Female–female competition for male 'friends' in wild chacma baboons, *Papio cynocephalus ursinus*

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Lactating female chacma baboons, *Papio cynocephalus ursinus*, maintain close associations, or 'friendships', with particular males that may protect infants from sexually selected infanticide by a newly immigrated alpha male. In a 2-year study, we sought evidence of female–female competition for male friends in cases where two mothers maintained friendships with the same male simultaneously. In this context, relative competitive abilities of the rival females influenced social access to the shared male friend: dominant females maintained higher levels of close proximity and allogrooming with the male than their subordinate counterparts. This disparity was greatest when younger dominant females and older subordinate females shared a male friend. This pattern resulted from social displacement: subordinate females experienced a significant decrease in time spent near the male friend immediately after a dominant female began associating with him (but the converse was not true). Changes in time male–female friends spent near one another were due primarily to changes in the behaviour of the females. Females may compete for friends based on male rank and probability of paternity of their current infants. Evidence that lactating females may pursue alternative anti-infanticide strategies besides friendship formation came from two sources. First, subordinate females displaced from a friendship made compensatory changes in their relationships with the potentially infanticidal alpha male: spatial proximity and the rate of contact with him fell significantly in the period immediately following displacement. Second, across the entire sample of friendships, female social behaviour and age were significantly correlated. Compared to younger mothers, older females showed: (1) a smaller relative contribution to maintaining close proximity to the male friend; (2) less close proximity to the male friend; and (3) greater proximity to relatives (this association applied to higher-ranking females). Thus, avoidance of infanticidal threat and protective association with maternal kin may constitute two alternative counterstrategies for some lactating females.

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Charles Darwin (1871) postulated that sexual selection operates through two mechanisms: intrasexual competition and intersexual mate choice. Intrasexual selection has long been accepted as an important cause of behavioural and morphological evolution in males (Bradbury & Davies 1987), particularly in polygynous species, but its relevance for understanding female biology is much less clear. The emphasis of current theoretical and empirical studies on males rather than females is understandable given that secondary sexual characteristics and contests

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for mates are conspicuous among males of many species, but relatively uncommon among females (Andersson 1994). Females do compete with one another in many circumstances, but the commodities at stake are generally considered to be resources related directly to their own and their offspring's survival (nest sites, food, safety from predators) rather than to that of males. Consequently, although competition for resources is implicated in diverse aspects of female behavioural ecology, such as reproductive suppression (Wasser & Barash 1983; Abbott 1987), maternal aggression (Maestripieri 1992), territoriality (Waser & Wiley 1979), infanticide (Wolff 1993), matrilineal dominance hierarchies (Silk 1993) and group fission (Dittus 1988), female–female competition for males remains 'a vast area of ignorance' (Berglund et al. 1993). Indeed, the extent to which the competitive

interactions of females concern access to limited resources or access to males remains largely unresolved (Breiehagen & Slagsvold 1988; Martin et al. 1990).

Female–female competition for males has been studied predominantly in the so-called 'sex role-reversed' systems, in which males provide most or all parental care of young. The skew in operational sex ratio resulting from this rare arrangement generates intense competition among females for access to 'choosy' males (Trivers 1972; Emlen & Oring 1977), as exemplified by polyandrous pipefishes and shorebirds (reviewed by Andersson 1994). It is important to remember, however, that sex role reversal is not a prerequisite for female competition (Petrie 1983; Berglund et al. 1993). Regardless of the relative parental investment of the sexes, females should compete for males whenever two conditions occur: males vary in their ability to provide a limiting resource or service that affects female fitness; and the benefits of successful competition exceed the costs. Avian studies reveal that females breeding with a polygynous male may compete intensely for his parental care, and that competitive exclusion of secondary females maintains social monogamy in some populations (Slagsvold & Lifjeld 1994; Sandell & Smith 1996, 1997; Sandell 1998). Thus, in this context female–female competition concerns access to high-quality males, not necessarily as sires, but as providers of fitness-enhancing investment.

Because individual differences in offspring mortality account for much of the variation in lifetime reproductive success of female vertebrates (Clutton-Brock 1988), a male's ability to enhance offspring survival is especially likely to attract female competition. Male birds can improve survivorship of young by incubating, brooding, or provisioning them, but in mammals other forms of parental investment may prevail (Clutton-Brock 1991). In particular, males may protect offspring against infanticide (Palombit 2000), a major cause of infant mortality in many mammalian species (Hausfater & Hrdy 1984; van Schaik & Janson 2000).

We studied female competition for males in a social system in which lactating females at risk of infanticide associate closely with potential male protectors. Savanna baboons, *Papio cynocephalus*, live in large groups comprising multiple adult males, adult females and youngsters of various ages organized into linear dominance hierarchies (Melnick & Pearl 1987). Among chacma baboons of southern Africa, adult males that have newly attained the alpha position in the male dominance hierarchy often commit infanticide. Infanticide appears to be a sexually selected strategy that accelerates the return to fertility in lactating females, and accounts for at least 40% of infant mortality in a population inhabiting the Moremi Game Reserve, Botswana (Palombit et al. 2000). The brevity of male alpha status among these baboons, 6–7 months on average, may be a chief cause of infanticide (Collins et al. 1984; Hamilton & Bulger 1990; Palombit et al. 2000). Infanticide should exert selection pressure on females to adopt anti-infanticide counterstrategies (Hrdy 1979; Ebensperger 1998), which in chacma baboons seem to involve the cultivation of defensive alliances with protector males.

As in other populations of savanna baboons (Ransom & Ransom 1971; Seyfarth 1978; Altmann 1980; Smuts 1985; Collins 1986; Bercovitch 1991), lactating female chacma baboons form close, affiliative relationships, or 'friendships', with specific adult males. Recent evidence suggests that reduced risk of male infanticide is a principal adaptive benefit of these bonds to female chacma baboons (Busse 1984; Palombit et al. 1997, 2000; Palombit 1999; Weingrill 2000). Mothers with infants vulnerable to infanticide invest heavily in friendships through spatial proximity, allogrooming and tolerance of male–infant interactions. If a female's infant should die, however, her close association with the male friend typically ends. Observational and experimental data independently indicate that male friends are more likely than other males to aid females under attack, especially when the aggressor is the potentially infanticidal alpha male (Palombit et al. 1997, 2000).

If males vary in their propensity or ability to protect against infanticide, and if this protection critically affects offspring survival, then females should compete for access to these male companions. Our study, therefore, differs from previous research on competition among oestrous female baboons for access to males as mates (e.g. Wasser 1983; Dunbar & Sharman 1983) in that we examine competition among anoestrous females for males providing a potentially fitness-enhancing, postnatal service.

The potential for competition in chacma baboons was first noted by Seyfarth (1978), who reported that the alpha female of his study group seemed to prevent the formation of close bonds between the alpha male and other anoestrous females. Competition should be especially conspicuous when rival females associate simultaneously with the same male friend, just as it is in some birds when multiple females contend for the brood-rearing assistance of a single, polygynously breeding male. In chacma baboons, the joint 'sharing' of friends occurs when two females give birth within weeks of one another and each establishes a friendship with the same male.

We sought evidence of female competition in this context by examining the effect of female competitive ability, as measured by their relative dominance ranks, on social access to a male friend. We predicted that when two rival females affiliated with the same friend, the higher-ranking female would associate with him at a higher rate. In those cases when a mother attempted to establish a friendship with a male that currently held a friendship with another lactating female, her success should also depend on her rank relative to the other female. A more dominant female should be able to displace the current female from her friend, whereas a more subordinate female might be prevented from associating with any male that already had a female friend. Finally, we examined whether the mechanism of displacement from friendships involved higher rates of agonistic interaction between rival females.

In a complementary analysis, we examined whether subordinate females that had been displaced from a preferred male friend made compensatory changes in their behaviour, either by forming a new friendship with

another male, increasing their avoidance of the potentially infanticidal male, or increasing their association with kin. The latter two patterns could provide the basis for an alternative female strategy based more on minimizing exposure to infanticide risk and less on alliance with a male defender. We explored further the possibility of alternative strategies by examining whether lactating females of different ages or dominance status differed in the nature of their friendships with males.

METHODS

Study Area and Subjects

The study site lies in the Moremi Game Reserve in the Okavango Delta, a large, seasonal wetlands created by the annual flooding of the Okavango River in northwestern Botswana. The habitat comprises seasonally inundated grasslands separating elevated woodland areas of variable size (Tinley 1966; Buskirk et al. 1974; Hamilton et al. 1976).

The study group comprised 65–75 individuals, including at any given time 4–8 adult non-natal males, 4–7 adult (sexually mature) natal males (≥8 years), 22–25 adult (cycling) females, and their immature offspring. The group has been studied from 1977 to 1991 by W. J. Hamilton III and colleagues (e.g. Hamilton et al. 1976; Busse & Hamilton 1981; Hamilton & Bulger 1992) and since 1992 by D. L. Cheney, R. M. Seyfarth and colleagues (e.g. Cheney et al. 1996; Palombit et al. 1999; Rendall et al. 1999; Silk et al. 1999). The ages and maternal relatedness of all natal individuals were known.

Male and female savanna baboons form linear dominance hierarchies that are maintained by communicative displays and occasional aggression (Hall & DeVore 1965; Rowell 1966; Hausfater 1975; Seyfarth 1976). Females attain ranks adjacent to their mothers and sisters in the hierarchy, which remains relatively unaltered for long periods (Hausfater et al. 1982; Samuels et al. 1987). Male baboons typically emigrate to neighbouring groups at around 8–10 years of age (Smith 1992; Alberts & Altmann 1995). In the Moremi population, males occasionally remain in their natal groups, attaining high rank and breeding there successfully (Bulger & Hamilton 1988). Dominance relationships among males are considerably more dynamic than those of females, and are influenced by age and size (Hamilton & Bulger 1990; Bulger 1993).

Behavioural Observations

We collected data in approximately 3450 10-min focal animal samples of 11 adult males and 20 adult females, and through ad libitum observation (Altmann 1974) distributed over a continuous 2-year period.

We assigned baboons dominance ranks based on the direction of dyadic agonistic interactions (i.e. 'supplants', 'bare-teeth' visual displays and overt aggression; Hall 1962). An individual's dominance position was expressed as the percentage of same-sex adults that ranked below it. Dominance hierarchies were strictly linear (Smith 1986; Bulger 1993). As with other sexually dimorphic mammals, male chacma baboons were dominant to females.

We used two behavioural measures to assess direct competitive interactions between females: the rate of supplanting and the rate of aggression. A 'supplant' occurred if a female withdrew within 5 s of another female's approach to within 2 m. 'Aggressive' interactions included threat signals (e.g. exposing white eyelids, lunging, slapping the ground, 'open-mouth' display, threat vocalizations), overt physical attack (biting, chasing, hitting), or any other interaction that caused a female victim to scream.

Heterosexual friendships were identified quantitatively using behavioural criteria described in full by Palombit et al. (1997). We used the dispersion of males and females to initially differentiate friendships from other heterosexual relationships, and then analysed social interactions within this context. We used two measures of spatial relations.

Close proximity

We measured the proportion of time that each female spent in 'close proximity' of each male by recording the time that the focal animal and another individual came within 2 m of one another (defined as an 'approach') and the time that either moved more than 2 m away (a 'withdrawal').

2–6 m range

We measured the proportion of time a female spent within 2–6 m of males by instantaneously recording the identities of all individuals within this distance of the subject at 2-min intervals during the focal session. If no adults were within 6 m of the focal individual, we then recorded the nearest neighbours of each sex and their distances to the subject.

For each female–male dyad in the group, we calculated a composite proximity score by summing the percentage of time that they spent within 0–2 m and 2–6 m of one another, weighted appropriately (Smuts 1985). A discontinuous distribution of these scores for a given female revealed distinctively strong spatial associations between the female and a particular male (see Palombit et al. 1997, for further details). We identified 23 heterosexual friendships involving 13 lactating females and eight adult males in this manner. These females engaged in significantly higher rates of allogrooming with male friends, and tolerated higher rates of affiliative infant handling by them (Palombit et al. 1997).

We assessed investment in a friendship by evaluating relative responsibility for maintenance of close proximity between friends, as measured by 'Hinde's index'. This index is the difference between the percentage of approaches due to the female and the percentage of withdrawals due to the female (Hinde & Atkinson 1970; Hinde 1977): a negative score indicates that the male is responsible for maintaining proximity, while a positive score indicates that the female is responsible. We previously reported Hinde indices demonstrating that the

close spatial proximity of chacma baboon friends was due primarily to the behaviour of the female partner (Palombit et al. 1997). We calculated Hinde indices only for friendship dyads with 15 or more approach–withdrawal interactions.

The analysis below comprises two related components. The first part investigates competition among females for male friends by focusing on 'overlapping' friendships that multiple females maintained simultaneously with the same male. The second part examines how females may modify their friendship behaviour in light of their competitive interactions with other females as well as their age and dominance status.

'Overlapping' Friendships With the Same Male

Operational definitions

When spatial and behavioural data designated two lactating females as bonded simultaneously to the same male, their friendships were defined as 'overlapping'. During the study, there were 14 cases of overlapping friendships, involving 12 females and six non-natal, adult males. Eight (57%) of these friendships occurred when two females affiliated with the same male; the other cases occurred when three mothers associated with the same male. Females that shared a friend were never closely related to one another (i.e. mothers–daughter, grandmother–granddaughter, or sisters).

Twelve (86%) cases of overlapping friendships were initiated when a female gave birth and immediately began associating with a male that already had an established friendship with one or more females. The two other cases involved females with infants 3–4 months old when they began an overlapping friendship. Overlapping friendships ended in four ways: (1) when one of the female's infants died or was killed (seven cases); (2) when a female and her infant both disappeared from the group (two cases); (3) when the male friend disappeared from the group (two cases); and (4) when a female abandoned her current friend and established a new friendship with another male (two cases). In a final case, the overlapping friendship was still active when the study ended.

Predictions

We hypothesized that the relative rank of the female attempting to establish an overlapping friendship would affect the nature and intensity of competition with the female that already had a friendship with the male. When the succeeding female was dominant, we predicted that she would partially or wholly displace the antecedent female from her friendship. When the succeeding female was subordinate, we predicted that her presence would have little effect on the antecedent female's friendship. For each antecedent female, therefore, we compared proximity, grooming and Hinde index measures with her male friend before and after the initiation of the overlapping friendship. 'Before' and 'after' data were available for 13 of the 14 overlapping friendships. In seven of these cases, the antecedent female was subordinate to the

succeeding female; in the other six overlapping friendships, the antecedent female was dominant. The median durations of before and after periods were 54 and 46 days, respectively.

Variation in Female Friendship Behaviour

We sought evidence of variability in female friendship behaviour from two sources: (1) compensatory changes in the behaviour of subordinate females following displacement from male friends by dominant females; and (2) general age- and rank-related differences in female social interactions with male friends across all friendships.

Behaviour of displaced females

If a male friend's protection against infanticide depends upon a cohesive bond with the female benefactor, then low-ranking females that have been displaced from a friendship by a dominant female may modify their behaviour in potentially compensatory ways. We predicted that a displaced subordinate female would either form a new friendship with another male, intensify avoidance of the alpha male, or increase association with adult or subadult kin in the group.

The spatial and social relations of females and potentially infanticidal males provided data on avoidance. We operationally defined a potentially infanticidal male as the current alpha male. We emphasize that alpha male chacma baboons do not always commit infanticide, particularly if they have resided in the group for long periods. Current alpha males during our study were considered potentially infanticidal for two reasons. First, each alpha male was either a new immigrant to the group or, in one case, a recently risen, formerly lower-ranking male. Infanticide by alpha males is more likely in these contexts. Second, we observed each of the four alpha males to attack and kill unweaned infants during his alpha tenure (Palombit et al. 2000).

We measured the time females spent within 6 m of the alpha male before and after initiation of overlapping friendships. In addition, we measured the rate of a female–alpha male social interaction designated 'long-distance retreat'. This was the flight response shown when a female with an infant detected the alpha male and ran off conspicuously with either the stereotyped 'tailup' display, or screaming, or both (Busse 1984). This unambiguous avoidance followed visual contact with the alpha male over distances ranging from 3 to 50 m, depending upon the arousal of the individual female or specific conditions of the encounter. The behaviour is likely to reflect active retreat from a potential but immediate threat of infanticide since, as Busse (1984) originally described, nonlactating females rarely show this reaction to the alpha male, and, furthermore, mothers with infants generally do not respond in this fashion to males that are low-ranking or long-term residents of the group.

We also measured time spent within 6 m of closely related, maternal kin before and after partial displacement from a friendship. A close 'relative' was defined

operationally as any adult or subadult individual (≥ 5 years old) that was the grandmother, mother, offspring, sibling, aunt, uncle, cousin, niece or nephew of the displaced subordinate female. In all cases of displacement, the total number of relatives potentially available to a particular subordinate female was the same in both the before and after periods.

Friendship behaviour and female age and rank

We investigated whether the spatial cohesiveness of a female's friendship and the magnitude of her investment in maintaining it varied systematically with her age and dominance status. The proportion of time a female spent within 6 m of and in close proximity (2 m) to the male measured spatial cohesion. We used variation in Hinde indices for close proximity (see above) as an assay of investment in friendships.

We surveyed the complete sample of friendships for evidence of covariation between female age or rank and the time spent within 6 m of close kin. Data for subordinate females displaced from friendships (see above) came from predisplacement periods. Close relatives were defined using the criteria presented above. To control for the possibility that older lactating females had more relatives in the group, the dependent variable was the percentage of time spent within 6 m of relatives divided by the total number of relatives in the group during the period the focal female maintained her friendship.

We conducted an exploratory multiway analysis of variance in which there were three independent variables: female age, female dominance rank and the interaction of age with rank. Dominance rank was expressed as the percentage of females ranking below the focal female. The dependent variables were the spatial measures described above.

The ages of subjects ranged from 6.9 to 20+ years; their dominance ranks varied from the highest- to lowest-ranking female in the group, as the percentage of adult females that ranked below each individual.

All statistical tests are two tailed.

RESULTS

Overlapping Friendships with the Same Male

Three results revealed that the simultaneous sharing of a male friend by two females was relatively common. First, 14 of 23 friendships (61%) experienced overlap at some time. Second, overlap periods accounted for $60 \pm 37\%$ (mean $\pm$ SD) of the total duration of females' friendships (range 0–100%, $N=23$). Overlap periods lasted 48 ± 29 days (mean $\pm$ SD, $N=14$). Third, overlapping friendships involved 12 of the 13 lactating females that formed friendships during the study.

When two females each maintained a simultaneous friendship with the same male, they spent a similar amount of time within 2–6 m of him (Wilcoxon matched-pairs signed-ranks test: $T=46$, $N=14$, NS). However, the dominant female spent significantly more time
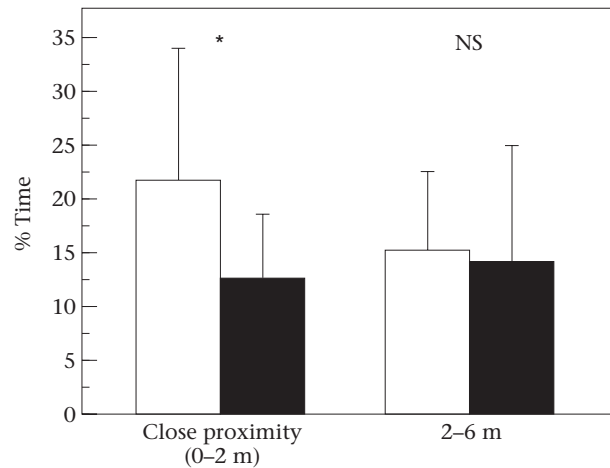

Figure 1. Mean $\pm$SD percentage of time a dominant female ($\square$) and a subordinate female ($\blacksquare$) spent within 0–2 m (close proximity) and within 2–6 m of a mutual male friend during the period that both females simultaneously maintained a friendship with him. The difference in close proximity time was significant ($P<0.05$, see text).
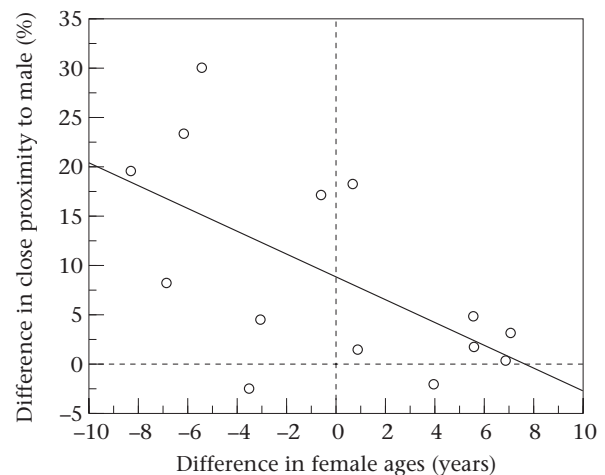
Figure 2. Association ($r=-0.61$, $P<0.05$) between differences in age and time in close proximity of two females sharing a male friend. The difference in age between the two females (dominant's age minus subordinate's) is plotted along the X axis, and the difference in time spent in close proximity to the mutual male friend (dominant's close proximity time minus subordinate's) is shown on the Y axis.

in close proximity (<2 m) to the friend than did the subordinate female (Fig. 1; $T=9$, $N=14$, $P<0.01$). This proportion of time varied from as little as 1% to as much as 30% and was related in part to age differences between the two females. The difference between rival females in time spent in close proximity to their friend was negatively correlated with their age disparity (Fig. 2). In other words, when a young dominant female and an old subordinate female shared a male friend, the dominant generally spent a great deal more time than the subordinate in proximity to the male. Conversely, when an old dominant female and a young subordinate shared a male friend, the dominant's priority of access to the male was only slightly greater than the subordinate's.
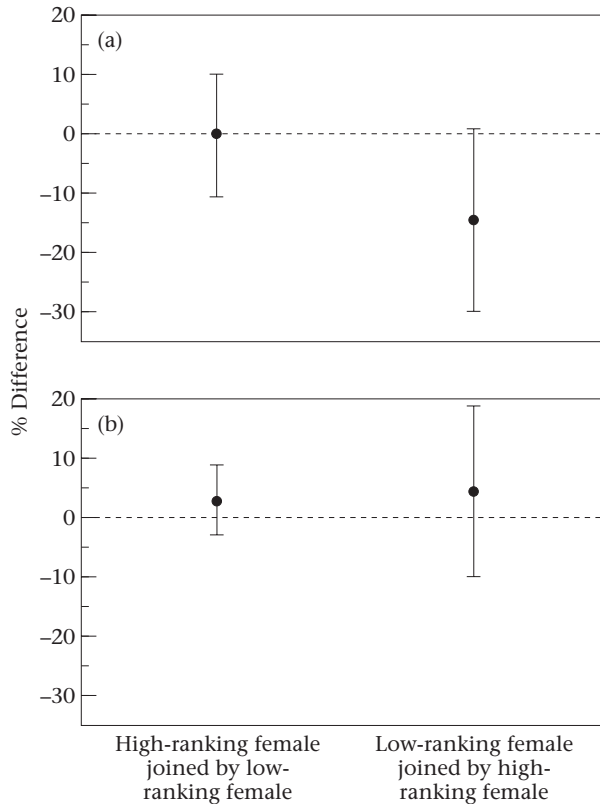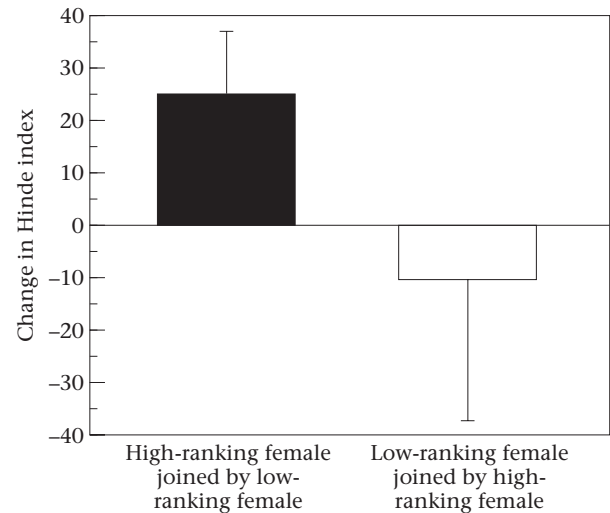
Figure 3. Change in a female's spatial relationship to male friend when a second female establishes a friendship with the same male. Shown is the mean ±SD difference in the percentage of time females spent (a) in close proximity to and (b) within 2–6 m of the male friend in the periods before and after a second female formed a friendship with the same male.

Transition to Overlap Periods: Changes in Social Behaviour

The different amounts of time that high- and low-ranking females spent in close proximity to the male friend suggested that dominants somehow excluded subordinates from the male. We therefore examined the social changes surrounding the transition to overlap periods.

Spatial association with the male friend

Initiation of a new female's friendship with a male had contrasting effects on a dominant and subordinate female's existing friendship with the same male. All subordinate females experienced a decline in close proximity to the male after a dominant female began associating with him (Fig. 3a; Mann–Whitney U test: $U=6$, $N_1=7$, $N_2=6$, $P<0.05$). On the other hand, a dominant female's close proximity to the male friend was unaffected by a subordinate forming a friendship with him. The contrasting responses of dominants and subordinates were not due to a difference in the developmental states of their infants: the ages of infants belonging to dominant and subordinate antecedent females did not differ when overlap began (median age=54 days) ($U=18$, $N_1=7$, $N_2=6$, NS).


Figure 4. Change in a female's relative contribution to close proximity maintenance to male friend when a second female establishes a friendship with the same male. Shown is the mean ±SD difference in Hinde indices for females' friendships in the periods before and after another female formed a friendship with the same male.

In contrast to close proximity, dominant and subordinate females experienced similar changes in time spent within 2–6 m of the male friend when another female formed a new friendship with him (Fig. 3b) ($U=18$, $N_1=7$, $N_2=6$, NS). Both high- and low-ranking females spent slightly more time within 2–6 m of the male during overlap periods than in the period before.

The slight increase in time that subordinates spent within 2–6 m of the friend did not compensate for the large decrease in time spent in close proximity following the arrival of a dominant female (Fig. 3b). Indeed, these subordinate females began to spend a significantly greater proportion of time beyond 25 m of their friend (see below).

We examined Hinde indices to determine whether altered female investment in maintaining close proximity accounted for the reduction in subordinates' close proximity to male friends. For some friendships, observed approaches and withdrawals in either the before or after (overlap) period were too infrequent to calculate Hinde indices in both periods (e.g. a subordinate female was rarely near the male friend after a dominant female began associating with him). Nevertheless, among those dyads providing sufficient data, transitions in Hinde indices appeared to differ for dominant and subordinate females (Fig. 4). Hinde indices for subordinate females tended to decline after a more dominant female began associating with the same male friend; conversely, indices increased among high-ranking females that were joined by a subordinate female (Mann–Whitney U test: $U=2$, $N_1=6$, $N_2=4$, $P=0.03$). The change in Hinde index was more pronounced for high- than for low-ranking females.

Hinde & Atkinson (1970) argued that parallel increases or decreases in both an individual's proximity to another and its role in maintaining that proximity suggest the observed change in proximity is due to its behaviour, rather than its partner's behaviour. The preliminary
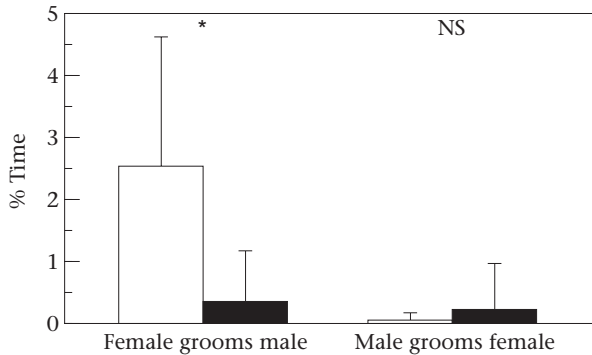
Figure 5. Mean±SD percentage time subordinate females and male friends spent grooming one another in the period before (□) and after (■) the subordinate female was displaced from the friendship by a dominant female. The difference in the percentage of time that a female groomed a male friend was significant (Wilcoxon matched-pairs signed-ranks test: $T=1$, $N=7$, $P<0.05$).

pattern suggested, therefore, is that the fall in subordinate females' close proximity to male friends after a dominant female began associating with him resulted from subordinates contributing less to proximity maintenance. Consistent with this interpretation is the observation that Hinde indices during overlap (after) periods retained their positive values (mean ± SD=19.9 ± 29, $N=6$), indicating the subordinate females remained more responsible than male friends for proximity maintenance. In only one case was the Hinde index negative, indicating a greater male contribution to proximity maintenance. It may be significant, incidentally, that the subordinate female that associated with this male experienced the smallest reduction in her close proximity time to the male after the dominant female arrived and formed a friendship with him.

The converse pattern seems to characterize high-ranking females. After a subordinate female established a new friendship with a male already associating with a dominant female, the dominant's time in close proximity to the shared male remained largely unaltered, but her relative contribution to maintaining proximity to him increased substantially.

Social interaction with the male friend

Reduced close proximity of females to males predicts diminished opportunity for other social interactions used to maintain friendships, notably grooming. Males generally groomed their female friends at low rates (Palombit et al. 1997), and their grooming behaviour was unaffected by the arrival of a second friend (Fig. 5). This was true also of dominant females, whose grooming of male friends was unaltered by the presence of a second female. The arrival of a rival female, however, did influence the grooming behaviour of subordinate females. For subordinate females, the percentage of time engaged in grooming male friends was approximately four times lower in the overlap period than in the period before they were joined by a more dominant female (Fig. 5; Wilcoxon matched-pairs signed-ranks test: $T=2$, $N=7$, $P<0.05$).

Female–female social interactions

Lower-ranking females were supplanted by their dominant counterpart at higher rates during the period when they shared a friend (mean ± SD=1.2 ± 1.8 supplants/h) than in the period before the second friendship was established (during which no supplants were observed) ($T=0$, $N=5$, $P<0.05$, two ties). There was no difference, however, in the rate at which the same dominant females supplanted lower-ranking females involved in friendships with other males (mean ± SD: before=0.01 ± 0.03 supplants/h; after=0.06 ± 0.10 supplants/h, $N=7$). Similarly, their rates of aggression to subordinate females sharing a male friend remained unaltered (mean ± SD, before=0.30 ± 0.54 supplants/h; after= 0.26 ± 0.34 supplants/h).

Male Attributes and Female Competition

Females that established a friendship with a male that was already the friend of another female did not do so because there were no other potential males available in the group. There were always at least three to four long-term resident, non-natal adult males present in the group that were currently unengaged in a friendship. Each of these males participated in at least one friendship at some time during the study. These results suggest that females chose males as friends based on their attributes. Two potentially important criteria are a male's dominance rank and likelihood of paternity of the female's infant.

Of the eight adult males involved in friendships during the study, only two never participated in simultaneously overlapping friendships with multiple females. These two males were each the lowest-ranking non-natal male in the group at the time, suggesting that male dominance influences female choice of friends. A positive correlation between the ranks of female and male friends at the time that friendships were formed (Spearman rank correlation: $r_S=+0.42$, $N=23$, $P=0.05$) supported this supposition. Thus, high-ranking females obtained high-ranking males as their friends. A female preference for high-ranking males did not extend to the current alpha male, however. None of the alpha males engaged in a friendship with a lactating female during his alpha tenure. This may have been because these males' recent immigration in the group (or recent ascent to alpha status) made them potentially infanticidal.

Although we could not determine genetic paternity, 68% of friendships involved pairs previously observed to copulate during the cycle in which the female conceived her current infant (Palombit et al. 1997). Most males, therefore, seemed to have some probability of having fathered their friend's infant.

An additional experimental result suggested that paternity may influence male predisposition to protect friends from aggression (Palombit et al. 1997). As in other cercopithecines (Gouzoules et al. 1984; Gouzoules & Gouzoules 1989), female savanna baboons often scream when attacked by conspecifics, and these calls function in part to recruit the aid of others in defence (Cheney &

Seyfarth 1999). When females' screams were played back to males under controlled field conditions, friends responded significantly more strongly than nonfriends did, but there was considerable variation in the strength of friends' responses (Palombit et al. 1997). Additional analysis of these previously reported data (Figure 4 in Palombit et al. 1997) revealed a strong positive correlation between the male friend's response and his dominance rank at the time the female conceived her infant ($r_S = +0.70$, $N=10$, $P<0.05$), but no correlation between male response and dominance rank at the time of the playbacks, when the friendships had already been established (NS). Thus, the higher a male's rank at the time his future friend conceived her infant, the stronger was his response to playback of her distress call over 6 months later. Given the strong positive association between male mating success and dominance rank in this population (Bulger 1993), the result suggests a potentially important relationship between probability of paternity and male protection.

Behaviour of Displaced Subordinate Females

How did subordinate females respond to spatial and social displacement from their friendships by a dominant female? In two of seven cases of displacement, the subordinate female eventually abandoned her overlapping friendship and established a new friendship with a currently unbonded male. More generally, however, all seven displaced subordinate females showed three changes in behaviour suggesting that they intensified avoidance of the potentially infanticidal alpha male.

First, following displacement from their male friend, all seven females ceased to spend any time within 6 m of the alpha male (Fig. 6a) (Wilcoxon matched-pairs signed-ranks test: $T=0$, $N=7$, $P<0.05$). Second, displaced females spent twice as much time beyond 25 m of all resident males (Fig. 6b) ($T=2$, $N=7$, $P<0.05$). This avoidance of all males was not due to a general avoidance of conspecifics, however, because time spent beyond 25 m of all females in the group remained constant during the corresponding periods. Third, the rate of 'long-distance retreat' of subordinate females from the alpha male fell following displacement (Fig. 6c) ($T=0$, $N=6$, $P<0.05$), as expected given increased spatial segregation from him. Recall that long-distance retreat is a social interaction with two components: first, long-distance visual contact with the alpha male, followed by a female's conspicuous evasion of him (Busse 1984). The reported result reflects the lower rate at which displaced females encountered the alpha male and subsequently had to flee from him. Ad libitum observations of subordinate mothers' responses to the alpha male supported this interpretation by suggesting that their aversion to him remained as high after displacement as it was immediately before.

Furthermore, the proportion of time subordinate females spent within 6 m of maternal relatives did not differ in the periods before and after they were displaced from friendships ($T=8$, $N=7$, NS). Thus, spatial relations with close kin did not change.
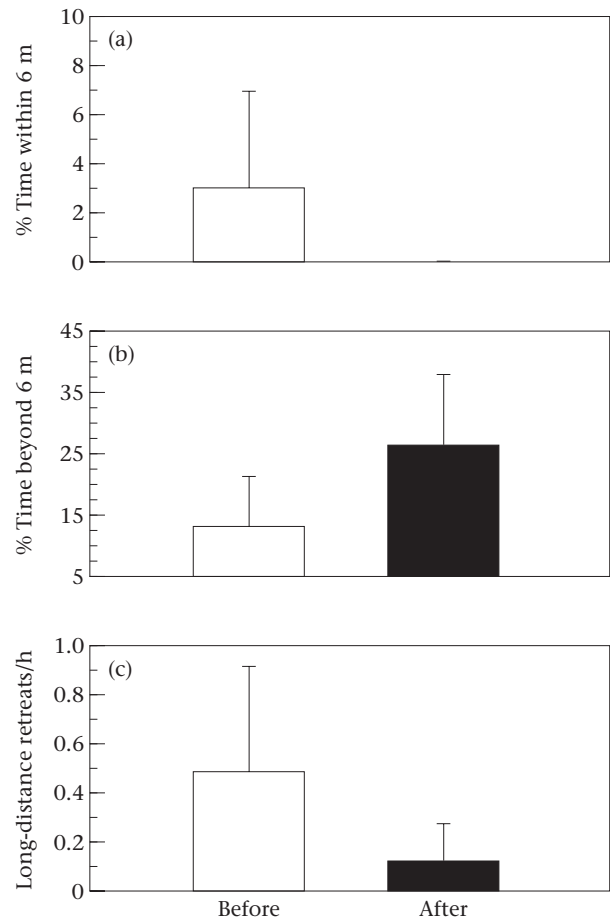
Figure 6. Change in behaviour of seven subordinate females before (□) and after (■) displacement from a friendship with a male by a dominant female: (a) mean±SD percentage of time spent by the female within 6 m of alpha male; (b) percentage of time spent by the female beyond 25 m of all resident males; (3) mean±SD hourly rate of 'long-distance retreat' (see text) from the resident alpha male.

Variation in Female Friendship Behaviour with Age and Dominance

Preliminary patterns of proximity maintenance suggested that a female's age influenced the nature of her bond with a male friend. First, female age, but not female rank or the interaction of age with rank, predicted the proportion of time she spent within 6 m of her male friend (overall F test: $F_{3,22}=3.24$, $P<0.05$; F test for 'female age': $F_{1,19}=4.38$, $P<0.05$). Older females spent less time within 6 m of their male friends than younger females.

Second, the Hinde index for friendships declined with increasing female age, but was unaffected by rank or the interaction of age with rank (overall F test: $F_{3,20}=3.56$, $P<0.05$; F test for 'female age': $F_{1,19}=5.25$, $P<0.05$). Recall that this index expresses the relative contribution of both partners to maintaining close proximity. Again, following Hinde & Atkinson (1970), an observed corresponding negative correlation between female age and the proportion of time friends spent in close proximity ($r=-0.44$, $N=23$, $P<0.05$) suggests that changes in

female, rather than male, behaviour are primarily at work here. That is, older lactating females had less spatially cohesive friendships because they invested less in maintaining close proximity to the male. Indeed, as a group, females older than 12 years, spent roughly as little time in close proximity to the male friend (mean ± SD=12 ± 8%, N=11) as did subordinate females that had been displaced from a male friend by a dominant rival (see Fig. 1). Unlike these displaced subordinate females, however, older females did not generally spend more time far from the males of the group: female age, rank and the interaction of rank with age did not explain variation in time spent beyond 25 m of all males. On the other hand, the interaction of female age and rank was significantly associated with the proportion of time spent within 6 m of close kin in the group (overall F test: $F_{3,22}$=9.51, P<0.001; F test for 'female age × rank': $F_{1,19}$=4.30, P=0.05): older, dominant females spent more time within 6 m of relatives than younger, subordinate females.

DISCUSSION

Female–Female Competition for Male Friends

Overlapping friendships of multiple lactating females with a single male were relatively common in chacma baboons. Sharing a friend with another female produced changes in the female's sociospatial relationships with the male, but primarily among subordinate females. After a more dominant rival began associating with the same male, a lower-ranking female invested less effort in maintaining proximity to him, and spent less time in close proximity to him, less time grooming him, and twice as much time far (>25 m) from him.

These changes constitute social costs of female–female competition to subordinate females. Allogrooming is one 'tool' by which cercopithecines maintain and defend valuable social relationships and long-term alliances (Dunbar & Sharman 1984; Stammbach & Kummer 1982; Dunbar 1988). Likewise, close proximity is socially important, not only because it permits or increases diverse affinitive interactions (such as grooming and infant handling), but also because simple 'sitting together' is a long recognized mechanism of social attachment in anthropoid primates (Carpenter 1954; Mason 1971; Kummer 1978; Rowell & Olson 1983).

Ultimately, reduced protection by male friends is the predicted cost to subordinate females of weakened friendships with males. This protection may shield females from harassment from dominant females (Altmann 1980), or adult males (Smuts 1985), but accumulating evidence suggests that infanticide deterrence is the primary benefit of friendships to female chacma baboons (Busse & Hamilton 1981; Palombit et al. 1997, 2000; Weingrill 2000). Available demographic data are too few to test if subordinate females displaced from friendships become more vulnerable to infanticide, but indirect evidence suggests a clear potential for elevated risk. First, ad libitum observations of alpha male attacks on infants suggest that propinquity of the male friend may critically determine the effectiveness and outcome of his defence

(Palombit et al. 2000). Thus, the substantial increase in the time displaced subordinate females spend beyond 25 m of their male friends may diminish their ability to intervene successfully against infanticidal attacks. Second, long-term defence against infanticide may depend upon an ongoing, strong social relationship between protector and benefactor (Palombit 1999, 2000). During aggressive interactions in nonhuman primates, as well as some other mammals, individuals preferentially aid those with whom they have interacted affinitively in the past (Harcourt 1992). The cost of intrasexual competition to subordinate females, therefore, is not simply an increase in the distance to the male defender, but disruption of the mechanisms fundamental to the male–female relationship, upon which effective infanticidal protection ultimately hinges.

Competition among lactating females for access to male friends differs both proximately and functionally from competition among cycling female baboons for mating access to males (Dunbar & Sharman 1983; Wasser 1983; Wasser & Starling 1986, 1988). In competition for friends, lactating females contend for social bonds with males that provide a postnatal service to females. This system is broadly reminiscent of that found occasionally in birds, but relatively rarely in mammals, in which rival 'primary' and 'secondary' females obtain unequal shares of male provisioning of food for young (e.g. Kempenaers 1994, 1995).

At a proximate level, dominant females' priority of access to male friends relies less on aggressive interference and overt harassment of subordinates than competition among cycling female baboons for males as mates. High-ranking mothers did not increase attacks on lower-ranking rivals associating with the same male, although they did supplant them more often. More frequent supplanting may reflect heightened intolerance of the subordinate competitor, increased avoidance of the dominant by the subordinate, or simply an increase in interaction rate arising inevitably from closer proximity. Given that no supplanting occurred prior to the overlap period in this study, more data on female–female interactions are needed to test among these three possibilities and confirm that supplanting rates remain stable after proximity time between rival females is controlled. In any case, however, even an increase in the absolute rate of supplanting may help peripheralize the subordinate female from the male. Future research must also examine how affiliation between females affects competition for friends. This effect was minimal in this study, however, since rival females were never close kin, and, therefore, lacked a close affiliation prior to the period they shared a male friend.

Dominant females contributed more to proximity maintenance with the male friend once a subordinate began associating with him. This did not result in dominants spending significantly more time in close proximity to the male, but the pattern raises the possibility that dominants sharing a male friend must invest more in order to maintain their current affiliation with him. Thus, competition may also affect the time budgets of dominant females, even if less deleteriously than their

subordinate rivals. Males appear to play a minor role in mitigating female competition. In only one case did a male's effort to maintain proximity to his subordinate female friend apparently buffer her from the detrimental effects of competition with his other, dominant female friend.

An important question is: why do female chacma baboons compete at all for access to male defenders? Females should not compete for access to a nondepreciable resource (Kleiman & Malcolm 1981), and it is not intuitively obvious why males cannot distribute protection equally among several mothers at once. Indeed, somewhat analogous protection against predation has been viewed as a nondepreciable service provided by male primates to multiple females (van Schaik & van Noordwijk 1989; Rose & Fedigan 1995).

At least two possible reasons explain why female chacma baboons compete for access to male friends. First, females may act 'spitefully' to lower the fitness of competitors by depriving them of a critical resource that is, in fact, shareable without incurring significant costs (Knowlton & Parker 1979; Berglund et al. 1993). A similar benefit may underlie aggressive disruption of ovulatory cycles and fertilization schedules of low-ranking female baboons (Dunbar & Sharman 1983). Alternatively, the substantial investment of female chacma baboons in maintaining their friendships suggests a depreciable commodity is, in fact, at stake. Social, spatial and temporal access to a particular male, in order to 'service' a relationship with him and thereby obtain his protection, is not necessarily equally shareable among several females at the same time. That is, the 'opportunity' to develop the social relationship itself becomes the effectively depreciable resource for which females compete.

Overlapping friendships imply variation in male quality. When establishing friendships, lactating females often overlook several 'unbonded' adult males in the group in favour of males that already possess a female 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 costs on them. Thus, the distribution of lactating females across male friends cannot be understood solely in terms of the numerical abundance of males; a process analogous to the 'polygyny threshold' model (Verner & Willson 1966) may be more likely to underlie friendship formation. It is unclear how subordinates' choices of friends is influenced by male quality versus the distribution of higher-ranking females already associating with males (e.g. Milinski 1984).

The critical attributes determining male quality require further study, but acquisition of high-ranking friends by high-ranking females suggests that male dominance status is relevant. Females may benefit from friendships with higher-ranking males in several ways. First, given that male rank is partly dependent upon body and canine size (Hamilton & Bulger 1990), the possible physical superiority of higher-ranking males may improve their ability to defend infants from attacking infanticidal males.

Second, because male dominance status and copulatory success are positively associated with one another (Bulger 1993), higher-ranking males may have a higher probability of paternity and, therefore, a greater predisposition to defend the infant. Genetic data are unavailable to test this hypothesis directly, but most friends were at least observed to copulate with one another during the female's previous conceptive cycle. A result of playback experiments further implicates the possible influence of rank and paternity certainty on defensive intervention. Males responded more strongly to their female friend's screams if they had previously held higher rank at the time she conceived her current infant (but male rank at the time of the friendship was unrelated to response magnitude). Experimental playback of infant vervet monkey, *Cercopithecus aethiops*, screams similarly elicited stronger responses from adult males with (an assumed) higher probability of paternity (Hauser 1986).

Third, high rank in male friends may improve chances that other males will help defend an infant. Palombit et al. (2000) propose that the alacrity and vigour of a male friend's response to an infanticidal attack sometimes prompts nonfriend adult males to join in defence. Typically, the protective efforts of these males are not well coordinated with the more pronounced and direct protection of male friends, but in some circumstances, they may nevertheless help to safeguard infants. High rank in the male friend may facilitate nonfriend involvement since the dominance relationships and relative fighting abilities of opponents and allies influence monkeys' decisions to intercede in ongoing aggression (Harcourt 1992; Noë & Sluijter 1995; Silk 1999).

It is important to reiterate that although high rank in male friends offers several potential benefits, in this study female preference for friends excluded alpha males that were recent immigrants and, therefore, potentially infanticidal (Palombit et al. 2000). Former alpha males, however, may be particularly valuable candidates for friendships since they are likely to have sired many of the infants conceived during their tenure, and they may still retain relatively high rank at the time friendships form later. Thus, these males may become the targets of intense competition among anoestrous females.

Overall, the data suggest that sexually selected infanticide has been a crucial selective agent structuring not only male–female social relationships in this species, but also female–female social interactions.

Evidence for Alternative Female Strategies?

Friendship formation appears to be the principal reproductive strategy of female chacma baboons vulnerable to infanticide. But is it the only one? Competition should promote the evolution of alternative strategies as the cost:benefit ratio of the primary strategy becomes unfavourable (Dawkins 1980; Gross 1996). Variation in behaviour is, by itself, insufficient evidence for alternative strategies, but it alerts us to their possible presence (Dunbar 1983; Caro & Bateson 1986). Thus, we propose two hypothetical anti-infanticide counterstrategies for further testing. The preliminary evidence for these alternative strategies emerges from two patterns: the behavioural changes of subordinate females displaced

from friendships, and the decreased investment in friendships by older females.

Subordinate females displaced from a friendship compensated for diminished social access to the male friend by reducing spatial proximity and interaction rate with the current alpha male. These females' more frequent interaction with the alpha male before displacement probably reflects the divergent short-term goals of male and female friends: anoestrous females typically follow their male protectors (Palombit et al. 1997), but male movements are often motivated by sexual pursuit of oestrous females, which then brings both partners into the vicinity of the alpha male. In this sense, friendships confront females with a fundamental trade-off: they gain a relationship with a potential male defender, but at the cost of greater exposure to the infanticidal threat (Palombit 2000). Once a female's friendship is weakened by competition with a dominant female, however, this trade-off may become intolerable. Thus, a subordinate female partially displaced from her friendship may adopt an alternative strategy based on avoidance of the infanticidal threat, even if this requires spending much time far from the (contested) male friend.

Preliminary evidence for a second counterstrategy derives from observed variation in female investment in friendships generally. Compared to younger females, older females contributed less to proximity maintenance with male friends, and consequently, were near them less often. Indeed, in terms of close proximity time with the male, their friendships were roughly comparable to those of subordinate females that had been displaced from friendships by dominant competitors. Unlike these displaced subordinates, however, older females did not compensate for reduced proximity to the male friend by evasive peripheralization from the alpha male. Rather, older dominant females spent more time near maternal relatives of both sexes. Taken together, these patterns suggest a possible alternative strategy based on protective association with kin. Protection in this context may rely more on enhanced vigilance and early detection of the infanticidal alpha male rather than direct, aggressive defence of the kind provided by a male friend (although subadult or young adult sons are known to defend mothers under attack; Palombit et al. 2000).

Declining friendship behaviour with age suggests that younger mothers derive greater potential benefits from friendships than older females. Preliminary data suggesting that primiparous female chacma baboons may suffer higher rates of infanticide than multiparous females (Palombit et al. 2000) support this possibility. If so, then younger females may not only have more to gain from friendships, they may also have more to lose from unsuccessful competition with other females. This may help to explain our observation that young dominant females monopolized close proximity to a shared male friend much more than older dominant females.

Acknowledgments

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