Proximate Factors Mediating "Contact" Calls in Adult Female Baboons (*Papio cynocephalus ursinus*) and Their Infants

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"Contact" calls are widespread in social mammals and birds, but the proximate factors that motivate call production and mediate their contact function remain poorly specified. Field study of chacma baboons (*Papio cynocephalus ursinus*) revealed that contact barks in adult females were motivated by separation both from the group at large and from their dependent infants. A variety of social and ecological factors affect the probability of separation from either one or both. Results of simultaneous observations and a playback experiment indicate that the contact function of calling between mothers and infants was mediated by occasional maternal retrieval rather than coordinated call exchange. Mothers recognized the contact barks of their own infants and often were strongly motivated to locate them. However, mothers did not produce contact barks in reply unless they themselves were at risk of becoming separated from the group.

Vocalizations labeled *contact calls* are widespread among primates and other social mammals and birds. In primates, they include loud calls given periodically by widely separated individuals, as well as comparatively quiet calls given at high rates while groups move or forage in dense vegetation in which the risk of becoming separated is high (e.g., Boinski, 1991, 1993; Byrne, 1981; Dittus, 1988; Gautier & Gautier, 1977; Itani, 1963; Marler & Hobbett, 1975; Palombit, 1992; Robinson, 1982). Given the individualistic nature of social relationships in many primate groups, researchers often have suggested that, in addition to allowing individuals to maintain contact with the group at large, contact calls serve the more specific function of allowing individuals to maintain contact with particular social companions (e.g., Cheney, Seyfarth, & Palombit, 1996; Dittus, 1988; Rendall, Rodman, & Emond, 1996). This hypothesis has received indirect empirical support from several studies demonstrat-

ing individual differences in the acoustic structure of contact calls (reviewed in Snowdon, 1986) and, in a few cases, explicit vocal recognition (Hansen, 1976; Rendall et al., 1996). Hence, the structure of contact calls is often compatible with monitoring the location of specific group members. However, few studies have tested the extent to which calling is in fact motivated by separation from particular individuals, as opposed to the group at large (cf. Cheney et al., 1996; Mitani & Nishida, 1993).

At the same time, although some studies have reported chorused, or antiphonal, calling implying active vocal exchanges (Biben, 1993; Smith, Newman, & Symmes, 1982; Snowdon & Hodun, 1981; Sugiura & Masataka, 1995; Winter, Ploog, & Latta, 1966), few studies have tested whether such "exchanges" result from a synchronization of activity and underlying motivational state among group members or whether they occur because individuals are selectively answering the calls of specific social companions. The distinctions between these various alternatives need not affect ultimate explanations of the contact function of calling. However, they may reflect important differences in the proximate mechanisms governing call production.

In this article, we report on a study of the contact barks of wild chacma baboons. Contact barks are loud, harmonically rich calls (see Figure 1) that are given at low rates, are transmitted over considerable distances (>200 m), and often are accompanied by overt behaviors consistent with a contact function, such as visual scanning and climbing to an elevated position from which to survey the area (Byrne, 1981; Cheney et al., 1996; Hall & DeVore, 1965; Ransom, 1981). At times, widely separated individuals can be heard calling at about the same time, creating the impression that they are exchanging calls.

In the only systematic research to date on the contact barks of chacma baboons, Cheney et al. (1996) found that adult females called primarily when alone or when moving in the last one third of the travel progression, suggesting that separation from the group at large (or at least the risk of
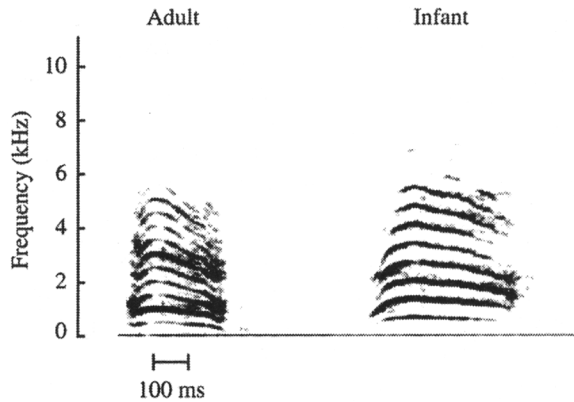
Adult Infant

Figure 1. Narrow-band (21-Hz) spectrogram of baboon contact barks for an adult female and an infant.

becoming separated) was the principal determinant of calling. However, females occasionally gave contact barks when they were in the midst of the group, suggesting that calling also may have been motivated by separation from particular social companions. Given the general importance of kinship in the regulation of spatial and social relationships among female baboons, Cheney et al. examined whether separation from adult female kin might underlie calling by testing whether females answered the calls of their adult female relatives. Although the authors could not conclude that separation from adult female kin never motivated females to call, they found little evidence that females selectively replied to the calls of their female relatives.

Cheney et al.'s (1996) findings suggest that female baboons did not answer the calls of social companions but instead called primarily only when they themselves were at risk of becoming separated from the group. However, there are other individuals from whom separation might be important and with whom a mechanism of selective call exchange might be especially beneficial, namely, infants. Female baboons invest heavily in their infants' development, and selection should favor mechanisms that allow mothers to efficiently maintain contact with their infants to provide support when needed. Such mechanisms might be particularly important when the risks of predation and infanticide are high, as they are for baboons in the Okavango Delta (Busse, 1980; Busse & Hamilton, 1981; Palombit et al., in press; Palombit, Seyfarth, & Cheney, 1997; Tarara, 1987).

In fact, female baboons have been found to produce contact barks at times when their infants are away from them (Cheney et al., 1996; Ransom, 1981), and they often behave at such times as though they are trying to locate their infants. Likewise, infants sometimes call and appear to be anxious when they become separated from their mothers. These observations suggest that the production of contact barks in adult female baboons may be motivated by separation not only from the group at large but also from their infants. They also suggest that mothers and infants may exchange calls to facilitate reunion.

In this article, we extend the study of baboon contact

barks to address more systematically the proximate factors mediating contact calls in female baboons and their infants. We begin with behavioral observations examining the factors that affect call production in adult females. We then report on the production of contact barks by infants and on the responses of mothers from natural observations and a playback experiment.

Part 1: Proximate Factors Affecting Call Production in Adult Females

Method

Study site and subjects. We conducted research on free-ranging baboons (*Papio cynocephalus ursinus*) in the Okavango Delta of northern Botswana, a vast wetland created by seasonal flooding of the Okavango River. The habitat is a mixture of grassy floodplains and wooded "islands" that rise a few meters above the floodplains and in years of heavy flooding are completely surrounded by water. Because of low flood levels during this study, the islands were surrounded by open grasslands.

Baboons at this site have been studied since 1977 (Bulger & Hamilton, 1988; Busse & Hamilton, 1981; Cheney, Seyfarth, & Silk, 1995; Rendall, Seyfarth, Cheney, & Owren, 1999). Hence, they are fully habituated to human observers and are readily identified on an individual basis. The matrilineal relatedness of all natal baboons is known. Subjects were the 22 adult females of one group that numbered approximately 75 individuals at the time of this study (February 1996–March 1997). Adult females could be ranked in a stable, linear dominance hierarchy on the basis of the outcome of approach–retreat interactions (Silk, Seyfarth, & Cheney, 1999).

Observational protocol. The goal of behavioral observation of the adult females was to identify factors responsible for call production, including in particular the importance of separation from their infants versus separation from the group at large. Observational data were gathered during 1-hr "focal animal" samples (Altmann, 1974) on the adult females sampled in random order. Observations were conducted throughout the day but were concentrated between 6 a.m. and 2 p.m. because our routine was to locate and then follow the baboons for 5–7 hr beginning early in the day as they left their sleeping site. A total of 734 hr of data were gathered, split roughly evenly among the 22 females. Because several females gave birth during the course of the study, our sample included data from 27 different immature offspring (infants or young juveniles) ranging in age from birth to 671 days. At the beginning of the study, 15 females had young infants between 0 and 6 months old, 5 females had older infants or young juveniles between 7 and 18 months old, and 2 females had no immature offspring. Three infants died or disappeared during the study. One is suspected to have been the victim of leopard predation, another died from wounds inflicted by an infanticidal male, and the third disappeared with no prior signs of ill health.

Observations included continuous data on the focal female's general activity state (e.g., resting, foraging, grooming), social behavior, and production of contact barks. In addition, point samples were taken at 15-min intervals during the 1-hr samples and included a global positioning satellite (GPS) reading (accurate to within 100 m), a measure of habitat visibility, and estimates of the focal female's proximity both to the group and to her infant.

We used the GPS readings to establish the female's average rate of travel and location within the home range during each 15-min interval. We predicted that both factors would affect spacing and calling behavior. Travel rates for each interval were calculated

using trigonometric relations to determine the straight line distance between GPS readings from successive point samples. The resulting value was then multiplied by 4 to express the distance traveled during that 15-min interval as an hourly rate (m/hr). To establish the female's location within the home range, we used the complete sample of GPS readings to create a scatter plot map of the group's ranging activities over the course of the study. Using this map and a scaled aerial photo of the region, we delineated a core region encompassing two thirds of all GPS readings and many of the group's preferred sleeping, resting, and feeding sites. Locations inside of this core region were labeled *central*, whereas locations outside of this core region were labeled *peripheral*.

At each point sample, we scored the type of habitat where the focal female was located. Experience indicated that certain gross distinctions in habitat corresponded to different levels of visibility, which we predicted would also affect spacing and calling behavior. We delineated four habitat types reflecting a continuum from high to low visibility: (a) floodplain—the open grasslands; (b) island edge—the transitional area surrounding an island, separating it from the floodplain; (c) island wood—forested areas on the raised islands; and (d) island scrub—areas of dense bush in the middle of large islands.

We scored a female's proximity to the group in one of two categories: either "with the group" if she was within 50 m of at least one other adult or "alone" if she was not. Females that were not within 50 m of another adult still may have been within 50 m of one or more juveniles or subadults and thus were not always truly alone. However, our observations suggested that separation from other adults by more than 50 m precluded visual contact in most habitats and posed a real risk of losing track of the direction of group travel.

We also scored a female's proximity to her infant in two categories, but we used a different criterion of separation. Mother and infant were scored as "in proximity" if they were within 5 m of one another. Otherwise, they were scored as "separated." Of course, mothers that were more than 5 m from their infants were not always out of sight of their infants. However, several factors made it difficult to evaluate separation between mother and infant in a fashion more comparable to that between a female and the rest of the group. For example, it was relatively easy to identify a baboon as an adult at distances up to (and beyond) 50 m, but it was considerably more difficult to locate and determine the individual identity of small infants at similar distances because of their size. In fact, in low-visibility habitats, it was sometimes difficult (for us, and potentially also for mothers) to see and identify small infants at a distance of more than a few meters. Thus, we evaluated mother–infant separation only with respect to 5-m proximity.

The only departure from application of this measure of mother–infant separation concerned episodes of calling. Each time a female produced a contact bark, we immediately scored her proximity both to the group and to her infant. The former was scored as outlined above. In scoring the latter, however, we made a special effort to establish whether the infant was truly out of sight by searching the surrounding area. It is important to note that this disparity in our evaluations of mother–infant separation between baseline conditions and episodes of calling was conservative with respect to the research hypothesis. That is, if separation from one's infant is an important determinant of calling, then a female should call more when she is separated from her infant than when the two are in proximity to each other. Our measure of separation in baseline conditions using the 5-m criterion, however, greatly overestimated the proportion of time that mothers and infants were truly out of sight. As a result, our calculation of the rate at which females called in this condition was necessarily low. This served to reduce the difference between the rates of calling when mothers and infants

were in proximity versus separated and made it harder for us to detect an effect of infant separation on call production.

We conducted the statistics by using the Number Cruncher Statistical System (Hintze, 1989) and SYSTAT (Wilkinson, 1992) software packages. All tests were two-tailed except where noted. Because of a strongly right-skewed distribution, average travel rates were square-root transformed before statistical testing.

Results

A total of 328 calls were recorded from 17 different females during focal sampling. Some females contributed many calls, whereas others contributed very few calls. Although contact barks are given singly, females often call repeatedly over short intervals such that their calls are clumped in time (Cheney et al., 1996). To improve the independence of calling episodes, we lumped calls produced by the focal female within each 15-min interval into a single calling bout, yielding 86 different bouts of calling. Hence, our primary measure of calling behavior in the analyses was whether or not females gave at least one contact bark in a given 15-min interval. In cases in which females gave multiple calls in a given interval, we used the number of calls produced as a supplemental measure of calling. Of the 86 bouts of contact barks, 5 were by females with no immature offspring in the group at the time. We omitted these cases from analyses related to infant proximity.

Factors affecting the production of contact barks. The majority of contact bark bouts could be accounted for by females' proximity to the group or to their infants: Of the 81 bouts involving females with immature offspring, 74 occurred when they were separated from the group ($n = 21$), their infants ($n = 19$), or both ($n = 34$). Females did not invariably call when separated from the group or their infants. Females called approximately 1 time in every 6 that they were separated from the group and 1 time in every 30 that they were separated from their infants. However, in only 7 cases did females call when they were both with the group and in proximity to their infants. Thus, the rate of calling was significantly higher when females were alone than when they were with the group (Wilcoxon $T = 4, p < .001, N = 17$; see Figure 2), and despite the conservative effect of our scoring of mother–infant separation during baseline conditions versus episodes of calling, the rate of calling was also higher when females were separated from their infants than when they were in proximity to them (one-tailed Wilcoxon $T = 37, p = .0545, N = 16$; see Figure 2).

Although separation from the group or from an infant accounted for most instances of calling, the probability of calling varied according to several other factors. For females that called more than once, the production of contact barks was inversely related to dominance rank ($r_s = -.60, p < .05, N = 13$). Thus, lower ranking females called more frequently than higher ranking females, replicating an earlier finding (Cheney et al., 1996). Call production also varied according to the age of the infants, with mothers of older infants calling more frequently than mothers of younger infants, analysis of variance: $F(1, 2934) = 4.25, p < .05$. In addition, females called at higher rates in peripheral as opposed to central areas of the group's home range (Wil-
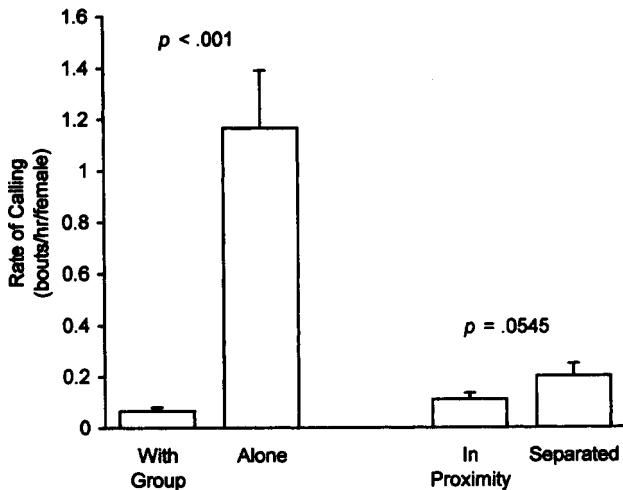
Figure 2. The mean (+*SE*) rate of calling by adult female baboons as a function of their proximity to the group (with the group or alone) and to their infants (in proximity or separated).

coxon $T = 32, p < .05, N = 17$), and this was especially true when females became separated from the group. Thus, when alone and on the periphery of their range, females called at rates that were nearly double those when they were alone and in the core of their range (Wilcoxon $T = 11, p < .01, N = 15$).

Across females, call production also varied with habitat, $\chi^2(3, N = 17) = 10.55, p < .05$. The rate of calling was highest in the island scrub habitat, where visibility was low, and lowest on the floodplain, where visibility was comparatively high. Calling was also more likely to occur as the rate of travel increased, $F(1, 2934) = 18.19, p < .001$; the average travel rate during intervals in which females called (554 m/hr) was almost double that of intervals in which no calls were given (316 m/hr). These two factors were interrelated: Analysis of variance revealed significant variation ($p < .05$) in the rate of travel across the four habitat types for 17 of the 22 females. For 15 of these females, travel rates were highest in island scrub habitats, where visibility was low. In addition to affecting the probability that a female would call, the rate of travel also affected the number of calls a female produced in a given 15-min interval. For those intervals in which a female called, the number of calls that were produced was positively correlated with the rate of travel ($r_s = .33, p < .01, N = 86$). The number of calls produced did not vary systematically with any of the other factors (e.g., habitat type, location in the range, dominance rank).

To evaluate the relative importance of each of the above factors in the production of contact barks, we used the data on all females combined to conduct a stepwise logistic regression with calling (yes or no) as the dependent variable (see Table 1). Only proximity to the group and proximity to one's infant made statistically significant ($p < .05$) contributions to explaining variation in calling. The rate of travel and location in the range were nearly significant additional predictors of calling. Noteworthy in this respect is the fact

that, in five of the seven instances of calling unaccounted for by separation from the group or their infants, females were at the time traveling rapidly (853 m/hr, or 2.5 times the overall average rate of travel of 322 m/hr) on the periphery of their range.

Separation from the group. On average, females were separated from the group approximately 10% of the time. However, there was considerable variation among individuals in the percentage of time that they spent alone (ranging from less than 4% to 22%), which was significantly correlated with female rank: Low-ranking females were alone significantly more often than were high-ranking females ($r_s = .50, p < .01, N = 22$). The likelihood of the females becoming separated from the group also varied as a function of travel rate: The rate of travel was significantly greater during intervals in which the females were alone than during intervals in which they were with the group (Wilcoxon $T = 6, p < .0001, N = 22$). Of course, it is possible that the increased rate of travel in intervals when females were separated from the group was a consequence rather than a cause of being separated, reflecting efforts to locate and catch the group rather than being a factor contributing to the separation. If true, then the rate of travel in the interval immediately preceding that in which females were alone should not have differed significantly from the baseline rate. In fact, this was not true. Rates of travel in the interval immediately preceding separation were significantly higher than the baseline rate of travel for each of the 22 females (Wilcoxon $T = 0, p < .0001, N = 22$), on average more than double the baseline rate. Hence, high rates of travel are better interpreted as a cause rather than an effect of separation.

A female's proximity to the group also varied as a function of her location within the group's home range: Of the 22 females, 16 were alone more often in central than peripheral areas of the range (sign test: $p = .052, N = 22$). Finally, across females, habitat type also affected the likelihood of becoming separated from the group. Females were alone more than expected in island scrub habitats and less than expected on the floodplain, $\chi^2(3, N = 22) = 34.00, p < .0001$.

Table 1

Results of Stepwise Logistic Regression Using the Production of Contact Barks (Yes or No) by Adult Female Baboons (N = 22) as the Dependent Variable

Variable	χ^2	p
Proximity to the group	115.31[a]	<.0001
Proximity to one's infant	4.77[a]	.0289
Rate of travel	3.49[a]	.0618
Location in the range	3.12[a]	.0773
Dominance rank	0.46[a]	.4968
Habitat type	0.36[a]	.5473
Infant age	0.13[a]	.7201
Overall stepwise model	161.46[b]	<.0001

Note. All variables that varied significantly with calling in univariate tests were entered in the analysis. Variables are listed in the order in which they were entered in the stepwise model.
[a]$df = 1, N = 2,936.$ [b]$df = 7, N = 2,936.$

Separation from infants. Infants in our sample spent approximately 53% of their time in proximity to (within a distance of 5 m from) their mothers. Not surprisingly, the percentage of time spent in proximity to mothers varied considerably with the infants' age. For purposes of analysis, we divided the infants into two age categories: younger infants less than 6 months of age and older infants between 6 and 22 months of age. Averaged across individuals, younger infants were in proximity to their mothers 91% of the time, whereas older infants were in proximity to their mothers only 40% of the time.

Younger infants were especially likely to be in proximity to their mothers as the rate of travel increased: For these infants, the rate of travel when in proximity to their mothers (307 m/hr) was more than twice that when they were separated (142 m/hr; Wilcoxon $T = 1$, $p < .01$, $N = 11$). There was no significant effect of travel rate on the likelihood that older infants would be in proximity to their mothers (Wilcoxon $T = 96$, *ns*, $N = 20$). The likelihood that these older infants would be in proximity to their mothers did vary significantly according to their mothers' proximity to the group. The percentage of time spent by older infants in proximity to their mothers was greater when the mothers were with the group than when the mothers were alone (Wilcoxon $T = 30$, $p < .01$, $N = 20$). In other words, older infants were more likely to be separated from their mothers at times when their mothers were themselves separated from the group. Younger infants were never separated from their mothers when their mothers were separated from the group.

These results suggest that infants' age may be the best predictor of the likelihood that they will be separated from their mothers. Indeed, the data on calling tended to confirm this relation. Only 1 bout of calling was recorded from a mother separated from a younger infant, whereas 52 bouts of calling were recorded from mothers separated from older infants.

Discussion

The results indicate that in adult female baboons, separation both from the group and from their infants affected the production of contact barks. These two factors accounted for more than 85% of calling bouts. This result does not imply that females called invariably whenever they became separated from the group or their infants. In fact, females called approximately only 1 time in every 6 that they were separated from the group and only 1 time in every 30 that they were separated from their infants. This substantial difference in calling rates between group and infant separation was probably largely artifactual, due to our conservative scoring of mother–infant separation during baseline observations (>5 m). Thus, in many cases when females were scored as being separated from their infants, they probably could still see their infants or knew where they were located. Hence, the rate at which females called when they were truly separated from their infants was probably much higher than our estimate reflects and was probably closer to the rate at which they called when they were separated from the group. Although females did not invariably call when they were

separated from the group or their infants, they seldom called if they were not separated from one or the other.

The finding that separation from the group often appeared to motivate calling supports an earlier study in which females called most often when traveling alone or in the last one third of the group progression (Cheney et al., 1996). The production of contact barks was also affected by habitat visibility, travel rate, and the caller's dominance rank. However, these factors appeared to influence calling indirectly by affecting the probability that females would become separated from the group. Thus, the probability of becoming separated was greater at higher rates of travel, the rate of travel was highest in low-visibility habitats, females became separated more often in low-visibility habitats, and lower ranking females were more often separated than were higher ranking females.

Females also called more in peripheral areas of their range, particularly when they became separated from the group. That females were separated from the group less frequently in peripheral as opposed to central parts of their range suggests that they may have actively avoided separation in these areas and that when they did become separated in peripheral areas there was a lower threshold to calling. This combination of findings might be explained by higher risks associated with the females becoming separated from the group in peripheral areas, where individuals are less likely to reencounter their own group by chance, are potentially more likely to encounter neighboring groups, and are less familiar with predator habits and refuge sites.

Part 2: Processes Mediating Contact Between Mothers and Infants

Behavioral observations indicated that female baboons' contact barks were motivated in part by separation from their infants, suggesting that these barks may function to maintain contact between mothers and infants. However, it is not clear how calling by mothers might facilitate such contact. For example, do mothers and infants actively exchange calls? Do mothers even recognize the calls of their own infants? To examine these questions, we conducted simultaneous observations and a playback experiment on mothers and infants.

Method

Simultaneous observations of mothers and infants. In a subset of our behavioral observations of mothers, we conducted simultaneous observations of infants to evaluate the possibility that the mothers and infants might exchange contact barks. While one observer followed a particular focal female, a second observer followed that female's infant. These observations focused on 6–18-month-old infants, because at that age, infants were frequently separated from their mothers (see Part 1). Because this subset of our observations was conducted using two observers, it was possible for us to more accurately evaluate proximity between mothers and infants. Proximity between mothers and infants was evaluated at 3-min intervals during 1-hr samples and scored in one of five categories: 0–5 m, 5–15 m, 15–50 m, >50 m, or out of sight.

Observations of mothers were conducted as described in Part 1, except that we now also recorded females' responses to all audible contact barks by infants. We then synchronized each female's record of responses with the simultaneous record of contact barks produced by her infant.

Playback experiment. To more systematically examine mothers' responses to contact barks, we designed a series of matched playback trials in which females heard either their own infants' contact barks or those of an unrelated infant of the same age and sex. Playback trials were conducted in two different contexts: (a) when the female was with the group and (b) when the female was alone (i.e., more than 50 m from any other adult). The basic design of the experiment, therefore, involved four conditions.

The contact barks used in the experiments were originally recorded on Sony Type IV metal tapes using a Sony WM-D6C Professional Walkman cassette recorder and a Sennheiser ME 80 directional microphone (with K3U powering module). Recordings were digitized at 22.05 kHz on a laptop computer by using the Canary software package (Version 1.2.1; Charif, Mitchell, & Clark, 1995). Playback stimuli were then constructed by using two calls from the same infant recorded at the same age. Because playback trials were conducted over a 9-month period, we updated our stimuli for particular infants every 3 months to control for potential developmental changes in the acoustic structure of their contact barks.

Our set of playback stimuli consisted of 23 pairs of calls (46 different exemplars) originally recorded from 15 different infants. Each playback stimulus consisted of 2 calls from the same infant separated by a 1-s interval of silence. We chose this stimulus arrangement for several reasons. First, in field playback experiments, it is often difficult to predict short-term changes in ambient noise created by environmental disturbances or conspecific (or heterospecific) signaling. Therefore, we felt that a stimulus consisting of 2 calls would better ensure that subjects would hear the contact barks we were broadcasting. Furthermore, it was our impression that rapidly repeated calls reflect greater distress on the part of the caller (see below). A stimulus consisting of 2 closely spaced calls, therefore, might be more likely to evoke a strong response from listeners.

The choice of subject and experimental context for each trial was determined by the ongoing regimen of behavioral sampling. The order of "own" versus "unrelated" infant trials was balanced across subjects. Trials were conducted only if there had been no contact barks from anyone in the group in the preceding 30 min and only if the mother's infant (and, in the case of control trials, the unrelated infant whose calls were to be played) had not been seen by observers for at least 10 min. The latter criterion was included to ensure that the infant whose calls were to be played could realistically be calling from some distance away. Because mothers and infants were frequently separated from one another without calling by either one, these conditions occurred regularly. Calls were played through a Nagra DSM speaker positioned an average distance of 30 m from the subject in the direction from which the infant was last seen. Amplitude settings were the same for all playback trials and were chosen to simulate an infant calling at a distance of approximately 100 m.

We conducted 89 playback trials on 19 different females (that all had an infant between 6 and 18 months old at the time) over a 9-month period. On average, a playback trial was conducted once every 3 days, a rate far lower than the rate of natural call production by infants (approximately two bouts per hour). Playback trials were split roughly evenly between own-infant (n = 46 trials) and unrelated-infant (n = 43 trials) conditions. Because females were not often separated from the group, more trials were conducted in the "with group" context (n = 56 trials) than in the "alone"

context (n = 33 trials). In some cases, a female served as a subject for more than 1 trial in a given condition. In these cases, the subject either heard the calls of a different infant (in the case of unrelated-infant trials) or heard a different pair of calls from her own infant (in the case of own-infant trials). In matched-comparison tests of these data, females' responses were averaged across the trials.

Results

Simultaneous observations of mothers and infants. We conducted 230 one-hour simultaneous samples of 19 different females and infants. Like adults, infants produced contact barks in bouts of repeated calls. During follows of focal females, we recorded 556 bouts of infant contact barks that were clearly audible to the females themselves. Of these, 93 bouts were produced by the focal females' own infants. Calling infants were typically widely separated from their mothers, with calling rate increasing as the distance between infants and mothers increased, $\chi^2(3, N = 19) = 65.53, p < .001$ (see Figure 3).

Mothers' responses to infants' contact barks varied considerably. Mothers often showed no overt response, or they simply oriented briefly in the direction of the caller. At other times, however, mothers appeared to wait for calling infants by sitting down and orienting in the direction of the caller or remaining stationary even as the rest of the group continued to move away. Occasionally, mothers responded more dramatically by climbing to an elevated position and scanning the area or approaching the caller. On a few occasions, mothers retrieved infants that called persistently. Rarely, however, did females respond with contact barks themselves.

For purposes of analysis, mothers' responses were grouped into three categories: orient in the direction of the caller; stop, wait, or move toward the caller; and produce a contact bark in reply within 5 min. The latter 5-min criterion for a vocal reply was generous but was used to facilitate comparison with an earlier study of females' responses to the contact barks of adult kin (Cheney et al., 1996). Because the sample of 93 bouts of contact barks by the focal females' own infants was too small when it was distributed across 19 different mother–offspring pairs to permit analyses by individual females, the data on females' responses were lumped.

Across mother–infant pairs, females were significantly more likely to orient toward their own calling infants than they were to other calling infants in the group, $\chi^2(1, N = 19) = 20.42, p < .001$ (see Figure 4). Females also were significantly more likely to stop, wait, or move toward their own infants, $\chi^2(1, N = 19) = 21.64, p < .001$ (see Figure 4), and the probability that they would do so was significantly greater when the infants gave multiple calls (Mann–Whitney $U = 4,804, p < .001, N = 19$). Females produced contact barks within 5 min of hearing infants call on only nine occasions, two following calls by their own infants and seven following calls by other infants. This sample of calling responses was too small to permit any statistical test.

Playback experiment. Mirroring the results from naturally occurring bouts of calling, females' responses to playbacks of contact barks varied considerably, although
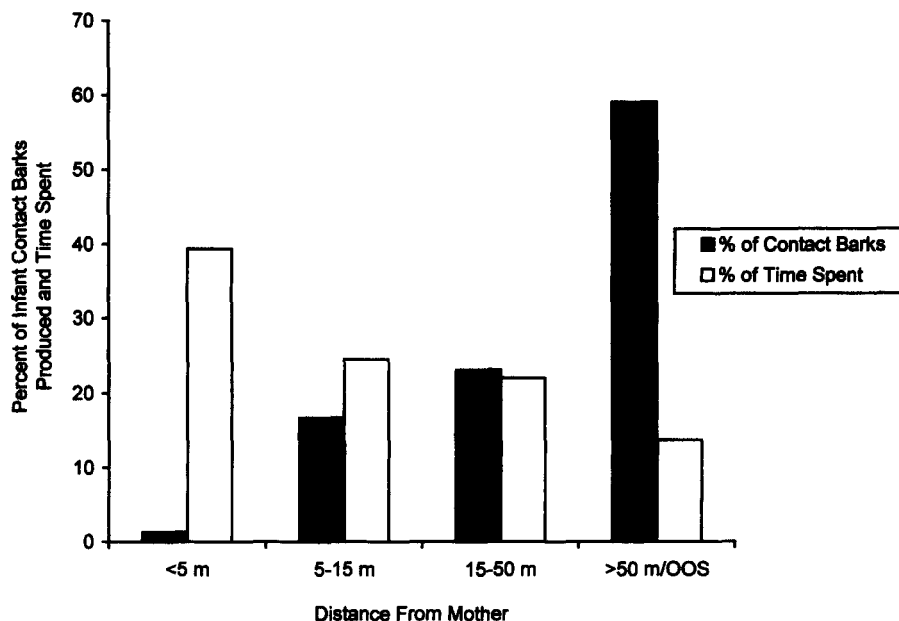
Figure 3. The percentage of contact barks produced by infant baboons as a function of the distance separating them from their mothers compared with the percentage of time infants spent at the same distances from their mothers. OOS = out of sight (see the *Method* section).

their responses to playbacks were typically stronger than their responses to naturally occurring calls. Females oriented in 52 of 89 trials (58%). Their overall mean latency to orient was 1.22 s, or within 0.25 s of hearing the second call in the

playback sequence. In 27 trials, females showed qualitatively exaggerated responses, abruptly abandoning their current activity (foraging or moving) and scanning rapidly and repeatedly in the direction of the speaker. In many trials
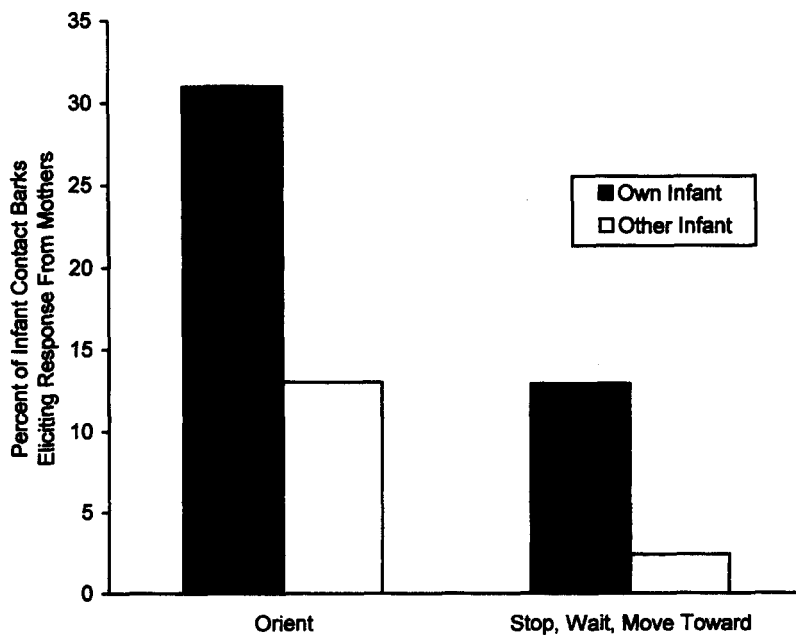

Figure 4. The percentage of naturally occurring infant baboon contact barks to which mothers responded either by orienting toward the caller or by stopping, waiting, or moving toward the caller (see the *Results* section for descriptions). Responses are plotted according to whether the caller was the mother's own infant or another infant in the group.

$(n = 15)$, females moved—and even ran—toward the speaker; stood bipedally or climbed to a better vantage point in a tree or on a stump to scan in the direction of the speaker; or stopped in their tracks and sat down to wait, facing in the direction of the speaker.

Females were clearly able to recognize the contact barks of their own offspring. Subjects oriented in significantly more own-infant trials than in unrelated-infant trials (Wilcoxon $T = 11.5$, $p < .05$, $N = 14$; see Figure 5). Furthermore, their orienting responses were both faster and longer to the calls of their own infants as opposed to those of unrelated infants. In the unmatched comparison across all subjects and trials, the latency to orient was shorter (Mann–Whitney $U = 142$, $p < .01$, $N = 19$) and the duration of orientation longer ($U = 399$, $p < .01$) in own-infant trials than in unrelated-infant trials (see Figure 6). Results were the same in the within-subjects matched comparison, in which again the latency to orient was shorter (Wilcoxon $T = 16$, $p < .05$, $N = 14$) and the duration of orientation was longer ($T = 19$, $p < .05$) in own-infant trials as opposed to unrelated-infant trials. Moreover, of the 27 trials in which subjects showed qualitatively exaggerated responses, 20 were own-infant trials, $\chi^2(1, N = 19) = 7.78, p < .01$.

Mothers responded by producing contact barks themselves in 16 of 89 trials (18%). However, the probability of calling was unaffected by infant identity (Wilcoxon $T = 24.5$, ns, $N = 14$, including 6 ties; see Figure 5). Females called in 9 own-infant trials and in 7 unrelated-infant trials. Hence, females did not selectively "answer" the contact barks of their own infants.

Instead, the probability of producing contact barks within 5 min of playback was strongly affected by the females' own state of separation from the group. Females were significantly more likely to call in trials in which they were alone ($n = 13$) than in trials in which they were with the group ($n = 3$; Wilcoxon $T = 0$, $p < .01$, $N = 13$; see Figure 5). Across subjects and trials, there was no association between orienting and calling responses, $\chi^2(1, N = 19) = 0.86$, ns, and although a few females called within seconds of hearing the contact barks of an infant, on average, the delay between broadcast of infant calls and the production of contact barks by females was 2 min, 25 s. These two findings suggest that females' production of contact barks was independent of their interest in the contact barks of infants (as manifested by their orienting and moving responses).
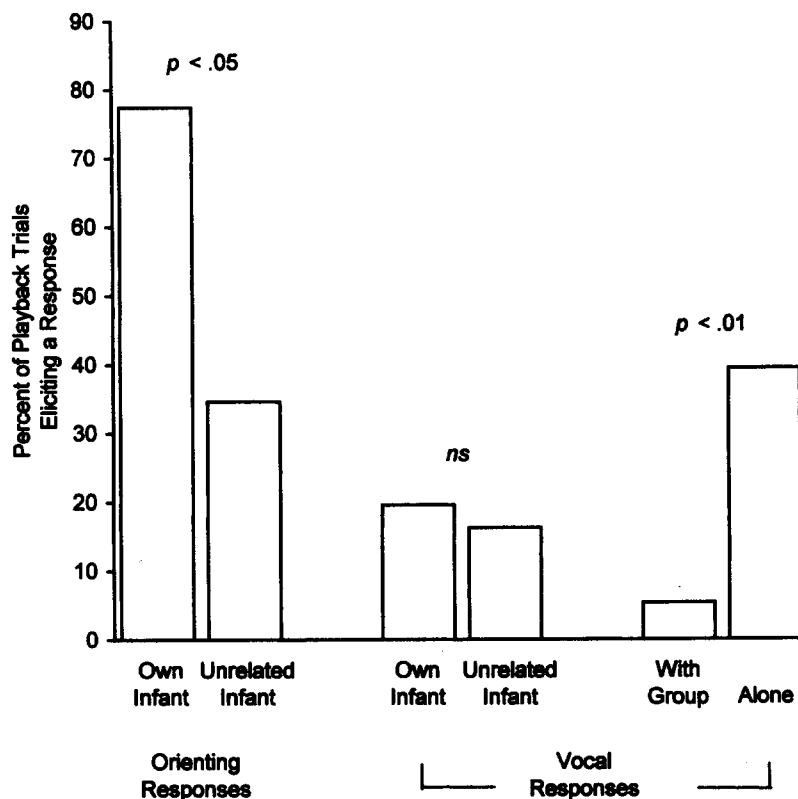

Figure 5. The percentage of trials in which female baboons responded to experimental playback of infant contact barks by either orienting toward the speaker playing the calls or producing a contact bark themselves. Orienting and vocal responses are plotted as a function of the identity of the infant whose calls were broadcast (one's own infant or an unrelated infant) and the female's proximity to the group (with the group or alone). Orienting responses were scored from frame-by-frame analysis of the videotape record and were defined as a change in the subject's orientation toward the playback speaker within 10 s of stimulus presentation.
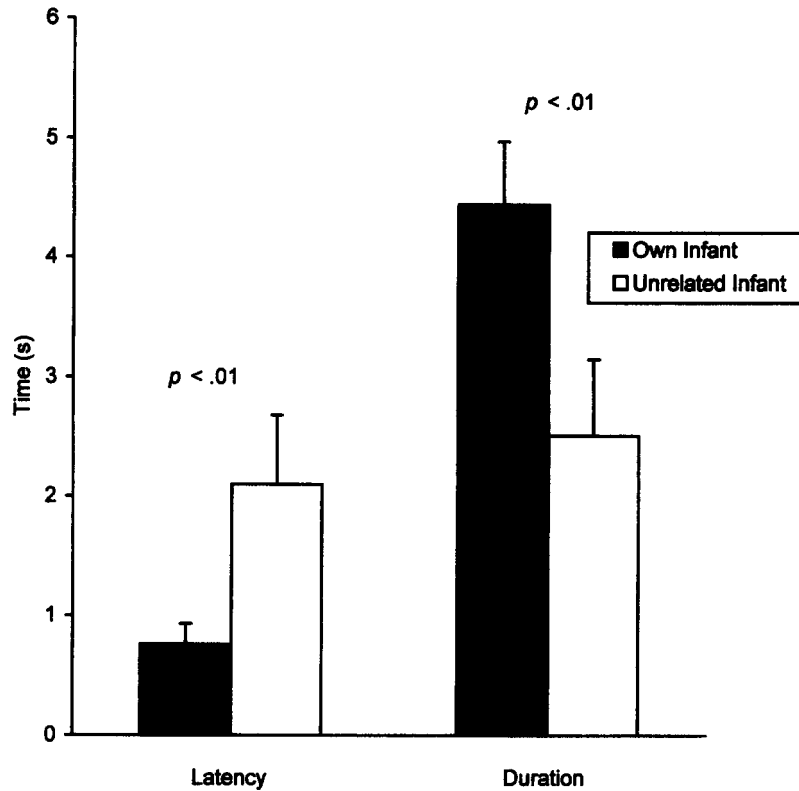
Figure 6. The mean (+*SE*) latency and duration of orienting responses by female baboons in playback trials to the contact barks of their own or unrelated infants. Latency and duration measures were calculated by using sound onset of the first call in the playback sequence.

Discussion

Results of both simultaneous observations of mothers and infants and the playback experiment indicate that mothers recognized their infants' contact barks and were motivated to locate the calling infants. In many playback trials involving their own infants, females immediately abandoned their current activity and either walked or ran toward the speaker; climbed a tree to scan toward the speaker; or sat on the ground facing the speaker, apparently waiting for their infant.

Overall, females responded more strongly and more frequently to the playback sequences than to naturally occurring calls. This was probably due to the fact that the sequences used for playback were deliberately designed to mimic infant distress. Observations of naturally occurring calls indicated that mothers were more likely to respond and search for their infants when their infants gave multiple calls. The increased incidence of calling by mothers following playback trials probably occurred because many trials were deliberately conducted when subjects were separated from the group. Under natural conditions, females gave more contact barks when they were separated from the group than when they were in proximity to other adults. Females were separated from the group during only 10% of all behavioral observations; however, 37% of playback trials were conducted in this condition.

Although mothers were clearly interested in the contact barks of their infants and were motivated to locate them, they did not exchange calls with their infants. Females seldom responded to the contact barks of their infants by producing calls themselves. Moreover, despite their strong behavioral responses to the playback sequences, mothers still did not answer their infants' calls. They were as likely to give a contact bark in response to unrelated infants' calls as they were to their own infants' calls, and their production of calls seemed to be unrelated to their attempts to locate their infants. In fact, mothers' call production appeared to be motivated primarily by their own state of separation from the group rather than that of their infants.

Females' responses to playbacks of their infants' contact barks, therefore, were comparable to their responses when the contact barks of adult female kin were played (Cheney et al., 1996). In those trials, too, subjects gave vocal responses primarily when they themselves were separated from the group. Similar responses have also been reported for the long-distance contact calls of other primate species. For example, both Dittus (1988) and Robinson (1982), studying toque macaques (*Macaca sinica*) and wedge-capped capuchins (*Cebus nigrivittatus*), respectively, found that group members seldom answered the loud calls of isolated individuals, despite showing an interest in their calls by scanning and sometimes moving in the direction of the caller. Likewise, in

a playback experiment on rhesus monkeys, Rendall and colleagues found that adult females seldom called in response to the contact calls ("coos") of their adult female kin, despite orienting strongly to their calls and even occasionally approaching the playback speaker (Rendall, 1996; Rendall et al., 1996).

General Discussion

We now briefly consider the two main issues raised at the outset of this article: (a) What factors motivate the production of contact calls? (b) What processes mediate the contact function of calling? In answer to the first question, it is clear that separation both from the group and from infants motivates calling by adult females. In addition, a variety of other social and ecological factors (e.g., age, social rank, habitat type, travel rate, and location within the home range) appear to indirectly influence call production by affecting the probability that individuals will become separated from the group or from particular social partners.

The second question is more difficult to answer. Our results suggest that the contact function of loud barks by adult female baboons and their infants is not mediated by a system of selective call exchange. Mothers did sometimes call when separated from their infants, and infants also sometimes called when separated from their mothers. However, we found no evidence that calling by mothers and infants was coordinated. Instead, contact between mothers and infants appeared to be achieved by occasional retrieval by mothers of calling infants.

There are at least two possible explanations for these findings. First, the fact that mothers did not selectively answer their infants' calls may indicate that vocal replies are not the most effective means to achieve a reunion. When the risks of predation and infanticide to unaccompanied infants are high (Busse, 1980; Busse & Hamilton, 1981; Palombit et al., 1997, in press; Tarara, 1987), it may be more adaptive for mothers simply to retrieve their infants rather than to answer them. This explanation is not entirely satisfactory, however, because mothers did not invariably retrieve calling infants, and when they did, it was only after persistent calling by the infants, which would seem merely to advertise the infants' vulnerability and therefore increase the likelihood of predation or infanticidal attack. Furthermore, this explanation cannot account for the finding that adults in several species also do not answer each other's calls (Cheney et al., 1995; Dittus, 1988; Rendall, 1996; Rendall et al., 1996; Robinson, 1982).

An alternative explanation for the lack of selective vocal replies in this study and the others noted above may be that individuals do not appreciate the plight of others that are separated or at least how calling in reply might help them to rejoin the group. The ability to understand another's perspective and how one's own behavior (and communication) can influence that of others is deemed to be an important component of human social cognition and language (Grice, 1957). It has become a focal point of research on nonhuman species because of the potential evolutionary implications. Converging evidence from various aspects of behavior and

communication suggests that monkeys (though perhaps not apes) do not fully appreciate the behavioral and mental perspectives of others (reviewed in Cheney & Seyfarth, 1990, 1996; Povinelli, 1993; Tomasello & Call, 1997). The fact that mothers in this study failed to answer their infants' calls despite calling when separated themselves is consistent with these findings and suggests that call production may be governed more by internal states associated with one's own condition of separation than by cognitive evaluations of the circumstances of others.

On the surface, a system like this that lacks vocal replies seems to present an evolutionary challenge because calling does not appear to provide obvious benefits to callers. However, self-motivated calling could be beneficial if, on many occasions, multiple animals were simultaneously at risk of becoming separated and were therefore calling with respect to their own state, thereby indirectly maintaining contact with one another. Exactly this sort of synchronization of activity and calling does seem to account for the contact function of many forms of quiet contact call given at high rates during dispersed foraging and travel in other species. It is possible that loud calls given by isolated individuals are an extension of this system, maintained in the absence of significant cognitive mediation by the frequent synchronization of activity and motivational states of others and, in the case of infants, by occasional maternal retrieval.

However, this explanation of the proximate mechanisms governing call production is not entirely satisfactory either. First, evidence that mothers answered their infants' calls would not by itself constitute proof that they understood their infants' perspective or mental state. Some other simple, contingency-based mechanism could also induce a vocal response. Second, the fact that mothers often began to search for their infants after hearing them call could be interpreted as evidence that they were able to understand their infants' perspective, at least to some degree.

On the basis of current evidence, then, it is not possible to determine whether mothers do not answer their infants' calls because (regardless of what they know about their infants' perspective) occasional physical retrieval minimizes the risks to infants or because females do not fully appreciate their infants' perspective or the effect that answering calls might have on achieving reunion. Given recent interest in the cognitive mechanisms underlying the behavior and communication of nonhuman species, future research would profit from experimental methods that can distinguish between these alternatives under naturalistic conditions.

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