

Preventing, Correcting, and Anticipating Female Infidelity

Three Adaptive Problems of Sperm Competition

GEOFFREY PARKER INTRODUCED the idea of sperm competition in 1970. Based on his work on insects, PARKER defined sperm competition as the competition between the sperm of two or more males for the fertilization of one or more ova (PARKER 1970a, 1970b). In the decades since PARKER's groundbreaking work, sperm competition has been documented or inferred to exist in many species, including humans and birds (BAKER/BELLIS 1995; BIRKHEAD/MØLLER 1998; SHACKELFORD/LEBLANC 2001; SHACKELFORD et al. 2002; SMITH 1984). Sperm Competition Theory provides the framework for a body of work that examines the adaptations in males and in females that evolved to solve problems associated with sperm competition.

In this article, I review work inspired by Sperm Competition Theory suggesting that male humans and paternally investing, socially monogamous male birds have a psychology that includes mechanisms designed to solve at least three specific adaptive problems of a female partner's infidelity. Over the evolutionary history of humans and paternally investing, socially monogamous birds, males faced the adaptive problems of (1) preventing a partner's

Abstract

Sperm competition occurs when the sperm of two or more males simultaneously occupy the reproductive tract of a female and thereby compete to fertilize an egg. Sperm competition has been documented or inferred to exist in many species, including humans and birds. Female infidelity creates the primary context for sperm competition. In animals that practice social monogamy and in which there is substantial paternal investment, males incur costs associated with a female partner's infidelity. A principle cost is investing resources in genetically unrelated offspring. Female sexual infidelity and the resulting sperm competition generated several adaptive problems for males over evolutionary history. In humans and in birds, these adaptive problems include preventing female infidelity, correcting female infidelity, and anticipating female infidelity. I review empirical work suggesting that males have evolved physiological and psychological mechanisms designed to solve these problems.

Key words

Female infidelity; sperm competition, evolutionary psychology, social monogamy.

infidelity, (2) correcting a partner's infidelity, and (3) anticipating a partner's infidelity. Although there are likely other adaptive problems concerning sperm competition, such as detecting infidelity or evaluating the timing of a female's infidelity, I limit the discussion to preventing, correcting, and anticipating female infidelity. The discussion of these specific adaptive problems highlights several directions for future work that may clarify our understanding of male psychology and behavior as it relates to female infidelity and sperm competition in birds, humans, and other socially monogamous, paternally investing species.

Overview

DALY and WILSON (1999) recently noted that the study of human evolutionary psychology shares much conceptually with the study of non-human animal behavior. Research on sperm competition in non-human animals—particularly birds—has clear implications for understanding human mating psychology and behavior. Because of the similarities in the mating systems of birds and humans, for example, research on sperm competition in birds (see

Adaptive problem	Evolved solution in birds	Evolved solution in humans
Preventing female infidelity	Mate guarding behaviors (BIRKHEAD/MØLLER 1992)	Mate guarding behaviors (FLINN 1988)
Correcting female infidelity	Copulation immediately upon reunion (HATCHWELL/DAVIES 1992) Forced copulation following extra-pair copulation (BIRKHEAD et al. 1989)	Adjusted number of sperm inseminated (BAKER/BELLIS 1989) Increased sexual interest in partner (SHACKELFORD et al. 2002) Increased perceived attractiveness of partner (SHACKELFORD et al. 2002)
Anticipating female infidelity	Frequent copulation (MØLLER 1988)	Frequent copulation (BAKER/BELLIS 1995) Morbid jealousy (DALY/WILSON 1988; TURBOTT 1981)

Table 1. Three adaptive problems associated with sperm competition and proposed solutions

BIRKHEAD/MØLLER 1992) provides a model for research on sperm competition in humans. Sperm competition has been studied in many animals, including several non-human primates (BIRKHEAD/MØLLER 1998; HARVEY/HARCOURT 1984). I limit comparisons of human behavior and psychology primarily to various bird species, because of the similarities in mating systems between humans and birds (see below). In addition, comparing humans and birds provides a unique approach for evaluating the adaptive problems generated by sperm competition.

Like most species of birds, humans practice social monogamy (BAKER/BELLIS 1995; BIRKHEAD/MØLLER 1992). In this mating system, males and females form long-term pair bonds. Males benefit through uncontested sexual access to their female partner, whereas females benefit through exclusive investment of a male in her and her offspring (BIRKHEAD/MØLLER 1992; TRIVERS 1972). For both birds and humans, however, these pair bonds are not always sexually exclusive. Extra-pair copulation by males and by females of socially monogamous birds have been observed and documented by various methods, such as DNA fingerprinting tests of paternity (BIRK-

HEAD/MØLLER 1992; SAINO/PRIMMER/ELLEGREN/MØLLER 1997). Likewise, there is cross-cultural evidence of extra-pair copulation by male and female humans. Blood grouping studies of humans indicate a cross-cultural paternity discrepancy rate of about 10% (SMITH 1984).

BIRKHEAD and MØLLER (1992) argue that female infidelity creates the primary context for sperm competition in birds. SMITH (1984) and BAKER/BELLIS (1995) provide parallel arguments for humans. For both birds and humans who practice social monogamy, female infidelity places a male at risk of cuckoldry, or investing in offspring to whom he is genetically unrelated. I propose that male humans and male birds faced similar adaptive problems within the domain of sperm competition. Specifically, I propose three sets of adaptive problems associated with sperm competition in birds and in humans. These are problems that deal with the prevention, correction, and anticipation of a female partner's infidelity. In the following sections, I describe the nature of these adaptive problems and identify behaviors that may be the output of evolved mechanisms designed to solve these problems. Table 1 provides a summary outline with relevant references.

Preventing Female Infidelity

A principle cost that males incur as a result of their partner's sexual infidelity is the risk of cuckoldry. There would have been tremendous selection pressures over evolutionary history for males to behave in ways that reduced the risk of investing in genetically unrelated offspring. These behaviors would prevent a partner from being sexually unfaithful or, barring that, prevent the rival male's sperm from reaching a partner's ovum or ova. The goal in this case, from the male's perspective, is to prevent insemination by a rival.

Male birds and male humans have a psychology that appears well designed to prevent or minimize sperm competition by reducing a partner's opportunity for extra-pair copulation. BIRKHEAD and MØLLER (1992) describe several behaviors in birds that function to prevent rival insemination. Mate guarding behaviors, for example, include the vigilant watch that male birds keep over their partner. The mate guarding behaviors documented in birds parallel some of the mate guarding behaviors documented in humans. These behaviors range from vigilance over a partner's whereabouts to rifling through a partner's personal mail (BUSS 1988; BUSS/SHACKEL-

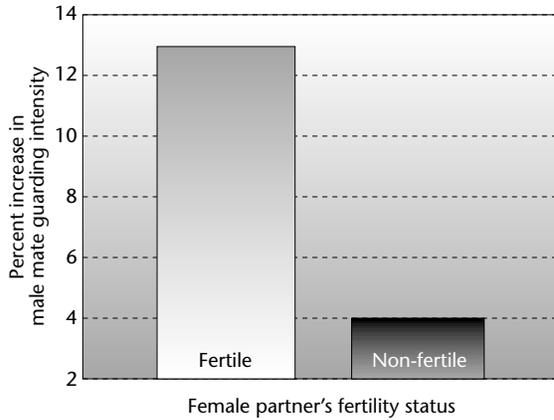


Figure 1: Percent increase in mate guarding intensity in male swallows following experimental detainment from female partner as a function of partner's fertility status. Data from MØLLER (1987). Adapted from BIRKHEAD/MØLLER (1992), Figure 9.7, p130.

FORD 1997; FLINN 1988). Additionally, in many species of birds and in humans, male mate guarding behaviors are more frequent and more intense with a more reproductively valuable partner (BIRKHEAD/MØLLER 1992; BUSS/SHACKELFORD 1997; FLINN 1988). MØLLER (1987) showed that, following experimental detainment from their partner, male swallows increase the intensity of mate guarding more for fertile than for non-fertile partners (see Figure 1). Likewise, BUSS and SHACKELFORD (1997; see also FLINN 1988) documented that a man's mate guarding is positively correlated with his wife's reproductive value, as indexed by her age, even after controlling for the man's age and the length of the relationship. A woman's mate guarding, however, is not correlated with her husband's age after the woman's age and the length of the relationship are controlled statistically (see Figure 2). These behavioral similarities suggest psychological similarities in male birds and male humans.

Preventing sperm competition is one solution to the adaptive problem of female sexual infidelity. Acts of mate guarding have costs, however. Male birds engaged in mate guarding expend time and energy that could be used to locate food or acquire additional mates, for example. Significant weight loss has been documented in male ducks that spend more time mate guarding and, consequently, less time feeding (ASHCROFT 1976). In humans, a man may be unable to maintain a successful career if too much time and effort is spent watching his partner's every move. Furthermore, despite the best mate

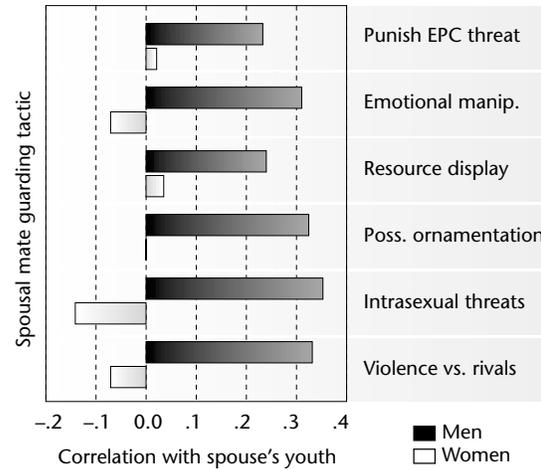


Figure 2: Partial correlations between human spousal mate guarding and partner's age, controlling for own age and length of relationship. All spousal mate-guarding tactics (punishment of extra-pair copulation (EPC) threat, emotional manipulation, resource display, possessive ornamentation, intrasexual threats, and violence against rivals) are significantly correlated with wife's age, but not husband's age ($p \leq .05$). Following are example behaviors included in each mate-guarding tactic. Punishment of EPC threat includes behaviors such as, "Hit spouse when he/she caught spouse flirting with someone else". Emotional manipulation includes behaviors such as, "Threatened to harm self if spouse ever left him/her". Resource display includes behaviors such as, "Spent a lot of money on spouse". Possessive ornamentation includes behaviors such as, "Gave spouse jewelry to signify that he/she was taken". Intrasexual threats include behaviors such as, "Threatened to hit the person who was making moves on spouse". Violence against rivals includes behaviors such as, "Got friends to beat up the person who had made a pass at spouse". Adapted from BUSS/SHACKELFORD (1997), Table 3, p351.

guarding efforts, neither a male bird nor a male human can be certain of his partner's fidelity.

Given that preventative measures are not fool-proof, males may be equipped with another set of mechanisms designed to "correct" a female partner's infidelity. These mechanisms might generate behaviors that allow a male to compete for paternity if his partner has been unfaithful.

Correcting Female Infidelity

In the case of preventing infidelity, the goal, from the male's perspective, is to avoid sperm competition. When a female partner's infidelity is detected or suspected, however, the chance to compete is desired. Biologists and psychologists studying humans and birds have identified factors linked with the risk of female infidelity (BAKER/BELLIS 1995; BIRKHEAD/

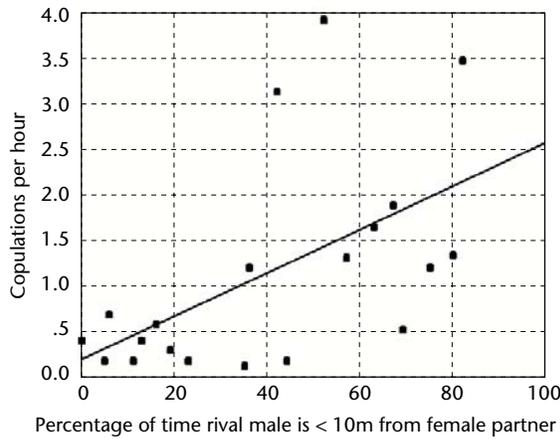


Figure 3: In-pair copulation rate as a function of the proportion of time female dunnocks spent within 10 m of a rival male. Males initiated significantly more copulations as their partner spent more time near rivals ($p < .05$). Adapted from DAVIES (1983), Figure 3, p336.

MØLLER 1992; SHACKELFORD/BUSS 1997). One of these factors is the percentage of time a pair or a couple has spent together since their last copulation. As the percentage of time that a couple has spent together since their last copulation decreases, the risk that a female has copulated with a rival male increases (BAKER/BELLIS 1995; BIRKHEAD/MØLLER 1992).

Males who suspect or detect a partner's infidelity can address this adaptive problem in at least two ways. The first is to copulate with their partner. Without copulation, there is no chance for sperm competition and, therefore, no chance for the in-pair male to sire his partner's offspring. The second is to increase the number of sperm inseminated during copulation. The psychology and physiology of male humans appear to be designed to gauge the risk of infidelity and to take appropriate corrective action by adjusting the number of sperm inseminated into their partner (BAKER/BELLIS 1995; SHACKELFORD et al. 2002). Although this sperm number adjustment is not yet documented in birds, some birds might be equipped with an alternative mechanism for correcting a partner's infidelity. DAVIES (1983) showed that male dunnocks increase the rate at which they copulate with their partners as a function of the percent of time that a rival spends in close proximity to her (see Figure 3). Male dunnocks also have been shown to copulate immediately upon reunion with their partners as a way of correcting possible infidelity (HATCHWELL/DAVIES

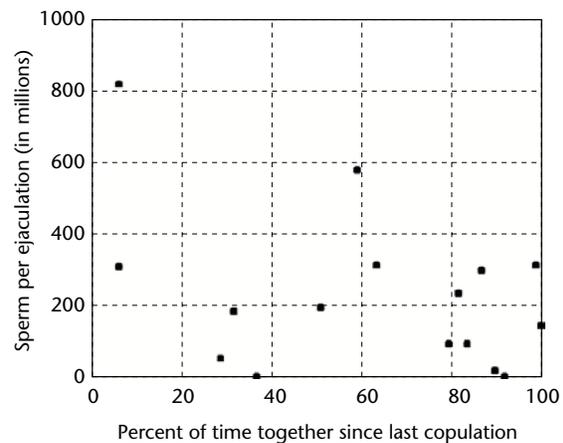
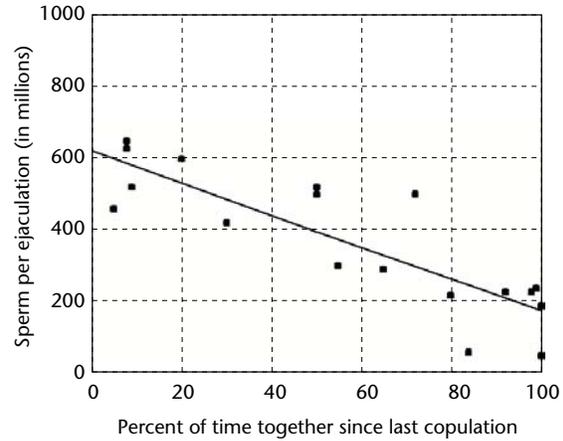


Figure 4: *Top:* Number of sperm ejaculated at human couple's next copulation as a function of the percent of time couple spent together since their last copulation. Correlation is significant ($p < .001$). Adapted from BAKER/BELLIS (1989), Figure 1, p868. *Bottom:* Number of sperm ejaculated at next masturbation as a function of the percent of time human couple spent together since their last copulation. Correlation is not significant ($p > .05$). Adapted from BAKER/BELLIS (1989), Figure 1, p868.

1992). Additionally, forced copulation following extra-pair copulation may serve the function of correcting infidelity. Forced copulation following extra-pair copulation has been documented in zebra finches (BIRKHEAD/HUNTER/PELLAT 1989), carrion rooks (GOODWIN 1955), and in many species of waterfowl (see, e.g., MCKINNEY/DERRICKSON/MINEAU 1983).

Biologists studying humans have documented a negative correlation between the percentage of time a couple has spent together since their last copulation and the number of sperm a male inseminates at the couple's next copulation (BAKER/BELLIS 1989, 1995). This adjustment occurs only at the couple's

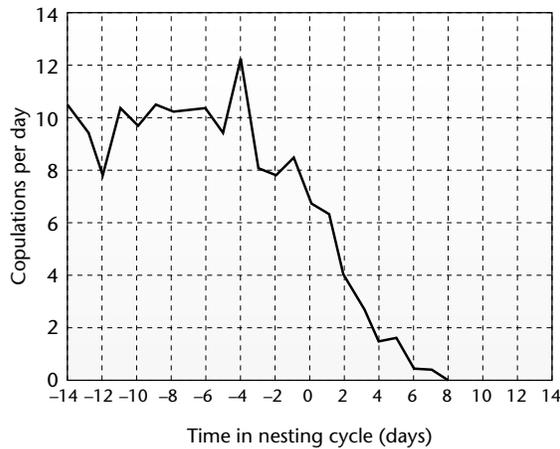


Figure 5: Number of osprey copulations per day as a function of time in nesting cycle. Day 0 is the day that the first egg was laid. Female fertility peaks in the days just before the first egg is laid and rapidly declines to zero following the onset of egg laying. Data from BIRKHEAD/LESSELS (1988). Adapted from BIRKHEAD/MØLLER (1988), Figure 1, p1674.

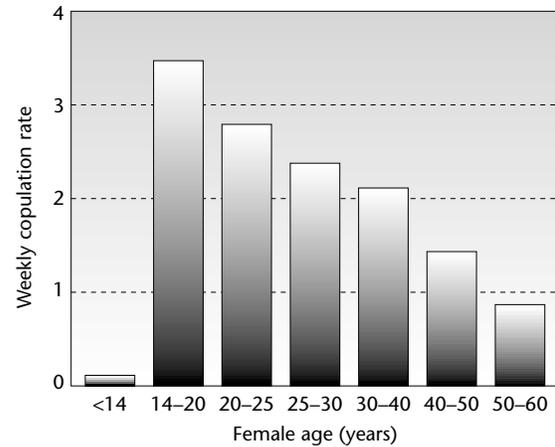


Figure 6: Weekly human copulation rate as a function female age. Adapted from BAKER/BELLIS (1995, Box 4.8, p63).

next copulation (see Figure 4 top), and not at the male's next masturbation (see Figure 4 bottom). The effectiveness of this adjustment decreases with the time that passes after a suspected extra-pair copulation, however. Males who were motivated to copulate as soon as possible following a suspected infidelity would have benefited reproductively (BAKER/BELLIS 1995; BIRKHEAD/MØLLER 1992). Recent research on humans documents that the percentage of time that a couple has spent *apart* since their last copulation (in which the risk of sperm competition and subsequent cuckoldry is higher), and not the total amount of time since their last copulation, predicts men's ratings of their partner's attractiveness (SHACKELFORD et al. 2002). Men's interest in copulating with their partner also is predicted by the percentage of time the couple has spent apart since their last copulation (SHACKELFORD et al. 2002). Copulatory interest and ejaculate competitiveness, both sensitive to the risk of a female partner's infidelity, may be outputs of evolved mechanisms designed to solve the adaptive problem of correcting a female partner's infidelity.

Anticipating Female Infidelity

Anticipating infidelity is another problem that male humans and paternally investing, socially monogamous male birds may have faced recurrently over evolutionary history. Implicit in the act of preventing a partner's infidelity is anticipating that infidel-

ity. Anticipating infidelity, however, is not equivalent to preventing infidelity. A male might anticipate an infidelity, but he may be unable to prevent it. The costs of mate guarding may be too high, for example (BIRKHEAD/MØLLER 1992; KEMPENAERS/VERHEYEN/DHONDT 1995). But a male can do better than standing by and waiting until the infidelity has happened before taking action. BIRKHEAD and LESSELS (1988) showed that although a male osprey must *decrease* his mate guarding intensity in order to forage for food for his partner during her fertile phase, he *increases* the rate at which he copulates with her during this period (see Figure 5). BAKER and BELLIS (1995) documented an analogous pattern in humans. Figure 6 shows that men mated to younger, more reproductively valuable women copulate more frequently with their partners than do men mated to older, less reproductively valuable women. This work on birds and on humans suggests that frequent copulation and insemination might maintain a male's competitive status in his partner's reproductive tract during the time that he cannot account for her behavior (BAKER/BELLIS 1995; MØLLER 1988).

In birds and in humans, past female infidelity and sexual promiscuity are good predictors of future female infidelity (BAKER/BELLIS 1995; BIRKHEAD/MØLLER 1992). Male humans and male birds may use information about a female partner's previous infidelities to predict her future infidelity, and then adjust their preventative and anticipatory behaviors accordingly. I hypothesize, for example, that male humans and male birds that anticipate a partner's infidelity in the near future will initiate more frequent copulation

with their partners, especially nearer to the time of the anticipated, but unpreventable, infidelity. A prediction derived from this hypothesis is that males who anticipate a future infidelity, and who are about to spend time apart from their partner, will pursue copulation immediately prior to their separation. The closer this copulation is to separation, the greater the chances that a later ejaculate of a rival will meet competitive sperm in the female's reproductive tract. As another example, I hypothesize a relationship between anticipated sperm competition and "morbid jealousy" in human males (DALY/WILSON 1988; TURBOTT 1981): Men who display intense, frequent, and often violent jealousy toward their partner may be reacting to real or imagined cues to their partner's future infidelity.

Summary and Concluding Remarks

Male humans and paternally investing, socially monogamous male birds may have a psychology and physiology that includes mechanisms designed to solve at least three adaptive problems of a female

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partner's infidelity and subsequent sperm competition. These three adaptive problems are preventing a partner's infidelity, correcting a partner's infidelity, and anticipating a partner's infidelity. Although I focused on humans and birds in this review,

these adaptive problems are likely to have been recurrently confronted by ancestral males of other socially monogamous, paternally investing species. The males of these species, like male humans and male birds, may have evolved psychological and physiological mechanisms designed to solve these adaptive problems. Future work can profitably test these hypotheses, in addition to other hypotheses presented in this review, all of which are inspired by modern Sperm Competition Theory.

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