

## 6

## The Causes and Consequences of Male Aggression Directed at Female Chacma Baboons

*Dawn M. Kitchen, Jacinta C. Beebner, Thore J. Bergman,  
Dorothy L. Cheney, Catherine Crockford, Anne L. Engb,  
Julia Fischer, Robert M. Seyfarth, and Roman M. Wittig*

At least once in every 10 hours of observation, a female chacma baboon (*Papio hamadryas griseipes*) can be heard screaming as she runs from a hostile adult male. Why do fairly protracted attacks like this occur so frequently outside of a feeding context? To the casual observer, it may not seem remarkable that male baboons assault females—given their huge sexual size dimorphism, it would appear they do so because they can. To determine whether there are any functional explanations for the phenomenon, in this chapter we search for underlying patterns to male aggression directed at females. Are some victims targeted while others ignored? Are all attacks as violent as they could be, or do males show restraint? Do all males use intimidation tactics equally?

Most savannah baboons of sub-Saharan Africa live in large multimale, multifemale groups. Females are philopatric and maintain close bonds with matrilineal kin, forming matrilineally based, stable dominance hierarchies (Silk et al. 1999; Cheney and Seyfarth 2007). Conversely, most male baboons emigrate to neighboring groups at 9 to 11 years of age, and rank is largely determined by condition and fighting ability (Kitchen et al. 2003b, 2005). Although males form linear dominance hierarchies that are stable over the short term, rank reversals are common.

By the time they are 5 or 6, juvenile male baboons typically outrank adult females. As adults, only males possess large, sharp canines, and they outweigh females by approximately 70% (Figure 6.1). Thus, these formidable males are capable of capriciously abusing females within otherwise female-bonded social groups.

-1 \_\_\_  
0 \_\_\_  
+1 \_\_\_



**Figure 6.1** Baboons throughout Africa are sexually dimorphic in size and other features. Here a male olive-hamadryas hybrid baboon threatens an adult female who is fear-grimacing, a submissive expression. Photo by Jacinta Beehner.

Predation and infanticide are the primary factors affecting reproductive success among female chacma baboons at our study site in the Okavango Delta of northwestern Botswana (Cheney et al. 2004). Although females can reduce the probability of a predator attack by remaining near conspecifics, close proximity to individuals (especially adult males) also increases the likelihood of intragroup aggression. For example, adult males easily supplant or chase females from food resources, although such bouts of malice are usually mild and brief.

Other aggressive encounters with males, seemingly unrelated to feeding competition, can be even more disruptive to a female's daily life. For example, male chacma baboons frequently engage in aggressive loud call ("wahoo") displays that are thought to function in intra- and intergroup male-male competition (Kitchen et al. 2003b). During most wahoo displays, males chase females. When a female is targeted, she often runs up a tree and hangs from a thin branch (Figure 6.2) or cowers out of reach, deep inside a thorny bush. Meanwhile, the displaying male swats at her and shakes the vegetation—eventually

— -1  
— 0  
— +1



**Figure 6.2** An adult male chacma baboon chased this cycling female up a tree. Here he is producing loud “wahoo” vocalizations while swatting at her as she hangs from a branch. He jumped up and down on the branch until she eventually fell from the tree. Photo by Dawn Kitchen.

she may fall from the tree or flee to another bush. Despite sometimes falling from 5 m or more and receiving contact aggression by the males, females rarely exhibit obvious injuries following an assault. Nevertheless, attacks can be protracted (wahoo displays can last for over an hour), and the incessant screaming of the victim, and sometimes members of her family, indicates that it is a disturbing event.

A similar story seems to unfold among East African baboons. In an extensive study of olive baboons (*P. b. anubis*), Smuts (1985) described the most common contexts in which males attacked females. Although females were frequently assaulted during feeding competition or when a male defended a third-party female, many attacks occurred during male-male competitive contexts (26%) or were seemingly unprovoked (32%). In this chapter, we focus on the latter two categories and ask whether any of three possible functional explanations apply to male-female aggression among chacma baboons. Although

closely related, we also highlight relevant differences between eastern and southern savannah baboons in our discussion.

It is possible that male-female hostility is fairly arbitrary. Aggression is commonplace in all age and sex classes, at least in chacma baboons, and frequently observers note a domino effect: an individual attacks a lower-ranking individual, this victim subsequently attacks an even lower-ranking animal, and so on. In many cercopithecine species, this method may be used by each individual to assert and maintain his dominance ("random acts of aggression": Silk 2002). However, this mechanism is unlikely to explain male aggression directed at female baboons because females are not a threat to any adult male's rank. More likely, this pattern could emerge as a by-product of male-male aggression (hereafter, the *redirected aggression hypothesis*). In other words, because all males outrank all females, a male who lost a fight with another male, or who is unwilling to risk injury in an escalated male-male contest, could aggressively target a female either to relieve stress or to focus attention away from himself (e.g., Castles and Whiten 1998). If this hypothesis explains the majority of nonfeeding-related male-female attacks, then we expect that most aggression will be conducted by low-ranking males following male-male aggression, that males will target the nearest adult female regardless of her reproductive state, and that males will also frequently attack juveniles of both sexes.

Male-female attacks may be more than random acts, however, and may instead function to communicate information about the assailant. First, males may be more successful at securing future mating if they harass estrous females with violence or the threat of violence (hereafter, the *sexual coercion hypothesis*: Smuts and Smuts 1993). The sexual coercion hypothesis assumes that females have some ability to control which males they mate with and that there are physical and physiological consequences of attacks that influence their choices. As an extension of the sexual coercion hypothesis, the *mating conflict model* (van Schaik et al. 2004) suggests that high-ranking males in particular may employ aggression to constrain female sexuality. In infanticidal species such as chacma baboons (Palombit et al. 2000), females may benefit from diluting paternity concentration by mating with multiple males. Female reproductive interests conflict most with the dominant male who maximizes his fitness by maintaining exclusive mating access. Thus, high-ranking males should be more motivated than low-ranking males to attack estrous females to prevent them from mating polyandrously. If attacks function to communicate intent to the female, they should also be surreptitious rather than part of an attention-grabbing loud

\_\_\_ -1  
 \_\_\_ 0  
 \_\_\_ +1

call display, and there is no reason to predict that they should either follow or incite male-male aggression.

Second, male attacks on females may function to communicate information about the male's dominance, stamina, or fighting ability (1) to choosy females (although we currently have no data available to address this hypothesis) or (2) to competitive male rivals (hereafter, the *male-male competition hypothesis*). Elsewhere we report that loud wahoo calls are honest indicators of a male's fighting ability (Kitchen et al. 2003b, 2005; Fischer et al. 2004)—only males in good condition produce frequent, intense, and high-quality wahoo displays. Furthermore, males may use this information to assess rivals; preliminary experimental playback data suggest that males attend to the acoustic quality of their rival's wahoos (Kitchen et al. unpublished), and, following the predictions of game theory, males preferentially target rivals of comparable fighting ability during antiphonal calling contests, chases, and physical altercations. Displays are clearly energetically draining—for example, the acoustic quality of even the highest ranking male's wahoos decline during a protracted calling bout. Probably as a result, males alter their investment in displays depending on the caliber of rival they face. Producing a prolonged bout of good-quality wahoos at a fast rate while also running up and down trees and chasing another individual might provide even more reliable information to rivals.

If chasing females is part of a collection of honest signals that communicate information about a male's prowess to a mixed-sex audience, then it must be energetically costly and thus conducted more often by high-ranking males in the best physical condition. Even so, attacks need not have major fitness consequences to the victims. In addition, attacks should occur as part of an otherwise stereotypical wahoo display and should incite rather than follow male-male aggression. Furthermore, this hypothesis predicts that a male should either be just as likely to choose any lower-ranking animal or, if the victim's screaming bolsters a male's display, he should choose an individual that would generate the most noise. Although adult females and juveniles seldom physically assist each other when a male attacks one of them, they often lend "vocal support" to a victim by grunting, fear-barking, or screaming during attacks (Wittig et al. 2007). Because high-ranking adult females should generate the most vocal support when attacked (Cheney and Seyfarth 2007), males could target these females to maximize the din they generate. Alternatively, given the potential for infanticide in this population, lactating females would be good targets for a male attempting to generate the most commotion.

But if the goal of many such attacks is just to goad other males, why not direct *all* attacks at low-ranking male rivals? Males may sometimes avoid victimizing other adult males in order to reduce the substantial risk of injury through retaliation, even by inferior competitors. For example, the winner of one observed altercation retained his rank but permanently lost vision in his left eye after a subordinate rival punctured it with his canine. When possible, males may avoid the more dangerous, direct confrontations with other males by focusing on females or juveniles. Still, these attacks are not risk free—the plight of the victim may elicit aggression from other males (e.g., Smuts 1985; Palombit et al. 2000; Kitchen et al. 2005) or at least might challenge other males to engage in a prolonged vocal battle.

Table 6.1 summarizes the predictions of the three possible hypotheses. This is not an exhaustive list of hypotheses, nor do all hypotheses have mutually exclusive predictions. In fact, we think it is likely that attacks serve multiple functions, sometimes simultaneously. We discuss this possibility in more depth after we summarize the patterns and consequences of male aggression toward females and review the counterstrategies females use to avoid male aggression. Although we generate our results from nine years of systematically collected data (both published and unpublished), the majority of the data were not collected to specifically address this topic. We hope that our preliminary analysis will direct future studies specifically designed to test the questions raised here.

### **Study Site, Population, and Methods**

The Okavango Delta lies within the Moremi Game Reserve in the northwest corner of Botswana. This area floods from approximately June through October, and only “islands,” elevated tree-lined areas (1 to >100 ha), remain above water. The baboons ford or swim through the water to get from island to island in search of food within their approximately 5 km<sup>2</sup> home range (described in Cheney and Seyfarth 2007).

The main study group has been observed since 1978 (Bulger and Hamilton 1987; Bulger 1993). The group is fully habituated to observers on foot and has been followed almost daily since 1992 (Cheney and Seyfarth 2007). The age and matrilineal relationships of all natal animals are known. The main study group averages 75 members, including 19 to 26 adult females and 3 to 12 adult males (Cheney et al. 2004).

All researchers at this site follow essentially the same data collection protocols

— -1  
— 0  
— +1

*Table 6.1* Predictions of three possible hypotheses explaining chacma baboon patterns of male aggression directed at female, with symbols indicating which predictions were supported.

	Redirected Aggression	Male-Male Competition	Mating Conflict/Sexual Coercion
Attacker identity	Lower-ranking male	+ Higher-ranking male	+ Higher-ranking male
Victim identity	Any individual, based on proximity	Any, or lactating/high-ranking females	+ Estrous females
Context	Follows male-male aggression	+ Precedes male-male aggression	No relationship predicted
	Unrelated to male vocal behavior	+ Aggression occurs while male vocalizes	Aggression occurs while male silent
Consortship challenges	Lower-ranking males should redirect at female	(+) Males should target each other rather than contested female	(+) Males, particularly higher-ranking, should target contested female rather than each other
Female mate choice	No relationship predicted	No relationship predicted	+ Females should have some control over consort formation
Fitness consequences	+ No relationship predicted	+ No relationship predicted	Females should evade higher-ranking consort partners in effort to dilute paternity
	None necessarily	(+) None to females necessarily; energetic costs to males	(+) Attacks should be costly to females

+ Results support prediction. (+) Results provide partial support for prediction.

(see Cheney and Seyfarth 2007): (1) Handheld computers are used to conduct 10-minute focal samples on target animals, during which all social interactions between the focal animal and others are recorded; (2) a daily census is taken to record any immigrations, emigrations, disappearances, and the number of adult females available in each reproductive category: pregnant, lactating and cycling, with cycling females further subdivided based on whether or not they are in estrus and the size of the perineal swelling (Dixson 1998); (3) all “friendships” (formed between lactating females and some resident males: Palombit et al. 1997), “consortships” (exclusive mate-guarding relationships between males and estrous females: Crockford et al. 2007), and changes in the male or female hierarchy (updated daily using approach-retreat interactions) are recorded; (4) specific information is systematically collected during major events (predation, infanticide, intragroup male competitive displays, and intergroup encounters); (5) digital audio recordings are collected opportunistically of vocalizations of interest for acoustic analysis or playback experiments; and (6) fecal hormones are collected and extracted in the field from targeted individuals (Beehner and Whitten 2004).

Periodically at our site, certain behaviors or different age/sex classes are targeted to address specific research questions. Here we attempt to use the most complete and appropriate data sets to address each of our predictions. Although many of our analyses are conducted on data collected in 1999–2001 and 2006 when male aggression was the focus, we also incorporate relevant data sets from other time periods when possible. In the text, we cite the years of data collection available for each test.

Here we define “attacks” as any intense chase (> 50 m for > 30 s) and/or aggressive physical contact (hitting, biting, grappling). Attacks are often but not always produced as part of a male “wahoo display” (wahoos are two-syllable, loud, repetitive vocalizations). More than one male can participate in a display, and each participant may attack multiple individuals.

Data collected during male competitive displays are considered independent if attacks on females are separated by more than an hour and produced in a new context (i.e., typically involving different participants in a new location). Data from different focal sampling periods are also considered independent because subjects are randomly chosen and no subject is sampled twice until all animals are sampled once. However, as in any study of individuals who live together for long periods of time and who interact repeatedly in various dyadic or larger combinations, the data presented here cannot be perfectly independent. Therefore,

\_\_\_ -1  
 \_\_\_ 0  
 \_\_\_ +1



other statistical methods employed to avoid pseudoreplication are discussed in this chapter or in the cited references.

### Patterns of Male-Female Aggression

To test whether male aggression toward adult females supports the *redirected aggression*, *male-male competition*, or *sexual coercion hypothesis*, we examine patterns in attacker identity, victim identity, context, and consortships (Table 6.1).

#### *Attacker Identity*

At least one male chased at least one female in 138 of 183 independent wahoo displays from 1999 to 2001. To avoid pseudoreplication in our analysis, we only counted males once per display regardless of the number of individuals they attacked, and we used each male's average rank over the entire study period. Even with this conservative approach, we found that high-ranking males were more likely to chase females than low-ranking males ( $n=16$  males,  $r_s=-0.72$ ,  $p<0.050$ ). To control for individual differences, we examined the chases of females by one male who occupied the most rank positions during the study. The same relationship emerged in this case study, with the subject more likely to chase females when he was high-ranking than low-ranking ( $n=7$  rank positions,  $r_s=-0.80$ ,  $p<0.050$ ).

Next, we restricted analysis to the subset of displays involving only two males. This approach eliminated the effect of overall rank (i.e., both rivals might be low- or high-ranking) and focused only on the relative rank between two rivals. For analysis, males were counted only once per display regardless of the number of females they chased. Because females were chased by one of the two males in 41 of 61 observed dyadic displays and by both participants in 14 of these displays, we used 56.6% for the expected value (i.e., the likelihood that a male in a dyadic display would chase a female was  $= (14 + (41/2))/61$ ). Contrary to the predictions of the redirected aggression hypothesis, low-ranking males were less likely than expected by chance to chase females ( $\chi^2_1=5.29$ ,  $p<0.050$ ). Although the higher-ranking of the two males chased females more often (50.8% of 61 displays) than lower-ranking males (39.3%), they did not do so more often than expected by chance ( $\chi^2_1=0.59$ ,  $p>0.100$ ). A likely explanation for these equivocal results is that chasing females serves multiple functions, particularly for males of different rank.

-1 \_\_\_  
0 \_\_\_  
+1 \_\_\_

Male rank was previously shown to be unrelated to age or size in this population (Kitchen et al. 2003b). Using data from 1999–2001, we also found no effect of a male's estimated age class (Kruskal-Wallis:  $n=12$  males,  $H_2=3.73$ ,  $p>0.100$ ) or size class (Mann-Whitney: height:  $n=10$ ,  $U_1=18$ ,  $p>0.100$ ; weight:  $n=8$ ,  $U_1=9$ ,  $p>0.100$ ) on the likelihood he would attack a female (using the average monthly rate of attacks per male per class).

### *Victim Identity*

1. Attacks on juveniles vs. adults: Despite the fact that the juvenile age class typically constitutes about 60% of a baboon group (e.g., Cheney et al. 2004), males only directed attacks at them during 16% of displays (based on 286 displays in a two-year period: Kitchen et al. 2005, unpublished), whereas they attacked adult females (approximately 30% of the group) during 68% and other adult males (approximately 10% of the group) during 57% of displays. Therefore, although the redirected aggression hypothesis predicts that male baboons should be equally likely to attack anyone ranking below them, they seemed to ignore juveniles of either sex ( $\chi^2_1=32.27$ ,  $p<0.001$ ) and focused their attacks on adult males ( $\chi^2_1=336.40$ ,  $p<0.001$ ) and females ( $\chi^2_1=24.30$ ,  $p<0.001$ ).

Redirected aggression might still explain this pattern of attacks if adults happen to be in closer proximity than juveniles. For 4.5 months in 2006, we collected data to examine this possibility. We used instantaneous scan samples at the beginning and end of each 10-minute focal sample, noting all individuals over one year of age sitting within 5 m of the male subject. We collected 501 samples from 12 adult males. On average, males had 1.9 neighbors within 5 m. Of the 951 neighbors identified, 38% were juveniles, 12% were adult males, and 50% were adult females. Using these data as expected values, adult males were targeted more than expected based on chance ( $\chi^2_1=261.33$ ,  $p<0.001$ ), juveniles were targeted less than expected ( $\chi^2_1=12.74$ ,  $p<0.001$ ), and females were targeted as expected ( $\chi^2_1=0.98$ , ns). Below we explore whether males target specific adult females.

2. Female rank and age: We examined the identity of all female victims in 369 chases by adult males observed in 1999–2001. Each female was only entered once in our analysis based on her average rank or average age throughout the study. Contrary to predictions, males did not target high-ranking females ( $n=28$  females,  $r_s=-0.28$ ,  $p>0.100$ ). Females were also not targeted based on age ( $n=28$ ,  $r_s=0.07$ ,  $p>0.100$ ).

\_\_\_ -1  
\_\_\_ 0  
\_\_\_ +1

3. Reproductive state: We used 47,660 min of focal data collected in 2001–2003 to compare the rate of male aggression (lunging, chasing, biting, hitting) toward adult females with the average number of females available in each reproductive category. As predicted by sexual coercion, males attacked females with an estrus swelling more than expected by chance ( $n=13$  males, observed: 16.8% of 101 acts of aggression; expected: 10%;  $\chi^2=4.62$ ,  $p<0.050$ ), whereas all other cycling (obs: 21.8%; exp: 30%;  $\chi^2=2.24$ ,  $p>0.100$ ), lactating (obs: 33.7%; exp: 40%;  $\chi^2=0.99$ ,  $p>0.100$ ), and pregnant females (obs: 27.7%; exp: 20%;  $\chi^2=2.96$ ,  $p>0.088$ ) were attacked as expected based on their availability. By comparison, we found no evidence that adult females were aggressive to other females based on the victim's reproductive state ( $n=33$  females; estrous: obs: 12.9% of 186 incidents of aggression; exp: 10%;  $\chi^2=0.84$ ; nonestrous cycling: obs: 27.4%; exp: 30%;  $\chi^2=0.23$ ; lactating: obs: 44.1%; exp: 40%;  $\chi^2=0.42$ ; pregnant: obs: 15.6%; exp: 20%;  $\chi^2=0.97$ ; all  $p>0.100$ ). These data replicate results obtained in 1999–2001, when males targeted estrous females 2.5 to 3.9 times as often (based on availability) as females in any other reproductive category.

We used 36,910 min of nonconsortship focal data collected from 2004 to 2005 to examine aggression toward cycling females in different phases. In further support of the sexual coercion hypothesis, we found that aggressive acts were more likely to be directed at cycling females *with* an estrous swelling (70% of 30 aggressive acts) than at nonestrous cycling females ( $\chi^2=4.80$ ,  $p=0.028$ ). Furthermore, focusing just on females with estrous swellings (for this analysis, it was necessary to combine consorting and nonconsorting data), we found an effect of swelling size and male rank on aggression patterns. Low-ranking males ( $n=4$ ) distributed aggression evenly between all estrous females (females in detumescence received 57.1% of 14 aggressive acts, females with an increasing or maximally sized swelling received 42.9%;  $\chi^2=0.29$ ,  $p>0.100$ ). Conversely, the aggressive acts of high-ranking males ( $n=5$ ) were more focused on females whose swellings were increasing or maximally sized (83.3% of 12 aggressive acts) than on females in detumescence who were unlikely to conceive (16.7%;  $\chi^2=5.33$ ,  $p=0.021$ ). This lends support to the mating conflict model, which predicts that high-ranking males should be more likely to use sexual coercion as a reproductive strategy.

4. Proximity to females: Redirected aggression might still explain why males target estrous females if these individuals happen to be in closer proximity to males than females in other reproductive states. Contrary to this hypothesis,

-1 \_\_\_  
0 \_\_\_  
+1 \_\_\_

however, we found that females in all reproductive states were equally likely to be within 5 m of an adult male according to their availability within the group; using the same data collected in 2006 described above, 45.6% of a male's female neighbors were lactating (expected: 35.6%;  $\chi^2=2.81$ ,  $p>0.100$ ), 17.9% were pregnant (exp: 26.8%;  $\chi^2=2.96$ ,  $p>0.100$ ), 27.2% were in estrus (exp: 21.0%;  $\chi^2=1.83$ ,  $p>0.100$ ), and 9.3% were cycling but had no sexual swelling (exp: 16.6%;  $\chi^2=3.21$ ,  $p>0.100$ ).

The specific effect of male rank on aggression toward estrous females was also not a result of proximity; of cases where a focal male's nearest neighbor was an estrous female (controlling for number of observation days per male), high-ranking males were no more likely to be near an estrous female (29% of 129 samples) than middle- or low-ranking males (46% and 25%, respectively). Results did not change if samples collected during consortships were examined separately. Thus, we find no evidence that estrous females are targeted simply because they spend more time near high-ranking males than other females.

We did, however, find some evidence that adult males and estrous females were attracted to each other outside of aggressive acts. Using 7410 min of non-consortship focal data on 12 males and 23 females collected in 2006, we found that females with sexual swellings approached or were approached by males twice as often (30.1% of all approaches) as cycling females without a sexual swelling (15.4%). When we examined all reproductive states (estrous, non-estrous cycling, pregnant, lactating), we found that only estrous females approached or were approached more than expected based on availability within the group (expected: 16.6%,  $\chi^2=10.979$ ,  $p<0.001$ ). However, we did not record "leave" behavior in this study; thus, we had no information on how long males and females were within 2 m of each other, nor did we know which sex was responsible for maintaining this proximity. In a study that did quantify duration of male-female proximity, it was the lactating females, not cycling or pregnant females, that spent significantly more time within 25 m of males (Palombit et al. 1997). In addition, because it was almost impossible to record data on nearest neighbors when males were displaying, it was unclear whether estrous females in the 2006 study were within 2 m immediately before displays (evidence that might suggest they were targeted by chance). Rather, it was our impression, based on detailed observations of displays in 1999–2001, that males began most displays by first walking through the group and then selecting a female to chase, often from some distance away. To adequately test this proposition, a study needs to be specifically designed to record which females

— -1  
— 0  
— +1

are near a male immediately before a chase begins, as well as victim behavior toward an attacker following a chase (Smuts and Smuts 1993).

5. Intergroup contests: Baboon density is high in this area of Botswana (approximately 24/km<sup>2</sup>: Cheney et al. 2004), with the home ranges of at least five groups overlapping our main study group. Perhaps as a result, intergroup interactions are common. These meetings often result in aggressive loud call displays in which males herd the female members of their own group in the opposite direction of the rival group. Adult males often immigrate into new groups following such encounters.

We found that all males were more likely to loud call and chase a female during an intergroup encounter if at least one female in the group was in estrus than if no females were in estrus (Kitchen et al. 2004). As in intragroup contests, estrous females were preferentially targeted for chasing during intergroup contests (17.9% of those available per day, 2 to 12 times more than any other reproductive category), even though most of these estrous female victims were not involved in a consortship during the encounter. We also found that subjects (n=6 males in paired comparisons) were more likely to chase a female during intergroup encounters when they were involved in an exclusive mate-guarding consortship than when they were not. Finally, high-ranking males (whether or not in a consortship) were more likely to attack females than low-ranking males.

Overall, these data suggest that males target estrous females during intergroup encounters and these attacks function to herd females away from other groups (possibly reducing female opportunities for extragroup copulations) and/or to coerce females into mating with the aggressor in the future. Although this is strong support for the sexual coercion hypothesis, the fact that males chase females typically as accompaniment to a loud call display does not negate the male-male competition hypothesis. We address this idea in more detail in the following discussion.

#### *Display Context*

Contrary to the sexual coercion hypothesis, we found a contextual relationship for female attacks using 128 independent displays that included chases of both sexes from 1999 to 2001. In support of the male-male competition hypothesis, we found that male-female chases were more likely to precede (64.1% of 128) than to follow male-male chases (35.9%;  $\chi^2_1 = 10.13$ ,  $p = 0.001$ ). Thus, attacks on females seemed more likely to prompt male aggression than vice versa.

-1 \_\_\_  
0 \_\_\_  
+1 \_\_\_

Often group members are spread out in tall grass or in wooded areas; as a result, not all baboons can see the details of all the attacks that occur in a group. If a male does not vocalize during an attack, he does not necessarily draw attention to himself. Therefore, males should silently chase females if male attacks function to coerce females into mating with the assailant. On the other hand, males should produce loud wahoo calls while chasing females if male attacks on females are meant to call attention to the aggressor's stamina. Of 294 male-female chases in 1999–2001, 172 (58.5%) were accompanied by loud calls from the attacker ( $\chi^2_1 = 8.50, p = 0.004$ ), lending support to the latter hypothesis. Although a statistically significant result, males still silently attacked females 42.5% of the time; therefore, at least some chases of females might be explained by sexual coercion or redirected aggression.

#### *Patterns in Consortships*

In this population, males of all ranks form consortships with estrous females for a period of hours or days. When a low-ranking male is in a consortship with a female nearing ovulation, he is eventually challenged by a higher-ranking male who will likely seize control of the female (a “takeover”). Thus, the alpha male typically monopolizes females when they are maximally swollen and most likely to conceive (Bulger 1993; Cheney and Seyfarth unpublished data). Consortship challenges often escalate to physical fights, and participating males also frequently attack the contested female.

1. Consort formation: Male harassment can only increase the likelihood of future mating if females have some influence over which males they copulate with. There is some published evidence of female choice in baboons (e.g., Seyfarth 1978a, b; Smuts 1985; Beehner and Bergman 2006; Swedell 2006; Palombit, Chapter 15 in this volume). Anecdotal evidence suggests that females in our population allow some consort partners to successfully sequester them. For example, a fourth-ranking male in consort with an estrous female stayed far away from the rest of our study group for several days in 2000. The female was in estrus while they were absent, and the pair did not return until she was in detumescence. Thus, the alpha male never had an opportunity to take over the consortship during what turned out to be a conceptive cycle for this female.

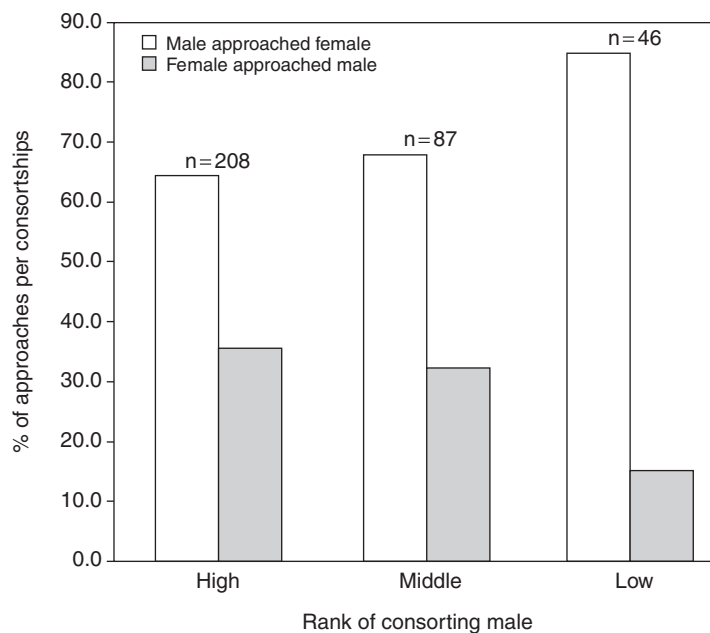
To examine the potential effects of females on consort formation and maintenance (as a proxy measure of female choice), we examined the number of times males and females approached each other in 2006. We found that

\_\_\_ -1  
\_\_\_ 0  
\_\_\_ +1

estrous females approached males more often than males approached females when not in a consortship (57.8% of 225 approaches;  $\chi^2=5.44$ ,  $p=0.020$ ) or when cycling but with no sexual swelling (61.7% of 115 approaches;  $\chi^2=6.34$ ,  $p=0.012$ ), whereas males were more than twice as likely to approach females than the reverse when the pair was in consort (68.1% of 342 approaches;  $\chi^2=44.96$ ,  $p<0.001$ ). Overall, these approach data suggest that females influence consort formation, but, once paired, males maintain proximity. As a comparison, approaches were just as likely to be made by either sex when females were pregnant (55.3% of 159 approaches;  $\chi^2=1.82$ ,  $p>0.100$ ), whereas lactating females approached males more often than the reverse (72.6% of 248 approaches;  $\chi^2=50.58$ ,  $p<0.001$ ), most likely in an effort to maintain spatial proximity with a male “friend” as an anti-infanticide strategy (see also Palombit et al. 1997).

2. Female behavior: Because high-ranking males are more likely than low-ranking males to thwart consort takeover attempts and thus sustain exclusive access to a female, the mating conflict model predicts that females should try to evade high-ranking consort partners to increase their ability to mate with multiple males during a given cycle (van Schaik et al. 2004). Using approach data gathered in 2006 to specifically address this question, we found that females tended to approach low-ranking male consorts less than expected (observed: 6.4%; expected: 13.5%;  $\chi^2=3.73$ ,  $p=0.054$ ), but approached mid-ranking (obs: 25.7%; exp: 25.5%;  $\chi^2=0.00$ ,  $p>0.100$ ) and high-ranking males (obs: 67.9%; exp: 61%;  $\chi^2=0.78$ ,  $p>0.100$ ) as often as expected. Therefore, contrary to this variation of the sexual coercion hypothesis, females did not try to avoid high-ranking partners and instead avoided low-ranking partners (Figure 6.3). Outside of consortships, we have no indication that females avoid the advances of low-ranking males in “sneaky” copulations, which can occur when a female temporarily becomes separated from her consort partner (Cheney and Seyfarth 2007).

3. Male behavior: If attacks on females function to coerce them into immediate or future mating, males who attempt to take over a consortship, or males who defend their consort partner from a possible takeover, should target the female rather than the defending or challenging male (van Schaik et al. 2004). Using data collected on 81 consortships from 1999 to 2001 during which aggression was directed at the female or at one of the males, or both, we found that 6.2% involved only male-male aggression, 39.5% involved only male-female aggression, and the majority involved both types of aggression (54.3%).



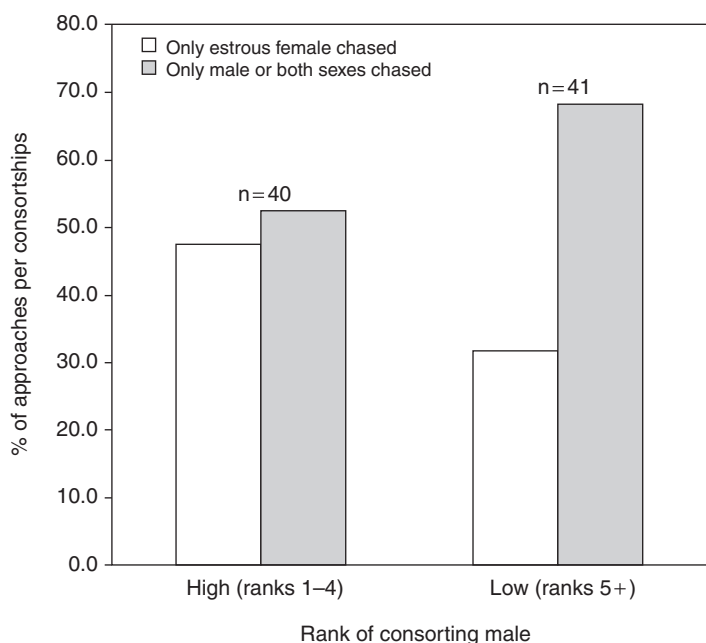
**Figure 6.3** The percentage of all approaches to within 2 m by the male or female member of a consorting pair based on the rank of the consorting male.

Thus, results were equivocal; although females were more likely to be targeted overall ( $\chi^2_1 = 5.37$ ,  $p = 0.021$ ), attacks were as likely to be solely directed at females as they were to be at both sexes ( $\chi^2_1 = 1.90$ ,  $p > 0.100$ ). In addition, the style of attacks varied with the sex of the victim; aggressive acts toward females were typically threats or short chases, whereas male-male attacks more frequently escalated from chases to grappling and biting. In fact, 27% of the 93 male-male physical fights observed in this study period were in the context of estrous female defense (Kitchen et al. 2005).

Following the mating conflict model, high-ranking males should be more coercive to consort partners than low-ranking males in order to dissuade females from polyandrous mating (van Schaik et al. 2004). We did not find strong support for this prediction using consortship challenge patterns. Although low-ranking consort males were less likely to direct aggression solely at females than at both sexes ( $\chi^2_1 = 5.49$ ,  $p = 0.019$ ; Figure 6.4), we found that high-ranking consort partners were just as likely to attack both sexes as to focus only on the contested female ( $\chi^2_1 = 0.10$ ,  $p > 0.100$ ).

— -1  
— 0  
— +1





**Figure 6.4** The percentage of consortship conflicts resulting in attacks on females alone or on both sexes based on the rank of the consorting male.

### Discussion

When feeding, chacma baboons of all age and sex classes frequently redirect aggression—one animal supplants another from a food source, and the victim subsequently threatens or lunges at a third, lower-ranking animal. However, in nonfeeding contexts, the consistent and sometimes violent attacks on females by males seem less random. For example, if these attacks are simply redirected aggression, low-ranking males should be more likely to attack females than high-ranking males, and males should target the closest lower-ranking animal available. In contrast, we found that males virtually ignored some individuals in close proximity and targeted others. Furthermore, high-ranking males were the most common attackers, a result that instead supports both alternative hypotheses for male-female aggression (male-male competition and sexual coercion). By definition, male aggression redirected at females would also have to be *provoked* by male-male aggression, yet this did not explain the majority of cases in which female-male aggression *preceded* rather than followed male-male aggression.

-1 \_\_\_  
0 \_\_\_  
+1 \_\_\_

We found strong support for the sexual coercion hypothesis in terms of which female victims were targeted. Contrary to the predictions of the other two hypotheses, attacks were preferentially focused on estrous females during intra- and intergroup displays. We did find some evidence that estrous females and males approached each other more often than other male-female dyads. However, whether this attraction (1) influences male choice of targets and (2) is a result of female mate choice or of successful male harassment will require collection and analysis of proximity data immediately before and after an attack. The pattern of aggression by males of different ranks to females in different phases of their cycles also supports the mating conflict/sexual coercion hypothesis (van Schaik et al. 2004). We found that high-ranking males were more likely than low-ranking males to focus attacks on those estrous females nearing ovulation.

Sexual coercion can only work if females have some choice in their mating partners. Although males were responsible for maintenance of proximity once paired, our approach data did suggest that estrous females were responsible for some portion of consort formation. However, females in a consortship were more likely to approach high-ranking than low-ranking partners, suggesting they did not avoid these males as would be expected under the mating conflict model. This hypothesis also predicts that during a consortship challenge, male aggression should be focused on the contested females. Although we found that females received more attacks overall, we found that attacks on females were relatively mild and that it was common for both male-female and male-male aggression to occur simultaneously during an attempted consort takeover. Thus, our consortship data provide only weak support for the mating conflict/sexual coercion hypothesis.

The strongest support for the male-male competition hypothesis is based on the context of attacks on females. First, male-female aggression typically occurs prior to rather than following male-male aggression, suggesting female attacks might be partially responsible for inciting other males. Second, contrary to the predictions of the sexual coercion hypothesis, the majority of attacks on females are accompanied by male wahoo displays, suggesting males are calling attention to themselves.

Still, enough of the attacks on females follow male-male aggression or occur when males are silent to suggest that attacks could serve more than one function. Furthermore, if males use female screams solely to bolster their displays, they would not need to target estrous females over other females. Moreover,

\_\_\_ -1  
 \_\_\_ 0  
 \_\_\_ +1

males could just as easily choose from among the numerous juveniles in the group. Yet juveniles are rarely attacked and nonestrous females are only attacked as expected based on proximity and availability. For these and other reasons given above, we suspect that male attacks on females serve a variety of functions. Testing this multifunction hypothesis would require a more detailed analysis than our data presently allow. For example, we predict that (1) *vocal* attacks should *precede* male-male aggression; (2) *silent* attacks should be targeted at *estrous* females; and (3) attacks by *low-ranking* males should *follow* male-male aggression.

Whether attacking a female during a wahoo display incurs sufficient energy cost to be part of a collection of honest signals about a male's stamina requires further investigation. First, a fine-scale analysis of calling bouts could be used to determine whether running and chasing have an effect on wahoo acoustic quality. We would predict that even high-ranking males' wahoos would decline in quality while chasing, but the decline would be less precipitous than among low-ranking males. Second, playback experiments could be used to simulate wahoo bouts with and without female chases (e.g., by pairing male wahoos and threat-grunts with the sound of a female screaming) to see if the inclusion of such attacks increases a rival's interest in the display.

### Consequences of Male Coercion

If male attacks on females are coercive, then females should change their mating preference as a direct or an indirect result of an attack. In chacma baboons, aggressive acts directed at estrous females do not immediately result in copulation, nor do they lead to immediate formation of a consortship. Assuming instead that there are "indirect" coercion effects (Muller et al., Chapter 8 in this volume), it is still difficult to test whether targeted harassment of estrous females actually reduces a female's tendency toward polyandrous mating and thereby increases the attacking male's exclusive mating access. Even if we could confirm this using copulation or paternity data, we would still have difficulty distinguishing the mechanism. In other words, are males successful because they frighten uncooperative females with violence, because they use their protracted aggressive displays as an honest signal of quality to impress females, or because they scare off other male contenders with their demonstrations of power?

There is another predicted consequence of sexual coercion that we can begin to address here. That is, female attacks should result in tangible fitness

-1 \_\_\_  
0 \_\_\_  
+1 \_\_\_

costs to the females involved (Smuts and Smuts 1993). In contrast, we would not anticipate clear fitness costs if attacks were redirected aggression or purely part of male-male competitive displays.

#### *Female-Female Aggression*

Using 794.3 h of focal data collected in 2001–2003 during feeding and non-feeding contexts, we found that male-female aggression was no more frequent than female-female aggression. Female-female attacks (0.234 incidents/h) were 1.84 times as common as male-female attacks (0.127/h). Given that there were 2.54 times as many females in the group as males (33 vs. 13), attacks on females were just as likely to be by males or by other females ( $\chi^2_1 = 0.19$ ,  $p > 0.100$ ).

#### *Physical Injuries*

Of the individuals we were able to weigh at this site, males ( $n = 9$ ) were 1.23 to 2.38 times heavier than females ( $n = 14$ ; Kitchen et al. 2003b). This size difference makes an attack by a male risky to females in terms of physical injuries. From 1999 to 2001, we noted any visible injuries (cuts, blood) or limping by adult females, adult males, and juveniles. We also described any altercations involving the victim just prior to the injury. Females received more injuries from males than from other females, but overall they were injured less frequently than males. We observed 45 injuries on 12 males, and all were a result of male-male physical fights. We observed 11 injuries on 19 adult females that resulted from male attacks, 1 due to a female attack, 3 presumably from unsuccessful predator attacks, and 18 that were unexplained. Even if all unexplained injuries were due to male aggression, this would be a rate of 1.53 injuries per female in 23 months versus 3.75 per male. Injuries to male baboons were also more severe, probably because male victims fight back (see also Smuts 1985). For example, in our population most male injuries were to the face or shoulders (80% of 45 injuries) because males turned to face each other before grappling, whereas females rarely received injuries to the face (24% of 33 injuries). Instead, most female injuries were cuts to the back, probably as the female fled.

Although injuries inflicted by males were more severe and frequent than injuries caused by other females, there have been no known fatal conspecific attacks on females in this population. By comparison, we attributed at least one male death in our group to injuries incurred in a fight with another male (Cheney et al. 2004). Nevertheless, even minor injuries may have impacts on

— -1  
— 0  
— +1

female fitness, such as reduced foraging/traveling efficiency and increased risk of infection.

### *Infanticide*

In addition to the time lost feeding, the risk of physical injury, and the psychological and physiological stress experienced during aggressive attacks by males, females with dependent offspring face a more tangible fitness cost. If one of the displaying males is a high-ranking recent immigrant, he may commit infanticide. Because the average tenure of an alpha male is shorter than the typical interbirth interval, infanticide may be a strategy that potentially increases the number of offspring that a male is able to sire by hastening the mother's return to reproductive condition (Palombit et al. 2000). Infanticide represents the largest source of mortality for infants in this population (Cheney et al. 2004; see also Palombit, Chapter 15 in this volume).

### *Physiological Effects*

One way to examine how stressful an event is to an individual is by measuring changes in glucocorticoid hormones, the so-called stress hormones. Though associated with some costs if prolonged, an acute stress response is adaptive and related to mobilizing glucose for immediate use (mainly, to escape from a predator or another aggressor: reviewed in Sapolsky et al. 2000). Changes in levels of glucocorticoids can provide a direct measure of the physiological (and possibly psychological) responses of females to aggression or the threat of aggression by males (reviewed in Beehner et al. 2005).

A study examining stress and glucocorticoid production was first conducted at our site from 2001 to 2003. Fecal glucocorticoids were collected from 18 females during four consecutive periods, each approximately one month long. Two periods were marked by stability in the upper ranks of the male hierarchy, and there were two "takeover" periods (Beehner et al. 2005). A takeover occurs when the alpha male identity changes, usually accompanied by general male instability and an increase in male-male aggressive displays. One takeover was a natal male that ascended the hierarchy, and one was a recent immigrant male. In a second study, from 2003 to 2004, 21 females were sampled over the course of 16 months (Engh et al. 2006). Several potentially infanticidal males immigrated during this study, and two bouts of actual infanticidal attacks occurred approximately one year apart. In these two studies, the physiological impact of male aggression on females in different reproductive stages was assessed.

-1 \_\_\_  
0 \_\_\_  
+1 \_\_\_

Although estrous females are preferentially targeted during male aggressive displays in this group, estrous females exhibited no variation in mean glucocorticoids across time periods—whether stable or unstable. In fact, individual victims targeted during one takeover period in 2002 did not show elevated glucocorticoids when compared with females who were not chased by these immigrant males (Beehner et al. 2005). As a further test, we compared the glucocorticoid levels of cycling females in different phases ( $n=209$  fecal samples from 17 females not in consortships). We found no difference in the glucocorticoid levels of cycling females with estrous swellings (mean + SE =  $116.95 + 1.05$  ng/g) compared to nonestrous cycling females ( $109.90 + 1.06$  ng/g; General Linear Mixed Model:  $F_{1,195,758} = 0.079$ ,  $p > 0.100$ ). Our results remained the same when females were differentiated further based on the phase of their estrous cycle (those with increasing or maximally sized swellings vs. those in detumescence) or on whether consorting females were included. Thus, although being attacked by a male is probably temporarily traumatic for any female, no physiological evidence exists that this aggression causes an enduring stress response in the victims.

Conversely, the glucocorticoids of *lactating* females increased dramatically following the immigration of potentially infanticidal males, and this increase was significantly higher following actual infanticidal attacks than following the mere threat of infanticide. By comparison, the glucocorticoid levels of lactating females did not increase during the takeover by the natal male (in our population, natal males who become the alpha rarely commit infanticide: Palombit et al. 2000).

Finally, lactating females exhibited an increase in glucocorticoids, even though rates of male aggression directed toward them did not increase following male immigration (they even declined in one study). Thus, it seems that physiological changes and perceived danger among females in this population are not due to male attacks or even the threat of violence, but rather to the psychological threat of one particular male behavior: infanticide, the most extreme form of sexual coercion.

### Discussion

Many researchers consider infanticide to be the ultimate act of sexual coercion (or at least of “sexual conflict”; see Palombit, Chapter 15 in this volume). As predicted, when immigrant males ascend to the alpha position in our population, the female baboons most at risk of infanticidal attacks—lactating females—exhibit the strongest physiological stress response.

— -1  
— 0  
— +1

Otherwise, contrary to the predictions of the sexual coercion hypothesis, we found little evidence that male harassment and abuse of females incur a substantial fitness cost. Although attacks are likely an immediately disturbing event (see Silk 2002 for discussion of self-directed behaviors as measures of stress), targeted females do not demonstrate any lasting physiological stress response.

Although males injure females, injuries do not occur at a high rate and male-female aggression is no more common than female-female aggression. Males have the capability of doing great damage with their canines, and their size relative to females means little risk of victim retribution. Yet the tactics of males in their conflicts with females are very different from those they employ with other males. Male attacks on females sometimes appear savage, but looks can be deceiving: males seem to restrain themselves and avoid inflicting injuries that could harm a female's reproductive potential.

It is interesting that, although male chacma baboons are more frequently aggressive to females (once every 10 h including only chases and violent attacks) than male olive baboons (every 17 h including mild threats: Smuts 1985), olive males inflict more severe injuries on females and at higher rates (1/y per female) than chacmas (less than 0.76/y per female). Differences between baboon populations do not end there. Although few systematic comparative studies have been published, accounts between geographic areas differ. For example, male dominance hierarchies below the rank of alpha might be slightly more stable in East African than in chacma baboons (e.g., rank reversals occur at a rate of 1.5/mo in our population vs. approximately 0.75/mo in a yellow baboon population: Alberts et al. 2003). Although dominance rank typically correlates with mating success in both East and South Africa, it seems that "queue-jumping" is more likely among East African baboons (at least in one long-term study of yellow baboons: Alberts et al. 2003). Alpha male East African baboons might have less exclusive mating privileges based on a potentially stronger influence of female choice than in chacma baboons and on male coalition formation, which does not occur in chacmas (reviewed in Bulger 1993 and Alberts et al. 2003). Furthermore, in contrast to our population, infanticide is rare in East Africa (reviewed in Henzi and Barrett 2003), and male-female friendships there seem to function for more than infant protection (Smuts 1985; Palombit et al. 1997; Lemasson et al. 2008). Therefore, perhaps *direct* female coercion has more impact on mating success in East African baboons, which might explain the severity of male-female attacks in the olive population. Conversely, male mating

success in chacma baboons may be more related to placement in the male dominance hierarchy and infanticide strategies (*indirect* coercion). This might explain the common use of repetitive vocal displays as indicators of fighting ability in chacmas—displays that are rarely or never used in most East African baboon populations (e.g., Beehner and Bergman, personal observation). We are not aware of any published reports of vocal contests among East African baboons.

### **Female Counterstrategies**

Assuming that male aggression might have at least some fitness costs, we expect to see female counterstrategies to male aggression. We briefly summarize some here (see also Palombit, Chapter 15 in this volume).

#### *Avoidance*

It seems possible that females can monitor when a male display is about to erupt and avoid males during these critical times. Certainly, a human observer can effectively anticipate that a male is about to initiate a display based on several behavioral cues (e.g., a male has a specific stride prior to a display). Our observations suggest that females and juveniles are also sensitive to these visual cues because they usually flee from males just before the onset of a wahoo display. Male loud calls could also alert females to displays, particularly when they cannot see approaching males because of tall grass or trees. Although one set of playback experiments suggests that females respond more strongly to alarm wahoos than to contest wahoos (Kitchen et al. 2003a), these trials were carried out during a period of time when there were no potentially infanticidal males resident in the group. It seems likely that lactating females would respond strongly to the contest wahoos of a high-ranking, recent immigrant.

#### *Female Allies*

Female–female alliances against adult male attackers are rare in this population (Cheney and Seyfarth 2007). For example, during a 23-month study on male displays (1999–2001), females only came to the aid of their kin during an attack by an adult male in two instances, one of which was an unsuccessful infanticidal attempt by a new immigrant male (personal observation; see also Palombit et al. 2000). Although females regularly provide vocal support during

— -1  
— 0  
— +1



male-female aggression (Wittig et al. 2007), females' relatively small body size largely prevents them from providing physical support to each other against males.

### *Male Allies*

The support of male friends during attacks considerably reduces the likelihood of infant injuries or deaths (Palombit et al. 1997, 2000). Moreover, fecal glucocorticoid (measured in 2003–2004) increased among lactating females following two separate bouts of infanticidal attacks within the group compared to other time periods, but only among those females *without* male friends (Engh et al. 2006). Thus, it appears that females with male friends perceive themselves to be at reduced risk of infanticide (see also Beehner et al. 2005).

### *Discussion*

Females might use visual and auditory cues to anticipate and avoid the aggression that inherently surrounds male-male competitive displays. However, whether females attend to these cues and successfully avoid displaying males has not been explicitly tested. Although females cannot rely on kin to protect them during male attacks, lactating females with male friends can anticipate support (see also Palombit, Chapter 15 in this volume). Probably as a consequence, the physiological stress levels of these females are lower than those of other lactating females following infanticidal attacks.

### **Summary and Conclusions**

During nonfeeding contexts, the behavioral patterns of chacma baboons suggest that male aggression toward females is not simply explained as redirected aggression. Rather, most acts of aggression toward females are cases of high-ranking males targeting sexually receptive females during loud call displays, and these attacks typically precede and perhaps prompt the involvement of other males. By preferentially pursuing estrous females, males may use female attacks as an indirect method of sexual coercion. However, male aggression toward females may sometimes have less to do with the victim and more to do with the broader audience. Males may incorporate a screaming female into their energetic loud call displays to showcase their stamina and condition to competitive rivals. In other words, can a male continue to produce good qual-

ity wahoos at a fast rate while also chasing a female up and down trees? Although other adult males are also targeted in such attacks, including females as potential targets lowers an assailant's immediate risk of injury from victim retaliation, while still serving to impress and challenge other males.

Our results also suggest that this aggression might have more fitness implications for males than for females than was previously assumed. Using our preliminary analysis of physical injuries and physiological stress levels of targeted estrous females, we did not find strong evidence that attacks had substantial fitness costs to females. Nevertheless, the baseline stress hormones of lactating females rose significantly under the threat of the most extreme form of sexual coercion: infanticide.

In sum, male aggression toward females in this highly dimorphic species is not as random as expected and probably serves a variety of functions such as impressing rivals and coercing females. Likewise, Rodseth and Novak (Chapter 12 in this volume) suggest that in humans some aggression toward women is "private" violence used to intimidate and dominate, whereas other aggression is meant for the public arena and functions to impress others in the community. Similarly, male baboons probably target females both as a low-cost, noisy addition to a loud call display advertising their endurance and fighting ability *and* as a means of harassing and controlling specific females nearing ovulation. Thus, both males and females in the "audience" (watching or participating) probably use the information conveyed in these displays. This possibility warrants more investigation in other highly competitive multimale species.

### **Acknowledgments**

We thank M. Muller and R. Wrangham for organizing the symposium leading to this volume. We are also grateful for the helpful comments on our chapter by M. Muller, R. Wrangham, and two anonymous reviewers. Our research would not have been possible without the vital assistance in the field from our colleagues K. Hammerschmidt, R. Hoffmeier, M. Metz, A. Mokupi, M. Mokupi, J. Nicholson, C. Seyfarth, L. Seyfarth, and E. Wikberg. We thank the Botswana government and the Department of Wildlife and National Parks for permission to conduct the research, and W. J. Hamilton III and colleagues for initiating research in this area. We are grateful for the support of Ian Clark, Game Trackers, the former and current managers and staff at Eagle Island Camp, Mack Air, and our many other dear friends in Botswana over the years.

\_\_\_ -1  
 \_\_\_ 0  
 \_\_\_ +1

We thank Liza Moscovice for comments on an early version of this manuscript and Pat Whitten for assistance with hormonal analysis. Funding was provided at different times by the Ohio State University, the Deutsche Forschungsgemeinschaft, the University of Pennsylvania, the National Institute of Health, and the National Science Foundation.

## References

- Alberts, S. C., H. E. Watts, and J. Altmann. "Queuing and Queue-Jumping: Long-Term Patterns of Reproductive Skew in Male Savannah Baboons, *Papio cynocephalus*." *Animal Behaviour* 65 (2003): 821–840.
- Beehner, J. C., and T. J. Bergman. "Female Behavioral Strategies of Hybrid Baboons in the Awash National Park, Ethiopia." In *Reproduction and Fitness in Baboons: Behavioral, Ecological, and Life History Perspectives*, eds. Larissa Swedell and Steven R. Leigh, pp. 53–79. New York: Springer, 2006.
- Beehner, J. C., T. J. Bergman, D. L. Cheney, R. M. Seyfarth, and P. L. Whitten. "The Effect of New Alpha Males on Female Stress in Free-Ranging Baboons." *Animal Behaviour* 69 (2005): 1211–1221.
- Beehner, J. C., and P. L. Whitten. "Modifications of a Field Method for Fecal Steroid Analysis in Baboons." *Physiology and Behavior* 82 (2004): 269–277.
- Bulger, J. "Dominance Rank and Access to Estrous Females in Male Savanna Baboons." *Behaviour* 127 (1993): 67–103.
- Bulger, J., and W. J. Hamilton III. "Rank and Density Correlates of Inclusive Fitness Measures in a Natural Chacma Baboon (*Papio ursinus*) Troop." *International Journal of Primatology* 6 (1987): 635–650.
- Castles, D. L., and A. Whiten. "Post-Conflict Behaviour of Wild Olive Baboons. I. Reconciliation, Redirection and Consolation." *Ethology* 104 (1998): 126–147.
- Cheney, D. L., and R. M. Seyfarth. *Baboon Metaphysics*. Cambridge: Cambridge University Press, 2007.
- Cheney, D. L., R. M. Seyfarth, J. Fischer, J. Beehner, T. Bergman, S. E. Johnson, D. M. Kitchen, R. A. Palombit, D. Rendall, and J. B. Silk. "Factors Affecting Reproduction and Mortality among Baboons in the Okavango Delta, Botswana." *International Journal of Primatology* 25 (2004): 401–428.
- Crockford, C., R. M. Wittig, R. M. Seyfarth, and D. L. Cheney. "Baboons Eavesdrop to Deduce Mating Opportunities." *Animal Behaviour* 73 (2007): 885–890.
- Dixson, A. F. *Primate Sexuality: Comparative Studies of the Prosimians, Monkeys, Apes and Human Beings*. Oxford: Oxford University Press, 1998.
- Engh, A. L., J. C. Beehner, T. J. Bergman, P. L. Whitten, R. R. Hoffmeier, R. M. Seyfarth, and D. L. Cheney. "Female Hierarchy Instability, Male Immigration and Infanticide Increase Glucocorticoid Levels in Female Chacma Baboons." *Animal Behaviour* 71 (2006): 1227–1237.

- Fischer, J., D. M. Kitchen, R. M. Seyfarth, and D. L. Cheney. "Baboon Loud Calls Advertise Male Quality: Acoustic Features and their Relation to Rank, Age, and Exhaustion." *Behavioral Ecology and Sociobiology* 56 (2004): 140–148.
- Henzi, S. P., and L. Barrett. "Evolutionary Ecology, Sexual Conflict and Behavioral Differentiation among Baboon Populations." *Evolutionary Anthropology* 12 (2003): 217–230.
- . "The Historical Socioecology of Savanna Baboons (*Papio hamadryas*)." *Journal of Zoology, London* 265 (2005): 215–226.
- Kitchen, D. M., D. L. Cheney, and R. M. Seyfarth. "Female Baboons' Responses to Male Loud Calls." *Ethology* 109 (2003a): 401–412.
- . "Factors Mediating Inter-group Encounters in Savannah Baboons (*Papio cynocephalus ursinus*)." *Behaviour* 141 (2004): 197–218.
- . "Contextual Factors Mediating Contests between Male Chacma Baboons in Botswana: Effects of Food, Friends and Females." *International Journal of Primatology* 26 (2005): 105–125.
- Kitchen, D. M., R. M. Seyfarth, J. Fischer, and D. L. Cheney. "Loud Calls as Indicators of Dominance in Male Baboons (*Papio cynocephalus ursinus*)." *Behavioral Ecology and Sociobiology* 53 (2003b): 374–384.
- Lemasson, A., R. A. Palombit, and R. Jubin. "Friendships between Males and Lactating Females in a Free-Ranging Group of Olive Baboons (*Papio hamadryas anubis*): Evidence from Playback Experiments." *Behavioral Ecology and Sociobiology* 62 (2008): 1027–1035.
- Palombit, R. A., D. L. Cheney, J. Fischer, S. Johnson, D. Rendall, R. M. Seyfarth, and J. B. Silk. "Male Infanticide and Defense of Infants in Chacma Baboons." In *Infanticide by Males and Its Implications*, eds. Carel P. van Schaik and Charles H. Janson, pp. 123–152. Cambridge: Cambridge University Press, 2000.
- Palombit, R. A., R. M. Seyfarth, and D. L. Cheney. "The Adaptive Value of "Friendships" to Female Baboons: Experimental and Observational Evidence." *Animal Behaviour* 54 (1997): 599–614.
- Sapolsky, R. M., L. M. Romero, and A. U. Munck. "How Do Glucocorticoids Influence Stress Responses? Integrating Permissive, Suppressive, Stimulatory, and Preparative Actions." *Endocrine Reviews* 21(2000): 55–89.
- van Schaik, C. P., G. R. Pradhan, and M. A. van Noordwijk. "Mating Conflict in Primates: Infanticide, Sexual Harassment and Female Sexuality." In *Sexual Selection in Primates: New and Comparative Perspectives*, eds. P. Kappeler and C. P. van Schaik, pp. 131–150. Cambridge: Cambridge University Press, 2004.
- Seyfarth, R. M. "Social Relationships among Adult Male and Female Baboons. I. Behaviour during Sexual Consortship." *Behaviour*, 64 (1978a): 204–226.
- . "Social Relationships among Adult Male and Female Baboons. II. Behaviour Throughout the Female Reproductive Cycle." *Behaviour* 64 (1978b): 227–247.
- Silk, J. B. "Practice Random Acts of Aggression and Senseless Acts of Intimidation: The Logic of Status Contests in Social Groups." *Evolutionary Anthropology* (2002): 221–225.

- Silk, J. B., R. M. Seyfarth, and D. L. Cheney. "The Structure of Social Relationships among Female Baboons in the Moremi Reserve, Botswana." *Behaviour* 136 (1999): 679–703.
- Smuts, B. B. *Sex and Friendship in Baboons*. Cambridge, Mass.: Harvard University Press, 1985.
- Smuts, B. B., and R. W. Smuts. "Male Aggression and Sexual Coercion of Females in Nonhuman Primates and Other Mammals: Evidence and Theoretical Implications." *Advances in the Study of Behavior* 22 (1993): 1–63.
- Swedell, L. *Strategies of Sex and Survival in Hamadryas Baboons: Through a Female Lens*. Upper Saddle River, N.J.: Pearson Prentice Hall, 2006.
- Wittig, R. M., C. Crockford, R. M. Seyfarth, and D. L. Cheney. "Vocal Alliances in Chacma Baboons (*Papio hamadryas ursinus*)." *Behavioral Ecology and Sociobiology* 61 (2007): 899–909.