
CHAPTER 16

Evolution of Paternal Investment

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REPRODUCTION INVOLVES TRADE-OFFS between mating and parenting (Trivers, 1972; Williams, 1966), and attendant conflicts between males and females and parents and offspring (Hager & Johnstone, 2003; Trivers, 1974). Conflicts arise because the ways in which each sex and each parent distribute limited reproductive resources is not always in the best interest of the other sex or offspring. Still, males and females have overlapping interests, as do parents and offspring, and thus the evolution and proximate expression of reproductive effort reflects a coevolving compromise between the best interest of the two sexes and of parents and offspring. For the majority of species, the evolutionary is males invest more in mating (typically competition for access to reproductive females) than in parenting, and females invest more in parenting than in mating (Andersson, 1994; Darwin, 1871), although there are readily understandable exceptions (Reynolds & Székely, 1997). Females benefit from male-male competition and the male focus on mating, because their offspring are sired by the most fit males, and successful males benefit because they produce more offspring by competing for access to multiple mates than by investing in parenting. The basic pattern is especially pronounced in mammals, where male parenting is found in less than 5% of species and where females invest heavily in offspring (Clutton-Brock, 1991). The reasons for the large mammalian sex difference are related to the biology of internal gestation and obligatory post-partum suckling, and the associated sex differences in the opportunity and potential benefits of seeking multiple mating partners (Clutton-Brock & Vincent, 1991; Trivers, 1972).

Given this, the phenomenon of human paternal investment is extraordinary and the focus of this chapter (see also Draper & Harpending, 1988; Flinn & Low, 1986; Geary, 2000; Geary & Flinn, 2001; Marlowe, 2000). Human paternal investment is considered in terms of the benefits of providing care to children and the costs of investment from the males' perspective, as well as cost-benefit trade-offs from the females' perspective. In the first section, I provide an introduction to these trade-offs in nonhuman species, and discuss them in relation to human paternal investment in the second section. In the third section, I discuss the

proximate correlates of men's parenting, and in the final section focus on their potential ultimate correlates.

PARENTAL INVESTMENT

Parents invest in offspring indirectly and directly (Qvarnström & Price, 2001). Indirect investment is genetic inheritance, although the quality of this investment (e.g., as it effects growth rate) often varies from one parent to the next (Savalli & Fox, 1998). Direct investment involves providing offspring with nutrients during gestation or egg production and postnatally, as well as protecting them from predators (Clutton-Brock, 1991). For highly social species, direct investment can also involve assistance in establishing position in the social hierarchy and navigating social discourse (Alberts & Altmann, 1995; Buchan, Alberts, Silk, & Altmann, 2003). Separating the effects of direct from indirect parental investment is complicated by potential interactions between genetic and environmental influences on offspring. Indirect, genetic influences can, for instance, affect the traits of offspring and thus the quantity and quality of direct investment provided by parents (Moore, Wolf, & Brodie, 1998).

The details of these potential genotype-environment interactions are not well understood and thus my discussion of direct parental effects must be tempered by the possibility of indirect effects. Despite these complications, parenting is generally associated with lower offspring mortality due to protection from predators and conspecifics (i.e., member of the same species) and parental provisioning (Clutton-Brock, 1991). The result is healthier adults that are better able to compete for mates and that produce larger and healthier offspring themselves (Clutton-Brock, Albon, & Guinness, 1988). In short, parents pay the cost of investing in offspring, because these offspring are more likely to survive and reproduce than are offspring that receive reduced or no direct parental investment.

PATERNAL INVESTMENT

Although uncommon in mammals, paternal investment is found in many species of bird, fish, and in some species of insect (Perrone & Zaret, 1988; Thornhill, 1976; Wolf, Ketterson, & Nolan, 1988). The study of the attendant cost-benefit trade-offs is complicated by the evolutionary history of the species, as well as by whether paternal investment is obligate or facultatively expressed (Arnold & Owens, 2002; Clutton-Brock, 1991; Fishman, Stone, & Lotem, 2003). Obligate investment means that male care is necessary for the survival of his offspring. In these species, selection will favor males who invest in offspring and could eventually result in males showing high levels of paternal investment, independent of proximate conditions (Westneat & Sherman, 1993).

Human paternal investment and that of many other species is facultatively expressed, that is, it is not always necessary for offspring survival and thus can vary with proximate conditions (Westneat & Sherman, 1993). The facultative expression of paternal investment is typically found when there is a high degree of paternity certainty; when investment improves offspring survival rates; and, when it does not severely restrict opportunities to mate with multiple females (Birkhead & Møller, 1996; Møller & Cuervo, 2000; Perrone & Zaret, 1988; Trivers, 1972). The

facultative expression of male parenting thus reflects trade-offs between the costs and benefits of this direct investment in the social and ecological contexts in which the male is situated.

TRADE-OFFS

Male parenting in fish species is typically associated with external fertilization and male defense of nesting sites to exclude competitors (Perrone & Zaret, 1979). Under these conditions, paternal certainty is high. Males are also able to fertilize the eggs of more than one female, and thus investment does not reduce mating opportunities. In contrast, paternal investment is uncommon in fish species with internal fertilization, presumably because paternity is not certain and because males can abandon females after fertilization and avoid the cost of investment.

Paternal investment does occur in some species with internal fertilization, including most species of bird and a few mammals, mostly carnivores and some primates (Dunbar, 1995; Mock & Fujioka, 1990). Again, the degree of paternal investment varies with potential benefits to offspring, paternity certainty, and availability of other mates. The former benefit of paternal investment has been demonstrated by removing fathers from nests, which results in lower offspring survival rates. In an analysis across 31 bird species, Møller (2000) determined that 34% of the variability in offspring survival was due to paternal investment. In some species, removal of the male results the death of all nestlings (obligate investment) and in other species male removal has lesser effects, as females compensate for lost provisions (facultative investment).

As noted, variability in male provisioning is related to the likelihood of paternity (Arnold & Owens, 2002; Møller, 2000). For many species, female cuckoldry of their social partner involves trade-offs between the risk of losing his investment versus gaining better genes and thus healthier offspring from another male (Møller & Tegelström, 1997). In species in which male investment is obligate, cuckoldry rates are very low, that is, females do not risk losing paternal investment (Birkhead & Møller, 1996). For species in which male investment is not obligate, cuckoldry rates vary with male quality; females often risk loss of male investment and copulate with healthier males, if they are paired with low-quality males (Møller & Tegelström, 1997). These cross-species relations have been supported by some (Dixon, Ross, O'Malley, & Burke, 1994; Sheldon, Räsänen, & Dias, 1997), but not all (Kempnaers, Lanctot, & Robertson, 1998) studies of the within-species relation between paternal investment and extra-pair paternity. Some of the inconsistencies may be related to the ability of males to detect their partner's extra-pair copulations or extra-pair paternity of offspring (Neff & Sherman, 2002). Ewen and Armstrong (2000) studied this relation in the socially monogamous stitchbird (*Notiomystis cincta*); males provide between 16% and 32% of the food to the nestlings, depending on age of the brood. Extra-pair copulations occur in the pair's territory and are thus easily monitored by the male. Males counter this paternity threat by chasing off extra-pair males. Despite this male strategy, extra-pair copulations do occur. In this study, as the frequency of female extra-pair copulations increased, male provisioning of the brood decreased ($r = -.72$).

Neff (2003) studied these relations in the bluegill sunfish (*Lepomis macrochirus*), where parental males defend a territory, externally fertilize and then fan and

protect eggs. One type of cuckold male hides behind rocks or plants and attempts to sneak into the nest to fertilize the eggs. Before the eggs hatch, threats to paternity can be thus be determined by presence or absence of cuckold males. After the eggs hatch, parental males can determine paternity based on olfactory cues from fry urine. As predicted, parental males reduced fanning and protecting of eggs, if cuckold males were present. Once the fry hatched and parental males could determine paternity, they protected them only if they were the father, whether or not cuckold males were present before the fry hatched. This and other well-controlled studies (Ewen & Armstrong, 2000) suggest that when males detect non-paternity risks, they reduce their level of paternal investment and often do so in direct relation to the magnitude of the risk (Møller, 2000). However, provisioning and protecting offspring is not always parental investment, as male provisioning is sometimes related to mating effort; specifically, to obtain sexual access to the offspring's mother (Rohwer, Herron, & Daly, 1999; Smuts & Gubernick, 1992).

In any case, paternity certainty and an improvement in the survival rate of his offspring are not sufficient for the evolution or facultative expression of paternal investment. The benefits of paternal investment must also 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 large litters (Asa & Valdespino, 1998). 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 parental investment strategy than with a polygynous strategy. Paternal investment might also evolve if females are ecologically dispersed and thus males do not have the opportunity to pursue multiple mating partners, as with *callitrichid* monkeys, such as marmosets (*Callithrix*; Dunbar, 1995). In these species, paternal investment is related to male-female joint defense of a defined territory, which limits the male's ability to expand his territory to include other females; female-on-female aggression that prevents males from forming harems; concealed ovulation, which prolongs the pairs' relationship to ensure conception; and, females often have twins, which increases the benefits of paternal care.

INTEGRATION

The patterns associated with the facultative expression of paternal investment are described in Table 1. Male's reproductive behavior is especially complicated when paternal investment improves offspring survival rate and offspring quality, and when the reproductive benefits of seeking additional mates do not always outweigh the reproductive benefits of paternal investment. These dynamics appear to parallel those found in humans. Under these conditions, selection will favor a mixed reproductive strategy, with different males varying in their emphasis on mating and parenting, and individual males varying in emphasis on mating and parenting in their relationship with different females. Individual differences in paternal investment, in turn, are likely to be related to male condition (e.g., social status), ecological factors (e.g., available mates), female strategies to induce paternal investment, female quality, and to genetically-based differences in male reproductive strategy (Krebs & Davies, 1993).

Table 16.1
Factors Associated with the Evolution and Facultative Expression
of Paternal Investment

Offspring Survival

1. If paternal investment has little or no effect on offspring survival rate or quality, selection will favor male abandonment if additional mates can be found (Trivers, 1972; Westneat & Sherman, 1993; Williams, 1966).
2. If paternal investment results in relatively but not an absolute improvement in offspring survival rate or quality, selection will favor males that show a mixed reproductive strategy. Males can vary in degree of emphasis on mating and parenting, contingent on social (e.g., male status, availability of mates) and ecological (e.g., food availability) conditions (Westneat & Sherman, 1993; Wolf et al., 1988).

Mating Opportunities

1. If paternal investment is not obligate and mates are available, selection will favor:
 - A. Male abandonment, if paternal investment has little effect on offspring survival rate and quality (Clutton-Brock, 1991).
 - B. A mixed male reproductive strategy, if paternal investment improves offspring survival rate and quality (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, will reduce the opportunity cost of paternal investment. Under these conditions, selection will favor 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; Thornhill, 1976; Westneat & Sherman, 1993).

Paternity Certainty

1. If the certainty of paternity is low, selection will favor male abandonment (Clutton-Brock, 1991; Møller, 2000; Westneat & Sherman, 1993).
 2. If the certainty of paternity is high, selection will favor paternal investment if:
 - A. 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 (Dunbar, 1995; 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, selection will favor 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).
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HUMAN PATERNAL INVESTMENT

The evolution and maintenance of human paternal investment must involve trade-offs between benefits to children, paternity certainty, and lost mating opportunities. The relation between paternal investment and the well-being of children is reviewed in the first subsection, whereas paternity certainty and the reproductive strategies of women and associated mating opportunities of men are reviewed in the second subsection.

PHYSICAL AND SOCIAL WELL-BEING OF CHILDREN

As noted in Table 16.1, to evolve, human paternal investment and its facultative expression must reduce child mortality rates or improve in child quality (e.g., as it enhances their social competitiveness). Support is found in the relation between paternal investment and children's well-being in extant populations and the historical record (Hill & Hurtado, 1996; Richner, Christe, & Oppliger, 1995; Schultz, 1991).

Physical Well-Being In traditional and developing societies and in the historical record, there is a consistent relation between paternal investment and children's mortality rates, but a strong causal relation cannot be drawn. First, higher quality men are typically paired with higher quality (e.g., better gatherers) women (Blurton Jones, Hawkes, & O'Connell, 1997); thus the higher survival rates of their children cannot be attributed solely to men's parenting. Second, the interaction between indirect genetic and direct parental effects on children is not well understood (e.g., Caspi et al., 2002) and thus complicates the assessment of direct investment. Finally, men's parenting may at times be mating effort and is thus not paternal investment per se (Borgerhoff Mulder, 2000; Marlowe, 2000).

Despite these complications, men's providing of care, food, and other resources lowers infant and child mortality risks in some contexts and generally improves the physical health of children. In the hunter-gatherer Ache (Paraguay), about 1 of 3 children die before reaching the age of 15 years, with highly significant differences in mortality rates for father-present and father-absent children (Hill & Hurtado, 1996). Father absence triples the probability of child death due to illness and doubles the risk of the child being killed by other Ache. 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 to a mortality rate of about 20% for children whose father resides with them until their 15th birthday.

There is a consistent relation between marital status and infant and child mortality rates in developing countries. "Both univariate and multivariate results show that mortality of children is raised if the woman 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" (United Nations, 1985, p. 227). The same pattern was found throughout preindustrial and industrializing Europe and the United States (Herlihy, 1965; Klindworth & Volland, 1995; Morrison, Kirshner, & Molho, 1977; Schultz, 1991). In an analysis of demographic records from eighteenth century Berlin, Schultz found a strong correlation ($r = .74$) between socioeconomic status (SES, a composite of income, educational level, and occupational status) and infant and child mortality rates; SES was defined in part by paternal occupation. During the 1437 to 1438 and 1449 to 1450 epidemics in Florence, Italy, child mortality rates increased 5- to 10-fold and varied inversely with SES (Morrison et al., 1977). In nineteenth century Sweden, infant mortality rates were 1½ to 3 times higher for children born to unmarried mothers than children born to married couples (Brändström, 1997).

An analysis of mortality risks in early twentieth century England and Wales suggested that "a child's chance of survival was strongly conditioned by. . . what

job its father did" (A. Reid, 1997, p. 151). Children of professional fathers had a 54% lower mortality rate than children whose fathers were unskilled laborers. Even when SES, environment (urban versus agricultural setting), maternal age, and other factors were controlled, infants and young children of working mothers had a 34% higher mortality rate than did children whose mothers did not work because women married to men with a sufficient income often stayed home to breast-feed, which was associated with significantly lower infant mortality (Rollet, 1997). Resources provided by fathers also allowed the family to live in healthier environments and provide a more stable food supply, which contributed to the relation between SES and infant and child mortality rates (A. Reid, 1997). In keeping with paternal effects, within-family studies-which control for maternal and child characteristics-indicate increased infant and child mortality rates following paternal death in developing nations today and in preindustrial Europe (Klindworth & Volland, 1995; Kok, van Poppel, & Kruse, 1997; United Nations, 1985).

The relation between SES and the physical well-being of children is still found in industrial nations today (e.g., I. Reid, 1998), even with low infant and child mortality. Adler et al. (1994, p. 22) 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." The relation between SES and health holds for all members of the family 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 an individual is treated by other individuals and the degree to which he or she can control the activities of everyday life, which appear to influence physical health (Lachman & Weaver, 1998). Across industrial societies today, paternal income and occupational status are an important, and sometimes the sole, determinant of the family's SES and are thus correlated with the physical well-being of the children.

Social Well-Being Because human paternal investment is not obligate, men have the option of focusing their reproductive energies on mating or on parenting. Given that some level of paternal investment is found in most human societies (Geary, 2000), it is almost certain that under some conditions, and at some point in our evolutionary past, men benefited by shifting some portion of reproductive effort from mating to parenting (Lovejoy, 1981). Men's parenting is, nonetheless, puzzling in contexts with low infant and child mortality rates. Under these conditions, selection should favor men who reduced or eliminated parenting in favor of mating. Evolutionary inertia is one potential reason for the continuation of paternal investment in these environments; specifically, it reflects selection for such investment in environments with high infant and child mortality. If so, then men may no longer experience benefits from paternal investment, and successful high-investment men may be disadvantaged in terms of lost mating opportunities. A second potential reason is that men's parenting provides social-competitive advantages to children; that is, it is designed to improve the "quality" of offspring (Davis & Daly, 1997). If so, then paternal investment should improve social competitiveness, and a smaller number of socially competitive children should result in reproductive advantages.

COMPETITIVENESS In industrial societies, one trait associated with social competitiveness is educational achievement, which is related to heritable individual differences in cognitive ability and to home environment (Cleveland, Jacobson, Lipinski, & Rowe, 2000; Geary, 2005). In these societies, paternal investment, including income provided to the family and direct care, is correlated with better academic skills in children and higher SES in adulthood (Kaplan, Lancaster, & Anderson, 1998; Pleck, 1997). However, a causal relation between paternal investment and these outcomes has not been established (Parke & Buriel, 1998). Indirect, genetic influences cannot be ruled out, nor can the effects of assortative mating. With respect to the latter, high investing men tend to marry women who are more competent, intelligent, and better educated and thus more effective parents than women married to lower investing men (Luster & Okagaki, 1993). Indeed, the strength of the relation between paternal characteristics and child outcomes is reduced considerably, once maternal characteristics are controlled (Amato, 1998). There are, however, unique relations between paternal investment and some child outcomes. Paternal investment of time (e.g., helping with homework) and income (e.g., for tutoring or college) is associated with upward social mobility of children, even when maternal characteristics (e.g., years of education) are controlled (Amato, 1998; Kaplan, Lancaster, Bock, & Johnson, 1995; Kaplan et al., 1998).

Moreover, withdrawal of paternal investment is correlated with decrements in children's later social success. In industrial societies, 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 to 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 the divorce (Cherlin et al., 1991; Furstenberg & Teitler, 1994). Still, some differences between children from intact and divorced families are found, after controlling for pre-divorce levels of family conflict and other confounding variables. It appears that divorce results in small to moderate increases in aggressive and noncompliant behaviors, especially in boys; an early onset of sexual activity for adolescent boys and girls; and lowered educational achievement in adulthood for men and women (Amato & Keith, 1991; Belsky, Steinberg, & Draper, 1991; Ellis et al., 2003; Florsheim, Tolan, & Gorman-Smith, 1998). These findings suggest paternal investment can improve children's later social competitiveness, given the strong relation between delayed sexual activity, educational outcomes, and later SES (Belsky et al., 1991; Parke & Buriel, 1998).

There is also evidence for direct paternal effects on the well-being of children (Parke, 1995; Pleck, 1997). Paternal involvement in play 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 than are children who do not regularly engage in this type of play (Carson, Burks, & Parke, 1993). Qualitative features of fathers' relationships with their children, such as positive emotional tone of the interactions, 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).

Girls with a warm relationship with their father and a father who is highly invested in the family experience menarche later than do girls living in father-absent homes or with an emotionally distant father (Ellis, McFadyen-Ketchum, Dodge, Pettit, & Bates, 1999); high familial stress and presence of a stepfather or mother's boyfriend also contribute to early sexual maturation in girls (Ellis & Garber, 2000). Later sexual maturation should enable girls to acquire additional social-competitive competencies (e.g., more education) and thus greater ability to eventually invest in their children. The associated traits may also include competencies that support high cooperation with a spouse and thus high paternal investment in their children (MacDonald, 1992).

All of these relations are, however, confounded by genetic and child evocative effects and by the earlier mentioned maternal effects (Comings, Muhleman, Johnson, & MacMurray, 2002; Park & Buriel, 1998; Scarr & McCarthy, 1983). Motivated and intelligent children are more likely to receive education-related paternal investment than are other children (Kaplan et al., 1998), and even these effects might be due to shared genes (e.g., for intelligence). Genetic influences on personality traits, such as impulsivity, might contribute to the relation between parental divorce and children's later reproductive relationships, rather than simply the experience of parental conflict and divorce (McGue & Lykken, 1992). 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 (Reiss, 1995).

SELECTION In industrial societies, a man's SES influences his mating options before marriage but is unrelated to reproductive success, due to socially imposed monogamy and birth control (Perusse, 1993). The finding that SES is unrelated to reproductive outcomes suggests that paternal investment in the competitiveness of children does not result in reproductive advantages. In fact, under these conditions, high levels of paternal investment might be associated with reproductive disadvantages due to the costs of investment. However, prior to the substantive reductions in infant and child mortality in Western culture, higher SES was associated with lower mortality, as described earlier.

When SES and social competitiveness reduce child mortality risks, paternal investment can be a viable strategy if it enables children to maintain or improve their SES and competitiveness in adulthood. Improved social competitiveness would enhance children's ability to acquire resources in adulthood (e.g., generating wealth), which would reduce the mortality risks of their children and the investor's grandchildren. Such investment would have been particularly advantageous in populations subject to frequent but unpredictable population crashes and when mortality varied inversely and strongly with SES, as it often did (Post, 1985). Because fluctuating mortality risks were unpredictable and disproportionately affected lower SES children, selection would have favored paternal investment that enabled their children to maintain or improve their later SES. To be effective, this investment would have to be provided even when current mortality risks are low.

Although not certain, the pattern suggests that paternal investment is an evolved reproductive strategy that enhances the physical well-being of children and their social competitiveness. In environments with intense social competition over scarce resources and with unpredictable mortality risks, paternal investment

in children's social competitiveness is, in effect, insurance against unforeseen risks (Boone & Kessler, 1999; Geary, 2000; Geary & Flinn, 2001; Lancaster & Lancaster, 1987). Given the uneven distribution of social capital (e.g., intelligence) and wealth, not all men have the means to improve children's social competitiveness. And, some resource-holding men will invest in multiple wives rather than in their children's social competitiveness (Borgerhoff Mulder, 2000; Marlowe, 2000).

PATERNITY CERTAINTY AND WOMEN'S REPRODUCTIVE STRATEGIES

Men's parenting appears to reduce infant and child mortality risks and improve children's social competitiveness, but these outcomes are not sufficient for the evolution of paternal investment. As described in Table 16.1, the evolution and facultative expression of paternal investment is also related to paternity certainty and alternative mating opportunities.

Paternity Certainty Because human paternal investment is not obligate in many contexts, some women may attempt to cuckold their partners. The benefits would include additional social and material support from the extra-pair man and perhaps higher quality genes for her children (Geary, Vigil, & Byrd-Craven, 2004). As with other species, the risks include mate guarding, male-on-female aggression, and abandonment (Betzig, 1989; Daly & Wilson, 1988). The definitive study of human cuckoldry has not been conducted, although it clearly happens. Bellis and Baker (1990), for example, found that when women initiated an infidelity it often occurred around the time of ovulation. For this sample, 7% of the copulations during the time of ovulation were with an extra-pair man and were less likely to involve use of contraceptives than copulations with their social partner.

Definitive conclusions cannot be reached, but it appears that men are cuckolded about 10% of the time (Bellis & Baker, 1990; Flinn, 1988; Gaulin, McBurney, & Brakeman-Wartell, 1997; McBurney, Simon, Gaulin, & Geliebter, 2002). The issues are complex, however, as the rate varies significantly across cultural settings and SES. Sasse, Muller, Chakraborty, and Ott (1994) reported that nonpaternity rates were 1% in Switzerland, but others have reported rates greater than 20% in low SES settings (Cerdeña-Flores, Baron, Marty-Gonzalez, Rivas, & Chakraborty, 1999; Potthoff & Whittinghill, 1965). Still, paternity certainty is higher in humans than in our two closest relatives (chimpanzees, *pan troglodytes*, and bonobos, *pan paniscus*), suggesting that most women do not cuckold their social partners. The pattern is consistent with coevolving reproductive strategies, whereby women's tendency toward sexual fidelity is traded for men's paternal investment.

Women's Reproductive Strategies Several features of women's sexuality might be considered strategies, at least in part, to reduce men's mating opportunities and thus create conditions that could facilitate the evolution and facultative expression of paternal investment. These include concealed ovulation, aversion to casual sex, and female-on-female aggression (Geary, 1998; Oliver & Hyde, 1993). To ensure conception, concealed ovulation requires men to maintain a longer relationship with women than is necessary in most other primate species (Dunbar, 1995), but this is not sufficient to ensure paternal investment. If other proximate mechanisms were not operating, such as pairbonding (Miller & Fishkin,

1997), then once physical signs of pregnancy were evident men could easily abandon women. Concealed ovulation and the period of extended sexual activity may, in fact, be one mechanism that fosters pairbonding and later paternal investment (MacDonald, 1992).

Women's aversion to casual sex greatly restricts men's mating opportunities (Buss & Schmitt, 1993) and thus the opportunity cost of paternal investment. And finally, women compete over mates, often through relational aggression. This involves gossiping about and attempting to socially manipulate other women (Crick, Casas, & Mosher, 1997) and excluding potential competitors (over mates) from the social group (Geary, 2002b). When effective, the strategy reduces men's mating opportunities and thus lowers the opportunity cost of parenting.

FACULTATIVE EXPRESSION OF HUMAN PATERNAL INVESTMENT

The first subsection describes potential proximate influences on facultative expression of men's parenting, and the second describes wider social correlates of this investment.

PROXIMATE CORRELATES

The respective subsections provide reviews of the genetic, hormonal, social, and developmental correlates of men's parenting.

Genetic and Hormonal Correlates Across species, sex differences and within-sex individual differences in parental behavior are associated with a suite of hormonal and neuroendocrine mechanisms (Wynne-Edwards, 2001), some of which are genetically mediated (Schneider et al, 2003; Young, Roger, Waymire, MacGregor, & Insel, 1999). Men's parenting also appears to be influenced by many of these same mechanisms, but it is not known if individual differences in these mechanisms (e.g., sensitivity to oxytocin) are heritable in humans. In any case, maternal and paternal cortisol levels are correlated with attentive and sensitive parenting of newborns (Corter & Fleming, 1995; Stallings, Fleming, Corter, Worthman, & Steiner, 2001), although there are also hormonal correlates that differ across mothers and fathers (Fleming, Ruble, Krieger, & Wong, 1997; S. E. Taylor et al, 2000). Expectant fathers who respond to infant distress cues (e.g., crying) with concern and a desire to comfort the infant have higher prolactin levels and lower testosterone levels than other men (Storey, Walsh, Quinton, & Wynne-Edwards, 2000). "Men with more pregnancy symptoms (couvade) and men who were most affected by the infant reactivity test had higher prolactin levels and greater post-test reduction in testosterone" (Storey et al., 2000, p.79).

Based on a parenting survey administered to twins, Pérusse and colleagues found evidence for modest genetic contributions to two features of parental investment, care (e.g., sensitivity to emotional state) and protection (e.g., keeping the child close; Pérusse, Neale, Heath, & Eaves, 1994). Genetic models explained 18% to 25% of the individual differences on these dimensions of paternal parenting and 23% to 39% of the individual differences in maternal parenting. These

same models suggested unique environmental effects account for the majority of the individual differences in both paternal and maternal care and protection, at least as measured by this survey. A similar study found parental reports of positive support (e.g., affection, encouragement) of their children were moderately heritable, although separate estimates were not provided for mothers and fathers (Losoya, Callor, Rowe, & Goldsmith, 1997).

These results are intriguing but in need of replication with more direct measures of parental investment. Moreover, the reported effects might not reflect genetic influences on paternal investment per se but rather heritable personality factors that are not directly related to the evolution of paternal care but nonetheless influence parenting. Particularly important are heritable personality factors such as conscientiousness, associated with the stability of long-term relationships, especially with a spouse, and factors such as irritability that would affect responsiveness to children (Graziano & Eisenberg, 1997; Jockin, McGue, & Lykken, 1996; Rowe, 2002). Still, it is likely that individual differences in both paternal and maternal investment reflect some degree of heritable variability in the hormonal and neuroendocrine systems associated with parenting behavior. At the same time, parental behavior and the underlying hormonal and neuroendocrine systems are almost certainly influenced by social factors, including the child's behavior, the nature of the spousal relationship, and wider ecological conditions (S. E. Taylor et al., 2000; Geary & Flinn, 2002), although the relative influence of these factors cannot be determined from existing studies.

Social Correlates The quality of the spousal relationship is related to the ways in which both mothers and fathers interact with their children (Amato & Keith, 1991; Cox, Owen, Lewis, & Henderson, 1989; Davies & Cummings, 1994; Howes & Markman, 1989), but "paternal parenting is more dependent on a supportive marital relationship than maternal parenting" (Parke, 1995, p. 37). Observational studies have found that "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, Nash, & Aschenbrenner, 1983, p. 1634; see also Belsky, Gilstrap, & Rovine, 1984). Basically, marital conflict often results in fathers' withdrawal from children and spouse (Christensen & Heavey, 1990), although this 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 spousal relationships show higher levels of paternal investment than other men do. It is possible that women's efforts to maintain an intimate and cooperative spousal relationship is a strategy to induce and maintain 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, or it is possible that the relation between marital satisfaction and paternal investment reflects genetic and not social effects. Most likely, it is a combination of heritable biases and reactivity to marital dynamics that influence paternal investment, but definitive answers must await research designs that assess social and genetic factors and their interaction (Parke & Buriel, 1998).

Developmental Correlates Childhood experiences have been proposed as influencing later reproductive strategies (Belsky et al., 1991; Chisholm, 1993; Miller & Fishkin, 1997). Local mortality risks and low resource availability, in particular, are hypothesized to be associated with how men later distribute their reproductive effort. When mortality risks are high and/or resources are scarce, investment in more rather than fewer offspring is assumed to ensure that at least some will survive to adulthood. Specifically, Belsky et al. and Chisholm argued that mortality risks and low resource availability influence the nature of parent-child relationships. In risky, low resource environments, the psychological and physiological stressors on parents are high, resulting in less attentive and more conflicted parent-child relationships. The prediction is that these relationships will be associated with a later tendency to form unstable, low parental investment relationships, that is, a focus on mating rather than parenting. In less risky, high resource environments, parent-child relationships are warmer and reflect higher levels of paternal and maternal investment (MacDonald, 1992). The prediction is that these relationships will be associated with a tendency to later form stable, high parental-investment relationships.

Aspects of the model have been supported in several recent studies. Wilson and Daly (1997) found age of first reproduction, number of children born per woman, mortality risks, and local resource availability are interrelated in modern-day Chicago. With low resource availability, men compete intensely for resource control. The result is higher premature death rates and an average life span difference of 23 years (54 versus 77 years) comparing the least and most affluent neighborhoods. Shorter life spans are associated with earlier age of first reproduction for both sexes 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 (see also Geary, 2002a; Korpelainen, 2000).

Consistent with the Belsky et al. (1991) model, paternal absence and marital conflict are also associated with reproductive events. For boys, paternal absence and marital conflict are associated with more risk taking and higher age-specific mortality rates, due largely to more accidents and violent deaths (Peterson, Seligman, Yurko, Martin, & Friedman, 1998). In relation to men whose parents had not divorced, these men are also more likely to divorce and thus show reduced paternal investment themselves (Tucker et al., 1997), but, again, genetic and social contributions to these effects were not separated.

Other studies, however, are inconsistent with the psychosocial stress model. For Ache and Mayan men, Waynforth, Hurtado, and Hill (1998, p. 383) 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." Father absence was 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 of human populations and of other species suggest low resource availability and other stressors are associated with delayed, not early, reproduction (Krebs & Davies, 1993; MacDonald, 1997). In all, there appears to be a relation between early experiences and men's later focus on mating or parenting. However, without studies that control for genetic effects and conditions (e.g.,

reproductive opportunity) at the time of reproduction, causal relations between developmental experiences and later reproductive activities cannot be drawn.

CULTURAL AND ECOLOGICAL CORRELATES

Draper and Harpending (1988) described human cultures as tending to be father-absent or father-present, reflecting differences in the relative emphasis of men on mating or parenting, respectively. I contrast father-absent and father-present societies in the first subsection (see also Marlowe, 2000) and discuss how men's reproductive strategies vary with mating opportunities in the second.

Cultural Correlates Father-absent societies are characterized by aloof spousal relationships, polygynous marriages, local warfare, male social displays, and inconsistent direct paternal investment (Draper & Harpending, 1988; Hewlett, 1988; Marlowe, 2000; West & Konner, 1976; Whiting & Whiting, 1975). These conditions "are particularly prevalent in so-called middle-range societies, that is, 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 provision their children without the direct contribution of the father (Draper, 1989), although the father may control the land and other resources women use to feed their children (Borgerhoff Mulder, 2000). In these societies, polygynous marriages are not prohibited, and wealthy men often invest resources or social power in attempting to secure additional wives, often to their reproductive advantage (Chagnon, 1988) and often at a risk of increased child mortality and thus a reproductive cost to individual wives (Marlowe, 2000).

Father-present societies are common in harsh ecologies and in industrial societies (Draper & Harpending, 1988). These societies are characterized by ecologically or socially imposed monogamy (Flinn & Low, 1986). In harsh ecologies, most men are unable to acquire the resources (e.g., meat) needed to support more than one wife and family; thus their reproductive options are restricted to monogamy. In many industrial societies, legal and moral prohibitions against polygynous marriages, combined with women's preference for monogamous marriages (Geary, 1998), limit men's mating opportunities and thereby reduce the opportunity cost of paternal investment. The result is a relative shift in men's reproductive efforts from mating to parenting.

Ecological Correlates The ratio of reproductive-age men to reproductive-age women in the local ecology is called the operational sex ratio (OSR). In human populations, the OSR is determined by sex differences in birth rates, death rates, and migration patterns. One factor that particularly skews the OSR in industrial societies is population growth rate, with expanding populations yielding an "oversupply" of women. This results from a preference of women for slightly older marriage partners (Kenrick & Keefe, 1992). With an expanding population, the younger generation of women compete for marriage partners among a smaller cohort of older men.

With an oversupply of women (e.g., from 1965 through the 1970s in the United States), men are better able to pursue their reproductive preferences. These historical periods are generally characterized by liberal sexual mores, 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 women's participation in the work-

force, and lower levels of paternal investment (see Guttentag & Secord, 1983). 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 (Miller & Fishkin, 1997). When there is an oversupply of men (Guttentag & Secord, 1983), women are better able to enforce their preference for a monogamous, high-investment spouse. 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.

Hurtado and Hill (1992) reported a similar pattern in the Ache and Hiwi (hunter-gatherers in southwestern Venezuela). In the Ache, there are more reproductive-age women than men (OSR of 1.3), whereas in the Hiwi, there are more reproductive-age men than women (OSR of .78). These 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 some men are more influenced by mating opportunities than child mortality risks (Marlowe, 2000).

EVOLUTIONARY PRESSURES

The construction of models of the evolution of human paternal behavior can be guided by the proximate and evolutionary correlates of paternal investment in other species (see Table 16.1) and by comparative analyses of evolutionarily related species. For humans, the most appropriate comparisons would involve other species of *Homo* and australopithecine species, but these are all extinct. Thus, a common approach is to use patterns in the two species most closely related to humans, chimpanzees and bonobos. However, it is not clear that these are appropriate comparison species because males show little to no paternal investment, among other differences in reproductive dynamics. If our ancestors were like chimpanzees or bonobos, multiple changes in male (e.g., increase in parenting) and female (e.g., emergence of concealed ovulation) reproductive behavior would have had to occur to create the current human pattern. Geary and Flinn (2001) proposed the reproductive dynamics of our ancestors might instead have been more similar to that of our distant cousin, the gorilla (*Gorilla gorilla*), because moving from a gorillalike pattern to the current human pattern would require fewer evolutionary changes.

The modal social organization of gorillas is single-male harems, which typically include one reproductive male, many females, and their offspring (Fossey, 1984; Stewart & Harcourt, 1987; A. B. Taylor, 1997). In lowland gorillas (*Gorilla gorilla gorilla*), several families may occupy the same geographical region and are often in proximity, whereas in mountain gorillas (*Gorilla gorilla beringei*) they are geographically isolated. In both cases, adult male and female gorillas often form long-term social relationships, and male gorillas show high levels of affiliation with their offspring, presumably due to high levels of paternity certainty associated with single-male harems. “Associated males hold, cuddle, nuzzle, examine,

and groom infants, and infants turn to these males in times of distress" (Whitten, 1987, p. 346).

If the launching point was a gorillalike pattern, then current patterns of human parenting and family structure (i.e., one adult male, one or several adult females and their children), as well as long-term male-female relationships, have been a feature of the hominid social structure for millions of years. The primary evolutionary change needed to move from a single-male harem to the multimale, multifemale communities found with humans is the formation of male kin-based coalitions. The first evolutionary step to multimale communities would simply involve greater stability and cooperation among adult males. Such coalitions could easily arise from a gorillalike system, with the formation of father-son coalitions or coalitions among brothers. In fact, groups of bachelor males are common in mountain gorillas (Robbins, 1996). Among lowland gorillas, several families will occupy the same geographical region and encounters between groups are often friendly, especially among the males (Bradley et al., 2004). Bradley et al.'s DNA fingerprinting of male and female relatedness among these families indicates that males tend to be organized as clusters of kin, whereas females tend to be unrelated to other group members. This form of social organization provides the social context from which kin-based male coalitions could evolve. Once formed, stable groups of cooperating males could easily displace a lone male (Wrangham, 1999). As with chimpanzees, once they evolved early hominid communities were likely characterized by coalitions of related males that defended a territory against groups of conspecific males (Foley & Lee, 1989; Goodall, 1986). Unlike chimpanzees, the gorillalike family structure would have been retained.

Unlike female chimpanzees or bonobos, female gorillas do not typically have conspicuous sexual swellings, although they often have minor swellings and primarily solicit copulations behaviorally (Stewart & Harcourt, 1987). Thus, moving from a gorilla like pattern of female sexual solicitation to the current human pattern (e.g., concealed ovulation) requires fewer changes than evolving from the promiscuous chimpanzeelike or bonobolike pattern. Still, there may have been a strengthening of male-female pairbond during hominid evolution to reduce cuckoldry risks and maintain male parenting in a multimale, multifemale community. Evolution from a gorillalike pattern would simply require a quantitative change in the strength of the pairbond, whereas evolution from a chimpanzeelike or bonobolike pattern would require a more substantive and qualitative change in the nature of male-female relationships. If correct, male parenting, long-term female-male relationships, and a family structure following the gorillalike pattern may have been in place since the emergence of our australopithecine ancestors (Lovejoy, 1981).

CONCLUSIONS

When viewed from the perspective of mammalian reproduction, the most extraordinary feature of human parental care is men's parenting. Although definitive conclusions cannot be drawn at this time, what is known suggests the evolution and proximate expression of human paternal investment is related to many of the same factors associated with such investment in other species (e.g., Perrone & Zaret, 1979; Thornhill, 1976). These factors include reductions in infant and child mortality rates and improvements in children's social competitiveness

(Kaplan et al., 1998). As with other species where males parent, men's parenting appears to be related to comparatively high levels of paternity certainty and reduced mating opportunities. The latter likely 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 net result is that men and women benefit from paternal investment, but his investment is not obligate. Rather, men's parenting is facultatively expressed, contingent on personal, social, and ecological conditions. Among these conditions are heritable individual differences in emphasis on mating or parenting, personality, the quality of the spousal relationship, and child characteristics (Kaplan et al., 1998; Luster & Okagaki, 1993; Rowe, 2002). Childhood experiences such as parental divorce, as well as wider social and ecological factors such as laws against polygynous marriages, are also correlated with the degree to which men invest in the well-being of their children (Belsky et al., 1991; Flinn & Low, 1986; 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, or whether some interaction between heritable risks and early stressors are involved (Losoya et al., 1997; Reiss, 1995). The challenge for researchers is to design evolutionarily informed studies that enable the simultaneous assessment of many of these factors and to more critically explore the causes and correlates of individual differences in men's parenting.

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