

6 Evolution of Fatherhood

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There is considerable discussion in academic, political, and social circles about the role of fathers in the family and in society in general (Cherlin 2005, Geary & Flinn 2001, Hewlett 1992, Tamis-LeMonda & Cabrera 1999). Much of the discussion centers on the importance of fathers for the health and development of their children, differences in the parenting contributions made by mothers and fathers, and often on how to increase the participation of fathers in the family (Booth & Crouter 1998, Silverstein & Auerbach 1999). The discussions rarely address the deeper question: Why is fatherhood found at all in humans? This question is central to our understanding of men and families, because human fathers are a scientific riddle. This is because men's parenting is highly unusual when placed in the context of little, if any, male parenting in at least 95% of other mammalian species (Clutton-Brock 1989), including the two species most closely related to humans, that is, chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*). In this chapter, I attempt to explain some aspects of this riddle and, in doing so, hope to provide a wider perspective on human fatherhood, its evolution, and its expression in various social and cultural contexts (see also Geary 2000, 2005). In the first section, I focus on the cross-species patterns of male parenting or paternal investment and the implications for understanding the conditions that promote the evolution and proximate expression of this form of parenting. In the second section, I use the basic patterns described in the first section to analyze the evolution and expression of men's parenting.

MALE PARENTING IN NONHUMAN SPECIES

Male parenting has to be considered in the wider context of the costs and benefits of parenting in general, whether provided by the mother or the father. For many species, there is little investment in offspring by either parent. For species in which investment does occur, it is always at some cost to the parent, including increased risk of illness and premature death (Clutton-Brock 1991, Trivers 1974). Given these costs, parenting can evolve only if there are considerable benefits to offspring and thus considerable reproductive benefits to the parent providing the investment. These benefits are well documented in species in which parenting is found. In these species, 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 offspring that develop into healthier adults that in turn are better able to compete for mates and that produce larger and healthier offspring themselves (e.g., Clutton-Brock, Albon, & Guinness 1988). In short, in species in which it is found, 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

Evolution

Although rare in mammals, male protection or provisioning of offspring is found in most species of bird, and in some species of fish and insect (Perrone & Zaret 1979; Thornhill 1976; Wolf, Ketterson, & Nolan 1988). Determining the costs and benefits that influence the expression of this male parenting is complicated by the evolutionary history of the species, as well as by whether paternal investment is obligate or is facultatively expressed (Arnold & Owens 2002; Clutton-Brock 1991; Fishman, Stone, & Lotem 2003). Obligate investment means that male care is absolutely necessary for the survival of his offspring, and thus evolution favors males that always invest in offspring. One potential result is that males could show high levels of parental investment, even if conditions change and the investment is no longer critical to offspring survival (Westneat & Sherman 1993).

For many species, including humans, male parenting is facultatively expressed; that is, it is not always necessary for offspring survival and, thus, the quantity and quality of this investment varies with social and ecological conditions (Westneat & Sherman 1993). Across species, the facultative

expression of male parenting varies with the influence of this investment on offspring survival prospects and quality; the degree of paternity certainty or risk of being cuckolded (i.e., raising the offspring of another male) by his partner; and, the extent to which parenting restricts opportunities to mate with multiple females (Birkhead & Møller 1996, Møller & Cuervo 2000, Perrone & Zaret 1979, Trivers 1972). These tradeoffs suggest that the evolution of facultative male parenting was driven by balancing the benefits to offspring survival and later competitiveness with the risks of cuckoldry and the costs of lost mating opportunities.

Costs and Benefits

Evidence for the just noted tradeoffs in the costs and benefits of male parenting can be found in species in which this parenting occurs and when males vary this investment with cuckoldry risk and mating opportunities lost. For instance, 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 because males directly fertilize eggs after the female deposits them. Males are also able to fertilize the eggs of more than one female, and thus investment does not reduce mating opportunities. In contrast, male parenting is rare 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.

Although male parenting is uncommon in fish with internal fertilization, it does occur in most species of bird and a few mammals (Dunbar 1995, Mock & Fujioka 1990). Across and within these species, the degree of paternal involvement again varies with the potential benefits to offspring, cuckoldry risks or paternity certainty, and availability of other mates. The benefit to offspring has been demonstrated by removing fathers from nests, which results in lower offspring survival rates, and from naturalistic studies that have documented reduced paternal investment following partner infidelity and a corresponding increase in offspring mortality (Arnqvist & Kirkpatrick 2005). In an analysis across 31 bird species, Møller (2000) determined that 34% of the variability in offspring survival was due to paternal investment.

Given the risks of male abandonment or reduction in parental investment, it is not surprising that cuckoldry rates are very low in species in which male investment is obligate (Birkhead & Møller 1996). For species in which male investment is not obligate, cuckoldry rates appear to vary with male quality. In some species, females paired with low-quality males will sometimes risk loss of male investment and copulate with healthier males (Møller & Tegelström 1997). One potential benefit is that the offspring sired

by healthier males, and in at least one species their grand-offspring, may be healthier and suffer less mortality (e.g., J. M. Reid et al. 2005; Saino, Møller, & Bolzern 1995), but the strength of this benefit is currently debated (Arnqvist & Kirkpatrick 2005; Westneat & Sherman 2003). In any event, cuckoldry risks are more consistently related to reductions in male provisioning and protection of offspring (Arnqvist & Kirkpatrick 2005). Although the strength of the relation between cuckoldry risk and male parenting is mixed (Dixon, Ross, O'Malley, & Burke 1994; Kempenaers, Lanctot, & Robertson 1998; Sheldon, Räsänen, & Dias 1997), some of the inconsistencies may be related to the ability of males to detect their partner's extra-pair copulations or risks of extra-pair paternity of offspring (Neff & Sherman 2002).

As an example, Neff (2003) studied the relation between mate protection of eggs and paternity certainty in the bluegill sunfish (*Lepomis macrochirus*). In this species, there are different types of males, some dads and others cads. Parental males defend a territory, then externally fertilize and fan and protect eggs. One type of cad or cuckolder 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 thus be determined by the presence or absence of cuckolder males. After the eggs hatch, parental males can determine paternity based on olfactory cues from fry urine. If parental males have evolved to vary their investment in offspring with the probability that the offspring are theirs, then these males are predicted to reduce fanning and protecting of eggs if cuckolder males are present. This is exactly what happened. Moreover, once the fry hatched and parental males could determine paternity, they protected them only if they had fathered them, whether or not cuckolder males were present before the fry hatched. This and other well-controlled studies (Arnqvist & Kirkpatrick 2005, Ewen & Armstrong 2000) suggest that when males detect risks to paternity, they reduce their level of paternal investment, often in direct relation to the magnitude of the risk (Møller 2000). However, provisioning and protecting offspring is not always parental investment, as these behaviors are sometimes related to mating effort, that is, 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 most species of mammal, female investment through postpartum suckling is sufficient for offspring survival and development, and dominant males are able to reproductively monopolize the majority of these females (Andersson 1994). Under these conditions, it is in males' reproductive best interest to compete for mates rather than to parent. Nevertheless, social monogamy and high levels of paternal investment are found in some

mammals, mostly carnivores and some primates (Mock & Fujioka 1990; van Schaik & Kappeler 2003). In these species, males are able to contribute to the direct care or protection of offspring and often have better reproductive options with such a strategy than by engaging in intense competition for mates.

For instance, male parenting is common in canids, such as 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. Additional examples and extended discussion of monogamy in mammals and birds can be found in Reichard and Boesch (2003).

HUMAN FATHERHOOD

As noted, humans are among the 5% of mammalian species in which males invest in the well-being of their offspring, although this investment is facultatively expressed (Geary 2000). To understand the evolution and proximate expression of men’s parenting, it is necessary to consider the relation between this investment and the just described factors related to male parenting in other species, that is, benefits to offspring, cuckoldry risk, and lost mating opportunity. I address the former issue in the first section and the two latter issues in the second. In the third section, I outline the conditions associated with the facultative expression of men’s parental investment, and in the final section, I discuss the potential evolutionary history of this investment.

Children’s Wellbeing

The evolution and maintenance of men’s parenting could occur only if the added benefits—above and beyond those resulting from the mother’s parenting—to children were substantial. As with other species, the most

obvious benefits would be better health and reduced mortality. For a highly social and slow-developing species, men's parenting might also enable children to better acquire social and culturally important competencies that will contribute to their reproductive competitiveness in adulthood (Geary & Flinn 2001).

Physical Wellbeing

In traditional and developing societies and in the historical record, there is a consistent relation between men's investment and children's mortality rates, but disentangling the direct effect of paternal investment from potential confounds is difficult. This is because healthier and culturally successful men are typically paired with healthier and culturally successful women (Blurton Jones, Hawkes, & O'Connell 1997), and thus the higher survival rates of their children cannot be attributed solely to men's parenting. Moreover, men's parenting may at times be part of mating effort and is thus not paternal investment per se (Borgerhoff Mulder 2000, Marlowe 2000).

Nevertheless, men's providing care, food, and other resources is associated with lower infant- and child-mortality risks and generally better physical health of children in most traditional societies today and during the preindustrial era of Western societies. Among the hunter-gatherer Ache (Paraguay), about 1 out of 3 children die before reaching the age of 15, with highly significant differences in mortality rates for father-present and father-absent children (Hill & Hurtado 1996). Father absence triples the probability of child's death due to illness and doubles the risk of the child's 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. In developing countries today, there is a consistent relation between marital status and infant- and child-mortality rates, with the lowest rates for children living with both biological parents, and higher rates for single, divorced, and widowed women (United Nations 1985).

The same pattern is found in the historical record of 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 18th-century Berlin, Schultz found a strong correlation ($r = .74$) between socioeconomic status (SES, a composite of income, educational level, and father's occupational status) and infant- and child-mortality rates. In 19th-century Sweden, infant-mortality rates were 1.5 to 3 times higher for children born to unmarried mothers than for children born to married couples (Brändström 1997). An analysis of mortality risks in

early-20th-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 did children whose fathers were unskilled laborers. Even when SES, environment (urban vs. 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. This is because women married to men with a sufficient income often stayed home to breastfeed, which significantly lowered infant mortality (Rollet 1997).

The best evidence for a direct effect of father’s investment on child health is found with studies of changes within families. These studies control for maternal and child characteristics and reveal increased infant- and child-mortality rates following paternal death in developing nations today and in the historical record (Klindworth & Volland 1995; Kok, van Poppel, & Kruse 1997; United Nations 1985).

Social Wellbeing and Competitiveness

In addition to improving the health of their children, men’s parenting may also provide a number of social competitive advantages to children, that is, its evolution may have been influenced in part by the effect of this parenting on their children’s ability to later compete for resources in adulthood (Davis & Daly 1997; Geary 2002; Geary & Flinn 2001). If this is the case, then paternal investment should improve social competitiveness, and even though the men would have a smaller number of children, the children’s social competitiveness should result in reproductive advantages for these men.

In industrial societies, one trait associated with social competitiveness is educational achievement, which is related to a combination of heritable individual differences in cognitive ability and to home environment (Cleveland, Jacobson, Lipinski, & Rowe 2000). 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 when these children reach adulthood (Kaplan, Lancaster, & Anderson 1998; Pleck 1997). However, a causal relation between men’s investment and these outcomes has not been firmly established (Parke & Buriel 1998). Indirect, genetic influences—more-able fathers have more-able and thus more-competitive children—cannot be ruled out, nor can the effects of mate choices. 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 are women married to lower-investing men (Luster & Okagaki 1993). Indeed, the strength of the relation between father characteristics and child outcomes is reduced

considerably once maternal characteristics are controlled (Amato 1998). Nonetheless, it does appear that the father's investment of time (e.g., helping with homework) and income (e.g., for tutoring or college) is associated with children's upward social mobility, even when maternal characteristics (e.g., years of education) are controlled for (Amato 1998; Kaplan, Lancaster, Bock, & Johnson 1995; Kaplan et al. 1998).

Moreover, withdrawal or reduction of paternal investment, as often happens following divorce, is associated with costs to children's later social success. But again, causal relations are difficult to determine. Although many differences comparing children from divorced and intact families can be traced to differences in family functioning before the divorce (Cherlin et al. 1991, Furstenberg & Teitler 1994), some differences remain after controlling for pre-divorce levels of family conflict and other confounding variables. Following divorce, there are small-to-moderate increases in aggressive and noncompliant behaviors in boys, and an earlier onset of sexual activity and lower long-term educational achievement for both sexes (Amato & Keith 1991; Belsky, Steinberg, & Draper 1991; Ellis et al. 2003; Florsheim, Tolan, & Gorman-Smith 1998).

Father's play and social engagement may also contribute to the social competencies of their children (Parke 1995; Pleck 1997). Men's involvement in play is associated with children's skill at regulating their emotional states and with 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 who have a warm relationship with their father and whose father is highly invested in the family experience menarche later than do girls living in father-absent homes or with an emotionally distant father (Ellis 2004; Ellis, McFadyen-Ketchum, Dodge, Pettit, & Bates 1999). In contrast, high familial stress, presence of a stepfather or mother's boyfriend, and sexual abuse contribute to early sexual maturation in girls and, in some cases, earlier sexual activity (Ellis & Garber 2000; Vigil, Geary, & Byrd-Craven 2005). Age of sexual maturation and initiation of sexual activity is important because delaying these developmental milestones provides girls with a greater opportunity to acquire additional social-competitive competencies (e.g., more education), and thus greater ability to compete socially in adulthood and eventually invest in their children (Geary & Flinn 2001, Vigil & Geary

2006). The traits that may be fostered by a warm relationship with the father may also contribute to the development of competencies that support high cooperation with a spouse and thus high paternal investment in their children (MacDonald 1992).

Cuckoldry Risks and Mating Opportunity

As with other species, men's parenting comes at a cost, in terms of risk of cuckoldry and lost mating opportunity (see Platek & Shackelford 2006). If there has been an evolutionary history of male parenting in humans, comparatively high levels of paternity certainty (i.e., low risk of cuckoldry) and restricted mating opportunities are predicted (Geary 2000). This is not to say that men are never cuckolded or never seek additional mates; they sometimes are and do. Rather, women are predicted to risk cuckoldry, that is, risk partner aggression and abandonment, only when his contributions to the family are small or when he is in poor physical and thus presumably genetic health (e.g., Daly & Wilson 1985; Daly, Wilson, & Weghorst 1982; Flinn 1992; Shackelford & Larsen 1997). I address the issues related to paternity certainty and reliance on paternity cues in the first section. In the second section, I address the issue of women's sexuality and men's mating opportunities.

Paternity

Paternity certainty. There have been no large-scale studies of cuckoldry, or nonpaternity, using representative samples, and thus definitive conclusions cannot be drawn regarding the overall certainty of paternity. Estimates of the frequency of nonpaternity range from about 1% to more than 30% of children (Anderson 2006; Bellis & Baker 1990; Bellis, Hughes, Hughs, & Ashton 2005; Flinn 1988; Gaulin, McBurney, & Brakeman-Wartell 1997; McBurney, Simon, Gaulin, & Geliebter 2002). In a meta-analysis, Anderson reported that when the father suspected he had been cuckolded, nonpaternity is found in about 30% of the cases. When the father is confident of paternity, nonpaternity is found for about 2% of their children. In another meta-analysis, Bellis et al. found the median non-paternity rate to be about 4%. One of the more intriguing examples of cuckoldry is the occasional finding of twins who have been sired by two different men (e.g., Lebeau-Le Guiner, Guidet, Bompoil, Marka & Pascal 2003). In any case, nonpaternity varies considerably across social and economic contexts. Sasse, Muller, Chakraborty, and Ott (1994) reported that nonpaternity rates were 1% in Switzerland, but others have reported rates greater than 20% in low socioeconomic settings

(Cerdeña-Flores, Baron, Marty-Gonzalez, Rivas, & Chakraborty 1999; Potthoff & Whittinghill 1965).

The other side of these nonpaternity estimates is a high degree of paternity certainty. In our two closest relatives, chimpanzees and bonobos, paternity is uncertain because females mate with multiple males. In this circumstance, little if any male parenting is predicted to evolve, and little is found (Whitten 1987). Overall, human paternity certainty is likely to be greater than 90% and possibly as high as 95%. When there are large deviations from these percentages, it appears to be in situations with low levels of male parenting or low male quality, as is found in other species with the facultative expression of paternal investment, variation in male quality, and female benefits to cuckoldry (Møller & Cuervo 2000).

Paternity Cues. Even though paternity certainty is high for human fathers, it is never 100%. Given this and the high and prolonged costs of parental care, men are predicted to have evolved biases that orient them to cues to the paternity of the children in which they are investing, much like those found for bluegill sunfish. Moreover, women are predicted to bias the use of these same cues as a means of maintaining paternal investment, especially in situations in which paternity is ambiguous (Daly & Wilson 1982; McLain, Setters, Moulton, & Pratt 2000; Pagel 1997). Of particular importance is men's sensitivity to cues of resemblance to their putative children and the corresponding prediction that they will invest more heavily in children they perceive as resembling themselves. These predictions are not related to step-parenting or adoption, because in these situations the man knows he is not the biological father and is providing some investment for other reasons, primarily to maintain a relationship with the children's mother (Anderson, Kaplan, Lam, & Lancaster 1999; Anderson, Kaplan, & Lancaster 1999; Flinn 1992).

Several studies suggest that fathers, more so than mothers, do indeed bias their investment in children based on their perceived resemblance to the child (Apicella & Marlowe 2004; Burch & Gallup 2000; Platek, Burch, Panayavin, Wasserman, & Gallup 2002; Platek et al. 2004), although results are mixed as to whether infants and young children do in fact resemble fathers more than mothers (Christenfeld & Hill 1995, McLain et al. 2000). There is also evidence that men who are not yet fathers show the same preference. In one study, Platek et al. (2002) morphed digital photographs of men and women to create the face of a preschool child that resembled them. Participants were then presented with a set of five morphed photos of children (the self-morph was in half of these sets) and asked to choose the child whom they were more likely to adopt, find most attractive, be most likely to spend time with, and invest other resources on. Men were significantly more likely than were women to indicate that they would invest in their self-morph. DeBruine (2004), however, found this effect in both men and women. As a follow-up

and to address DeBruine's failure to find a sex difference, Platek et al. (2004) replicated their original sex difference finding and, in a brain-imaging study, showed different patterns of brain activation in men and women when they evaluated children that resembled themselves and children that did not. Men's activation patterns suggested attentional focus, active evaluation of the self-morph, and inhibition of potentially negative affect.

If men are sensitive to paternity cues, regardless of cuckoldry risk, and their investment is beneficial to children, as it is, then women are predicted to have an evolved bias to manipulate information regarding paternity (Pagel 1997). In a study of spontaneous interactions in maternity wards in the United States, Daly and Wilson (1982) found that mothers stated the newborn resembled the father more than that the newborn resembled her, but fathers were more skeptical of this resemblance. Follow-up studies confirmed the pattern in Canada and Mexico and suggested it extends to maternal kin (Daly & Wilson 1982, McLain et al. 2000, Regalski & Gaulin 1993). Men are thus biased to invest in children whom they perceive as resembling themselves, and women and their kin are biased such that they are much more likely to provide social cues suggesting greater paternal than maternal resemblance to children; in other words, women and their kin either implicitly or explicitly attempt to manipulate social information in ways that would result in increased paternal investment.

Women's Sexuality

Because women and their children benefit from men's parental investment, evolution will favor women with behavioral and other traits that will increase the likelihood men will invest in these children. These would include traits that resulted in, or at least suggested, high levels of paternity certainty, and also traits that reduced the primary cost of paternal investment, lost mating opportunities. There are, in fact, several features of women's sexuality consistent with these predictions, including concealed ovulation, women's aversion to casual sex, and pair bonding (Geary 1998, Miller & Fishkin 1997, Oliver & Hyde 1993). To ensure conception, concealed ovulation requires men to maintain a longer relationship with women than is found in most other primates (Dunbar 1995), but this, in and of itself, is not sufficient to ensure paternal investment. If other proximate mechanisms were not operating, such as pair bonding (Miller & Fishkin 1997), 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 continued paternal investment (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 parenting. 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 (Symons 1979). Men are, however, highly variable in this regard, with many men biased toward monogamous relationships and others toward polygynous relationships (Miller & Fishkin 1997). Nonetheless, any evolved tendency toward monogamy on the part of men was potentially predated by restricted mating opportunities, as found in monogamous primates (Dunbar 1995).

When and Where Do Men Parent?

The evolution of the facultative expression of men's parental care is predicted to have involved the same cost-benefit tradeoffs described in the Male Parenting in Nonhuman Species section. These involve the benefits to children's survival prospects and later social competitiveness and the man's paternity certainty, as these are balanced against the cost of lost mating opportunities. The when and where of men's actual investments in a family and children are thus predicted to vary with the benefits this investment provides to children, and the quality of the relationship with his wife. The latter is important because this is likely to be a paternity cue and reflects women's efforts to maintain men's investment in the family. Men's tendency to invest in children or not also appears to be influenced by their experiences while growing up and by social and cultural influences on mating opportunities. Of course, many of these effects are also influenced by genes and hormones, as I discuss in the first section. In the second section, I discuss the family and background correlates of men's parenting, and in the third section I focus on wider cultural and social influences on this parenting.

Genetic and Hormonal Correlates

In addition to social and ecological context, sex differences and within-sex variation in parenting are associated with hormones and other biological mechanisms (Wynne-Edwards 2001). The expression of these hormones and, through this, parental behavior can be influenced by individual differences in genes (Schneider et al. 2003; Young, Roger, Waymire, MacGregor & Insel 1999) or by social context (Storey, Walsh, Quinton, & Wynne-Edwards 2000). For both mothers and fathers, high levels of the stress hormone

cortisol are correlated with the attentive and sensitive parenting of newborns (Corter & Fleming 1995; Stallings, Fleming, Corter, Worthman, & Steiner 2001), although there are other 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 do other men (Storey et al. 2000). It is not yet fully understood whether these differences cause more attentive parenting by fathers, change in response to exposure to their children, or both.

In any case, it is clear that individual differences in the quality of maternal and paternal care are related, in part, to genetic differences. In a study of twins, Pérusse, Neale, Heath, and Eaves (1994) 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). Genetic models explained 18% to 25% of the individual differences on these dimensions of men's parenting and 23% to 39% of the individual differences in women's parenting. At the same time, this study also suggested that unique environmental effects—experiences unique to each person—account for the majority of the variation in paternal and maternal care and protection. A similar study found that 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 interesting but in need of replication with other measures of parental investment. Moreover, the findings 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. Of particular importance are heritable personality factors, such as conscientiousness, 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; Jockin, McGue, & Lykken 1996; Rowe 2002). Still, it is likely that individual differences in both fathers' and mothers' investment in children reflect some degree of heritable variability in the hormonal systems associated with parenting behavior, although whether or not these hormonal differences are expressed may depend on experience.

Social Correlates

The most consistently found predictor of men's engagement with their children and satisfaction with parenting is the quality of the spousal relationship (Amato & Keith 1991; Belsky, Gilstrap, & Rovine 1984; Cox, Owen,

Lewis, & Henderson 1989; Davies & Cummings 1994; Feldman, Nash, & Aschenbrenner 1983; Howes & Markman 1989). Marital conflict, in contrast, often results in men's withdrawal from children and spouses (Christensen & Heavey 1990), although this is sometimes more pronounced for daughters than for sons (Kerig, Cowan, & Cowan 1993). The bottom line is that men in satisfying spousal relationships show higher levels of investment in their children than other men do. It follows from this that women's efforts to maintain an intimate and cooperative spousal relationship is a strategy, though not necessarily conscious, 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 are other men, or 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

Certain childhood experiences have been proposed as influencing if men will be biased to invest in parenting or in mating as adults (Belsky et al. 1991; Chisholm 1993; Miller & Fishkin 1997). Local mortality risks and low resource availability, in particular, are hypothesized to be associated with this bias. When mortality risks are high 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 relationships that focus on mating rather than parenting. In less-risky, high-resource environments, parent-child relationships are warmer and reflect higher levels of investment by both parents (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 studies. As an example, Wilson and Daly (1997) found age of first reproduction, number of children birthed per woman, mortality risks, and local resource availability to be interrelated in modern-day Chicago. With few resources in the local

environment, men compete intensely for resource control. The result is higher premature-death rates and an average lifespan of 54 years, as compared to 77 years in the most affluent neighborhoods. Shorter life spans are associated with earlier age of first reproduction for both men and women, and nearly twice as many children birthed per woman, comparing the least and most affluent neighborhoods. In other words, the early and frequent reproduction of women and men in these contexts, and low levels of maternal and often no paternal investment might be, at least in part, a facultative response to high mortality risks (see also Geary 2002; Korpelainen 2000). Other studies are, however, 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).

Vigil and Geary (2006) approached parental investment in terms of the ability of parents to add to children’s social competitiveness before these children reach adulthood (see also Geary 2002; Geary & Flinn 2001). In this view, children and parents are predicted to be sensitive to children’s social competitiveness vis-à-vis the children’s peer group, as this is the most likely representation of the social competition the children will face in adulthood. Peer relations and wider community conditions suggest men’s investment should increase with increases in the level of competition their children will face as adults. To test this hypothesis, 623 low-income women reported on various reproductive milestones—including ages at menarche, first sexual intercourse, and first childbirth—indicators of social competitiveness (e.g., years of education), community background (e.g., wealth of community), and family history, including amount of time spent with their father. There was a counterintuitive relation between time spent with their father, the community’s background, and reproductive delay, that is, delaying having their first child to get a better education. It appeared that fathers invested the most time in their daughters when they lived in wealthier and highly competitive communities, that is, when their daughters required additional investment to keep them competitive with their peer group.

A similar pattern was reported by Harris and Marmer (1996). They found that the often-reported positive correlation between warm father-child relations and children’s long-term economic and educational success is stronger in wealthier families, and concluded that “the positive effect of

father's behavioral involvement . . . [is] less effective for children who experience long-term poverty" (Harris & Marmer 1996, p. 632). These results, and those of Vigil and Geary (2006), suggest that fathers may vary their investment in response to what their children need to be socially competitive in their peer group, or at least in their perceived peer group.

Men's Parenting Across Cultures and Social Circumstances

Across cultures, there are differences in men's relative emphasis on investing their time and other resources in parenting or in finding multiple mates. Draper and Harpending (1988) described this variation, in terms of human cultures, as tending to be father-absent or father-present. I provide a brief contrast of father-absent and father-present societies in the first section and discuss how men's reproductive biases vary with the social circumstances that influence mating opportunities in the second.

Father-Absent and Father-Present Cultures

In father-absent societies, spousal relationships tend to be aloof, paternal investment is inconsistent, and polygynous marriages are allowed and pursued by many men. A correlate of polygyny is an increase in male-on-male aggression and thus more local warfare and male social displays (Draper & Harpending 1988, Hewlett 1988, Konner 2005, 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 for their children without the direct contribution of the father (Draper 1989), although fathers often control the land and other resources women use to feed their children (Borgerhoff Mulder 2000). In these societies, 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 large 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, and thus their parental investment is functionally obligate. In other words, in these difficult conditions, children's

survival is often dependent on heavy investment by both parents. In Western and some other industrial societies, men's ability to mate polygynously is limited by legal and moral prohibitions against these marriages, combined with women's preference for monogamy (Geary 1998). One result is a relative shift in men's efforts from mating to parenting.

Social Circumstances

Independent of cultural rules for marriage, mating opportunities vary with the ratio of reproductive-age men to reproductive-age women in the local social group, which is called the operational sex ratio (OSR). In human populations, the OSR is influenced by sex differences in birth rates, death rates, and migration patterns. In industrial societies, the population growth rate is particularly important because expanding populations yield an "oversupply" of women. This is because women prefer 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.

In historical periods in which there is an oversupply of women, as from 1965 through the 1970s in the United States, men are better able to pursue their reproductive preferences. These 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 workforce, and lower levels of men's parenting (Guttentag & Secord 1983). These patterns emerge because men 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 historical 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 among 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 willing to risk the lives of some of their children to pursue a polygynous reproductive strategy.

Evolutionary History

The evolutionary history of men's parental behavior has almost certainly been influenced by the same cost and benefit tradeoffs associated with paternal investment in other species, but reconstructions of the history of these tradeoffs are never certain. The possibilities can, nevertheless, be guided by comparative analyses of evolutionarily related species. A common approach is to use patterns among our two closest relatives, chimpanzees and bonobos. However, for a variety of reasons discussed elsewhere (Geary 2006; Geary & Flinn 2001), Flinn and I have argued that 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 reproductive pattern. In contrast, we proposed that the reproductive behaviors of our ancestors might have been more similar to that of our distant cousin, the gorilla (*Gorilla gorilla*). This is because moving from a gorilla-like pattern to the current human pattern would require fewer evolutionary changes than would be necessary to move from a chimpanzee- or bonobo-like pattern to the modal human pattern.

The typical social organization of gorillas is often described as isolated single-male harems, which typically include one reproductive male, two to four females, and their offspring (Fossey 1984, Stewart & Harcourt 1987, A. B. Taylor 1997). However, there is considerable variation in this social structure, even in the most isolated groups of mountain gorillas (*Gorilla gorilla beringei*); Robbins (1999) found that 40% of these groups included several, often related, males (e.g., brothers or father-sons). Groups of lowland gorillas (*Gorilla gorilla gorilla*) also maintain a harem structure but, in contrast to mountain gorillas, are less socially isolated. Several families will occupy the same geographical region, and encounters between groups are often friendly, especially among the males (Bradley et al. 2004). With the exception of strong male coalitions, the family groupings among these gorillas are very similar to the embedding of polygynous and monogamous families in human male kinship groups that is found in most traditional societies (Pasternak, Ember, & Ember 1997).

Moreover, the dynamics that emerge within families of lowland gorillas is similar to that found in human families. Unlike the multiple mating of female chimpanzees (during estrous) and bonobos, and a corresponding low level of paternity certainty (de Waal & Lanting 1997, Goodall 1986), adult male and female gorillas often form long-term social relationships. DNA fingerprinting indicates that male gorillas show high levels of paternity certainty (> 95%; Bradley et al. 2004), and behavioral observation has revealed high levels of affiliation with their offspring. As Whitten (1987) observed, "Associated males hold, cuddle, nuzzle, examine, and groom infants, and infants turn to these males in times of distress" (p. 346). Unlike female chimpanzees and bonobos, female gorillas do not typically have conspicuous sexual swellings and primarily solicit copulations behaviorally (Stewart & Harcourt 1987). The gorilla-like pattern of female sexual solicitation is more similar to the current human pattern (e.g., concealed ovulation) than is the pattern of female solicitation in chimpanzees or bonobos.

Other similarities between the human family and men's parenting and the social and reproductive relationships found among gorillas are presented elsewhere (Geary 2006; Geary & Flinn 2001). My point is that if this hypothesis is correct, then a family structure that includes mothers and fathers and high levels of paternal investment has been part of our evolutionary history for millions years (see also Lovejoy 1981).

CONCLUSION

Cultural debates regarding men's contributions to families and their children and the occasional rancor over the unequal contributions of men and women to parenting (Cherlin 2005, Silverstein & Auerbach 1999) belie a deeper and rarely considered scientific riddle; specifically, on the basis of little or no male parenting in nearly all other mammalian species and among our two closest living relatives (Clutton-Brock 1989, Whitten 1987), it is a scientific curiosity that men invest in families and children at all (Geary 2000). To understand how men's parenting evolved and how it is maintained in the here and now, we must consider the factors related to the evolution and expression of male parenting across other species. These factors involve tradeoffs that balance the benefits of male protection and provisioning to the health and later competitiveness of his offspring, weighed against the risk of cuckoldry and the cost of lost mating opportunities. Of course, it is likely that male parenting would benefit offspring even in species where this parenting does not occur. However, in these species, males that compete for access to mates out-reproduce any parental fathers, and thus any tendency toward the latter does not evolve (Andersson 1994).

Men's parenting is consistent with the same cost-benefit tradeoffs in other species in which paternal investment is found. In traditional and developing societies today and in the historical record, men's investment in families substantively reduced children's morality risks and improved their physical health and development (e.g., Morrison et al. 1977, Schultz 1991, United Nations 1985). In these societies and in Western societies today, men's investment often facilitates their children's ability to acquire the skills needed to compete in adulthood (Kaplan et al. 1998, Vigil & Geary 2006). Children who become successful adults are able to better care for and thus lower the mortality risks and enhance the later competitiveness of men's grandchildren. Men also benefit because of comparatively high levels of paternity certainty, although cuckoldry does occur and men and women show evidence of corresponding adaptations (e.g., Platak & Shackelford 2006). Women's reluctance to engage in casual sex greatly reduces men's mating opportunities, and in so doing, lowers the opportunity cost of paternal investment.

Even with an evolved bias to invest in children, there is considerable variation among men as to when and with whom they will invest in a family. The influences on the expression of men's parental behaviors are multifaceted and range from the genes that influence the expression of parenting-related hormones to the quality of the marital relationships to cultural mores regarding marriage practices (e.g., whether or not polygyny is allowed; Belsky et al. 1984, Flinn & Low 1986, Guttentag & Secord 1983, Storey et al. 2000). A comparative and evolutionary perspective on men's parenting provides a broader perspective for understanding these patterns and allows us to more fully understand when, where, and with whom men will invest in families.

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