

Sperm Competition In Insects, Birds, and Humans

Insights from a Comparative Evolutionary Perspective

THE APPLICATION OF evolutionary thinking to animal behavior and psychology offers a number of benefits. A comparative evolutionary psychological approach can provide insight into differences and similarities between species by encouraging rigorous examination of the adaptive problems and evolved solutions to these problems (DALY/WILSON 1998). Different species sometimes share a similar suite of evolved mechanisms because they recurrently confronted similar classes of adaptive problems. In this sense, the study of non-human animal behavior and psychology can shed light on human behavior and psychology (WILSON 1997). TRIVERS' (1972) theory of parental investment and sexual selection, for example, has been successful in explaining sex differences in courtship behaviors in a number of species, including humans. Analogously, Sperm Competition Theory has generated a wealth of information about the mating systems of a number of species (BIRKHEAD/MØLLER 1998; PARKER 1970a, 1970b). In this review, we present a comparative approach to evolutionary psychology, demonstrating that an understanding of the adaptive problems, evolved psychologies, and manifest behaviors

Abstract

An understanding of the adaptive problems, evolved psychologies, and manifest behaviors of one species can offer insights into the evolved psychologies of other species. Sperm competition provides an arena within which to assess the heuristic value of such a comparative evolutionary perspective. Sperm competition occurs when the sperm of two or more males simultaneously occupy a female's reproductive tract. We describe mechanisms of sperm competition in insects and in birds. We suggest that the adaptive problems and evolved solutions in these species provide insight into evolved human sexual behaviors and psychology. We review recent theoretical and empirical arguments for the existence of human sperm competition. Using a comparative evolutionary psychological approach, we discuss features of male psychology and female psychology that may have evolved as solutions to the adaptive problems presented by sperm competition. We conclude with a discussion of future directions for work on human sperm competition, highlighting the heuristic value of a comparative evolutionary psychological approach in this field.

Key words

Sperm competition, evolutionary psychology, cognitive mechanisms, comparative psychology.

of one species can offer insight into the evolved psychologies of other species. The focus of this article is on cross-species similarities, although a comparative evolutionary perspective also can be valuable in identifying cross-species differences (DALY/WILSON 1995).

Along with the benefits of a comparative evolutionary perspective come a number of difficulties (see DALY/WILSON 1998). For example, there are no rules for identifying whether a set of conditions that thwart reproduction across different species represent (a) a similar adaptive problem confronted by these different species, or (b) different adaptive problems that share qualitative features. In addition, there are no rules for judging the similarity or dissimilarity

of the behaviors displayed by different species. As a final example, apparently similar adaptive problems confronted by different species are not always solved by the same evolved mechanisms. For example, many species faced the adaptive problem of thermal regulation. Solutions to this adaptive problem vary across species, however, ranging from sweating in humans, to the adjustment of wings and feathers in birds.

Our goal in this article is not to resolve these and other difficulties associated with adopting a comparative evolutionary perspective (see DALY/WILSON 1998). Instead, our goal in this article is to demonstrate that, these difficulties notwithstanding, a comparative evolutionary perspective can offer some insight into the adaptations and manifest behaviors of different species that have recurrently confronted similar classes of adaptive problems. Of key interest in this article is the value of a comparative evolutionary perspective for gaining a better understanding of human behavior and psychology. For example, because humans share with some insects the adaptive problem of mate retention, BUSS (1988) looked for and identified several behavioral similarities across these species that appear designed to prevent a mate from copulating with a rival. It is our intention to demonstrate in this article that sperm competition generated similar adaptive problems for some species of insects, many species of birds, and for humans. We suggest that cross-species behavioral similarities often may be the output of psychological mechanisms designed to solve qualitatively similar adaptive problems.

Brief Overview of Sperm Competition

Sperm competition is the result of the simultaneous occupation of sperm from two or more males in a single female's reproductive tract (PARKER 1970a, 1970b). Although important contributions to Sperm Competition Theory come from researchers studying many different species, PARKER's initial review was based on observations of three species of flies. PARKER's discovery of sperm competition in insects was facilitated by the fact that insects can store sperm for long periods of time in specialized organs, coupled with the ease with which females can be observed in multiple matings. PARKER's interest in game theory led him to consider the potential for an evolutionary arms race. On one hand, there would have been selection pressure for males to remove from a female the sperm deposited by previous suitors. On the other hand, selection would have favored those males that were able to prevent removal of their own sperm. PARKER noted that the last male to inseminate a female typically would fertilize 80% of her eggs. Investing more time and energy into copulating with a single female could produce a fertilization rate of 100%. Observations of male behaviors led PARKER to conclude that males maximized their offspring production not by monopolizing a single female, but by mating with multiple females. These observations

and theoretical considerations formed the basis of Sperm Competition Theory (PARKER 1970a; for theoretical extensions and refinements, see PARKER 1982, 1984, 1990a, 1990b, 1993, 1998; PARKER et al. 1996; PARKER/BEGON 1993; PARKER/SIMMONS/KIRK 1990).

Sperm competition serves as a good 'test case' for the heuristic value of a comparative evolutionary psychological perspective. There is a wealth of information about sperm competition in many non-human animals, notably in insects and in birds (see, e.g., BIRKHEAD/MØLLER 1992, 1998). In addition, there is a growing body of work suggesting that sperm competition was an important selective force in shaping modern human psychology and behavior (see, e.g., BAKER/BELLIS 1995; SHACKELFORD et al. in press). One approach for furthering our understanding of human sexuality is to apply a comparative evolutionary psychological perspective to the study of sperm competition. When we examine human sexuality using a comparative evolutionary psychological approach to sperm competition, we can better understand our similarities to and differences from other sexually reproducing species.

Sperm Competition and Sexual Selection

In addition to natural selection, Charles DARWIN (1871) proposed sexual selection. Sexual selection describes (a) the competition between males for the opportunity to mate with females (intrasexual selection), and (b) the selection of male mates by females (intersexual selection). SMITH (1998) suggested that a more precise way of thinking about sexual selection is that it is not a competition between males to gain sexual access to females, but rather a competition between the ejaculates of different males to fertilize a female's eggs. In this sense, sperm competition can be considered an integral component of sexual selection (MØLLER 1998).

Sperm competition and sexual selection likely played an important role in the evolution and design of genitalia and reproductive physiology (EBERHARD 1985; SHORT 1979). For example, sexual selection could have acted upon ejaculate size. Larger ejaculates often are more successful in sperm competition (BAKER/BELLIS 1995). Comparatively, the ejaculates of more monogamous primate species experience less opportunity for sperm competition. Males in these species have smaller testicles relative to body weight (and consequently produce smaller ejaculates) compared to species with higher rates of sperm competition (GOMENDIO/HARCOURT/ROLDÁN 1998; HARCOURT et al. 1981).

Penis size and shape also may have evolved in response to the pressures of sperm competition and sexual selection. A longer penis that deposited sperm nearer to the site of fertilization may be the result of such selection (EBERHARD 1985; SHORT 1975). The shape of the human penis may be designed to remove sperm previously inseminated by a rival male (BAKER/BELLIS 1995). Empirical work on other species provides comparative, corroborative support for this hypothesis. The penis of the damselfly, for example, is designed such that it removes up to 99% of the stored sperm in the female before the male deposits his own ejaculate (WAAGE 1979).

Sperm Competition in Insects and in Birds

The first examination of sperm competition was in insects (PARKER 1970a). Insects provide a model of sperm competition that is applicable to a number of species. Male insects, like the males of other species, benefit by avoiding sperm competition. This avoidance can be accomplished in several ways. One method is to avoid competition with sperm that have been stored in a female by previous copulation with another male. Another method is to avoid competition with the sperm of males that might copulate with the female in the future (SIMMONS/SIVA-JOTHY 1998).

Many insects have anatomical features that facilitate avoidance of sperm competition. The penis of the male tree cricket, for example, is structurally designed to deliver an ejaculate into the anterior portion of the female's spermatheca (the sperm storage organ). Sperm that were stored there previously are collected on the male's penis and are removed prior to insemination of the male's own ejaculate (ONO/SIVA-JOTHY/KATO 1989; see also GAGE 1992).

Another method of avoiding sperm competition may exist. This is killing or incapacitating rival sperm. Some evolutionary biologists suggest that this mechanism operates in humans (BAKER/BELLIS 1995). Different sperm morphs are thought to 'seek and destroy' the sperm of rivals within a female's reproductive tract. No conclusive evidence has been collected to support this idea, however (for additional criticisms and a review of related empirical and theoretical work, see GOMENDIO/HARCOURT/ROLDÁN 1998).

In addition to the evolution of mechanisms designed to avoid competition with sperm already stored inside a female, some male insects are equipped with mechanisms that are designed to pre-

vent the opportunity for future sperm competition (THORNHILL/ALCOCK 1983). These 'mate guarding' mechanisms can be classified as proximate or remote. Proximate mate guarding involves a male staying within close physical distance of the female with whom he has recently copulated (TSUBAKI/SIVA-JOTHY/ONO 1994). Remote mate guarding involves tactics designed to aid the male in avoiding competition with sperm from rival males when he is not physically present with his partner to do this guarding himself. In insects, for example, a copulatory plug is sometimes formed after copulation (DRUMMOND 1984). This plug is the result of chemical reactions between the seminal fluid and oxygen in the air. The plug blocks the female's genital orifice and thereby prevents future insemination by other males. Another form of remote mate guarding involves the post-copulatory release of a substance in the seminal fluid that reduces the receptivity of the female to rival males (THORNHILL 1976).

Birds have been studied extensively within the context of sperm competition. There are similarities between the mechanisms of sperm competition documented in birds and the mechanisms documented in insects. For example, the males of many species of birds and insects recurrently had to solve problems of avoiding sperm competition. Sperm competition mechanisms in birds also have important implications for the study of human sperm competition. Not only have male birds and male humans faced many of the same adaptive problems with respect to avoiding sperm competition, but also the majority of bird species engage in social monogamy, the mating system characteristic of humans (BAKER/BELLIS 1995; BIRKHEAD/MØLLER 1992). Social monogamy is a mating system in which a male and a female form a long-term pair bond. Within this mating system, males benefit by gaining exclusive sexual access to the reproductive resources of a female, whereas females benefit by gaining exclusive access to the investment of the male in her and her offspring (BIRKHEAD/MØLLER 1992; TRIVERS 1972). Human males and the males of many bird species invest substantially in offspring, which places these males at risk of investing in offspring to whom they are genetically unrelated. These and other similarities suggest the possibility of discovering similar mating behaviors, motivated by similar evolved psychologies, in birds and in humans.

Paternity guarding is a term used to describe behaviors designed to avoid sperm competition, or to avoid the key costs of sperm competition—failure to transmit genes into the next generation and pa-

ternal investment in genetically unrelated offspring. Researchers have identified two broad categories of paternity guarding in birds. These are paternity guarding through mate guarding and paternity guarding through frequent copulation (BIRKHEAD/MØLLER 1992). It was once thought that males guard their mates as a result of the pair bond that they form (BIRKHEAD/MØLLER 1992). Sperm Competition Theory offers a clearer understanding of the underlying mechanisms and processes. As males spend greater amounts of time away from their partners, the incidence of female extra-pair copulation increases (ALATALO/GOTTLANDER/LUNDBERG 1987). Accordingly, male birds adjust the intensity with which they guard their partners—particularly their proximate mate guarding behaviors—so that this mate guarding is most intense when their partners are at peak fertility (MØLLER 1987). But there are costs to mate guarding. Male birds engaged in mate guarding expend time and energy that could be used to locate food or to acquire additional mates. For example, significant weight loss has been documented in male ducks who spend more time mate guarding and, consequently, less time feeding (ASHCROFT 1976).

Although many species of birds engage in mate guarding, not all do. Ecological constraints prevent some birds of prey from mate guarding. The male osprey, for example, locates and acquires for his partner the majority of the food she eats (BIRKHEAD/LESSELS 1988). These males cannot simultaneously and successfully collect food for their partners and guard their partners. Furthermore, some male birds trade food for copulations, increasing not only their paternity certainty, but also the health of their putative offspring (TASKER/MILLS 1981). For the males in this species, frequent copulation can serve as a successful paternity guard. This is because (a) the number of copulations is positively related to the number of offspring sired by the male, and (b) the last male to copulate with a female fertilizes a relatively high percentage of her eggs (BIRKHEAD/MØLLER 1992).

Like mate guarding, the psychology motivating copulatory frequency appears to be sensitive to female fertility. Male ospreys copulate as many as 10 times per day with their partner when she is at peak fertility—just prior to egg laying. Copulatory frequency approaches zero after the first egg is laid, when her fertility is at a minimum (BIRKHEAD/LESSELS 1988). These behavioral patterns suggest that these birds are sensitive to the potential costs of sperm competition, and that they behave so as to reduce the likelihood of incurring these costs.

The preceding sections introduced key physiological and behavioral mechanisms of sperm competition. We presented information that provides a basis for comparing the adaptive problems and evolved solutions in insects and in birds to those in humans. The similarities in the mating system and parenting system of some birds and humans generated similar adaptive problems for these species in the domain of sperm competition. The next sections review theoretical arguments and empirical evidence for the existence of human sperm competition.

Theoretical Arguments for Human Sperm Competition

SMITH (1984) presented theoretical arguments for the existence of sperm competition in humans. SMITH (1984) explored the possible benefits that females might reap through manipulating the outcome of such competition. Sperm competition in humans requires that a female copulate with more than one male within roughly a five-day period. This can happen in several contexts. Communal sex, including wife-swapping, orgies, and 'swinging', is one such context. Studies conducted over the past 30 years indicate that these behaviors are rare and probably did not represent a recurrent context over the evolutionary history of humans in which sperm competition could act as a selective force (see, e.g., ATHANASIOU 1973; SMITH 1984).

Rape is another context that can place the sperm of different men into competition. BAKER/BELLIS (1995), SMITH (1984), THORNHILL/THORNHILL (1992; see also THORNHILL/PALMER 2000), and others argue that rape of females by males was a recurrent feature of human evolutionary history. Despite cultural institutions that punish and discourage rape, over half a million rapes occur annually in the United States alone (GREEN 1980). There also is a strong association between rape and war, a key feature of our evolutionary past (BROWNMILLER 1975; BUSS 1999; THORNHILL/PALMER 2000). These reports suggest that rape could have provided a recurrent context for sperm competition to act as a selection pressure on human physiology and psychology.

Finally, female infidelity is a context for human sperm competition. Female extramarital sex has been documented in three-fourths of indexed societies (BROUDE/GREENE 1976; BUSS 2000; SHACKELFORD/BUSS 1997). According to SMITH (1984) and BAKER/BELLIS (1995), female infidelity may have been the primary context for sperm competition throughout human evolutionary history. If female infidelity

was the primary context for sperm competition, females must have sometimes received substantial benefits for infidelity, because the potential costs to the female of detected infidelity are high. An unfaithful female risks the loss of her long-term partner's investment, and she risks injury and even death at the hands of her jealous partner (BUSS 2000; DALY/WILSON 1988; SHACKELFORD/BUSS/PETERS 2000). If the potential for female infidelity is a universal feature of human psychology, then the benefits of female infidelity must have outweighed these costs, on average. Such benefits include the contribution of superior genes to offspring, material resources, and protection for a woman and her offspring (GREILING/BUSS 2000; SMITH 1984). These are some of the same benefits gained by female birds that mate with extra-pair males (BIRKHEAD/MØLLER 1998). In addition to theoretical arguments for sperm competition being a recurrent feature of human evolutionary history, there is mounting corroborative empirical data.

Empirical Evidence for Human Sperm Competition

The size and structure of genitalia and other reproductive anatomy are key products of an evolutionary history of sperm competition. For example, relative to body size, male humans have testes that are larger than those of gorillas and orangutans, but smaller than those of chimpanzees (SMITH 1984). Humans are more monogamous than chimpanzees, but more promiscuous than gorillas and orangutans (GOMENDIO/HARCOURT/ROLDÁN 1998; SMITH 1984; WRANGHAM/PETERS 1996). Humans, chimpanzees, gorillas, and orangutans thus appear to have a reproductive physiology that is designed to 'expect' a certain level of sperm competition brought about by multiple mating by females.

Another form of evidence that suggests an evolutionary history of human sperm competition is that human sperm are produced in a variety of types or morphs. BAKER/BELLIS (1988, 1995) argue that human sperm is produced in different morphs, each performing a specific, evolved function. The authors classify human sperm into 'egg-getters', those that move most directly to fertilize the egg; 'blockers', those that take up larger areas in the mucus channels and prevent rival sperm from reaching the egg; and 'seek-and-destroyers', those that search for and upon detection kill rival sperm (see BAKER/BELLIS 1995, for a review of sperm polymorphism in other species). In addition to documenting different sperm morphs, BAKER/BELLIS (1989, 1993a, 1993b, 1995) con-

ducted a series of experiments that tested hypotheses about human ejaculate adjustment in relation to the risk of female infidelity and subsequent sperm competition.

A key hypothesis derived from Sperm Competition Theory is that males will adjust the number of sperm they inseminate as a function of the risk that their sperm will encounter competition from the sperm of other males. This hypothesis has been tested and confirmed in numerous studies of various insects (e.g., GAGE 1991; GAGE/BAKER 1992; GAGE/BARNARD 1996; for a review of this work, see SIMMONS/SIVA-JOTHY 1998). Extending this work to humans, BAKER/BELLIS (1989, 1993a, 1995) documented a negative relationship between the proportion of time a couple has spent together since their last copulation and the number of sperm ejaculated at the couple's next copulation. As the proportion of time a couple spends together since their last copulation decreases, there is a predictable increase in the probability that the man's partner has been inseminated by another male (BAKER/BELLIS 1995). Additional regression analyses documented that the proportion of time a couple spent together since their last copulation is a significant predictor of sperm number ejaculated at the couple's next copulation, but not at the male's next masturbation (BAKER/BELLIS 1989, 1995). This class of observations inspired evolutionary psychologists to investigate the psychological mechanisms that might have been designed as solutions to the adaptive problems presented by sperm competition.

The Evolved Psychology of Sperm Competition

A comparative evolutionary psychological perspective predicts that species that recurrently faced similar adaptive problems may have evolved similar psychological mechanisms to solve these problems. The sperm competition that results from female infidelity presents a similar class of adaptive problems for individuals across many species. The fact that humans and birds share similar mating systems suggests additional parallels between the evolved psychologies of humans and birds. Male humans and the males of many bird species are faced with the problems of preventing, correcting, and anticipating their partner's infidelity (SHACKELFORD/LEBLANC 2001). Failure to solve these problems would have had devastating consequences—including failure to pass genes into the next generation and investing finite resources in genetically unrelated offspring. Fe-

males are faced with the problems of maximizing the benefits of infidelity relative to the costs of infidelity, and manipulating ejaculates in the presence of sperm competition. Evolutionary psychologists have recently begun to document that these adaptive problems may have designed psychological mechanisms that function to solve them (BAKER/BELLIS 1993a, 1995; SHACKELFORD et al. in press; THORNHILL/GANGESTAD/COMER 1995).

Men who prevented their partner's infidelity would have benefited reproductively over the course of human evolution. Human mate guarding behaviors may be the output of psychological mechanisms designed to prevent sperm competition (BUSS 1988; BUSS/SHACKELFORD 1997; FLINN 1988; SHACKELFORD/LEBLANC 2001). These mate guarding behaviors range from vigilance over a female partner's whereabouts to female-directed violence for a suspected infidelity. Similar mate guarding behaviors have been observed in many species of birds (BIRKHEAD/MØLLER 1992). As predicted by a comparative evolutionary perspective, there are similarities between many classes of mate guarding behaviors in humans and mate guarding behaviors in birds. For example, male humans and male birds adjust the intensity of their mate guarding behaviors according to the reproductive value and fertility of their partners (BUSS/SHACKELFORD 1997; FLINN 1988; MØLLER 1987). Furthermore, just as for male birds, mate guarding is not always possible for male humans. Male humans may be equipped with another mechanism that 'corrects' female infidelity by motivating a man to copulate as soon as possible after a partner's absence, in an apparent effort to compete for paternity in the event of rival insemination (SHACKELFORD et al., in press).

In a study modeled after BAKER and BELLIS' (1993a) research on male ejaculate adjustment as a function of the risk of female infidelity, SHACKELFORD et al. (in press) found psychological evidence suggesting a long evolutionary history of human sperm competition. The ejaculate adjustment documented by BAKER/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. (in press) 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 partners' sexual attractiveness and men's ratings of their interest in copulating with their partner.

Male humans also face the adaptive problem of anticipating a female partner's infidelity. Men are sensitive to cues to a partner's infidelity (SHACKEL-

FORD/BUSS 1997). One cue to the likelihood of female infidelity is the female's age. Younger, reproductive age women are more likely to promote sperm competition through extra-pair copulations than are older, post-reproductive age women (BAKER/BELLIS 1995; BUSS 1994, KINSEY/POMEROY/MARTIN 1953). Men appear to have psychological mechanisms that are sensitive to this risk. Men mated to younger women copulate more frequently with their partners than do men mated to older women (BAKER/BELLIS 1995). This pattern suggests that men mated to younger women might anticipate the possibility of sperm competition and engage in frequent copulation in an attempt to remain competitive inside their partner's reproductive tract. Anticipating sperm competition also represents an adaptive problem for many male birds. For example, the more time that a female spends in the immediate vicinity of other male birds, the more likely it is that one or more of those males will inseminate her. Male dunnocks appear to be designed to assess and combat this risk by increasing the rate at which they copulate with their partner as a function of the number of rival males close to her (DAVIES 1983).

Less work has been done on the mechanisms of human female psychology that may have been forged by an evolutionary history of sperm competition. Research on birds suggests that there are genetic benefits associated with mating with multiple males and thereby promoting sperm competition. A growing body of empirical work on non-human animals, particularly many species of birds, documents positive relationships between heritable male traits, paternity, and offspring survival (KEMPENAERS/VERHEYEN/DHONDT 1997; MØLLER 1994; SHELDON et al. 1997). There may be similar benefits of multiple mating for human females. BAKER/BELLIS (1993b, 1995) hypothesized that human female orgasm is an adaptation for preferentially retaining the sperm of certain males. BAKER/BELLIS (1993b, 1995) documented that women are more likely to report a 'high retention orgasm' with an extra-pair sexual partner than with their regular, in-pair partner. These researchers also found that, relative to the timing of sexual intercourse with their in-pair partner, women report a greater likelihood of sex with an extra-pair partner during the most fertile phase of their menstrual cycle (BELLIS/BAKER 1990, BAKER/BELLIS 1995). These results suggest an active female role in sperm competition, and they are consistent with the argument that female infidelity was the primary context for the evolution of sperm competition mechanisms. THORNHILL/GANGESTAD/COMER (1995) and SHACKELFORD et

al. (2000) provide evidence that the attractiveness of a woman's partner is a strong predictor of her orgasm. If male attractiveness is an honest signal of genetic quality, and if female orgasm is an adaptation for retaining preferentially the sperm of favored males, then ancestral women would have benefited by experiencing orgasm with physically attractive males.

Future work from an evolutionary psychological perspective continues to explore the hypothesis that human and non-human minds are equipped with psychological mechanisms designed to solve the problems of sperm competition. One important research area that is starting to be examined in humans is the link between sperm competition and violence perpetrated by a male against his female partner. For example, domestic abuse and marital rape might be predictable from men's perceptions that their partners are currently or have recently been sexually unfaithful, thus placing them at risk of sperm competition (SHACKELFORD/LEBLANC 2001; THORNHILL/PALMER 2000).

Summary and Conclusion

Sperm competition presents individuals of a variety of species with similar adaptive problems. Over the evolutionary history of these species, sperm competition was an integral component of sexual selection. We reviewed the development of Sperm Competition Theory and highlighted some of the evolved mechanisms in insects that were identified in

early sperm competition research. This initial work on insects paved the way for a tremendous amount of empirical research on sperm competition in birds. From a comparative evolutionary psychological approach, it is predicted that the similarities in the adaptive problems recurrently faced by socially monogamous birds and humans sometimes led to similarities in the evolved psychologies of these species. Converging research suggests that this is the case. Human females and the females of socially monogamous birds may benefit by mating with multiple males and thereby promoting sperm competition. Socially monogamous male birds and male humans faced similar adaptive problems of preventing, correcting, and anticipating their female partners' infidelities. Analogous evolved solutions to these problems are evidenced by similar classes and patterns of male mate guarding behaviors in birds and in humans.

Early applications of a comparative evolutionary perspective were successful in identifying and explaining the similarities and differences in human and non-human mate selection and parenting behaviors (TRIVERS 1972). A review of the sperm competition literature from a comparative evolutionary perspective suggests the possibility of a similarly successful cross-species analysis and integration. The adaptive problems of sperm competition and their evolved solutions in non-human species, notably insects and birds, provide a model for better understanding human sexual behaviors and psychology.

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References

- Alatalo, R. V./Gottlander, K./Lundberg, A. (1987) Extra-pair copulations and mate guarding in the polyterritorial pied flycatcher, *Ficedula hypoleuca*. *Behavior* 101:139-155.
- Ashcroft, R. E. (1976) A function of the pairbond in the common eider. *Wildfowl* 27:101-105.
- Athanasiou, R. (1973) A review of public attitudes on sexual

issues. In: Zubin, J./Money, J. (eds) *Contemporary Sexual Behavior*. Johns Hopkins University Press: Baltimore, pp. 361-390.

Baker, R. R./Bellis, M. A. (1988) 'Kamikaze' sperm in mammals? *Animal Behaviour* 36:937-980.

Baker, R. R./Bellis, M. A. (1989) Number of sperm in human ejaculates varies in accordance with sperm competition theory. *Animal Behaviour* 37:867-869.

- Baker, R. R./Bellis, M. A. (1990)** Do females promote sperm competition? Data for humans. *Animal Behaviour* 40: 997–999.
- Baker, R. R./Bellis, M. A. (1993a)** Human sperm competition: Ejaculate adjustment by males and the function of masturbation. *Animal Behaviour* 46:861–885.
- Baker, R. R./Bellis, M. A. (1993b)** Human sperm competition: Ejaculate manipulation by females and a function for the female orgasm. *Animal Behaviour* 46:887–909.
- Baker, R. R./Bellis, M. A. (1995)** Human sperm competition. Chapman & Hall: London.
- Birkhead, T. R./Lessels C. M. (1988)** Copulation behavior of the osprey *Pandion haliaetus*. *Animal Behaviour* 36:1672–1682.
- Birkhead, T. R./Møller, A. P. (1992)** Sperm competition in birds. Academic Press: London.
- Birkhead, T. R./Møller, A. P. (eds) (1998)** Sperm competition and sexual selection. Academic Press: San Diego.
- Broude, G. E./Greene, S. J. (1976)** Cross-cultural codes on twenty sexual attitudes and practices. *Ethnology* 15:410–429.
- Brownmiller, S. (1975)** *Against our will*. Simon & Schuster: New York.
- Buss, D. M. (1988)** From vigilance to violence: Tactics of mate retention in American undergraduates. *Ethology and Sociobiology* 9:291–317.
- Buss, D. M. (1994)** *The evolution of desire*. Basic Books: New York.
- Buss, D. M. (1999)** *Evolutionary psychology*. Allyn & Bacon: Needham Heights MA.
- Buss, D. M. (2000)** *The dangerous passion*. The Free Press: New York.
- Buss, D. M./Shackelford, T. K. (1997)** From vigilance to violence: Mate retention tactics in married couples. *Journal of Personality and Social Psychology* 72:346–361.
- Daly, M./Wilson, M. (1988)** *Homicide*. Aldine de Gruyter: Hawthorne NY.
- Daly, M./Wilson, M. (1995)** Evolutionary psychology: Adaptationist, selectionist, and comparative. *Psychological Inquiry* 6:34–37.
- Daly, M./Wilson, M. (1998)** Human evolutionary psychology and animal behaviour. *Animal Behaviour* 57:509–519.
- Darwin, C. (1871)** *The descent of man, and selection in relation to sex*. John Murray: London.
- Davies, N. B. (1983)** Polyandry, cloaca-pecking and sperm competition in dunnocks. *Nature* 302:334–336.
- Drummond, B. A. (1984)** Multiple mating and sperm competition in the lepidoptera. In: Smith, R. L. (ed) *Sperm competition and the evolution of animal mating systems*. Academic Press: San Diego, pp. 547–572.
- Eberhard, W. G. (1985)** *Sexual selection and animal genitalia*. Harvard University Press: Cambridge MA.
- Flinn, M. V. (1988)** Mate guarding in a Caribbean village. *Ethology and Sociobiology* 9:1–28.
- Gage, M. J. G. (1991)** Risk of sperm competition directly affects ejaculate size in the Mediterranean fruit fly. *Animal Behaviour* 42:1036–1037.
- Gage, M. J. G. (1992)** Removal of rival sperm during copulation in a beetle, *Tenebrio molitor*. *Animal Behaviour* 44:587–589.
- Gage, M. J. G./Baker, R. R. (1991)** Ejaculate size varies with socio-sexual situation in an insect. *Ecological Entomology* 16:331–337.
- Gage, M. J. G./Barnard, C. J. (1996)** Male crickets increase sperm number in relation to competition and female size. *Behavioral Ecology and Sociobiology* 38:349–353.
- Gomendio, M./Harcourt, A. H./Roldán, E. R. S. (1998)** Sperm competition in mammals. In: Birkhead, T. R./Møller, A. P. (eds) *Sperm competition and sexual selection*. Academic Press: San Diego, pp. 667–755.
- Green, R. (1980)** Variant forms of human sexual behavior. In: Austin, C. R./Short, R. V. (eds) *Reproduction in mammals*, book 8, human sexuality. Cambridge University Press: New York, pp. 68–97.
- Greiling, H./Buss, D. M. (2000)** Women's sexual strategies: The hidden dimension of extra-pair mating. *Personality and Individual Differences* 28:929–963.
- Harcourt, A. H./Harvey, P. H./Larson, S. G./Short, R. V. (1981)** Testes weight, body weight, and breeding systems in primates. *Nature* 293:55–57.
- Kempnaers, B./Verheyen, G. R./Dhondt, A. A. (1997)** Extra-pair paternity in the blue tit (*Parus caeruleus*): Female mate choice, male characteristics, and offspring performance. *Behavioral Ecology* 8:481–492.
- Kinsey, A. C./Pomeroy, W. B./Martin, C. E. (1953)** *Sexual behavior of the human female*. Saunders: Philadelphia.
- Møller, A. P. (1987)** Copulation behavior in the goshawk *Accipiter gentilis*. *Animal Behaviour* 35:755–763.
- Møller, A. P. (1994)** Male ornament size as a reliable cue to enhanced offspring viability in the barn swallow. *Proceedings of the National Academy of Science USA* 91:6929–6932.
- Møller, A. P. (1998)** Sperm competition and sexual selection. In: Birkhead, T. R./Møller, A. P. (eds) *Sperm competition and sexual selection*. Academic Press: San Diego, pp. 55–90.
- Ono, T./Siva-Jothy, M. T./Kato, A. (1989)** Removal and subsequent ingestion of rival's semen during copulation in a tree cricket. *Physiology and Entomology* 14:195–202.
- Parker, G. A. (1970a)** Sperm competition and its evolutionary consequences in the insects. *Biological Review* 45:525–567.
- Parker, G. A. (1970b)** Sexual selection and its evolutionary effect on copula duration in the fly, *Scatophaga stercoraria*. *Journal of Insect Physiology* 16:1301–1328.
- Parker, G. A. (1982)** Why are there so many tiny sperm? Sperm competition and the maintenance of two sexes. *Journal of Theoretical Biology* 96:281–294.
- Parker, G. A. (1984)** Sperm competition and the evolution of animal mating strategies. In: Smith, R. L. (ed) *Sperm competition and the evolution of animal mating systems*. Academic Press: San Diego, pp. 2–60.
- Parker, G. A. (1990a)** Sperm competition games: Raffles and roles. *Proceedings of the Royal Society of London B* 242:120–126.
- Parker, G. A. (1990b)** Sperm competition games: Sneaks and extra-pair copulations. *Proceedings of the Royal Society of London B* 242:127–133.
- Parker, G. A. (1993)** Sperm competition games: Sperm size and sperm number under adult control. *Proceedings of the Royal Society of London B* 253:245–254.
- Parker, G. A. (1998)** Sperm competition and the evolution of ejaculates: Towards a theory base. In: Birkhead, T. R./Møller, A. P. (eds) *Sperm competition and sexual selection*. Academic Press: San Diego, pp. 3–54.
- Parker, G. A./Ball, M. A./Stockley, P./Gage, M. J. G. (1996)** Sperm competition games: Individual assessment of sperm competition intensity by group spawners. *Proceedings of the Royal Society of London B* 263:1291–1297.
- Parker, G. A./Begon, M. (1993)** Sperm competition games: Sperm size and number under gametic control. *Proceedings of the Royal Society of London B* 253:255–262.

- Parker, G. A./Simmons, L. W./Kirk, H. (1990) Analyzing sperm competition data: Simple models for predicting mechanisms. *Behavioral Ecology and Sociobiology* 27:55–65.
- Shackelford, T. K./Buss, D. M. (1997) Cues to infidelity. *Personality and Social Psychology Bulletin* 23:1034–1045.
- Shackelford, T. K./Buss, D. M./Peters, J. (2000) Wife killing: Risk to women as a function of age. *Violence and Victims* 15:273–282.
- Shackelford, T. K./LeBlanc, G. J. (2001) Preventing, correcting, and anticipating female infidelity: Three adaptive problems of sperm competition. Manuscript under editorial review.
- Shackelford, T. K./LeBlanc, G. J./Weekes-Shackelford, V. A./Bleske, A. L./Euler, H. A./Hoier, S. (in press) Psychological adaptation to human sperm competition. *Evolution and Human Behavior*.
- Shackelford, T. K./Weekes-Shackelford, V. A./LeBlanc, G. J./Bleske, A. L./Euler, H. A./Hoier, S. (2000) Female coital orgasm and male attractiveness. *Human Nature* 11:299–306.
- Sheldon, B. C./Merilä, J. Qvarnström, A./Gustafson, L./Ellegren, H. (1997) Paternal genetic contribution to offspring condition predicted by the size of male secondary sexual character. *Proceedings of the Royal Society of London B* 264:297–302.
- Short, R. V. (1979) Sexual selection and its component parts, somatic and genital selection, as illustrated by man and the great apes. *Advances in the Study of Behavior* 9:131–158.
- Simmons, L. W./Siva-Jothy, M. T. (1998) Sperm competition in insects: Mechanisms and the potential for selection. In: Birkhead, T. R./Møller, A. P. (eds) *Sperm competition and sexual selection*. Academic Press: San Diego, pp. 341–434.
- Smith, R. L. (1984) Human sperm competition. In: Smith, R. L. (ed) *Sperm competition and the evolution of animal mating systems*. Academic Press: San Diego, pp. 601–660.
- Smith, R. L. (1998) Foreword. In: Birkhead, T. R./Møller, A. P. (eds) *Sperm competition and sexual selection*. Academic Press: San Diego, pp. xv–xxiii.
- Tasker, C. R./Mills, J. A. (1981) A functional analysis of courtship-feeding in the red-billed gull (*Larus novaehollandiae*). *Behaviour* 77:222–241.
- Thornhill, R. (1976) Sexual selection and nuptial feeding behavior in *Bittacus apocalis*. *American Naturalist* 110:529–548.
- Thornhill, R./Alcock, J. (1983) *The evolution of insect mating systems*. Harvard University Press: Cambridge MA.
- Thornhill, R./Gangestad, S. W./Comer, R. (1995) Human female orgasm and mate fluctuating asymmetry. *Animal Behaviour* 50:1601–1615.
- Thornhill, R./Palmer, C. T. (2000) *A natural history of rape*. MIT Press: Cambridge MA.
- Thornhill, R./Thornhill, N. W. (1992) The evolutionary psychology of men's coercive sexuality. *Behavioral & Brain Sciences* 15:363–421.
- Trivers, R. L. (1972) Parental investment and sexual selection. In: Campbell, B. (ed) *Sexual selection and the descent of man 1871–1971*. Aldine: Chicago, pp. 136–179.
- Tsubaki, Y./Siva-Jothy, M. T./Ono, T. (1994) Re-copulation and post-copulatory mate guarding increase immediate female reproductive output in the dragonfly, *Nannophya pygmaea*. *Behavioral Ecology and Sociobiology* 35:219–225.
- Waage, J. K. (1979) Dual function of the damselfly penis: Sperm removal and transfer. *Science* 203:916–918.
- Wilson, M. (1997) Our roots and our colleagues. *Human Behavior and Evolution Society Newsletter* 6:1–2.
- Wrangham, R./Peterson, D. (1996) *Demonic males*. Houghton Mifflin: Boston.