parenting" (Parke, 1995, p. 37). For instance, a number of observational studies of parent-infant and parent-child interactions have found a significant sex difference in the relation between marital satisfaction and parental engagement with children (Belsky et al., 1984; Feldman et al., 1983; Lamb & Elster, 1985).

In all, "the quality of the marital dyad, whether reported by the husband or wife, is the one most consistently powerful predictor of paternal involvement [with his infant] and satisfaction [with the parenting role]" (Feldman et al., 1983, p. 1634). Belsky et al. (1984) and Lamb and Elster (1985) also found that fathers' engagement with their children was related to the quality of the marital relationship, but, at the same time, they found little relation between the level of marital interaction (e.g., degree of communication) and mothers' involvement with their children. Basically, it appears that marital conflict results in the fathers' withdrawal—emotional or physical—from his children and his spouse (see, e.g., Christensen & Heavey, 1990). However, this withdrawal is sometimes more pronounced for daughters than for sons (Kerig, Cowan,

& Cowan, 1993) and varies with the nature of the interpersonal dynamics between husband and wife (Gottman, 1998).

In sum, men in satisfying relationships with their wives show higher levels of paternal investment than other men do, and it is possible that women's efforts to maintain an intimate and cooperative relationship with their husbands is a strategy to induce greater levels of paternal investment. It is also possible that men biased toward paternal investment are more cooperative and prone to monogamy—and thus less likely to incite conflict with their wives—than other men are and that the relation between marital satisfaction and paternal investment reflects genetic and not social effects (MacDonald, 1997). Most likely, it is a combination of heritable biases and reactivity to marital dynamics that influences paternal investment, but definitive answers must await the use of research designs that assess both social and genetic factors (Parke & Buriel, 1998).

Developmental correlates. One influential model predicts that men's (and women's) focus on mating effort or parental effort varies with childhood experiences (Belsky, 1997; Belsky et al., 1991; Chisholm, 1993; L. C. Miller & Fishkin, 1997). Local mortality risks and low resource availability, in particular, are hypothesized to be associated with the degree to which men later focus on mating or parenting. In environments where mortality risks are high and resources are scarce, investment in more rather than fewer offspring is assumed to ensure that at least some of these offspring will survive to adulthood (Chisholm, 1993). Investing limited resources in one or a few offspring might improve the social competitiveness of these offspring, but if mortality risks are high, such an investment is very risky, that is, all of the investment would be lost if the child were to die.

Belsky et al. (1991) and Chisholm (1993) argued that mortality risks and low resource availability influence the nature of parent-child relationships, in particular, the attachment style of the children (see also Belsky, 1997; L. C. Miller & Fishkin, 1997). In risky, low-resource environments, the psychological and physiological stressors on parents are high, which, in turn, results in less attentive and more conflicted parent-child relationships. These relationships are predicted to be associated with a tendency of offspring to form unstable, low-parental-investment relationships in adulthood, that is, relationships focused on mating effort and not on parental effort. In less risky, high-resource environments, parent-child relationships are warmer and reflect higher levels of parental investment (MacDonald, 1992). These relationships are predicted to be associated with a tendency of offspring to form stable, high-parental-investment relationships in adulthood, that is, relationships focused on parental effort and not on mating effort.

Aspects of this model have been supported in several recent studies (see Belsky et al., 1991, and Chisholm, 1993, for reviews). For instance, M. Wilson and Daly (1997) found that age of first reproduction, number of children born per woman, mortality risks, and local resource availability were all interrelated in modern-day Chicago. In neighborhoods with low resource availability, men competed intensely for these limited resources. The associated increase in mortality rates resulted in a shorter average life span, relative to more affluent neighborhoods. For men, this resulted in an average life span difference of 23 years (54 vs. 77 years), comparing the least and most affluent neighborhoods. Shorter life spans, in turn, were associated with earlier age of first reproduction for both men and women and nearly twice as many children born

per woman, comparing the least and most affluent neighborhoods. In other words, the early and frequent reproduction of women and men in these contexts might be, at least in part, a facultative response to high mortality rates.

Consistent with the Belsky et al. (1991) model, paternal absence and marital conflict are also associated with reproductive events. For girls, these factors are associated with an earlier age of menarche and earlier sexual activity relative to girls living in more stable home environments and with both biological parents, although genetic influences might also contribute to both marital conflict and early menarche (Moffitt, Caspi, Belsky, & Silva, 1992; Rowe, 1994). For boys, paternal absence and marital conflict are associated with greater risk taking and higher age-specific mortality rates in adulthood. Individuals (male and female) whose parents divorced before these individuals were 21 years old have shorter average life spans than do individuals whose parents did not divorce. One of the causes of increased mortality risks in these men is a higher frequency of accidental and violent deaths (Peterson, Seligman, Yurko, Martin, & Friedman, 1998). In relation to men whose parents had not divorced, these men were also more likely to divorce and thus showed reduced paternal investment themselves (Tucker et al., 1997), but, again, genetic and social contributions to these effects were not separated in these studies.

Moreover, there are other studies that are inconsistent with this psychosocial stress model of parental investment. In samples of Ache and Mayan men, Waynforth, Hurtado, and Hill (1998) found that "measures of family stress and violence were unsuccessful in predicting age at first reproduction, and none of the psychosocial stress indicators predicted lifetime number of partners" (p. 383). Father absence was, however, related to less "willingness to pay time and opportunity costs to maintain a sexual relationship" (Waynforth et al., 1998, p. 383), although this could easily reflect genetic and not psychosocial effects. Other studies indicate that in many human populations and, in fact, in many other species, low resource availability and other stressors are associated with delayed, not early, reproduction (Krebs & Davies, 1993; MacDonald, 1997). The pattern of low resource availability being associated with delayed reproduction led MacDonald to critically evaluate the Belsky et al. (1991) model. On the basis of this evaluation, MacDonald concluded that some of the correlations between early family stressors and reproductive strategies reflect, in part, heritable differences in reproductive strategy rather than a strong causal relation between early experience and later mating strategy.

At this point, there does appear to be a relation between early experiences—particularly mortality risks, parental conflict, and early attachment to parents—and men's later focus on mating effort or parental effort. However, without studies that control for genetic effects, causal relations between these developmental factors and later reproductive activities cannot be drawn.

Cultural and Ecological Correlates

Draper and Harpending (1988) have characterized human cultures as tending to be father absent or father present, reflecting differences in the relative emphasis of men on mating and parenting, respectively. A brief contrast of father-absent and father-present societies is provided in the first section below, and the second provides a description of the relation between the OSR and the reproductive strategies of men.

Father-absent and father-present societies. Father-absent societies are characterized by aloof husband–wife relationships, a polygynous marriage system, local raiding and warfare, male social displays—verbal and with ornamentation—and little or inconsistent direct paternal investment in children (Draper & Harpending, 1988; Hewlett, 1988; West & Konner, 1976; Whiting & Whiting, 1975). These conditions “are particularly prevalent in so-called middle-range societies, i.e., those where agriculture is practiced at a very low level” (Draper & Harpending, 1988, p. 349), and in resource-rich ecologies. In the latter, women can often provide adequate care to their children—for example, through small-scale agriculture—without the direct contribution of the father (Draper, 1989; E. M. Miller, 1994). Under these conditions, paternal investment does not appear to influence child mortality rates to the same extent as is found in other ecologies, and thus, the reproductive benefits of paternal investment are often smaller than the benefits associated with a focus on mating effort (E. M. Miller, 1994).

In mid-range societies (e.g., pastoral, agricultural), many men are able to accumulate resources beyond what is needed to sustain a single wife and her family (see below). The issue for these men is whether to invest these additional resources in a monogamous relationship and the children of one woman, which would result in somewhat reduced child mortality risks and would improve their social competitiveness, or invest these resources in mating effort (i.e., to obtain additional wives). In societies in which polygynous marriages are not prohibited, most wealthy men opt for the latter strategy. In these societies, men compete with each other for the establishment of social dominance or for the control of those material resources (e.g., land and cattle) that women need to raise their children (see, e.g., Borgerhoff Mulder, 1990). The achievement of social or economic dominance, in turn, influences the number of women the man can marry and the number of surviving children (see, e.g., Chagnon, 1988; Irons, 1993). Given this, the investment of “excess wealth” in mating effort is typically a successful reproductive strategy for men in these societies.

Father-present societies, in contrast, are more commonly found in harsh or unstable ecologies and in industrial, or other relatively large, stratified societies (Draper & Harpending, 1988). These are societies that are generally characterized by ecologically or socially imposed monogamy (Flinn & Low, 1986). Under harsh ecological conditions, the vast majority of men are unable to acquire the resources (e.g., meat obtained through hunting) needed to support more than one wife and family. The reproductive aspirations of men are thus ecologically restricted to monogamy. This is because high levels of paternal investment are often necessary to ensure the survival of children and because these ecologies limit the ability to accumulate excess wealth and thus limit mating opportunities.

In many industrial societies, monogamy is socially imposed, that is, there are formal laws that prohibit polygynous marriages. Although the factors that led to the cultural evolution of socially imposed monogamy are not fully understood (see Betzig, 1995, and MacDonald, 1995, for discussion), the net result is a relative shift in men’s reproductive efforts, from mating effort to parental effort. This is because legal and moral prohibitions against polygynous marriages, combined with women’s preference for high-investment monogamous marriages, limit men’s mating opportunities and thereby reduce the opportunity cost of paternal

investment. With a reduced opportunity cost of paternal investment, investing excess wealth in the well-being of children is a viable reproductive strategy for men, especially in ecologies where mortality risks fluctuate greatly and vary inversely with level of paternal investment (e.g., during epidemics); it is of interest that greatly fluctuating mortality risks were common in preindustrial Europe, where socially imposed monogamy evolved.

Nevertheless, there are important individual differences within both father-absent and father-present societies. For instance, even though direct paternal investment in children tends to be lower in cultures that allow polygynous marriages, in comparison with cultures in which monogamy is ecologically or socially imposed, most of the men (>80%) in most polygynous societies are monogamously married (Murdock, 1981). Even so, there is some indication that in cultures that allow polygyny, monogamously married men often divert social and material resources from the family to their mating efforts, that is, their attempts to attract and obtain a second wife (see, e.g., Hames, 1992, 1996). Many men engage in polygynous relationships in monogamous societies as well (e.g., serial marriages), although socially imposed monogamy likely restricts these activities to some degree.

Moreover, under some conditions high-status polygynously married men are able to invest more material and social resources in their many children than are lower status and monogamously married men. On the Ifaluk islands, in the Western Pacific, chiefs tend to have more wives (serial monogamy in this case) and children than do lower status men but associate with their children twice as often as these lower status men (Betzig & Turke, 1992). This is possible because high-ranking men receive tributes from other families and relatively more food from communal fishing than do low-ranking men. The net result is that chiefs spend less time working than other men and have more material resources and time to invest in their children.

The most important point is that when social and ecological conditions do not impose monogamy, many men focus more on mating (e.g., achieving social dominance through male–male competition) than on parenting. In contrast, when social and ecological factors impose monogamy, many men focus more on parenting than on mating. There are, of course, individual differences in all of these societies, and these are likely to be related to both genetic and social factors (e.g., spousal relationship), as described earlier.

Operational sex ratio. At this point, it should be clear that there is not a simple biologically determined level of paternal investment, given that men’s investment in their families is influenced by a host of interpersonal (e.g., spousal relationship) and cultural (e.g., socially imposed monogamy) factors. In addition to these factors, the OSR—the ratio of marriage-age men to marriage-age women—appears to influence the degree to which men focus on mating effort or parental effort (Guttentag & Secord, 1983; Pedersen, 1991; Secord, 1983). In human populations, the OSR is determined by sex differences in birth rates, death rates, and migration patterns.

Sex ratios by themselves do not bring about societal effects, but rather that they combine with a variety of other social, economic, and political conditions to produce the consequent effects on the roles of men and women and the relationship between them. (Guttentag & Secord, 1983, p. 137)

In recent years, one factor that has skewed the OSR in industrial societies is the population growth rate, with expanding populations yielding an "oversupply" of women. An oversupply of women results from a preference of women for slightly older marriage partners and of men for slightly younger marriage partners (Kenrick & Keefe, 1992). With an expanding population, the younger generation of women select marriage partners from a smaller cohort of older men. The resulting imbalance in the numbers of marriage-age men and women is correlated with a variety of general social patterns, including divorce rates, sexual mores, and levels of paternal investment, among other things (Guttentag & Secord, 1983; Pedersen, 1991; Secord, 1983).

During periods when there is an oversupply of women—such as from 1965 through the 1970s in the United States—men are better able to pursue their reproductive preferences than women are. This is because an oversupply of women creates increased mating opportunities for men. These historical periods are generally characterized by liberal sexual mores (i.e., many sexual partners for both men and women), high divorce rates, an increase in the number of out-of-wedlock births and the number of families headed by single women, an increase in female participation in the workforce, and generally lower levels of paternal investment (see Guttentag & Secord, 1983). Basically, during these periods, men, on average, are able to express their preference for a variety of sexual partners and relatively low levels of paternal investment (Pedersen, 1991), although some men remain monogamous (L. C. Miller & Fishkin, 1997). A very different pattern is associated with historical periods in which there is an oversupply of men (Guttentag & Secord, 1983). Here, women are better able to enforce their preferences for a monogamous, high-investment spouse. As a result, these periods are generally characterized by an increase in the level of commitment of men to marriage, as indexed by declining divorce rates and greater levels of paternal investment (Pedersen, 1991).

Hurtado and Hill (1992) reported a similar pattern with a comparison of marital stability—that is, men's focus on mating or parenting—in the Ache and Hiwi (hunter-gatherers in southwestern Venezuela). Ache men live in a social environment that provides many mating opportunities, whereas a large imbalance in the ratio of men to women (more men than women) greatly restricts Hiwi men's mating opportunities.

Differences in levels of mating opportunities between the Ache and the Hiwi occur alongside marked contrasts in marital stability. Whereas serial monogamy and extramarital promiscuity are very common among the Ache, stable lifetime monogamous unions with almost no extramarital copulation is the normative mating pattern among the Hiwi. (Hurtado & Hill, 1992, p. 40)

These patterns are found despite high infant and child mortality risks associated with paternal abandonment with the Ache and low risks with the Hiwi, suggesting that the reproductive strategy of some men is more strongly influenced by mating opportunities than by child mortality risks, at least in the Ache.

Evolutionary Pressures

Even among the few mammalian species in which paternal investment is common, human paternal care is unique in many ways. Unlike female canids, women do not typically give birth to

more than one child at a time and, in fact, give birth to only a few children in their lifetime. Thus, the principle benefit of paternal investment in canid species—large litter sizes and thus greater reproductive success with a monogamous than polygynous mating strategy—is not found in humans. Humans are unique even among monogamous primates, as most of these species are small arboreal monkeys or gibbons that live in relatively isolated family groups (Dunbar, 1995). Humans, in contrast, are large terrestrial apes that live in multimale, multifemale communities. The males of most terrestrial species of ape and monkey that live in multimale, multifemale communities focus most of their reproductive efforts on mating and not on parenting (Goodall, 1986; Smuts, 1985; Smuts & Gubernick, 1992). Indeed, the large sex differences in the physical size of our ancestors (e.g., *A. afarensis*) suggests that hominid males invested more in mating than in parenting as well.

Given the general mammalian pattern and the many unique features of human paternal investment, it is unlikely that a single factor contributed to its evolution. Rather, the evolution of human paternal investment likely resulted from a confluence of factors reflecting the coevolution of the reproductive strategies of women and men (Alexander, 1990; Clark, Begun, & Prout, 1999; Darwin, 1871; Dawkins, 1989; E. O. Wilson, 1975). In other species, these factors include improvements in offspring survival rate or quality, increased paternity certainty, and reduced mating opportunities (see Table 1). It is likely that these same factors in combination contributed to a shift over of the course of human evolution from an exclusive male focus on mating effort to at least a partial emphasis on parental effort.

Indeed, on the basis of patterns in preindustrial and developing nations, it is likely that hominid paternal investment resulted in reduced offspring mortality rates and in improvements in their offspring's ability to compete for scarce social and material resources in adulthood. The latter is consistent with the threefold increase in brain volume and presumably in intelligence from *Australopithecines* to modern-day humans (McHenry, 1994a; Miller, 1994; Rushton & Ankney, 1996) and with a near doubling of the estimated length of the juvenile period (from 10 to 16 to 20 years; McHenry, 1994b; Tanner, 1990). Although increased brain size is almost certainly associated with advantages in social competition (Alexander, 1990), it entails the costs of increased vulnerability in infancy and prolonged dependency, which, in turn, increase the costs of male abandonment to pursue additional mates (Lovejoy, 1981). In other words, to ensure that large-brained and socially competitive offspring reached adulthood, some shift from mating effort to parental effort (e.g., provisioning and social protection) was likely to have been necessary for hominid males.

In comparison with our two closest relatives (chimpanzees and bonobos), men enjoy a high degree of paternity certainty and provide prolonged levels of parental care. Although this care may have initially been mating effort (i.e., females making sexual access contingent on male investment), as is found in some extant primates (Smuts & Gubernick, 1992), a number of factors indicate true paternal investment in humans. Included among these is a universal concern of men over the paternity of their children, sexual jealousy, social controls on the sexual behavior of women, and higher levels of investment in biological children than in stepchildren, the latter being largely mating effort (Buss, 1994; Daly & Wilson, 1985; Daly, Wilson, & Weghorst, 1982; Dicke-mann, 1981). Equally important, the majority of women who

receive adequate levels of paternal care appear to be sexually monogamous and thus increase the benefits of paternal investment (i.e., increased paternity certainty) and the costs of abandonment (e.g., increased mortality rates of their biological children). Even with high levels of paternity certainty and benefits to offspring, for human paternal investment to have evolved, mechanisms that reduced the mating opportunities of our male ancestors and therefore reduced the opportunity cost of paternal investment were likely to have been necessary. The offspring in many mammalian species would likely benefit from paternal investment, but such investment is not typically found because in nearly all of these species, males who focus on mating effort have a reproductive advantage over males who focus on parental effort (Clutton-Brock, 1989).

Because it is in women's best interest to secure paternal investment at a cost of lost mating opportunities for men, any mechanism that reduced these opportunities was likely to have originated in our female and not our male ancestors. In fact, it is likely that the evolutionary course toward paternal investment was initiated by reproductive and social adaptations in our female ancestors, given the strong bias of mammalian males toward mating effort. Although it is not certain, these mechanisms appear to include concealed ovulation, women's aversion to casual sex, and female-female competition to exclude competitors from the social group, as described earlier (Geary, 1998).

The relation between concealed ovulation and paternal investment is complex, however, and merits further discussion. Dunbar's (1995) analysis of primate species indicates that social monogamy and high levels of paternal investment are almost always associated with concealed and sometimes synchronized ovulation but that concealed ovulation is most common in primate species with high risks of infanticide (Hrdy, 1979). In other words, concealed ovulation is not always associated with high levels of paternal investment, but high levels of paternal investment are typically associated with concealed ovulation. One possibility is that reduced infanticide risk—that is, mating with many males and thus confusing paternity—was the initial selection pressure for concealed ovulation in hominids (see Hrdy, 1979), although men do not appear to be biologically biased toward infanticide (Daly & Wilson, 1988). Concealed and later synchronized ovulation (which prevents males from mating with more than one fertile female at a time) appears to be a further evolved strategy in some primate species, a strategy to reduce the mating opportunities of males and thereby reduce the opportunity cost of paternal investment (Dunbar, 1995). Although concealed ovulation increases the amount of affiliation between males and females, it is not sufficient to ensure paternal investment, especially in multimale, multifemale communities where alternative mating opportunities are possible.

As noted earlier, once physical signs of pregnancy were evident, males could abandon females and pursue other mates if an additional mechanism was not operating. It appears that this mechanism is pair-bonding (Lovejoy, 1981; MacDonald, 1992; Miller & Fishkin, 1997). In this view, concealed ovulation increased the amount of male-female affiliation time and resulted in prolonged sexual activity, which, in turn, reduced the mating opportunities of males and, at the same time, provided the initial conditions for the evolution of pair-bonding (MacDonald, 1992). In addition to reducing the risk of male abandonment during pregnancy, pair-bonding would facilitate the type of spousal relationship that

appears to facilitate paternal investment. Pair-bonding would also increase the sexual fidelity of females and thereby increase paternity certainty, which, in turn, would result in reproductive benefits for those males who invested in offspring. Once male investment resulted in reproductive benefits, such as reduced offspring mortality rates and increased social competitiveness, the stage would be set for the further evolution of paternal investment.

On the other hand, if the benefits of hominid paternal investment were similar to those found in extant preindustrial and developing societies and in Western nations prior to the demographic shift, then lower levels of paternal than maternal investment would be expected (and are found). If paternal investment yields reproductive benefits but is not obligate—and it does not appear to be in humans—then focuses on mating effort, parental effort, or some combination are all viable reproductive strategies for men. When both mating effort and parental effort are viable options, considerable variability in men's reproductive strategies would be expected (and are found). Moreover, because paternal investment does not appear to be obligate, it is in the best interest of some women to attempt the cuckoldry of their social partners. Cuckoldry risks, in turn, would reduce the level of paternity certainty and, through this, militate against paternal investment. All of these factors lead to the prediction of greater levels of maternal than paternal investment and continued conflict between men and women over this investment (Buss, 1994).

Conclusion

When considered in terms of mammalian reproduction, it is unremarkable that mothers throughout the world show a much greater availability for and engagement with their children than fathers do (Whiting & Edwards, 1988). This is because the biology of mammalian reproduction necessarily results in higher levels of maternal than paternal investment and creates a faster potential rate of reproduction for men than for women (Andersson, 1994; Clutton-Brock & Vincent, 1991). Under these conditions, the cross-species pattern is for the reproductive strategy of females to be focused on parental effort and the reproductive strategy of males to be focused on mating effort (Trivers, 1972). When viewed from this perspective, the most noteworthy feature of human parental care is that many fathers show some degree of direct and indirect investment in their children. Although the level of paternal care is far from satisfactory for those individuals who call for equal maternal and paternal investment, it is nonetheless remarkable in comparison with the relatively little paternal care found in the two species most closely related to humans and in terms of the more general pattern found with mammals (Clutton-Brock, 1989; Whitten, 1987).

At this point, definitive conclusions cannot be drawn about the evolutionary and proximate mechanisms associated with human paternal investment, but what is known suggests that many of the same features that are associated with such investment in other species are also important in humans (see, e.g., Perrone & Zaret, 1979; Thornhill, 1976). These factors include reductions in infant and child mortality rates in high-risk environments and improvements in children's later ability to compete for essential social and material resources (see, e.g., A. Reid, 1997; Kaplan et al., 1998). The evolution and proximate expression of human paternal investment also appear to be related to relatively high—though not

100%—levels of paternity certainty and to reduced mating opportunities. The latter appears to have resulted from physical (e.g., concealed ovulation) and social (e.g., aversion to casual sex) adaptations in our female ancestors, as appears to be the case with socially monogamous primates (Dunbar, 1995).

The proximate expression of human paternal investment is correlated with many factors, including heritable individual differences in emphasis on mating effort or parental effort, personality, the quality of the spousal relationship, and child characteristics (Luster & Okagaki, 1993; MacDonald, 1997; Pérusse et al., 1994). Childhood experiences—such as attachment to parents, level of parental conflict, and parental divorce—and wider social and ecological factors—such as laws against polygynous marriages and the OSR—are also correlated with the degree to which men invest in the well-being of their children (Belsky et al., 1991; Flinn & Low, 1986; L. C. Miller & Fishkin, 1997). However, the relative contribution of each of these factors is not currently known. For instance, it is not clear whether early experiences in conflicted households cause later low-investment parenting, whether shared genes cause unstable relationships across generations regardless of rearing environment, or whether some interaction between heritable risks and early stressors is involved (Reiss, 1995; MacDonald, 1997). The challenge for researchers is to design studies that enable the simultaneous assessment of many of these factors and to more critically explore the causes and correlates of individual differences in human paternal investment.

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