
Introduction to theory and research on anti-cuckoldry tactics: overview of current volume

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Female infidelity

In most cultures, marriage vows entail the promise of fidelity and life-long commitment. In principle, marriage vows are a contract – a reproductive contract – between two individuals to maintain both emotional *and* sexual fidelity to one another ‘til death do them part.’ Monogamy. There are few species that maintain monogamous relationships between the sexes. It is commonly believed that males are more promiscuous, but new research is shedding light on the prominence of female infidelity as well as the consequences of such behavior.

Female infidelity is common in the animal kingdom as well as among humans. According to an analysis of 280 000 paternity tests conducted in 1999 by the American Association of Blood Banks, approximately 30% of children are fathered by extra-pair copulations; that is, 30% of children in this sample were fathered by someone other than the woman’s long-term romantic partner. Several case studies exemplify this phenomenon and the associated psychological and social consequences. The *New York Times* reported a case of a Texas man who was faced with the unnerving news that not one, but several, of his children were the product of extra-pair paternity. The bittersweet news came when the man was being tested as a carrier for a debilitating genetic disorder that his youngest daughter had suffered with since birth. When the genetic test came back negative he should have been elated, but knowing that both

parents must be carriers for any child to be inflicted with the disorder raised obvious concerns. Either the doctor misdiagnosed his child or his child was the product of infidelity on the part of his wife. DNA paternity testing confirmed that he did not father his youngest daughter. This motivated him to obtain paternity tests for his three other children, only one of which had been sired by him.

A team of scientists in Italy (Barbaro *et al.*, 2004) was asked to conduct DNA paternity tests to reveal relatedness among individuals involved in a murder case. The case involved three victims (two males, one female) that were brutally murdered. The suspected killer was later found hanged, a presumed suicide. The police conducted a series of DNA paternity tests to determine the paternity of the murdered female's child. It was presumed that the child had been fathered by the suspect, the man who had hanged himself, because he had been in a long-term relationship with the slain female. However, DNA paternity testing revealed that the child was actually fathered by one of the other murdered young men. A judge in another case ordered a team of scientists to solve a disputed paternity case among a set of twin girls when one of the girls raised doubts about her father's paternity, because she felt the man favored her twin sister. DNA testing confirmed that the man had only sired one of the twin girls and was genetically excluded from having sired the twin who raised doubts about paternity. It is not uncommon in the animal literature to find organisms that will have offspring (of a single litter) fathered by several males. For example, in most passerine birds, any given clutch can contain eggs fathered by two or more males. However, this phenomenon has rarely been described or discussed in humans.

The problem of paternal uncertainty: how males deal with female infidelity

Because of concealed ovulation, internal fertilization, and female infidelity, human parental certainty is asymmetrical: unlike females, who are always 100% certain of *maternity*, males can never be certain of *paternity*. Current estimates of extra-pair paternity (paternity by someone other than the putative and domestic father, or cuckoldry) are between 1 and 30%, with the best estimate at about 10% (Baker & Bellis, 1995; Cerda-Flores *et al.*, 1999; Neale, Neale, & Sullivan, 2002; Sasse *et al.*, 1994; Sykes & Irven, 2000). In other words, approximately 1 in 10 children are the product of female infidelity. This asymmetry in parental certainty has contributed to an asymmetry in human parental investment (Bjorklund & Shackelford, 1999; Dawkins, 1976; Geary, 2000; Trivers, 1974). As a consequence of having to carry a child to term,

females, by default, invest more in and provision more for children than do males. Additionally, if a female nurses her offspring she could be bound to several additional years of parental investment.

Males, however, are not obligated to invest resources in offspring, and tend to provide care proportional to their confidence or certainty of paternity (Burch & Gallup, 2000; Daly & Wilson, 1996, 1998). The risk of cuckoldry appears to have driven the evolution of male anti-cuckoldry tactics; tactics designed to limit and control female infidelity in an attempt to reduce the risk of cuckoldry (Buss, 1988, 1994, 1999; Buss & Shackelford, 1997; Platek, 2002; Platek *et al.*, 2002, 2003; Shackelford *et al.*, 2002).

We can observe a similar pattern among many other mammals. For example, paternal care is usually only manifest in those mammals with relatively high paternal certainty, whereas for most mammals (95–97%) males provide little or no direct investment in their offspring. For those few species that do engage in paternal provisioning, it appears that the males have evolved several anti-cuckoldry tactics that increase the certainty that they are the source of paternity (e.g. Lacy & Sherman, 1983). In an attempt to limit provisioning for offspring that are the consequence of female extra-pair copulations, males of some species sometimes perform what may appear to be extreme behaviors. For example, when a male langur overthrows another male and gains dominance within a troop, he will systematically kill infants that were fathered by the previous alpha male. By resorting to infanticide when the paternity of an offspring is ostensibly foreign (e.g. Hrdy, 1974), his behavior serves two functions: (1) it eliminates the possibility that he will invest valuable resources in unrelated offspring and (2) it induces sexual receptivity in those females whose offspring he killed. This allows the new dominant male to use the females for his own reproductive best interests. Additionally, male baboons have been found to invest resources in offspring proportional to the degree to which he monopolized the females prior to insemination (Buchan *et al.*, 2003).

There is growing evidence that human males are similarly affected by these evolutionary pressures to invest in offspring as a function of paternal certainty. As a way of elucidating the importance of paternity for males, Daly and Wilson (1982) and Regalski and Gaulin (1993) (see also Brédart & French, 1999; Christenfeld & Hill, 1995; Nesse *et al.*, 1990) observed family interactions following the birth of a child. They measured the number of times people remarked who the infant looked like. Both studies found that people were more likely to comment that the children resembled the putative fathers than they were to comment that the children resembled the mothers. Both studies also documented that the mother and her family were more likely to attribute resemblance to the putative father than to the mother, whereas the putative father and his

family showed no such bias. The authors interpreted these behaviors as attempts on the part of the female and her family to reassure the putative father and his family about paternity. Daly and Wilson (1982) report that one male was so adamant about the importance of paternity that he stated, "... if the child does not look like me I'll abandon them both!"

It is also well known that men preferentially invest resources in children to whom they are likely to be related genetically. For example, it is not uncommon for stepchildren to be treated significantly worse than genetic children (e.g. Anderson *et al.*, 1999). Burch and Gallup (2000) have shown that males spend less time with, invest fewer resources in, and are more likely to abuse ostensibly unrelated children than children they assume to be their genetic offspring. They also found that the less a male thinks a child (unrelated or genetic) looks like him, the worse he treats the child and the worse he views the relationship with that child. Daly and Wilson (1988; and see Daly, Wilson, & Weghorst, 1982) estimate the incidence of filicide (child-killing) among stepchildren to be as much as 100 times that of genetic children. In Daly and Wilson's (1988) landmark book, *Homicide*, they interpret spousal homicide as a byproduct of cuckoldry fear and sexual jealousy among men. These data suggest a strong link between paternity uncertainty and the treatment of children.

As a result of paternal uncertainty, human males appear to have evolved an arsenal of anti-cuckoldry tactics to limit and perhaps control the incidence of female infidelity and thereby increase the likelihood that the children they provision are genetically their own. Emerging data suggest that males have evolved at least three types of tactic that help to reduce the likelihood of being cuckolded. Each of these tactics is the focus of a section of this volume, with chapters contributed by leading experts in the field of evolutionary science.

This volume takes the form of an integration of new data with newly emerging theory about human paternal uncertainty and the evolution of male anti-cuckoldry tactics in an attempt to consolidate a base of literature into a new model for the evolution of male anti-cuckoldry tactics. The conception of this volume was the result of a symposium, chaired by the editors, at the 15th annual meeting of the Human Behavior and Evolution Society at the University of Nebraska-Lincoln in June 2003. Dr. David Buss, Dr. Steven Gangestad, and Dr. Randy Thornhill, internationally renowned experts in evolutionary psychology, served as discussants to this symposium and Dr. Gangestad has contributed a chapter to the volume. The book consists of both papers presented as part of the symposium and other independent contributions that were not presented as part of the symposium, but represent significant advances in the relevant fields.

The first anti-cuckoldry tactic (addressed in Part II) involves attempts by a man to limit his mate's opportunities for extra-pair copulations that could result

in pregnancy. Males have evolved psychological adaptations that produce mate guarding and jealousy (Buss, 1988; Buss & Shackelford, 1997; see Buss, 2000, for a review) to reduce or to prevent a mate from being inseminated by another male. Recent evidence suggests that males maximize the utility of their mate-guarding strategies by implementing them at ovulation, a key reproductive time in a female's menstrual cycle (Gangestad, Thornhill, & Garver, 2002). Further, jealousy appears to fluctuate with a man's mate value and, hence, risk of cuckoldry. Brown and Moore (2003), for example, found that males who were less symmetrical were significantly more jealous. These and other data suggest that jealousy has evolved as a means by which males can attempt to deter extra-pair copulations (Buss, 2000; Daly & Wilson, 1982; see also Buss *et al.*, 2000; Buss & Shackelford, 1997). Chapters 3–5 address events that might lead up to female infidelities and the mate-guarding tactics employed to deter these behaviors. In Chapter 3, Steven Gangestad provides a discussion of the evidence for adaptations for female extra-pair mating in humans, how female extra-pair mating can lead to extra-pair paternity, and the likelihood that these behaviors are being driven by a female's search for "good genes" – genes that provide an advantage to offspring in the form of pathogen resistance and developmental stability.

In Chapter 4, Todd Shackelford and Aaron Goetz discuss commitment, devotion, and other mate-retention tactics as predictors of violence against women. Male sexual jealousy is a primary cause of violence in romantic relationships (Buss, 2000; Daly & Wilson, 1988). Mate-retention tactics are behavioral manifestations of jealousy designed to thwart a partner's infidelities or relationship defection (Buss, 1988; Buss & Shackelford, 1997; Flinn, 1988). Although some mate-retention tactics appear to be innocuous romantic gestures, some may be harbingers of violence. Shackelford and colleagues investigated the relationships between male mate-retention tactics and female-directed violence in romantic relationships. In an initial study, men reported their use of mate-retention tactics and violence in romantic relationships. Because research has shown that men underreport the violence they inflict on their partners, whereas women report this violence with relative accuracy, a second study assessed women's reports of their partners' behaviors. As predicted, and across both studies, men's use of particular mate-retention tactics was related positively to female-directed violence. A third study secured husbands' reports of their own mate retention and wives' reports of their husbands' use of violence. Again, men's use of particular mate-retention tactics and female-directed violence were related positively. Shackelford and colleagues conclude with a discussion of mate-retention tactics as unique predictors of violence in romantic relationships and suggest directions for future work. Concluding Part II

(Chapter 5), Goetz and Shackelford address the issue of forced in-pair copulation as an anti-cuckoldry tactic and provide interesting new data to support their theoretical model.

In Part III (Chapters 6–10), intra-vaginal anti-cuckoldry strategies such as sperm competition and semen displacement are discussed. In species with internal fertilization, sperm competition occurs when the sperm of two or more males simultaneously occupy the reproductive tract of a female and compete to fertilize an egg (Baker & Bellis, 1995; Parker, 1970, 1984). Sperm-competition theory provides the theoretical framework for a body of work investigating anatomical, behavioral, and psychological adaptations in males and females designed to solve problems posed by sperm competition (Parker, 1970; Smith, 1984). Although much current research on the evolutionary causes and consequences of sperm competition focus primarily on birds (Birkhead & Møller, 1992) and insects (Cooke & Gage, 1995; Gage, 1991; Thornhill & Alcock, 1983), studies of human sperm competition have become a recent focus by evolutionary biologists and evolutionary psychologists (Baker & Bellis, 1988, 1989a, 1989b, 1993a, 1993b, 1995; Bellis & Baker, 1990; Gangestad & Thornhill, 1997, 1998; Gangestad, Thornhill, & Garver, 2002; Pound, 2002; Shackelford & LeBlanc, 2001; Shackelford *et al.*, 2000, 2002; Singh *et al.*, 1998; Thornhill, Gangestad, & Comer, 1995).

Baker and Bellis (1993a, 1995), for example, documented that male humans, like male birds, male insects, and other male non-human primates, appear to be physiologically designed to solve the adaptive problems of sperm competition. Baker and Bellis studied couples in committed, sexual relationships and reported that, consistent with sperm-competition theory, when copulating with their partner men inseminate more sperm when the risk of sperm competition is high. Specifically, controlling for the time since last ejaculation, they documented a large positive correlation between the number of sperm ejaculated and the proportion of time a couple has spent apart since their last copulation.

In a study modeled after research by Baker and Bellis (1993a) on male-ejaculate adjustment as a function of the risk of female infidelity, Shackelford *et al.* (2002) found psychological evidence suggesting a long evolutionary history of human sperm competition. The ejaculate adjustment documented by Baker and Bellis (1993a, 1995) would not be functional if men were not motivated to copulate with their partners sooner rather than later following the possibility of rival insemination. Shackelford *et al.* (2002) documented a positive relationship between the proportion of time a couple has spent apart since their last copulation and, for example, men's ratings of their partner's sexual attractiveness and men's ratings of their interest in copulating with their partner.

Opening up Part III (Chapter 6) Aaron Goetz and Todd Shackelford introduce intra-vaginal anti-cuckoldry tactics with a thorough review of the sperm-competition literature. They synthesize existing and new data that suggest that human (and animal) male physiology adjusts the delivery of sperm quantity and semen chemistry as a function of cuckoldry risk and that there may be specific psychological adaptations associated with sperm competition.

In Chapter 7, Gordon Gallup and Rebecca Burch introduce the semen-displacement hypothesis, which suggests that the morphology of the human penis may act to plunge another male's ejaculate from the reproductive tract of his partner. Gallup and Burch (2004) documented that men's and women's perceptions of a male's sexual behavior (e.g. depth, vigor, and speed of penile thrusting) change as a function of cuckoldry risk. Additionally, by utilizing prosthetic male and female genitalia, they provide evidence that the morphology of the human penis, specifically the glans penis, the frenulum, and the coronal ridge, may be designed for successful semen displacement. This chapter capitulates this hypothesis and raises some interesting predictions based on their findings. Burch and Gallup also contribute a chapter (Chapter 8) that discusses a series of working hypotheses that involve the effects of semen chemistry and its psychobiological effects as an intra-vaginal means by which males may be able to reduce the likelihood of cuckoldry or alter the hormonal status of a reproductive partner. This chapter provides great detail about the chemical composition of semen and the impact this cocktail may have on human mating patterns.

In Chapter 9, Aaron Goetz and colleagues describe how semen displacement, sperm competition, and mate-retention tactics represent a cluster of psychological adaptations that have all evolved to deal with female extra-pair mating. Goetz and colleagues have discovered that the use of mate-retention tactics (e.g. Buss, 1988; including vigilance, emotional manipulation, verbal and physical possession signals, and violence against rivals) correlates with the likelihood of sperm competition and, consequently, copulatory behaviors designed to displace rival male semen. Jennifer Davis and Gordon Gallup conclude Part III (Chapter 10) with a chapter that outlines a new hypothesis suggesting that the reproductive endocrinological disorder known as preeclampsia, an immune disorder that results from genetic incompatibilities between the parents, may have been selected for as a response in females to unfamiliar semen.

Part IV consists of two chapters and introduces the last in this line of cuckoldry defenses: assessing paternity post-parturition. It has been hypothesized that one way a male ancestor assessed paternity was by assessing the degree to which a child resembled him (Daly & Wilson, 1982, 1998; Regalski & Gaulin, 1993). In Chapter 11 Rebecca Burch and her colleagues summarize the "social mirror" effect; the degree to which social perceptions of paternal resemblance

impact parental/paternal behaviors. Finally, in Chapter 12 Steven Platek and Jaime Thomson summarize the evidence that facial resemblance may act as a cue to kinship and, in particular, a cue to paternity for males. They summarize recent findings demonstrating unique neurobiological correlates for processing facial resemblance and the expression of sex differences. They also present evidence that males use self-child resemblance in their decisions to provision for offspring. Using facial morphing, Platek *et al.* (2002, 2003) have shown that males, but not females, respond favorably to facial resemblance in children when queried about hypothetical investment behaviors (e.g. which child would you spend the most time with?). Using functional magnetic resonance imaging (fMRI), Platek and his colleagues have shown that the brains of males react differentially to children's faces that resemble them. Male brain activity displayed when looking at children's faces that do not resemble their own does not differ from the brain activity displayed by females viewing faces of children, and females do not show differential activation as a function of self-child facial resemblance. These data suggest that males have evolved specific neurocognitive mechanisms that influence their decisions to provision for children.

This volume represents the inter-disciplinary and integrated approach to the study of paternal uncertainty and should shed new light on the topic both from a research and an applied perspective. This new three-stage theory - (1) mate-guarding strategies, (2) intra-vaginal strategies, and (3) post-partum strategies - generates many new testable hypotheses that we hope will further our understanding of female infidelity and anti-cuckoldry tactics.

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