

“Friendship” with Males: A Female Counterstrategy to Infanticide in Chacma Baboons of the Okavango Delta

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The fundamental conflict of reproductive interests between males and females, originally articulated by Trivers (1972) and Parker (1979), may have diverse evolutionary consequences at multiple levels: genetic, morphological, physiological, social, ecological, life historical (Arnqvist and Rowe 2005; Chapman 2006). This volume addresses one dramatic manifestation of this conflict: coercive behavior directed at females by adult males. This phenomenon draws our attention immediately to selection on females for adaptive strategies countering the costs of male coercion.

In this chapter, I examine evidence for one such proposed counterstrategy in one particular system: “friendship” in a population of chacma baboons. “Friendship” refers to a cohesive social relationship between an anestrous female and an adult male (Figure 15.1). Smuts (1985) originally developed the concept in her classic study of olive baboons (*Papio hamadryas anubis*). Though sometimes labeled differently by various researchers, friendships have been observed in other olive baboon populations (Ransom and Ransom 1971), as well as in yellow baboons (*P. h. cynocephalus*) (Altmann 1980) and chacma baboons (*P. h. ursinus*, *P. h. griseipes*) (Seyfarth 1978; Anderson 1983; Palombit et al. 1997; Weingrill 2000). Friendship is a general feature of multimale, multifemale baboon societies, though it is not limited to baboons (Manson 1994; Palombit 1999) and does not necessarily have a unitary functional explanation.

This chapter focuses on research conducted for over a decade on a population of chacma baboons inhabiting the Okavango Delta in northwestern Botswana. These baboons live in relatively large groups (mean = 75 individuals)



Figure 15.1 A “friendship” in the Okavango chacma baboons, comprising an adult male, and an anestrus female (with her dependent infant). Photograph by Ryne Palombit.

comprising multiple adult males, adult females, and their offspring. As with baboons in other parts of Africa, groups are organized around linear dominance hierarchies and matrilineal relationships among female kin (for additional details concerning the study group and site, see Kitchen et al., Chapter 6 in this volume). This population is of special interest because a diverse array of data collectively suggests that male–female friendships are a female counterstrategy to a particular manifestation of sexual conflict: infanticide.

The “Coercive” Problem: Infanticide by Males

Male infanticide is the killing of unweaned infants by conspecific adult males. Clarke et al. (Chapter 3 in this volume) summarizes the increasing evidence supporting the sexual selection hypothesis that infanticide is a reproductive strategy of males: killing an unrelated infant prematurely terminates its mother’s lactational amenorrhea, returning her to ovulatory status much sooner, thereby making her available for fertilization to an infanticidal male whose own mating opportunities are constrained by intrasexual competition.

At first glance, male infanticide might seem to depart in two ways from Smuts and Smuts’s (1993) original definition of 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." First, the potential mating opportunities afforded by male aggression are less proximate when directed at anestrus females than at currently cycling females. If, however, loss of an infant accelerates a mother's availability as a potential mate to the male, infanticide can in principle be examined within a sexual coercion framework. Nevertheless, it is worthwhile to appreciate that the more extended temporal course for coercion of anestrus females may involve different conditions, decision making, and proximate mechanisms than coercion of cycling females.

A second issue is that infanticide may not be usefully viewed as aggression to females or perhaps even as "aggression" *per se*. The target of infanticide is the infant. In primates, with the apparent exception of chimpanzees and mountain gorillas, aggression to mothers during infanticidal attacks is relatively infrequent or erratic, being usually a response to maternal defense rather than an inherent tactical feature of the attack itself. Also, it is rarely injurious (van Schaik 2000; Palombit 2003). Indeed, some primarily anecdotal evidence suggests that males may preferentially improve the probability of success by attacking when an infant's mother is unlikely to be involved (i.e., she is some distance away). Several workers have also argued that infanticide "is best understood as a motivational system separate from general aggressiveness" (Hrdy et al. 1995; van Schaik 2000:46), partly in light of evidence that, at least in rodents, the neuroendocrine bases of infanticide are distinct from those mediating conspecific aggression (vom Saal 1984; Schneider et al. 2003).

Whether or not inclusion of infanticide improves our analysis of "sexual coercion," there is no doubt that infanticide is an arresting example of "sexual conflict" in the broader sense (Arnqvist and Rowe 2005), in which a male reproductive strategy imposes costs on female fitness. The cost becomes particularly acute in organisms with slow rates of reproduction such as in primates. The potential fitness consequences of infanticide are so significant that it is rightly regarded as being as important as "traditional" socioecological factors, such as predation, in models of primate social evolution in general and female biology in particular (Kappeler and van Schaik 2002; Hrdy 1979; Agrell et al. 1998; Ebensperger 1998). Confusion of paternity through female promiscuity may perhaps be the best known of these female counterstrategies (Clarke et al., Chapter 3, in this volume), but protective association with a male defender has received increasingly focused scrutiny (van Schaik and Kappeler 1997; Palombit 2000).

Infanticide in the Okavango Chacma Baboons

Infanticide is seldom observed partly because attacks are typically unpredictable, opportunistic, and rapid, but also because opportunities for successful infanticide are rare. Sometimes, however, infanticide occurs at relatively high rates. The chacma baboons of the Okavango Delta are one such population. Enlarging the original data sets of Busse and Hamilton III (1981) and Collins et al. (1984), Palombit et al. (2000) reported that infanticide accounts for at least 38% of infant mortality, though relative rates as high as 75% may occur in certain years. A subsequent demographic analysis over a longer period not only confirmed this figure, but demonstrated that infanticide was comparatively more important than any other cause of death, including disease and predation (Cheney et al. 2004).

The patterning of infanticide in this population is more consistent with Hrdy's sexual selection hypothesis than alternative models (such as the generalized aggression hypothesis or the social pathology hypothesis). Infanticide is usually perpetrated by an adult male who has recently immigrated into the group and attained the alpha position in the dominance hierarchy (Figure 15.2). Targeted infants are not only those in the group at the time of alpha male turnover, but also those born within one gestation period after the new



Figure 15.2 An infanticidal male with his victim. Photograph by Ryne Palombit.

alpha's immigration. His status as a new immigrant largely eliminates the possibility of killing his own offspring. And his dominance rank positions him to benefit reproductively since (1) the mother's resumption of menstrual cycling is greatly accelerated by loss of her infant; and (2) alpha male chacma baboons largely monopolize periovulatory matings (Bulger 1993). The full significance of this benefit is made clear by the brief tenure of alpha males, averaging only seven to eight months. In other words, an alpha male chacma baboon has near exclusive sexual access to females, but only for a brief period. This scenario intensifies the potential benefit of infanticide. And the benefit is realized: following the majority of infanticides, mothers were observed to copulate with infanticidal males during subsequent conceptive cycles (Palombit et al. 2000).

Occasionally, a long-term resident male in the group may rise to the alpha position. We might expect that these males would be less inclined toward infanticide than a new immigrant male who has never copulated with the females of the group. But infanticide following such "resident male" turnover has been observed, and in all cases the male had not been observed to previously consort with the female during the cycle in which she conceived the infant he killed. The noteworthy ability of the alpha male to monopolize copulations may be responsible: mating may be so skewed in his favor that other resident males run little risk of killing their own offspring. Because the sample size of "resident male alpha turnovers" is relatively small, however, this supposition awaits further tests.

Demographic data from the Okavango not only suggest the potential reproductive value of infanticide to males, but also illuminate the dire problem it poses to females. Consider that a new adult male immigrates into the group every few months on average (Palombit 2003), that alpha male tenure averages only seven months, and that gestation lasts about six months (Gilbert and Gillman 1951). In principle, then, a female could be faced with a steady succession of infanticidal alpha males: following the death of her infant, she would resume cycling within a month or two, mate with the male and conceive a month or so after that, only to give birth six months later when, once again, a new immigrant male is now alpha, who then kills her infant, and so on. Females do succeed in rearing infants, of course, for at least four reasons. First, not all new immigrant males attain alpha status rapidly or at all (Cheney et al. 2004). Second, not all alpha males become "infanticidal." Rather, evidence of infanticide and high infant mortality is associated with one-third to one-half of new alpha males, indicating that infanticide may be pursued facultatively by

males, depending on currently unclear criteria (Palombit et al. 2000). Third, older infants are more likely to survive wounds inflicted by infanticidal males (Palombit et al. 2000). Finally, the threat of infanticide may be mitigated to variable degrees by female counterstrategies, notably an association with a male defender.

The Counterstrategy: Recognizing “Friendships”

A necessary first step is reliably differentiating a friendship from the social relationships an anestrus female has with the other adult males in her group. Heterosexual friendships are, by and large, highly conspicuous associations, even to casual observers. Since social relationships are a function of the nature, patterning, and diversity of social interactions between individuals (Hinde 1983), the distinctiveness of friendships is best appreciated through consideration of multiple behavioral dimensions.

A useful initial indicator of an association is pronounced spatial proximity. A commonly used technique utilizes the so-called Composite Proximity Score (or C Score), which sums the amount of time two individuals are found within variable distances of one another. For example:

$$C = 1(T_{0-2m}) + 0.25(T_{2-6m})$$

where T_{0-2m} and T_{2-6m} are the percentages of time that a male and female spend within 0–2 m and 2–6 m, respectively (Palombit et al. (1997) (corresponding constants of 1 and 0.25 are weighting factors for each spatial category—see Smuts [1985]). A C-score is calculated for each male-female dyad in the group, and then the distribution of scores for a particular female is examined: a discontinuous distribution indicates a distinctive spatial association of this female with a particular male (or two) (Figure 15.3). Thus, friendships are male-(anestrus) female dyads characterized by a high degree of spatial proximity.

A striking feature of the Okavango chacma baboons is that this propinquity typically becomes conspicuous only after a female gives birth to an infant, usually quickly thereafter (Palombit et al. 1997). In the period immediately preceding the birth of an infant *and* also, in the relevant cases, immediately following the death of an infant, a female’s spatial relations do not clearly reveal “special relationships” with any adult males in particular. Friendships are tied closely to the presence of a dependent infant.

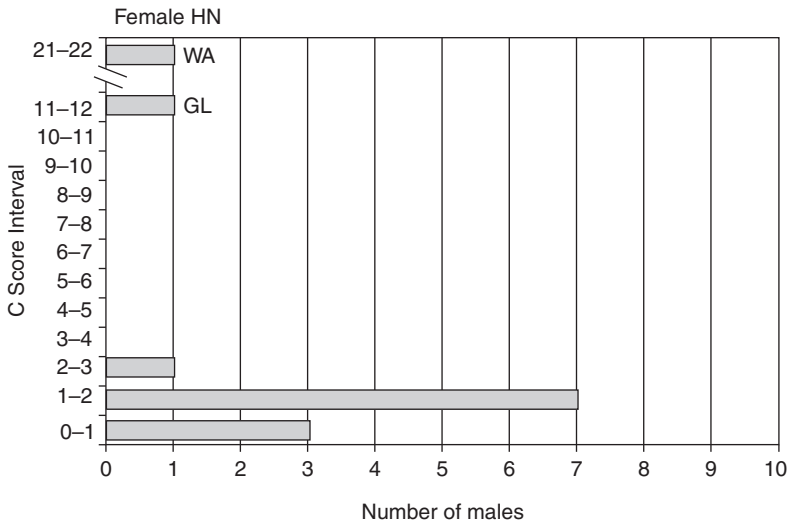
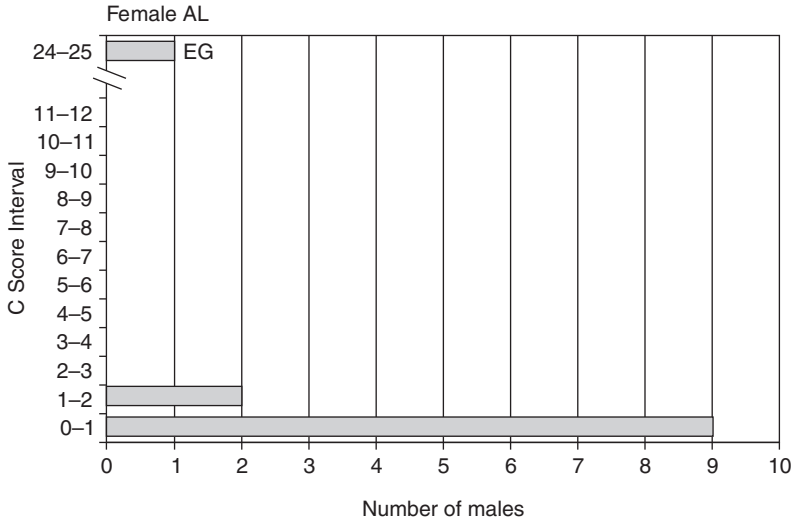


Figure 15.3 The distribution of composite proximity scores (C scores) for two representative females, AL and HN. The number of males in the group (on the *x*-axis) with a C score falling within the range given (on the *y*-axis) is shown for each female. “EG,” “WA,” and “GL” designate the names of male friends identified based on discontinuities in the distributions.

There is much more to friendship than simple spatial association, however, as reflected by the additional social interactions of friends. One of these is “infant handling,” the prolonged, relaxed touching and manipulation of an infant attended or carried by its mother (Figure 15.4). A female’s baby is frequently handled by multiple adult females (Silk et al. 2003), but when it comes to males, her friend handles an infant at nearly three times the rate of all other (non-friend) males, even after controlling for the greater propinquity of friends. Indeed, for nearly two-thirds of lactating females, friends are the *only* males who handle infants. The functional significance of infant handling remains unclear, though this behavior is not “agonistic buffering,” in which a male uses an infant to shield himself from aggression from another male (e.g., Busse 1984a). The relevance of infant handling for distinguishing friendships is that it reflects a pronounced level of maternal tolerance (“trust”) of a particular male and his attitude toward her infant.

Allogrooming is also significantly more common between friends. Approximately 7% of the time that friends are in close proximity is devoted to grooming, compared to no more than 2% (and usually far less) for nonfriend males. As with infant handling, the male friend is the *only* male grooming partner for many lactating females.



Figure 15.4 “Infant handling” by an adult male friend. Photograph by Ryne Palombit.

Finally, there is a distinct vocal dimension of friendships. The importance of vocalizations in regulating social behavior was first revealed in this population by study of female-female interactions. Adult females sometimes emit low-amplitude, tonal grunts when approaching one another (Cheney et al. 1995). Compared to "quiet approaches," this grunting increases the probability of both sustained proximity and ensuing affiliative interaction (such as grooming) between the females, especially if they have disparate dominance ranks. Grunts by males have a similar function, but with one important qualification (Palombit et al. 2000). In male approaches to females, grunts by males are also associated with elevated rates of affiliative interaction, if the female is cycling or pregnant. When the female is lactating, however, grunts have this mollifying effect *only* when they are performed by an approaching male friend (Figure 15.5). In other words, a female with infant shuns affiliative interaction with a nonfriend male, whether he grunts or not. Thus, females appear to classify males on the basis of their friendship status and accordingly moderate their response to a signal that normally paves the way for friendly interaction.

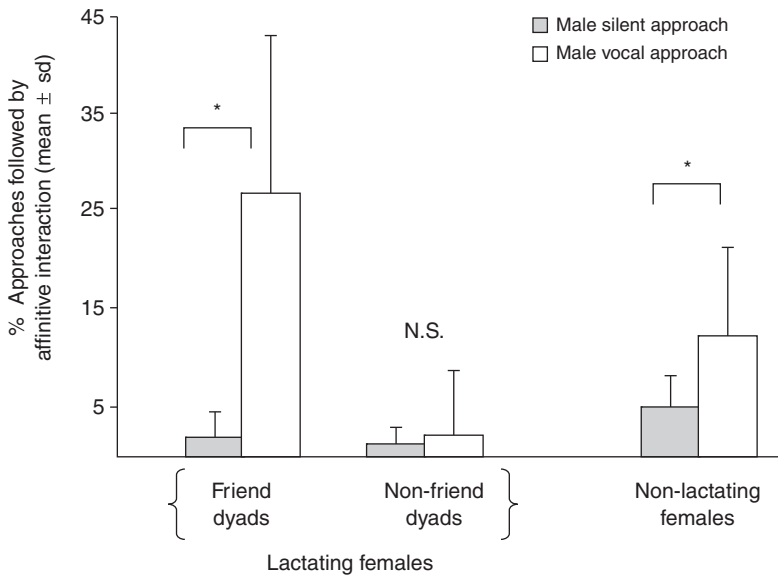


Figure 15.5 The effect of male grunting on subsequent affiliative interaction with females.

* Indicates significantly higher rates of affiliative interaction following vocal approaches by males ($p < 0.05$).

Who Are the Friends?

The variables we have described set friendships clearly apart from lactating females' relationships with other males in the group, but which individuals engage in friendship behavior? The vast majority of female chacma baboons have friendships with an adult male during at least some part of their lactation period. For example, of 19 births monitored among 14 females by Palombit et al. (1997), in only two cases did a parturient female fail to establish a friendship (in one case, the infant survived to weaning; in the other case, it was killed a few hours after birth). Females of all dominance ranks have male friends, although competition among females may sometimes influence the distribution of friendships in the group and over time. Similarly, both multiparous and primiparous mothers engage in friendship behavior. The modal pattern is for a lactating female to have one male friend at a time. In Palombit et al.'s (1997) study, for example, only 3 of 12 lactating females had multiple male friends simultaneously. None had more than two. In summary, any female who gives birth to an infant is likely to develop a friendship, regardless of her dominance and parity status.

Male friends are almost always fully adult, nonnatal individuals (in one case, a lactating female's friend was her young adult son). Males of all dominance rank may be potentially involved in friendships; thus most males participate in friendships at some point in their lives. The current alpha male is rarely a friend to females, however, unless his tenure exceeds one gestation period (i.e., unless he copulated with the lactating female during her previous conceptive cycle). Although lactating females avoid the current alpha male as friend, about 60% of the friend dyads involve *former* alpha males (Palombit et al. 1997), and females may preferentially seek out such males as associates.

The Adaptive Value for Females: Do Male Friends Make a Difference?

A useful starting point for understanding the purpose of friendships concerns the *costs* of friendships. Relationships are usefully viewed as elements of an individual's social world that it must develop, maintain, and "service" (Kummer 1978). If females benefit from associating with a male friend, we predict that they will invest in these relationships. Two behavioral measures reflect this investment.

First, the "Hinde Index" (Hinde 1977) usefully assesses which partner in a dyad is responsible for the close proximity (≤ 2 m) they share. In the current context, the index is obtained by subtracting the percentage of withdrawals due to the female from the percentage of approaches due to her action. The resulting index varies from -100 , signifying complete male responsibility, to $+100$, reflecting female responsibility. Hinde indices for chacma baboon friends are almost all positive, and the average value is strongly positive. Thus, it is the female who is responsible for the fact that friends are often near one another. A second assay of investment concerns grooming. Because allogrooming is a primary mechanism for establishing and maintaining social relationships in primates (Dunbar 1988; Harcourt 1988), its distribution may indicate the "value" individuals ascribe to their different social relationships (*sensu* Simpson 1991). Notably, nearly 90% of the grooming exchanged between friends is done by the female (Figure 15.6). Male friends rarely reciprocate grooming. In this sense, too, the female commitment to maintaining the relationship is conspicuously greater than the male's involvement. The existence of these costs of friendships to females implies compensatory benefits. Three hypotheses address the adaptive benefits of friendships to females:



Figure 15.6 Adult female grooming her male friend. Photograph by Ryne Palombit.

The *infanticide protection hypothesis* argues that males protect their female friends' infants from infanticidal attack.

The *female harassment hypothesis* posits that male friends protect lactating females from aggressive interactions with higher-ranking females. Dominant females may harass mothers (Altmann 1980) or handle roughly or temporarily "kidnap" their infants (e.g., Wasser 1983).

The *future male caretaker hypothesis* suggests that there are no immediate, protection-related benefits of friendship to females. Rather, a female establishes a friendship with a particular male in order to promote the development of a relationship (even perhaps attachment) between her infant and the male (Ransom and Ransom 1971; Seyfarth 1978). The proposed benefit of this bond comes later, when the youngster is an older infant or a juvenile, and the male may reduce its travel costs through occasional carrying (Anderson 1992), defend it from predators or from nonlethal aggression from other immatures or adult females (Altmann and Altmann 1970; Buchan et al. 2003), increase its access to food (Altmann 1980; Packer 1980), or accelerate its socialization and attainment of independence (Altmann 1980).

Four independent lines of evidence—demography, behavioral observations, playback experiments, and hormonal profiles—strongly suggest that the benefit of male friends to females relates more to infanticide protection than alternative contingencies. This evidence can be described with reference to these hypotheses' respective predictions, as follows.

Prediction 1: Friendship reduces infanticide risk to mothers.

Directly demonstrating this fitness benefit of male associates is difficult because there are not enough data to compare rates of infanticide suffered by females who have male friends and those *very* few females who do not. Another way to test this prediction, however, is to rephrase it:

Prediction 2: Friendship status enhances a male's willingness to invest in the anti-infanticide defense of particular females and their infants.

This prediction can be tested in two ways. First, we can compare the behavior of males during potential (or actual) infanticidal attacks by a new alpha male. Such comparisons are necessarily qualitative because these attacks do not lend themselves to systematic collection of behavioral data. Typically, many individuals are rushing about, covering relatively long distances, calling loudly, chasing, seeking cover, fleeing. It is important to understand that the commotion surrounding these attacks does not mean that infanticide is a side effect of ongoing aggression escalating "out of control" to fatally injure bystanders (*sensu* Bartlett et al. 1993). On the contrary, infanticidal attacks are typically sudden

and precipitous, and are not preceded by other aggression. The pronounced arousal of other baboons is a *response* to the attack (e.g., chasing a male who has clutched an infant in his mouth). Even with the limitations on observations, two general features of infanticidal defense emerge.

One feature is that male friends are not the *only* respondents to these attacks. In a majority of cases (at least 60%), other nonfriend males and females are unambiguously aroused and move rapidly to the site of an attack, vocalize (e.g., scream or grunt), or even chase the attacker (Palombit et al. 2000). In one such attack, for example, an infant was saved when its 5-year-old sister snatched it up and carried it quickly away from the pursuing alpha male.

Another feature is the qualitative difference in the responses of adult males: males observed to directly engage the attacker (e.g., approach, chase, or fight him) or the infant (e.g., carry it) are always the friend of the infant's mother (Table 15.1; Figure 15.7). Although these males may be actively confronting a rival male who is arguably superior in fighting ability, their defense may still be effective in part because the distribution of injuries in escalated male-male fights is largely independent of the interactants' rank (Drews 1996). In other words, a middle-ranking male may still inflict a serious injury during a prolonged fight with a physically superior alpha. As predicted by the infanticide protection hypothesis, friends are more willing than other males to participate in the energetically costly and risky forms of anti-infanticide defense.

Table 15.1 Qualitative differences in male response to potentially infanticidal attacks by alpha male (summarized from Palombit et al. 2000).

Response Dimension	Friend Males	Non-friend Males
Move rapidly to attack site?	+	+
Remain at attack site for prolonged period in state of "aroused vigilance"	+	+
Vocalize in response to attack	+	+
Chase attacker	+	+
Initiate chase of attacker	+	-
Direct threats, appeasement signals, vocalizations at attacker at close range	+	-
Initiate and maintain close proximity to attacker	+	-
Physically fight attacker	+	-
Carry infant for extended travel	+	-



Figure 15.7 A vigilant adult male watches an infant he is protecting. Photograph by Ryne Palombit.

A second way to test Prediction 2 is through field playback experimentation, which provides supplemental data on male defensive predispositions under more controlled conditions. The experimental rationale derives from the fact that female cercopithecines typically emit screams when attacked by others, and these calls may function in part to recruit defensive aid from conspecifics (Gouzoules et al. 1984; Cheney and Seyfarth 1990; Bergman et al. 2003). The response of male chacma baboons to naturally occurring screams from out-of-sight females does not always involve movement toward the caller. Sometimes males respond simply by looking and visually scanning—albeit intently—for variable amounts of time.

Experimental playbacks exploit this natural variation in male responsiveness by selectively presenting female screams to male friends or nonfriend males under uniform conditions that control for numerous potentially relevant variables (e.g., immediately preceding social interaction) (Palombit et al. 1997). With this technique, we can now obtain a better sense of how males vary in their solicitude toward females in distress. Such experiments reveal that (1) a

particular female scream elicits a stronger response from her male friend than a control male of similar rank and friendship status (i.e., the control male also has a female friend in the group, but not the one whose scream he hears); and (2) any given male responds more strongly to his female friend's scream than to the scream of another lactating female of similar dominance rank (Figure 15.8a). Visual scanning is likely to reflect the listener's investment in obtaining further information about the specific circumstances surrounding the vocalization (Marler et al. 1992) and is generally predictive of imminent changes in behavior (Rowell and Olson 1983).

Consequently, the results support the conclusion suggested by the *ad libitum* observations of infanticidal attacks that friendship with a female heightens a male's predisposition to protect her. Although this finding was partly unanticipated by the experimental design, in two trials a male subject did move immediately and quickly in the direction of the playback speaker—these males were both friends of the (playback) caller. Thus, as predicted by the infanticide protection hypothesis, a female's male friend seems to "care" more than other males about her safety and security. This hypothesis also specifies the temporal patterning of this male solicitude:

Prediction 3: A male's willingness to invest in defense is strictly tied to the presence of the female friend's infant.

The playbacks revealed striking support for this prediction: the solicitude of male friends vanishes with the infant. At various times during our study, infants died (usually, but not always, due to infanticide). When we repeated the same playbacks shortly after the deaths of these infants, male friends responded far less strongly; in fact, the magnitude of their responses was significantly *weaker* than that of control males (Figure 15.8b). Thus, as predicted by the infanticide protection hypothesis, a female's male friend seems to "care" more than other males about her safety and security, but only when she has an infant. Similarly, as noted earlier, a female ceases investment in her friendship behavior shortly following the death of her infant. For both sexes, then, the function of friendships is closely tied to neonates.

The empirical support for Predictions 2 and 3 is inconsistent with the future male caretaker hypothesis, which holds that the advantage does not lie in immediate protection by males at the time of the friendship, but rather in the bonds that form later between males and youngsters.

The female harassment hypothesis, however, cannot be rejected on the basis of Predictions 2 and 3 since it also predicts that male friends will come to

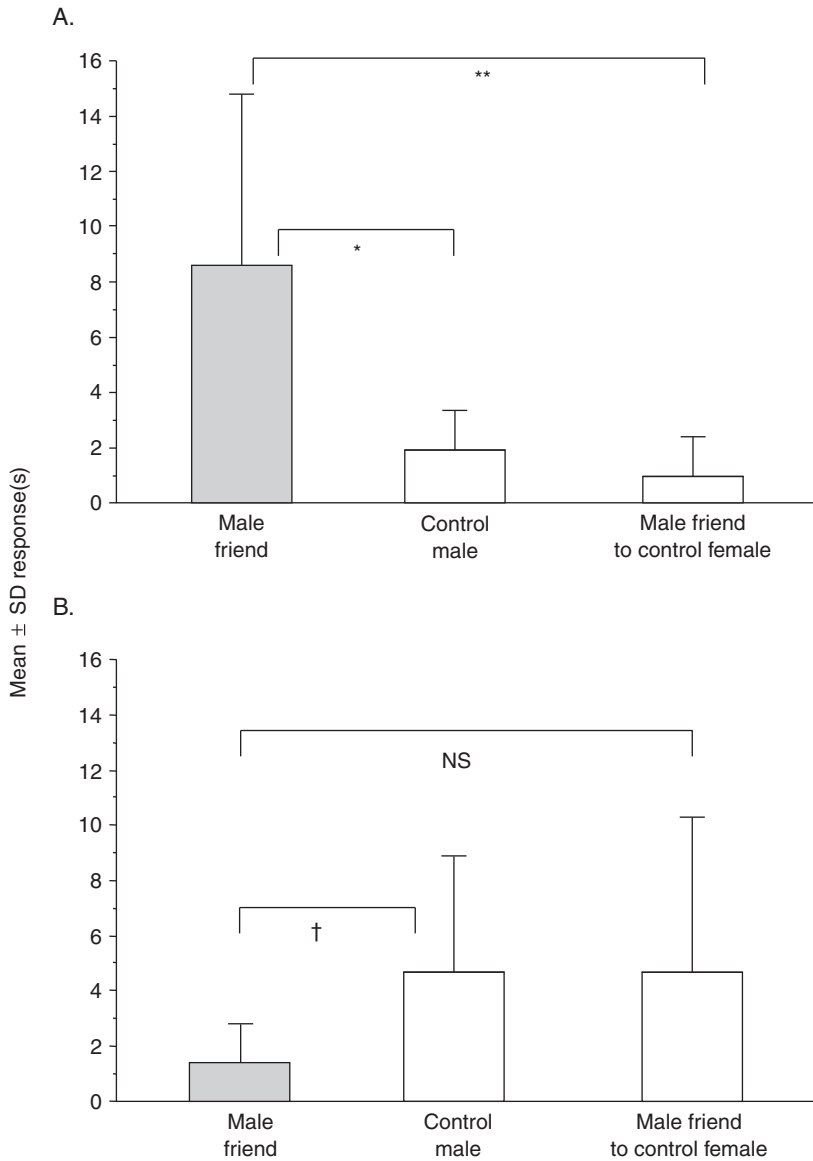


Figure 15.8 Experimental audio playback of female screams to adult male chacma baboons. The first two bars show the responses to the same stimulus scream of her male friend (black bar) or a control male of similar dominance rank and friendship status; that is, he has a female friend (white bar). The hatched bar is the response of the original male friend to the scream of a control (lactating) female. Part a presents results of some text is dragged here performed when the male friend's female partner had a living infant: male friends showed significantly ($p < 0.01$) stronger responses than control males to the same scream (*), and male friends responded significantly stronger to the screams of their female friends than control females (**).

the aid of females in distress. To further test between the Infanticide Protection and the Female Harassment hypotheses, two additional predictions focus on their respective sources of danger.

Prediction 4: Male friends will respond more strongly than control males to attacks on females by the potentially infanticidal alpha male (infanticide protection hypothesis) or by higher-ranking females (female harassment hypothesis).

A final series of playback experiments reveal that it is the infanticidal contingency that most clearly differentiates the responses of friend versus nonfriend males. These experiments utilized a stimulus comprising a female victim's screams (as above), but now combined with the threat calls of the (simulated) attacker (Palombit et al. 1997). In these trials, male friends respond more strongly than control males when the aggressor was an infanticidal alpha male rather than a high-ranking female (or even a high-ranking, but noninfanticidal [beta-ranking] adult male). In other words, males seem to perceive that a potentially infanticidal attack threatens greater danger to their friends (and their infants) than does female harassment (or attack by nonalpha males), and they respond accordingly.

Prediction 5: Lactating females will exhibit avoidance of the potentially infanticidal alpha male (infanticide protection hypothesis) or higher-ranking females (female harassment hypothesis).

Lactating females unambiguously avoid new immigrant alpha males, as expressed by rapid retrieval of infants and flight from proximity of the male, often accompanied by highly intense displaying, such as screaming and the "tail-up" display (Busse 1984b; Palombit et al. 2000). This conspicuous pattern of avoidance is much less common among other females or among lactating females whose infants happen to be elsewhere at the time. Another striking feature of

Part b presents results of playbacks conducted within 1 to 4 weeks of the death of an infant: at this time, male friends showed significantly ($p < 0.05$) weaker responses to control males (\dagger), and the male friends' response to friends' screams did not differ significantly from their response to the control female's scream. The response measure is the duration of the subject's looking in the direction of the playback speaker in the 20s after the vocal stimulus is played back minus the duration of looking in the same direction in the 20s preceding playback (Mean \pm SD for pooled subjects.) All tests were the relevant paired comparisons as indicated, performed with two-tailed, Wilcoxon signed ranks tests for 30 playbacks (Part A) or 18 playbacks (Part B) distributed equally across conditions See Palombit et al., 1997 for details).

this avoidance is that the new alpha is often simultaneously directing affiliative or conciliatory signals such as lip-smacking or grunting at these fleeing, screaming females; these signals fail to mollify mothers carrying infants.

Behavioral data do not support the analogous prediction of the female harassment hypothesis, however: lactating females approach and avoid higher-ranking, unrelated females at the same rate they do when they are cycling. Finally, the fact that high-ranking females all the way up to the group's alpha female pursue friendships as reliably and vigorously as low-ranking individuals do (see later in this chapter) suggests that protection from harassment from other females is not the primary benefit offered by male friends.

Thus, behavioral data from the Okavango chacma baboons support the infanticide protection hypothesis more than the two alternative hypotheses. Recent hormonal data further support the infanticide protection hypothesis. Glucocorticoid hormones, such as cortisol, have long been considered physiological assays of stress (Sapolsky 1993; Palme et al. 2005). It is not surprising that immigration of a new male chacma baboon elevates glucocorticoid levels among group members. Not only does he destabilize the male dominance hierarchy by his arrival, but he pursues alpha status through increased aggression and threat displays, such as loud "wahoo" calling contests and vigorous chases (Kitchen et al. 2003; Fischer et al. 2004). Thus, circulating cortisol levels rise in males (including the immigrant) at this time (Bergman et al. 2005). It is the corresponding hormonal responses among females that are of interest in testing the infanticide protection hypothesis, which posits that:

Prediction 6: Compared to other females, females at risk of infanticide will experience greater stress following immigration of a new male, and therefore show higher levels of circulating cortisol.

Alternatively, however, we might argue that the social disturbance caused by intensified male-male competition would affect females generally, or, if anything, cycling females in particular, for they among females are disproportionately targeted in the protracted, aggressive chases that seem to advance a new male's rise to alpha status (Kitchen et al., Chapter 6 in this volume):

Prediction 7: Emigration of a new male will be followed by cortisol increases in all females, or more in cycling females.

The hormonal data support Prediction 6 but reject Prediction 7. It is not cycling, but lactating (and pregnant) females who exhibit a significant rise in glucocorticoids following immigration of a new male (Beehner et al. 2005). These data demonstrate that this hormonal spike is not due to changes in rates

of (noninfanticidal) aggression from males, female-female grooming, female-female aggression, and male-male aggression. The implication is clear: females at risk of infanticide from the new male undergo peculiarly high stress upon his arrival. This is borne out by observed *additional* increases in glucocorticoid concentration among lactating females when a new alpha commits infanticide (Engh et al. 2006). Finally, and most importantly, the infanticide protection hypothesis predicts that:

Prediction 8: Compared to mothers with male friends, lactating females without male friends are at higher risk of infanticide, and therefore will exhibit higher levels of stress-related hormones.

The data demonstrate that the few lactating females who do not have male friends not only sustain higher circulating levels of cortisol generally, but they also experience this predicted higher cortisol spike at alpha male turnover (Beehner et al. 2005). In light of the fact that males rarely—if ever—groom their female friends, this hormonal difference cannot be attributed simply to less grooming from a male friend.

Is Infanticide Protection from Friends Worth Competing For?

Competition among females for males is relatively rare in mammals, and consequently little studied (Berglund et al. 1993; Andersson 1994). Sexual selection theory (Darwin 1871) predicts that such female-female competition is most likely in two contexts: (1) a “sex role reversed” mating system (Petrie 1983), which certainly does not apply to the chacma baboon; and (2) when males provide a resource or service crucial to female reproduction. It is difficult to imagine a male service more critical to a female chacma baboon than preventing the death of her infant, particularly in light of the clear demographic impact of infanticide. Thus, more so than its alternatives, the infanticide protection hypothesis generates several additional predictions:

Prediction 9: Females will compete for male friends.

Female competition implies that males vary in their effectiveness as protectors of infants and hence in their value as friends. A male's dominance rank and paternity status are likely focal points of female-female competition because they imply greater competitive ability and defensive motivation, respectively:

Prediction 10: Females will compete for access to male friends who are high ranking and/or fathers of their infants.

Finally, we ultimately need to demonstrate the benefit of female-female competition:

Prediction 11: Competitively superior females will gain access to better male protectors and therefore suffer less risk of infanticide than less successful females.

Beginning with Prediction 9, several lines of evidence suggest that such competition occurs among lactating female chacma baboons.

Differential Access to the Male Friend. First, sometimes two mothers maintain friendships with the same male simultaneously (Figure 15.9). In such cases, the higher-ranking female maintains greater levels of close proximity and interaction (e.g., allogrooming) with him than her subordinate counterpart. The magnitude of this disparity is especially pronounced when the dominant is a young female and the subordinate is an old female. This may be partly because primiparous females appear to be more vulnerable than their multiparous counterparts to infanticide (Palombit et al. 2000; Cheney et al. 2004). That is, younger females not only have more to gain from friendships, but they may also have more to lose from unsuccessful competition with other females.

Competitive Exclusion from a Male Friend. Second, the pattern of differential access to the male friend results from competitive “displacement” of the lower-ranking female by the dominant rival. We can observe this progression



Figure 15.9 Two lactating females who are simultaneously engaged in friendships with the same adult male. Photograph by Ryne Palombit.

in situations when one lactating female has an exclusive friendship with a particular male, and then another female gives birth and establishes a friendship with him as well. The consequences for the first female's friendship depend on the dominance ranks of the females. If the first female is low-ranking, and she is then "joined" by a higher-ranking mother, the subordinate female experiences a quick and dramatic decline in her propinquity and social interaction with the male friend. The converse does not occur, however: a dominant's friendship remains largely unchanged if a second, newly parturient low-ranking female begins associating with the male (Palombit et al. 2001).

These changes in friendships are the result of female behavior rather than of male friend behavior. These females do not usually physically fight or aggressively interfere with each other, but dominants supplant subordinates from male friends in much the same way that they supplant them from foods. In other words, dominant females compel low-ranking rivals to withdraw from the contested resource, the male friend. Males apparently do little to influence this outcome. In many cases, a low-ranking female is entirely supplanted from her friendship with a male; that is, she abandons the relationship and pursues an alternative strategy.

Attributes of Male Friends. Is there evidence that certain male characteristics are particularly "valued" in female competition for male friends (Prediction 10)? One initial piece of evidence is the fact that two females' simultaneous sharing of a single male friend does not simply derive from a lack of males. In all cases where we observed this phenomenon, there were three to four long-term resident, nonnatal adult males who were unengaged in friendships at the time (though each of them participated in friendships at other times). Thus, when establishing friendships, lactating females overlook "unbonded" adult males in favor of males who already possess a male friend. Notably, subordinate females are just as likely as dominants to choose a male that already has a friend, even though sharing a friend imposes higher competitive costs on them. This pattern already implies variation in male quality.

Two features of males stand out in this regard: dominance rank and probability of paternity of the female's infant. The importance of male rank in female competition is suggested by the positive correlation between friends' ranks: high-ranking females acquire high-ranking males as friends (Figure 15.10). There are several potential advantages of high rank in a male protector against infanticide. First, the physical superiority of dominant males may make them more effective defenders. Second, as described earlier, the vigor and speed of

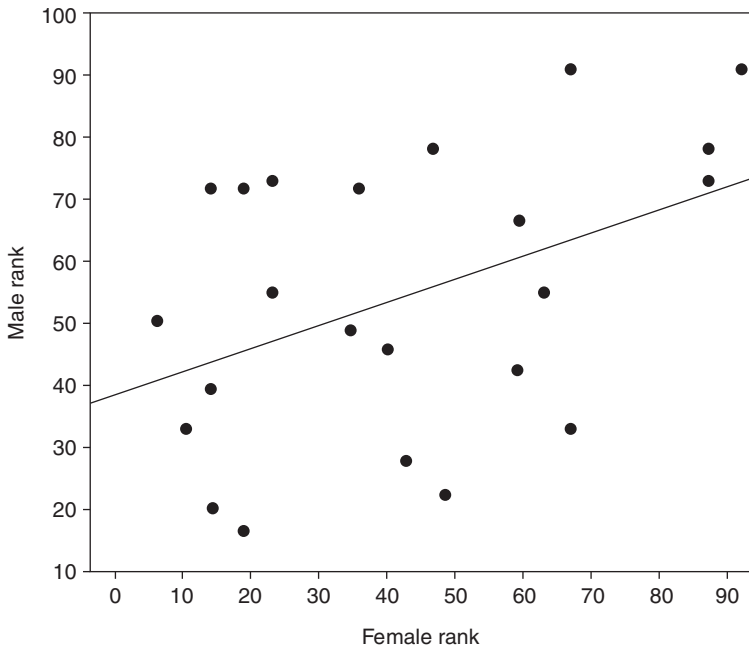


Figure 15.10 Association between the dominance ranks of male and female friends ($r_s = +0.42$, $p < 0.05$). Rank is expressed as the percentage of individuals dominated.

the male friend's response to infanticidal attack may facilitate indirect defensive participation from other baboons. High rank in the male friend may facilitate this involvement by nonfriends, since rank and the relative fighting abilities of opponents influence monkeys' decisions about intercession in ongoing aggression (Harcourt 1992; Noë and Sluiter 1995; Silk 1999). Finally, of course, dominant males may have a higher probability of paternity of a female's infant and, therefore, a greater predisposition to defend it.

The potential importance of paternity is indicated by the fact that in at least 68% of friendships, the male had previously copulated with the female in the cycle in which she conceived her current infant (Palombit et al. 1997). Since females typically mate with only one or two adult male partners per cycle (Bulger 1993), this result suggests that females preferentially target possible fathers as friends. Without direct genetic analyses, however, it is difficult to specify how paternity influences male defense or friendship behavior, but one unexpected result of the experimental playbacks is intriguingly suggestive. There is a positive correlation between the magnitude of a male friend's response to the

female's scream and the dominance rank he held when his female friend conceived her infant (6–10 months earlier) ($r_s = +0.70$, $N = 10$, $p < 0.05$). There was no such correlation between the male's response and his rank at the time of the actual playback, however. Hauser (1986) similarly found that playback of infant vervet monkey (*Cercopithecus aethiops*) screams elicited stronger responses from males with a presumed higher probability of paternity. Thus, to the extent that male rank is correlated with mating success, this result may reflect the importance of paternity in male protectiveness. If paternity influences chacma male protectiveness, it becomes a resource that females should seek to acquire and, if necessary, compete for.

Benefits of Competition: In light of these patterns, we can test Prediction 11 by answering this question: If high-ranking males are better protectors, and high-ranking females usually acquire them as friends, then are high-ranking females less vulnerable to infanticide? Demographic data collected to date do not suggest improved survivorship among the infants of high-ranking females (Cheney et al. 2004). If anything, *middle-ranking* mothers seem to suffer less infanticide than either their high- or low-ranking rivals. If we divide the female hierarchy into equal thirds, we find that approximately 12% of infanticide victims were born to mid-ranking females, compared to 53% and 36% being the offspring of high- and low-ranking females, respectively.

The implications of this demographic result for understanding female competition for friends is unclear. The fact that a decade of demographic data have not yet revealed any clear-cut reproductive advantage of high rank to females generally (Cheney et al. 2004) recommends further study of this long-lived, slowly reproducing primate. Conversely, high- and low-ranking females may be more vulnerable to infanticide. High-ranking females may be more vulnerable because they enjoy priority of access to feeding sites, as does the (infanticidal) alpha male, thereby bringing them together frequently. Low-ranking females may be more susceptible because their (lower-ranking) male friends are less effective deterrents. In any case, longitudinal data are needed to test this prediction.

Is Infanticide Protection Worth Competing For? Infanticide protection in chacma baboons raises a fundamental question: why is competition for male friends necessary at all? A "nondepreciable" resource should not stimulate competition (Kleiman and Malcolm 1981), and it is not immediately obvious why a male friend cannot guard several mothers (and their infants) at the same time, especially in light of the female responsibility for proximity maintenance.

After all, analogous protection against predation has been considered a service males can provide to multiple females simultaneously (van Schaik and van Noordwijk 1989; Rose and Fedigan 1995).

So, why do females compete for males? There are at least two possible reasons. First, females may act “spitefully” to lower the fitness of rivals by depriving them of a critical resource that is, in fact, shareable (Knowlton and Parker 1979; Berglund et al. 1993). Current data do not allow a test of this hypothesis in the chacma baboon. Alternatively, and more plausibly, the substantial investment female chacma baboons make in friendships suggests that social, spatial, and temporal access to a particular male, in order to “service” a relationship with him, is not necessarily equally shareable among several females at once. In other words, the opportunity to develop the friendship itself—which seems to crucially influence male defense—becomes the effectively depreciable resource for which females compete.

The Costs and Benefits of Friendships to Males

The adaptive significance of friendships as a female counterstrategy cannot be fully understood until we consider males. From a male perspective, it does not matter that females stand to benefit reproductively from their association. If friendship-based protection is costly to males, there must be compensatory fitness advantages for them in order for females to garner infanticide protection.

One might reasonably argue that at one level the costs of friendships to male chacma baboons appear trivial, or at least considerably less substantive than those impacting females. Even the casual observer of chacma baboon friendships is struck by the conspicuous female contribution to the relationship—through maintaining proximity and allogrooming—and the contrasting modicum that males seem to invest in this regard. In this situation, however, experimental playbacks usefully distill out the significant commitment of male friends. That is, although indifference may seem to characterize a male’s daily interactions with an attentive female friend, playbacks under controlled conditions reveal that he does “care” disproportionately for her (and her infant) in circumstances that are potentially dangerous. The consequential costs of this solicitude are suggested by the nature of these males’ direct defense during infanticidal attacks. Vigilance, active protection, and risk of injury are costs to males that direct our attention to potential benefits, which can be grouped into three hypothetical alternatives.

The parental effort hypothesis suggests that males are the fathers of the infants they protect, and thus they directly enhance their individual fitness

through friendships. Observations that male friends are usually one of several former sexual consorts of their female partners in their previous conceptive cycle support this hypothesis. Thus, there is clear potential for paternity to motivate baboon social behavior.

The mating effort hypothesis suggests that males are unrelated to the infants of their current female friends, but friendship increases the probability of siring *future* offspring with these females through preferential mating (Smuts 1985). This scenario seems unlikely to operate in the Okavango chacma baboons in light of the apparent capacity of alpha males to competitively exclude other males from periovulatory matings, but only genetic data can conclusively test the hypothesis.

A third set of hypotheses can be subsumed under the diverse "Social Advantages" males may derive directly or indirectly from association with females. For example, friendship with an anestrus female may facilitate an immigrating male's integration into a group (Smuts 1985). Although there is one recorded case of a pregnant female chacma baboon befriending an immigrant male in this manner (Palombit unpublished data), this hypothesis cannot generally explain chacma baboon friendships because new immigrants are virtually never chosen as friends by lactating females (almost certainly because they constitute the primary risk of infanticide). Alternatively, male and female friends may mutually support each other in aggressive interactions. For example, the aid male rhesus macaques (*Macaca mulatta*) receive from their female friends crucially helps them achieve and maintain high rank (Smuts and Smuts 1993). There is currently no evidence, however, that male status in the Okavango chacma baboons depends in any meaningful way on assistance from females or, for that matter, from other males. In this population, coalitionary support is rare among females (even among kin) (Silk et al. 1999) and is virtually nonexistent among adult males. Finally, friendship with a female may facilitate a male's access to her infant to use as an "agonistic buffer" when another (higher-ranking) male threatens or attacks him (Deag and Crook 1971; Ransom and Ransom 1971). This hypothesis has not been studied intensively, but there is evidence that males may be able to use friends' infants as buffers more frequently than other infants (Busse 1984a; Palombit unpublished data). What is lacking, however, is a clear understanding of the quantitative fitness benefits of agonistic buffering to males and of whether these compensate for the costs of protecting these infants.

In summary, the fitness consequences for males—both costs and benefits—remain one of the least understood aspects of friendship behavior, not only in

chacma baboons, but in baboons and primates generally (van Schaik and Paul 1996). At present, the parental effort hypothesis seems most plausible, but additional data are needed for direct tests. To this end, the relevant paternity analyses of DNA from the Okavango chacma baboon population is currently underway.

Conclusions and Future Directions

Taken together, these diverse data suggest that heterosexual friendships in this population are best understood as a female counterstrategy to infanticide. The Okavango chacma baboons are not unique in this regard. Weingrill (2000) came to the same conclusion in his study of chacma baboons in the Drakensberg Mountains of South Africa. More generally, there is accumulating evidence that female association with a male protector has evolved as an anti-infanticide strategy in a variety of mammals, birds, and insects (Palombit 2000). Of course, infanticide avoidance is not the only adaptive reason for male-female bonds generally (e.g., Gubernick and Teferi 2000), and even perhaps for baboon friendships in particular. As noted, infanticide does not appear to be nearly as important in male reproductive strategies among East African baboons (Palombit 2003), though friendships are widespread and prominent. In olive baboons, the benefits of friendships to females appear to relate to protection from nonlethal harassment (Smuts 1985; Palombit unpublished data).

Many of the questions remaining about chacma baboon friendships, infanticide, and their functional bases require much more study. Even the nature of the friendship itself warrants greater scrutiny. One intriguing question, for example, concerns whether baboon friendships involve distinctive psychoneuroendocrine foundations of the kind characterizing pair bonds in neotropical monkeys (e.g., Mendoza and Mason 1997), which appear to constitute adult attachment relationships (Mason and Mendoza 2002) *sensu* Bowlby (1977). Anecdotal behavioral evidence (see especially Smuts 1985, 1999), preliminary hormonal data, and their highly consequential fitness implications raise compelling possibilities that baboon friendships may indeed constitute strong, emotionally salient bonds for their participants, but this question awaits further study. Are perhaps these relationships as important to individuals as the matrilineal dominance relationships usually emphasized in descriptions of baboon societies? Indeed, it is the transient, but reproductively significant, nature

of friendships makes them valuable foci of new explorations of social cognition (e.g., Cheney and Seyfarth 2004).

One particularly important question concerns how variation in the nature of friendships affects male defense, infanticide risk, and, especially, female lifetime reproductive success. Reproductive data accumulate slowly in baboons, but ancillary questions can be examined. For example, in light of the apparent differences in infant mortality due to infanticide, do friendships involving high- and low-ranking mothers differ systematically from those of middle-ranking females? The same question can be usefully extended across baboon populations; that is, do friendships vary in meaningful ways with infanticide risk intraspecifically?

Our understanding of the costs of friendships for females and especially males is relatively poor. It is difficult to measure the costs of anti-infanticide defense for males, but other costs, such as female-female competition, also merit attention. A female displacing a lower ranking mother from her friendship potentially imposes a significant cost on the relevant male if he is the father of the supplanted female's infant and if weakened friendship status heightens infanticide risk. If paternal or mating benefits underpin male involvement in friendships, it is surprising that males apparently do little to forestall this competitive outcome.

Intimately related to this understanding of costs is a related question: how does friendship compare with other anti-infanticide strategies available to females? Even the precise nature and limits of the alternatives are unclear. In this sense, a prominent association with a male has been argued to be a relatively *undesirable* anti-infanticide strategy for females because it effectively "advertises" the distribution of paternity, thereby *increasing* a female's vulnerability to infanticide (Harcourt and Greenberg 2001). This potential cost is probably insignificant in this chacma baboon population, however. Infanticide is usually perpetrated by a new immigrant male whose lack of any copulatory history in the group whatsoever makes the distribution of friendships in his new group largely superfluous to paternity-based contingencies. The cost is potentially more relevant when a long-term resident male rises to alpha rank, but even in this case, the argued ability of alpha male chacma baboons to skew mating in their favor once again implicates sexual history as more important. The degree of reproductive skew is, in fact, another deficiency in our knowledge, and it bears directly on the question of how much opportunity female chacma baboons have to avoid infanticide by confusing paternity (O'Connell and Cowlshaw 1994;

Henzi 1996; Cowlshaw and O'Connell 1996). Although confusion of paternity may not offer anti-infanticide benefits to female chacma baboons, Palombit et al. (2001) have suggested two other possible counterstrategies. First, older, dominant mothers may spend more time with female kin, at the expense of time spent with the male friend. Second, low-ranking females "displaced" from access to a male friend by a higher ranking female may become peripheral, avoiding all males generally. We know little about the adaptive significance of these possible counterstrategies, however. Presently, friendships appear to be the best option available to females confronted by this significant risk of infanticide.

In summary, then, study of friendships in the Okavango chacma baboons suggests that although males are a preeminent problem for female reproductive success, they are also, in a different context, the (best?) solution.

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