

MALE GRUNTS AS MEDIATORS OF SOCIAL INTERACTION WITH FEMALES IN WILD CHACMA BABOONS (*PAPIO CYNOCEPHALUS URSINUS*)

by

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Summary

Previous research has suggested that the quiet, tonal grunts given by female savanna baboons (*Papio cynocephalus ursinus*) function to mollify lower-ranking females and thereby facilitate friendly social interaction with them (Cheney *et al.*, 1995). In a two-year study of wild chacma baboons, we assessed whether or not grunts given by adult males function similarly to facilitate heterosexual interaction. Two patterns of male vocal behavior initially suggested this function. First, males grunted more often when approaching females with which social interaction was potentially highly beneficial and/or unlikely (due to female evasion), *i.e.* estrus females and lactating females (particularly friend females); males rarely grunted when

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approaching pregnant females. Second, higher-ranking males grunted significantly more often than subordinates when approaching females in most reproductive states.

In spite of these two patterns, however, male grunts had contrasting effects on the probability of supplanting a female and interacting affinitively with her. Supplanting of females was just as common when the approaching male grunted as when he did not. Instead, variance in supplanting was better explained by female avoidance of high-ranking and non-friend males than by the male's vocal behavior. Results suggest that male grunts themselves do not generally determine whether a supplant of the female occurs. Rather, the female's reproductive state and social relationship with the male (*i.e.* his 'friendship' status and/or rank) affect *both* the male's tendency to call to her and the female's tendency to move away from him.

In contrast to supplanting, affinitive interaction occurred significantly more often when males grunted than when they silently approached females. Taken together, results suggest that a female chacma baboon's 'spatial' response to a male's approach ('stay or leave') depends upon her assessment of non-vocal factors, but her 'social' response ('interact or not') is influenced by the grunts given by the male.

Keywords: Chacma baboon, *Papio cynocephalus ursinus*, friendship, pair bond, vocalization, vocal behavior, immigration, affiliation.

Introduction

Since the modern study of primate vocal communication began thirty years ago (Rowell, 1962; Rowell & Hinde, 1962; Andrew, 1963), a substantial body of data describing vocal repertoires and the contexts of calling has been collected from many species (reviewed by Gautier & Gautier, 1977; Snowdon *et al.*, 1982; Snowdon, 1986; Seyfarth, 1987; Todt *et al.*, 1988). These data have clarified the functioning of certain primate vocalizations, notably, alarm calls (*e.g.* Seyfarth *et al.*, 1980; Zuberbühler *et al.*, 1997), long-distance intergroup calls (*e.g.* Robinson, 1979; Mitani, 1985), and distress calls (*e.g.* Gouzoules *et al.*, 1984). These conspicuous calls, however, account for a small proportion of vocalizations given by most nonhuman primates (Marler & Mitani, 1988). With some exceptions (*e.g.* chimpanzees, *Pan troglodytes* [Mitani, 1996]), the most frequently heard calls are the less conspicuous coos, grunts, and trills that accompany intragroup social interaction in many species such as callitrichids (*Saguinus oedipus*, *Cebuella pygmaea*) (Snowdon & Hodun, 1981; Cleveland & Snowdon, 1982), vervet monkeys (*Cercopithecus aethiops*) (Cheney & Seyfarth, 1982), macaques (*Macaca* sp.) (Green, 1975; Palombit, 1992), and gorillas (*Gorilla gorilla beringei*) (Harcourt *et al.*, 1993). These vocalizations are characterized

by relatively short duration, low amplitude, considerable acoustic variability, and obscurity of function. As Snowdon (1988, 1997) has argued, the use of these vocalizations in mediating complex intragroup social interactions remains a major unexplored area in the study of primate communication.

In spite of an observed conjunction of vocalizing and affiliation in some primates (reviewed by Smith *et al.*, 1982), only a few studies have examined how short-range calls may mediate affiliative social interaction within primate groups. For example, the staccato grunts of stump-tail macaques (*Macaca arctoides*) appear to facilitate maternal tolerance of 'infant handling' by conspecifics (Bauers, 1993), while grunts of Japanese macaques (*Macaca fuscata*) often precede female-female grooming (Masataka, 1989). In a recent study of the use of tonal grunts in female-female interaction in chacma baboons (*Papio cynocephalus ursinus*), Cheney *et al.* (1995) found that: (1) dominants grunt in 23% of all approaches to subordinates; (2) dominants are less likely to supplant subordinates and more likely to engage in affiliative interactions with them if they grunt than if they approach silently; (3) grunts reconcile opponents following aggression (returning inter-individual tolerance to baseline, pre-aggression levels); and (4) dominants are more likely to grunt if the subordinate has an infant, thereby suggesting that females use these grunts to promote interaction with those individuals that are most desirable to them (see also Rendall *et al.*, in press).

Male-female social relationships in savanna baboons in general and chacma baboons in particular are characterized by a striking combination of aggressive and affiliative interaction. Harassment from males occurs relatively frequently and in a variety of contexts (Smuts, 1985; Cowlshaw, 1995). Moreover, among chacma baboons, males that have recently immigrated into the group and attained alpha status may attempt infanticide (Collins *et al.*, 1984; Palombit *et al.*, 1997). Immigrant males thus elicit varying degrees of aversive behavior from females including 'tail-raising', screaming, rapid flight, and maintenance of close proximity to male friends (Busse, 1984; Palombit *et al.*, 1997). On the other hand, male-female relationships may also be affiliative. A 'friendship' is the cohesive, affiliative bond between an anestrus female and an unrelated adult male (*e.g.* Seyfarth, 1978a; Smuts, 1985; Bercovitch, 1991). Female chacma baboons establish and maintain these bonds by directing disproportionately greater spatial proximity, grooming, and tolerance of infant handling to one (or two)

males in the group, but only while they are lactating (Palombit *et al.*, 1997). Similarly, the 'consortships' of males and estrus females are also characterized by close proximity and a high rate of sociosexual interaction, although unlike the friendship, these temporary associations are typically maintained primarily (though not exclusively) by males (*e.g.* Seyfarth, 1978b; Bulger, 1993; Bercovitch, 1995).

The existence of such affiliative relations and the potential for aggression prompted us to ask how a male baboon manages to 'appease' or 'mollify' a female so that social interaction is possible. The use of grunts by females to facilitate interaction with one another (Cheney *et al.*, 1995) and the fact that male chacma baboons produce narrow-spectrum grunts similar to those described for females (Owren *et al.*, 1997) suggested that grunting may be the crucial signal.

We studied male-female social interactions to test the following hypotheses: (1) a male approaching a female is less likely to supplant her and more likely to interact affinitively with her when he grunts than when he does not; (2) males that are potentially most aggressive to females — *e.g.* high-ranking males or newly immigrant males — grunt when approaching females more often than do other males; and (3) males grunt at the highest rates to females that are either most evasive (females with dependent infants) or to females that are most desirable (estrus females). Thus, we expect a male's vocal behavior to differ depending on the reproductive state of the female he is interacting with.

Methods

Study area and subjects

The study site is situated in the Moremi Game Reserve in the Okavango Delta, northwestern Botswana (23° 02' E, 19° 31' S). The Okavango Delta is a seasonal wetlands comprising grasslands and raised 'islands' ranging in size from less than one hectare to hundreds of hectares and covered with trees and shrubs (*e.g.* *Diospyros*, *Kigelia*, *Ficus*, *Acacia*). From May through August the grasslands are inundated as rainwater descends from Angola, thereby causing the Okavango River and its ancillary channels to expand gradually beyond their banks. Further descriptions of the study area are provided by Tinley (1966), Buskirk *et al.* (1974), Hamilton *et al.* (1976), and Ross (1987).

The study group, C Troop, comprised 60-70 individuals, including at any given time 4-8 fully adult males, 22-26 adult (cycling) females, and their immature offspring. The study group has been observed from 1977-1991 by W.J. Hamilton III and colleagues (*e.g.* Hamilton *et al.*, 1976; Busse & Hamilton, 1981; Hamilton & Bulger, 1992) and since 1991

by D.L. Cheney, R.M. Seyfarth and colleagues (*e.g.* Cheney *et al.*, 1996; Palombit *et al.*, 1997). Because of this long history of observation, maternal relatedness was known for all females and natal males. All subjects were fully habituated to observers on foot (to within 1-3 m) and were individually identifiable.

The 26 adult females of the group (aged at least 6 years and exhibiting monthly perineal swellings) and all adult males that resided in the study group for more than 3.5 months ($N = 18$) served as subjects. Since male baboons of this population often remain in the groups they were born in well into adulthood and may reproduce as frequently as immigrants (Bulger & Hamilton, 1988; Hamilton & Bulger, 1990), the adult male subjects included both natal males aged at least 8 years at the beginning of the study ($N = 6$) and non-natal males of unknown age, but judged as adults on the basis of body and canine size ($N = 12$).

Behavioral observations

Data on heterosexual social interaction were collected in approximately 3450 ten-minute focal animal samples of males and females, and through *ad libitum* observation (Altmann, 1974) distributed over a continuous two-year period. When a male approached (*i.e.* came within 2 m) of a female, we noted whether or not the male grunted to the female. We also noted the subsequent behavior of both participants. A 'supplant' occurred if the female withdrew within 5 s of a male's approach. The following behaviors were classified as affiliative interactions and could all be initiated by either sex: allogrooming, touching, genital presenting, embracing, handling a female's dependent infant, and copulation, occurring within 10 s of a male's approach. Affinitive interactions with pregnant and lactating females did not involve copulation or genital presenting. 'Aggressive' interactions included threat signals (*e.g.* exposing white eyelids, lunging, slapping the ground, 'open-mouth' head bobbing) or overt physical attack (biting, chasing, hitting), or any behavior that caused the female to scream.

The analysis below excludes interactions between females and males that were close maternal relatives (defined as sons, brothers, uncles, nephews, cousins). Individual males were assigned dominance ranks in the field based on the direction of intrasexual agonistic interactions, *i.e.* 'supplants', 'bare-teeth' visual displays, and overt aggression. In order to account for changes in the male hierarchy over the study period, each male was assigned a weighted mean rank, which was the cumulative sum of the percentage of males dominated in each time period of stasis in the hierarchy weighted by percentage of the study period represented by that time period.

Because male-female interactions in baboons are known to change dramatically with the birth of an infant (*e.g.* Altmann, 1980; Smuts, 1985; Palombit *et al.*, 1997), data analysis differentiated between interactions with lactating and non-lactating females. And because male interactions with lactating females are known to differ markedly between those dyads that constitute a heterosexual friendship and those that do not, we differentiate throughout between friends and non-friends. Since friendships in chacma baboons are restricted only to periods when females have dependent infants (Palombit *et al.*, 1997), this dichotomy between friend and non-friend refers only to lactating females. Finally, where data permit, we evaluate male interactions with cycling females by the 'consort' or 'non-consort' status of the dyad. The number of females in each reproductive condition with which males interacted were as follows: 23 cycling, consort females, 26 cycling, non-consort females, 20 pregnant females, and 16 lactating females (of which 12 females were involved in 22 friendships with males during the study).

Case studies of immigrant males

Male savanna baboons typically leave their natal groups and immigrate into other groups around the time they reach sexual maturity at 8-10 years of age (Hamilton & Bulger, 1990; Smith 1992; Alberts & Altmann, 1995). In chacma baboons, immigrants generally rise quickly to the alpha position in the male hierarchy of their new group (Hamilton & Bulger, 1990). Female aversion to these immigrant males can be pronounced, probably because some immigrant males attempt infanticide (Collins *et al.*, 1984; Palombit *et al.*, 1997). Female aversion wanes with time, however, as male residency increases and as infants mature (although even after 9-12 months lactating females may still be wary of a particular male) (Busse, 1984; unpubl. data).

Changes in immigrant males' vocal behavior and developing relationships with females provide a valuable means of assessing the social function(s) of grunts. For example, does an immigrant male call more or less as his social relationships with resident females stabilize and as general female avoidance of him declines? Interactions of immigrant males with females provide a particularly useful context for evaluating whether grunts function to facilitate sustained male proximity to females.

Immigrant male baboons provided data from three case studies to test further how male grunting mediates interactions with females. One male, GL, became alpha male approximately three months after his immigration, held that rank for about eight months, then remained in the group as a middle-ranking male. After about two years' residency in the study group, he emigrated to a neighboring group. A second individual, EG, failed to reach alpha male status, but occupied the beta position in the hierarchy for approximately six months. He disappeared without prior indications of illness or poor condition after one year's residency in the group. A third male, DG, attained the alpha position in the male hierarchy within two weeks of immigration, and maintained that rank for approximately one year. He was still alpha male in the study group when data collection ended, but he fell in rank to a new immigrant male shortly thereafter.

We focus on the possible role of grunts in facilitating proximity maintenance by summarizing co-variation in three variables for each male: (1) male residency in the group (in 10-week time periods), (2) the percentage of male approaches towards females accompanied by grunts, and (3) the percentage of silent approaches resulting in the immediate withdrawal (supplant) of the female. Temporal variation in supplants after quiet approaches is assumed to reflect changing female aversion to immigrant males. Specifically, we examined how male vocal behavior varied with changes in female aversion over time. Finally, the rate of vocal approaches to females was sufficiently high in one male (GL) across all time periods to permit assessment of the percentage of this male's vocal approaches that resulted in either female withdrawal or sustained proximity.

Statistical analysis

We analyzed the vocal and social behavior of males using nonparametric statistics primarily. We also conducted an exploratory multi-way analysis of variance to evaluate the relative importance of grunting *versus* other factors in accounting for variation in the occurrence of supplants and affiliative interaction following male approaches. For all heterosexual dyads in which at least 10 male approaches were observed, two dependent variables were calculated: (1) the proportion of male approaches resulting in a supplant; and (2) the proportion of

male approaches followed by affiliative behavior. The independent variables consisted of: (1) the proportion of approaches when the male grunted; (2) mean male dominance rank (percentage of males dominated); (3) duration of male tenure in the group; (4) mean female dominance rank; (5) female age; (6) friendship status; (7) reproductive state of the female. Because the ages of a few very old adult females were not precisely known, females were assigned to one of five age categories (4-7 years, 7-10 years, 10-13 years, 13-16 years, > 16 years). As noted by Hamilton & Bulger (1990), immigrant male chacma baboons typically enter a group at high dominance rank and then progressively decline with time. This was reflected in a clear tendency for male rank to decline with tenure in the group among the subject non-natal males ($r_s = -0.573$, $N = 12$, $p = 0.06$). In order to address the possible effects of this correlation, the interaction between male rank and tenure in the group was included as an eighth variable. Interactions among the variables pertaining to females were not examined because these were not correlated with one another, *i.e.* females of all age categories and dominance ranks experienced various reproductive states and maintained friendships with males during the study. Rank acquisition via 'youngest ascendancy' within matrilineal (*e.g.* Moore, 1978; Hausfater *et al.*, 1982; Bulger & Hamilton, 1988) likewise generates age-independent variation in dominance rank across all females in the group. The percentage of vocal approaches was square-root transformed, and male rank and tenure were log transformed to increase homogeneity of variance. Finally, scattergrams of residuals *versus* the fitted values of the dependent variables lacked evidence of pronounced heteroscedasticity.

Results

General patterns of male grunting behavior

On average, individual males grunted in 11.6% of their approaches to females (SD = 7.4, $N = 18$ males, 2743 approaches). The relative frequency of male grunting upon approaching a female varied with her reproductive state (Fig. 1a). Males grunted significantly less often when approaching pregnant females than when approaching cycling females (Wilcoxon matched-pairs, signed-ranks $T = 7$, $N = 12$, $p = 0.01$) or lactating females ($T = 9$, $N = 18$, $p < 0.001$). Grunting accompanied a larger percentage of male approaches to lactating females than to cycling females ($T = 22$, $N = 18$, $p < 0.01$). To summarize, males vocalized rarely when approaching pregnant females, more often when approaching cycling females, and most of all when approaching lactating females. Male grunting did not differ significantly within the class of cycling females (*i.e.* consort *versus* non-consort dyads) or within the class of lactating females (*i.e.* non-friend *versus* friend dyads).

A male's vocal behavior also varied systematically with his dominance rank. High-ranking males were significantly more likely than subordinates

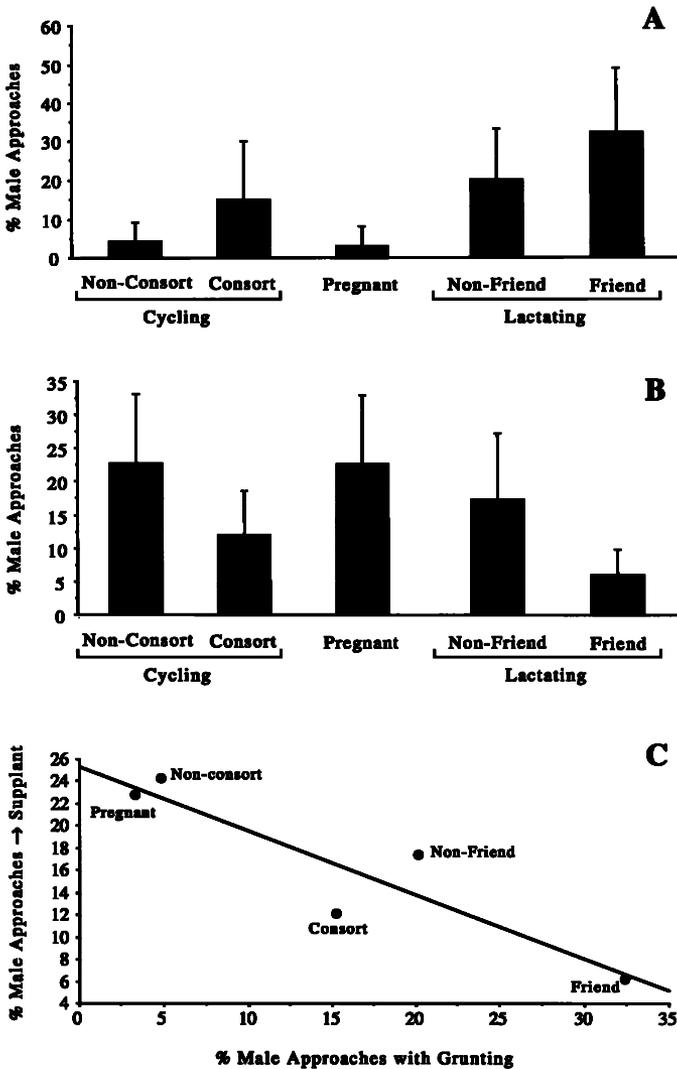


Fig. 1. Mean (\pm SD) percentage of male approaches towards adult females that was (A) accompanied by male grunting; and (B) followed by a supplant of the female. Males are separated on the basis of the reproductive state of the females they approached: non-consort ($N = 11$), consort ($N = 17$), pregnant ($N = 17$), lactation non-friend ($N = 17$), lactation friend ($N = 6$); Part (C) presents the correlation between mean percentage of vocal approaches by males (data in 1a) and mean percentage of male approaches resulting in supplant (data in 1b) across female reproductive states.

to call when approaching females in most reproductive states (non-consort females: $r_s = +0.76$, $N = 18$, $p < 0.01$; pregnant females: $r_s = +0.69$, $N = 17$, $p < 0.01$; lactating, non-friend females: $r_s = +0.54$, $N = 17$, $p < 0.05$). Only when approaching estrus females with which they were consorting did subordinate males call more often than dominants ($r_s = -0.65$, $N = 11$, $p < 0.05$). When approaching a lactating female friend, however, a male's rank was unrelated to the relative frequency of grunting.

Effect of grunts on subsequent supplants

Supplants and female reproductive state

Supplanting was significantly less common when a male approached a female with which he had a social relationship of either of two types: a friendship or a sexual consortship (Fig. 1b). Males supplanted female friends at significantly lower rates than when they approached pregnant females, non-consort (cycling) females, or lactating, non-friend females (Wilcoxon $T = 0$, $N = 6$, $p < 0.05$, for all three tests). The rate of supplanting was lower when a male interacted with consort females than with pregnant females ($T = 9$, $N = 11$, $p < 0.05$) or non-consort females ($T = 4$, $N = 11$, $p < 0.05$), but not with lactating females (of either friendship status). Thus, the existing sociosexual relationship of a male and female was implicated as a potentially important factor behind supplants.

Supplants: vocal *versus* silent approaches

Male grunting and supplanting were strongly negatively correlated with one another across the different reproductive conditions ($r = -0.91$, $p < 0.05$), as shown in Fig. 1c. This relation, however, did not hold when we examined data *within* each of these conditions, *i.e.* the consequences of grunts for individual males approaching females. As Fig. 2 shows, supplants of females were as common after the males' vocal approaches as following their silent approaches to non-lactating females (Wilcoxon $T = 15$, $N = 9$, $p > 0.10$), lactating non-friend females ($T = 15$, $N = 11$, $p > 0.10$), and lactating friend females ($T = 5$, $N = 5$, $p > 0.10$).

In summary, across the different classes of females and reproductive conditions, there was a significant relation between grunting and supplanting: when males approached pregnant females, for example, they rarely grunted and the females were often supplanted, whereas when males approached

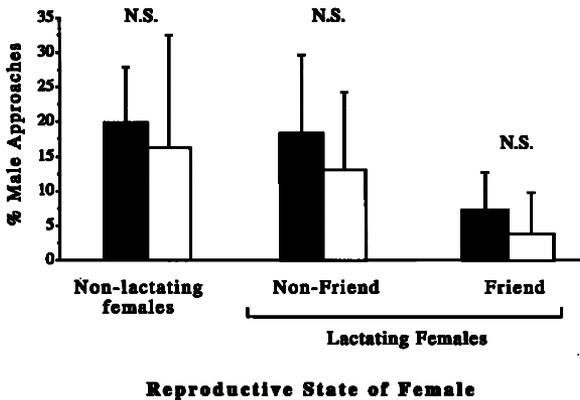


Fig. 2. Mean (\pm SD) percentage of vocal (white bars) and silent (black bars) male approaches towards unrelated females that was followed by a supplant of the female. Males are differentiated on the basis of the reproductive state of the females approached: non-lactating ($N = 9$), lactation non-friend ($N = 11$), lactation friend ($N = 5$). 'NS' = non-significant difference by Wilcoxon matched-pairs, signed-ranks (see text).

their lactating female friends, the males often grunted and the females were rarely supplanted (Fig. 1c). Within each female-reproductive condition, however, the apparent relation between grunting and supplanting disappeared. When a male approached a pregnant female, for example, a supplant was equally likely regardless of whether he grunted or remained silent. The data suggest that grunts themselves did not determine whether or not a female was supplanted; instead, the female's identity and/or reproductive condition affected both the male's tendency to grunt and the female's tendency to move away.

Additional evidence that grunts did not discourage supplants derives from the positive correlation between the relative frequency of vocal supplants and the relative frequency of silent supplants in male interactions with females of all reproductive states ($r = +0.5$, $N = 14$, $p = 0.05$). This correlation indicates that certain males tended to elicit supplants consistently and independently of their vocal behavior.

Effect of grunts on subsequent affiliative interaction

Affiliative interaction and female reproductive state

The percentage of a male's approaches followed by affiliation was similar (approximately 4-8%) in interactions with females in all reproductive classes

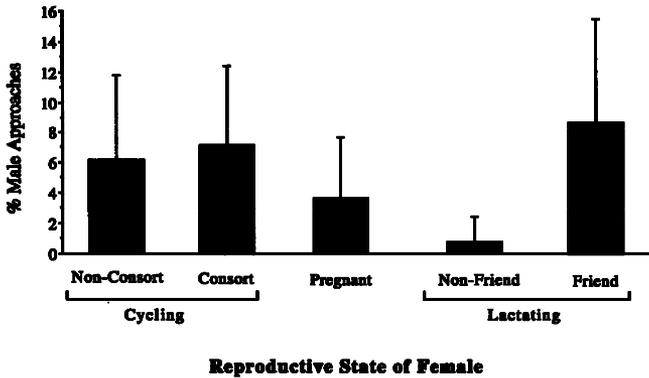


Fig. 3. Mean (\pm SD) percentage of male approaches towards adult females that was followed by affiliative interaction. Males are separated on the basis of the reproductive state of the females they approached: non-consort ($N = 11$), consort ($N = 17$), pregnant ($N = 17$), lactation non-friend ($N = 17$), lactation friend ($N = 6$).

except one: lactating non-friend females (Fig. 3). Females in this class were affiliative interactants with males significantly less often (following fewer than 1% of male approaches) than females in all other reproductive states (Wilcoxon test between non-friend females and: non-consort females, $T = 3.5$, $N = 15$, $p < 0.01$; consort females, $T = 1$, $N = 8$, $p < 0.05$; pregnant females, $T = 7$, $N = 12$, $p = 0.01$; lactating friend females, $T = 0$, $N = 5$, $p < 0.05$).

Vocal *versus* silent approaches

In contrast to supplanting (see above), affiliative interaction was significantly more likely to occur when a male grunted as he approached than when he approached silently (Fig. 4). This was true for two classes of females. In male interactions with non-lactating females, affiliative interactions followed twice as many vocal approaches as silent approaches (Wilcoxon $T = 9$, $N = 11$, $p < 0.05$). This disparity was even larger for male approaches to lactating friend females, where affiliative behavior was nearly 20 times more common after vocal approaches than after silent approaches (Wilcoxon $T = 0$, $N = 5$, $p < 0.05$). Grunting by males, however, had no effect on the probability of affiliative interaction with lactating, non-friend females, primarily because males virtually never interacted affiliatively with such females when they approached them. For 11 of 14 males, the percentage of approaches followed by affiliative interaction was zero for *both* vocal and silent approaches.

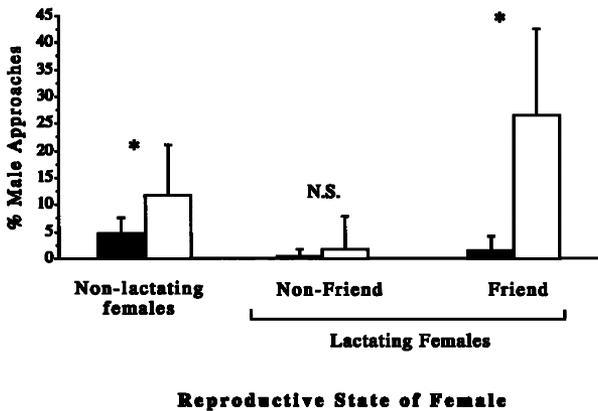


Fig. 4. Mean (\pm SD) percentage of vocal (white bars) and silent (black bars) male approaches towards unrelated females that was followed by affiliative interaction with the female. Males are differentiated on the basis of the reproductive state of the females approached: non-lactating ($N = 11$), lactation non-friend ($N = 14$), lactation friend ($N = 5$). '*' = significant difference ($p < 0.05$) by Wilcoxon matched-pairs, signed-ranks (see text).

Predictor variables of supplanting and affiliative interaction

Only two of the variables tested with an analysis of variance accounted significantly for variation in the percentage of male approaches followed by supplants of females: male dominance rank ($F_{1,41} = 4.21, p < 0.05$) and the friendship status of the dyad ($F_{1,41} = 7.69, p < 0.01$). Supplants were more likely following approaches by high-ranking or non-friend males. The other six variables — percentage of male approaches with grunting, male tenure, the interaction of male tenure with dominance rank, female dominance rank, female age, and female reproductive state — did not explain significant proportions of the variation in supplant behavior. Three significant predictors variables for affiliative interaction were: friendship status (friends interacted at higher rates; $F_{1,41} = 5.80, p < 0.05$); female reproductive state (cycling females experienced more affiliative interaction than lactating females, which showed higher rates than pregnant females; $F_{2,48} = 3.53, p < 0.05$); and, finally, female age category (old females in the category 'greater than 16 yr' experienced significantly higher rates of affiliative interaction with males than other age classes; $F_{2,48} = 2.58, p = 0.05$).

Case studies of immigrant males

When he first enters a group, an immigrant male chacma baboon often elicits avoidance among resident females (see above) and, therefore, is likely to supplant females often following his approaches. The hypothesis that grunts function to promote proximity to females predicts co-variation in male grunting and female tolerance. For example, a newly immigrant male is expected to grunt often to females in his approaches, but as time progresses and female aversion to the male wanes, he may use grunts less often. Over time, then, the relative rate of supplants following silent approaches (a measure of female tolerance of the male's proximity) and the overall rate of grunting in approaches will both decline. More generally, a positive association between these two variables is anticipated.

This prediction was fulfilled for all three immigrant males (Fig. 5). For two males (DG and EG), female aversion (as reflected by the percentage of silent supplants) was initially high and then declined substantially (Mean \pm SD = $44 \pm 5\%$) over the 20-30 weeks following immigration. Male grunting in approaches to females also declined correspondingly. That is, as females became more tolerant of male proximity after silent approaches, these males used grunts in progressively fewer of their approaches. The pattern for the third male, GL, was different but still consistent with the general prediction of the hypothesis. Female spatial intolerance of this male rose sharply when he attained the alpha position in the hierarchy and it generally increased over the remainder of his residency *along with* his use of grunts in approaches. These two variables were positively correlated over the entire residency of male GL ($r = +0.7$, $N = 9$, $p < 0.05$). Thus, this male used grunts in a larger proportion of approaches as female aversion to his (silent) approaches increased with time, in accordance with the view that grunts and proximity maintenance are functionally related. Further evidence for this view is the distinct, though nonsignificant tendency for GL to supplant females less often after his vocal approaches than following his silent approaches over the post-immigration period (sign test, $x = 7$, $N = 8$, $p < 0.10$).

Discussion

Do male grunts serve an 'appeasing' function in interactions with females? To answer this question we must differentiate between two measures of

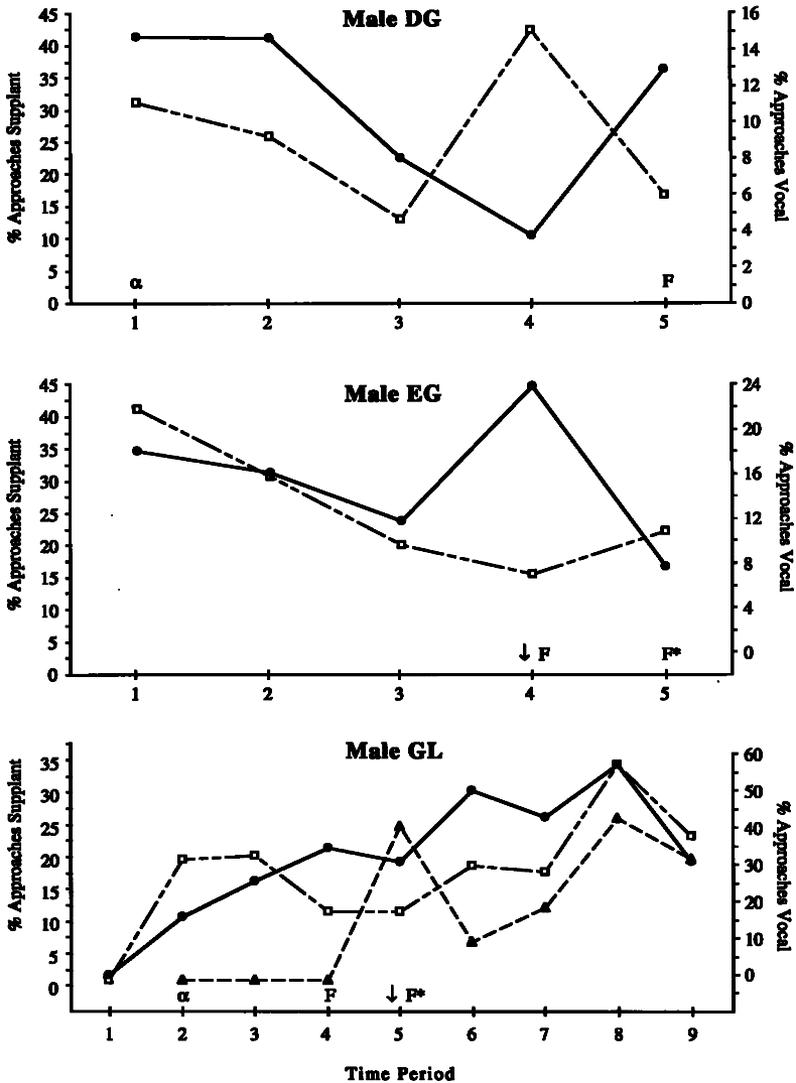


Fig. 5. Temporal changes in the vocal and social behavior of three immigrant adult males. The per cent of male silent (open squares, dashed line) and vocal (closed triangles, dotted line) approaches to females resulting in a supplant, and the per cent of male approaches accompanied by vocalization (closed circles, solid line) are graphed across contiguous 10-week periods following immigration. Symbols along the x-axis indicate the timing of changes in rank in the male hierarchy and in heterosexual friendship status with females: α = attainment of alpha position in hierarchy; \downarrow = fall in rank below the beta position; 'F' = onset of friendship formation with female(s); 'F*' period with largest number of friendships involving male.

appeasement: sustained proximity (*i.e.* reduced probability of supplanting) and affiliative interaction.

Evidence in favor on an appeasing function of male grunts: Affinitive interaction

Three sorts of data support the view that grunting by male baboons makes further friendly interaction with females more likely. First, affiliative interactions were significantly more likely to occur when a male grunted as he approached a non-lactating female or a lactating female friend than when he approached silently (Fig. 4).

Second, males grunted more often when approaching an estrus or lactating female than when approaching a pregnant female. Although a male may potentially benefit from interacting with a particular female in any reproductive state, estrus and lactating females would seem to have a particularly high 'resource value' (*sensu* Kummer, 1978). Estrus females (especially consorts) offer males opportunities for direct enhancement of reproductive success. Lactating females offer males the potential benefits of interacting with friends or their infants (*e.g.* protection and investment in offspring, access to infants for use in 'agonistic buffering' against higher-ranking males, access to females as targets of redirected aggression from higher-ranking males, hygienic advantages of the extensive grooming proffered by female friends, and future copulatory success with females that mate preferentially with past friends when they resume cycling). Moreover, the pronounced reluctance of females with infants to interact with most males, especially immigrant males, provides an additional context in which males may potentially benefit from grunting. The fact that males direct more of their grunts to females (and/or their infants) with which the potential benefits are relatively higher and/or the probability of interaction is relatively low is consistent with the view that these calls are given in an attempt to facilitate interaction.

Third, high-ranking males grunted at significantly higher rates than did low-ranking males when approaching all females except those involved in sexual consortships with them (which elicited more grunts from subordinate males) and those involved in friendships with them (which elicited similar rates of grunting from males of all ranks). If dominant males pose a greater threat of harassment to females than subordinate males (Smuts & Smuts, 1993), this result suggests that males grunted in order to appease

females with which they did not have an ongoing affiliative relationship. Analogously, grunts may confer a greater net benefit to subordinate males than dominant males during consortships with females. Smuts & Smuts (1993) note that male cercopithecines may use aggression to initiate or maintain consortships with 'uncooperative' females, and that subordinate males are particularly frequent aggressors of estrus females, presumably because they are at a mating disadvantage compared to higher-ranking males. Consistent with this view, Bulger (1993) found that subordinate male chacma baboons in the study group had significantly shorter consortships than dominant males. Thus, the more frequent use of grunts by subordinate males in consort may reflect an additional tactic these males use to mitigate female 'noncooperation' (*sensu* Bercovitch, 1995), and the consequently greater difficulty they experience in maintaining sexual consortships.

Evidence against an appeasing function of male grunts: Supplanting

At the same time, a variety of data argue against the view that male grunting to females serves a mollifying function in the context of supplants. First, although there was a strong relation between male grunting and the probability of a supplant across females and reproductive conditions, when females and reproductive conditions were held constant this relation disappeared. Data suggest that reproductive condition affected both the tendency of males to grunt and the tendency of females to be supplanted, not that grunts themselves affected supplanting.

Second, for male interactions with females in general, the probability of a supplant following a vocal approach was positively correlated with the probability of a supplant following a silent approach. This positive correlation suggests that females avoided particular males whether or not they grunted. The results of the ANOVA implicate high-ranking and non-friend males in particular. Note that this correlation did not exist between the probability of affiliative interactions following vocal and silent approaches, suggesting that affiliative behavior *was* influenced by grunting.

General conclusions

We examined how grunting influenced two consequences of male approaches to females: supplants and friendly interaction. There is little compelling evidence that the grunts given by the long-term male residents of a group consistently reduce the probability of supplanting females. Although these males

may grunt at high rates when approaching a female in a particular reproductive state, her decision to stay near or withdraw immediately appears to be influenced more by non-vocal factors, particularly the male's dominance and friendship status. So, for example, a female is likely to avoid the approach of a high-ranking male that is not a friend, whether or not he grunts.

These results contrast with patterns of interactions among female chacma baboons, where grunts reliably reduce the probability of supplants regardless of the social (dominance) relationships of the females (Cheney *et al.*, 1995). A possible explanation of this difference is that in female-female interactions, where dominance and long-term relationships are typically highly stable (*e.g.* Hausfater *et al.*, 1982; Samuels *et al.*, 1987), grunts have an immediate, causal effect on subsequent behavior because participants assume that grunts are accurate correlates of an approaching female's subsequent behavior. That is, "through past experience, and perhaps also by observing the interactions of others, [females] learn that grunts *honestly signal* a low probability of aggression" from other females (Cheney & Seyfarth, 1996; our italics). By contrast, this may be less the case in the more dynamic social interactions of adult males and females. Consequently, grunting by the male is a less important determinant of events following an approach than other factors — notably, aspects of a female's social relationship with the male.

On the other hand, there was some evidence that grunting by *immigrant* males may have reduced supplanting and served to keep females nearby after approaches. This result is consistent with the view that current social relationships are generally more important than grunts in influencing a female's reaction to an approaching male. Because females and newly immigrant males have no previous history of interaction, and because the rank position of immigrants in the male hierarchy may be unstable for some time, females may attend more to grunts in responding to their approaches. Moreover, grunts may, in fact, predict the subsequent behavior of immigrant males more reliably than of resident males. Immigrant males grunt at extremely high rates to females, not just during approaches, but from a distance as well. By grunting often at females and — more importantly — by frequently following such vocal signals with non-aggressive (or even friendly) behavior, an immigrant male may promote increasing tolerance by the group's females, which initially avoid him, but may begin to associate these signals with a low probability of male aggressiveness. As female

aversion declines with time, so, too, may the calling rates of immigrant males in approaches (albeit at a slower rate, Fig. 5). Thus, grunts may lose much of their appeasing function later, not only because males may generally call less often as residents, but also because, once they are established in the group, they occasionally exploit this system of grunt-facilitated proximity to a female's disadvantage. That is, males sometimes grunt as they approach a female only then to attack or harass her or her infant (*e.g.* in the context of re-directed aggression). Even if such episodes are rare, their potentially high costs to females should prompt them to subsequently 'devalue' grunts in favor of their memory of the history of interaction — *i.e.* their social relationships — with particular males. Immigrant males may be generally less likely to exploit females in this way, not only because the potential costs of doing so may be greater for them than for well-established residents, but simply because the opportunity to 'cheat' in this fashion requires a prior history of 'honest' interaction with females, which these males lack (and, which, in fact, they are establishing in the period following their arrival in the group).

In contrast to supplanting behavior, there was strong evidence that male grunting consistently promotes subsequent affiliative interaction with females. Even so, however, the nature of the social relationship between a male and female is a critical intervening variable influencing this function. In approaches to lactating females, for example, male grunts significantly enhance the probability of friendly interaction, but only in the context of an established friendship. Lactating females rarely interact affiliatively with non-friend males, even though these males vocalize when approaching at an equally high rate as friend males do. Moreover, to the extent that a male's grunts to a female friend are also directed at her dependent infant, a male may use grunting (in conjunction with affiliative behavior such as gentle handling of infants) to establish a bond with the developing youngster in a way analogous to that proposed for immigrant males grunting to adult females. The fitness benefits of this relationship with an infant may include facilitating (subsequent) use of infants in agonistic buffer episodes against high-ranking males (Strum, 1983), or protecting probable offspring from infanticide or harassment from others (Palombit *et al.*, 1997).

In summary, the overall scenario that seems to emerge is that a female chacma baboon's 'spatial' response to a male's approach (*e.g.* 'stay or leave') may be influenced in part by his vocal behavior for some males (*i.e.* new

immigrants), but, more generally, this response is based largely upon an assessment of non-vocal factors (such as the male's rank and their social relationship). Conversely, the female's 'social' response to a male's approach (e.g. 'interact or not interact') is influenced by the grunts given by the male. Thus, these results support the conclusion of previous research that grunting may facilitate social interaction and tolerance among members of a chacma baboon group. The results also indicate, however, that these quiet, intragroup vocalizations do not necessarily possess a simple, unitary function, but may variably mediate the social interactions of nonhuman primates within the context of specific and dynamic conditions.

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