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Coevolution of paternal investment and cuckoldry in humans

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Introduction

The social dynamics of reproduction emerge as individuals compete for control of the reproductive potential and reproductive investment of members of the opposite sex. Reproductive potential is the individual's ability to invest in the growth, development, and later social and reproductive competencies of offspring and the potential genetic benefits that might be passed to offspring (Alexander, 1987; Geary, 2002). Reproductive investment is the expenditure of the behavioral components (e.g. provisioning) of this potential to enhance the survival and later reproductive prospects of one offspring at the expense of other offspring or the parent (Trivers, 1972). As identified by Darwin (1871), the dynamics of reproduction - termed sexual selection - take the form of *intra-sexual competition* for access to mates or for control of the resources that potential mates need to reproduce, and *intersexual choice* of mating partners (see also Andersson, 1994). For most species of mammal, intrasexual competition takes the form of physical contests, whereby males attempt to exclude other males from access to females or access to the resources that females need to reproduce. Intersexual choice often involves female choice of mates, based on the results of male-male competition or on indicators of male genetic fitness or the males' ability and willingness to invest reproductive potential in her offspring.

To the extent that reproductive interests of males and females differ, sexual selection will also involve *intersexual conflict*, which traditionally involves conflict over the allocation of parental investment (Haig, 1993; Trivers, 1972). Intrasexual conflict will be most extreme for species in which reproduction involves prolonged male and female interdependence and when one or either

sex can benefit by diverting reproductive investment from the core relationship to alternative relationships. Diversion of reproductive investment is of course related to intersexual choice and intrasexual competition. As an example, cuckoldry – whereby the male social partner is deceived into raising the offspring of another male – involves female choice but is complicated by the simultaneous need to maintain the relationship with the social partner while engaging in a sexual and potentially reproductive relationship with an extra-pair male. Among other things, this dynamic creates conditions that will favor the evolution of female strategies that function to deceive the primary male social partner into investing his reproductive potential in offspring that may be those of another male (i.e. cuckoldry), and male counter-strategies that function to reduce this risk. I discuss this form of intersexual conflict in the second section of this chapter. In the first section, I discuss paternal investment and its evolution, as well as women's strategies to secure this investment from one or several men.

Paternal investment

In the first part of this section, I briefly describe the cross-species conditions that favor the evolution of paternal investment, and in the second part I elaborate on a model of the social ecology in which human paternal investment may have evolved (see Geary, 2006; Geary & Flinn, 2001). In the final part, I describe cuckoldry risks in extant human populations and relate these to the social ecology described in the second part of the section.

EVOLUTION

Paternal investment is found in many species of bird and fish, and in some species of insect and mammal (Clutton-Brock, 1989; Perrone & Zaret, 1979; Thornhill, 1976; Wolf, Ketterson, & Nolan, 1988). Across species, paternal investment involves cost-benefit trade-offs; specifically, this investment is typically associated with a higher degree of paternity certainty and improved offspring survival and later reproductive prospects, but at a cost of lost mating opportunity (Birkhead & Møller, 1996; Møller & Cuervo, 2000; Perrone & Zaret, 1979; Trivers, 1972). The trade-offs are a reflection of the evolutionary history of the species and of the current social and ecological conditions in which the individual is situated. Evolutionary history is important because it determines 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 and thus selection will favor males who always invest in offspring. One potential

long-term result is that males will show high levels of paternal investment, independent of proximate conditions (Westneat & Sherman, 1993). Moreover, given the costs of abandonment by the male, females rarely cuckold in these species (Birkhead & Møller, 1996).

Paternal investment in humans and many other species is facultatively expressed: it often benefits offspring but is not always necessary for their survival and thus the quantity and quality of human paternal investment often varies with proximate conditions (Geary, 2000; Westneat & Sherman, 1993). The facultative expression of male parenting reflects the just-noted cost-benefit trade-offs as these relate to the current social and ecological contexts in which the male is situated. The degree of male investment (1) increases with increases in the likelihood that investment will be provided to his own offspring (i.e. paternity certainty), (2) increases when investment increases the survival and later reproductive prospects of offspring, and (3) decreases when there are opportunities to mate with multiple females. Equally important, the conditional benefits of paternal investment in these species results in simultaneous cost-benefit trade-offs in females. Sometimes it is in the females' best interest (e.g. when paired with an unhealthy male) to cuckold their partner and mate with higher-quality males (Birkhead & Møller, 1996). It is in these species – which includes humans – that prolonged intersexual conflict is predicted to evolve.

HUMAN PATERNAL INVESTMENT

Humans are among the 5% of mammalian species in which males invest in the well-being of their offspring, although as noted this investment is facultatively expressed (Geary, 2000). Here I outline the potential evolutionary history of human paternal investment and then the conditions associated with the facultative expression of this investment. The combination provides a context for understanding the issues of paternity certainty, mate guarding, and cuckoldry, as described in the final part of this section.

Evolutionary history

The evolution of human paternal behavior has almost certainly been influenced by the same cost-benefit trade-offs associated with paternal investment in other species. The evolutionary history of these trade-offs is never certain, but can be guided by comparative analyses of evolutionarily related species. For humans, the most appropriate comparisons would involve other species of *Homo* and australopithecines, but these are all extinct. Thus, a common approach is to use patterns in the two species most closely related to humans: chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*). Because

males show little or no paternal investment in these species, it is not clear that they are appropriate comparison species (see also Geary & Flinn, 2001). 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. Geary and Flinn (2001) proposed that the reproductive dynamics of our ancestors might instead 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 modal 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; Taylor, 1997). However, there is considerable variation in this social structure, even in the most isolated groups of mountain gorillas (*G. gorilla beringei*); Robbins (1999) found that 40% of these groups included several often related males (e.g. brothers or father-sons). Encounters between groups are rare but when they do occur they result in intense and physical male-male competition over females, and male mate guarding of the females in their group (e.g. gathering them together and placing themselves between the females and the intruding male or males).

Groups of lowland gorillas (*G. gorilla gorilla*) also maintain a harem structure, but in contrast to mountain gorillas they 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). 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 patrilocal social structure is similar to that found in chimpanzees (*P. troglodytes*; Goodall, 1986) and humans in traditional societies today (e.g. Pasternak, Ember, & Ember, 1997); that is, males tend to stay in or near the territory of their birth group whereas females tend to emigrate from their birth group to the group of their mate. The kinship organization of male lowland gorillas provides a ready explanation for the lower levels of male-male competition in comparison with that found with mountain gorillas.

In any case, the dynamics that emerge within families of lowland gorillas is similar to that found in human families. Unlike the unrestricted mating of female chimpanzees (during estrous) or bonobos, and a corresponding low level of paternity certainty for conspecific chimpanzees (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 low levels of mate guarding (e.g. compared to chimpanzees) and high levels of affiliation with their offspring. "Associated males hold, cuddle, nuzzle, examine, and groom infants, and infants turn to these males in times of distress" (Whitten, 1987, 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.

The primary evolutionary change needed to move from a single-male harem to the multi-male, multi-female communities found with humans is the formation of male kin-based coalitions. Bradley *et al.*'s (2004) findings indicate that, at least for lowland gorillas, the male-kinship structure is very close to that currently found with humans. The primary difference is the degree of cooperation among adult males as related to coalitional competition with other groups of male kin. Such coalitions could easily arise from the social structure described by Bradley *et al.* (2004). The formation of more closely knit male kinship coalitions would create greater proximity of males and through this the creation of multi-male, multi-female communities. Indeed, if gorilla families were placed in closer proximity and if male-kinship bonds were strengthened, the common structure of human families, including polygynous families, in traditional societies would be formed. If this model is close to being correct, then paternal investment has a long evolutionary history in humans, as suggested by Lovejoy (1981), as do long-term male-female reproductive relationships.

The formation of tightly knit patrilocal communities, however, results in several additional and important changes in social organization. The pressure to maintain a male coalition creates pressures that facilitate within-group cooperation and this in turn is likely to result in reduced polygyny and a higher percentage of males that reproduce (see also Geary & Flinn, 2002). The cost of less reproductive skew among males is that more lower-quality males enter the reproductive pool and thus more females are paired with these males. The existence of multi-male groups and the pairing of lower-quality males results in greater potential for extra-pair relationships and great potential benefits to females if they cuckold lower-quality social partners. The resulting predictions are that paternity certainty is lower than that found in lowland gorillas, but much higher than that found in chimpanzees or bonobos. Paternity certainty should be associated with coevolving mechanisms, such as pair bonding, that maintain the male-female reproductive relationship in multi-male,

multi-female communities (MacDonald, 1992). There will also be sex-specific adaptations that, under some conditions (e.g. when paired with an unhealthy mate), will enable the seeking of extra-pair relationships and corresponding counter strategies that will disrupt these relationships. The focus of this chapter is on cuckoldry and male mate guarding, but these are not the only adaptations predicted to evolve in this social ecology.

Proximate expression

If the above scenario is correct, then male parenting, long-term female–male relationships, and a family structure following the gorilla-like pattern were in place before the emergence of our australopithecine ancestors, as proposed originally by Lovejoy (1981). Even with a long evolutionary history, paternal investment would not have been maintained during human evolution, if it did not confer reproductive benefits to males. The benefits would occur in the context of the same trade-offs described in the previous section; specifically, as related to paternity certainty and offspring survival and later reproductive prospects, as these benefits are balanced against lost mating opportunities. These trade-offs are indeed expressed in many human populations with the facultative expression of men's parenting.

The details of the family-dynamic, cultural, and other correlates of men's paternal investment are described elsewhere (Flinn & Low, 1986; Geary, 2000, 2006). The point here is that in many contexts men's provisioning and other forms of parental investment can substantively reduce children's morbidity and mortality risks (Adler *et al.*, 1994; Hill & Hurtado, 1996; Morrison, Kirshner, & Molho, 1977; Richner, Christe, & Oppliger, 1995; Schultz, 1991) and enhance their social-competitive competencies (Amato, 1998; Kaplan *et al.*, 1995). In many contexts the latter can influence later reproductive prospects (Irons, 1979). These relations have been considerably muted during the past century in industrialized societies, but are nonetheless evident in traditional societies today (e.g. Hill & Hurtado, 1996; United Nations, 1985) and prior to industrialization in modern societies (e.g. Morrison *et al.*, 1977) and thus were almost certain to have been crucial during human evolutionary history.

CUCKOLDRY RISKS

The benefits of paternal investment and the coevolution of this investment with paternity certainty result in potential reproductive trade-offs for women. Because men vary in quality (e.g. health; Shackelford & Larsen, 1997) and are readily available in multi-male, multi-female communities, women have the opportunity to cuckold their social partner and can sometimes benefit from doing so. As with other species (e.g. Birkhead & Møller, 1996), men are

predicted to and do reduce their levels of parental investment when they are not investing in their own children or suspect they have been cuckolded by their partner (e.g. Daly & Wilson, 1985; Daly, Wilson, & Weghorst, 1982; Flinn, 1992). As a result, women must balance the costs of reduced paternal investment or male retaliation against the benefits of cuckoldry; that is, having their children sired by a more fit man while having their social partner assist in the rearing of these children.

Although definitive conclusions cannot be reached at this time, it appears that men may be cuckolded about 10% of the time, on average (Bellis & Baker, 1990; Flinn, 1988; Gaulin, McBurney, & Brakeman-Wartell, 1997; McBurney *et al.*, 2002). The issues are complex, however, as the rate varies significantly across cultural settings and socioeconomic status. Sasse *et al.* (1994) reported that nonpaternity rates were 1% in Switzerland, but others have reported rates greater than 20% in settings of low socioeconomic status (Cerdeña-Flores *et al.*, 1999; Potthoff & Whittinghill, 1965). It is also possible that some of these men are aware of the nonpaternity of the children they are raising, and thus have not been technically cuckolded.

In any case, human paternity certainty is greater than 90% and considerably higher in some populations. This level of paternity certainty is much closer to that found in gorillas (>95%) than in chimpanzees and bonobos where there is little certainty of paternity given that females have multiple mates. The level of paternity certainty in human populations is what would be predicted on the basis of the gorilla-like model. More precisely, the formation of male coalitions and the resultant emergence of multi-male, multi-female communities, along with an increase in the number of lower-quality males entering the reproductive pool, will increase the opportunity for and the benefits of cuckoldry, but the pre-existing social structure would remain largely intact. The structure, as noted, would include polygynous and monogamous families with long-term male-female relationships, moderate to high levels of paternal investment, and high levels of paternity certainty. The formation of larger communities would result in increased male intrasexual competition but muted by kinship ties, and increased intersexual conflict. The latter would result in a drift, so to speak, from higher to lower levels of paternity certainty due to cuckoldry, but this drift would be countered by risk of lost paternal investment and male retaliation.

Intersexual conflict

As noted earlier, intersexual cooperation occurs when the reproductive interests of the male and female overlap and intersexual conflict arises as

individuals attempt to secure more reproductive investment from other individuals than is in the latter's best interest, as often happens with parent-offspring relationships (Haig, 1993; Trivers, 1974). Among unrelated adults the most extreme forms of intersexual conflict are rape (Thornhill & Palmer, 2000) and cuckoldry. My focus is on women's and men's behavioral and psychological adaptations that may have evolved in the context of intersexual conflict and cuckoldry. The potential for this specific form of intersexual conflict arises when women have the opportunity to develop relationships with extra-pair men and under conditions when it is in women's best interest to develop potentially reproductive relationships with one or more of these men. In the first part of this section I present an overview of the conditions most clearly associated with women developing relationships with more than one man, and in the second part I explore the social and psychological aspects of the dynamics of the relationships that are most likely to result in cuckoldry.

SERIAL MONOGAMY AND POLYANDRY

In theory, the reproductive best interest of most women can be achieved by marriage to a socially dominant and wealthy man who is able and willing to invest his high reproductive potential in her children, but this is not always achievable (Buss, 1989; Gangestad & Simpson, 2000; Geary, 1998). This appears to be particularly true in contexts populated by many low-status men who do not have the material resources to support a family. As one potential adaptation to these conditions, women might develop a successive series of relationships with a number of these men or several simultaneously, each of whom provides some investment during the course of the relationship (Buss & Schmitt, 1993; Campbell, 2002; Greiling & Buss, 2000). These women are practicing serial monogamy and sometimes polyandry, and they and their children are often healthier than women living in the same contexts but who are monogamously married to low-status men with few resources (Lancaster, 1989).

In several South American Indian societies, such as the Ache and Barí, women will engage in sexual relations with men who are not their social partner, especially after becoming pregnant (Beckerman *et al.*, 1998; Hill & Hurtado, 1996). By tradition, these men are called secondary fathers and are socially obligated to provide material resources and social protection to the woman's child, although not all of them do so. The result seems to be a confusion of paternity such that both primary and secondary fathers invest in the child. The mortality rate of Ache children with one secondary father is about half that of children with no secondary father or two or more secondary fathers (Hill & Hurtado, 1996). With more than one secondary father, paternity is too uncertain and thus these men do not invest in the child. The benefit of a secondary father

cannot be attributed to qualities of the mother, as Beckerman *et al.* (1998) found that 80% of Barí children with a secondary father survived to adulthood, as compared with 61% of their siblings without a secondary father. Under these conditions, the reproductive benefits of multiple sexual relationships are clear.

In the Ache and Barí, the primary and secondary fathers of children are known to the wider social group, and in situations in which women practice serial monogamy the nonpaternity of children from previous relationships is clear. In other words these are situations in which many of the men providing some form of investment to children – presumably to maintain a sexual relationship with the children’s mother – are explicitly aware that they are not the biological father. In many other contexts, women’s extra-pair sex is duplicitous and often involves cuckoldry of their social partners. In these situations, women must maintain two explicit heterosexual relationships, resulting in implicit intrasexual competition between the associated males. If this type of dynamic has occurred repeatedly during human evolutionary history then there are likely to have evolved social and psychological biases that increase the prospects that women can successfully deceive cuckolded males into providing paternal investment, and coevolving male counter strategies (Daly & Wilson, 1982).

WOMEN’S CUCKOLDRY STRATEGIES

In several large but unrepresentative samples, 20–25% of adult women reported having had at least one extra-pair sexual relationship during their marriage (Essock-Vitale & McGuire, 1988; Glass & Wright, 1992), and another 25% reported developing an intimate but not sexual (at that point) extra-pair relationship (Glass & Wright, 1992). Using a nationally representative sample in the USA, Wiederman (1997) found that 12% of adult women reported at least one extra-pair sexual relationship during their marriage, and about 2% reported such a relationship during the past 12 months; Treas and Giesen (2000) found similar percentages for another nationally representative sample. These may be underestimates, given that people are reluctant to admit to extra-pair relationships. In any case, the results indicate that some women develop simultaneous and multiple opposite-sex relationships, many of which become sexual and are unknown to their social partner. The studies reviewed in the Cuckoldry risks section make it clear that some of these extra-pair relationships result in pregnancy, and appear to occur with much higher frequency for women paired with lower-quality men, as is found in other species.

The dynamics of these extra-pair relationships are likely to involve a mix of implicit (i.e. unconscious) and explicit (i.e. conscious) psychological processes (e.g. attention to symmetric facial features) and social strategies. In fact, the finding that attraction to extra-pair partners is influenced by hormonal

fluctuations points to the importance of implicit mechanisms. In particular, women, as a group, show systematic changes in sexual fantasy and attractiveness to extra-pair men, among other sex-related traits, around the time of ovulation (Bellis & Baker, 1990; Gangestad & Thornhill 1998; Gangestad, Thornhill, & Garver, 2002; Geary *et al.*, 2001; Macrae *et al.*, 2002; Penton-Voak *et al.*, 1999; Penton-Voak & Perrett, 2000; Thornhill & Gangestad, 1999). Women are not only more likely to fantasize about (Gangestad *et al.*, 2002) and sometimes engage in (Bellis & Baker, 1990) an affair during this time, they are also more sensitive to and attracted by male pheromones. Gangestad and Thornhill (1998) and Thornhill and Gangestad, (1999) found that the scent of facially symmetric and thus physically attractive men was rated as more attractive and sexy than was the scent of less symmetric men, but only during this fertile time frame. Penton-Voak and colleagues found that women rate masculine faces, those with a more prominent jaw, as especially attractive around the time of ovulation (Penton-Voak *et al.*, 1999; Penton-Voak & Perrett, 2000). Scent, facial symmetry, and a masculine jaw bone may, in turn, be proximate cues to the man's genetic fitness and social dominance (Shackelford & Larsen, 1997).

The emerging picture is one in which women appear to have an evolved sensitivity to the proximate cues of men's fitness, a sensitivity that largely operates automatically and implicitly and peaks around the time women ovulate. The implicit operation of these mechanisms enables women to assess the fitness of potential extra-pair partners without a full awareness that they are doing so. In this way, women are psychologically and socially attentive to the relationship with their primary partner and most of the time have no explicit motive to cuckold this partner. If their social partners monitor for indications of attraction to extra-pair men, which they often do (see below), then these cues are only emitted during a short time frame. Moreover, given that attraction to a potential extra-pair partner is influenced by hormonal mechanisms, often combined with some level of pre-existing and non-sexual emotional intimacy with the extra-pair male (Banfield & McCabe, 2001), many of these women may have no intention of an extra-pair sexual relationship before it is initiated. Under these conditions, the dynamics of cuckoldry may involve some level of self deception on women's part, a mechanism that facilitates their ability to keep the extra-pair relationship hidden from their social partners.

MEN'S ANTI-CUCKOLDRY STRATEGIES

As with women, men's anti-cuckoldry biases almost certainly involve a mix of implicit processes and explicit behavioral strategies that can be directed toward their mates, toward potential rivals, and toward the evaluation of the likely paternity of children born to their partners (Buss, 2002; Schmitt & Buss,

2001; Symons, 1979). I provide a brief overview of some of the better studied of these mechanisms in the following sections; specifically, relationship jealousy, mate guarding, and use of paternity cues, respectively.

Relationship jealousy

Jealousy is an affective experience that is triggered by risks to a central relationship, especially relationships with parents and mates. The most salient trigger for men's jealousy in adulthood is predicted to be real or imagined threats to paternity certainty; that is, a risk of partner infidelity (Buss *et al.*, 1992; Daly & Wilson, 1982; Symons, 1979). The psychological manifestation is sexual jealousy, which has a near-universal influence on the dynamics of men's and women's relationships (e.g. Buss *et al.*, 2000; Geary *et al.*, 1995), although the evolutionary interpretation of these dynamics and associated sex differences have been questioned (e.g. Harris, 2000, 2003). In keeping with predictions derived from evolutionary theory, Sagarin and colleagues (2003) provided evidence that men's jealousy is especially likely to be triggered by paternity threats and not to other aspects of their mates' relationships with other people. Here, it was found that men were distressed by the prospect of their partner having an extra-pair sexual relationship with another man and thus risking pregnancy, but were not distressed by the prospect of their partner having a sexual relationship with a woman and thus not risking pregnancy (Sagarin *et al.*, 2003).

When triggered, jealousy often results in a variety of behavioral responses, including male-on-female aggression (Daly *et al.*, 1982; Daly & Wilson, 1988), divorce (Betzig, 1989), the monitoring and attempted control of the social and sexual behavior of their partners (Dickemann, 1981; Flinn, 1988), enhancement of their attractiveness as a mate (Buss & Shackelford, 1997), and the monitoring of and aggression toward actual or perceived sexual rivals (Wilson & Daly, 1985). In total, these behaviors encompass tactics that function to ensure, through coercion or enticement, that their reproductive investment and that of their mate is directed toward the man's biological children.

Mate guarding

One of the more common behavioral responses to relationship jealousy is mate guarding. For men this involves reducing their partner's opportunity to mate with other men. The attendant dynamics are well illustrated by Flinn's observational study of spousal and other heterosexual relationships in a rural Trinidadian village. In this village, "13 of 79 (16.4%) offspring born . . . during the period 1970–1980 were putatively fathered by males other than the mother's coresident mate. Clearly, mate guarding could have significant effects on fitness" (Flinn, 1988, p. 10). Indeed, mate guarding by men but not women

was found to be a common feature of long-term relationships, although the guarding varied with the pregnancy risks of the man's partner, as found by Sagarin *et al.* (2003). Men monitored the activities less diligently and had fewer conflicts with pregnant and older wives than they did with younger and non-pregnant wives. In a related study, women reported that their partner engaged in more mate guarding during the week when the women were most likely to ovulate, the time frame when these same women reported an increase in sexual fantasy and interest in an extra-pair man (Gangestad *et al.*, 2002).

The cues that trigger men's increased mate guarding during the ovulatory time frame are not well understood, but might involve sensitivity to behavioral, physical, and perhaps olfactory changes that occur during this time (Gangestad *et al.*, 2002). One obvious change might be that women become more behaviorally attentive (e.g. flirtatious) to attractive extra-pair men, which their partners will likely monitor. There are also soft-tissue changes that result in greater symmetry in many of the traits that influence men's mate choices and through this there is an increase in women's physical attractiveness (e.g. Scutt & Manning, 1996). These changes would make the woman more attractive to their partner, as well as to extra-pair men. Although the results are not conclusive, it appears that women are not only more symmetric during the time of ovulation, they may also produce olfactory cues that signal ovulation (Singh & Bronstad, 2001; but see Thornhill & Gangestad, 1999). In the better controlled of these studies, Singh and Bronstad asked women to wear t-shirts during the time of ovulation and during a non-ovulatory phase of their menstrual cycle. Men then rated the t-shirt odors in terms of pleasantness, sexiness, and intensity. Shirts worn during the ovulatory phase were rated as more pleasant and sexy than shirts worn by the same women during the non-ovulatory phase. There were, in contrast, no phase differences for rated intensity. Men may thus be sensitive to cycle-related fertility cues.

Paternity cues

The patterns described in the previous two sections are consistent with the prediction that a variety of emotional and behavioral anti-cuckoldry biases are evident in men (Daly *et al.*, 1982). These biases largely operate prior to pregnancy. Because men parent during some or all of their children's development and often beyond this, they are also predicted to have biases that serve as post-partum paternity cues. Women, in turn, 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 *et al.*, 2000; Pagel, 1997). Men in particular should be sensitive to cues of resemblance

to their putative offspring and invest more heavily in children they perceive as resembling themselves.

Several studies suggest that fathers do indeed bias their investment in children based on their perceived resemblance to the child (Burch & Gallup, 2000; Platek *et al.*, 2002), 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). Platek *et al.* (2002) took digital photographs of men and women and morphed them to create the face of a preschool child. Participants were then presented with a set of five such photos (their morphed photo was in half of the sets) and asked to choose the child whom they were more likely to adopt, find most attractive, most likely to spend time with and invest resources on, among other investment related items. Men were significantly more likely than women to indicate that they would invest in their self-morph. Burch and Gallup (2000) assessed men who were in mandated treatment for domestic violence and also found a child-resemblance bias for the biological children or putative biological children of these men. As the perceived resemblance to their children increased, the quality of the reported relationship with the children increased ($r = 0.60$), the severity of the injuries inflicted on the children's mothers during the domestic violence decreased ($r = -0.31$), and indicators of spousal commitment improved.

In species in which cuckoldry occurs on a regular basis and in which paternal investment is important and contingent on perceived biological relatedness to offspring, as with humans, it is in the females' and the offspring's best interest to confuse paternity (Pagel, 1997). Daly and Wilson (1982) found that in videos of spontaneous interactions in maternity wards in the USA, mothers stated that the newborn resembled the father more than the newborn resembled her but fathers were more skeptical of this resemblance. Follow-up studies confirmed the pattern in Canada and Mexico and suggest that it extends to maternal kin as well as the mother (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 attempt either implicitly or explicitly to manipulate social information in ways that would result in increased paternal investment.

Men may also assess the likelihood of their partner seeking an extra-pair relationship based on their partner's personality, and on the overall quality of the relationship. Men married to women who are conscientious and emotionally stable report higher levels of marital satisfaction and lower perceived risk of partner infidelity (Shackelford & Buss, 2000). When it comes to an actual

infidelity, women who regularly participate in religious activities are less likely to engage in an extra-pair relationship, whereas women who are unhappy in their current relationships, have been previously divorced, and earn more money (and thus less dependent on spousal support) are more likely to engage in such a relationship, although cause and effect are difficult to separate (Atkins, Baucom, & Jacobson, 2001; Previti & Amato, 2004). In any case, a 17-year longitudinal study of family functioning revealed that beliefs about the inherent stability of the current relationship were predictive of later infidelities. In other words, individuals who believed the relationship was unstable and couples who discussed dissolution of the relationship were more likely to experience an infidelity by one or both of them in subsequent years. It follows that men may be more prone to suspect infidelity or mate guard partners who express a dissatisfaction with the relationship or who believe that relationships are generally unstable.

Sperm competition

Cuckoldry, of course, occurs when women maintain more than one sexual relationship and engage in sexual intercourse with both partners within roughly a 5-day time frame (Baker & Bellis, 1995). Under these conditions, the women's partners are implicitly competing through sperm competition. In modern populations, it is clear that some women do engage in multiple and simultaneous sexual relationships and thus create conditions that could promote sperm competition. Bellis and Baker (1990) 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 these relationships were less likely to involve the use of contraceptives than were copulations with their social partner. In a national probability survey of the sexual behavior of adults in Britain, Johnson *et al.* (2001) found that 15% of the 16–24-year-old women and 8% of the 25–34-year-old women reported concurrent sexual relationships during the past year.

Although these patterns and other evidence support the hypothesis that sperm competition may have occurred during human evolutionary history (Baker & Bellis, 1993; Pound, 2002; Shackelford *et al.*, 2002), the extent of such competition and its importance in shaping human reproductive behavior is debated (e.g. Nicholls, 2002). If human paternal investment evolved in a social context that is closely related to a gorilla-like social structure embedded in multi-male, multi-female communities then sperm competition would have been considerably less important than if our evolutionary history was closer to that of the chimpanzee- or bonobo-like reproductive pattern.

Conclusion

Paternal investment and cuckoldry are necessarily linked, proximately and ultimately, and the attendant dynamics reflect a balance of cost-benefit trade-offs for both males and females (Clutton-Brock, 1991; Fishman *et al.*, 2003). Paternal investment has evolved for species in which such investment is likely to be directed toward biological offspring (i.e. high paternity certainty), is associated with improved survival and later reproductive prospects for these offspring, and does not substantively reduce mating opportunity. When paternal investment is necessary for offspring survival it is obligate and nearly all males invest and very few females cuckold (Birkhead & Møller, 1996). When paternal investment is helpful but not obligate, then it is facultatively expressed. This contingent expression of male parenting is influenced by the local ecology and social group in which the male is situated and the associated trade-offs between the male's mating opportunities, paternity certainty, and the benefits accrued by his offspring. These same conditions create the potential for females to risk cuckolding their social partners. The risks are male abandonment and retaliation and the primary benefits are having offspring sired by a more fit male - their offspring have higher survival rates - while securing investment for her offspring from the social partner.

The evolutionary history of human paternal investment is not fully understood, although it is clear that it is facultatively expressed in most ecologies and social groups (Flinn & Low, 1986) and almost certainly expressed in accordance with the same cost-benefit trade-offs found in other species (Geary, 2000, 2006). Our understanding and interpretation of these proximate patterns will be influenced by our understanding of the contexts in which human paternal investment evolved (Lovejoy, 1981). If the evolutionary history is similar to that found in extant groups of chimpanzees and bonobos, where there is little paternal investment or paternity certainty, then human paternal investment, long-term male-female relationships, and relatively high levels of paternity certainty are recently evolved traits. In contrast, if male parenting evolved in a context similar to that found in extant lowland gorillas, then these traits have a long evolutionary history. In fact, reductions in paternity certainty and cuckoldry would be the more recent evolutionary changes; these would coincide with the formation of close-knit male kin groups and the formation of large multi-male, multi-female communities.

If the gorilla-like model is correct, then men are biased as a group to invest in the well-being of their children, though still basically polygynous in their mate preferences (as with gorillas), and both men and women are biased to develop long-term (though not necessarily exclusive) reproductive relationships. From

this perspective, cuckoldry risks are predicted to be greater than but still close to those found in extant gorillas, as they are. Although we await definitive results, cuckoldry rates across human populations appear to be about 10% for humans as compared with less than 5% in gorillas (Bradley *et al.*, 2004). As is found in other species with the facultative expression of paternal investment, women appear to be much more likely to cuckold lower-quality social partners or partners with whom a long-term relationship seems unlikely than they are to cuckold other men. The gist of this model is that the facultative expression of men's parenting may be closer to our evolutionary history and women's polyandrous mating and cuckoldry further from our evolutionary history than implied by evolutionary models that start from chimpanzee- or bonobo-like reproductive behavior.

References

- Adler, N. E., Boyce, T., Chesney, M. A., *et al.* (1994). Socioeconomic status and health: the challenge of the gradient. *American Psychologist*, **49**, 15–24.
- Alexander, R. D. (1987). *The Biology of Moral Systems*. Hawthorne, NY: Aldine de Gruyter.
- Amato, P. R. (1998). More than money? Men's contributions to their children's lives. In A. Booth and A. C. Crouter, eds., *Men in Families: When Do They Get Involved? What Difference Does it Make?* Mahwah, NJ: Erlbaum, pp. 241–78.
- Andersson, M. (1994). *Sexual Selection*. Princeton, NJ: Princeton University Press.
- Arnold, K. E. and Owens, I. P. F. (2002). Extra-pair paternity and egg dumping in birds: life history, parental care and the risk of retaliation. *Proceedings of the Royal Society of London B*, **269**, 1263–9.
- Atkins, D. C., Baucom, D. H., and Jacobson, N. S. (2001). Understanding infidelity: correlates in a national random sample. *Journal of Family Psychology*, **15**, 735–49.
- Baker, R. R. and Bellis, M. A. (1993). Human sperm competition: ejaculate adjustment by males and the function of masturbation. *Animal Behaviour*, **46**, 861–85.
- Baker, R. R. and Bellis, M. A. (1995). *Human Sperm Competition: Copulation, Masturbation, and Infidelity*. London: Chapman and Hall.
- Banfield, S. and McCabe, M. P. (2001). Extra relationship involvement among women: are they different from men? *Archives of Sexual Behavior*, **30**, 119–42.
- Beckerman, S., Lizarralde, R., Ballew, C., *et al.* (1998). The Barí partible paternity project: preliminary results. *Current Anthropology*, **39**, 164–7.
- Bellis, M. A. and Baker, R. R. (1990). Do females promote sperm competition? Data for humans. *Animal Behaviour*, **40**, 997–9.
- Betzig, L. (1989). Causes of conjugal dissolution: a cross-cultural study. *Current Anthropology*, **30**, 654–76.
- Birkhead, T. R. and Møller, A. P. (1996). Monogamy and sperm competition in birds. In J. M. Black, ed., *Partnerships in Birds: The Study of Monogamy*. New York: Oxford University Press, pp. 323–43.

- Bradley, B. J., Doran-Sheehy, D. M., Lukas, D., Boesch, C., and Vigilant, L. (2004). Dispersed male networks in Western gorillas. *Current Biology*, **14**, 510–13.
- Burch, R. L. and Gallup, Jr., G. G. (2000). Perceptions of paternal resemblance predict family violence. *Evolution and Human Behavior*, **21**, 429–35.
- Buss, D. M. (1989). Sex differences in human mate preferences: evolutionary hypothesis tested in 37 cultures. *Behavioral and Brain Sciences*, **12**, 1–49.
- Buss, D. M. (2002). Human mate guarding. *Neuroendocrinology Letters*, **23** (Suppl. 4), 23–9.
- Buss, D. M. and Schmitt, D. P. (1993). Sexual strategies theory: an evolutionary perspective on human mating. *Psychological Review*, **100**, 204–32.
- Buss, D. M. and Shackelford, T. K. (1997). From vigilance to violence: mate retention and tactics in married couples. *Journal of Personality and Social Psychology*, **72**, 346–61.
- Buss, D. M., Larsen, R. J., Westen, D., and Semmelroth, J. (1992). Sex differences in jealousy: evolution, physiology, and psychology. *Psychological Science*, **3**, 251–5.
- Buss, D. M., Shackelford, T. K., Choe, J., Buunk, B. P., and Dijkstra, P. (2000). Distress about mating rivals. *Personal Relationships*, **7**, 235–43.
- Campbell, A. (2002). *A Mind of Her Own: The Evolutionary Psychology of Women*. New York: Oxford University Press.
- Cerda-Flores, R. M., Barton, S. A., Marty-Gonzalez, L. F., Rivas, F., and Chakraborty, R. (1999). Estimation of nonpaternity in the Mexican population of Nuevo Leon: a validation study with blood group markers. *American Journal of Physical Anthropology*, **109**, 281–93.
- Christenfeld, N. J. S. and Hill, E. A. (1995). Whose baby are you? *Nature*, **378**, 669.
- Clutton-Brock, T. H. (1989). Mammalian mating systems. *Proceedings of the Royal Society of London B*, **236**, 339–72.
- Clutton-Brock, T. H. (1991). *The Evolution of Parental Care*. Princeton, NJ: Princeton University Press.
- Daly, M. and Wilson, M. (1982). Whom are newborn babies said to resemble? *Ethology and Sociobiology*, **3**, 69–78.
- Daly, M. and Wilson, M. I. (1985). Child abuse and other risks of not living with both parents. *Ethology and Sociobiology*, **6**, 155–76.
- Daly, M. and Wilson, M. (1988). *Homicide*. New York: Aldine de Gruyter.
- Daly, M., Wilson, M., and Weghorst, S. J. (1982). Male sexual jealousy. *Ethology and Sociobiology*, **3**, 11–27.
- Darwin, C. (1871). *The Descent of Man, and Selection in Relation to Sex*. London: John Murray.
- de Waal, F. and Lanting, F. (1997). *Bonobo: The Forgotten Ape*. Berkeley, CA: University of California Press.
- Dickemann, M. (1981). Paternal confidence and dowry competition: a biocultural analysis of purdah. In R. D. Alexander and D. W. Tinkle, eds., *Natural Selection and Social Behavior*. New York: Chiron Press, pp. 417–38.
- Essock-Vitale, S. M. and McGuire, M. T. (1988). What 70 million years hath wrought: sexual histories and reproductive success of a random sample of American

- women. In L. Betzig, M. Borgerhoff Mulder, and P. Turke, eds., *Human Reproductive Behaviour: a Darwinian Perspective*. Cambridge: Cambridge University Press, pp. 221–35.
- Fishman, M. A., Stone, L., and Lotem, A. (2003). Fertility assurance through extrapair fertilizations and male paternity defense. *Journal of Theoretical Biology*, **221**, 103–14.
- Flinn, M. V. (1988). Mate guarding in a Caribbean village. *Ethology and Sociobiology*, **9**, 1–28.
- Flinn, M. V. (1992). Paternal care in a Caribbean village. In B. S. Hewlett, ed., *Father-Child Relations: Cultural and Biosocial Contexts*. New York: Aldine de Gruyter, pp. 57–84.
- Flinn, M. V. and Low, B. S. (1986). Resource distribution, social competition, and mating patterns in human societies. In D. I. Rubenstein and R. W. Wrangham, eds., *Ecological Aspects of Social Evolution: Birds and Mammals*. Princeton, NJ: Princeton University Press, pp. 217–43.
- Fossey, D. (1984). *Gorillas in the Mist*. Boston, MA: Houghton Mifflin Co.
- Gangestad, S. W. and Simpson, J. A. (2000). The evolution of human mating: trade-offs and strategic pluralism. *Behavioral and Brain Sciences*, **23**, 573–644.
- Gangestad, S. W. and Thornhill, R. (1998). Menstrual cycle variation in women's preferences for the scent of symmetrical men. *Proceedings of the Royal Society of London B*, **265**, 927–33.
- Gangestad, S. W., Thornhill, R., and Garver, C. E. (2002). Changes in women's sexual interests and their partner's mate retention tactics across the menstrual cycle: evidence for shifting conflicts of interest. *Proceedings of the Royal Society of London B*, **269**, 975–82.
- Gaulin, S. J. C., McBurney, D. H., and Brakeman-Wartell, S. L. (1997). Matrilateral biases in the investment of aunts and uncles: a consequence and measure of paternity uncertainty. *Human Nature*, **8**, 139–51.
- Geary, D. C. (1998). *Male, Female: The Evolution of Human Sex Differences*. Washington, DC: American Psychological Association.
- Geary, D. C. (2000). Evolution and proximate expression of human paternal investment. *Psychological Bulletin*, **126**, 55–77.
- Geary, D. C. (2002). Sexual selection and human life history. In R. Kail (Ed.), *Advances in child development and behavior* (Vol 30, pp. 41–101). San Diego, CA: Academic Press.
- Geary, D. C. (2006). Evolution of paternal investment. In D. M. Buss, ed., *The Evolutionary Psychology Handbook*. Hoboken, NJ: John Wiley & Sons (in press).
- Geary, D. C. and Flinn, M. V. (2001). Evolution of human parental behavior and the human family. *Parenting: Science and Practice*, **1**, 5–61.
- Geary, D. C. and Flinn, M. V. (2002). Sex differences in behavioral and hormonal response to social threat: commentary on Taylor *et al.* (2000). *Psychological Review*, **109**, 745–50.
- Geary, D. C., Rumsey, M., Bow-Thomas, C. C., and Hoard, M. K. (1995). Sexual jealousy as a facultative trait: evidence from the pattern of sex differences in adults from China and the United States. *Ethology and Sociobiology*, **16**, 355–83.

- Geary, D. C., DeSoto, M. C., Hoard, M. K., Sheldon, M. S., and Cooper, L. (2001). Estrogens and relationship jealousy. *Human Nature*, **12**, 299–320.
- Glass, S. P. and Wright, T. L. (1992). Justifications for extramarital relationships: the association between attitudes, behaviors, and gender. *Journal of Sex Research*, **29**, 361–87.
- Goodall, J. (1986). *The Chimpanzees of Gombe: Patterns of Behavior*. Cambridge, MA: The Belknap Press.
- Greiling, H. and Buss, D. M. (2000). Women's sexual strategies: the hidden dimension of extra-pair mating. *Personality and Individual Differences*, **28**, 929–63.
- Harris, C. R. (2000). Psychophysiological responses to imagined infidelity: the specific innate modular view of jealousy reconsidered. *Journal of Personality and Social Psychology*, **78**, 1082–91.
- Harris, C. R. (2003). A review of sex differences in sexual jealousy, including self-report data, psychophysiological responses, interpersonal violence, and morbid jealousy. *Personality and Social Psychology Review*, **7**, 102–28.
- Haig, D. (1993). Genetic conflicts in human pregnancy. *Quarterly Review of Biology*, **68**, 495–532.
- Hill, K. and Hurtado, A. M. (1996). *Ache Life History: The Ecology and Demography of a Foraging People*. New York: Aldine de Gruyter.
- Irons, W. (1979). Cultural and biological success. In N. A. Chagnon and W. Irons, eds., *Natural Selection and Social Behavior*. North Scituate, MA: Duxbury Press, pp. 257–72.
- Johnson, A. M., Mercer, C. H., Erens, B., et al. (2001). Sexual behaviour in Britain: partnerships, practices, and HIV risk behaviors. *Lancet*, **358**, 1835–42.
- Kaplan, H. S., Lancaster, J. B., Bock, J. A., and Johnson, S. E. (1995). Does observed fertility maximize fitness among New Mexican men? A test of an optimality model and a new theory of parental investment in the embodied capital of offspring. *Human Nature*, **6**, 325–60.
- Lancaster, J. B. (1989). Evolutionary and cross-cultural perspectives on single-parenthood. In R. W. Bell and N. J. Bell, eds., *Interfaces in Psychology: Sociobiology and the Social Sciences*. Lubbock, TX: Texas Tech University Press, pp. 63–72.
- Lovejoy, C. O. (1981). The origin of man. *Science*, **211**, 341–50.
- MacDonald, K. (1992). Warmth as a developmental construct: an evolutionary analysis. *Child Development*, **63**, 753–73.
- Macrae, C. N., Alnwick, K. A., Milne, A. B., and Schloerscheidt, A. M. (2002). Person perception across the menstrual cycle: hormonal influences on social-cognitive functioning. *Psychological Science*, **13**, 532–6.
- McBurney, D. H., Simon, J., Gaulin, S. J. C., and Geliebter, A. (2002). Matrilateral biases in the investment of aunts and uncles: replication in a population presumed to have high paternity certainty. *Human Nature*, **13**, 391–402.
- McLain, D. K., Setters, D., Moulton, M. P., and Pratt, A. E. (2000). Ascription of resemblance of newborns by parents and nonrelatives. *Evolution and Human Behavior*, **21**, 11–23.

- Møller, A. P. and Cuervo, J. J. (2000). The evolution of paternity and paternal care. *Behavioral Ecology*, **11**, 472–85.
- Morrison, A. S., Kirshner, J., and Molho, A. (1977). Life cycle events in 15th century Florence: records of the Monte Delle Doti. *American Journal of Epidemiology*, **106**, 487–92.
- Nicholls, H. (2002). Sperm control. *Trends in Cognitive Sciences*, **6**, 185.
- Pagel, M. (1997). Desperately concealing father: a theory of parent-infant resemblance. *Animal Behaviour*, **53**, 973–81.
- Pasternak, B., Ember, C. R., and Ember, M. (1997). *Sex, Gender, and Kinship: a Cross-Cultural Perspective*. Upper Saddle River, NJ: Prentice-Hall.
- Penton-Voak, I. S. and Perrett, D. I. (2000). Female preference for male faces changes cyclically: further evidence. *Evolution and Human Behavior*, **21**, 39–48.
- Penton-Voak, I. S., Perrett, D. I., Castles, D. L., et al. (1999). Menstrual cycle alters face preference. *Nature*, **399**, 741–2.
- Perrone, Jr., M. and Zaret, T. M. (1979). Parental care patterns of fishes. *American Naturalist*, **113**, 351–61.
- Platak, S. M., Burch, R. L., Panyavin, I. S., Wasserman, B. H., and Gallup, Jr., G. G. (2002). Reactions to children's face resemblance affects males more than females. *Evolution and Human Behavior*, **23**, 159–66.
- Potthoff, R. F. and Whittinghill, M. (1965). Maximum-likelihood estimation of the proportion of nonpaternity. *American Journal of Human Genetics*, **17**, 480–94.
- Pound, N. (2002). Male interest in visual cues of sperm competition risk. *Evolution and Human Behavior*, **23**, 443–66.
- Previti, D. and Amato, P. R. (2004). Is infidelity a cause or a consequence of poor marital quality? *Journal of Social and Personal Relationships*, **21**, 217–30.
- Regalski, J. M. and Gaulin, S. J. C. (1993). Whom are Mexican infants said to resemble? Monitoring and fostering paternal confidence in the Yucatan. *Ethology and Sociobiology*, **14**, 97–113.
- Richner, H., Christe, P., and Oppliger, A. (1995). Paternal investment affects prevalence of malaria. *Proceedings of the National Academy of Sciences USA*, **92**, 1192–4.
- Robbins, M. M. (1999). Male mating patterns in wild multimale mountain gorilla groups. *Animal Behaviour*, **57**, 1013–20.
- Sagarin, B. J., Becker, D. V., Guadagno, R. E., Nicastle, L. D., and Millevoi, A. (2003). Sex differences (and similarities) in jealousy: the moderating influence of infidelity experience and sexual orientation of the infidelity. *Evolution and Human Behavior*, **24**, 17–23.
- Sasse, G., Muller, H., Chakraborty, R., and Ott, J. (1994). Estimating the frequency of nonpaternity in Switzerland. *Human Heredity*, **44**, 337–43.
- Schmitt, D. P. and Buss, D. M. (2001). Human mate poaching: tactics and temptations for infiltrating existing mateships. *Journal of Personality and Social Psychology*, **80**, 894–917.
- Schultz, H. (1991). Social differences in mortality in the eighteenth century: an analysis of Berlin church registers. *International Review of Social History*, **36**, 232–48.

- Scutt, D. and Manning, J. T. (1996). Symmetry and ovulation in women. *Human Reproduction*, **11**, 2477–80.
- Shackelford, T. K. and Buss, D. M. (2000). Marital satisfaction and spousal cost-infliction. *Personality and Individual Differences*, **28**, 917–28.
- Shackelford, T. K. and Larsen, R. J. (1997). Facial asymmetry as an indicator of psychological, emotional, and physiological distress. *Journal of Personality and Social Psychology*, **72**, 456–66.
- Shackelford, T. K., LeBlanc, G. J., Weekes-Shackelford, V. A., et al. (2002). Psychological adaptation to human sperm competition. *Evolution and Human Behavior*, **23**, 123–38.
- Singh, D. and Bronstad, P. M. (2001). Female body odour is a potential cue to ovulation. *Proceedings of the Royal Society of London B*, **268**, 797–801.
- Stewart, K. J. and Harcourt, A. H. (1987). Gorillas: variation in female relationships. In B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham, and T. T. Struhsaker, eds., *Primate Societies*. Chicago, IL: University of Chicago Press, pp. 155–64.
- Symons, D. (1979). *The Evolution of Human Sexuality*. New York: Oxford University Press.
- Taylor, A. B. (1997). Relative growth, ontogeny, and sexual dimorphism in gorilla (*Gorilla gorilla gorilla* and *G. g. beringei*): evolutionary and ecological considerations. *American Journal of Primatology*, **43**, 1–31.
- Thornhill, R. (1976). Sexual selection and paternal investment in insects. *American Naturalist*, **110**, 153–63.
- Thornhill, R. and Gangestad, S. W. (1999). The scent of symmetry: a human sex pheromone that signals fitness? *Evolution and Human Behavior*, **20**, 175–201.
- Thornhill, R. and Palmer, C. T. (2000). *A natural history of rape: biological bases of sexual coercion*. Cambridge, MA: MIT Press.
- Treas, J. and Giesen, D. (2000). Sexual infidelity among married and cohabitating Americans. *Journal of Marriage and the Family*, **62**, 48–60.
- Trivers, R. L. (1972). Parental investment and sexual selection. In B. Campbell, ed., *Sexual Selection and the Descent of Man 1871–1971*. Chicago, IL: Aldine Publishing, pp. 136–79.
- Trivers, R. L. (1974). Parent-offspring conflict. *American Zoologist*, **14**, 249–64.
- United Nations (1985). *Socio-Economic Differentials in Child Mortality in Developing Countries*. New York: United Nations.
- Westneat, D. F. and Sherman, P. W. (1993). Parentage and the evolution of parental behavior. *Behavioral Ecology*, **4**, 66–77.
- Whitten, P. L. (1987). Infants and adult males. In B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham, and T. T. Struhsaker, eds., *Primate Societies*. Chicago, IL: University of Chicago Press, pp. 343–57.
- Wiederman, M. W. (1997). Extramarital sex: prevalence and correlates in a national survey. *Journal of Sex Research*, **34**, 167–74.
- Wilson, M. and Daly, M. (1985). Competitiveness, risk taking, and violence: the young male syndrome. *Ethology and Sociobiology*, **6**, 59–73.
- Wolf, L., Ketterson, E. D., and Nolan, Jr., V. (1988). Paternal influence on growth and survival of dark-eyed junco young: do parental males benefit? *Animal Behaviour*, **36**, 1601–18.