
Male Aggression and Sexual Coercion of Females in Nonhuman Primates and Other Mammals: Evidence and Theoretical Implications

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I. INTRODUCTION

The single most important difference between the sexes is the difference in their investment in offspring. The general rule is this: females do all of the investing; males do none of it. (Trivers, 1985, p. 207)

Although Trivers' general rule has many exceptions, it accurately identifies the primary source of conflict between the sexes: in most sexual organisms most of the energy and time invested in offspring comes from females. From this basic fact it follows that, for males more than females, reproductive success is limited by the number of matings with fertile partners. For females more than males, on the other hand, reproductive success is limited by the time and effort required to garner and transfer energy to offspring and to protect and care for them (Bateman, 1948; Trivers, 1972). Males therefore are usually more eager than females to mate at any time with any partner who may be fertile, while females are usually more careful than males to choose mates who seem likely to provide good genes, protection, parental care, or resources in addition to gametes (Trivers, 1972; Alexander and Borgia, 1979).

Combined with female interest in mate quality, male interest in mate quantity creates a widespread conflict of interest between the sexes (Borgia, 1979; Parker, 1979; Hammerstein and Parker, 1987). The conflict is

mitigated when males court females by offering them the benefits females want from males, such as food, protection, or help in rearing young. These benefits are typically costly in terms of male time and energy, however, and males may often be able to overcome female reluctance at lower cost to themselves by using force or the threat of force, behavior that we call "sexual coercion."

Theoretical treatments (e.g., Hammerstein and Parker, 1987) indicate that sexual coercion can function as an important selective force influencing the evolution of both male and female behaviors. However, male aggression toward females, including sexual coercion, has rarely been a focus of study, and for the vast majority of animals, including most mammals, quantitative information is unavailable. These limitations severely constrain our ability to determine the evolutionary significance of sexual coercion.

This article aims to stimulate research and theorizing about sexual coercion by reviewing the relevant evidence for nonhuman primates and some other mammals in which sexual coercion is especially well documented. Two contrasting goals guide this review. On the one hand, we hope to persuade the reader that sexual coercion is an important phenomenon worthy of further study. On the other, we wish to highlight important gaps in our knowledge of sexual coercion. We have tried to balance these two goals by using limited evidence from a small number of species to generate hypotheses, while emphasizing that, to test these hypotheses, we need much better information from a larger number of species.

We begin by describing aggressive male behaviors that appear to function as sexual coercion, the costs that this male aggression imposes on females and young, and the counterstrategies that females employ to reduce these costs. The data that we review for primates and other mammals reveal extensive variation in the form and frequency of male aggression against females, and we propose several hypotheses to help account for this variation. We also consider the kinds of evidence needed to determine whether particular cases of male aggression against females function as sexual coercion. In the final section, we argue that sexual coercion has been underestimated as a significant force in social evolution, and indicate how more attention to intersexual coercion as a form of sexual selection can enhance our understanding of animal societies.

THE CONCEPT OF SEXUAL COERCION

We define sexual coercion as use by a male of force, or threat of force, that functions to increase the chances that a female will mate with him at a time when she is likely to be fertile, and to decrease the chances that

she will mate with other males, at some cost to the female. The functional consequences of male sexual coercion distinguish it from other instances of male aggression against females (e.g., in the context of feeding competition) that do not appear to involve manipulation of sexual opportunities.

Our definition of sexual coercion as a subset of aggressive male behaviors toward females that is delineated by their function means that sexual coercion is not a purely behavioral concept, but involves a combination of behavioral description and functional explanation. Sexual coercion cannot be identified by observing only the immediate behavior of the aggressor; it is also necessary to observe the subsequent behavior of the aggressor, the target, and even of other individuals. It is not an easy concept to work with, but we believe it is nevertheless useful because it accurately reflects the complexity of agonistic sexual behavior in animals. Toward the end of this article, we consider in some detail how one can test the hypothesis that particular acts of male aggression against females fit the functional definition of sexual coercion given here. We delay this discussion until later because it requires a basic understanding of the wide variety of male aggression toward females that is observed in nature. Thus, we will proceed for the moment on the assumption that sexual coercion does indeed exist, while keeping in mind the need to examine functional consequences before accepting the hypothesis that a particular aggressive act (or set of acts) actually functions as sexual coercion.

Our definition also limits sexual coercion to behavior that involves the use or the threat of force. Although males can (and do) manipulate female mating behavior to their own advantage by inflicting other kinds of costs or by withholding benefits, such a broad definition of sexual coercion would encompass so large a part of all interactions between males and females that it would prove useless.

II. MALE AGGRESSION AND SEXUAL COERCION IN NONHUMAN PRIMATES

In what follows, we concentrate on polygynous primates living in groups in which a single male monopolizes matings with two or more females, or multiple males compete for mating opportunities with multiple females. Because polygyny is typically associated with much more intense male-male competition for mates (Clutton-Brock and Harvey, 1976, 1978), these species are expected to show more male sexual coercion than species living in monogamous or polyandrous groups. Reduced sexual coercion is especially likely in monogamous and polyandrous primates, because these species invariably establish long-lasting pair bonds and defend territories

against other groups (Goldizen, 1987; Robinson *et al.*, 1987; Robbins Leighton, 1987), minimizing opportunities for contact between opposite-sex individuals other than mates. This is in contrast to the situation in many monogamous birds and in most human groups, in which, because of high mobility and/or communal living, mated individuals may frequently encounter opposite-sex individuals other than their mates (Westneat *et al.*, 1990; Rodseth *et al.*, 1991). Although, on theoretical grounds, sexual coercion is expected to be considerably less common in monogamous and polyandrous nonhuman primates, we do not imply that it is entirely absent in these species, and, indeed, the possible significance of sexual coercion of females by mates (e.g., Goldizen, 1989) or male neighbors during encounters between family groups, or by strange males when they encounter lone females, or by mates when females approach territory boundaries, deserves further attention.

We focus on information from wild primates, when it is available, because wild groups are more likely to reflect socioecological conditions that obtained during the species' evolutionary history, but we also include relevant evidence from provisioned and captive animals. Caution is necessary when such information is used to support an argument related to selection pressures in the wild. However, evidence from captive or provisioned animals can provide useful indications of behavioral potentials not typically shown in the wild, which may nevertheless reflect a species' evolved capacity to respond adaptively to novel circumstances (R. W. Smuts, 1993).

Finally, we conclude our discussion of primates with a special section on chimpanzees. We discuss chimpanzees as a separate "case study" because much more information is available on male aggression against females in this species than in any other primate, and we wish to present this information as a coherent whole.

A. FREQUENCY OF MALE AGGRESSION AGAINST FEMALES AND CONTEXTS OF OCCURRENCE

Male aggression against females is frequently mentioned in passing or briefly described in the literature on wild nonhuman primates, which suggests its widespread occurrence through the Primate order (Tracy and Crawford, 1992). However, few quantitative data are available on male aggression against female nonhuman primates. Smuts (1985) determined rates of male aggression toward anestrus (i.e., pregnant and lactating) females in a troop of wild olive baboons. During daylight hours, the average anestrus adult female was a victim of male aggression five times per week. One-quarter of these episodes involved physical attack, and

roughly 1 of every 50 attacks resulted in a serious wound. Put another way, each adult pregnant or lactating female baboon in the troop could expect to receive at least one serious wound from a male every year (Smuts, 1985). The rate at which female mountain gorillas receive aggression from the silverback male is even higher (ranging from 1 to 4.3 times per female per 12-hour day, depending on the group and time period), but, in contrast to baboons, this aggression very rarely leads to injury (Watts, 1992). In some other species, male aggression toward females occurs much less often. Among red howlers, for example, Sekulic (1983a) observed male aggression toward females at a rate of less than 0.04 times per female per day.

The contexts in which males show aggression toward females also vary widely, both within and between species. In many species, a significant proportion of male-female agonism occurs during feeding competition (e.g., olive baboons: 20% [Smuts, 1985]; mountain gorillas: 5–20% [Watts, 1992]; wedge-capped capuchins: 63% [O'Brien, 1991]; chimpanzees: about 18% [Goodall, 1986, fig. 12.3]). Smuts (1985) found that males were also aggressive toward anestrus females in a wide variety of social situations, including defense of other females and young who were affiliated with the aggressor. Mountain gorilla males and macaque males also frequently direct aggression toward females in order to break up fights between females (Kaplan, 1977; Harcourt, 1979; Bernstein and Ehardt, 1986; Oi, 1990; Watts, 1992). Smuts (1985) also observed young, high-ranking males attacking the close female associates of older, lower ranking rivals, apparently in order to provoke the older males into aggressive confrontations that they were likely to lose. Similarly, de Waal (1982) described how, during a power struggle between captive chimpanzee male allies Nikki and Luit on the one hand, and alpha male Yeroen on the other, Luit and Nikki often attacked one of Yeroen's female supporters near Yeroen, apparently to test his willingness to protect females against the rivals. These examples indicate that bonds with particular males sometimes make females vulnerable to manipulative aggression by rival males.

The examples just given highlight the fact that not all male aggression toward females functions as sexual coercion. However, quantitative data from several species show that male aggression toward females is more likely when the females are in estrus (macaques: Tokuda, 1961; Kurland, 1977; Enomoto, 1981; Fedigan, 1982; Eaton, 1984; Teas, 1984 [but see Ruehlmann *et al.*, 1988, for an exception]; savanna baboons: Hausfater, 1975; chimpanzees: Goodall, 1986; mountain gorillas: Nadler, 1989b). This widespread tendency for males to show more aggression toward potentially fertile females is consistent with the hypothesis that male aggression often functions to increase access to mates.

B. POSSIBLE EXAMPLES OF MALE SEXUAL COERCION

The primate literature contains numerous descriptions of behaviors that appear to satisfy our definition of sexual coercion. For example, male rhesus monkeys attack females caught mating or consorting with lower ranking rivals and sometimes injure them severely (Carpenter, 1942; Lindburg, 1983; Manson, 1991). Manson (1991), studying free-ranging, provisioned rhesus monkeys on Cayo Santiago, reported a significant positive relationship between the frequency with which estrous females associated with lower ranking males and the rate at which they received aggression from high-ranking males, who were apparently intent on disrupting these mating relationships. Chimpanzees, like male macaques, also tend to attack the female, rather than the lower ranking rival, if the two are caught courting (de Waal, 1982; Goodall, 1986; Hauser, 1990). Male chimpanzees (Goodall, 1986; see also Section V,A), rhesus monkeys (Carpenter, 1942; Lindburg, 1983), Japanese macaques (Enomoto, 1981), and savanna baboons (Hausfater, 1975) also use aggression to try to initiate or maintain consortships with uncooperative females.

The most dramatic examples of apparent sexual coercion come from wild orangutans, in which most copulations by subadult males (MacKinnon, 1971; Rodman, 1973; Rijksen, 1978; Galdikas, 1985; Mitani, 1985) and nearly half of all copulations by adult males (Mitani, 1985) occur after the female's fierce resistance has been overcome through violent restraint. Similar forced copulations have occasionally been observed among wild chimpanzees; in most cases these involved incestuous matings (Goodall, 1986; Nishida, 1990). In a series of studies of captive chimpanzees, lowland gorillas, and orangutans, Nadler (1982, 1988; Nadler and Miller, 1982) found that, when heterosexual pairs were housed alone together, males in all three species used aggression to force females to copulate throughout the estrous cycle. When females were given control over proximity to the male, however, copulations occurred only with female cooperation and only at mid-cycle. These observations indicate that males in all three of these species of apes will employ sexual coercion when the opportunity for females to escape is minimized.

Even when a female is not sexually receptive, male aggression may be designed to increase, or maintain, future mating access. A well-known example involves the male hamadryas baboon, who uses coercion to keep the females he gathers around him away from other males at all times. Should one of "his" females stray toward another male, the hamadryas male will instantly threaten the female with an eyebrow flash; if she fails to approach him immediately he will attack her with a neckbite (Kummer, 1968). Male use of aggression to herd mates away from strange males

during encounters with other groups has been reported for species in all major primate taxa, including prosimians (M. E. Pereira, personal communication), cercopithecines (Cheney and Seyfarth, 1977; van Noordwijk and van Schaik, 1985; Byrne *et al.*, 1987), colobines (Stanford, 1991), New World monkeys (Goldizen, 1989), and apes (Nishida and Hiraiwa-Hasegawa, 1987; Sicotte, 1989; Watts, 1991).

Our definition of sexual coercion in functional as well as behavioral terms means that it may sometimes be difficult to determine whether a particular behavior qualifies as sexual coercion. For example, in several primates, male ritualized courtship displays incorporate aggressive behaviors that are typically directed against other males (e.g., stalking in rhesus macaques: Manson, 1991; hair erection and bipedal swagger in chimpanzees: Goodall, 1986; charging in gorillas: Nadler, 1989b). The functional significance of "ritualized" aggression during courtship is not well understood; such displays could possibly function to demonstrate a male's health and vigor and might thereby facilitate female mate choice. Thus, the fact that a male directs aggression toward an estrous female does not in and of itself constitute evidence for sexual coercion (see Section VIII for further discussion of this issue).

On the other hand, male aggression that has no obvious sexual significance may nevertheless function to increase female sexual cooperation in the future and thus qualify as a form of sexual coercion. Goodall (1986), for example, notes that 83% of severe male attacks on females that occurred in no obvious context involved cycling females whose sexual swellings had not yet reached the stage of full tumescence associated with ovulation. She suggests that these attacks intimidate the female so that, when she is close to ovulation, she will respond positively to the male's mating initiatives.

Another possible example of sexual coercion involves the frequent cooperative aggression against single females by allied male spider monkeys (black-handed spider monkeys: Fedigan and Baxter, 1984; black spider monkeys: McFarland Symington, 1987). This aggression has not been observed to injure females, but it can be intense; McFarland Symington (1987, p. 153) describes "frenzied chases involving three males and lasting up to 15 minutes." The functional significance of this aggression remains obscure; although it is directed only at cycling females (McFarland Symington, 1987), it has not been observed as a prelude to copulation (Fedigan and Baxter, 1984; McFarland Symington, 1987). Spider monkeys are among a handful of primates in which males remain in their natal groups and form lifelong bonds with one another, while females transfer to other groups. They are also one of the few polygynous anthropoid primates that show little sexual dimorphism, but females are nevertheless consistently

subordinate to males and relations between the sexes are “generally tense” (McFarland Symington, 1987, p. 161). Given the slight sexual dimorphism in these species, it seems reasonable to hypothesize that male dominance over females is a product of aggression by male coalitions and that, by increasing their power over females, cooperating males also increase their ability to gain sexual access to them. Since courtship and copulation have rarely been observed in wild spider monkeys (Fedigan and Baxter, 1984; McFarland Symington, 1987), further evidence is needed to evaluate this hypothesis.

Male primates’ use of force to increase sexual access to females can also involve considerably longer-term strategies such as infanticide (Hrdy, 1979). Males from a wide variety of nonhuman primates, including Old and New World monkeys, apes, and prosimians, kill infants sired by other males (Hausfater and Hrdy, 1984; Crockett and Sekulic, 1984; Struhsaker and Leland, 1987; Pereira and Weiss, 1991). Male infanticide occurs most often in species that live in groups with a single breeding male after a strange male aggressively usurps the breeding position and attempts to kill the immature offspring of the previous male (grey langurs: Hrdy, 1977; red howlers: Sekulic, 1983a; Crockett and Sekulic, 1984; mantled howlers: Clarke, 1983; red-tail monkeys: Struhsaker, 1977; blue monkeys: Butynski, 1982). Male infanticide can also occur when immigrant males enter groups with multiple breeding males (baboons: Collins *et al.*, 1984), in association with a change in male status relationships within multimale groups (red colobus: Struhsaker and Leland, 1985), or after a breeding male dies, leaving vulnerable mothers and infants without protection (gorillas: Watts, 1989). Because a return to sexual cycling is inhibited by lactation, death of the infant typically brings the mother into estrus sooner than would occur otherwise. In many instances, the infanticidal male subsequently mates with the female (reviewed by Struhsaker and Leland, 1987). Although the aggression involved in infanticide targets the infant rather than the mother, it is appropriate to view infanticide as a form of sexual coercion for two reasons. First, like other forms of sexual coercion, it involves the use of force to manipulate the female’s sexual state and mating behavior to the male’s advantage; killing the infant is simply a means to this end. Second, like other forms of sexual coercion, it imposes a cost on the female.

C. A NOTE ON TERMINOLOGY

In the following section, we discuss the costs to females of male aggression that we hypothesize functions as sexual coercion. However, below and in later sections, we refer to specific behaviors as “male aggression”

rather than "sexual coercion" because, in most cases, the functional consequences of these behaviors have yet to be demonstrated conclusively.

III. COSTS TO PRIMATE FEMALES OF MALE AGGRESSION

Although the reproductive costs to females of male aggression have seldom been measured, they may often be considerable. Lindburg (1983) saw a top-ranking rhesus male fatally injure his consort partner after she repeatedly approached another male, and B. B. Smuts (personal observation) saw an adult male olive baboon kill an adolescent, estrous female. Rajpurohit and Sommer (1991) reported the death of a grey langur female as a result of wounds inflicted by a male, but the context of the attack was not described.

Enomoto (1981) and Manson (1991) reported frequent male aggression toward estrous female macaques (Enomoto: 0.86 times per day per female; Manson: 0.26–0.44 times per day per female). These two studies and Teas' (1984), study of wild rhesus "temple monkeys" in India agree that male aggression against estrous females often resulted in serious wounds. These results should be regarded with caution, however, because they are from provisioned troops living in crowded conditions, which may increase rates of male aggression and wounding. At Gombe, observers have witnessed numerous brutal attacks by male chimpanzees on females from other communities, and some of these females died from their wounds (Goodall, 1986). Finally, even when females themselves are not severely injured by male attacks, male violence can lead to abortion (baboons: Pereira, 1983), disruption of estrous cycles (chimpanzees: Goodall, 1986; rhesus macaques: J. Manson and S. Perry, personal communication), and perhaps other deleterious, stress-related effects.

The reproductive costs of male infanticide are easier to ascertain. Among grey langur troops near Jodhpur, when the previous resident male was replaced by a new male, 40% of infants present at the time of replacement ($n = 81$ in 12 different troops) and 35% of the infants born shortly thereafter ($n = 34$) were victims of infanticide (Sommer, 1992). Since male takeovers occurred on average every 26.5 months (Sommer and Rajpurohit, 1989), infanticide is clearly an important source of infant mortality. Among mountain gorillas, at least 37% of infant mortality is due to male infanticide (Watts, 1989). Crockett and Rudran (1987) and Clarke and Glander (1984) give similar estimates (44 and 40%) for red howler monkeys and mantled howlers, respectively. Male infanticide may also be responsible for a significant proportion of infant mortality in chimpanzees

(Goodall, 1986; Nishida, 1990; Nishida *et al.*, 1990), baboons (Collins *et al.*, 1984), and probably a number of other species. Potential costs of infanticide for females are probably even higher, since rates of infanticide are undoubtedly reduced, sometimes substantially, by female counterstrategies (see below).

In addition to the obvious costs due to severe injuries or death, male aggression can inflict subtle but perhaps significant costs by constraining female behavior in many ways. For example, male herding in hamadryas baboons sometimes prevents a female from joining her female kin in a different group, thus depriving her of potential allies (Abegglen, 1984). In mountain gorillas, male infanticide constrains female movements between groups. Mothers with young infants must remain in their current group until the infant is older, abandon the infant and transfer without it (as sometimes occurs), or transfer with the infant, which nearly always leads to infanticide (Watts, 1989).

When males employ aggression to exact female sexual cooperation, the benefits females derive from free mate choice will be reduced (for discussion of possible benefits of mate choice, see Smuts, 1987a; Small, 1989; Manson, 1991). Manson (1991), for example, found that among rhesus macaques on Cayo Santiago, estrous females preferentially maintained proximity to lower ranking males, and such proximity-maintaining behavior correlated with higher copulation rates. However, after higher ranking males chased or attacked females in consort with lower ranking males, the females often failed to restore proximity to their previous partners. This suggested to Manson that male aggression disrupted females' attempts to express their mating preferences.

The time and energy involved in maintaining vigilance toward potentially aggressive males may sometimes be costly, although such costs are difficult to measure. Female baboons with young infants consistently avoid proximity to recent male immigrants (the males most likely to commit infanticide; Collins *et al.*, 1984; Busse, 1984), female vervets restrain their infants significantly more often in the presence of new males (Fairbanks and McGuire, 1987), and female ring-tailed lemurs carefully monitor the movements of recently immigrated males who are likely to commit infanticide (Pereira and Weiss, 1991).

Finally, it is important to note that the costs discussed here occur in spite of whatever female counterstrategies exist to resist or reduce male aggression. In the absence of such counterstrategies, the costs to females of male aggression presumably would often be considerably higher. These "original," higher costs are the selective forces that promote the evolution of female counterstrategies. In addition, the counterstrategies that females

employ to resist or reduce male aggression themselves often involve costs, as indicated below.

IV. PRIMATE FEMALE COUNTERSTRATEGIES TO MALE AGGRESSION

A. FIGHTING BACK

The most obvious first line of defense against male aggression is to fight back. In extreme cases, particularly when protecting vulnerable infants, this is just what female primates tend to do. Mountain gorilla females, for example, usually fight back against male attacks on their infants. However, because male gorillas are twice as large as females, female resistance is usually futile, and resistant females risk severe injury (Watts, 1989). Red howler and grey langur females also attempt to physically thwart infanticidal males, and occasionally wound them, but they are rarely able to prevent infanticide (Hrdy, 1977; Sekulic, 1983a; Crockett and Sekulic, 1984). Similarly, orangutan females struggle free only rarely during forced copulations (Mitani, 1985).

In most nonhuman primates in which male aggression toward females has been reported, males are larger than females and dominate them in one-on-one encounters (reviewed by Smuts, 1987b), which limits the effectiveness of retaliatory aggression by single females. A few striking exceptions exist, however. In ring-tailed, crowned, and ruffed lemurs, females consistently win dyadic agonistic encounters with males (Kappeler, 1990; Pereira *et al.*, 1990; Kaufman, 1991). Among patas monkeys, individual females often defeat males in one-on-one fights, and males "appear extremely reluctant to use force against females in almost all contexts, presumably because of the threat of female retaliation" (Loy, 1989, p. 39). Similarly, in macaques, vervet monkeys, brown capuchins, wedge-capped capuchins, and several other species, individual females sometimes win agonistic encounters against males (e.g., stumptail macaques: Bernstein, 1980; Japanese macaques: Johnson *et al.*, 1982; vervets: Bramblett *et al.*, 1982; brown capuchins: Janson, 1984; wedge-capped capuchins: Robinson 1981; O'Brien, 1991; see Smuts, 1987b, for further details). Since, with the exception of lemurs, males are larger than females in all of these species (and much larger than females in patas monkeys), these observations are puzzling; they are discussed further below.

Because of the limited effectiveness in most primates of individual retaliation by females, evolution has favored a variety of other female counterstrategies. These are not trivial, but involve critical aspects of

female life histories, including timing of sex and reproduction, mate choice, choice of group, and the development of social relationships and alliances. Below we give some examples of each.

B. TIMING OF SEXUAL ACTIVITY AND REPRODUCTION

In grey langurs (Agoramoorthy *et al.*, 1988), gelada baboons (Mori and Dunbar, 1985), and captive hamadryas baboons (Colmenares and Gomendio, 1988), takeover of the unit by a new male induces spontaneous abortions in pregnant females, which has been interpreted as female termination of investment in infants who are likely to be victims of infanticide (Mori and Dunbar, 1985; Sommer, 1987). In addition, in all three species, lactating females confronted with a new male may rapidly return to cycling, shortening lactational amenorrhea (Sigg *et al.*, 1982; Mori and Dunbar, 1985; Colmenares and Gomendio, 1988; Winkler, 1988). In the captive hamadryas group, all six lactating females quickly resumed cycles, regardless of the age of their infants, and one grey langur female resumed cycling only 7 days after giving birth (Winkler, 1988). Thus, the presence of a new male overrode the role that infant suckling normally plays in the control of female reproduction (Colmenares and Gomendio, 1988). Whether rapid return to cycling by lactating females has evolved to prevent infanticide, however, remains an open question. In several wild gelada females (Mori and Dunbar, 1985) and in the single case reported for wild langurs (Winkler, 1988), the infants of the nursing mothers who resumed cycles early were not killed, but in the captive hamadryas group, some were, which led the observers to reject the infanticide hypothesis (Colmenares and Gomendio, 1988). However, the hamadryas data are ambiguous because all four victims of infanticide were killed by a single male described as so aggressive in temperament that he was removed from the colony (Colmenares and Gomendio, 1988), and because of abnormal crowding in captivity.

In many primates, pregnant females may solicit copulations when confronted with an unfamiliar male (red colobus: Struhsaker and Leland, 1985; grey langurs: Hrdy, 1977; captive patas: Loy, 1985; gelada baboons: Mori, 1979; redbellied monkeys: Cords, 1984; mountain gorillas: Watts, 1989). Hrdy (1977, 1979) first argued that such situation-dependent sexual receptivity may reduce the likelihood of infanticide by confusing paternity. Sommer (1987, 1992) rejects this hypothesis for grey langurs, because the pattern of postconception estrus observed over many years at Jodhpur was virtually the same whether the sire was still resident in the troop or a new male had taken over (in other words, it was not "situation-dependent"), and because the presence or absence of copulations with a

new male did not affect whether or not the female's infant was subsequently killed by that male. In contrast, female red colobus monkeys who were pregnant when a male attacked infants in their group mated more frequently and later into their pregnancy than did pregnant females either before or after these attacks. A large fraction of these copulations was with the infanticidal male, who did not attack infants of the pregnant females after they were born (Struhsaker and Leland, 1987, p. 96). Thus postconception estrus may serve different functions in different species. Other species in which infants are vulnerable to infanticide, such as red howlers, fail to show postconception estrus in response to invading males (Sekulic, 1983c).

When some infants are killed by infanticidal males, others in the same group often escape harm. At Jodhpur, for example, a substantial proportion of vulnerable langur infants (44%) were not attacked by new males, even though other infants in the troop were killed (Sommer, 1992). The fact that some infants go unharmed raises intriguing questions about the factors that may be responsible for their survival, including, perhaps, presently unidentified female counterstrategies.

After red howler females experience invasion and infanticide from immigrant males, they rapidly return to cycling but do not conceive immediately. Crockett and Sekulic (1984) hypothesize that the rapid return to cycling incites male-male competition, hastening resolution of the identity of the new alpha male; similarly, delayed conception may benefit females because it increases the probability that their next infant will be sired by the new alpha male.

C. MATE CHOICE

In primates that live in multimale troops, females often show preferences for mating with dominant males; these preferences have usually been interpreted in terms of the proven genetic quality of the males (reviewed by Small, 1989). The alternative hypothesis that females choose dominant males in order to reduce harassment of themselves or their infants by other males (Wrangham, 1979; Trivers, 1985) has received little attention and deserves further scrutiny. Manson (1991), for example, showed that when rhesus monkey females consort with high-ranking males, they are attacked significantly less often by rival males than when they consort with low-ranking males. Since, as noted above, such attacks can lead to severe injury or even death, mate choice could significantly reduce the costs to females of male aggression. Pereira and Weiss (1991) hypothesize that female ring-tailed lemurs choose to mate with males that indicate superior ability to maintain high rank throughout the subsequent birth season,

because such males will be more effective in protecting infants from infanticide by rival males. Similarly, Pope (1990) and O'Brien (1991) suggest that, among red howlers and wedge-capped capuchins, respectively, females benefit from mating with the alpha male, because he provides the most effective protection against infanticide by other males. Janson (1984, 1986) suggests that female brown capuchins benefit from mating with dominant males because the protection they provide enables females and their infants to forage undisturbed at rich food sources.

In many Old World primates, female mate choice appears designed to facilitate copulation with a number of different males (reviewed by Smuts, 1987a; Small, 1989). Hrdy (1979) and Wrangham (1980a) suggested that, by mating with many males, a female can confuse paternity and thus reduce the probability of infanticide. This hypothesis predicts that females will be particularly interested in mating with males who are most likely to commit infanticide, namely, males that have recently entered a group, or extragroup males who might later transfer into the group (Hrdy, 1979). Indeed, in a number of primate species, females are sexually attracted to such males (reviewed by Smuts, 1987a; Small, 1989). This has been documented both for species living in multimale troops (e.g., Japanese macaques: Wolfe, 1981; rhesus macaques: Brereton, 1981; Manson, 1991; vervet monkeys: Henzi and Lucas, 1980; savanna baboons: Packer, 1979) and species living in one-male troops (grey langurs: Hrdy, 1977; Mohnot, 1984; Sommer, 1988; blue monkeys: Tsingalia and Rowell, 1984; patas monkeys: Olson, 1985). Sommer (1988) has suggested, in addition, that female grey langurs solicit copulations from male invaders in order to incite male-male competition and induce takeover by the strongest possible male. Sommer's hypothesis could apply to many other species living in one-male troops in which females copulate enthusiastically with invading males (e.g., redbellied monkeys: Cords, 1984; blue monkeys: Tsingalia and Rowell, 1984; patas monkeys: Harding and Olson, 1986). Alternatively, females may induce takeover by the strongest male not by mating, but by inciting male-male competition through other means, such as howling (Sekulic, 1983c).

Despite promiscuous tendencies, females in many species living in multimale groups show marked mating preferences for particular male partners (reviewed by Smuts, 1987a). For example, in savanna baboons, females often prefer to mate with males with whom they have developed a long-term, affiliative relationship (Seyfarth, 1978; Smuts, 1983a,b, 1985). Smuts (1985) argued that females form such friendships with males, and prefer them as mates, in exchange for protection by these males against aggression from other males toward themselves and their infants. Indeed, when a male defended a female or her immature offspring against other

baboons, in 91% of the cases he was the female's friend (Smuts, 1985). Females form friendships with both high- and low-ranking males. This reflects the fact that, in olive baboons (unlike macaques; see below), even low-ranking males are useful allies, because they are willing to challenge higher ranking males, especially when they receive agonistic support from other males (Packer, 1977; Strum, 1982; Smuts, 1985; Noë, 1990). M. E. Pereira (personal communication) has documented similar special relationships among captive redfronted brown lemurs, which are also characterized by male protection of the female against other males in exchange for enhanced mating opportunities. The significance of such special relationships was highlighted when, after a male transferred from one enclosure to another, he killed the infants of one female and "bonded" with the other, leaving her infants alone (M. E. Pereira, personal communication).

D. CHOICE OF GROUP

A female's choice of which group to live in may be strongly influenced by potential male aggression, particularly in those species in which females commonly transfer. In red colobus monkeys (Marsh, 1979) and grey langurs (Sugiyama, 1967), females sometimes emigrate in response to the presence of a potentially infanticidal male immigrant. In howler monkeys, in contrast, patterns of female emigration seem to be more related to female-female competition than to attempts to avoid infanticide (Jones, 1980; Crockett and Sekulic, 1984).

Since mountain gorilla infants are vulnerable to infanticide by extra group males, mothers will clearly benefit from association with a male who can protect their infants effectively. In two of three cases in which an infant was killed despite the resident male's presence, the female subsequently deserted the male for another (in the third case, it is not known whether or not she transferred)(Fossey, 1984). Even for females who have not experienced infanticide, evaluation of a potential mate's ability to protect her infants may be the most important criterion for mate choice (Wrangham, 1979, 1982; Watts, 1983, 1989; Stewart and Harcourt, 1987).

In chimpanzees, both females and their infants are vulnerable to severe aggression from males from neighboring communities, particularly when their own community range is shrinking due to intercommunity male-male competition (Goodall, 1986; see below). Consistent with this danger, at Mahale Mountains, when all but one of the adult males of K-group disappeared, K-group females transferred en masse to the neighboring M-group, which contained many adult males (Nishida *et al.*, 1985). However, for the first few years after transfer, most male infants of transferred females were killed by M-group males, even though they were often the infants'

likely fathers (Kawanaka, 1981; Nishida and Kawanaka, 1985; Nishida, 1990; Nishida *et al.*, 1990). Observers speculate that the M-group males may have regarded these infants as offspring of K-group males, because the ranging habits of females that had transferred from K-group made their community identity ambiguous (Nishida and Kawanaga, 1985. Nishida, 1990).

E. DEVELOPMENT OF SOCIAL RELATIONSHIPS AND ALLIANCES

As indicated above, in savanna baboons, gorillas, and chimpanzees, females choose to associate and mate with males who, in turn, help protect females and infants from aggression by other males. In several species, females who have recently given birth increase the time they spend near male "friends" (savanna baboons: Altmann, 1980; Smuts, 1985; Japanese macaques: Takahata, 1982) or near the probable fathers of their infants (gorillas: Harcourt, 1979; red howlers: Sekulic, 1983b; black spider monkeys: McFarland Symington, 1987; long-tailed macaques: Van Noordwijk and van Schaik, 1988; blue monkeys; Tsingalia and Rowell, 1984). Through these close associations with males, females probably gain protection from potential infanticide.

Male-female relationships in macaques appear to involve mutual protection against males who threaten the established social order—maturing males and male immigrants. Like female savanna baboons, female macaques form long-term, affiliative bonds with particular males who selectively protect their female affiliates and the infants of those females from aggression by other males (Kaufman, 1967; Takahata, 1982; Chapais, 1983b,c). In macaques, however, unlike baboons, females consistently prefer high-ranking males as associates (Takahata, 1982; Chapais, 1983a,c; Hill, 1990; Manson, 1991). This is consistent with the fact that, in macaques, in contrast to baboons, only high-ranking males can effectively protect females from other males, since aggression directed up the male hierarchy is extremely rare. High-ranking males, in turn, prefer high-ranking females as associates (Takahata, 1982; Chapais, 1983a,c; Hill, 1990; Manson, 1991), and these females support the males during aggressive competition with other males (Koyama, 1970; Fedigan, 1976; Gouzoules, 1980; Chapais, 1983a,c; de Waal, 1989). This mutual support provides the females with protection against aggression from male immigrants and young natal males (Chapais, 1983a,c; Bernstein and Ehardt, 1986; Oi, 1990), and it helps the resident males to achieve and maintain high rank (Koyama, 1970; Bernstein, 1969; Gouzoules, 1980; Chapais, 1983a,c; de Waal, 1980). Studies of naturalistic, captive groups of vervet monkeys indicate the existence of similar, mutually supportive relationships be-

tween high-ranking females and dominant males (Raleigh and McGuire, 1989; Keddy Hector and Raleigh, 1992). In wild brown and wedge-capped capuchins, as well, females preferentially associate and groom with the dominant male, and both females and the dominant male direct aggression toward all subordinate males (Robinson, 1981, 1988; Janson, 1984; O'Brien, 1991). Since infanticide has been observed in capuchins (Valderama *et al.*, 1990), O'Brien (1991) speculates that a strong association with the dominant male may help females to obtain protection for their infants.

Bonds with other females can also prove critical in reducing male aggression toward females and young (Smuts, 1987b; Nadler, 1989a; Strier, 1990). Females form coalitions against males in a wide variety of nonhuman primates, including lemurs; New World monkeys, such as howlers and capuchins; and Old World monkeys, such as macaques, baboons, vervets, patas monkeys, and several colobines (reviewed in Smuts, 1987b; see also Robinson, 1981, 1988; Sekulic, 1983a; Pope, 1990; O'Brien, 1991, for New World monkeys). Female coalitions are especially likely in response to male harassment of females or infants. In many species, females gang up on males when they attack, herd, or frighten other females (rhesus macaques: Bernstein and Ehardt, 1985; Japanese macaques: Watanabe, 1979; pig-tailed macaques: Oi, 1990; olive baboons: B. B. Smuts, personal observation; chacma baboons: Hall, 1962; silver-leaf monkeys: Bernstein, 1968; captive chimpanzees: de Waal, 1982). In common squirrel monkeys (Baldwin, 1968), patas monkeys (Hall, 1967; Loy, 1989), vervets (Andelman, 1985), and captive chimpanzees (de Waal, 1982), several females may turn on a male who solicits sex from an unwilling female. The most frequent context in which females form aggressive coalitions against males involves potential, or actual, threat to an infant (grey langurs: Boggess, 1979; Hrdy, 1977; Jay, 1963; blue monkeys: Butynski, 1982; redtail monkeys: Struhsaker, 1977; vervet monkeys; Lancaster, 1972; patas monkeys: Hall, 1968; rhesus monkeys; Bernstein and Ehardt, 1985; Lindburg, 1971; Japanese macaques; Kurland, 1977; Watanabe, 1979; long-tailed macaques: Chance *et al.*, 1977; olive baboons: Ransom, 1981; Smuts, 1985; common squirrel monkeys: Baldwin, 1968; red-backed squirrel monkeys: Baldwin and Baldwin, 1972; wedge-capped capuchin monkeys: Valderama *et al.*, 1990; red howlers: Sekulic, 1983c; Pope, 1990; ring-tailed lemurs: Pereira and Weiss, 1991).

In species in which females normally remain in their natal groups, female-female coalitions typically involve close kin and are usually directed against females and juveniles from other matriline (reviewed by Walters and Seyfarth, 1987). In striking contrast, when the target is an adult male, females often form coalitions with females to whom they are not closely related (rhesus monkeys: Bernstein and Ehardt, 1985; red-

backed squirrel monkeys; Baldwin and Baldwin, 1972; grey langurs: Hrdy, 1977; olive baboons: B. B. Smuts, personal observation; vervets: Cheney, 1983b; bonobos: Kano, 1987; Furuichi, 1989). Such coalitions can mobilize very quickly in response to male aggression, since any females nearby can be recruited (B. B. Smuts, personal observation). This may help to explain why, as noted above, females can sometimes individually dominate males in spite of the females' smaller size: Males may sometimes defer to individual females because of the ever-present possibility that one female opponent may suddenly become many (cf. Robinson, 1981, 1988, for wedge-capped capuchins). Thus, female cooperation against males may benefit females both in the short-term, by halting male aggression, and in the long-term, by making males more hesitant to harass females or young because of the risks of counterattack by a female mob.

How effective are female coalitions in reducing male aggression? In Japanese macaques (Packer and Pusey, 1979), vervet monkeys (Cheney, 1983a,b), and patas monkeys (Hall, 1967), female coalitions can drive males from the troop or prevent them from entering in the first place. Among capuchins, female coalitions probably help to keep non-alpha males peripheral, both socially and spatially (Robinson, 1981; O'Brien, 1991). In wild red colobus monkeys, female-female coalitions have been observed to kill immigrant males (Starin, 1981), and among captive talapoin monkeys, female-female coalitions have also resulted in killing of males (Rowell, 1974). In grey langurs and red howlers, however, female coalitions are not very effective against infanticidal males (Hrdy, 1977; Crockett and Sekulic, 1984). Few data are available to evaluate the effectiveness of female coalitions against males. For instance, no published data indicate whether female coalitionary aggression toward a male reduces the likelihood that he, or male witnesses, will show subsequent aggression toward females or young. Clearly, this topic deserves further attention.

F. FORM OF THE SOCIAL SYSTEM

Until this point, we have considered how, given particular features of the social system (e.g., presence of related females; one-male vs. multimale groups), females may develop counter strategies to resist male aggression. Here, we briefly consider how sexual coercion and female strategies to resist it may influence the form of the social system itself.

Mountain gorillas provide the clearest evidence that male sexual coercion and female counterstrategies can determine the form the social system takes. In these apes, almost all infants who lose the protection of a mature silverback male (in most cases, because he has recently died) are soon

killed by other males (Watts, 1989). In contrast, contrary to Fossey's earlier (1984) suggestion, recent data indicate that infants living in a group with a mature silverback are rarely killed (Watts, 1989). These observations provide strong support for Wrangham's hypothesis that infanticide is the selective force responsible for group-living in gorillas (Wrangham, 1979, 1982, 1987a; Watts, 1983). Because females rely for protection primarily on the silverback male, rather than on other females (Watts, 1989), the gorilla social system is based not on bonds between related females, but on bonds between (usually unrelated) females and the adult male(s) in the group (some gorilla groups have more than one mature male: Harcourt, 1979; Stewart and Harcourt, 1987).

Male sexual coercion may also help to explain the distribution of one-male versus multimale polygamous primate groups—a problem that remains unresolved despite numerous attempts to explain it in terms of male competitive strategies (Clutton-Brock *et al.*, 1977; Ridley, 1986). Several people have argued that we also need to consider the effect of female strategies on the number of males in the group (Wrangham, 1980a; van Schaik and van Noordwijk, 1989; Altmann, 1990). Altmann (1990) proposes that the threat of male infanticide may result in the evolution of synchronized female ovulation, which in turn will make it more difficult for one male to control all of the fertile females in his group. This will result in a transformation from one-male to multimale groups (see Section VII for a discussion of why infanticide is generally reduced in multimale groups).

V. MALE AGGRESSION AGAINST FEMALES IN CHIMPANZEES

Chimpanzees have been studied continuously and intensively for more than 25 years at two study sites in Tanzania, Gombe National Park (Goodall, 1986) and Mahale Mountains National Park (Nishida, 1990). Although they have also been studied at other sites in East, Central, and West Africa (Heltne and Marquardt, 1989), these studies have not yet produced detailed information on male aggression against females. Thus, it remains to be seen whether the patterns observed at Gombe and Mahale characterize all chimpanzees or are limited to populations living in particular areas.

Chimpanzee males show two main kinds of aggression against females: aggression against potential mates from the same community and aggression against nonestrous females from neighboring communities. Each kind is reviewed in turn.

A. MALE AGGRESSION TOWARD POTENTIAL MATES

Goodall succinctly summarizes the role of male aggression in chimpanzee sex as follows: "Almost always, unless he is crippled or very old, an adult male can coerce an unwilling female into copulating with him" (1986, p. 481). In chimpanzees, males copulate under three different circumstances (Tutin, 1979; Hasegawa and Hiraiwa-Hasegawa, 1983, 1990): promiscuous, opportunistic mating, which involves frequent copulations with many different males in the group setting; possessive mating, which involves a single male's attempts to monopolize copulations in spite of the presence of other males; and consortships, in which mating takes place between one male and one female who travel apart from the rest of the community for several days or weeks. Promiscuous, opportunistic mating typically occurs early in the female's cycle before her swelling reaches maximum tumescence, and is unlikely to result in fertilization. As she nears ovulation, she will typically either participate in a possessive mating relationship (most likely involving the alpha male), or form a consortship. Male aggression against females occurs in all three contexts but especially during consort formation (Goodall, 1986).

Among chimpanzees at Gombe, Tanzania, consortships are probably responsible for at least one-third of all conceptions, and they greatly improve a lower ranking male's chances of fathering offspring (Goodall, 1986). It is thus not surprising that males appear highly motivated to form consortships. In order to do so, they must convince a female to follow them away from other males and to remain with them for at least several days (sometimes as long as 5–6 weeks) until her sexual swelling begins to subside, which indicates that ovulation has occurred. In order to accomplish this end, males employ what Goodall terms "a fair amount of brutality" (1986, p. 453).

Males often try to initiate consortships with a female long before her sexual swelling reaches the full size associated with ovulation. The male's apparent goal is to escape the rest of the group early, before competition for the female becomes too intense, and then to sequester the female through the period of ovulation. Aggression is most common during the early stages of consortship, when the male is trying to lead the female away from other males by traveling away from the core area of the community range (Tutin, 1979; Goodall, 1986). During this time, the female often refuses to follow the male, and she may scream, which sometimes attracts other males. If she is approaching ovulation, a higher ranking male may disrupt the consortship and she can escape her suitor. However, if she is not fully swollen, other males show little interest and she has a harder time escaping.

Goodall (1986) reports that if the female refuses to accompany the consorting male, he will often use violence to force her to follow him. For example, Evered spent 5 hr leading Winkle north across a valley, away from other males. During these 5 hr, he repeatedly displayed at her aggressively and attacked her six times, twice severely (Tutin [1975, 1979] and Goodall [1986] provide numerous additional vivid examples of male aggression in this context). Once the pair has moved far from the core of the community range, the female becomes more cooperative (probably because she is in an unfamiliar area and relies on the male for protection) and the male becomes more relaxed and tolerant (probably because he has left his mating competition far behind)(Goodall, 1986).

Male aggression appears to be quite effective in convincing females to go on consort. This is well illustrated by the case of Jomeo, an adult male who showed the lowest rates of punitive aggression toward consort partners. He was also least successful in forming consortships and was the only adult male who is thought not to have sired any offspring.

The significance of male aggression during consort formation may help to explain why males frequently conduct severe, apparently unprovoked attacks on cycling females whose sexual swellings have not reached full tumescence. Goodall (1986) hypothesizes that these attacks function as intimidation designed to increase the chances that the female will submit to the male's advances in the future. Similarly, she argues that when a female appears to follow a male on consort voluntarily, her lack of resistance does not necessarily indicate willing participation; rather, it may simply reflect previous experiences with male aggression. Along the same lines, the low frequency with which females ignored adult male invitations to copulate (4.1%) may also reflect previous experience with male aggression. When a female did ignore a male's invitation to copulate, on one out of every five occasions he responded with aggressive displays or chases and she gave in. These hypotheses linking female acquiescence to previous aggression, or to the expectation of future aggression, seem intuitively reasonable but are difficult to test (see Section VIII,B for further discussion).

B. MALE AGGRESSION AGAINST FEMALES FROM OTHER COMMUNITIES

At Gombe (Pusey, 1979; Goodall, 1986) and Mahale Mountains (Nishida, 1979; Nishida and Hiraiwa-Hasegawa, 1985), young, sexually cycling, nulliparous females typically transfer, either temporarily or permanently, to neighboring communities; while there, they mate with community males. Males welcome such females and sometimes even pro-

protect them from hostility by resident females. In dramatic contrast, when chimpanzee males encounter mature, anestrus females from another community, they typically respond with intense, sometimes lethal aggression, as illustrated by the killing of the old female, Madam Bee, at Gombe. The attacked females are not immigrants but are encountered in areas of overlap between the ranges of the two communities or in their own community range during invasions by neighboring males (Bygott, 1972; Goodall *et al.*, 1979; Goodall, 1986; Nishida and Hiraiwa-Hasegawa, 1985).

From 1975 until 1982, observers at Gombe witnessed 25 encounters between adult males from the habituated community and strange, anestrus mothers from neighboring communities (Goodall, 1986). Nineteen of these encounters were aggressive, involving chases or attacks. Fifteen attacks were observed, and, with one exception, they were extremely severe. Three attacks resulted in the death of the female's infant. In 10 cases, observers were able to see the victim after the attack. Each time she was bleeding heavily from wounds on the limbs and/or back and, in at least 8 cases, on the face or head; some females may have died of their wounds.

Males showed a marked degree of cooperation in this context. All of the attacks involved aggression by more than one male; some involved as many as six males. The males often embraced one another before attacking the female. In one case the males persistently "hunted" (Goodall's term) a strange female before attacking her, and, in another case the males cooperated to surround the female as they sometimes do when hunting baboons (Goodall, 1986, p. 494).

Several similar attacks have also been observed at Mahale Mountains (Nishida and Hiraiwa-Hasegawa, 1985). In two instances involving the same female, observers intervened because they were certain she would be killed (Nishida and Hiraiwa-Hasegawa, 1985). At both Gombe and Mahale, although infants may be killed and even cannibalized during these attacks, observers gained the impression that the males' aggression was directed primarily at the mother (Goodall, 1986; Nishida and Hiraiwa-Hasegawa, 1985).

Several explanations have been proposed to account for aggression toward anestrus females from other communities. Wolf and Schulman (1984) argued that males attack older females because they have low reproductive value, and, if killed, additional habitat becomes available for younger females of higher reproductive value who may eventually mate with the killers. Many of the females attacked by males from other communities were not, however, especially old (Goodall, 1986; Nishida and Hiraiwa-Hasegawa, 1985), so this explanation cannot account for all of the cases. Nishida and Hiraiwa-Hasegawa (1985, p.12) speculated that, by attacking neighboring females who may compete with resident females for

food and other resources, the males may “court the favor” of resident females. However, resident females will rarely witness such attacks, since they are relatively uncommon, and typically only one or two resident females are likely to be present (at Gombe, on average, only 1.25 resident females were present during attacks on strange females, based on data in Goodall, 1986, Table 17.2).

Goodall (1986) provides a third hypothesis, suggesting that repeated brutal attacks on mothers may facilitate recruitment of their daughters to the attacker’s group. In support of this idea, she notes that, at least at Gombe, many daughters retain close bonds with their mothers and remain as residents in their natal groups. If the mother–daughter bond is weakened due to repeated attacks, or destroyed because the mother is killed, the daughters may be more likely to transfer permanently to the neighboring group. Consistent with this explanation, all but one of the (at least) five attacks on the old female, Madam Bee, occurred when the attacking males were recruiting her daughter, Little Bee; during this period, Little Bee transferred to their community. After Madam Bee’s death, her other daughter, Honey Bee, associated with the attackers’ community off and on for 3 years. If Goodall’s explanation is correct, then male aggression toward females from other communities would qualify as a form of sexual coercion (although in this instance the individual who directly suffers the cost of the coercion is not the males’ potential mate, but her mother).

Whatever the explanation for the brutal attacks on strange females, they clearly occur regularly at Gombe and Mahale, and thus constitute an important selection pressure influencing the behavior of female chimpanzees. Female chimpanzees forage, often on their own with dependent young, in dispersed, but overlapping, home ranges. Males range more widely and cooperate in defending a community range that encompasses that of several females. As adults, and often after transferring from their natal communities, female chimpanzees become clearly identified with a particular community, i.e., with a particular group of males (Goodall, 1986; Nishida and Hiraiwa-Hasegawa, 1987). Although female dispersion is probably a product of feeding competition (Wrangham, 1975, 1979), the fact that females “belong” to a particular male community, rather than ranging and associating freely regardless of community boundaries, is probably a response to violence by males from neighboring communities. This conclusion is supported by observations from Mahale Mountains indicating that infants of lactating females with ambiguous community identity are especially vulnerable to infanticide by males (Kawanaka, 1981; Nishida and Kawanaka, 1985; Nishida, 1990; Nishida *et al.*, 1990). Thus, among chimpanzees, as among gorillas (see above), male aggression against females appears to have influenced the form the social system takes.

VI. MALE AGGRESSION AGAINST FEMALES IN OTHER MAMMALS

Table I summarizes information on male aggression against females in selected mammals. It is not exhaustive, and it is biased toward large, diurnal mammals whose behavior has been studied in the wild. We present the information in Table I to illustrate (a) the fact that male aggression against females and infants occurs in a variety of mammals, (b) the varied contexts and forms of this aggression, (c) the potential costs to females, and (d) the different kinds of counterstrategies that females exhibit. Most of the instances of male aggression toward females were interpreted by the authors as sexual coercion, as defined in this article. In surveying the literature on nonprimate mammals, we encountered few instances of male aggression toward females in nonsexual contexts.

A. TYPES OF MALE AGGRESSION

Females in many mammalian species experience both sexual aggression and infanticide by males. Male sexual aggression appears to be most common in gregarious species in which females do not form long-term bonds with a single male (or, as in lions, with a group of allied males), so that females are exposed to a number of males competing for sexual access to them (e.g., fallow deer, bighorn sheep, African elephants, several pinnipeds, bottlenose dolphins). In contrast, females that do form long-term bonds with particular males (wild horses, lions) are usually protected from routine sexual harassment by other males and do not experience sexual aggression from their long-term male associates. These females, however, are vulnerable to infanticide (in lions) or induced abortion (in horses) during male takeovers. Female rodents and farm cats also experience infanticide when they encounter strange males.

In species in which estrous females are exposed to several competing males, they are typically chased and herded, and sometimes kicked, pushed, or bitten by males attempting to mount. In some species (such as fallow deer or African elephants), males apparently do not frequently injure females, and the main costs to females of sexual aggression are probably loss of feeding time and energy expended in escape. In other species, sexually aggressive males sometimes severely injure and even kill females (e.g., several pinnipeds). In addition, in their aggressive attempts to gain access to estrous females, males sometimes cause death of infants (e.g., crabeater seals, sea lions, elephant seals). Little information is available on species in which females are solitary. In sea otters (Foote, 1970) and many other mustelids (martens, weasels, skunks, mink) and viverrids (civets, fossas, some mongooses), copulation is accompanied by intersex-

TABLE I
MALE AGGRESSION AGAINST FEMALES AND INFANTS IN SELECTED NONPRIMATE MAMMALS^a

Species	Social/mating system	Context of male aggression	Potential costs to females	Female counterstrategies	References
Fallow deer (<i>Dama dama</i>)	Polygynous; dominant males defend territories on leks	Prolonged chases of fertile females by nonterritorial males	Energetic costs of avoiding male "sexual harassment"; potential wounding by male antlers	Remaining in territories of dominant males provides protection from other males	Clutton-Brock <i>et al.</i> (1988); Clutton-Brock (1991)
Rocky Mountain bighorn sheep (<i>Ovis canadensis</i>)	Promiscuous; multimale, multifemale groups	Single males or groups of subordinate males chase females and push, butt, and kick them until they submit to copulation. "Blocking": male forcefully sequesters female and mates with her; prevents her from approaching other males by herding, kicking, and pushing	Potential injury from attacks by blocking males; prevention of female mate choice; disruption of feeding; restricted movements; energetic costs of fleeing	Females try to escape chasing and blocking males; if unsuccessful, female mates, perhaps to avoid further attacks	Geist (1971); Hogg (1984)
Wild horses and Assateague ponies (<i>Equus caballus</i>)	Polygyny; single-male, multifemale bands	Males invade bands and try to steal females by herding, or try to take over band by challenging resident male; after a male acquires new females by either method, he forces copulation by chasing, biting, and mounting	Females occasionally suffer bite wounds; in wild horses, 86% of females <6 months pregnant aborted when acquired by a new male; abortions were highly correlated with forced copulations; also stress, reduced feeding efficiency	Wild horses: females kick, turn away, and run from males trying to force copulation; 4/18 attempts at forced copulation were blocked by female. Ponies: females transfer bands several times and appear to remain with males best able to protect them from harassment by other males	Horses: Berger (1983, 1986) Ponies: Rutberg (1990)
African elephants (<i>Loxodonta africana</i>)	Promiscuous; females associate in groups with female kin; solitary males seek estrous females	Males chase estrous females and try to copulate	Energetic costs of escape; stress	Females protest copulation attempts by young, subordinate males and maintain proximity to larger, older males who protect them from other males	Moss (1983); Poole (1989)

(continues)

TABLE I (Continued)

Species	Social/mating system	Context of male aggression	Potential costs to females	Female counterstrategies	References
Northern elephant seals (<i>Mirounga angustirostris</i>)	Polygynous; dominant males defend "harems" of up to 50 females from other males	When females leave harem to return to sea, subordinate males chase females, bite them, pin them to the ground, and force copulations; subordinate males also invade harems and try to force copulations	Out of 14,419 females 11 died on land from injuries inflicted during forced copulations; unknown number died at sea; many more suffer wounds	On way to sea, females sometimes permit copulation, because copulating male escorts female to sea and protects her from aggression by other males; females may aggregate on land to facilitate protection by dominant male from sexual coercion by other males	Le Boeuf and Mesnick (1991); Mesnick and Le Boeuf (1991)
Crabeater seals (<i>Lobodon carcinophagus</i>)	Solitary; promiscuous and/or polygynous	Males approach female with pup and try to mate; males sometimes force mothers and pups apart; males bite neck and upper back when trying to copulate	Females incur serious, bleeding wounds; if male separates mother and pup, pup dies	Females counterattack and try to force males away; females move away from approaching males	Siniff <i>et al.</i> (1979)
Southern sea lions (<i>Otaria byronia</i>)	Polygynous; dominant males defend "harems" from other males	Subordinate males raid harems and then hit, bite, throw, and abduct females and force copulations; subadult males abduct pups and try to mate with them	At end of season, 26% of females had fresh, bloody wounds; some pups die when separated from mothers	Females flee raiding males and sometimes escape; females may aggregate to facilitate protection by dominant male from harassment by other males	Campagna <i>et al.</i> (1988)
Australasian sea lions (<i>Neophoca cinerea</i>)	Polygynous; dominant males defend "harems" from other males	Dominant males herd females back into their territories by pushing and knocking females over; invading males pin female down and force copulation	Potential injury from herding; forced copulation	Females struggle when invading males force copulation, but are rarely able to escape	Marlow (1975)
Hawaiian monk seal (<i>Monachus schauinslandi</i>)	Polygynous; mating occurs in water	Groups of males mob females and try to mate; males bite females on neck, head, and back during copulation attempts	Serious wounds; some fatalities	Avoiding males and fighting back; once bitten, females become passive, perhaps to avoid further wounding	Alcorn and Buelna (1989); Johnson and Johnson (1979)

Bottlenose dolphins (<i>Tursiops truncatus</i>)	Bisexual communities; promiscuous	Stable coalitions of 2–3 males cooperate to herd estrous females; males prevent females from escaping by chasing, hitting, biting	Females are hit and bitten; some females have rakelike scars from bites; energetic costs of fleeing	Females sometimes escape from male coalitions	Connor <i>et al.</i> (1992b)
Lions (<i>Panthera leo</i>)	Bisexual groups; promiscuous	Stable coalitions of 2–7 males kill infants during group takeovers	Infanticide accounts for 27% of all cub mortality; females sometimes mortally wounded while protecting cubs from males	Mothers cooperate to defend young cubs from males and sometimes succeed; females may leave pride with older cubs when new males take over; females delay conception after infanticide to increase probability that strong male coalition will join their pride; protection from infanticidal males may be one important selection pressure favoring association with female kin	Packer and Pusey (1983a,b); Packer <i>et al.</i> (1990)
Farm cats (<i>Felis catus</i>)	Polygynous or promiscuous	Strange male may kill kittens	Loss of kittens	Cooperative defense by related females; protection from infanticidal males may be one important selection pressure favoring association with female kin	Macdonald <i>et al.</i> (1987)
Sea otters (<i>Enhydra lutris</i>)	Probably polygynous	During copulation, the male grasps female by nose or face with his teeth and sinks his teeth in	Deep puncture wounds to nose and face; eye damage; many females are scarred on nose and face; one female known to have died from infection in facial wound that hindered breathing	Females fight back and sometimes struggle free	Foote (1970)
Arctic ground squirrels (<i>Spermophilus parryi</i>)	Polygynous or promiscuous	Infanticide by intruding males	Loss of young	After juveniles emerge, related females share burrows and cooperatively maintain vigilance and defend young against intruding males	McLean (1982, 1983)

(continues)

TABLE I (Continued)

Species	Social/mating system	Context of male aggression	Potential costs to females	Female counterstrategies	References
White-footed mice (<i>Peromyscus leucopus</i>)	Promiscuous	Infanticide by immigrating males and resident males that had not sired young	Loss of young	Maternal aggression against male intruders deters infanticide; females mate with several males; males that have mated may be less likely to commit infanticide	Wolff (1985); Wolff and Cicirello (1989)
Water voles (<i>Arvicola terrestris</i>)	Polygynous	Potential infanticide by strange males	Potential loss of young	Pregnant females mate when they enter home range of strange male, and he does not subsequently harm their offspring	Jeppsson (1986)
Collared lemmings (<i>Dicrostonyx groenlandicus</i>)	Polygynous	Infanticide by introduced males	Loss of young	Mothers attack unfamiliar males and often prevent infanticide, especially after day 2 postpartum	Mallory and Brooks (1978)
Laboratory mice (<i>Mus domesticus</i>)	Promiscuous	Infanticide by introduced males	Loss of young	Mothers selectively attack males shown to be infanticidal in separate tests	Elwood <i>et al.</i> (1990)

^a All evidence is from studies conducted in the wild, except for the last two entries and data on maternal aggression in white-footed mice (Wolff, 1985).

ual fighting (Enders, 1952; Ewer, 1973). With the exception of sea otters, little information is available on how serious the fighting is and whether females sustain serious injuries as a result.

B. COSTS OF MALE AGGRESSION AND FEMALE COUNTERSTRATEGIES

As among nonhuman primates, quantitative data on the costs of male aggression in nonprimate mammals are rare. Le Boeuf and Mesnick (1991) estimate the probability that an adult female elephant seal will be killed by a male as .001 per season, and conclude that "this could be a significant selection pressure . . . that might have the effect of shaping the behavior and morphology of females to avoid being victimized." Packer and Pusey (1983a) report that over one-fourth of all infant mortality in lions is due to infanticide by males.

Female counterstrategies include physiological responses that delay conception (lions) or abort fetuses (the Bruce effect in many rodents; Huck, 1984). Frequent copulation and delayed conception in lions are hypothesized to increase the probability that a large male coalition will join the group, which in turn increases the chances that the females will be protected from a subsequent male takeover for long enough to bear and raise cubs (Packer and Pusey, 1983a,b). The Bruce effect has been interpreted as a means by which females cut their losses when infanticide appears likely (Huck, 1984). In contrast, Berger (1983) argues that abortion in female horses subject to forced copulation provides no benefit to the females, since infanticide will not occur if the fetus survives. (Kirkpatrick and Turner [1991] point out that forced copulations and induced abortion do not occur in all wild horse populations.) Pseudo-estrus during pregnancy, as described for several female primates confronted with strange males (e.g., grey langurs and red colobus), also occurs in water voles, and Jeppsson (1986) argues that it functions to reduce the vulnerability of the females to male infanticide.

Behavioral counterstrategies frequently include attempting to escape sexually aggressive males. Fighting back occurs but is less common, presumably because of the risks of injury. Lionesses, for example, attack males trying to kill their young and are sometimes mortally wounded in the process (Packer and Pusey, 1983a). Experiments with laboratory mice show that females with pups can discriminate between infanticidal and noninfanticidal strange males and are more likely to attack the former (Elwood *et al.*, 1990). In some rodents, maternal aggression is very effective in preventing infanticide (e.g., white-footed mice: Wolff, 1985; collared lemmings: Mallory and Brooks, 1978), but in others, it is not (e.g., arctic ground squirrels: McLean, 1982).

Sometimes, females submit to copulation with an aggressive male. Several authors interpret such submission as a tactic to avoid further aggression (bighorn sheep: Hogg, 1984; Hawaiian monk seals: Johnson and Johnson, 1979). Mesnick and LeBoeuf (1991, p. 272) characterize such tactics as trading sex for protection.

Female association with particular, protective males appears to be the most common mammalian strategy to reduce vulnerability to male sexual aggression and infanticide. These protective associations range in duration from years (e.g., horses/ponies, lions) to weeks (elephant seal harems), days (fallow deer, mountain sheep), or mere minutes (elephant seals, when females attempt to return to sea). Wrangham (1986, p. 463) refers to such protective males as "hired guns" and emphasizes that females need to form these protective associations with some males only because of the coercive behavior of other males.

Females employ diverse tactics to obtain the protection of dominant males. Female northern elephant seals (Cox and Le Boeuf, 1977) and female African elephants (Moss, 1983; Poole, 1989) emit a loud vocalization when mounted by subordinate males. This "protest" call functions to attract a more dominant male, who will chase the subordinate away. The female then often mates with the dominant male. Female elephants, bighorn sheep, and fallow deer sometimes actively maintain proximity to a dominant male, who provides protection from other males (Moss, 1983; Poole, 1989; Geist, 1971). Female ponies transfer from band to band several times, apparently in search of males best able to protect them from harassment by other males (Rutberg, 1990). As noted above, after losing cubs to strange males, female lions adopt behaviors apparently designed to attract a large male coalition.

In a few cases, selection pressures for female association with "hired guns" may account for aspects of the species' social or mating system, as argued for gorillas and chimpanzees, above. Clutton-Brock *et al.* (1988), for example, hypothesize that female choice for protective males is responsible for the evolution of leks in fallow deer (see Wrangham, 1980b, for a similar explanation for the evolution of leks in birds). Trillmich and Trillmich (1984) hypothesize that the benefits of protection by dominant males from sexual aggression by other males explains female aggregations in several pinniped species. Finally, Packer *et al.* (1990) show that group-living in female lions cannot be explained by the benefits of cooperative hunting and argue instead that one of the most important selection pressures leading to female groups is the need for cooperative protection against male infanticide. In support of this hypothesis, survival of cubs after male takeovers was significantly enhanced when two or more females were present compared to just one (Packer *et al.*, 1990). Macdonald *et al.*

(1987) make a similar argument for the evolution of communal rearing of young by related females in domestic farm cats.

C. SIMILARITIES AND DIFFERENCES BETWEEN NONHUMAN PRIMATES AND OTHER MAMMALS

Male aggression against females and young in other mammals shows several striking parallels with nonhuman primates and also some intriguing differences. Parallels include female vulnerability to infanticide or induced abortion when strange males invade or take over their groups, male use of aggression to herd estrous females away from other males, and the high frequency of the female "hired gun" counterstrategy. Differences include the apparently higher frequency of aggression during copulation itself in other mammals (especially in pinnipeds, mustelids, viverrids) compared with nonhuman primates; the greater frequency of sexual harassment by more than one male at a time (e.g., several pinnipeds, bighorn sheep, fallow deer) in other mammals compared with nonhuman primates; and a bias among other mammals (with striking exceptions, e.g., horses) toward brief associations with dominant males compared to the more typical long-term heterosexual associations of nonhuman primates. In addition, the use of female coalitions to thwart aggressive males appears to be rare in other mammals compared with nonhuman primates. All of these generalizations must remain tentative until data are available to allow more systematic comparisons between different mammalian taxa. Such systematic comparisons should prove extremely useful in helping to identify the ecological, demographic, and social factors associated with different kinds and intensities of male aggression against females and young, and different kinds of female counterstrategies.

VII. VARIATION IN MALE AGGRESSION AGAINST FEMALES

Even in the absence of many quantitative data, it is clear that the frequency and intensity of male aggression against females vary considerably among nonhuman primates and mammals in general. For example, although male aggression against females is common in a number of primates, including gorillas (Watts, 1992), chimpanzees (Goodall, 1986), baboons (Hausfater, 1975; Smuts, 1985), macaques (Oi, 1990; Manson, 1991), white-fronted and wedge-capped capuchins (Janson, 1986; O'Brien, 1991), black spider monkeys (McFarland Symington, 1987), and brown lemurs (Pereira *et al.*, 1990; M. E. Pereira, personal communication), it is very uncommon in others, such as bonobos (Kano and Mulavwa, 1984; White,

1992), patas monkeys (Loy, 1989), red-backed squirrel monkeys (Boinski, 1987), brown capuchins (Janson, 1984, 1986), woolly spider monkeys (Strier, 1990, 1992), and black-and-white ruffed lemurs (Foerg, 1982; Kaufman, 1991). Similar variation exists among other mammals.

It is difficult at present to investigate the factors responsible for this variation, because of enormous gaps in the data. As indicated at the start of this article, for most mammals, information on the presence or absence of male aggression against females and male sexual coercion is entirely lacking. It might be argued that when a detailed account of a species' social behavior fails to highlight male aggression against females, it can safely be interpreted as an indication that such aggression is rare or absent. However, we disagree with this suggestion, since, until recently, many accounts of well-studied species such as baboons and chimpanzees (and humans), in which we now know that male aggression against females is common, failed to emphasize its frequency, or even failed to mention it at all. Thus, at present, our analysis of interspecific variation must be limited to those species in which authors describe male aggression against females or explicitly indicate its rarity or absence. Because these species represent a small proportion of all primates (and an even smaller proportion of all mammals), many of the hypotheses presented below will require modification in light of new data. Our purpose, then, is to stimulate further research and theorizing, rather than to attempt a definitive assessment of interspecific variation and its causes.

Since all but the first of the factors described below is an aspect of the social structure of mammalian groups, it is important to begin by stating our assumptions with respect to the relative influence of ecological and social factors on social structure. We follow Wrangham's model of primate social systems (1979, 1980a; see also van Schaik and van Hooft, 1983; van Schaik, 1989). Wrangham argues that food distribution is the primary determinant of the distribution and grouping of females, which, in turn, is the primary determinant of male mating strategies and the distribution of males. Since male strategies may impose costs or confer benefits on females, male strategies may, however, exercise a secondary influence on female social patterns, which may then have a secondary influence on males. The interaction is complex and the extent to which male aggression against females and female counterstrategies are facilitated or constrained by ecological factors is not well understood. In general, we assume that ecological factors are primarily responsible for philopatry and female-bonding, as occurs in most Old World monkeys (Wrangham, 1980a). On the other hand, we assume that there is little or no ecological pressure for female grouping in any of the apes (Wrangham, 1979, 1987a), and hypothesize that male aggression is the principal selection pressure leading

female gorillas to aggregate around (usually) one male and for female chimpanzees to associate loosely with a group of related males (see Sections IV,F and V,B).

1. *Phylogeny cannot explain variation in male aggression toward females.* The examples given at the beginning of this section indicate that phylogeny cannot account for much of the observed variation in male aggression against females, since all of the major primate taxa (apes, Old World monkeys, New World monkeys, prosimians), as well as several families, subfamilies, and genera, include species reported to show both high and low levels of this behavior.

2. *Although increased sexual dimorphism in body size and weaponry make females more vulnerable to male aggression (Strier, 1990; Le Boeuf and Mesnick, 1991), the effects of sexual dimorphism are often swamped by other factors (Fedigan and Baxter, 1984; Kappeler, 1991).* Clearly, the ability of males to physically dominate females will influence the likelihood of male aggression against females (Le Boeuf and Mesnick, 1991). For example, severe aggression in the context of copulation appears to characterize a number of pinniped species in which males are much larger than females (e.g., elephant seals, sea lions). However, sexual dimorphism alone clearly does not determine levels of male aggression against females. Consider, for example, common chimpanzees and bonobos, which show similar degrees of sexual dimorphism in body size (Jungers and Susman, 1984) but very different levels of male aggression against females (see below). Similarly, although all lemurs are monomorphic (Kappeler, 1991), in some species (e.g., brown lemurs) adult males show considerable aggression toward adult females, while in others (e.g., ring-tailed lemurs), they show none (but note that male ring-tailed lemurs do attack infants separated from their mothers [Pereira and Weiss, 1991]). In many of the monomorphic lemurs, and in hyenas, in which males and females differ little in size, females consistently dominate males (lemurs: Foerg, 1982; Young *et al.*, 1990; Kappeler, 1991; Pereira *et al.*, 1990; spotted hyenas: Frank, 1986a,b). Along the same lines, males may be very aggressive toward females in species in which there is little size difference between males and females (e.g., black spider monkeys: McFarland Symington, 1987; bottlenose dolphins: Connor *et al.*, 1992a; wild horses: Berger, 1986; crabeater seals: Siniff *et al.*, 1979) and even in species in which males are smaller than females (Hawaiian monk seals: Alcorn and Buelna, 1989). Finally, among species in which males are larger than females, the extent to which males dominate females and the frequency of male aggression against females do not appear to conform closely to the degree of sexual dimorphism. Patas monkeys, for example, are among the most sexually

dimorphic monkeys, and yet male patas rarely aggress against females (Loy, 1989). In contrast, male aggression against females is common in macaques and chimpanzees, although in these species females are 70–80% as large as males. These patterns, in turn, may reflect differences in the extent to which females form coalitions against males.

3. *Frequent coalitions among females will reduce male aggression against females.* In species in which females remain with their natal kin, they can improve their ability to resist male aggression by forming alliances with other females (Smuts, 1987b; Nadler, 1989a; Strier, 1990). Examples include lions, capuchins, and many species of “female-bonded” Old World monkeys. The effectiveness of female–female alliances may depend, in part, on the degree of confluence of female interests in their struggles against males. Patas monkeys, for example, live in small groups in which only one male remains in the group throughout the year, and patas females appear to present a consistently united front against this male, which may help to account for his very peripheral status and lack of aggression toward females, despite his much larger size (Loy, 1989; Chism *et al.*, 1984). Among macaques, in contrast, which live in groups containing several female matriline and more than one male, the interests of different females may often conflict, so that presenting a united front against particular males is not always possible. The contrast between bonobos (pygmy chimpanzees) and chimpanzees highlights the potential significance of female–female alliances against males. In bonobos, as in chimpanzees, females transfer from their natal groups around adolescence (Nishida and Hiraiwa-Hasegawa, 1987). However, bonobo females, in contrast to chimpanzee females, routinely ally with one another against males, both in the wild (Kano, 1987; Furuichi, 1989) and in captive groups (A. R. Parish, personal communication). Paralleling this difference in female alliances are striking differences in female–male dominance relationships and the frequency of male aggression against females. Among chimpanzees, males consistently dominate females (Goodall, 1986), and, as indicated above, male aggression against females is common. Among bonobos, in contrast, “almost all males of middle to lower ranks are subordinate to full [sic] adult females” and “even the alpha male is threatened or chased by a female or a group of females” (Kano, 1987, p. 60), and male aggression toward females is rare (Kano, 1987; Furuichi, 1989; White, 1992). The importance of female allies is further underscored by Idani’s (1991) observations that newly transferred females who have not yet formed strong bonds with resident females are considerably more vulnerable to male aggression. Wrangham (1986) argued that female bonobos associate with males in order to gain protection from sexual coercion

by other males. However, the evidence just described, combined with the absence of reports of male agonistic support of females against other males, indicates that, contrary to Wrangham's hypothesis, female bonobos gain protection from male aggression primarily through their alliances with other females.

The significance of female–female alliances against males is also suggested by data on chimpanzees, orangutans, and black spider monkeys. These three are among the few polygynous anthropoid primates in which, presumably as a result of feeding competition (Wrangham, 1979; Rodman, 1984; McFarland Symington, 1987), females cannot afford to forage routinely with other females, and in all three male aggression against females seems to be particularly common (see above).

4. *Females living in one-male groups and multimale groups will experience different types of male sexual coercion.* In species in which a single male typically lives with several females, sexual coercion by the breeding male should be minimal (since he is the only mate available), except at those times when outside males approach the group. (During these events, the breeding male may attempt to herd "his" females away from other males [e.g., mountain gorillas: Sicotte, 1989; capped langurs: Stanford, 1991; red deer: Clutton-Brock *et al.*, 1982]). In one-male groups, the breeding male may provide important benefits to his females by protecting them from sexual harassment and/or infanticide by outside males. However, females under such systems periodically suffer intense sexual coercion, in the form of infanticide, when the breeding male dies (e.g., mountain gorillas) or is challenged (e.g., grey langurs, wild horses). Estrous females living (or breeding) in multimale groups, in contrast, are expected to suffer higher rates of male sexual coercion routinely, because the constant presence of rival males will often select for sexually coercive strategies. Females living in multimale groups are also expected to suffer higher rates of nonsexual aggression, such as during feeding, because of the presence of many males. However, such females are expected to be less vulnerable to male infanticide than are females living in one-male groups, for two reasons. First, females will gain protection from infanticide by possible fathers of their infants, and/or by males who protect infants in exchange for future mating opportunities with the mother (Smuts, 1985; Smuts and Gubernick, 1992). Second, the presence of many rival males decreases the benefits to males of infanticide, since male–male competition reduces the probability that the infanticidal male will subsequently fertilize the mother.

5. *Associations with particular males will reduce female vulnerability to sexual aggression.* As noted above, females living in one-male groups

may gain protection from male aggression through their long-term association with the breeding male. In species living in multimale groups, females may form long-term bonds (e.g., savanna baboons) or associate on a short-term basis (e.g., elephant seals) with one, or a few, adult males, in order to gain protection from other males. In savanna baboons, male protection extends to the infants of female associates even when the protective male is unlikely to be the father (Smuts, 1985), apparently in exchange for future mating benefits. At least among nonhuman primates, these relationships may function as alternatives to protective alliances with other females. Therefore, affiliative heterosexual relationships are more likely, or will be more important, when sexual dimorphism is great (because female allies are less valuable), as in baboons and gorillas, and/or when females transfer from their natal groups (because related females are unavailable as allies), as in gorillas and chimpanzees.

6. *Male reliance on females for "political" support will reduce male sexual coercion.* When males rely on females as allies against other males, their need to recruit female coalition partners may reduce aggression, including sexual coercion, toward females. This hypothesis is consistent with the observation that male sexual coercion is relatively rare in captive chimpanzees, in which female political support is important to male status competition (de Waal, 1982), compared with wild chimpanzees, in which it is not (Goodall, 1986). In a group of free-ranging rhesus monkeys in which the alpha female's support was critical to the high-ranking males, they never showed aggression toward her, although lower ranking males did so (Chapais, 1983a,c). Similarly, in captive vervet monkeys, in which high-ranking females strongly influence male dominance status (Raleigh and McGuire, 1989), males typically leave a high-ranking female alone after she aggressively resists mounting attempts, but they often persist in trying to mate following similar refusals by lower ranking females (Keddy, 1986). It is not clear whether reliance on females for political support inhibits male aggression toward females in other mammals.

7. *The existence of male-male alliances increases female vulnerability to sexual coercion.* Male aggression against females or infants in nonhuman primates almost always involves single males, but notable exceptions include spider monkeys (Fedigan and Baxter, 1984; McFarland Symington, 1987), red-backed squirrel monkeys (Boinski, 1987), and chimpanzees (see above; Goodall, 1986; Nishida and Hiraiwa-Hasegawa, 1985), in which males sometimes gang up on females, and red howlers (Crockett and Sekulic, 1984; Pope, 1990), in which groups of males invade troops, evict the breeding male, and commit infanticide. In black spider monkeys, red-backed squirrel monkeys, and chimpanzees, males remain in their

natal groups and form long-term bonds with male kin, an unusual pattern among mammals. In red howlers, invading males are often closely related (Pope, 1990). Other mammals characterized by persistent male alliances also show cooperative male aggression against females (bottlenose dolphins: Conner *et al.*, 1992a,b) or infants (lions: Packer and Pusey, 1983a). Male cooperative coercion of females appears to be especially widespread and significant in our own species (B. B. Smuts, 1992, 1993).

For heuristic purposes, we have stated each of these hypotheses independently, but the challenge is to determine how these variables, and others, interact to produce observed levels of male aggression against females.

VIII. EVALUATING THE SEXUAL COERCION HYPOTHESIS

In this article, we have described many examples of male aggression against females that are hypothesized to function as sexual coercion, that is, aggressive acts that appear to increase the male's mating success at some cost to the female. Here we briefly consider the kinds of evidence needed to determine, in particular instances, whether (a) male aggression against females increases male mating success and (b) male aggression against females inflicts costs on females.

A. EVIDENCE SHOWING THAT MALE AGGRESSION AGAINST FEMALES CORRELATES WITH INCREASED MATING SUCCESS

Quantitative evidence exists for a few species showing that male aggression is correlated with increased mating activity. For example, among Southern sea lions, when a peripheral male uses aggression to abduct a female from the group, he copulates more often than peripheral males that did not abduct a female (Campagna *et al.*, 1988). Assuming that copulations with abducted females occasionally lead to fertilization, this evidence indicates that abduction leads to reproductive benefits. In other cases, it may be harder to interpret correlational evidence. Among Japanese macaques, for example, dyads in which the male showed aggression toward the female during the mating season were significantly more likely to copulate than dyads in which the male showed no aggression (Enomoto, 1981). It is not clear, however, whether aggression toward females caused increased male mating success; it is possible that dyads that copulated showed a higher frequency of male aggression toward the female simply because the members spent more time together.

B. EVIDENCE CONCERNING THE SPECIFIC SEQUELAE OF MALE AGGRESSION AGAINST FEMALES

The difficulties mentioned above in interpreting correlational evidence emphasize the importance of prolonged observations of particular individuals to document the specific events that follow male aggression against females. For example, during focal samples of estrous female rhesus monkeys, Manson (1991) documented the effects of escalated attacks by males on females. Most such attacks occurred when the female's nearest adult male neighbor was lower ranking than the attacker or from a different group. For each male attack on a female associating with another male, Manson determined whether the female subsequently first approached the attacker or her prior associate, and whether she eventually mated with either male. Following attacks, females approached their previous associates more often than they approached attackers, and they were also more likely subsequently to copulate with previous associates than with attackers. Manson (1991, p. 24) concludes that "male attacks on estrous females that were accompanying lower-ranking males did not, in the short run, induce the female to copulate with the attacker rather than the accompanying lower-ranking male. Attackers may have increased their chances of copulating with the victim on subsequent days, but these effects are more difficult to assess, because of problems in determining the 'expected' probability that a pair will copulate in the absence of attack." Huffman (1987) reached similar conclusions for Japanese macaques. These studies illustrate a serious difficulty involved in determining the consequences of male aggression against females: although we can document the events following an aggressive event, we have no way to know for certain what would have happened had the male not shown aggression toward the female.

There are several approaches to this problem. For a given time interval that is likely to encompass both male aggression toward females and male mating with those same females, one could compare rates of copulation by males with females they showed aggression toward compared with rates of copulation by those same males with females they did not show aggression toward. The results would have to be interpreted with caution, because the presence or absence of aggression in a particular dyad may reflect other aspects of the relationship. For example, if a male has reason to believe that a female is likely to prefer him as a mate, he may have less need to show aggression toward her than toward a female who does not prefer him. Data on frequency of aggression and rates of copulation would in this case be confounded by the effects of female preference. Another approach would be to compare the aggressive behavior and subsequent

mating activities of different males, to see whether those who showed more aggression mated more. Again, however, one would need to consider carefully the possibility that differences among the males in the frequency of aggression reflected differences in their need to use aggression as a reproductive tactic. Suppose some males are in a better position to offer females benefits that lead females to prefer them as mates. Males less able to provide benefits might improve their mating success through the use of aggression, but if this strategy is generally less successful than providing females with benefits, the data will show a negative correlation between rates of male aggression and mating success.

These hypothetical examples are not meant to indicate that it is impossible to determine whether male aggression sometimes increases mating success but rather to emphasize the need to examine male aggression against females in conjunction with detailed knowledge of individual life histories, particular social relationships, and the alternative reproductive strategies available to individuals. In investigating this phenomenon, it will be important to establish general patterns by collecting data on large numbers of individuals. However, because of the difficulties of interpretation discussed above, it will also be critical to obtain very detailed evidence on the relationship between aggression (or lack of it) and mating (or lack of it) in particular dyads over long periods of time. Such "case study" data should help to identify the significance male aggression toward females holds in particular species, or even among particular types of individuals (e.g., adolescents).

An example of such a case study approach comes from Nadler and Miller's (1982) research on mating in captive gorillas. Sexual behavior was quantified each day for four females paired with each of two males for two consecutive cycles. Several results suggested a causal relationship between male sexual aggression and copulation frequency. First, one male consistently showed more sexual aggression than the other, and he also consistently copulated more often. Second, when data for each male were examined separately, the frequency of copulation-days (days in which any copulation occurred) was directly related to the frequency of aggression shown toward different females. The authors considered two alternative explanations for these findings. First, perhaps the females were simply more attracted to the more aggressive male. This hypothesis was rejected, because females tried more often to avoid the more aggressive male. Second, perhaps the direction of causality was reversed, so that male aggression was stimulated by sexual interaction. To test this hypothesis, the authors examined the frequencies of female presenting (which typically preceded copulation) and of male aggression across the two consecutive cycles for each of seven pairs (one pair was removed from the study due

to illness). In each pair, the frequency of presenting increased from cycle 1 to cycle 2, the result "expected if the females learned during cycle 1 that such presenting reduced male aggression" (Nadler and Miller, 1982, p. 236). If female presenting stimulated male aggression then male aggression should also have increased from cycle 1 to cycle 2, but the reverse was found for all seven pairs. The authors conclude that "male aggression, most evident in the first cycle, stimulated heightened levels of female presenting and copulation, rather than the reverse" (p. 237). A similar case study approach could be employed in group-living animals, by documenting patterns of sexual aggression and mating within dyads across time.

C. EVIDENCE CONCERNING WHICH MALES ARE MOST LIKELY TO SHOW AGGRESSION AGAINST FEMALES, AND WHICH FEMALES ARE MOST OFTEN VICTIMS OF MALE AGGRESSION

Such evidence, particularly when it is combined with knowledge about life histories and social relationships, may help to identify the functional consequences of male aggression against females. For example, the fact that estrous females in many species receive more aggression from males than do anestrous females provides support for the hypothesis that males use aggression to obtain mates. The fact that peripheral and/or subordinate males are often the ones most likely to show aggression toward estrous females indicates that aggression may sometimes be a competitive tactic adopted by males that are at a mating disadvantage.

D. EVIDENCE CONCERNING THE EFFECTS OF PRESENCE OR ABSENCE OF OTHER MALES ON MALE AGGRESSION TOWARD FEMALES

In bighorn sheep, dominant males associating with estrous females away from other males exhibit slow and gentle courtship. These same males aggressively herd females when rival males are present (Geist, 1971). Similarly, in an experimental study of male-female pairs of crab-eating macaques housed together, the rate of male aggression toward the female increased from a low frequency of once every 3 to 4 hr when a male and female were housed alone to over seven times an hour in the presence of a rival male (Zumpe and Michael, 1990). Such evidence supports the hypothesis that males use aggression against females to reduce the likelihood of losing mating opportunities to rival males. In such cases, however, we must be able to rule out the alternative hypothesis that males show less aggression toward females when other males are not present simply

because females show less resistance when other males are not available as alternative mates.

E. EVIDENCE REGARDING THE COSTS TO FEMALES OF MALE AGGRESSION

For a behavior to qualify as sexual coercion by our definition, it must not only benefit the male but must also inflict a cost on the female. Many more data are needed quantifying the costs to females of male aggression, which may range from subtle costs, such as increased energetic expenditure or loss in feeding efficiency, to dramatic costs, such as severe injury or even death. If these costs can be translated into effects on female reproduction, we may discover that, as a result of the costs they impose on females, male reproductive strategies sometimes decrease the reproductive rate of a species or population (Mallory and Brooks, 1978).

The existence of male aggression against females does not in and of itself demonstrate a cost to females. In theory, a female might avoid an approaching male (i.e., be chased by him) or resist copulation or mate-guarding to determine his health and vigor or to incite competition among surrounding males in order to identify the "best" male present (Thornhill and Alcock, 1983; Westneat *et al.*, 1990). For example, female bighorn sheep repeatedly run away from groups of chasing males but eventually submit to copulation with the most dominant male of the chasing group. Is the female a victim of male aggression, or is she using the male tendency to chase estrous females as an efficient means of identifying the strongest male in the vicinity? The critical issue here is not whether the female benefits from mating with the strongest male (presumably she does benefit, given the alternatives) but whether the benefits the female receives are important in and of themselves (e.g., being chased allows her to mate with the male with the "best genes") or whether the benefits are meaningful only because male aggression exists (e.g., submitting to copulation with the dominant male is the best way for the female to avoid further costs, given the existence of male sexual aggression). In other words, we need to ask whether, if the female had complete control over male behavior, would she choose to be subject to male aggression or not?

Observational evidence alone may sometimes allow us to infer the answer to this question. If, for example, females routinely suffer serious injuries, presumably they would be better off if male aggression did not exist. Similarly, we may infer that male aggression is costly if females persistently resist it in ways that risk injury (e.g., fighting back) or endanger their infants. In contrast, female razorbills visit mating arenas, where they

have opportunities to mate with males other than the male they are paired with. In this situation, females frequently resist (always successfully) copulation attempts (Wagner, 1991). Because these visits are apparently completely voluntary, and because females sometimes visit the mating arenas after they have laid their final clutches (i.e., females do not need to visit these areas to be fertilized), Wagner (1991) concluded that exposure to male copulation attempts is beneficial rather than costly to females.

In other cases, experimental techniques may help to determine whether females will choose to avoid male aggression, or its consequences, when they have the option to do so. Nadler's experiments with captive apes, described earlier, showed that when females could completely control their associations with males, copulations at times other than mid-cycle, which were normally associated with male aggression, ceased entirely (Nadler, 1982, 1988; Nadler and Miller, 1982). More experiments examining the interplay between male aggression and female mate choice are needed.

F. EVIDENCE FROM A WIDE VARIETY OF SPECIES, INCLUDING THOSE IN WHICH MALE AGGRESSION AGAINST FEMALES AND INFANTS IS MINIMAL

As noted above, because male aggression against females has so far received little systematic attention, it is difficult to know whether the absence of reports of male aggression against females indicates that it does not occur, or that it has been overlooked. For this reason, we have focused on those species in which male aggression against females or infants has been reported, and have said little about those in which it has not. However, if we want to understand the selective significance of this phenomenon and the factors responsible for variation in its frequency and intensity, we need to know not only about its occurrence, but also about the species and circumstances in which it occurs only rarely or not at all. This will require the collection and reporting of "negative evidence." Such evidence could prove critical to identifying effective female counterstrategies. For example, among savanna baboons, male infanticide has been reported on numerous occasions (Collins *et al.*, 1984). In contrast, among their relatives the macaques, which have been studied equally intensively, it has been reported only once (Ciani, 1984). Macaques and savanna baboons have very similar social systems, but in macaques females routinely form coalitions against males, whereas in baboons they do not, presumably because baboons show much greater sexual dimorphism in body size and weaponry. This comparison suggests that the formation of female-female coalitions in macaques may be an effective counterstrategy against male

infanticide. More data are needed to test this hypothesis, but it illustrates the way that comparative data on variation in female and infant vulnerability to male aggression may deepen our understanding of this phenomenon.

IX. IMPLICATIONS OF MALE SEXUAL COERCION FOR SEXUAL SELECTION THEORY

The evidence reviewed above indicates the widespread existence of male aggression against female mammals. Although not all male aggression against females occurs in a sexual context, much of it does, and a significant proportion of such aggression apparently functions as sexual coercion; that is, it increases male mating success relative to other males, at some cost to the female. Male aggression in general, and sexual coercion in particular, also occur in other animals (e.g., insects: Borgia, 1980; Thornhill, 1980; Arnquist, 1980; birds: Beecher and Beecher, 1979; McKinney *et al.*, 1983; Emlen and Wrege, 1986). Male sexual coercion appears to have influenced myriad aspects of female behavior and life histories, including female choice of social partners and, in some cases, the form of the social system itself. These results suggest that sexual coercion is an important male reproductive strategy that can impose strong selection pressures on both sexes. Yet the significance of sexual coercion has not been widely recognized.

We suggest that this lack of recognition results from the failure to acknowledge sexual coercion (usually male coercion of females) formally as a third form of sexual selection comparable to the two forms that have been recognized ever since Darwin: intrasexual competition for mates (usually between males) and intersexual mate choice (usually by females) (Darwin, 1871). Like these other forms of sexual selection, sexual coercion involves behaviors that influence mate selection and retention through interactions with conspecifics (Darwin, 1871). Similarly, successful coercion of females can increase male mating success at the expense of other males, just as do successful fighting or successful mate attraction.

When sexually coercive strategies are discussed in the literature, they are usually treated either implicitly (e.g., Hogg, 1984) or explicitly (e.g., West-Eberhard *et al.*, 1987) as an aspect of male–male competition, probably because they are a means by which some males obtain mates at the expense of others. However, female choice is also a means by which some males obtain mates at the expense of others; yet Darwin (1871), Fisher (1930), Trivers (1972), and many others have clearly recognized the importance of conceptualizing mate choice as a distinct form of sexual selection. Similarly, it is imperative to identify intersexual coercion as a

form of sexual selection that is conceptually distinct from, but interacting with, intrasexual competition.

We suggest that all three forms of sexual selection are intimately related, and that each influences and is influenced by the others. Bradbury and Davies (1987) proposed that nearly all mating systems include a mix of intrasexual competition and intersexual mate choice, and they argued that improved understanding of animal mating behavior requires explicit consideration of how these two forces interact. Empirical studies increasingly support the validity and usefulness of this approach (e.g., McPeck, 1992; Rosser, 1992). We wish to extend Bradbury and Davies' argument to include explicit consideration of the potentially critical role that intersexual coercion and female resistance to it may play in this dynamic system. Thus, for example, previous theoretical treatments of social evolution have focused on how male–male competition and female choice interact in particular ecological circumstances to produce characteristic mating systems (e.g., Emlen and Oring, 1977; Clutton-Brock and Harvey, 1978). We suggest that an expanded theoretical perspective that emphasizes male sexual coercion and female strategies to resist such coercion will significantly improve our understanding of the evolution of social systems, mating systems, and related aspects of animal behavior (see Section IV, F for examples).¹

Increased attention to the potential significance of male sexual coercion and female resistance to it should help transform implicit assumptions into explicit hypotheses amenable to evaluation. A good example of the need to make assumptions explicit concerns the treatment of male–male contest competition (i.e., fighting, dominance displays, etc.) in the sexual selection literature. Authors frequently imply that the outcome of male–male contest competition largely determines differential male mating success. This conclusion treats females as passive resources. Others recognize the potential importance of female choice, but claim that it is often constrained, or negated, by the outcome of male–male competition (e.g., Thornhill, 1979). However, the outcome of male–male competition, in and of itself, constrains female choice only when dominant males succeed in keeping other males away from females, so that female options are limited to mating with the winners of male–male competition, or not mating at all.

¹ In this article, we have emphasized male sexual coercion of females, along with male–male mating competition and female mate choice, but a complete understanding of social evolution will require investigation of female sexual coercion of males, as well as female–female mating competition and male mate choice. Female sexual coercion is expected to occur, at least occasionally, in “sex-role reversed” species, in which females compete intensively for mating opportunities with males (Gwynne, 1991).

If winning males are not able to keep other males entirely away from some females, then winning males gain a reproductive advantage if and only if they either (a) coerce females into mating with them, or (b) are freely chosen by females as mates (because they offer "good genes," protection, resources, etc.). (Note that if females mate with dominant males because dominant males punish them if they do not, then it is not an instance of free choice but instead represents a response imposed by sexual coercion, and as such falls under [a], above.)

Thus, unless males succeed in keeping all other males away from females (which is probably relatively rare in most mammals), *the outcome of male-male contest competition has meaningful reproductive consequences only in conjunction with either female mate choice or male sexual coercion (or both).*

To realize the implications of this insight, we must explore the complex interactions between the different components of sexual selection. Consider, first, how the possibility of effective female resistance to male sexual coercion might influence the intensity of male-male competition. If males cannot coerce females into mating with them, two possibilities exist.

1. Males may compete intensively if females benefit from choosing males that have demonstrated superior fighting ability. For example, Clutton-Brock *et al.* (1988) suggest that female fallow deer benefit from associating and mating with dominant males because these males are best able to provide females with protection from sexual harassment by other males. In species in which females freely choose their mates, but males kill infants, females may choose to mate with dominant males because they provide the most effective protection against infanticide. Pereira and Weiss (1991) suggest that this is why female ring-tailed lemurs choose to mate with dominant males. These considerations may help to explain why in both species, despite the obvious exertion of female mate choice, males compete intensely and aggressively for dominance status.

2. In contrast, if females can freely exert mate choice but have no reason to mate with the males showing the highest competitive ability, male contest competition for mates should be minimal. Woolly spider monkeys may be a good example (Strier, 1990, 1992). In this species, females and males are the same size, perhaps because locomotor and energetic constraints set an upper limit on body size. Males show no sexual aggression toward females, and females freely choose their mates. Most strikingly, within groups, male woolly spider monkeys show absolutely no overt competition for mates (Strier, 1990, 1992). Spotted hyenas may be another example. This species, like many Old World monkeys, is characterized by strong female-female coalitions based on kinship (Frank,

1986a,b). However, unlike Old World monkeys, the sexes are similar in size, females consistently dominate males, and males do not try to coerce females into mating. Female ability to choose their mates may explain the mysterious absence in this species of overt aggression among males, although male hyenas do exhibit dominance relationships.

The relationship between male dominance rank and male mating success varies widely in animals (Dewsbury, 1982), including primates (Fedigan, 1983) and attempts to explain this variability have met with limited success. The above analysis suggests that differential ability of dominant males to coerce and sequester females, which has been almost entirely ignored, might help to explain why male dominance correlates with mating access much better in some studies than in others, and why males appear to compete more intensively in some species than in others. In most instances, of course, male ability to coerce females will not be uniform within species, but will vary within and between populations; similarly, some females will be better able to resist coercion than others (see examples given earlier for high-ranking female macaques and vervet monkeys) (Gowaty, 1992). In addition, the benefits to females of choosing "dominant" males (i.e., the winners of male contest competition) will also vary across females and across situations. Also, female mate "choice" and male sexual coercion will often be inextricably intertwined. For example, if dominant males are able to coerce females successfully, females may choose to mate with them to avoid the costs of coercion. On the other hand, (or in addition) females may choose dominant males because those males are best able to protect females (and/or their infants) from coercion by other males (Wrangham, 1979). These examples indicate that the interplay between male contest competition, male sexual coercion, and female choice will be dynamic and context-specific. Only by examining this interplay in all its subtlety and complexity will we be able to understand many critical aspects of animal societies.

One such aspect involves female behaviors traditionally interpreted as tactics to facilitate mating with males who provide the "best genes." Bartholomew (1970) argued that female pinnipeds congregate in tightly packed groups on land so that they can mate with dominant males who are genetically superior. Similarly, Cox and Le Boeuf (1977) argued that female elephant seals vocally protest copulations with subordinate males because they benefit from mating with dominant males who carry superior genes. A focus on male sexual coercion suggests the alternative hypothesis that female aggregation in pinnipeds, and female protest vocalizations in elephant seals, benefit females by increasing the probability that dominant males will protect them from sexual aggression by other males (Trillmich

and Trillmich, 1984). Indeed, it is possible that many cases in which females appear to prefer dominant males as mates are better explained by the protective benefits those males provide than by their "superior genes" (Wrangham, 1979).

Another aspect of animal societies that may be illuminated by consideration of sexual coercion as a selective force is the evolution of sexual dimorphism in body size and weaponry. Consistent with the views expressed here, Richard (1992) points out that in some polygynous mating systems female choice is paramount, and argues that, under such conditions, larger size in males may not be favored by natural selection even though variance in male mating success may be large. In addition, perhaps we need to rethink the assumption that intrasexual competition is the main selective force influencing relative body size in males and females. Attempts to account for variation in the degree of sexual dimorphism in body size in terms of male-male competition (Clutton-Brock *et al.*, 1977; Alexander *et al.*, 1979; Gaulin and Sailer, 1984) and/or female-female competition (Ralls, 1976; Hrdy, 1981; Jolly, 1984; Richard and Nicoll, 1987; Young *et al.*, 1990) have met with limited success (e.g., Shine, 1988). Both sets of explanations ignore the most obvious consequence of sex differences in size and weaponry: differential ability of one sex to dominate the other. The possibility that intersexual conflict may be a selective force influencing male and female body sizes deserves exploration. Under certain conditions, selection may favor larger body size in females because it results in decreased vulnerability to male aggression. This hypothesis may help to explain, for example, lack of sexual dimorphism in spotted hyenas and ring-tailed lemurs, species in which females dominate males and aggressively defend offspring against potentially infanticidal males (Kruuk, 1972; Pereira and Weiss, 1991).

Still another important aspect of animal societies that may be illuminated by recognition and study of male sexual coercion as a major selective force is the evolution and expression of long-term male-female associations and male parental behavior. We have argued above that male-male competition is usually ineffective as a reproductive strategy unless complemented by either male sexual coercion of females or female choice. We have also argued that female choice may often be based on female preference for effective male protection (Smuts and Gubernick, 1992) rather than for "good genes." If these arguments have some validity, they suggest that male tendencies to associate regularly with particular females may have evolved: (a) to protect females and their offspring from aggression by other males, and (b) as an alternative to sexual coercion in the repertoire of male reproductive strategies (see Smuts [1992] for application of this argument to human social evolution). This in turn suggests that to understand why

males sometimes pursue either one of these strategies we need to know why they sometimes pursue the other.

Whether males try to gain mates by imposing costs on females or by providing them with benefits should depend on the costs to the male of doing one or the other, a male's ability to provide females with benefits, and the significance of these benefits to females. Consider, for example, two closely related species, brown capuchins and white-fronted capuchins, living in the same environment (Janson, 1986). Both species live in matrilineal groups with several adults of both sexes, and the diet of both species includes large amounts of fruit. Brown capuchins feed on patchy, defensible resources, and, by tolerating females who mate with him and their young at food patches and helping to keep other males away from these patches, the alpha male offers females a critical benefit. As a result, Janson (1984, 1986) argues that the females consistently and actively choose the alpha male as their mate. Because females prefer to mate with the alpha male, he does not need to employ sexual coercion, and Janson never saw him do so. Critical to this system, perhaps, is the fact that the alpha male can offer important benefits to females as an incidental by-product of his own foraging strategies (which exclude subordinate males from food patches) at little apparent cost to himself. White-fronted capuchins, in contrast, specialize on foods that occur in larger, less defensible patches, and, in contrast to brown capuchins, females and young do not cluster around the alpha male while feeding. Janson (1986) argues that, because the alpha male cannot offer females foraging advantages, they have little to gain from mating with him and instead seek matings with all the males in their group. The alpha male pursues estrous females and tries to force copulations on them, but he cannot prevent the females from mating with subordinate males.

This example shows how an apparently slight difference in the ecological context can dramatically alter the dynamic interplay between male-male competition, female choice, and sexual coercion to produce a radically different outcome. It suggests two conclusions. First, simple, causal models that attempt to explain behavior by invoking relatively gross factors, such as the form of the mating system or the habitat type, need to be replaced by more dynamic models that consider complex interactions between specific variables (Bradbury and Davis, 1987). Second, because small changes in particular variables can produce large differences in the way the three components of sexual selection interact, we should expect to see considerable variation in behavioral outcomes both between and within species, and even within the same group at different times.

Sometimes, for example, females make friends with nonfathers, who provide protection to females and their offspring in return for future sexual

access, as reported by Smuts (1985) for savanna baboons near Gilgil. When such friendships endure for several years, however, the friends are likely to be protecting their own offspring (Smuts and Gubernick, 1992). Berkovitch (1991), in contrast, found that in a different troop in the same population, females formed friendships mainly with probable fathers of their infants *after* mating with them. He suggested that the difference between his findings and those of Smuts (1985) might reflect subtle demographic differences between the two troops. Sometimes females prefer dominant males as both protectors and mates, probably because dominant males are the most effective protectors (e.g., red howlers, Sekulic, 1983b; Pope, 1990; brown capuchins: Janson, 1984, 1986). Savanna baboon females sometimes choose subordinates for both roles (Smuts, 1985). Rhesus and Japanese macaque females sometimes prefer dominant friends but subordinate mates (Huffman, 1987; Manson, 1991). Since dominant males frequently attempt to gain sexual access to their friends but usually fail (Huffman, 1987), it is clear that this arrangement is imposed by females. Why females should prefer, and dominant males should accept, the arrangement is a mystery that is likely to be solved only through insightful investigation and analysis of the complex dynamics of macaque social life.

X. CONCLUSION

Although infanticide, physical aggression, and other modes of male sexual coercion of females have sometimes been viewed as important phenomena, they have not been recognized as manifestations of a single selective force comparable in evolutionary significance to competition between males and mate choice by females. We predict that the approach advocated here, by integrating a broad range of phenomena into a single theoretical framework, will generate new hypotheses to explain puzzling behavior and identify important problems that have previously gone unrecognized.

XI. SUMMARY

Male aggression against females is a prominent feature of many primate societies. Data on the frequency and contexts of male aggression against females in primates suggest that males often use force, or the threat of force, to increase the chances that females will mate with them, and/or to decrease the chances that they will mate with other males. Such aggression is labeled sexual coercion. Infanticide is considered a form of sexual

coercion, because it involves the use of force and often functions to increase male sexual opportunities. Male aggression against females and sexual coercion, including infanticide, also occur in many other mammals. Intriguing similarities to and differences from primates offer important opportunities for comparative studies. Females resist male aggression through a variety of counterstrategies, including alliances with other females and with male protectors, and modification of the timing of reproduction. Male aggression against females and sexual coercion impose substantial costs on females and provide important benefits to males and therefore represent a significant selection pressure influencing life histories and behaviors in both sexes. Variables hypothesized to account for interspecific differences in male aggression against females include sexual dimorphism in body size and weaponry, dispersal patterns, and differences in female–female, female–male, and male–male relationships. Recognition of intersexual coercion as a third form of sexual selection, along with intrasexual competition and intersexual mate choice, is critical to improving understanding of reproductive strategies and social systems in primates and other animals.

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