

Intended Receivers and Functional Significance of Grunt and Girney Vocalizations in Free-Ranging Female Rhesus Macaques

Jessica C. Whitham*, Melissa S. Gerald† & Dario Maestriperi*

* Animal Behavior Research Group, The University of Chicago, Chicago, IL, USA

† Cayo Santiago, Caribbean Primate Research Center, University of Puerto Rico, Punta Santiago, Puerto Rico

Correspondence

Dario Maestriperi, The University of Chicago, 5730 S. Woodlawn Avenue, Chicago, IL 60637, USA. E-mail: dario@uchicago.edu.

Received: February 9, 2007

Initial acceptance: April 17, 2007

Final acceptance: April 30, 2007
(S.A. Foster)

doi: 10.1111/j.1439-0310.2007.01381.x

Abstract

We investigated the intended receivers and contexts of occurrence of grunt and girney vocalizations in rhesus macaques (*Macaca mulatta*) to assess whether these calls are best interpreted as signals of benign intent or as calls that may function to attract the attention of other individuals or induce arousal. We focally observed 19 free-ranging adult female rhesus macaques. Female calls increased dramatically after infants were born, and most were directed toward mother–infant dyads. When infants were physically separated from their mothers, callers visually oriented toward infants in over 90% of the cases, suggesting that infants were the intended receivers of grunts and girneys. Approaches followed by vocalizations were more likely to lead to the caller grooming the mother, less likely to elicit a submissive response, and more likely to result in infant handling than approaches without calls. Infant handling, however, was not necessarily benign. Vocalizations were often emitted from a distance >1 m and were rarely followed by approaches or social interactions. Our results suggest that grunts and girneys are unlikely to have evolved as signals that encode information about the caller's intention or subsequent behavior. Whereas girneys may be acoustically designed to attract infants' attention and elicit arousal, grunts may have no adaptive communicative function. Mothers, however, may have learned that other females' grunts and girneys are unlikely to be associated with significant risk and, therefore, are generally tolerant of the caller's proximity and behavior.

Introduction

Animal behavioral signals can evolve by natural selection if the sender of the signal gains fitness benefits from the responses of others (e.g. Krebs & Davies 1993; Maynard Smith & Harper 2003). Demonstrating that behavior patterns have an adaptive communicative function requires rejecting the null hypothesis that there is no adaptive function, as well as the hypothesis that they are adaptive but their function is not communicative (Darwin 1872). Although people can infer from someone's sneezes that this person has a cold and

respond by wishing this individual well, sneezes are unlikely to have evolved for their communicative function. Rather, their adaptive function is to help eliminate bacteria or other extraneous particles from the oral–nasal cavities. Sneezes do convey information about the sneezing individual, but they are best interpreted as cues and not signals (e.g. Maynard Smith & Harper 2003). In this view, both signals and cues can convey information, but signals evolved for their communicative function whereas cues evolved to serve functions unrelated to communication, or are nonfunctional byproducts of other traits.

If the adaptive communicative function of putative signals has been established, a question arises as to the mechanisms by which these signals exert their effects on other individuals. One view of animal signals is that they contain encoded information from the sender, which requires decoding by the receiver. In this view, the signal may contain information about the sender (e.g. its size or physical strength, motivation, intentions, or subsequent behavior) or may refer to other individuals, objects, or events in the external environment (see Smith 1977; Seyfarth et al. 1980; Dittus 1984, for this interpretation of signals). The use of information-encoding signals is a form of knowledge-based communication, whereby the receivers' responses are prompted by the knowledge acquired from the information encoded in the signal. Animal signals, however, can elicit reliable responses in their receivers through mechanisms other than the transfer of information and knowledge modification (e.g. Owren et al. 2003). For example, attention-getting signals elicit orientation responses in receivers and facilitate further interactions with them without necessarily conveying encoded information and altering the receiver's knowledge (e.g. Call & Tomasello 2007). Similarly, signals may induce pleasant or unpleasant emotional states in receivers and increase the probability of eliciting particular responses by acting directly on specific neural circuits (e.g. Owren & Rendall 2001; Owren et al. 2003).

In this study, we addressed whether two types of vocalizations commonly used by rhesus macaque females, grunts and girneys, are best interpreted as signals that encode information about a benign intent (e.g. Silk et al. 2000) or whether other explanations are more appropriate. For example, these calls could be signals that function through attentional or affective mechanisms, or be best interpreted as cues and not signals.

Grunts are common vocalizations in macaques (*Macaca* spp.) and baboons (*Papio* spp.). Although macaque and baboon grunts are acoustically different (baboon grunts are tonal calls based on regular vocal-fold vibration, whereas macaque grunts are noise-based calls; M. Owren, pers. comm.; see also Rowell & Hinde 1962; Hall & DeVore 1965; Ransom 1971), these vocalizations occur in similar contexts in these cercopithecine monkeys. Females often emit these calls in the context of close-range social interactions with other group members, and particularly when exhibiting interest in other females' infants and engaging in infant handling (Rowell & Hinde 1962; Rowell et al. 1964; Chevalier-Skolnikoff 1974;

Bauers 1993; Silk et al. 2000). In rhesus and Japanese macaques (*Macaca fuscata*), girney vocalizations (first described by Rowell & Hinde 1962, as a quiet, 'nasal, grunting whine') often co-occur with grunts in the context of infant-handling interactions (e.g. Rowell et al. 1964; Green 1975; Blount 1985; Silk et al. 2000). Neither grunts nor girneys, however, are ever directed by mothers to their own infants (e.g. Green 1975; Blount 1985; Bauers 1993).

Both grunts and girneys are used by adults in several contexts other than infant handling, including group movement (Hauser & Marler 1993; Rendall et al. 1999; Fischer & Hammerschmidt 2002), grooming (Mori 1975), and establishing friendly interactions (Green 1975; Cheney et al. 1995). Grunts also occur in the contexts of feeding (Hauser & Marler 1993; Cheney & Seyfarth 1997), approaching others (Cheney & Seyfarth 1997), mating (Chevalier-Skolnikoff 1974; Fischer & Hammerschmidt 2002), and post-conflict reconciliation (Silk et al. 1996). Girneys have been reported to play a role in agonistic buffering (Fischer & Hammerschmidt 2002) and in communicating submission, appeasement, or non-aggressive tendencies (e.g. Itani 1963; Green 1975; Blount 1985).

Grunts and girneys have been reported to facilitate positive interactions between adult females and mother-infant dyads. In stump-tail macaques (*Macaca arctoides*), Bauers (1993) reported that adults exhibiting an interest in infants were less likely to receive aggression from infants' mothers when they grunted relative to when they did not vocalize. In chacma baboons (*Papio ursinus*), females were more likely to engage in infant handling if they emitted grunts after approaching mothers with infants than if they approached and remained silent (Silk et al. 2003). Finally, in rhesus macaques, Silk et al. (2000) found that females generally handled infants gently if their approaches were accompanied by grunts and/or girneys but handled them roughly if they did not vocalize. Furthermore, females which approached other females were less likely to initiate aggression, more likely to initiate grooming, and less likely to elicit submission when they vocalized than when they remained silent.

Based on these findings, both Bauers (1993) and Silk et al. (2000) argued that grunts and girneys are signals that communicate a 'benign intent.' According to this view, adult females vocalize to mothers to signal good intentions toward their infants. As a result of this exchange of information, mothers are more tolerant and more willing to allow infant handling. Although this interpretation of grunts and

girneys is consistent with the observed responses to these vocalizations, it is inconsistent with anecdotal observations suggesting that grunts and girneys are directed to infants instead of mothers (e.g. Rowell et al. 1964; Chevalier-Skolnikoff 1974; Green 1975; Blount 1985). Furthermore, this argument is also contradicted by reports that these vocalizations are not consistently followed by attempts at infant handling or affiliative interactions with the mothers. For example, Rowell et al. (1964) described captive rhesus females sitting against the wire mesh of the cage and grunting to infants in another enclosure, i.e. in a situation in which physical contact with infants was impossible. Rowell et al. interpreted grunts as 'comments' on individuals or interactions (see also Brumm et al. 2005). As grunts are often associated with head-bobbing and tail-wagging (e.g. Rowell et al. 1964), it is also possible that they are attention-getting or arousal-inducing signals directed to infants. Finally, these calls may have no adaptive communicative function, i.e. they might be cues but not signals. In this view, grunts and girneys may elicit tolerant responses from mothers not because they encode information about benign intent but because mothers find these vocalizations pleasant and/or have learned that these calls are unlikely to be associated with significant risk.

In the present study, we investigated the occurrence of female grunts and girneys among free-ranging rhesus macaques to identify the contexts of their production and to determine whether these calls are primarily directed to infants, their mothers, or other individuals. In doing so, we aimed to address whether these vocalizations are likely to have a communicative function and whether they encode information about benign intent or operate through different mechanisms. Specifically, we hypothesized that female grunts and girneys may be vocalizations used by adult females to arouse infants or simply get their attention. This, in turn, might facilitate further female observations of infant behavior, the establishment of visual contact between the female and the infant and the possible exchange of other signals between them, or the possible occurrence of direct physical interactions such as touching or grooming. Our null hypothesis is that grunts and girneys do not have an adaptive communicative function. For example, they might simply be a behavioral expression of arousal in the caller similar to some types of self-directed behavior (e.g. scratching; Maestripietri et al. 1992).

The benign intent hypothesis predicts that these vocalizations (1) should have a relatively high degree

of context specificity, (2) should be directed to mothers, (3) should be preceded and followed by specific interactions in a highly predictable manner (e.g. accompanied by approaches and followed by benign infant handling). In particular, as low-cost signals of benign intent are assumed to be honest (Silk et al. 2000), grunts and girneys should be very accurate predictors of the caller's subsequent behavior, whereas they may or may not be accurate predictors of the responses of other individuals. Furthermore, (4) the occurrence of these vocalizations should be affected by kinship and rank because these variables affect social tolerance and risk of aggression between rhesus females (e.g. Kapsalis & Berman 1996; Silk 2002) and therefore are relevant to exchange of information about benign intent. In contrast, the hypothesis that grunts and girneys are infant-directed attention-getting or arousal-inducing signals implies that these vocalizations should (1) be directed to infants, (2) be accompanied by other attention-getting or arousing signals such as tail-wagging, and (3) elicit infant orientation responses. Furthermore, (4) these calls need not accurately predict the caller's subsequent behavior and need not depend on kinship and rank relationships between adult females. Predictions (2) and (4) would also be consistent with the null hypothesis that grunts and girneys have no adaptive communicative function.

Methods

Study Site and Subjects

This study was conducted on the population of free-ranging rhesus macaques on Cayo Santiago, an island located roughly 1 km off of Puerto Rico's southeastern coast (Rawlins & Kessler 1986). Monkeys on Cayo Santiago forage on vegetation and are provisioned with water and commercial monkey chow. A daily census is taken to collect social and demographic data. Similar to rhesus macaques living in the wild (e.g. Lindburg 1971), the monkeys reside in multimale-multifemale groups with a clear matrilineal structure. In the Cayo Santiago population, females become reproductively mature at approximately 3 yr of age, and males reach maturity and disperse from their natal groups at about 4 yr of age (Bercovitch & Berard 1993). There is a distinct mating season (Mar.–Aug.) and birth season (Sep.–Feb.). During data collection, the population comprised approximately 850 animals distributed among six naturally formed social groups. Our study was conducted on group S, which included 60–75

individuals throughout the study. Nineteen of the 20 adult females in this group served as study subjects (one female was excluded because it did not exhibit normal behaviors in the presence of humans). All females in the study group descended from the same matriarch. The age of subjects ranged from 4.52 to 22.53 yr (mean \pm SE = 11.96 ± 1.31). Parity, determined as the total number of infants a female had given birth to before the start of the study, ranged from 0 to 14 (mean \pm SE = 5.84 ± 0.96). Two study animals (aged 4.62 and 22.53 yr) died of natural causes during the study.

Data Collection

We collected data from Sep. to Dec./Jan. for two consecutive years, in 2004 and 2005. In both years, observations began several weeks (mean \pm SE = 5.93 ± 1.50) prior to the first birth in the subject group (no-infants period) and continued throughout most of the birth season (infants period). Twelve of the 19 focal animals gave birth during the first year. Five of these individuals reproduced during the second year also. Subjects were observed in a random order, between 8:00 and 17:00 hours, during 40-min sessions using focal, continuous sampling (Martin & Bateson 1986). A total of 317 h of observations were made. The number of hours of observations per focal female ranged between 10.7 and 18.7 h (16.7 ± 0.5).

We recorded a number of behaviors initiated and received by the focal females. Approaches within 1 m, bouts of affiliation (touches, sitting in contact, episodes of allogrooming), acts of aggression (threat, lunge, chase, bite, hit, push, and grab), and submissive behaviors (cower, flee, grimace, and scream) exchanged between the focal subjects and other group members were recorded as events. The amount of time spent in proximity (within 1 m), in contact, and engaged in allogrooming with others was also recorded. Benign infant handling was scored when focal females touched, manually inspected, groomed, or held other females' infants (0–3.5 mo of age). Infant handling was considered 'rough' if it involved any of the following: bite, grab, hit, pull, drag, restrain, or push. Instances of self-scratching and tail-wagging by focal females, if any were also recorded.

We recorded the occurrence of all grunts and girneys during the observations. Macaque grunts and girneys can easily be discriminated by ear from each other, as well as from other vocalizations such as coos or screams. As grunts and

girneys were often emitted in close succession, vocalization units were lumped into bouts for the purpose of analysis. A bout began when a unit was produced and ended after 5 s passed with no units being emitted. If a grunt unit occurred and was followed by only grunt units within 5 s, it was considered a grunt bout. The same rule was applied to girney units. If a grunt unit was followed by a girney unit, or vice versa, the bout was categorized as mixed.

Whenever a grunt or girney was produced by a focal female, we recorded: eye gaze direction (e.g. whether it was looking at a mother, the mother's infant, individuals of other age/sex classes, or no one in particular), behavior of the recipient(s), distance to recipient(s), distance between a mother and its infant when receiving calls, and the attentional/behavioral responses of the recipient(s) [e.g. whether the recipient(s) looked at the vocalizing female and/or exhibited any social or nonsocial behaviors]. Recipients were identified based on the orientation of the caller in relation to other individuals in its vicinity (see below). When grunts or girneys were received by focal females, we recorded: visual orientation of the caller, behavior of the focal female's own infant at the time that the call occurred, distance between the focal female and both its own infant and the caller, distance between the caller and the focal female's infant, and attentional/behavioral responses of the focal female and its own infant.

All instances of unidirectional aggression and submission between females were recorded on an ad libitum basis and were combined with data from focal observations to construct a dominance hierarchy. All adult females in the group could be ranked in a linear hierarchy and were assigned a rank between 1 and 20 (highest to lowest).

Data Analyses

Effects of individual and dyadic characteristics on the occurrence of grunts and girneys

We first examined whether the age, parity, and dominance rank of the focal females influenced the rate at which these individuals produced and received vocalization bouts. Next, we focused on vocalizations produced by focal females and directed at mothers and/or infants to examine the relative dominance relationship and the degree of relatedness between the focal female and the mother. For kinship analyses, individuals with a coefficient

of maternal relatedness of 0.25 or higher were considered closely related to the caller and the remaining were considered distantly related. Analyses of rank and kinship controlled for differences in the number of higher-ranking and lower-ranking, and closely related and distantly related individuals available to each focal female (i.e. in the same social group).

Effects of presence of infants on the occurrence of grunts and girneys

To assess whether the presence of newborn infants in the group influenced the occurrence of grunts and girneys, we compared the rates of vocalization bouts produced by focal females across the 'no-infants' and the 'infants' periods. We also compared the rates of vocalization bouts received by females during the 'pregnancy' period (5 mo or less before the female gave birth) and the 'baby' period (5 mo or less after the baby was born). During the 'baby' period, vocalizations received by either member of the mother-infant dyad were included when calculating rates.

Orientation of the caller and identification of the recipients of the vocalizations

The potential recipients of grunts and girneys were identified using two methods. The first involved a qualitative assessment of the face or general body orientation of the caller in relation to other individuals in its vicinity. We assumed that grunts and girneys are close-range vocalizations emitted to individuals in close proximity and that the caller would orient its face or body toward the intended recipient. This method was used to assess whether grunts and girneys were directed to individuals of different age/sex classes, e.g. adult males or females, male or female juveniles, or mother-infant dyads.

A second, more precise method was used for grunts and girneys directed at mother-infant dyads. By recording the direction of the caller's eye gaze during the vocalization bouts, we attempted to ascertain whether the intended recipient was the mother or the infant. When mother and infant were in contact, however, it was often difficult to determine whether the vocalizing female was looking at the mother or its baby. Therefore, to assess whether mothers or their infants were the intended recipients, we only examined calls for which mothers and infants were out of contact at the start of the bout, and the caller only looked at one member of the dyad.

Context of occurrence of grunts and girneys and the behavioral responses to these vocalizations

We examined whether grunts and girneys were likely to be preceded or followed by particular behaviors. Only vocalizations produced by the focal females and directed to members of the mother-infant dyad were used for these analyses. Grunt bouts, girney bouts, and mixed bouts were combined, as preliminary analyses did not reveal any significant differences in their contextual occurrence. As vocalization bouts were often repeated and closely interspersed with other behaviors in quick and complex interactional sequences, we conducted a simplified analysis combining closely repeated bouts into strings. A 30-s time criterion was used, so that a string began with the first unit, and did not end until a unit was followed by 30 s of silence. For strings with more than one unit, the mean duration was 14.62 ± 1.58 s (range 1–128 s).

First, we analyzed all instances in which focal females approached mothers and/or infants and investigated whether or not the focal female produced a vocalization to either individual within 30 s. We also noted whether any affiliation, aggression, submission, benign infant handling, rough infant handling, scratching or tail-wagging occurred within 30 s of the approach or within 30 s of the end of a vocalization string. Second, we investigated all vocalization strings to determine whether particular behaviors were associated with the calls. We examined whether the subject was within 1 m of each member of the mother-infant dyad when the last unit of the string was produced, and if not, determined whether the focal female approached or received an approach from the mother or its infant within 30 s. Finally, we assessed which behaviors (affiliation, aggression, submission, benign or rough infant handling) were likely to occur after the last unit of the string was produced.

Statistical analyses

Data were analyzed using SPSS 14 (SPSS Inc., Chicago, IL, USA). Wilcoxon's signed-rank tests were used for within-subject comparisons. Spearman's ranks correlations were used for other analyses, as well as partial correlations. Statistical outliers (defined as individuals beyond 2.5 SD of the mean) were removed when performing correlations. All tests were two-tailed. Probabilities <0.05 were considered statistically significant.

Results

During the course of the study, focal females exchanged a total of 1792 grunt units (835 produced, 957 received) and 413 girney units (171 produced, 242 received) with other group members. Females produced 649 total vocalization bouts. Of these, 516 were grunt bouts (range of hourly rates: 0.613–4.676 bouts/h), 55 were girney bouts (0–1.135 bouts/h), and 78 were mixed bouts (0–1.699 bouts/h). All females produced grunt bouts, but six failed to produce girney bouts, and three never emitted a mixed bout. The focal females and/or their infants received 725 vocalization bouts. Of these, 525 were grunt bouts (range of hourly rates: 0–6.985 bouts/h), 65 were girney bouts (0–0.646 bouts/h), and 135 were mixed bouts (0–1.987 bouts/h). Two females never received grunt bouts, four did not receive girney bouts, and seven never received mixed bouts.

To assess whether the data collected in the two successive years were similar, we compared the hourly rates of grunt bouts, girney bouts, and mixed bouts produced by focal females for which we had data for both years, regardless of whether or not they had infants. The comparison was done separately for the 'no-infants' period and the 'infants' period, and no significant differences were found (Wilcoxon's signed-rank test: 'no-infants' grunts: $z = -0.153$, $n = 17$, $p = 0.878$; 'infants' grunts: $z = -0.876$, $n = 17$, $p = 0.381$; 'no-infants' girneys: $z = 0.000$, $n = 17$, $p = 1.000$; 'infants' girneys: $z = -0.471$, $n = 17$, $p = 0.638$; 'no-infants' mixed: $z = -0.447$, $n = 17$, $p = 0.655$; 'infants' mixed: $z = -1.477$, $n = 17$, $p = 0.140$). Therefore, data from the 2 yr were combined for individual females.

Effects of Individual and Dyadic Characteristics on the Occurrence of Grunts and Girneys

Age was not correlated with the rate at which females produced grunt bouts ($r_s = -0.118$, $n = 17$, $p = 0.653$) or girney bouts ($r_s = -0.413$, $n = 18$, $p = 0.088$). Age was significantly and inversely correlated with the rate at which females produced mixed bouts ($r_s = -0.640$, $n = 16$, $p = 0.008$), but this relationship was mostly driven by two females. Age was not correlated with the rates at which focal females received grunt bouts, girney bouts, or mixed bouts (grunts: $r_s = -0.349$, $n = 19$, $p = 0.143$; girneys: $r_s = -0.049$, $n = 19$, $p = 0.841$; mixed: $r_s = 0.031$, $n = 16$, $p = 0.910$). Parity did not influence rates at which vocalizations were produced

(grunts: $r = 0.043$, $df = 14$, $p = 0.876$; girneys: $r = -0.365$, $df = 15$, $p = 0.149$; mixed: $r = -0.079$, $df = 13$, $p = 0.781$; all partial correlations controlled for age). Similarly, there was no relationship between parity and the rates at which females received bouts of any type (grunts: $r = -0.043$, $df = 16$, $p = 0.866$; girneys: $r = 0.170$, $df = 16$, $p = 0.50$; mixed: $r = -0.240$, $df = 13$, $p = 0.389$). Rank did not predict the rate at which females emitted grunt bouts or mixed bouts (grunts: $r_s = 0.277$, $n = 17$, $p = 0.282$; mixed: $r_s = 0.233$, $n = 16$, $p = 0.385$). The relationship between rank and the hourly rate of girney bouts approached significance ($r_s = 0.460$, $n = 18$, $p = 0.055$), but this was largely driven by one female. Similarly, rank was not correlated with the rates at which bouts were received (grunts: $r_s = -0.110$, $n = 19$, $p = 0.655$; girneys: $r_s = -0.181$, $n = 19$, $p = 0.459$; mixed: $r_s = 0.111$, $n = 16$, $p = 0.684$).

Focal females were more likely to vocalize at mothers and/or their infants if mothers were higher-ranking than themselves than if they were of lower rank. Specifically, this was significant for grunt bouts and mixed bouts (Wilcoxon's signed-rank test: $z = -2.628$, $n = 17$, $p = 0.009$; and $z = -2.691$, $n = 17$, $p = 0.007$, respectively). Females were equally likely to girney to dyads of higher and lower rank ($z = -1.599$, $n = 17$, $p = 0.110$). Females were equally likely to emit both grunt bouts and mixed bouts to closely and distantly related dyads (grunts: $z = -1.630$, $n = 19$, $p = 0.103$; mixed: $z = -1.023$, $n = 19$, $p = 0.307$). However, females were more likely to girney at distant relatives than close relatives ($z = -1.98$, $n = 19$, $p = 0.047$).

Effects of Presence of Infants on the Occurrence of Vocalizations

Grunts and girneys were far more common when infants were present in the group than prior to the birth of the first infant (grunts: $z = -3.340$, $n = 19$, $p = 0.001$; girneys: $z = -2.481$, $n = 19$, $p = 0.013$; mixed: $z = -3.516$, $n = 19$, $p < 0.001$; Fig. 1). During the 'no-infants' period, only 48 grunt bouts, one girney bout, and two mixed bouts were recorded. Of the 48 grunt bouts, 38 had no clear recipient and were emitted while feeding or waiting to feed at the corral ($n = 32$), resting ($n = 5$), or in the context of aggression ($n = 1$). Of the 10 grunt bouts which appeared to have recipients, four were produced while watching yearlings or mother-yearling dyads, one was emitted while handling a yearling, three were aimed at males while feeding, and two were

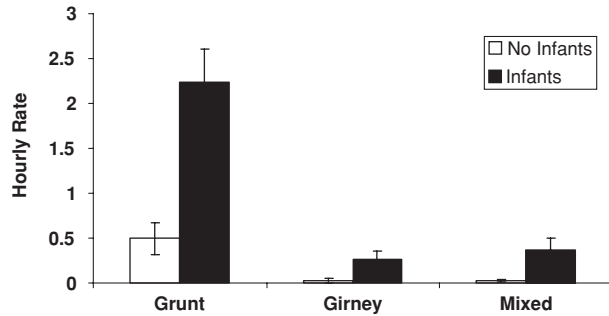


Fig. 1: Vocalization bouts produced by focal females during the 'no-infants' period (before the birth of the first infant in the study group) and the 'infants' period (after the birth of the first infant). Calculated by averaging hourly rates of bouts emitted for all females (mean \pm SE).

directed at adult females sitting in proximity. The only girney bout produced during the 'no-infants' period was by a focal female looking at a mother-yearling dyad. Both mixed bouts produced before infants were present in the group were emitted while watching a yearling.

Females received grunt bouts, girney bouts, and mixed bouts at significantly higher rates when they had infants than before giving birth (grunts: $z = -3.059$, $n = 12$, $p = 0.002$; girneys: $z = -2.803$, $n = 12$, $p = 0.005$; mixed: $z = -2.934$, $n = 12$, $p = 0.003$; Fig. 2). In fact, of all the vocalizations received by mothers, only five were received while they were pregnant.

Recipients of Vocalizations Produced by Focal Females

Females aimed a significantly higher proportion of grunts to mothers and/or infants than to other group

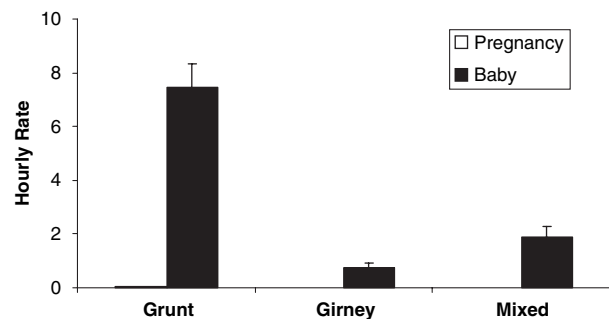


Fig. 2: Vocalization bouts received by mothers during the pregnancy period (5 mo or less before the female gave birth) and the 'baby' period (5 mo or less after the baby was born). During the 'baby' period, vocalizations received by either member of the mother-infant dyad were included. Calculated by averaging hourly rates of bouts received for all 12 females which gave birth at least once during the study (mean \pm SE).

members ($z = 3.641$, $n = 19$, $p < 0.001$). Specifically, of the 370 grunt bouts that appeared to be directed at clearly identifiable recipients, 318 were directed at mothers and/or infants, 17 bouts were aimed at yearlings or mother-yearling dyads, and the remaining calls were distributed as follows: adult females without infants ($n = 17$), adult males ($n = 9$), juvenile females ($n = 6$), subadult males ($n = 2$), and juvenile males ($n = 1$). Of the 50 girney bouts for which we could identify recipients, 40 had mothers and/or their infants as targets. However, there was no statistically significant difference between the proportion of girneys directed at mother-infant dyads vs. other individuals ($z = -1.458$, $n = 13$, $p = 0.145$). Recipients of the other girney bouts were yearlings or mother-yearling dyads ($n = 3$) and adult females with no infants ($n = 7$). Finally, a significantly higher proportion of mixed bouts were aimed at mothers and/or infants than at other individuals ($z = -3.136$, $n = 16$, $p = 0.002$) (Fig. 3). Specifically, of the 75 mixed bouts with identifiable recipients, 69 were directed at mothers and/or their babies, three at yearlings, and three at adult females without infants. When vocalization types were combined for analysis, a higher proportion of calls had mothers and/or infants as targets than other group members ($z = -3.703$, $n = 19$, $p < 0.001$).

Vocalizations Directed at Mothers and Infants

Focal females were significantly more likely to direct a higher proportion of calls to mothers and/or infants when mothers and infants were in contact vs. out of contact (all calls combined, $z = -3.322$, $n = 19$, $p = 0.001$). However, as mothers and infants generally spent more time in contact than out of contact during data collection, the occurrence of vocalizations may have been random with respect to these two conditions. Unfortunately, no accurate

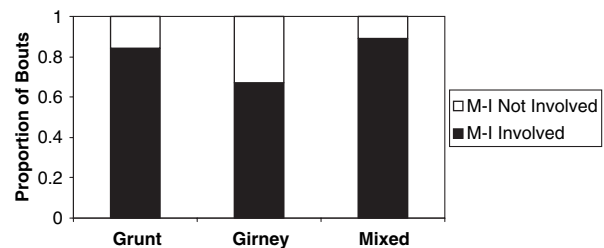


Fig. 3: Proportion of bouts produced by focal females and directed at members of the mother-infant dyad versus proportion directed at individuals of other age/sex classes. Calculated by averaging proportions for females that produced at least one bout.

quantitative data were available on the time recipients of vocalizations spent in contact or out of contact, to test whether vocalizations were random or significantly biased toward a particular condition.

When grunt bouts occurred and mothers and infants were out of contact, the vocalizing females were significantly more likely to visually attend to infants ($91.0 \pm 4.43\%$ of the cases) than to mothers ($z = -3.490$, $n = 15$, $p < 0.001$). Girney and mixed bouts were too rare for statistical analyses. However, infants were the subject of the caller's visual attention in five of the six girney bouts, and 13 of the 14 mixed bouts in which mothers and infants were out of contact. Infants visually oriented toward the caller after 26.86% of the girney bouts and 15.85% of the grunt bouts for which visual responses could be observed. In a few cases, infants also approached and touched the calling female.

Contextual Analyses of Vocalizations Directed at Mothers and Infants

Females approached mothers a total of 530 times. Only 65 of these approaches were followed by a grunt or girney within 30 s. The focal female behaved submissively in five cases, two of which were preceded by a vocalization. Females rarely initiated aggression against mothers after approaching ($n = 5$), and none of these rare aggressive episodes was preceded by a vocalization. Aggressive responses from mothers were also rare ($n = 9$), but receiving a submissive act from the mother occurred more frequently ($n = 53$). Only two bouts of aggression received and one submissive behavior received were preceded by a vocalization. Twenty-three approaches were followed by the focal female grooming the mother. Approaching females were significantly more likely to groom mothers if they called after approaching than if they did not vocalize ($z = -2.380$, $n = 14$, $p = 0.017$). Specifically, while $17.98 \pm 5.90\%$ of approaches with calls were followed by the initiation of grooming, only $2.45 \pm 0.89\%$ of silent approaches were followed by initiation of grooming. Mothers groomed the females which approached on 15 occasions, 11 of which were not preceded by a call.

Females approached infants 506 times. Females engaged in infant handling within 30 s of an approach only 17 times. A higher percentage of approaches with vocalizations was followed by infant handling ($13.03 \pm 6.93\%$) than approaches without vocalizations ($1.57 \pm 0.64\%$). However, the difference was not statistically significant ($z = -1.481$,

$n = 15$, $p = 0.139$). Approximately half of the infant-handling episodes were rough, regardless of whether they occurred after approaches with vocalizations (4/9 cases) or without them (4/8 cases).

Females were significantly more likely to self-scratch and tail-wag if they vocalized within 30 s after an approach to mothers and/or infants than if they approached without calling (scratching: $z = -3.238$, $n = 15$, $p = 0.001$; tail-wagging: $z = -2.524$, $n = 15$, $p = 0.012$). Specifically, while $42.88 \pm 6.7\%$ of approaches followed by calls were temporally associated with self-scratching, only $11.5 \pm 2.78\%$ of silent approaches were followed by scratching.

Females tail-wagged for $24.48 \pm 8.56\%$ of approaches that were followed by calls, but only $0.43 \pm 0.33\%$ of silent approaches. Thus, female approaches followed by grunts or girneys were also accompanied by expressions of arousal and attention-getting signals. While scratching was a common behavior displayed by females in a variety of contexts, tail-wagging was less frequent but more closely associated with grunts and girneys. Tail-wagging was displayed on 62 occasions by 11 of the 19 females. Almost all (94.33%) tail-wagging episodes were directed to mother-infant dyads and 78% of these were either preceded or followed a vocalization within 5 s.

The analyses of behaviors occurring after grunts or girneys focused on 346 vocalization strings directed at mothers and/or their infants, and particularly on cases in which the caller was not in proximity to the mother ($n = 135$) or infant ($n = 128$) when the last unit of the string occurred. A significantly higher proportion of these calls was not followed by approaches (made or received by the caller) than was followed by an approach (mother: $z = -3.889$, $n = 19$, $p < 0.001$; infant: $z = -3.799$, $n = 19$, $p < 0.001$; Fig. 4). When approaches did occur, females were equally as likely to approach or receive an approach from the mother and the infant.

To assess whether vocalizations were likely to be followed by social behaviors other than approaches, we examined whether any affiliation, submission, aggression, benign infant handling, or rough infant handling occurred within 30 s of the last unit of the string. In the vast majority of cases in which the female remained in view ($n = 335$), these vocalizations were not followed by any social behaviors being exchanged between the caller and the mother or the infant. When social behaviors occurred, they included benign infant handling ($n = 8$), rough infant handling ($n = 6$), aggression toward the

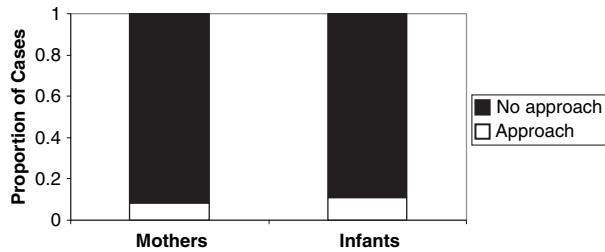


Fig. 4: Proportion of cases in which focal females either approached or received an approach from members of the mother–infant dyad vs. proportion in which an approach did not occur, after directing the last unit of a vocalization string to a member of the dyad from beyond 1 m. Calculated by averaging proportions for all females.

mother ($n = 3$) or received from it ($n = 6$), submission towards the mother ($n = 1$) or received from it ($n = 3$), and initiation of allogrooming of the mother ($n = 16$) or receipt of allogrooming from it ($n = 3$). Therefore, the end of a series of repeated vocalizations directed at mothers or infants was generally unlikely to be immediately followed by social interactions. When these social interactions occurred, they could involve the mother or the infant and be either positive or negative.

Discussion

Among rhesus macaque females, grunts are relatively common vocalizations. Our results suggest that grunts are used in a variety of contexts and can be directed to individuals of different age/sex classes, or to no one at all. Nearly 80% of the grunts produced prior to the beginning of the birth season did not appear to have a clear recipient, and the majority of these calls were emitted in the context of feeding. Previous studies of macaques and baboons have suggested that grunts given in the context of feeding, group movement, and close-range social interactions may have unique acoustic features (Owren et al. 1997; Rendall et al. 1999; Rendall 2003). In our study, grunts produced before infants were born rarely comprised more than one unit, whereas those emitted after the beginning of the birth season often included multiple units (see also Rowell & Hinde 1962; Bauers 1993). Furthermore, adult females received these multiple-unit grunts at much higher rates after they had an infant. Therefore, it is possible that infant-related grunts are acoustically distinct from grunts occurring in other contexts. Girneys, which were common during the birth season, were virtually nonexistent before infants were born. Although girneys were less frequent than

grunts (but see Blount 1985, for Japanese macaques), they tended to occur in very similar contexts. In fact, during the birth season, the two vocalizations often co-occurred in bouts that included multiple repetitions of both call types.

The visual orientation of the calling female during grunt and girney bouts suggests that most of these vocalizations were directed to mother–infant dyads. Aside from adult females and their infants, the most common recipients of grunts and girneys were yearlings and mother–yearling dyads. A small number of these vocalizations, particularly grunts, were also directed to adult males, and to subadults and juveniles. As individuals of any age/sex class can be the recipients of grunts and girneys, it is unlikely that these vocalizations reflect ‘comments’ on infants (e.g. Rowell et al. 1964; Brumm et al. 2005) or refer to a specific activity such as infant handling. It is possible, however, that the grunts and girneys directed to mother–infant dyads are acoustically different from other variants and are specific to infants or infant-related interactions.

When mother–infant dyads were in contact, it was difficult to discern whether the vocalizations were being directed to the mother or the infant. However, when infants were physically separated from their mothers, grunts and girneys were directed to infants in over 90% of the cases (see also Chevalier-Skolnikoff 1974; Green 1975). This finding contradicts the hypothesis that females direct these vocalizations to mothers to inform them of benign intentions toward their infants. The lack of significant effects of dominance rank on the rate of grunts and girneys emitted and received by adult females is also inconsistent with the benign intent hypothesis. This is because communication of benign intent can be interpreted as a form of appeasement, and appeasement signals in rhesus macaques are typically displayed by subordinates to dominants (e.g. Maestripieri & Wallen 1997). Within dyads, however, females directed more grunt and mixed bouts (but not girney bouts) to higher-ranking than to lower-ranking mothers and infants, and directed more girney bouts (but not grunt or mixed bouts) to distant than to close relatives. This is consistent with the notion that the exchange of vocalizations between adult females and mother–infant dyads might have been affected by the quality of the social relationships between the two females. However, it is also possible that calling females were more attracted to and more aroused by infants that were less accessible, such as the infants of high-ranking mothers and distantly related females, because of a

simple novelty effect. Age and parity had no significant effects on the rates of vocalizations emitted or received by adult females.

The benign intent hypothesis predicts that female grunts and girneys should be accompanied by approaches and followed by attempts to handle infants. To examine this, we investigated the behaviors that preceded and followed the calls within a short time interval. By examining which behaviors followed the last vocal unit of strings that included grunts or girneys, we found that less than 10% of vocalizations that were emitted from beyond 1 m of mothers or infants were followed by approaches to these individuals. Similarly, females initiated infant handling after fewer than 5% of the strings. This suggests that, at least in the particular circumstances considered in our analysis, grunts or girneys are unlikely to be associated with the behaviors predicted by the benign intent hypothesis. Moreover, when infant handling did occur, it was equally as likely to be benign or rough. In terms of behaviors directed toward mothers, study females rarely behaved aggressively toward these individuals after a vocalization string, and none of the initiated bouts of aggression that followed approaches were preceded by a call. The initiation of grooming was also relatively uncommon following approaches, but grooming episodes were significantly more likely to occur if females called after approaching (18.0% of approaches, on average) than if they did not vocalize (2.5%). The difference between these two conditions was more striking than in the study by Silk et al. (2000), in which calling only doubled the likelihood of occurrence of allogrooming (39% vs. 17% of approaches, on average). Grunts and girneys also occurred in situations in which the calling female was already in contact with the mother (8.7% of the vocalization strings) or in contact with or handling the infant (6.6% of the vocalization strings). In these situations, the calling female and the mother typically continued their ongoing interaction. However, in about half the cases in which the calling female began a new episode of infant handling after the vocalization, this handling was rough.

When taken together, our findings suggest that grunts and girneys are directed to infants and that they tend to be associated with a general friendly disposition toward the infant's mother. However, they do not appear to convey precise information about the caller's intentions or subsequent behavior to the mother or to the infant. This is because the caller's behavior following a grunt or girney was highly variable and, in many cases, these calls were

not followed by any social behavior at all (see also Rowell & Hinde 1962; Hinde et al. 1964; Rowell et al. 1964; Ransom 1971; Smuts 1985; Fischer & Hammerschmidt 2002). These results contradict the benign intent hypothesis (Silk et al. 2000) and are consistent with the nonrepresentational interpretation of grunts and girneys given by other authors (Owren et al. 2003; Rendall 2003).

Mothers' responses to grunts and girneys were generally consistent with the findings of a previous study (Silk et al. 2000). We found that when females approached mother-infant dyads, aggression received from mothers was uncommon, regardless of whether or not the female vocalized. However, a higher percentage of approaches with vocalizations were followed by infant handling (benign or rough) and by allogrooming of the mother than silent approaches. Submissive responses from the mother were also less likely to occur if approaches were accompanied by vocalizations than if they were not (see also Silk et al. 2000). The few cases in which the infant initiated contact with the calling female after an approach were also likely to be preceded by a vocalization.

Overall, these results indicate that that grunts and girneys allow females to gain access to infants and interact positively with their mothers, as previously suggested (Silk et al. 2000). Our results, however, show that grunts are more predictably associated with the responses of others, e.g. increased tolerance, than with the caller's subsequent behavior. This is consistent with Owren et al. (2003) and Rendall's (2003) nonrepresentational interpretation of these calls and not with the predictions of the benign intent hypothesis (Silk et al. 2000). Therefore, our results suggest that the calls do not contain encoded information about the caller's intentions and subsequent behavior, but rather that others are able to infer something about the general emotional or motivational disposition of the caller from its vocalizations. In other words, grunts and girneys may or may not have evolved as signals but they are almost certainly used as cues by mothers.

The hypothesis that grunts and girneys may be signals used to capture infants' attention and possibly to induce arousal (Owren et al. 2003; Rendall 2003) is consistent with the following observations: (1) these vocalizations are directed to infants and not to mothers; (2) another possible attention-getting or arousing signal, tail-wagging, often co-occurs with these vocalizations (tail-wagging is a rare behavior, which almost exclusively occurs during interactions with infants), (3) in at least some cases,

infants respond by orienting toward and approaching the caller, (4) the calls may or may not be followed by an attempt to interact with the infant or the mother, and (5) infant handling following the call may be benign or rough. We suggest that this hypothesis may be especially applicable to girneys, which seem to be more specific to interactions with infants than grunts and to have melodic acoustic features that are well distinct from any other vocalizations in the rhesus macaque repertoire. Therefore, we suggest that the acoustic structure of girneys may be adaptively designed to attract young infants and engage their attention (see also Owren et al. 2003), similar to how the acoustic structure of motherese, or baby talk, allows human adults to visually or socially engage with infants (e.g. Fernald 1992). Unlike humans, however, rhesus macaque females do not direct these vocalizations to their own infants.

Some of our results suggest that grunts and girneys may express infant-related arousal in the caller. Rhesus macaque females are clearly attracted to other females' infants and seem to become especially aroused when infants in a particular age range engage in specific activities. For example, although rhesus females do not appear to be highly attracted to newborn babies (e.g. of 0–4 wk of age; Gerald et al. 2006) which spend a considerable amount of time nursing or sleeping, they respond strongly to infants between 1 and 6 mo of age, which are much more active and independent (Gerald et al. 2006). Furthermore, adult females scratch themselves at high rates while observing infants breaking contact with their mothers and walking independently, or returning to their mothers after a short period of independent exploration (D. Maestripieri, pers. obs.). These are also the circumstances in which adult females are most likely to grunt to the infants (Rowell & Hinde 1962; Rowell et al. 1964). In fact, in the present study, females self-scratched at significantly higher rates following approaches to mothers and/or infants that were accompanied by vocalizations when compared with approaches without calls. The hypothesis that grunts and girneys express infant-related arousal would explain why macaque mothers do not vocalize to their own infants. Mothers are very familiar with their infants, but are aroused by the novelty and unfamiliarity of other females' infants.

Expressions of arousal such as scratching may not have been under selective pressure for their communicative function (Maestripieri et al. 1992) and the same may be true for grunts or girneys. Nevertheless, expressions of arousal might function as

cues for other individuals and elicit predictable responses. For example, mothers may respond with tolerance to females which become aroused by infants and vocalize because they have learned that these vocalizations are unlikely to be associated with behaviors that pose a significant risk. We suggest that the hypothesis that calls may function only as cues, and not as signals, is more likely to apply to grunts than to girneys because: (1) grunts given to infants are far more common and less acoustically distinctive than girneys, and (2) grunts are given in many other contexts (although they might be acoustically distinct from infant-related grunts) and in some cases do not appear to have clear recipients (see also Owren et al. 2003). Grunts appear to share many characteristics with scratching, another behavioral expression of arousal that lacks specificity of context and clear recipients. These characteristics argue against the hypothesis that grunts and scratching have been selected to serve a specific signaling function.

If our hypotheses concerning the nature and functional significance of grunts and girneys are correct, adult females emitting these vocalizations to another female's infant are expressing arousal as well as attempting to attract the attention of the infant or interact with it. According to these hypotheses, and consistent with the interpretation of these vocalizations proposed by Owren and Rendall (Owren et al. 2003; Rendall 2003), there is no specific information encoded in grunts or girneys, and these calls have no specific meaning. However, other individuals, such as mothers, have learned to interpret these calls as cues that the vocalizing female is aroused and is attempting to engage the infant, or more simply that the caller is unlikely to exhibit harmful behavior. As a result, the calls have the effect of increasing social tolerance in the mother and facilitating the exchange of friendly interactions between females in general. Thus, the attraction to other females' infants results in a relatively relaxed context of interaction where the main focus of attention is the baby. These infant-centered affiliative interactions, therefore, represent important opportunities for adult females to establish or strengthen their social bonds and may play an important role in the social dynamics within the group (see also Maestripieri 1994).

Acknowledgements

We are grateful to Breeane Geery for her help with data collection and to the staff of the Caribbean Primate Research Center on Cayo Santiago for their

assistance. We also thank Michael Owren and Drew Rendall for helpful comments on this manuscript. This research was supported by NIH grant K02-MH63097 to D.M., intramural funds from the University of Chicago, and the University of Puerto Rico, Medical Sciences Campus. This publication was made possible by grant number CM-5-P40RR003640 from the National Center for Research Resources (NCRR), a component of the National Institutes of Health (NIH). Its contents are solely the responsibility of the authors and do not necessarily represent the official views of NCRR or NIH.

Literature Cited

- Bauers, K. A. 1993: A functional analysis of staccato grunt vocalizations in the stump-tailed macaque (*Macaca arctoides*). *Ethology* **94**, 147–161.
- Bercovitch, F. B. & Berard, J. 1993: Life history costs and consequences of rapid reproductive maturation in female rhesus macaques. *Behav. Ecol. Sociobiol.* **32**, 103–110.
- Blount, B. 1985: 'Girney' vocalizations among Japanese macaque females: context and function. *Primates* **26**, 424–435.
- Brumm, H., Kipper, S., Riechelmann, C. & Todt, D. 2005: Do Barbary macaques 'comment' on what they see? A first report on vocalizations accompanying interactions of third parties. *Primates* **146**, 141–144.
- Call, J. & Tomasello, M. 2007: *The Gestural Communication of Apes and Monkeys*. Erlbaum, Mahwah, NJ.
- Cheney, D. L. & Seyfarth, R. M. 1997: Reconciliatory grunts by dominant female baboons influence victims' behaviour. *Anim. Behav.* **54**, 409–418.
- Cheney, D. L., Seyfarth, R. M. & Silk, J. B. 1995: The role of grunts in reconciling opponents and facilitating interactions among adult female baboons. *Anim. Behav.* **50**, 249–257.
- Chevalier-Skolnikoff, S. 1974: The ontogeny of communication in the stump-tail macaques (*Macaca arctoides*). *Contrib. Primatol.* **2**, 1–166.
- Darwin, C. 1872: *The Expressions of the Emotions in Man and Animals*. Murray, London.
- Dittus, W. J. 1984: Toque macaque food calls: semantic communication concerning food distribution in the environment. *Anim. Behav.* **32**, 470–477.
- Fernald, A. 1992: Human maternal vocalizations to infants as biologically relevant signals: an evolutionary perspective. In: *The Adapted Mind* (Barkow, J. H., Cosmides, L. & Tooby, J., eds). Oxford Univ. Press, New York, pp. 391–428.
- Fischer, J. & Hammerschmidt, K. 2002: An overview of the Barbary macaque, *Macaca sylvanus*, vocal repertoire. *Folia Primatol.* **73**, 32–45.
- Gerald, M. S., Waitt, C. & Maestriperi, D. 2006: An experimental examination of female responses to infant face coloration in rhesus macaques. *Behav. Process.* **73**, 253–256.
- Green, S. 1975: Variation of vocal pattern with social situation in the Japanese monkey (*Macaca fuscata*): a field study. In: *Primate Behaviour. Developments in Field and Laboratory Research* (Rosenblum, L. A., ed.). Academic Press, New York, pp. 1–102.
- Hall, K. R. L. & DeVore, I. 1965: Baboon social behavior. In: *Primate Behaviour: Field Studies of Monkeys and Apes* (De Vore, I., ed.). Holt, Rinehart & Winston, New York, pp. 53–110.
- Hauser, M. D. & Marler, P. 1993: Food-associated calls in rhesus macaques (*Macaca mulatta*): I. Socioecological factors. *Behav. Ecol.* **4**, 194–205.
- Hinde, R. A., Rowell, T. E. & Spencer-Booth, Y. 1964: Behaviour of socially living rhesus monkeys in their first six months. *Proc. Zool. Soc. Lond.* **143**, 609–649.
- Itani, J. 1963: Vocal communication of the wild Japanese monkey. *Primates* **4**, 11–66.
- Kapsalis, E. & Berman, C. M. 1996: Models of affiliative relationships among free-ranging rhesus monkeys (*Macaca mulatta*): II. Testing predictions for three hypothesized organizing principles. *Behaviour* **133**, 1235–1263.
- Krebs, J. R. & Davies, N. B. 1993. *An Introduction to Behavioural Ecology*, 3rd edn. Blackwell Science, Oxford.
- Lindburg, D. G. 1971: The rhesus monkey in North India: an ecological and behavioral study. In: *Primate Behaviour. Developments in Field and Laboratory Research* (Rosenblum, L. A., ed.). Academic Press, New York, pp. 1–106.
- Maestriperi, D. 1994: Influence of infants on female social relationships in monkeys. *Folia Primatol.* **63**, 192–202.
- Maestriperi, D. & Wallen, K. 1997: Affiliative and submissive communication in rhesus macaques. *Primates* **38**, 127–138.
- Maestriperi, D., Schino, G., Aureli, F. & Troisi, A. 1992: A modest proposal: displacement activities as an indicator of emotions in primates. *Anim. Behav.* **44**, 967–979.
- Martin, P. & Bateson, P. 1986: *Measuring Behaviour. An Introductory Guide*. Cambridge Univ. Press, Cambridge.
- Maynard Smith, J. & Harper, D. 2003: *Animal Signals*. Oxford Univ. Press, Oxford.
- Mori, A. 1975: Signals found in the grooming interactions of wild Japanese monkeys of the Koshima troop. *Primates* **16**, 107–140.
- Owren, M. J. & Rendall, D. 2001: Sound on the rebound: bringing form and function back to the forefront in understanding nonhuman primate vocal signaling. *Evol. Anthropol.* **10**, 58–71.

- Owren, M. J., Seyfarth, R. M. & Cheney, D. L. 1997: The acoustic features of vowel-like grunt calls in chacma baboons (*Papio cynocephalus ursinus*): implications for production processes and functions. *J. Acoust. Soc. Am.* **101**, 2951—2963.
- Owren, M. J., Rendall, D. & Bachorowski, J.-A. 2003: Nonlinguistic vocal communication. In: *Primate Psychology* (Maestripietri, D., ed.). Harvard Univ. Press, Cambridge, MA, pp. 359—394.
- Ransom, T. W. 1971: Ecology and social behavior of baboons (*Papio anubis*) at the Gombe National Park. PhD Thesis, Univ. California, Berkeley, CA.
- Rawlins, R. G. & Kessler, M. J. 1986: *The Cayo Santiago Macaques: History, Behavior and Biology*. State Univ. New York Press, Albany, NY.
- Rendall, D. 2003: The affective basis of referential grunt variants in baboons. *J. Acoust. Soc. Am.* **113**, 3390—3402.
- Rendall, D., Seyfarth, R. M., Cheney, D. L. & Owren, M. J. 1999: The meaning and function of grunt variants in baboons. *Anim. Behav.* **57**, 583—592.
- Rowell, T. E. & Hinde, R. A. 1962: Vocal communication by the rhesus monkey (*Macaca mulatta*). *Proc. Zool. Soc. Lond.* **138**, 279—294.
- Rowell, T. E., Hinde, R. A. & Spencer-Booth, Y. 1964: “Aunt”-infant interaction in captive rhesus monkeys. *Anim. Behav.* **12**, 219—226.
- Seyfarth, R.M., Cheney, D.L. & Marler, P. 1980: Vervet monkey alarm calls: semantic communication in a free-ranging primate. *Anim. Behav.* **28**, 1070—1094.
- Silk, J. B. 2002: Kin selection in primate groups. *Int. J. Primatol.* **23**, 849—875.
- Silk, J. B., Cheney, D. L. & Seyfarth, R. M. 1996: The form and function of post-conflict interactions between female baboons. *Anim. Behav.* **52**, 259—268.
- Silk, J. B., Kaldor, E. & Boyd, R. 2000: Cheap talk when interests conflict. *Anim. Behav.* **59**, 423—432.
- Silk, J. B., Rendall, D., Cheney, D. L. & Seyfarth, R. M. 2003: Natal attraction in adult female baboons (*Papio cynocephalus ursinus*) in the Moremi Reserve, Botswana. *Ethology* **109**, 627—644.
- Smith, W. J. 1977: *The Behavior of Communicating*. Harvard Univ. Press, Cambridge, MA.
- Smuts, B. B. 1985: *Sex and Friendship in Baboons*. Harvard Univ. Press, Cambridge, MA.