

Chapter 3

Conflict and Bonding Between the Sexes

Ryne A. Palombit

Locked together by their need for partners in sexual reproduction, the sexes undergo an antagonistic dance to the music of time.

Tracy Chapman and Linda Partridge (1996)

Abstract The derivation of human universals from nonhuman data is complicated by the immense diversity of patterns exemplified by both human and nonhuman primates. One approach is to elucidate processes that may operate universally, though the particular phenotypic patterns that result may differ, depending upon the distinctive features of species biology. Below, I argue that sexual conflict and its corollary, sexually antagonistic coevolution, are of central importance for understanding the evolution of reproductive strategies in nonhuman primates. Because sexual conflict is a relatively new area of theory and research, and because primate life histories limit the kinds of data that can be collected, relevant primate data are limited (with the possible exception of one form of conflict: infanticide). Consequently, I review sexual conflict theory, relevant comparative data from nonprimates, and preliminary evidence from select primate studies. Theoretical considerations and empirical evidence suggest significant potential for the widespread action of sexual conflict in nonhuman primates, in both precopulatory and postcopulatory domains of reproduction, and affecting characters ranging from morphology and physiology to sociosexual behavior. Female counterstrategies to male-imposed costs are diverse, but male–female association has been argued to forestall sexual conflict both in the form of precopulatory coercion and of infanticide. In light of evidence for pervasive and diverse effects of sexual conflict in nonhuman primate biology, it is likely that it also constitutes a universal process

R.A. Palombit

Department of Anthropology, Center for Human Evolutionary Studies, Rutgers University,
New Brunswick, NJ, USA

e-mail: rpalombit@anthropology.rutgers.edu

underlying human reproduction. I briefly explore several potential sources of human sexual conflict suggested by the nonhuman data.

3.1 An Approach to Universals

Universals are “*mechanisms of human behavior held in common among people all over the world. . .*” (Boyd and Silk 2006: 590). The variability of human behavior has always bedeviled the search for universals, prompting Fox (1989: 116) to ask how we get beyond the “ethnographic dazzle” to the universals of general, biological importance? The problem is only magnified when we expand the taxonomic context of the analysis to include nonhuman primates, a mammalian order famous for immense diversity in behavior, reproduction, life history, morphology, and physiology. One might say that ethological dazzle threatens to obscure this comparative analysis: how can one discern anything about human universals from this extraordinary variety? There are two solutions to this problem of deriving our family resemblances (*sensu* Fox 1989).

One approach is to search for specific *patterns* of behavior shared between human and nonhuman primates. This orientation towards *substantive* universals necessarily concentrates our attention on a relatively small number of species most closely related to us, notably the chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*), or perhaps the African great apes, or the great apes, generally. To remain useful, however, this approach, focused as it is on elucidating homologous patterns, cannot extend too far beyond this group of primates. This method offers advantages and insights (e.g., Goodall 1971; Wrangham and Peterson 1996; de Waal 2005).

An alternative approach, however, is suggested by Wittgenstein’s (1953) theory of universal family resemblances, as captured by the “Churchill face” metaphor (Aaron 1965). Among members of a family, such as the Churchills, there is a distinctive Churchill face, which is recognizable as the same, in some sense, but which cannot be said to have any *one* feature common to *all* faces. In other words, there is *no* shared pattern *per se*. The crucial aspect of this view is its emphasis on a *process* generating predictable patterns not necessarily defined by any one feature or character. The particular patterns will depend upon distinctive features of a species’ biology or a population’s conditions. It is the *process* that constitutes the universal.

It is this second perspective on behavioral universals that frames this chapter’s examination of nonhuman primates. Here, I focus on one process that I believe is paramount for understanding primate reproductive strategies: sexual conflict. Sexual conflict has attracted increasing attention over the last decade, and the studies of this process have now come to outnumber investigations of the conventional forms of sexual selection (intrasexual selection and mate choice) (Pizzari and Snook 2003). Most of this research has focused on invertebrates – particularly insects – although there have also been studies of sexual conflict in some vertebrates, such as fish, birds, and an occasional mammal (e.g., Arnqvist and Rowe 2005). In spite of

an early landmark article (Smuts and Smuts 1993), research on sexual conflict in primates has not progressed dramatically.

3.2 What is Sexual Conflict?

As with any relatively new field, there is considerable debate over the definitions, assumptions, and models of sexual conflict (Hosken and Snook 2005; Tregenza et al. 2006). Of course, the notion that male and female reproductive styles do not always coincide perfectly has a long history in evolutionary thinking, beginning with Darwin's (1871) exposition of sexual selection, demonstrated by Bateman's (1948) study of *Drosophila* reproduction, and elaborated by Williams's (1966) "battle of the sexes" metaphor. But it was Trivers (1972) who spotlighted the potential for sexual conflict with an ostensibly simple point: sex differences in parental investment, originating with anisogamy, but amplified in mammals by gestation, lactation, and postnatal care, will generate different reproductive strategies for the males and females, maximizing quantity vs. quality of offspring, respectively. The implication is that reproductive strategies of the sexes not only diverge, but may comprise elements that are *incompatible*. This incompatibility is crucial because different fitness optima for males and females will not generate conflict if they can be achieved simultaneously (Parker 2006). Sexual conflict emerges when strategies among members of one sex impose fitness costs on the other sex. In the resulting evolutionary dialectic, each sex attempts to mitigate these

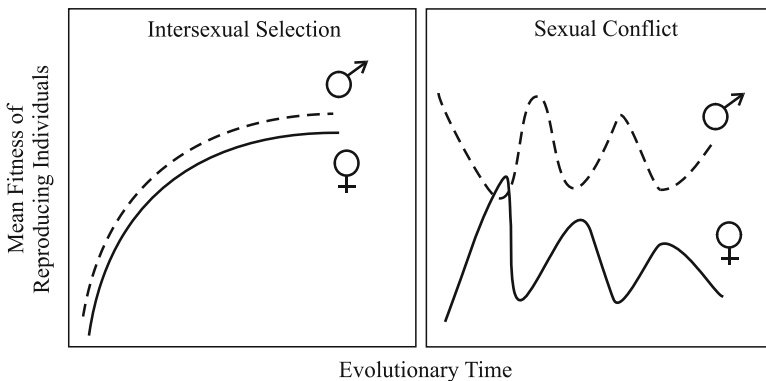


Fig. 3.1 A comparison of average fitness profiles of reproducing males and females over evolutionary time under “conventional” intersexual selection (female choice) (*left*) and sexual conflict (*right*). Under intersexual selection, male fitness (*dashed line*) and female fitness (*line*) often (though not invariably) increase to an asymptote set by natural selection. Under sexual conflict, mutations conferring a net mating benefit to males reduce female fitness, thereby selecting for a female counter-adaptation decreasing male fitness, etc. It is important to note that the figure does not represent the average fitness of males and females in a population, which will coincide with one another (Fisher 1930), but rather the average fitness profiles of reproducing individuals (see Arnqvist 2004; Pizzari and Snook 2004). Figure modified from Pizzari and Snook (2003)

costs and move members of the other sex closer to its own optimum (Gowaty 1997). This coevolutionary dynamic of sexually antagonistic strategies positions sexual conflict as a potential third form of sexual selection, in addition to intrasexual selection and mate choice (Smuts and Smuts 1993; Clutton-Brock and Parker 1995; Chapman et al. 2003; Zeh and Zeh 2003; Tregenza et al. 2006) (Fig. 3.1). It is female avoidance of male-imposed costs that drives sexual conflict, rather than the acquisition of benefits from preferred mating. Parker's (1979) ESS analyses gave rise to the current theoretical framework recognizing two general forms of sexual conflict as sexually divergent optima for either (1) alleles determining a specific trait – *intra*locus conflict – as in the evolution of sexual dimorphism (e.g., Lande 1987; Lindenfors 2002; Cox and Calsbeek 2009); or (2) the outcome of male–female interactions – *inter*locus conflict. This chapter is concerned only with the outcome of male–female interactions.

3.3 Approaches to Studying Sexual Conflict

There are three general approaches to studying sexual conflict. The first method is exemplified by the now classic study of seminal proteins in the fruit fly (*Drosophila melanogaster*) (Rice 1996; Holland and Rice 1999). These proteins originate in accessory glands, are transferred (with sperm) to female mates, and influence females in a number of ways that benefit males, such as: (1) increasing the rate of female egg-laying (Chen 1984); (2) decreasing female receptivity to additional matings (Ravi Ram and Wolfner 2007); and (3) improving sperm competition by displacing the sperm of previous copulators (Harshman and Prout 1994; Clark et al. 1995). Seminal fluids are apparently toxic, such that prolonged exposure to them elevates female mortality (Chapman et al. 1995; Clark et al. 1995; Lung et al. 2002). In order to test the prediction that monogamous mating systems engender less sexual conflict than polygynous systems, Holland and Rice (1999) randomly assigned individual *D. melanogaster* to one of two population treatments: imposed monogamy versus the (control) polygynous ancestral condition. After 47 generations, the monogamous lineage was characterized by lower toxicity of male seminal fluids and lower female resistance to seminal fluids (see also Rice et al. 2005). These data exemplify a key (though not inevitable) corollary of interlocus sexual conflict: *sexually antagonistic coevolution*. This historical approach, tracking changes over evolutionary time, can provide particularly compelling evidence of sexual conflict and sexually antagonistic coevolution, but it is feasible primarily with relatively short-lived animals that can be manipulated in the laboratory.

A second approach, based on quantitative genetics, defines sexual conflict as negative covariance between the sexes in fitness, particularly over generations (Rice and Chippindale 2001; Shuster and Wade 2003; Pizzari and Snook 2003, 2004). For example, red deer (*Cervus elaphus*) stags with greater lifetime reproductive success sired less successful daughters and more successful sons than stags with lower lifetime fitness (Foerster et al. 2007). The negative correlation between

the fitness of males and females suggests opposing optimal genotypes for males and females, i.e., sexually antagonistic coevolution. Again, this method is impractical for primates because we know relatively little about lifetime reproductive success, particularly for males, and even less about the selection coefficients and heritability of characters related to fitness.

A third approach considers how certain behavioral, anatomical, or physiological aspects of reproductive strategies among members of one sex impose costs on the other sex, and how phenotypic features of the second sex may function to mitigate those costs (as coevolutionary counterstrategies). The relevant data are collected over relatively short time periods, rarely long enough to demonstrate the effects of sexual conflict on the lifetime reproductive success of individuals. These kinds of analyses can reveal the extent and form of sexual conflict, but they can only indirectly imply the action of sexually antagonistic coevolution. This approach is the only one that is now tractable for studies of nonhuman primates.

3.4 Pre- and PostCopulatory Conflict over Mating: Sexual Coercion

3.4.1 Sexual Coercion: A Conceptual Framework

Aggression between the sexes surrounding mating is termed “sexual coercion” (Smuts and Smuts 1993). Clutton-Brock and Parker (1995) distinguish three forms of sexual coercion: forced copulation, sexual harassment, and sexual intimidation. Although few nonhuman primate studies explicitly differentiate these three categories of sexual coercion, there is evidence that all three may operate in primates.

3.4.2 Forced Copulation

This form of sexual coercion involves the physical restraint and forcible insemination of resistant females. Among primates, forced copulation has been noted occasionally in several species (chimpanzees Tutin 1979; patas monkeys Chism and Rogers 1997; spider monkeys Gibson et al. 2008), but it is regularly observed in only two species, the orangutan (*Pongo pygmaeus*) (van Schaik and van Hooff 1996) and *Homo sapiens* (Smuts 1992; Goetz et al. 2008).

Although forced copulation occurs in a number of different taxa (Table 3.1), it is a less common form of sexual conflict than harassment or intimidation. This may be because forced copulation is only possible under a restricted set of conditions, such as when males are much larger than females (Clutton-Brock and Parker 1995) or when females are isolated and unable to obtain social support. However, neither of these factors provides an entirely satisfactory explanation for the distribution of forced copulation in primates. Although the orangutan is a strongly dimorphic

Table 3.1 Potential forms of (interlocus) sexual conflict

Context	Category	Nature of sexual conflict	Example taxa ^a	Reference ^a
Precopulatory	Forced copulation	Catch and physically restrain female followed by forced insemination; incl. anatomical specializations to grasp and prevent escape of female prior to forced insemination	<i>Pongo pygmaeus</i> , <i>Homo sapiens</i> , Anseriform birds, some insects	Thornhill and Alcock 1983; Gowaty and Buschhaus 1998; Bertin and Fairbairn 2005; Siva-Jothy 2006; Vahed and Carron 2008, Knott in press
	Harassment, indirect costs of mating or mate guarding	Repeated, persistent courtship or copulation (attempts), by single or especially multiple males; physical aspects of courtship or copulation (e.g., posture, inexperienced males)	Insects, Fish, Anurans, Snakes, Artiodactyls <i>Microcebus murinus</i> ?	Howard 2008; Clutton-Brock and Parker 1995; Réale et al. 1996; Arnqvist and Nilsson 2000; Shine et al. 2000; Eberle and Kappeler 2004a; Bowcock et al. 2009
	Male dominance displays	Males target females in aggressive displays that function in acquisition and/or maintenance of intragroup dominance status or intergroup spacing	<i>Papio hamadryas griseipes</i> , <i>P. h. ursinus</i>	Henzi et al. 1998; Kitchen et al. in press
Postcopulatory (Prezygotic)	Sexual intimidation/punishment	Aggression to (estrus) females that refuse to associate or copulate with male, or that associate or copulate with other male(s)	Primates	Smuts and Smuts 1993; Clutton-Brock and Parker 1995, see text
	Seminal fluid proteins	Proteins beneficially affect outcomes of sperm competition for males, while imposing costs upon female viability and/or reproduction	Insects, Nematodes	Gems and Riddle 1996; Holland and Rice 1999, see text
	Non-fertile sperm	Anucleate sperm reduce female receptivity to subsequent mating	Insects	Cook and Wedell 1999
	Reproductive tract injury	Male-induced changes/injury of female genital tract, typically during copulation, results in decreased sexual interaction	Insects, Rodents, Strepsirrhines? <i>H. sapiens</i> ?	van der Schoot et al. 1992, Crudgington and Siva-Jothy 2000; Blanckenhorn et al. 2002; Stockley 2002; Low 2005
	Genital plugs, coagulates	Seminal coagulates may: improve sperm transport, reduce sperm loss, physically block intromission by other males, and/or physiologically induce female refractory period	Insects, Rodents, Primates	Matthews and Adler 1978; Simmons and Siva-Jothy 1998; Dixson and Anderson 2002

Genital lock	Prevention of penis removal from female reproductive tract for prolonged period following ejaculation; due to genital clasping structures or partial enlargement of penis and vaginal adhesion	Insects, <i>Galago crassicaudatus</i> , <i>Macaca arctoides</i>	Thornhill and Alcock 1983; Dixson 1998; Werner and Simmons 2008
Sexual intimidation/punishment (mate guarding)	Temporary male association with an inseminated female for a prolonged period following ejaculation to aggressively prevent subsequent mating by female	Insects, Primates	Eberle and Kappeler 2004b; Sato and Kohama 2007
Egg-sperm interaction	Genes of sperm and egg differentially influence processes surrounding capacitation, penetration of egg, and fertilization	Invertebrates, Fish	Rice and Holland 1997; Levitan 2008; Martin-Coello et al. 2009
Postcopulatory (Postzygotic)	Feticide	Equids, Primates	Berger 1983; Pereira 1983; Sommer 1987; Agoramoorthy et al. 1988; Pluháček and Bartoš 2000
	Male harassment (or forced copulation) of pregnant female promotes or induces spontaneous abortion of implanted zygote or fetus		van Schaik 2000a
Sexually selected infanticide	Killing of dependent infants to prematurely end lactational amenorrhea and return females to fertilizable (estrus) state	Primates, Fissiped carnivores, Toothed whales	
Parental investment & genomic imprinting	Activity of genes depends upon sex of parent from which inherited (e.g., paternally derived genes induce disproportionately greater maternal investment in offspring)	Rodents	Keveeme 2001; Roulin and Hager 2003
“Policing”	Male intervenes to curtail female-female aggression, mitigating or eliminating benefits a “winner” could derive via individual or coalitionary competitive superiority	<i>Gorilla gorilla</i> subspecies, <i>Pan troglodytes</i>	Boehm 1994; Watts 1997; Sicotte 2002; Stokes 2004; Harcourt and Stewart 2007

^aTaxa and references list are not exhaustive, but rather represent illustrative examples

species, forced copulation is frequently done by small males, who are either subadults or “unflanged” adults with arrested development of secondary sexual characters (Knott 2009). Moreover, in many strongly dimorphic monkeys, males do not exhibit the behavior at all. Social isolation may increase vulnerability to forced copulation. In contrast to the vast majority of highly gregarious anthropoid primates, female orangutans are often alone (Rodman and Mitani 1987). Humans are not solitary, but Emery-Thompson (in press: 361) argues that college-age women experience the highest rate of rape in the United States partly because “*they are the group most likely to be living away from natal kin but not yet with a domestic partner.*” However, social vulnerability does not explain why forced copulations are so rare in chimpanzees (0.2% of the copulations observed by Tutin (1979)) even though females typically disperse from their natal communities and spend much time alone. Possible explanations for the rarity of forced copulation in chimpanzees are female influence on male dominance relations (Stumpf and Boesch 2006) or simply the effectiveness of male sexual coercion in generating mating opportunities (see below), which reduces the benefits of physical restraint and forcible insemination.

Forced copulation in orangutans is commonly considered part of an alternative reproductive strategy of unflanged adult males. The males avoid direct mating competition with large, flanged males by retarding development of secondary sexual traits and relying on force to copulate with uncooperative females that generally prefer flanged males as mates (van Schaik and van Hooff 1996; Atmoko and van Hooff 2004; Maggioncalda et al. 1999). Knott (2009) argues, however, that since forced copulation is not restricted to unflanged males, it is better viewed as a *general* male orangutan strategy to overcome female resistance. Both models are consistent with sexual conflict arguments that forced copulation in nonhuman animals is an alternative mating strategy (Table 3.1).

Thornhill and Palmer (2000) have similarly proposed the controversial hypothesis that human rape reflects an alternative strategy of low-status, socially disadvantaged males to obtain conceptions. Emery-Thompson (2009) rejects this argument on several grounds, including observations that a substantial majority of rapes are perpetrated by men casually or intimately known to their victims (acquaintance rape) and that women often continue their relationships with these attackers. Thus, she contends instead that rape is one of several forms of sexual aggression used by men to maintain *long-term* reproductive access to female mates. Emery-Thompson has shifted the functional focus from immediate copulatory benefits (as in orangutans) to prospective reproductive gains via intimidation and punishment (see below). Again, both hypotheses are based on sexual conflict.

It is important to recognize that forced copulation in humans is an extremely heterogeneous phenomenon (Travis 2003). Some cases of rape may originate in pathological behavior (such as “stranger rape”) (Emery-Thompson 2009) or in male tactics of terror and control (e.g., violent rape in the context of warfare; Swiss and Giller 1993). Thus, although a comprehensive understanding of rape in humans will no doubt involve an array of processes and factors, sexual conflict theory seems likely to improve understanding of some forms of the behavior (Emery-Thompson 2009).

3.4.3 Sexual Harassment versus Sexual Intimidation

Sexual harassment refers broadly to the fitness costs of mating to females (*sensu* Daly 1978), particularly costs connected with persistent male courtship, repeated intromission attempts, or the nature of copulation itself. Sexual intimidation refers to situations in which “males punish females that refuse to associate with them or that associate with other males,” and is thus designed to reduce female resistance or promiscuity (Clutton-Brock and Parker 1995, p 1353). When males use sexual intimidation tactics, females learn to modify their behavior to minimize the costs of male aggression. This definition is directly similar to Smuts and Smuts’s (1993) original definition of sexual coercion. To illustrate the distinction between sexual harassment and sexual intimidation, consider the following examples:

1. During the rut, female sheep (*Ovis* spp.) may be pursued by up to 11 rams at a time, whose repeated attempts to charge, sniff, and mount result in exhaustion and injury to females (Réale et al. 1996) as well as increased mortality, as females evade male suitors on precipitous terrain (Festa-Bianchet 1987).
2. When a female dung fly (*Scatophaga stercoraria*) lands on a dropping occupied by several males, their struggles to copulate and exclude rivals from mating may trample her into the patty, covering her with dung that impairs her ability to fly and sometimes even drowns her (Parker 1970).
3. A male chimpanzee severely attacks an estrous female for “no obvious reason,” i.e., in circumstances *unrelated* to ongoing mating, and when the female’s sexual swelling is small or flat; many days later, during the period of maximal swelling and mating, she restricts copulations to this male (Goodall 1986: 341).

The various costs imposed on female sheep and dung flies are classified as sexual harassment because they are the indirect by-product of female mate discrimination and male competition, which are particularly relevant when mating attempts are made *repeatedly* or by *multiple* males (or both). The chimpanzee example highlights aggression designed to reduce female resistance or promiscuity, in this case, to promote *future* female mating compliance. Harassment and intimidation can operate in either pre- or postcopulatory contexts. For example, mate guarding is a common manifestation of coercion that can precede or follow copulation. It may comprise threats and attacks on the female herself (*sensu* intimidation) or aggression directed at rival males, thereby imposing indirect mating costs on females (*sensu* harassment).

Harassment and intimidation are behavioral examples of a general distinction in sexual conflict theory between *negative pleiotropic side effects* and *adaptive harm* to females, respectively (Partridge and Hurst, 1998). Many students of sexual conflict maintain that the costs accrued by females are incidental (pleiotropic) by-products of male mating strategies, selected for *not* because of, but *in spite of* the harm to females (Hosken et al. 2003; Morrow et al. 2003; Arnqvist 2004). Conversely, proponents of the adaptive harm hypothesis posit that males benefit from *directly* harming females, if an existing system of phenotypic plasticity promotes female responses that benefit males (e.g., a female injured by a male may increase

her resting time, thereby limiting copulation with other males, or she may invest more in her current offspring due to the harm-induced reduction in her reproductive value) (Lessells 1999; Lessells 2005; Johnstone and Keller 2000).

Of crucial importance for understanding these forms of sexual coercion are data addressing not just the magnitude of costs to females, but also the nature of those costs. There are few such data for primates, but studies of other animals reveal costs in the form of reduced foraging efficiency (Rubenstein 1986; Magurran and Seghers 1994; Pilastro et al. 2003; Erez et al. 2005; Heubel and Plath 2008), increased exposure to predation (Magellan and Magurran 2006), injury and associated increased mortality (Hiruki et al. 1993; Miller et al. 1996; Réale et al. 1996; Mühlhäuser and Blanckenhorn 2002), and physiological stress (Moore and Jessop 2003; Shine et al. 2004). These costs are in addition to those associated with suboptimal reproduction due to fertilization by a lower quality male or to lost opportunities for polyandry.

3.4.4 Is Sexual Coercion Beneficial to Females?

It is possible that sexual coercion may actually enhance female fitness by providing a behavioral filter for higher quality males as mates or guaranteeing that females' sons will carry sexually antagonistic traits that enable them to achieve higher reproductive success (Eberhard 1996; Cordero and Eberhard 2003). If the net effect on female fitness is therefore positive, then sexual conflict becomes a mechanism of female choice, which Eberhard (2005) contends explains most male mating aggression to resistant females. This hypothesis has not been supported by some mathematical models (Kirkpatrick and Barton 1997), but there is some related evidence for benefits of coercion to females (Valero et al. 2005).

Most primate researchers assume that sexual coercion reduces the effectiveness of female mate choice and that female preference for *less* aggressive males is a likely counterstrategy to sexual coercion (Smuts and Smuts 1993). This view derives in part from the intensity of both male aggression and toward females and female resistance, which seems to impose high costs on the victims (e.g., chimpanzees: Goodall 1986; Muller et al. in press). Moreover, for most anthropoid primates, group life may provide females with less costly means of evaluating mates than provoking male attacks upon themselves. An arguably more relevant variant of this hypothesis, however, is that females prefer to mate with high-quality males (e.g., dominant males), who also happen to be more aggressive *generally* (which constitutes an indirect cost of mating).

3.4.5 Sexual Harassment and Intimidation in Non-Human Primates

Three conditions promote sexual harassment that occurs when multiple males attempt to mate simultaneously with a single female (Réale et al. 1996; Head and Brooks 2006; Smith and Sargent 2006): (1) a male-biased operational sex ratio;

(2) asynchrony in female estrous; and (3) weak dominance among males (i.e., reduced or incomplete male ability to control sexual access to females).

All three conditions prevail in nocturnal mouse lemurs (*Microcebus murinus*) studied at Kirindy, western Madagascar: reproducing males tend to outnumber estrous females; females breed on only one night each year, but are receptive on individually different nights of the mating season; male–male competition sometimes involves contests, but scramble competition via extensive roaming behavior is more common (Eberle and Kappeler 2004a, b). On her night of receptivity, a female is typically approached by 2–15 males and mates with almost all of them up to 11 times. Notably, the usual social dominance of females wanes during the mating season, prompting Eberle and Kappeler (2004a: 97) to interpret the high rates of mating with multiple males as “harassment” stemming from a temporary female inability to reject suitors. Postcopulatory mate guarding does occur occasionally, raising the possibility of sexual intimidation. But this mate-guarding is based less on aggression directed at the female than on chasing rival males away. Attacks on females occurred in only 4 of the 55 cases of mate guarding and were also largely ineffectual in light of the fact that three of the four females succeeded in deserting the male. These patterns of sexual coercion are generally more consistent with multi-male harassment than with sexual intimidation, as predicted by the demographic, social, and reproductive conditions.

The gregarious (diurnal) strepsirrhines are of comparative interest for distinguishing between harassment and intimidation because intimidation relies particularly on learned cooperation in explicitly gregarious contexts (Clutton-Brock and Parker 1995). Unfortunately, few relevant new data have become available since Smuts and Smuts (1993) to address this question. Brockman’s (1999) description of sexual aggression by male sifakas (*Propithecus verreauxi*) suggests harassment rather than intimidation. Multiple males attempt simultaneously to mate with most estrous females during the mating season. Intersexual sexual aggression increases significantly at this time, but the vast majority of it is female aggression to males (not vice versa). Harassment typically takes the form of disrupting an ongoing copulation, and can be perpetrated by either males or females. Although interfering females direct aggression at either copulating partner, males virtually always focus exclusively on the rival male instead of the female. These patterns are collectively inconsistent with the definition of sexual intimidation. Indeed, the data support Smuts and Smuts’s (1993) hypothesis that female dominance in some lemurs effectively deters coercion in the form of sexual intimidation. Even so, indirect costs via sexual harassment apparently persist for female sifakas. The nature and magnitude of these costs for female fitness remain unclear, however. Limitation of female choice seems likely, but this possibility needs to be clarified quantitatively (do less harassed females achieve their preferences more often?) as well as tested against the alternative that female resistance functions as mate choice (see below). Moreover, the mating benefits of harassment for the males remain obscure.

A quasi-experimental anecdote concerning ring-tailed lemurs (*Lemur catta*) further supports the notion that female dominance limits sexual intimidation (Parga and Henry 2008). Partly due to the effects of provisioning, a young female reached sexual maturity at an earlier age than usual, but *before* she had developed

social dominance over males. This young estrous female subsequently became the target of direct aggression and even forced copulation attempts by a particular adult male.

Data on the diurnal, group-living strepsirrhines also provide a relatively rare primate example of support for the mate choice hypothesis for coercion. In ruffed lemurs (*Varecia variegata*), female conspicuously resist male sexual overtures, even resorting to physical aggression against them. Although males do not typically retaliate with aggression of their own, both Foerg (1982: 119) and Morland (1993) suggest that this sexual antagonism ensures that a female copulates with higher quality (“strong”) males who “are more likely to overcome her beating” long enough to achieve insemination.

Studies of anthropoid primates have made little effort to test between indirect and direct costs to females. Japanese macaques (*Macaca fuscata*) were among the first primates to provide data on sexual coercion, primarily in the form of chases of estrous females or “possessive following” (Carpenter 1942; Itani 1982; Enomoto 1981). As Huffman (1987) points out, these patterns were often interpreted as incidental components of male courtship or “precourtship” behavior (Itani 1982: 362), thereby implicating sexual harassment. Likewise, a key form of sexual harassment – the costs of mating with *multiple* males – is reflected in the decreased foraging efficiency of females on days they mated polyandrously, compared with days they consorted with the alpha male only (Matsubara and Sprague 2004). Soltis et al. (1997, p 725; 2001, p 486) conclude that male aggression to estrous females is primarily a “side effect” of a general mating season increase in overall male aggressiveness and female-maintained proximity to males. Although sexual intimidation does occur, it accounts for a minority of instances of sexual coercion. Subsequent studies of mating-related aggression in this species, however, have emphasized sexual coercion in Clutton-Brock and Parker’s (1995) sense of intimidation (Jack and Pavelka 1997; Soltis 1999; Soltis et al. 2001).

Indeed, this interpretation tends to emerge from many recent studies of male aggression over mating in primates (e.g., Kuester et al. 1994; Perry 1997; Reed et al. 1997; Boinski 2000; Colmenares et al. 2002; Arlet et al. 2008; Table 3.1 and references above). This is partly because comparatively few investigations have addressed the Clutton-Brock and Parker (1995) distinction between harassment and intimidation (Soltis et al. (1997) being a notable exception) and have focused on the processes of intimidation implicit (or explicit) in (Smuts and Smuts 1993). But this emphasis may also reflect the fact that many of the species studied are characterized by gregariousness and male contest competition, which are conditions especially likely to promote sexual intimidation.

One of the more compelling demonstrations of intimidation is provided by the 10-year study of the Kanyawara population of chimpanzees, Kibale, Uganda. It is striking – as well as suggestive of the biological significance of sexual intimidation – that in a species well-known for male–male aggression, male–female aggression occurs at roughly the same rate at Kanyawara (Muller et al. 2009). The majority of this aggression involves male charging displays and chases, but approximately 35% of it entails physical attacks on females (often in coalition with

other males). Muller et al. (2007) provide data by directly testing three predictions of the Smuts and Smuts (1993) sexual coercion hypothesis:

Prediction 1: Sexual coercion is costly to females. The intensity of male aggression is difficult to quantify, but assaults on females can involve flailing with branches, pummeling with fists, pulling of hair, and inflicting injuries (Goodall 1986). These attacks are typically assumed to carry costs, such as risk of infection from wounds, but Muller et al. (2007) clarify potential costs with evidence that cycling parous females, who are the primary targets of male coercion, have elevated cortisol levels. The data cannot demonstrate that male coercion directly *causes* hormonally mediated stress in females. A causal connection is suggested, however, by the fact that, compared with parous females, nulliparous females copulated at equivalent rates, spent similar (if not more) time in the company of males, but received relatively less coercion from them (as less preferred sexual partners) *and* had cortisol levels that were not only lower but that did not differ significantly on estrous versus nonestrous days.

Prediction 2: Male mating success is improved by sexual coercion. Previous primate studies had rejected this prediction based on the lack of a positive correlation between overall rates of male aggression to females and male mating success (Bercovitch et al. 1987; Soltis 1999; Stumpf and Boesch 2006). Muller et al. (2009) provide a more direct assay of the selective impact of sexual coercion by demonstrating that male chimpanzees copulated at significantly higher rates with females that they were more aggressive to, than with females that they were less aggressive to (Fig. 3.2).

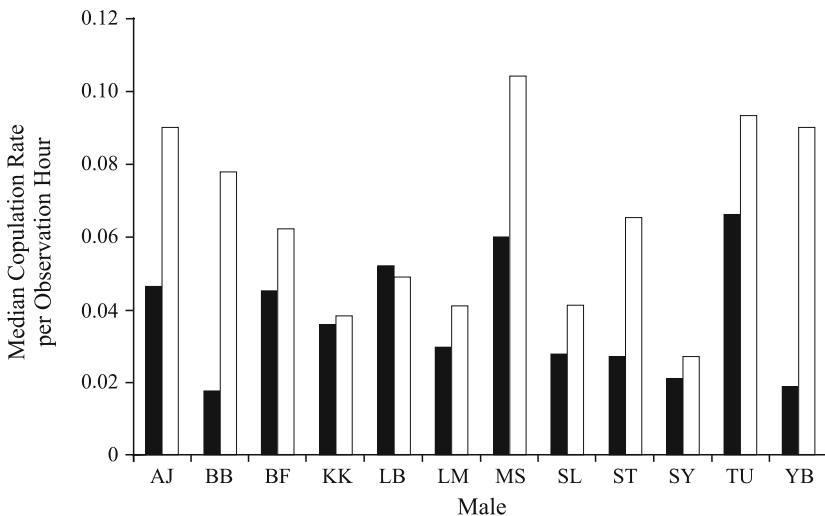


Fig. 3.2 Median dyadic rates of aggression for each of 13 male chimpanzees (*Pan troglodytes*) with 15 parous females. For each male, the median copulation rates were calculated with females who received above (*white*) or below (*black*) the median amount of aggression for that male. The difference was significant (Wilcoxon signed-rank test, $p = 0.002$). Data from Muller et al. (2007)

Prediction 3: Coercion is not simply an indirect cost of female choice. One of the noteworthy aspects of this study is its test of the alternative hypothesis that male aggression reflects female choice. Muller and colleagues marshal several lines of evidence to reject the possibility that intersexual aggression is a by-product of female mating preferences for aggressive males. First, male rank was uncorrelated with aggression directed at females. Second, the relationship between male coercion and mating success with targeted females also held for low-ranking males as well, who are arguably less preferred sexual partners. Finally, a matrix partial correlation analysis revealed a significant association between male aggression directed at individual females and the copulation rate with those females, controlling for time spent together.

3.5 PostCopulatory Sexual Conflict: Prezygotic

Sexual conflict after copulation may involve processes occurring at or prior to fertilization (prezygotic) or thereafter (postzygotic) (Table 3.1). The postcopulatory manifestation of intrasexual selection is sperm competition (along with associated factors such as genital locks, penis morphology, etc.), which has attracted much study (e.g., Birkhead and Møller 1998). Postcopulatory intersexual selection is cryptic female choice (Eberhard 1996), which primarily concerns the differential treatment of sperm in the reproductive tracts of polyandrously mating females (as well as associated phenomena, e.g., abortion). The important question here, however, concerns the potential for conflict between these two postcopulatory processes: how do the benefits to females of cryptic mate choice via multimale mating compare with the costs incurred from male adaptations for sperm competition? Current data are too few to answer this question for primates. Although sperm competition is relatively well investigated (Gomendio et al. 1998), cryptic female choice remains virtually unstudied (Reeder 2003), with the possible exception of *H. sapiens* (Baker and Bellis 1995; Thornhill and Gangestad 1996). Therefore, I highlight below two areas where postcopulatory-prezygotic sexual conflict might occur in primates.

3.5.1 Genital Coagulates

One possible source of conflict concerns enzymes acting on seminal vesicular proteins to congeal ejaculates into structures ranging from a soft coagulum to a more substantial, rubbery plug. Seminal coagulation is more pronounced in primates with multimale mating patterns (compared to unimale systems), suggesting a male strategy to block rival sperm access to the cervical Os (Dixson and Anderson 2002). What is not known, however, is whether these coagulates impose costs on females. Plugs can be dislodged by subsequent male partners or by inseminated

females in *L. catta* (Parga 2003) and *P. troglodytes* (Dixson and Mundy 1994), suggesting low potential for sexual conflict (at least over remating) or the existence of an effective female counterstrategy to male manipulation. Intersexual conflict may be more relevant in taxa where females cannot remove plugs, such as *M. murinus* (Eberle and Kappeler 2004a). But even in these cases, conflict cannot be assumed as plugs potentially confer benefits to females, such as facilitating fertilization via sperm retention or transport. This could be valuable in a species like *M. murinus*, in which females are in estrous for only a few hours on a single night each year.

3.5.2 Penis Morphology and Female Injury

In strepsirrhines, keratinized penile spines, plates, or papillae are so conspicuous, widespread, and variable as to have long informed taxonomy (Bearder et al. 1996). Similar, but generally simpler, anatomical features are also found in a few platyrrhines and catarrhines (Dixson 1998). Spines develop upon sexual maturity (Perkin 2007), suggesting testosterone mediation and a mating-related function, but the precise nature of that function remains obscure. Adaptive hypotheses include tactile facilitation of ejaculation, removal of sperm or copulatory plugs, genital locking of partners, stimulation of reproductive readiness in females or of synchrony between partners, and Fisherian female choice (Dixson 1989; Eberhard 1990; Harcourt and Gardiner 1994).

Comparative data from insects suggest an alternative explanation: sexual conflict. In the cowpea weevil (*Callosobruchus maculatus*), the penis is equipped with spines that damage the female genital tract during copulation, reducing her likelihood of subsequent mating, and thereby enhancing sperm competition outcomes for the male (Crudgington and Siva-Jothy 2000; Hotzy and Arnqvist 2009). In primates, the magnitude of spinosity is negatively correlated with the duration of female sexual receptivity during the ovarian cycle (Stockley 2002), suggesting that penile spines similarly improve male sperm competition success by restricting female mating. The precise mechanism underlying this association is unclear, however. Penile spines could stimulate ovulation or associated neuroendocrine reflexes, but they could also cause “*short-term local damage to the female genital tract, making continued sexual activity painful or aversive*” (Stockley 2002, p 130).

Correspondingly, sexual conflict theory may shed light on the function of human practices of genital modification (e.g., Wilson 2008). The patterns and frequency of female genital cutting vary substantially across populations, and the effects on female (and male) sexual behavior and reproduction are strongly debated (Gruenbaum 2001). Reason (2004) argues that in one West African population, the practice enhances female reproductive success because it is a virtual prerequisite for marriage and because men invest significantly more in the offspring of wives who are circumcised. Both patterns are consistent with a sexual conflict interpretation, but clearly more study of human behavioral ecology in the context of relevant

cultural influences is needed to test this hypothesis against alternative explanations. As Low (2005, p 76) concludes, although current data on genital modification “*may not prove [sexual] conflicts of interests, they are suggestive.*”

3.6 Postcopulatory Sexual Conflict: Postzygotic

Precopulatory intimidation by male chimpanzees can only be fully understood in the context of postcopulatory sexual conflict in the form of infanticide. Muller et al. (2009) argue that sexual coercion, particularly as practiced by high-ranking males, is a counterstrategy to limit female promiscuity, and that promiscuity is itself a counterstrategy to male infanticide (see also Stumpf et al. 2008). This scenario highlights the nature of sexually antagonistic coevolution: male infanticide favors female promiscuity, which favors male sexual coercion, etc.

Infanticide figures prominently in Smuts and Smuts’ (1993) original discussion of sexual coercion, but it does not fit easily within Clutton-Brock and Parker’s (1995) more general harassment-intimidation dichotomy. It is initially difficult to appreciate that male infanticide might constitute incidental harm to females, since an infant’s death seems so directly detrimental to the mother’s fitness. But this proposition becomes clearer when we consider that the specific “problem” that lactating females pose to reproducing males is a straightforward consequence of primate biology: a nursing infant is, in the words of Altmann et al. (1978: 1029), a “*perfect contraceptive.*” The function of sexually selected infanticide, then, is to disrupt this contraceptive system, not to harm the mother (or reduce her fitness) per se. Thus, following the broader theoretical logic of Partridge and Hurst (1998) and Lessells (2005), if, speculatively, males possessed other means of effectively counteracting the contraceptive – e.g., by manipulating the mother’s hormonal state or accelerating weaning – and if the costs of such a strategy did not exceed the costs of infanticide, then males would *not* be selected to kill infants (but could still achieve the same reproductive benefit). Under such conditions, the death of infant, if it occurred, would be an incidental by-product of the male manipulative strategy, not a necessary harmful component of that strategy. This is not to say that male attacks on infants can not, in principle, function as sexual intimidation, if their mothers’ mating compliance forestalls further aggression directed at them. As Clutton-Brock and Parker (1995) point out, however, this mechanism of *indirect* sexual intimidation predicts that male threats and attacks will also extend to *juveniles*, which is neither predicted by the sexual selection hypothesis nor is a common correlate of infanticidal behavior (Hrdy 1974; van Schaik and Janson 2000).

Male infanticide is still, however, a drastic form of sexual conflict. It reflects adaptive harm (*sensu* Johnstone and Keller 2000) insofar as infanticidal males exploit a preexisting feature of female reproductive plasticity, such that infant loss often accelerates resumption of ovulatory cycling. Although the adaptive significance of infanticide in primates continues to be debated, the available

evidence is more consistent with the sexual selection argument (Borries et al. 1999; Soltis et al. 2000; van Schaik 2000b) than with competing hypotheses, such as the generalized aggression model (Bartlett et al. 1993) and the social pathology argument (Dolhinow 1977). Thus, infanticide appears a likely manifestation of postcopulatory sexual conflict in primates, as well as, arguably, the most studied form of sexual conflict (Hausfater and Hrdy 1984; van Schaik and Janson 2000).

3.7 A Counterstrategy: Male–Female Association

The counterstrategies to sexual conflict are as diverse as the manifestations of conflict itself. They may be morphological, such as the thick skin of female blue sharks (*Prionace glauca*) vulnerable to bites from “courting” males (Pratt 1979), or the large body size of some female lemurs, which is argued to limit sexual coercion during the mating season (Foerg 1982; Taylor and Sussman 1985; Richard 1992; Morland 1993; Brockman 1999).

Female sexual behavior – particularly promiscuity – can limit sexual conflict, both in the form of precopulatory coercion and postcopulatory infanticide. The convenience polyandry hypothesis holds that conceding copulations allows females to avoid the costs of resistance to coercive males (Thornhill and Alcock 1983; Mesnick and le Boeuf 1991; Blyth and Gilburn 2006). This explanation is less often invoked as an anticoercion counterstrategy in primates than in other animals, but one example is Eberle and Kappeler’s (2004a, p 97) argument that the multimale mating of female mouse lemurs reflects “‘making the best of a bad job’ in the face of male harassment.” The counteractive value of convenience polyandry is improved when it is supplemented with postcopulatory mechanisms of cryptic female choice (e.g., spermicides) (Holman and Snook 2006), but this remains unstudied in nonhuman primates. In the postcopulatory domain, both theoretical models and empirical evidence suggest that female promiscuity offers significant potential to limit infanticide by confusing paternity (Hrdy 1979; Ebensperger 1998; van Schaik and Janson 2000; Wolff and MacDonald 2004; Pradhan and van Schaik 2008).

Association with males is a hypothesized female counterstrategy to sexual conflict, again in both the form of sexual coercion and of male infanticide. Sustained proximity to a large, dominant male reduces estrous female exposure to male harassment and intimidation in Japanese macaques (Matsubara and Sprague 2004) and chimpanzees (Wrangham 1986), as well as in many other taxa (insects: Thornhill and Alcock 1983; fish: Pilastro et al. 2003; Dadda et al. 2005; birds: Gowaty and Buschhaus 1998; bighorn sheep: Réale et al. 1996; elephant seals: Mesnick and le Boeuf 1991). This function has also been suggested for the temporary consortships of female orangutans at risk of forced copulation (Mitani 1985; Fox 2002; Setia and van Schaik 2007). Thus, protection from sexual coercion is an alternative functional hypothesis for consortships, independent (though not mutually exclusive) of mate guarding, and female choice hypotheses (Manson

1997). The relevance of this hypothesis for understanding variation in consortships has not been explored thoroughly.

Reducing the costs of precopulatory sexual harassment may similarly underlie sexual swellings. Previous analyzes have suggested that sexual swellings might benefit females because they incite male–male competition, which then facilitates insemination by high-quality males (Clutton-Brock and Harvey 1976) or copulation with many males (Hrdy and Whitten 1987). Alternatively, sexual swellings might serve to reduce the costs of harassment or intimidation by ensuring mate guarding by a dominant male who keeps other males away. The adaptive value of this counterstrategy, however, must be measured against the (coercion) costs of advertising estrous, the benefits of multimale mating, and the benefits of the alternative counterstrategy of reducing coercion via *concealment* of receptivity.

Male–female association is also a proposed counterstrategy to postcopulatory conflict in the form of infanticide (Wrangham 1979; van Schaik and Dunbar 1990; van Schaik and Kappeler 1997). Empirical evidence supports this hypothesis in numerous taxa, including insects, birds, and rodents, and a few primate species (reviewed by Palombit 2000). Mountain gorilla (*Gorilla beringei*) groups have long been viewed as associations of females with a male protector, but whether he deters infanticide or predation is debated. A recent mathematical simulation supports the antiinfanticide hypothesis (Harcourt and Greenberg 2001), but Harcourt and Stewart (2007) argue that rejection of the antipredation hypothesis is premature. Recently, this argument was extended to orangutans with Setia and van Schaik's (2007) suggestion that lactating females use male long calls to stay loosely associated with adult male protectors.

Van Schaik and Dunbar's (1990) hypothesis that social monogamy is an antiinfanticide strategy remains one of the most interesting versions of this hypothesis. Evidence that infanticide has selected for social monogamy is strong in some nonprimate taxa such as burying beetles (*Nicrophorus* spp.) and tropical house wrens (*Troglodytes aedon*), but interpretations of the gibbon data have generated divergent conclusions (Palombit 1999, 2000; Sommer and Reichard 2000; Fuentes 2002; van Schaik and Kappeler 2003). Recent tests of the hypothesis in prosimians, such as fork-marked lemurs (*Phaner furcifer*), avahis (*Avahi occidentalis*), and spectral tarsiers (*Tarsius spectrum*), have not consistently supported the hypothesis (Schülke and Kappeler 2001; Thalmann 2001; Gursky 2002). However, this intriguing hypothesis awaits further direct testing in the taxa it primarily addresses: the gibbons.

One population in which long-term data continue to suggest an antiinfanticide function of male–female bonding is the chacma baboon (*Papio hamadryas griseipes*) of the Okavango Delta, Botswana (see also Weingrill 2000). Like yellow baboons (*P. h. cynocephalus*) and olive baboons (*P. h. anubis*) of east Africa, these baboons live in relatively large, multimale, multifemale groups, with female philopatry and dominance relationships in both sexes. In contrast to its east African cousins, however, the chacma baboon exhibits comparatively high rates of infanticide (Palombit 2003). Infanticide is the primary source of mortality for infants, and accounts for at least 38% of infant mortality, though this rate may be as high as 75%

in some years (Cheney et al. 2004). The patterning of infanticide in this population is more consistent with the sexual selection hypothesis than with alternative hypotheses (Palombit et al. 2000). Infanticide is generally committed by males that have recently immigrated into a group and attained alpha status. The relatively short tenure of alpha males (approximately 7 months, on average) combined with their apparently greater monopolization of matings (Bulger 1993) creates conditions that enhance the potential benefits of infanticide. In other words, a new alpha male is confronted with a short period of relatively exclusive sexual access to females. Conversely, since loss of an infant significantly accelerates resumption of fertile cycling in females, lactating mothers are confronted with a significant threat of infanticide.

Unsurprisingly, lactating females exhibit conspicuous and aroused aversion to newly immigrated alpha males, including continual retrieval of infants, screaming, and tail-up displays (Busse 1984). They almost always establish a “friendship” with an unrelated, adult male shortly after parturition (Busse 1981; Palombit et al. 1997). Friendships can be unambiguously differentiated from a female’s relationships with other males in the group on the basis of spatial association, grooming, infant handling, and vocal interaction (reviewed by Palombit 2009). Ad libitum evidence suggests that friendship status increases a male’s defense of infants during potentially (or actual) infanticidal attacks. Although several males may rush to the scene of such attacks, it is primarily the male friend of the infant’s mother who provides direct, apparently costly forms of defense, such as fighting or threatening the alpha male, or carrying the infant. Experimental playback experiments further showed that male friends were more likely to respond to their female friends’ screams than to the screams of other females, and females’ screams were more likely to provoke responses from their male friends than from other males (Palombit et al. 1997). These experiments also revealed that the solicitude of male friends was tied closely to the presence of infants: playback of female screams shortly after infants died elicited similarly weak responses from all males, regardless of their friendship status. Alternative benefits of friendships to females, such as protection from harassment from higher-ranking females, lack empirical support (Palombit 2009).

Since these original observations, a series of hormonal studies in this population have further supported the antiinfanticide function of heterosexual friendships. Following the immigration of a new male, glucocorticoid levels rise in females generally, but remain high over subsequent weeks only among anestrus females, not among cycling females (Beehner et al. 2005; Wittig et al. 2008). This is a striking difference because cycling females are the primary targets of the protracted, aggressive chasing that seems to facilitate a new male’s rise to alpha status (Kitchen et al. 2009). Thus, hormonal patterns suggest that it is females at risk of infanticide (not simply of aggression) from the new male who experience greater stress upon his arrival in the group. This is further substantiated by *additional* increases in glucocorticoids among lactating females when a new alpha actually commits an infanticide (Engh et al. 2006) or among the (few) lactating females who lack male friends at the time of male immigration (Beehner et al. 2005).

A final indication of the potential importance of friendships is that females compete with one another for them (Palombit et al. 2001). This is reflected partly by the positive correlation between the dominance ranks of male and female friends, and partly by observations of high-ranking females displacing subordinate rivals from friendship with a particular male. Competition among females for males is relatively rare in mammals (Berglund et al. 1993; Andersson 1994), and in this case, it suggests that males provide a service with important fitness consequences for females. It is not immediately obvious why male protection is not shareable among multiple lactating females, but since *friendship* status appears so crucial, females may compete for social access to males in order to develop this relationship.

Sexual conflict hypotheses for male–female bonding are potentially relevant to understanding human pair-bonding, although space precludes a thorough treatment of this question here. Early models argued that a durable pairbond between the sexes was part of an adaptive suite of traits including reproductive monogamy and a division of labor between females and provisioning males (Murdock 1949; Washburn and Lancaster 1968; Lovejoy 1981). An alternative hypothesis emphasizes the importance of male protection of females from sexual conflict in the form of sexual coercion and/or infanticide (Betzig 1992; Smuts 1992; Mesnick 1997; Hrdy 1999; Hawkes 2004). A recent cross-cultural analysis rejected the male protection hypotheses partly because pairbond stability (overall divorce rates in a society) was uncorrelated with general male aggressiveness (overall rates of male homicides and assaults) (Quinlan and Quinlan 2007). However, this conclusion is limited in the same way that the lack of a correlation between overall male aggressiveness and mating success in chimpanzees may overlook the fact that sexual coercion significantly increases a male’s mating success with the *particular* females he targets (see above). Thus, the hypothesis must be tested with human data addressing *specifically* how risk of sexual coercion or infanticide to individual women varies with the nature of their pair bonds. Since male partners are themselves sometimes a source of sexual coercion to women (Rodseth and Novak 2009), these analyses must differentiate between the costs of pair-bonding with men and the protective benefits of pair bonds from other men. The variety of current evidence suggests the possibility that the different selective pressures proposed may each promote pair-bonding under different conditions (Quinlan 2008). This proposition merits greater scrutiny.

3.8 Conclusions and Future Directions

Sexual conflict is inevitable and ubiquitous: the question is not whether it occurs, but how and when, and to what degree sexually antagonistic coevolution has acted, compared with other mechanisms of sexual selection (Hosken and Snook 2005: S1, Andersson and Simmons 2006). Sexual conflict theory situates explanations in the “arms race” perspective previously reserved for more conventional coevolutionary

adversaries, such as predators and prey (Dawkins and Krebs 1979). The Red Queen hypothesis, that any gain in fitness by one unit of evolution is balanced by equivalent losses in fitness by others (van Valen 1973), may provide the most appropriate framework for analyzing reproductive strategies as a zero-sum game between opposing males and females (Chapman and Partridge 1996; Rice and Holland 1997). This does not mean, however, that conflict universally characterizes the *phenotypic* expression of male and female interaction. Affiliation and intersexual cooperation may be one outcome of this coevolutionary conflict, as suggested for chacma baboon friendships. Indeed, the chacma baboon and chimpanzee together highlight the view of universals as process, rather than as pattern. Current evidence suggests that sexually selected infanticide has generated two distinct modes of female counterstrategy in these species: promiscuity and association with males. The patterns are different, but the underlying process that generates the patterns is the same: sexual conflict. This chapter has focused mostly on sexual conflict over mating, but it may also occur at the level of sex chromosomes, gamete interaction, parental investment, group size and composition, and group dynamics (Table 3.1).

Sexual coercion via intimidation/punishment is likely to be a common, if not universal feature of life among animals that live gregariously and modify their behavior through learning (Clutton-Brock and Parker 1995). The attention following the publication of the Smuts and Smuts (1993) model has enlarged the data base for male mating aggression to females. Somewhat surprisingly, however, relatively few studies have rigorously tested the full set of constituent predictions (but see Muller and Wrangham 2009) or differentiated analytically between sexual harassment and intimidation. Costs to females are often an assumed rather than measured consequence of overt aggression, or are assessed qualitatively (e.g., as an “injury”). A key goal for future studies is quantitative measurement of these costs (as Muller et al. [2009] do). These data will help address some other questions: do females do worse reproductively when mating with more coercive or persistent males, as predicted by theory? The hypothesis that females may derive benefits from coercion also merits greater study. Likewise, the costs of coercion to males are virtually ignored, but may be significant. For example, the seminal fluids of bushcrickets inhibit receptivity of females to further mating in a manner similar to *D. melanogaster*, but males that deliver greater quantities of these fluids *also* experience longer sexual refractory periods themselves (Vahed 2007). Information on costs to males, combined with data addressing covariation in male coercion and fitness, will help to clarify the trade-offs of coercion or manipulation of females versus alternative mating strategies. Most primate studies of sexual conflict have focused on sexual coercion, but male manipulation in the form of antagonistic seduction, and concomitant females resistance (Holland and Rice 1999) merits more attention.

The life history of primates, as well as the practical constraints on an experimental study of them, significantly limit the kinds of data that can be collected. Nevertheless, there are compelling reasons to study sexual conflict in primates. Until fairly recently, much of the research on sexual conflict was conducted on (invertebrate) taxa that conform more or less to the Bateman (1948) principle that

males are selected to mate and females not (Partridge and Hurst, 1998, Tregenza et al. 2006). Our understanding of the full significance of sexual conflict will be improved by greater study of systems violating this assumption, i.e., taxa in which remating is potentially beneficial to females. Additionally, as Clutton-Brock and Parker (1995) emphasize, models of sexual conflict have generally focused on relatively simple social contexts. The study of highly social species promises to reveal important and subtle influences of social relationships on the economic trade-offs of sexual coercion and resistance. In spite of the methodological difficulties they pose, primates are excellent subjects to achieve all of these goals.

In summary, conflict among genes is “*a universal feature of life*” (Burt and Trivers 2006, p 3). This is true not only for genes within a genome, but also for genes residing in the genomes of the interacting entities we call “male” and “female.”

Acknowledgments I am extremely grateful to Peter Kappeler and Joan Silk for their generous cooperation and advice in the preparation of the manuscript. Field research was funded by NSF (BCS-0117213), the Leakey Foundation, the Wenner-Gren Foundation and the Center for Human Evolutionary Studies (Rutgers University).

References

- Aaron RI (1965) Wittgenstein’s theory of universals. *Mind* 74:249–251
- Agoramoorthy G, Mohnot SM, Sommer V, Srivastava A (1988) Abortions in free-ranging hanuman langurs (*Presbytis entellus*) - a male induced strategy? *Hum Evol* 3:297–308
- Altmann J, Altmann SA, Hausfater G (1978) Primate infant’s effects on mother’s future reproduction. *Science* 201:1028–1029
- Andersson M (1994) *Sexual selection*. Princeton University Press, Princeton, NJ
- Andersson M, Simmons LW (2006) Sexual selection and mate choice. *Trends Ecol Evol* 21:296–302
- Arlet ME, Molleman F, Chapman CA (2008) Mating tactics in male grey-cheeked mangabeys (*Lophocebus albigena*). *Ethology* 114:851–862
- Arnqvist G (2004) Sexual conflict and sexual selection: lost in the chase. *Evolution* 58:1383–1388
- Arnqvist G, Nilsson T (2000) The evolution of polyandry: multiple mating and female fitness in insects. *Anim Behav* 60:145–164
- Arnqvist G, Rowe L (2005) *Sexual conflict*. Princeton University Press, Princeton, NJ
- Atmoko S, van Hooft JARAM (2004) Alternative male reproductive strategies: male bimaturism in orangutans. In: Kappeler PM, van Schaik CP (eds) *Sexual selection in primates: new and comparative perspectives*. Cambridge University Press, Cambridge, pp 196–207
- Baker RR, Bellis MA (1995) *Human sperm competition: copulation, masturbation and infidelity*. Chapman & Hall, New York
- Bartlett TQ, Sussman RW, Cheverud JM (1993) Infant killing in primates: a review of observed cases with specific reference to the sexual selection hypothesis. *Am Anthropol* 95:958–990
- Bateman AJ (1948) Intrasexual selection in *Drosophila*. *Heredity* 2:349–368
- Bearder SK, Honess PE, Bayes M, Ambrose L, Anderson M (1996) Assessing *Galago* diversity – a call for help. *Afr Primates* 2:11–15
- Beehner JC, Bergman TJ, Cheney DL, Seyfarth RM, Whitten PL (2005) The effect of new alpha males on female stress in free-ranging baboons. *Anim Behav* 69:1211–1221

- Bercovitch FB, Sladky KK, Roy MM, Goy RW (1987) Intersexual aggression and male sexual activity in captive rhesus macaques. *Aggress Behav* 13:347–358
- Berger J (1983) Induced abortion and social factors in wild horses. *Nature* 303:59–61
- Betglund A, Magnhagen C, Bisazza A, König B, Huntingford F (1993) Female-female competition over reproduction. *Behav Ecol* 4:184–187
- Bertin A, Fairbairn DJ (2005) One tool, many uses: precopulatory sexual selection on genital morphology in *Aquarius remigis*. *J Evol Biol* 18:949–961
- Betzig LL (1992) Of human bonding: cooperation or exploitation? *Soc Sci Inform* 31:611–642
- Birkhead TR, Møller AP (1998) Sperm competition and sexual selection. Academic Press, New York
- Blanckenhorn WU, Hosken DJ, Martin OY, Reim C, Teuschl Y, Ward PI (2002) The costs of copulating in the dung fly *Sepsis cynipsea*. *Behav Ecol* 13:353–358
- Blyth JE, Gilburn AS (2006) Extreme promiscuity in a mating system dominated by sexual conflict. *J Insect Behav* 19:447–455
- Boehm C (1994) Pacifying interventions at Arnhem Zoo and Gombe. In: Wrangham RW, McGrew WC, de Waal FBM, Heltne PG (eds) Chimpanzee cultures. Harvard University Press, Cambridge, MA, pp 211–226
- Boinski S (2000) Social manipulation within and between troops mediates primate group movement. In: Boinski S, Garber PA (eds) On the move: how and why animals travel in groups. University of Chicago Press, Chicago, pp 421–468
- Borries C, Launhardt K, Epplen C, Epplen JT, Winkler P (1999) DNA analyses support the hypothesis that infanticide is adaptive in langur monkeys. *Proc Roy Soc Lond B* 266:901–904
- Bowcock H, Brown GP, Shine R (2009) Beastly bondage: the costs of amplexus in cane toads (*Bufo marinus*). *Copeia* 1:29–36
- Boyd R, Silk JB (2006) How humans evolved, 4th edn. WW Norton, New York
- Brockman DK (1999) Reproductive behavior of female *Propithecus verreauxi* at Beza Mahafaly, Madagascar. *Int J Primatol* 20:375–398
- Bulger JB (1993) Dominance rank and access to estrous females in male savanna baboons. *Behaviour* 127:67–103
- Burt A, Trivers RL (2006) Genes in conflict: the biology of selfish genetic elements. Belknap Press, Cambridge, MA
- Busse CD (1981) Infanticide and parental care by male chacma baboons, *Papio ursinus*. PhD Dissertation, Davis, University of California
- Busse CD (1984) Tail raising by baboon mothers toward immigrant males. *Am J Phys Anthropol* 64:255–262
- Carpenter CR (1942) Sexual behavior of free-ranging rhesus monkeys (*Macaca mulatta*). I. Specimens, procedures and behavioral characteristics of estrous. *J Comp Psychol* 33:113–142
- Chapman T, Partridge L (1996) Sexual conflict as fuel for evolution. *Nature* 381:189–190
- Chapman T, Liddle LF, Kalb JM, Wolfner MF, Partridge L (1995) Cost of mating in *Drosophila melanogaster* females is mediated by male accessory gland products. *Nature* 373:241–244
- Chapman T, Arnqvist G, Bangham J, Rowe L (2003) Sexual conflict. *Trends Ecol Evol* 18:41–47
- Chen PS (1984) The functional morphology and biochemistry of insect male accessory glands and their secretions. *Annu Rev Biochem* 29:233–255
- Cheney DL, Seyfarth RM, Fischer J, Beehner J, Bergman T, Johnson SE, Kitchen DM, Palombit RA, Rendall D, Silk JB (2004) Factors affecting reproduction and mortality among baboons in the Okavango Delta, Botswana. *Int J Primatol* 25:401–428
- Chism J, Rogers W (1997) Male competition, mating success and female choice in a seasonally breeding primate (*Erythrocebus patas*). *Ethology* 103:109–126
- Clark AG, Aguadé M, Prout T, Harshman LG, Langley CH (1995) Variation in sperm displacement and its association with accessory gland protein loci in *Drosophila melanogaster*. *Genetics* 139:189–201

- Clutton-Brock TH, Harvey PH (1976) Evolutionary rules and primate societies. In: Bateson PPG, Hinde RA (eds) *Growing points in ethology*. Cambridge University Press, Cambridge, pp 195–237
- Clutton-Brock TH, Parker GA (1995) Sexual coercion in animal societies. *Anim Behav* 49:1345–1365
- Colmenares F, Zaragoza F, Hernández-Lloreaga MV (2002) Grooming and coercion in one-male units of hamadryas baboons: market forces or relationships constraints? *Behaviour* 139:1525–1553
- Cook PA, Wedell N (1999) Non-fertile sperm delay female remating. *Nature* 397:486
- Cordero C, Eberhard WG (2003) Female choice of sexually antagonistic male adaptations: a critical review of some current research. *J Evol Biol* 16:1–6
- Cox RM, Calsbeek R (2009) Sexually antagonistic selection, sexual dimorphism, and the resolution of intralocus sexual conflict. *Am Nat* 173:176–187
- Crudgington HS, Siva-Jothy MT (2000) Genital damage, kicking and early death. *Nature* 407:855–856
- Dadda M, Pilastro A, Bisazza A (2005) Male sexual harassment and female schooling behaviour in the eastern mosquitofish. *Anim Behav* 70:463–471
- Daly M (1978) The cost of mating. *Am Nat* 112:771–774
- Darwin C (1871) *The descent of man, and selection in relation to sex*. Murray, London
- Dawkins R, Krebs JR (1979) Arms races between and within species. *Proc Roy Soc Lond B* 205:489–511
- de Waal FBM (2005) A century of getting to know the chimpanzee. *Nature* 437:56–59
- Dixon AF (1989) Sexual selection, genital morphology, and copulatory behavior in male galagos. *Int J Primatol* 10:47–55
- Dixon AF (1998) *Primate sexuality: comparative studies of the prosimians, monkeys, apes and human beings*. Oxford University Press, Oxford
- Dixon AF, Anderson MJ (2002) Sexual selection, seminal coagulation and copulatory plug formation in primates. *Folia Primatol* 73:63–69
- Dixon AF, Mundy NI (1994) Sexual behavior, sexual swelling, and penile evolution in chimpanzees (*Pan troglodytes*). *Arch Sex Behav* 23:267–280
- Dolhinow P (1977) Normal monkeys? *Am Sci* 65:266
- Ebensperger LA (1998) Strategies and counterstrategies to infanticide in mammals. *Biol Rev Camb Philos Soc* 73:321–346
- Eberhard WG (1990) Animal genitalia and female choice. *Am Sci* 78:134–141
- Eberhard WG (1996) *Female control: sexual selection by cryptic female choice*. Princeton University Press, Princeton, NJ
- Eberhard WG (2005) Evolutionary conflicts of interest: are female sexual decisions different? *Am Nat* 165:S19–S25
- Eberle M, Kappeler PM (2004a) Selected polyandry: female choice and inter-sexual conflict in a small nocturnal solitary primate (*Microcebus murinus*). *Behav Ecol Sociobiol* 57:91–100
- Eberle M, Kappeler PM (2004b) Sex in the dark: determinants and consequences of mixed male mating tactics in *Microcebus murinus*, a small solitary nocturnal primate. *Behav Ecol Sociobiol* 57:77–90
- Emery Thompson M (2009) Human rape: revising evolutionary perspectives. In: Muller MN, Wrangham RW (eds) *Sexual coercion in primates and humans: an evolutionary perspective on male aggression against females*. Harvard University Press, Cambridge, Massachusetts, pp 346–374
- Engh AL, Beehner JC, Bergman TJ, Whitten PL, Hoffmeier RR, Seyfarth RM, Cheney DL (2006) Female hierarchy instability, male immigration and infanticide increase glucocorticoid levels in female chacma baboons. *Anim Behav* 71:1227–1237
- Enomoto T (1981) Male aggression and the sexual behavior of Japanese monkeys. *Primates* 22:15–23

- Erez T, Schneider JM, Lubin Y (2005) Is male cohabitation costly for females of the spider *Stegodyphus lineatus* (Eresidae)? *Ethology* 111:693–704
- Festa-Bianchet M (1987) Bighorn sheep, climbing accidents, and implication for mating strategy. *Mammalia* 51:618–620
- Fisher RA (1930) *The genetical theory of natural selection*. Oxford University Press, Oxford
- Foerg R (1982) Reproductive behavior in *Varecia variegata*. *Folia Primatol* 38:108–121
- Foerster K, Coulson T, Sheldon BC, Pemberton JM, Clutton-Brock TH, Kruuk LEB (2007) Sexually antagonistic genetic variation for fitness in red deer. *Nature* 447:1107–1110
- Fox EA (2002) Female tactics to reduce sexual harassment in the Sumatran orangutan (*Pongo pygmaeus abelli*). *Behav Ecol Sociobiol* 52:93–101
- Fox R (1989) *The search for society: quest for a biosocial science and morality*. Rutgers University Press, New Brunswick, NJ
- Fuentes A (2002) Patterns and trends in primate pair bonds. *Int J Primatol* 23:953–978
- Gems D, Riddle DL (1996) Longevity in *Caenorhabditis elegans* reduced by mating but not gamete production. *Nature* 379:723–725
- Gibson KN, Vick LG, Palma AC, Carrasco FM, Taub D, Ramos-Fernández G (2008) Intra-community infanticide and forced copulation in spider monkeys: a multi-site comparison between Cocha Cashu, Peru and Punta Laguna, Mexico. *Am J Primatol* 70:485–489
- Goetz AT, Shackelford TK, Camilleri JA (2008) Proximate and ultimate explanations are required for a comprehensive understanding of partner rape. *Aggress Violent Behav* 13:119–123
- Gomendio M, Harcourt AH, Roldán ERS (1998) Sperm competition in mammals. In: Birkhead TR, Møller AP (eds) *Sperm competition and sexual selection*. Academic Press, San Diego, pp 667–756
- Goodall J (1971) *In the shadow of man*. Houghton Mifflin, Boston
- Goodall J (1986) *The chimpanzees of Gombe: patterns of behavior*. Belknap Press, Cambridge, MA
- Gowaty PA (1997) Sexual dialectics, sexual selection, and variation in reproductive behavior. In: Gowaty PA (ed) *Feminism and evolutionary biology: boundaries, intersections, and frontiers*. Chapman & Hall, New York, pp 351–384
- Gowaty PA, Buschhaus N (1998) Ultimate causation of aggressive and forced copulation in birds: female resistance, the CODE hypothesis, and social monogamy. *Am Zool* 38:207–225
- Gruenbaum E (2001) *The female circumcision controversy: an anthropological perspective*. University of Pennsylvania Press, Philadelphia
- Gursky SL (2002) Determinants of gregariousness in the spectral tarsier (Prosimian: *Tarsius spectrum*). *J Zool Lond* 256:401–410
- Harcourt AH, Gardiner J (1994) Sexual selection and genital anatomy of male primates. *Proc Roy Soc Lond B* 255:47–53
- Harcourt AH, Greenberg J (2001) Do gorilla females join males to avoid infanticide? A quantitative model. *Anim Behav* 62:905–915
- Harcourt AH, Stewart KJ (2007) *Gorilla society: conflict, compromise, and cooperation between the sexes*. University of Chicago Press, Chicago
- Harshman LG, Prout T (1994) Sperm displacement without sperm transfer in *Drosophila melanogaster*. *Evolution* 48:758–766
- Hausfater G, Hrdy SB (1984) *Infanticide: comparative and evolutionary perspectives*. Aldine, New York
- Hawkes K (2004) Mating, parenting, and the evolution of human pair bonds. In: Chapais B, Berman CM (eds) *Kinship and behavior in primates*. Oxford University Press, Oxford, pp 443–473
- Head ML, Brooks R (2006) Sexual coercion and the opportunity for sexual selection in guppies. *Anim Behav* 71:515–522
- Henzi SP, Lycett JE, Weingrill T (1998) Mate guarding and risk assessment by male mountain baboons during inter-troop encounters. *Anim Behav* 55:1421–1428

- Heubel KU, Plath M (2008) Influence of male harassment and female competition on female feeding behaviour in a sexual-asexual mating complex of mollies (*Poecilia mexicana*, *P. formosa*). *Behav Ecol Sociobiol* 62:1689–1699
- Hiruki LM, Stirling I, Gilmartin WG, Johanos TC, Becker BL (1993) Significance of wounding to female reproductive success in Hawaiian monk seals (*Monachus schauinslandi*) at Laysan Island. *Can J Zool* 71:469–474
- Holland B, Rice WR (1999) Experimental removal of sexual selection reverses intersexual antagonistic coevolution and removes a reproductive load. *Proc Natl Acad Sci USA* 96:5083–5088
- Holman L, Snook RR (2006) Spermicide, cryptic female choice and the evolution of sperm form and function. *J Evol Biol* 19:1660–1670
- Hosken DJ, Snook RR (2005) How important is sexual conflict? *Am Nat* 165:S1–S4
- Hosken DJ, Martin OY, Born J, Huber F (2003) Sexual conflict in *Sepsis cynipsea*: female reluctance, fertility and mate choice. *J Evol Biol* 16:485–490
- Hotzy C, Arnqvist G (2009) Sperm competition favors harmful males in seed beetles. *Curr Biol* 19:404–407
- Howard RD (1980) Mating behavior and mating success in woodfrogs, *Rana sylvatica*. *Anim Behav* 28:705–716
- Hrdy SB (1974) Male-male competition and infanticide among the langurs (*Presbytis entellus*) of Abu, Rajasthan. *Folia Primatol* 22:19–58
- Hrdy SB (1979) Infanticide among animals: a review, classification, and examination of the implications for reproductive strategies of females. *Ethol Sociobiol* 1:13–40
- Hrdy SB (1999) *Mother nature: a history of mothers, infants, and natural selection*. Pantheon Books, New York
- Hrdy SB, Whitten PL (1987) Patterning of sexual activity. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT (eds) *Primate societies*. University of Chicago Press, Chicago, pp 370–384
- Huffman MA (1987) Consort intrusion and female mate choice in Japanese macaques, *Macaca fuscata*. *Ethology* 75:221–234
- Itani J (1982) Intraspecific killing among non-human primates. *J Soc Biol Struct* 5:361–368
- Jack KM, Pavelka MSM (1997) The behavior of peripheral males during the mating season in *Macaca fuscata*. *Primates* 38:369–377
- Johnstone RA, Keller L (2000) How males can gain by harming their mates: sexual conflict, seminal toxins, and the cost of mating. *Am Nat* 156:368–377
- Keverne EB (2001) Genomic imprinting, maternal care, and brain evolution. *Horm Behav* 40:146–155
- Kirkpatrick M, Barton NH (1997) The strength of indirect selection on female mating preferences. *Proc Natl Acad Sci USA* 94:1282–1286
- Kitchen DM, Beehner JC, Bergman TJ, Cheney DL, Crockford C, Engh AL, Fischer J, Seyfarth RM, Wittig RM (2009) The causes and consequences of male aggression directed at female chacma baboons. In: Muller MN, Wrangham RW (eds) *Sexual coercion in primates and humans: an evolutionary perspective on male aggression against females*. Harvard University Press, Cambridge, Massachusetts, pp 129–156
- Knott C (2009) Orangutans: sexual coercion without sexual violence. In: Muller MN, Wrangham RW (eds) *Sexual coercion in primates and humans: an evolutionary perspective on male aggression against females*. Harvard University Press, Cambridge, Massachusetts, pp 81–111
- Kuester J, Paul A, Arnemann J (1994) Kinship, familiarity and mating avoidance in Barbary macaques, *Macaca sylvanus*. *Anim Behav* 48:1183–1194
- Lande R (1987) Genetic correlations between the sexes in the evolution of sexual dimorphism and mating preferences. In: Bradbury JW, Andersson MB (eds) *Sexual selection: testing the alternatives*. John Wiley & Sons, London, pp 83–94
- Lessells CM (1999) Sexual conflict in animals. In: Keller L (ed) *Levels of selection in evolution*. Princeton University Press, Princeton, NJ, pp 75–99

- Lessells CM (2005) Why are males bad for females? Models for the evolution of damaging male mating behavior. *Am Nat* 165:S46–S63
- Levitan DR (2008) Gamete traits influence the variance in reproductive success, the intensity of sexual selection, and the outcome of sexual conflict among congeneric sea urchins. *Evolution* 62:1305–1316
- Lindenfors P (2002) Sexually antagonistic selection on primate size. *J Evol Biol* 15:595–607
- Lovejoy CO (1981) The origin of man. *Science* 211:341–350
- Low BS (2005) Women's lives there, here, then, now: a review of women's ecological and demographic constraints cross-culturally. *Evol Hum Behav* 26:64–87
- Lung O, Tram U, Finnerty CM, Eipper-Mains MA, Kalb JM, Wolfner MF (2002) The *Drosophila melanogaster* seminal fluid protein Acp62F is a protease inhibitor that is toxic upon ectopic expression. *Genetics* 160:211–224
- Magellan K, Magurran AE (2006) Habitat use mediates the conflict of interest between the sexes. *Anim Behav* 72:75–81
- Maggioncalda AN, Sapolsky RM, Czekala NM (1999) Reproductive hormone profiles in captive male orangutans: implications for understanding developmental arrest. *Am J Phys Anthropol* 109:19–32
- Magurran AE, Seghers BH (1994) A cost of sexual harassment in the guppy, *Poecilia reticulata*. *Proc Roy Soc Lond B* 258:89–92
- Manson JH (1997) Primate consortships: a critical review. *Curr Anthropol* 38:353–374
- Martin-Coello J, Benavent-Corai J, Roldan ERS, Gomendio M (2009) Sperm competition promotes asymmetries in reproductive barriers between closely related species. *Evolution* 63:613–623
- Matsubara M, Sprague DS (2004) Mating tactics in response to costs incurred by mating with multiple males in wild Japanese macaques. *Int J Primatol* 25:901–917
- Matthews MK Jr, Adler NT (1978) Systematic interrelationship of mating, vaginal plug position, and sperm transport in the rat. *Physiol Behav* 20:303–309
- Mesnick SL (1997) Sexual alliances: evidence and evolutionary implications. In: Gowaty PA (ed) *Feminism and evolutionary biology: boundaries, intersections, and frontiers*. Chapman & Hall, New York, pp 207–260
- Mesnick SL, le Boeuf BJ (1991) Sexual behavior of male northern elephant seals. II. Female responses to potentially injurious encounters. *Behaviour* 117:262–280
- Miller EH, Ponce de León A, DeLong RL (1996) Violent interspecific sexual behavior by male sea lions (Otariidae): evolutionary and phylogenetic implications. *Mar Mamm Sci* 12:468–476
- Mitani JC (1985) Sexual selection and adult male orangutan long calls. *Anim Behav* 33:272–283
- Moore IT, Jessop TS (2003) Stress, reproduction, and adrenocortical modulation in amphibians and reptiles. *Horm Behav* 43:39–47
- Morland HS (1993) Reproductive activity of ruffed lemurs (*Varecia variegata variegata*) in a Madagascar rain forest. *Am J Phys Anthropol* 91:71–82
- Morrow EH, Arnqvist G, Pitnick S (2003) Adaptation versus pleiotropy: why do males harm their mates? *Behav Ecol* 14:802–806
- Mühlhäuser C, Blanckenhorn WU (2002) The costs of avoiding matings in the dung fly *Sepsis cynipsea*. *Behav Ecol* 13:359–365
- Muller MN, Wrangham RW (2009) Sexual coercion in primates and humans: an evolutionary perspective on male aggression against females. Harvard University Press, Cambridge, Massachusetts
- Muller MN, Kahlenberg SM, Thompson ME, Wrangham RW (2007) Male coercion and the costs of promiscuous mating for female chimpanzees. *Proc Roy Soc Lond B* 274:1009–1014
- Muller MN, Kahlenberg SM, Wrangham RW (2009) Male aggression against females and sexual coercion in chimpanzees. In: Muller MN, Wrangham RW (eds) *Sexual coercion in primates and humans: an evolutionary perspective on male aggression against females*. Harvard University Press, Cambridge Massachusetts, pp 184–217
- Murdock GP (1949) *Social structure*. Macmillan, New York

- Palombit RA (1999) Infanticide and the evolution of pair bonds in nonhuman primates. *Evol Anthropol* 7:117–129
- Palombit RA (2000) Infanticide and the evolution of male-female bonds in animals. In: van Schaik CP, Janson CH (eds) *Infanticide by males and its implications*. Cambridge University Press, Cambridge, pp 239–268
- Palombit RA (2003) Male infanticide in wild savanna baboons: adaptive significance and intra-specific variation. In: Jones CB (ed) *Sexual selection and reproductive competition in primates: new perspectives and directions*. American Society of Primatologists, New York, pp 367–412
- Palombit RA. 'Friendship' with males: a female counterstrategy to infanticide in the okavango chacma baboons. In: Muller MN, Wrangham RW (eds) *Sexual coercion in primates and humans: an evolutionary perspective on male aggression against females*. Harvard University Press, Cambridge Massachusetts, pp 377–409
- Palombit RA, Seyfarth RM, Cheney DL (1997) The adaptive value of 'friendships' to female baboons: experimental and observational evidence. *Anim Behav* 54:599–614
- Palombit RA, Cheney DL, Fischer J, Johnson S, Rendall D, Seyfarth RM, Silk JB (2000) Male infanticide and defense of infants in chacma baboons. In: van Schaik CP, Janson CH (eds) *Infanticide by males and its implications*. Cambridge University Press, Cambridge, pp 123–152
- Palombit RA, Cheney DL, Seyfarth RM (2001) Female-female competition for male 'friends' in wild chacma baboons (*Papio cynocephalus ursinus*). *Anim Behav* 61:1159–1171
- Parga JA (2003) Copulatory plug displacement evidences sperm competition in *Lemur catta*. *Int J Primatol* 24:889–899
- Parga JA, Henry AR (2008) Male aggression during mating: evidence for sexual coercion in a female dominant primate? *Am J Primatol* 70:1187–1190
- Parker GA (1970) The reproductive behaviour and the nature of sexual selection in *Scatophaga stercoraria* L. (Diptera: Scatophagidae). II. The fertilization rate and the spatial and temporal relationships of each sex around the site of mating and oviposition. *J Anim Ecol* 39:205–228
- Parker GA (1979) Sexual selection and sexual conflict. In: Blum MS, Blum NA (eds) *Sexual selection and reproductive competition in insects*. Academic Press, New York, pp 123–166
- Parker GA (2006) Sexual conflict over mating and fertilization: an overview. *Phil Trans Roy Soc B* 361:235–259
- Partridge L, Hurst LD (1998) Sex and conflict. *Science* 281:2003–2008
- Pereira ME (1983) Abortion following the immigration of an adult male baboon (*Papio cynocephalus*). *Am J Primatol* 4:93–98
- Perkin AW (2007) Comparative penile morphology of East African galagos of the genus *Galagoides* (family Galagidae): implications for taxonomy. *Am J Primatol* 69:16–26
- Perry S (1997) Male-female social relationships in wild white-faced capuchins (*Cebus capucinus*). *Behaviour* 134:477–510
- Pilastro A, Benetton S, Bisazza A (2003) Female aggregation and male competition reduce costs of sexual harassment in mosquitofish *Gambusia holbrooki*. *Anim Behav* 65:1161–1167
- Pizzari T, Snook RR (2003) Sexual conflict and sexual selection: chasing away paradigm shifts. *Evolution* 57:1223–1236
- Pizzari T, Snook RR (2004) Sexual conflict and sexual selection: measuring antagonistic coevolution. *Evolution* 58:1389–1393
- Pluháček J, Bartoš L (2000) Male infanticide in captive plains zebra, *Equus burchelli*. *Anim Behav* 59:689–694
- Pradhan GR, van Schaik CP (2008) Infanticide-driven intersexual conflict over matings in primates and its effects on social organization. *Behaviour* 145:251–275
- Pratt HL Jr (1979) Reproduction in the blue shark, *Prionace glauca*. *Fish Bull* 77:445–470
- Quinlan RJ (2008) Human pair-bonds: evolutionary functions, ecological variation, and adaptive development. *Evol Anthropol* 17:227–238
- Quinlan RJ, Quinlan MB (2007) Evolutionary ecology of human pair-bonds: cross-cultural tests of alternative hypotheses. *Cross-Cultural Res* 41:149–169

- Ravi Ram K, Wolfner MF (2007) Seminal influences: *Drosophila* Acps and the molecular interplay between males and females during reproduction. *Integr Comp Biol* 47:427–445
- Réale D, Bousset P, Chapuis J-L (1996) Female-biased mortality induced by male sexual harassment in a feral sheep population. *Can J Zool* 74:1812–1818
- Reason LL (2004) The behavioral ecology of female genital cutting in northern Ghana. *Res Econ Anthropol* 23:175–202
- Reed C, O'Brien TG, Kinnaird MF (1997) Male social behavior and dominance hierarchy in the Sulawesi crested black macaque (*Macaca nigra*). *Int J Primatol* 18:247–260
- Reeder DM (2003) The potential for cryptic female choice in primates: behavioral, anatomical, and physiological considerations. In: Jones CB (ed) *Sexual selection and reproductive competition in primates: new perspectives and directions*. American Society of Primatologists, New York, pp 255–303
- Rice WR (1996) Sexually antagonistic male adaptation triggered by experimental arrest of female evolution. *Nature* 381:232–234
- Rice WR, Chippindale AK (2001) Intersexual ontogenetic conflict. *J Evol Biol* 14:685–693
- Rice WR, Holland B (1997) The enemies within: intergenomic conflict, interlocus contest evolution (ICE), and the intraspecific Red Queen. *Behav Ecol Sociobiol* 41:1–10
- Rice WR, Holland B, Harrison R (2005) Experimentally enforced monogamy: inadvertent selection, inbreeding, or evidence for sexually antagonistic coevolution? *Evolution* 59:682–685
- Richard AF (1992) Aggressive competition between males, female-controlled polygyny and sexual monomorphism in a Malagasy primate, *Propithecus verreauxi*. *J Hum Evol* 22:395–406
- Rodman PS, Mitani JC (1987) Orangutans: sexual dimorphism in a solitary species. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT (eds) *Primate societies*. University of Chicago Press, Chicago, pp 146–154
- Rodseth L, Novak SA (2009) The political significance of gender violence. In: Muller MN, Wrangham RW (eds) *Sexual coercion in primates and humans: an evolutionary perspective on male aggression against females*. Harvard University Press, Cambridge Massachusetts, pp 292–321
- Roulin A, Hager R (2003) Indiscriminate nursing in communal breeders: a role for genomic imprinting. *Ecol Lett* 6:165–166
- Rubenstein DI (1986) Ecology and sociality in horses and zebras. In: Rubenstein DI, Wrangham RW (eds) *Ecological aspects of social evolution*. Princeton University Press, Princeton, NJ, pp 282–302
- Sato Y, Kohama T (2007) Post-copulatory mounting behavior of the West Indian sweet-potato weevil, *Euscepes postfasciatus* (Fairmaire) (Coleoptera: Curculionidae). *Ethology* 113:183–189
- Schülke O, Kappeler PM (2001) Protection from infanticide, male resource defense, over-dispersed females and the evolution of pair-living in a nocturnal lemur, *Phaner furcifer*. *Folia Primatol* 72:182–183
- Setia TM, van Schaik CP (2007) The response of adult orang-utans to flanged male long calls: inferences about their function. *Folia Primatol* 78:215–226
- Shine R, O'Connor D, Mason RT (2000) Sexual conflict in the snake den. *Behav Ecol Sociobiol* 48:392–401
- Shine R, Phillips B, Langkilde T, Lutterschmidt DI, Wayne H, Mason RT (2004) Mechanisms and consequences of sexual conflict in garter snakes (*Thamnophis sirtalis*, Colubridae). *Behav Ecol* 15:654–660
- Shuster SM, Wade MJ (2003) *Mating systems and strategies*. Princeton University Press, Princeton, NJ
- Sicotte P (2002) The function of male aggressive displays towards females in mountain gorillas. *Primates* 43:277–289
- Simmons LW, Siva-Jothy MT (1998) Sperm competition in insects: mechanisms and the potential for selection. In: Birkhead TR, Møller AP (eds) *Sperm competition and sexual selection*. Academic Press, San Diego, pp 341–434

- Siva-Jothy MT (2006) Trauma, disease and collateral damage: conflict in cicicids. *Phil Trans Roy Soc B* 361:269–275
- Smith CC, Sargent RC (2006) Female fitness declines with increasing female density but not male harassment in the western mosquitofish, *Gambusia affinis*. *Anim Behav* 71:401–407
- Smuts BB (1992) Male aggression against women: an evolutionary perspective. *Hum Nat* 3:1–44
- Smuts BB, Smuts RW (1993) Male aggression and sexual coercion of females in nonhuman primates and other mammals: evidence and theoretical implications. *Adv Stud Behav* 22:1–63
- Soltis J (1999) Measuring male-female relationships during the mating season in wild Japanese macaques (*Macaca fuscata yakui*). *Primates* 40:453–467
- Soltis J, Mitsunaga F, Shimizu K, Yanagihara Y, Nozaki M (1997) Sexual selection in Japanese macaques. I. Female mate choice or male sexual coercion? *Anim Behav* 54:725–736
- Soltis J, Thomsen R, Matusabayshi K, Takenaka O (2000) Infanticide by resident males and female counter-strategies in wild Japanese macaques (*Macaca fuscata*). *Behav Ecol Sociobiol* 48:195–202
- Soltis J, Thomsen R, Takenaka O (2001) The interaction of male and female reproductive strategies and paternity in wild Japanese macaques, *Macaca fuscata*. *Anim Behav* 62:485–494
- Sommer V (1987) Infanticide among free-ranging langurs (*Presbytis entellus*) at Jodhpur (Rajasthan/India): recent observations and a reconsideration of hypotheses. *Primates* 28:163–197
- Sommer V, Reichard U (2000) Rethinking monogamy: the gibbon case. In: Kappeler PM (ed) *Primate males: causes and consequences of variation in group composition*. Cambridge University Press, Cambridge, pp 159–168
- Stockley P (2002) Sperm competition risk and male genital anatomy: comparative evidence for reduced duration of female sexual receptivity in primates with penile spines. *Evol Ecol* 16:123–137
- Stokes EJ (2004) Within-group social relationships among females and adult males in wild western lowland gorillas (*Gorilla gorilla gorilla*). *Am J Primatol* 64:233–246
- Stumpf RM, Boesch C (2006) The efficacy of female choice in chimpanzees of the Taï Forest, Côte d'Ivoire. *Behav Ecol Sociobiol* 60:749–765
- Stumpf RM, Thompson ME, Knott CD (2008) A comparison of female mating strategies in *Pan troglodytes* and *Pongo* spp. *Int J Primatol* 29:865–884
- Swiss J, Giller JE (1993) Rape as a crime of war: a medical perspective. *J Am Med Assoc* 270:612–615
- Taylor LL, Sussman RW (1985) A preliminary study of kinship and social organization in a semi-free-ranging group of *Lemur catta*. *Int J Primatol* 6:601–614
- Thalmann U (2001) Food resource characteristics in two nocturnal lemurs with different social behavior: *Avahi occidentalis* and *Lepilemur edwardsi*. *Int J Primatol* 22:287–324
- Thornhill R, Alcock J (1983) *The evolution of insect mating systems*. Harvard University Press, Cambridge, MA
- Thornhill R, Gangestad SW (1996) The evolution of human sexuality. *Trends Ecol Evol* 11:98–102
- Thornhill R, Palmer CT (2000) *A natural history of rape: biological bases of sexual coercion*. MIT Press, Cambridge, MA
- Travis CB (2003) *Evolution, gender, and rape*. MIT Press, Cambridge, MA
- Tregenza T, Wedell N, Chapman T (2006) Sexual conflict: a new paradigm? *Phil Trans Roy Soc B* 361:229–234
- Trivers RL (1972) Parental investment and sexual selection. In: Campbell B (ed) *Sexual selection and the descent of man, 1871–1971*. Aldine, Chicago, pp 136–179
- Tutin CEG (1979) Mating patterns and reproductive strategies in a community of wild chimpanzees (*Pan troglodytes schweinfurthii*). *Behav Ecol Sociobiol* 6:29–38
- Vahed K (2007) Comparative evidence for a cost to males of manipulating females in bushcrickets. *Behav Ecol* 18:499–506

- Vahed K, Carron G (2008) Comparison of forced mating behaviour in four taxa of *Anonconotus*, the Alpine bushcricket. *J Zool Lond* 276:313–321
- Valero A, Hudson R, Luna EÁ, Macías Garcia C (2005) A cost worth paying: energetically expensive interactions with males protect females from intrasexual aggression. *Behav Ecol Sociobiol* 59:262–269
- van Schaik CP (2000a) Infanticide by male primates: the sexual selection hypothesis revisited. In: van Schaik CP, Janson CH (eds) *Infanticide by males and its implications*. Cambridge University Press, Cambridge, pp 27–60
- van Schaik CP (2000b) Vulnerability to infanticide by males: patterns among mammals. In: van Schaik CP, Janson CH (eds) *Infanticide by males and its implications*. Cambridge University Press, Cambridge, pp 61–71
- van Schaik CP, Dunbar RIM (1990) The evolution of monogamy in large primates: a new hypothesis and some crucial tests. *Behaviour* 115:30–62
- van Schaik CP, Janson CH (2000) *Infanticide by males and its implications*. Cambridge University Press, Cambridge
- van Schaik CP, Kappeler PM (1997) Infanticide risk and the evolution of male-female association in primates. *Proc Roy Soc Lond B* 264:1687–1694
- van Schaik CP, Kappeler PM (2003) The evolution of social monogamy in primates. In: Reichard UH, Boesch C (eds) *Monogamy: mating strategies and partnerships in birds, humans and other mammals*. Cambridge University Press, Cambridge, pp 59–80
- van Schaik CP, van Hooff JARAM (1996) Toward an understanding of the orangutan's social system. In: McGrew WC, Marchant LF, Nishida T (eds) *Great ape societies*. Cambridge University Press, Cambridge, pp 3–15
- van der Schoot P, van Ophemert J, Baumgarten R (1992) Copulatory stimuli in rats induce heat abbreviation through effects on genitalia, but not through effects on central nervous mechanisms supporting the steroid hormone-induced sexual responsiveness. *Behav Brain Res* 49:213–223
- van Valen L (1973) A new evolutionary law. *Evol Theory* 1:1–30
- Washburn SL, Lancaster CS (1968) The evolution of hunting. In: Lee RB, DeVore I (eds) *Man the hunter*. Aldine, Chicago, pp 293–303
- Watts DP (1997) Agonistic interventions in wild mountain gorilla groups. *Behaviour* 134:23–57
- Weingrill T (2000) Infanticide and the value of male-female relationships in mountain chacma baboons (*Papio cynocephalus ursinus*). *Behaviour* 137:337–359
- Werner M, Simmons LW (2008) The evolution of male genitalia: functional integration of genital sclerites in the dung beetle *Onthophagus taurus*. *Biol J Linn Soc* 93:257–266
- Williams GC (1966) *Adaptation and natural selection: a critique of some current evolutionary thought*. Princeton University Press, Princeton, NJ
- Wilson CG (2008) Male genital mutilation: an adaptation to sexual conflict. *Evol Hum Behav* 29:149–164
- Wittgenstein L (1953) *Philosophical investigations*. Blackwell, London
- Wittig RM, Crockford C, Lehmann J, Whitten PL, Seyfarth RM, Cheney DL (2008) Focused grooming networks and stress alleviation in wild female baboons. *Horm Behav* 54:170–177
- Wolff JO, MacDonald DW (2004) Promiscuous females protect their offspring. *Trends Ecol Evol* 19:127–134
- Wrangham RW (1979) On the evolution of ape social systems. *Soc Sci Info* 18:335–368
- Wrangham RW (1986) Ecology and social relationships in two species of chimpanzee. In: Rubenstein DI, Wrangham RW (eds) *Ecological aspects of social evolution*. Princeton University Press, Princeton, NJ, pp 352–378
- Wrangham RW, Peterson D (1996) *Demonic males: apes and the origins of human violence*. Houghton Mifflin, Boston
- Zeh JA, Zeh DW (2003) Toward a new sexual selection paradigm: polyandry, conflict and incompatibility. *Ethology* 109:929–950