

Food-associated calls in rhesus macaques (*Macaca mulatta*): II. Costs and benefits of call production and suppression

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In field experiments, free-ranging rhesus macaques (*Macaca mulatta*) gave food-associated calls in 45% of the trials in which they were presented with food, either monkey chow or coconut; they did not call in control trials when sticks were presented. Consistent with prior naturalistic observations, adult females called in a higher proportion of trials than adult males. Coconut, one of the most highly preferred food items in the diet, elicited different call types and a higher rate of calling from "discoverers" than did chow. The call types produced to coconut (warbles, harmonic arches, and chirps) were primarily those that, under nonexperimental conditions, were associated with relatively rare and preferred foods. In contrast, coos and grunts were primarily produced in response to chow. The relative hunger level of the discoverer had no significant effect on the call type produced but did affect the rate of call production; discoverers called at higher rates when they were hungry. Upon hearing food-associated calls, individuals within the vicinity of the discovery responded by rapidly approaching the caller. A larger number of individuals approached when discoverers called than when they did not. Discoverers who failed to call received significantly more aggression from group members and, in the case of females, actually consumed less food than discoverers who called. The probability of receiving aggression did not appear to be associated with the discoverer's dominance rank. Results suggest that food-associated calls are "honest" signals reflecting food possession. Those who fail to signal and are caught with food are apparently punished. *Key words*: food-associated calls, honest signaling, ownership, punishment, referential signaling, rhesus monkeys, withholding information. [*Behav Ecol* 4:206-212 (1993)]

Theoretical discussions of animal communication have suggested that there are significant benefits associated with withholding information from other group members (Cheney and Seyfarth, 1990; Dawkins and Krebs, 1978; Hauser and Nelson, 1991; Krebs and Dawkins, 1984). This form of deception, it is claimed, should occur more frequently than active falsification (e.g., Caldwell, 1986; Møller, 1988, 1990; Munn, 1986) because it is more difficult to detect cheaters. Although this argument is logically convincing, there are at least two weaknesses with regard to empirical observations of signal suppression or withholding information. First, few studies have explicitly explored the costs and benefits associated with the failure to signal. In studies that have addressed this issue (e.g., Cheney and Seyfarth, 1985; Hauser, 1990; Marler et al., 1986, 1991), the economics of the behavior have been examined from either the signaler's point of view or the perceiver's, but rarely from both perspectives. Second, studies of withholding information are, by definition, studies of a nonresponse, raising methodological problems that have not been satisfactorily addressed in studies to date (but see Cheney and Seyfarth, 1990).

To assert that an animal has voluntarily suppressed signal production, as some studies have, one must establish that (1) the necessary conditions of signal production are present, and (2) the subject has detected and is responding to such conditions (e.g., an alarm call-withholding animal shows signs of detecting a predator, such as crouching or flee-

ing). For example, Hauser (1990) has shown that in wild chimpanzees (*Pan troglodytes*), females give copulation calls significantly more often when they are mating with older and higher-ranking males than when they are mating with younger, and presumably lower-ranking males. In the absence of information about the function of copulation calls or the mechanisms underlying their production (Hamilton and Arrowood, 1978), it is reasonable to assume that the conditions that typically cause a female to call are the same for old and young males, but that the costs and benefits of calling differ between males of different age or rank. Because females who suppress their copulation calls often display the facial expressions accompanying call production, it seems likely that at least some of the necessary conditions for voluntary signal suppression have been met.

In nonhuman primate studies, research on withholding information has focused on the social and ecological factors leading to call suppression. For example, Cheney and Seyfarth (1985) have demonstrated that in vervet monkeys (*Cercopithecus aethiops*), adult females are more likely to give alarm calls to a predator if they are with close kin than if they are with unrelated individuals, and adult males are more likely to give alarm calls if they are with adult females (i.e., potential mates) than if they are with other adult males (i.e., potential competitors). Hauser and colleagues (Hauser and Wrangham, 1987; Hauser et al., in press) have shown that captive chimpanzees are relatively quiet when they dis-

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cover small amounts of food, but call frequently when larger quantities of shareable food items are encountered. None of these studies, however, has explored the possibility that call suppression is costly, perhaps resulting in targeted aggression. Aggression is a likely consequence, especially when other group members would profit from shared information (e.g., increased encounter rate with food).

This report describes results from field experiments on the conditions leading to the production and suppression of food-associated calls in rhesus macaques (*Macaca mulatta*). Three factors guided the decision to look at this form of deception in the context of food. First, we have already described the contexts leading to the production of food-associated calls in this population of rhesus monkeys, including acoustic analyses of the calls emitted (Hauser and Marler, 1993). These data indicate that the production of food-associated calls is not a necessary consequence of encountering food. Rather, the production or suppression of food-associated calls seems to be affected by the caller's sex, social status, and hunger level, in addition to the type of food discovered. Second, food, as a stimulus, can be readily described and manipulated, and consequently, the costs and benefits of gaining access to it can be quantified. Third, it is possible to assess the voluntary nature of call suppression (i.e., a nonresponse) because the conditions leading to call production are known, and the discoverer's recognition of the conditions can be documented.

Based on our descriptive account of food-associated calls in rhesus monkeys, together with theoretical and empirical insights from research on withholding information (reviewed in Cheney and Seyfarth, 1990; Hauser and Nelson, 1991; Marler et al., 1991), experiments were designed to answer the following questions: (1) How do food quality and hunger level affect the calling behavior of the discoverer? (2) How does the discoverer's sex and dominance rank affect calling behavior? (3) How does the probability of being seen by other group members at the food source affect the discoverer's probability of calling? (4) How does the discoverer's calling behavior (i.e., call production or suppression) affect the behavior of other group members?

METHODS

Subjects and study area

We conducted experiments on rhesus monkeys living on the island of Cayo Santiago, Puerto Rico (18°09' N, 65°44' W) from August to October 1990. Cayo Santiago is a relatively small island (15 ha) that, geographically, is subdivided into two smaller islets or "cays." There are no predators on the island, and more than 50% of the monkeys' diet consists of Purina monkey chow. A large proportion of the mortality on the island can be accounted for by starvation and injury (Berard, 1990). The general population structure was comparable to that described in the companion paper, with the exception that each of the seven social groups increased slightly in size (range, 80–360 individuals). Group L, the focal group for these experiments, was the largest and most dominant on the island

and maintained almost exclusive access to the smaller of the two cays.

Experimental design

Subjects

A pilot study indicated that it was inefficient to select a target individual in advance because at the time of testing, we required that focal subjects (hereafter referred to as "discoverers") should be out of view from other group members, an unpredictable event. A more opportunistic approach resulted in a higher yield with regard to the number of subjects that could be sampled, given the amount of time spent searching. We only selected adult males or adult females, rejecting individuals who had been previously tested. We tested 28 adult males and 21 adult females (only 1 subject was tested per trial) for a total of 49 successful trials; 87 trials were aborted before stimulus presentation because 1 or more of our experimental conditions were not satisfied. The most frequent cause of trial abortion was the appearance of other group members within 10 m of the targeted discoverer.

Factors potentially affecting discoverers' behavior

Two variables were directly examined during our experiments: time of day and food quality. We conducted trials between 0600 and 0700 h or between 1300 and 1500 h. The first time block precedes the strongest peak in feeding activity (Hauser and Marler, 1993) and the delivery of chow into the dispensers. Consequently, individuals tested during this period were unlikely to have eaten during the previous 12–14 h. The second time block coincides with the end of the daily feeding activity, and, in general, chow has been depleted from all of the dispensers by the start of this period. During this study, chow was depleted from the dispensers at approximately 1135 h (SD = 25 min; $n = 65$ sampling days).

We selected two food items as stimuli: chow and coconut. Based on our naturalistic observations, coconut is a highly preferred food and of sufficient rarity on the island that competition for access to even small pieces is intense, often escalating to aggressive chases and subsequent injury. In a given trial, 15 pieces of chow or coconut were presented to the discoverer; each piece of food was about the same size as an average piece of chow (approximately $3 \times 6 \times 2$ cm). We decided to use 15 pieces of food because they could not all be carried away by one individual, and this was a sufficiently large quantity to allow for co-feeding by other group members. As a control, we used 15 wooden sticks, each piece approximating the dimensions of a piece of chow.

Protocol

Three observers were involved in each experiment and were all responsible for searching for an adult male or an adult female discoverer. For the morning time block, we began searching at 0600 h, and for the afternoon period at 1300 h. If no subject could be located by either 0650 h or 1450 h, the experimental session was aborted. Because trials lasted 20 min (see below), morning experiments were completed no later than 0710 h and afternoon experiments by 1510 h. Once an appropriate sub-

Table 1
Variables examined and sample sizes (number of trials) obtained during experiments

Variable	Number of trials		
	Sticks	Chow	Coconut
Time period			
AM	4	10	10
PM	5	10	10
Gender			
Males	7	11	10
Females	2	9	10

ject was located, one observer, responsible for videotaping the trial, moved approximately 10 m away from the discoverer and in a position that maximized visibility. A second observer positioned herself at a 90° angle between the discoverer and the video camera. This second observer was responsible for presenting either the chow, coconut, or sticks and subsequently for describing (into a dictaphone) all interactions occurring outside of the camera's range; stimuli were carried in an opaque box attached to the waist and then dropped from the box during the trial. The third observer was also responsible for obtaining data on interactions that occurred outside of the camera's range as well as notes on the discoverer and food-drop area; the latter included a schematic map of the experimental set-up with the relative positions of the observers, discoverer, and all other individuals within a 10-m radius. Observers two and three alternated roles between successive trials to diminish the possibility that animals would learn to associate the box, and therefore food, with a particular observer.

Once each observer was in position, the trial started with a 30-s baseline period. At the end of the baseline, the second observer approached the midpoint between the camera and discoverer, dropped the stimulus items, and then continued to walk in the same direction, stopping after approximately 5 m; in a majority of trials ($n = 45$), the observer's approach and stimulus presentation was sufficient to alert the discoverer to the food's presence. In two trials, the discoverer did not notice the food for approximately 2 min after the drop, whereas in two other trials, it was necessary after 5 min for the second observer to approach the food area a second time, thereby causing the discoverer

Table 2
Variables examined in relation to gender

Variable	Number of trials	
	Males	Females
Time period		
AM	15	9
PM	13	12
Rank		
Low	10	6
Middle-low	9	3
Middle-high	4	7
High	5	5

to orient to the stimulus. For these four trials, we considered drop time as the first indication that the discoverer could see the food. If the discoverer moved outside of the camera's range (e.g., some animals grabbed a few pieces of food and then ran away), then the other observers would follow him or her. The video record of the drop area continued until all of the food had been depleted and then shifted back to the discoverer. The trial ended 20 min after the stimulus item had been dropped. We alternated between trials with coconut and with chow, with controls evenly distributed throughout the experimental series.

Several factors likely to influence the discoverers' response to food were recorded but not systematically controlled. These factors included the discoverer's rank and sex and the identity of all individuals within a 10-m radius of the focal but out of sight. Dominance ranks were established on the basis of aggressive interactions occurring in nonexperimental periods and collected during 30-min focal follows. For most of the analyses presented, individuals were classified into one of four dominance rank categories: low, middle-low, middle-high, and high. In rhesus macaques on Cayo Santiago, adult males outrank adult females (Berard, 1990; Rawlins and Kessler, 1987).

Sex of the discoverer was the only independent variable for which we could make reasonable predictions regarding its effect on the discoverer's response. Specifically, based on our naturalistic observations of food-associated calls in rhesus monkeys (Hauser and Marler, 1993), we expected females to call more frequently than males. Although no a priori hypotheses were generated with respect to the other independent variables, we had reason to believe that at least some of these variables would interact with those directly manipulated. For example, if there are significant costs to attracting others to a rich food source (e.g., higher-ranking individuals supplanting or chasing lower-ranking individuals from the food), then low-ranking discoverers might be expected to call less frequently than high-ranking individuals. Because of the number of parameters considered in this experiment, we present a summary of the variables, respective sample sizes, and a subset of potentially relevant interactions that are considered using nonparametric and parametric statistics (Tables 1 and 2).

Video records of each trial were transcribed using a Panasonic editing deck and a timer. Subsequently, we consulted notes collected by the observers; these notes were particularly important in trials where the discoverer moved out of the camera's range or into an area of poor visibility.

Data collected during nonexperimental periods

When our test stimuli dropped out of the carrying box, they landed and spread out in a random pattern on the ground. We made 10 test drops with chow away from the rhesus population in order to obtain an estimate of the average spread of food. The average distance between pieces was 142 cm, which we judged to be ample for two or more individuals to feed together. We reasoned that if an individual called during an experimental session, thereby recruiting others to the area, they would be able to co-feed. To determine whether a discoverer finding 15 pieces of chow or coconut would

be able to pick up and run away with the entire food source, we collected observations on the amount of chow an individual could carry away from the dispensers. During 3 months of observation, we never observed an individual carrying more than eight pieces of chow away from the dispensers.

In addition to observations collected during the experimental period, each discoverer was also observed in a 20-min focal follow within 1 week of the trial; each of these follows occurred at approximately the same time of day as when the trial was conducted (i.e., an average of 63 ± 12 min from the start time of the trial).

Because the costs and benefits associated with the discoverer's behavior might vary with changes in the group's activities at different times of the day, particularly the relative level of aggression, we recorded observations of aggressive interactions in the week ($n = 6$ days) following the completion of our experiments. Specifically, from 0600 to 0700 h and from 1300 to 1500 h, observations of four classes of aggression [lunge, mild chase, intense chase, and chase with physical contact (e.g., biting, hitting)] between adults were scored using *ad libitum* sampling.

Significance testing was conducted with parametric and nonparametric statistics. Throughout, statistical significance was set at $p < .05$. For a number of analyses, we performed log transformations on the data set, and they have been indicated in the text.

RESULTS

Discoverers' responses to sticks, chow, and coconut

Upon seeing the sticks drop, discoverers never called, nor did they approach the drop area. In general, discoverers showed no interest in the sticks except for a brief orientation. Consequently, any response exhibited in the presence of chow or coconut must represent a response to food, rather than to the observers' presence or actions.

When discoverers noticed either chow or coconut, they typically scanned the area around them first and then moved toward the food. A two-factor ANOVA revealed that the latency to approach the drop area and feed was significantly shorter in the morning (mean = 9.4 s) than in the afternoon (mean = 11.5 s; $F = 4.70, p < .04$) and significantly shorter in response to coconut (mean = 7.8 s) than to chow (mean = 13.1 s; $F = 3.96, p < .05$). The interaction between food type and time of day was not statistically significant ($p > .05$).

Once discoverers approached the food, there was considerable variation among individuals with regard to the amount of time spent eating at the drop area as opposed to taking food and moving away. An ANOVA revealed that this variation was not related to time of day, food type, or dominance rank, but was significantly influenced by gender: males spent more time at the drop area (mean = 164.1 s) than females (mean = 29.4 s; $F = 9.49, p < .004$).

Discoverers also differed with regard to the total amount of food they consumed. On average, discoverers ate 4.9 pieces of food (SD = 2.3, range =

Table 3

Food-associated calls elicited by chow and coconut for males and females under experimental conditions

Call type	Number of calls given			
	Chow		Coconut	
	Males	Fe-males	Males	Fe-males
Warble	0	1	1	33
Harmonic arch	0	0	0	2
Chirp	0	0	0	15
Grunt	0	49	1	1
Coo	0	61	3	13

0.25–9.0); a mean of 1.4 pieces was eaten before the discoverer was detected by another group member, and 3.6 pieces were consumed after detection. Time of day, food type, and gender did not have statistically significant effects on the amount of food consumed.

Calling behavior of the discoverer

On 18 of the 40 trials where food was presented (45%), the discoverer produced at least one food-associated call. Females called in 15 of 19 trials and males called in 3 of 21 trials ($\chi^2 = 14.34, p < .0002$). Chow elicited calls in 8 trials and coconut in 10 trials. The latency to call following the drop was 31.0 s (SE = 4.3). There was no statistically significant difference in the latency to call for trials involving chow as opposed to coconut or in tests conducted in the morning as opposed to the afternoon. Latency to call was, however, significantly longer for males (mean = 77.3 s, SE = 40.1, $n = 3$) than for females (mean = 22.0 s, SE = 7.6, $n = 15$; $t = 2.37, p < .03$). In four trials, the discoverer called only before eating, in seven trials the calls were produced only after eating at least one piece of food, and in seven trials, the calls preceded and followed eating. Including data from males and females, the number of calls given was significantly higher in the morning (mean = 2.5 calls, SE = 0.48, $n = 7$) than in the afternoon (mean = 1.2 calls, SE = 0.2, $n = 11$; $F = 5.87, p < .03$) and significantly higher with coconut (mean = 16.1 calls, SE = 8.6) than with chow (mean = 3.3 calls, SE = 1.4; data log-transformed: $F = 4.98, p < .04$); the interaction term was not statistically significant. The discoverer's rank had no statistically significant effect on either the probability of giving at least one call or the number of calls given.

Table 3 presents the number of calls of each type given by males and females to chow as compared to coconut. Results from a two-factor ANOVA revealed that more warbles, harmonic arches, and chirps were elicited by coconut than by chow ($F = 4.17, p < .05$), but time of day had no significant effect. Grunts were given with chow and coconut in the morning and afternoon test sessions. Results from a two-factor ANOVA revealed no significant effect of food type or time of day on the production of grunts. When coos were produced, they preceded food consumption on five of the seven trials. A two-factor ANOVA failed to detect a significant

Table 4
Aggression toward discoverer as a function of calling behavior

Discoverer's vocal behavior	Aggression					
	Time (s)		No. of acts		No. of severe acts	
	Mean	SE	Mean	SE	Mean	SE
Male and female discoverers						
Call	0.3	0.1	0.3	0.1	0.2	0.1
No call	1.7	0.4	1.4	0.2	1.7	0.2
Female discoverers						
Call	0.3	0.1	0.4	0.1	0.2	0.1
No call	3.6	1.0	2.3	0.4	1.8	0.2

Data log-transformed.

effect of food type or time of day on the production of coos.

Response of other group members to the discoverer

In 37 out of 40 food trials, the discoverer was detected at the drop area by at least one other group member. Mean time to detection was 40.4 s (SD = 8.4). The average number of individuals detecting the discoverer was three (range = 1–17). Of those individuals who were first to detect the discoverer (i.e., first detectors), 24 were higher ranking and 11 were lower ranking. Discoverers who called were not detected more rapidly (mean = 39.9 s) than discoverers who were silent (mean = 34.2 s; $t = 0.50$, $p > .05$). This result is not surprising because we could not control for the number and social composition of nearby individuals. A greater number of individuals (mean = 4.8, SD = 2.6) approached vocal discoverers than silent discoverers (mean = 3.1, SD = 1.5; $t = 2.43$, $p < .05$).

There was considerable variation in the pattern of response exhibited toward discoverers by first detectors. First detectors who were lower ranking typically sat nearby the discoverer, either attempting to steal a piece of food, waiting for the discoverer to leave, or in five trials, recruiting support from higher-ranking animals to chase the discoverer away. Lower-ranking animals recruited support by screaming, which typically caused other individuals to approach the food area. First detectors who were high ranking, in contrast, supplanted the discoverer in 18 of 24 trials and were physically aggressive toward the discoverer in five trials; such aggression typically involved a chase and physical contact. Individuals who appeared after the first detector tended to be significantly more aggressive and were generally responsible for a majority of aggressive acts targeted at the discoverer.

To determine why some discoverers received aggression and others did not, three measures of aggression were used: total amount of time the discoverer received aggression (regardless of the type of aggression; data log-transformed), number of aggressive acts received, and number of severe aggressive acts received (i.e., biting, hitting, tackling the subject and rolling him or her). Using a two-factor ANOVA, none of these types of aggression were affected by the discoverer's sex or by time of

day. High-ranking male discoverers in the top 10% of the hierarchy ($n = 4$) received no aggression, and the other rank classes did not differ statistically.

Aggression by detectors was most significantly related to the calling behavior of discoverers. Specifically, discoverers who gave at least one food-associated call, excluding coos (Hauser and Marler, 1993), received less aggression than those who did not call (Table 4); because of the relatively high variance in levels of aggression between trials, data were log-transformed for statistical testing. This relationship was statistically significant for the total amount of time receiving aggression ($t = 2.84$, $df = 38$, $p < .007$), total number of aggressive acts ($t = 2.30$, $df = 38$, $p < .03$), and total number of severe acts of aggression ($t = 2.55$, $df = 38$, $p < .02$). Restricting the data to females, the primary callers in these experiments, analyses revealed that vocal discoverers received less aggression ($t = 5.9$, $df = 17$, $p < .0001$), fewer acts of aggression ($t = 5.5$, $df = 17$, $p < .0001$), and fewer severe acts of aggression ($t = 5.9$, $df = 17$, $p < .0001$) than silent discoverers. The differences in aggression are especially striking given the fact already noted that more individuals approached vocal than silent discoverers.

When discoverers were detected by higher-ranking group members, their calling behavior was related to the amount of food consumed. Specifically, females who produced at least one food-associated call ate more food (mean = 4.9 pieces, $n = 15$) than females who did not call (mean = 2.8 pieces, $n = 4$; $F = 3.07$, $p < .05$), and this effect was not influenced by the type of food presented ($p > .05$); given the small number of vocal male discoverers, statistical tests could not be conducted. One reason why vocal discoverers ate more food than silent discoverers was because the latter received more aggression and often dropped pieces of chow or coconut while they were being chased. In three trials, females who were being chased pulled food out of their cheek pouches and dropped it in front of the higher-ranking animal in pursuit, after which the aggressor stopped chasing the discoverer.

On average, the amount of food eaten by animals arriving after the discoverer was 9.4 pieces per trial (SD = 3.6) and 1.7 pieces (SD = 0.9) per individual. Because of the large number of individuals within group L (> 350) and the lack of data on individuals within hearing distance of the discoverer, it is not possible to calculate the expected frequencies of

food pieces obtained. As an alternative, we looked at the average number of pieces obtained per individual per trial. Kin obtained less food (mean = 0.6) than nonkin (mean = 2.8; $t = 8.50$, $df = 39$, $p < .0001$). Because males typically have few relatives within the social group, analyses were rerun considering trials with female discoverers: kin obtained less food (mean = 1.3) than nonkin (mean = 3.3; $t = 3.95$, $df = 18$, $p < .001$). Moreover, kin did not obtain more food when females called (mean = 1.4) than when they were silent (mean = 1.0; $t = 0.63$, $df = 17$, $p = .54$).

In contrast to the vocal behavior of discoverers, in only three trials (all involving coconut) did other individuals arriving at the drop area give food-associated calls. Moreover, and in contrast to silent discoverers, we observed extremely little aggression targeted at other individuals who obtained food. Because discoverers were the only subjects being followed intensively, however, we cannot be certain that our sampling procedures did not result in an underestimate of aggression levels received by other group members.

Control data during nonexperimental period

During the 20-min nonexperimental control trials on the same subjects, individuals received significantly less aggression (mean = 0.37 acts) than during experimental trials (mean = 2.68 acts; $t = 4.02$, $p < .0001$). Moreover, only two cases of severe aggression were observed during control trials as compared to 48 during experimental trials. In the post-experimental period, observations revealed that the level of aggression in the morning (0.43/min) was not significantly different from that exhibited in the afternoon (0.46/min). Thus, it seems unlikely that the difference in calling rate between morning and afternoon was due to a difference in the probability of receiving aggression.

With the exception of two adult males, all individuals tested during experimental conditions produced at least one food-associated call during nonexperimental encounters with food. Thus, it seems unlikely that tests were being conducted on populations of callers and noncallers that also differed consistently in the frequency of aggression they received. Nonetheless, a more rigorous assessment of the hypothesis that noncalling food discovery is associated with heightened aggression by detectors would involve repeated trials with the same individuals.

DISCUSSION

Naturalistic observations of rhesus macaques on Cayo Santiago indicate that adult males and adult females produce a complex of vocal signals upon discovering food (Hauser and Marler, 1993). Results from our field experiments support this finding. Individuals discovering chow tended to produce coos and grunts. In contrast, warbles, harmonic arches, and chirps were primarily given in response to the more highly preferred coconut. In addition, the rate of food-associated calls was influenced both by hunger and food quality: the highest call rate was recorded from hungry animals discovering coconut and the lowest rate from relatively satiated animals finding chow. Sex of the

discoverer also had a significant effect on the production of food-associated calls. Adult females called significantly more than adult males. Finally, rank did not appear to have a significant effect on either the rate or probability of call production. These results provide additional support for the view (Hauser and Marler, 1993) that rhesus monkeys produce some food-associated calls that are functionally referential (*sensu* Marler et al., 1992).

There were also significant costs and benefits associated with the discoverer's calling behavior. Of those discoverers who were detected by other group members, there was less aggression toward vocal discoverers than toward silent discoverers. Among female discoverers, those who called obtained more food than those who were silent. Finally, discoverers who were not detected by other group members ate more food than discoverers who were detected. The sample size of undetected discoverers was, however, small.

Results suggest that whether a rhesus monkey produces food-associated calls depends on at least two factors: gender and the probability of receiving aggression. In general, females are more likely to call than are males. This difference may be due in part to the fact that in rhesus monkeys, as in many other nonhuman primate species, adult males outrank adult females, and consequently females are more likely to receive aggression.

What can be said about the function of food-associated calls in rhesus monkeys and the conditions that lead to their production as opposed to suppression? One interpretation of our data would be that call production represents an "announcement" of food possession or ownership. Recent research on captive long-tailed macaques (*Macaca fascicularis*; Kummer and Cords, 1991) indicates that ownership of a food item is dependent on the current owners' spatial relationship (i.e., proximity) to the item as well as its relationship to observant rivals. Specifically, individuals who were closer to the food item were more likely to maintain possession, whereas offspring were most likely to rob their mothers, and older males were most likely to be robbed by younger males. Kummer and Cords (1991) suggest that such ownership cues provide a foundation upon which conflict, involving various forms of asymmetry, is settled.

Our observations of rhesus vocal behavior in the context of food discovery fit well with the results presented by Kummer and Cords (1991). Specifically, if calls reflect possession, then in the absence of calling (i.e., failure to announce possession), individuals detected with food would be more likely to receive aggression. Consequently, silent discoverers would, on average, obtain less food. Differences in calling behavior between males and females also fit with this interpretation. Because males are less likely to be challenged over food possession than females, they would be expected to call less frequently. Confirmation or falsification of this hypothesis will require experimental manipulations of the discoverer's audience (*sensu* Marler et al., 1991) to determine how the identity of potential competitors influences calling behavior. Observations of audience effects would also enable us to explore the possibility that individuals intentionally (see Cheney and Seyfarth, 1990, for a review) withhold information from conspecifics.

Silent discoverers who were detected by other group members received significantly more aggression than vocal discoverers, and the aggression received was often severe, leading to injury. Nonetheless, a relatively high proportion (i.e., 55%) of all discoverers failed to call in the context of a rich food source. Thus, it seems that some individuals were attempting to obtain all of the food, even though the probability of detection and subsequent aggression was high. This suggests that the costs of detection are insufficient to deter call suppression, that some individuals have more to gain by calling than others, or that both factors figure into the final decision. Because so little is known about the functional constraints on deception (Grafen, 1990), it is difficult to establish whether the frequency of food-associated call suppression by rhesus monkeys on Cayo Santiago is within or outside of the theoretically expected range. Theoretical attention to these issues would help to sharpen our predictions about the probable limits on deception. Such theory would, in turn, serve to guide empirical investigations attempting to provide more quantitative measures of the costs and benefits of signaling behavior, both during deception and in honest usage.

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REFERENCES

- Berard J, 1990. Life histories of rhesus macaque males (PhD dissertation). Eugene: University of Oregon.
- Caldwell R, 1986. The deceptive use of reputation by stomatopods. In: Deception: perspectives on human and nonhuman deceit (Mitchel RW, Thompson NS, eds). Albany: State University of New York Press; 129-145.
- Cheney DL, Seyfarth RM, 1985. Vervet monkey alarm calls: manipulation through shared information? Behaviour 94:150-166.
- Cheney DL, Seyfarth RM, 1990. How monkeys see the world: inside the mind of another species. Chicago: Chicago University Press.
- Dawkins R, Krebs JR, 1978. Animal signals: information or manipulation. In: Behavioral ecology (Krebs JR, Davies NB, eds). Oxford: Blackwell; 282-309.
- Grafen A, 1990. Biological signals as handicaps. J Theor Biol 144:475-546.
- Hamilton WJ, Arrowood PC, 1978. Copulatory vocalizations of chacma baboons (*Papio ursinus*), gibbons (*Hyplobates hoolock*) and humans. Science 200:1405-1409.
- Hauser MD, 1990. Do chimpanzee copulatory calls incite male-male competition? Anim Behav 39:596-597.
- Hauser MD, Marler P, 1993. Food-associated calls in rhesus macaques (*Macaca mulatta*): I. Socioecological factors. Behav Ecol 4:194-205.
- Hauser MD, Nelson DA, 1991. 'Intentional' signaling in animal communication. Trends Ecol Evol 6:186-189.
- Hauser MD, Teixidor P, Field L, Flaherty R, in press. Food-elicited calls in chimpanzees: effects of food quantity and divisibility. Anim Behav.
- Hauser MD, Wrangham RW, 1987. Manipulation of food calls in captive chimpanzees: a preliminary report. Folia Primatol 48:207-210.
- Krebs JR, Dawkins R, 1984. Animal signals: mind-reading and manipulation. In: Behavioral ecology (Krebs JR, Davies NB, eds). Sunderland, Massachusetts: Sinauer Associates; 380-402.
- Kummer H, Cords M, 1991. Cues of ownership in long-tailed macaques, *Macaca fascicularis*. Anim Behav 42: 529-549.
- Marler P, Duffy A, Pickert R, 1986. Vocal communication in the domestic chicken. II. Is a sender sensitive to the presence and nature of a receiver? Anim Behav 34: 194-198.
- Marler P, Evans CE, Hauser MD, 1992. Animal vocal signals: reference, motivation, or both? In: Nonverbal vocal communication: comparative and developmental approaches (Papoušek H, Jürgens U, Papoušek M, eds). Cambridge: Cambridge University Press; 66-86.
- Marler P, Karakashian S, Gyger M, 1991. Do animals have the option of withholding signals when communication is inappropriate? The audience effect. In: Cognitive ethology: the minds of other animals (Ristau C, ed). Hillsdale, New Jersey: Lawrence Erlbaum Associates; 135-186.
- Møller AP, 1988. False alarm calls as a means of resource usurpation in the great tit, *Parus major*. Ethology 79: 25-30.
- Møller AP, 1990. Deceptive use of alarm calls by male swallows, *Hirundo rustica*: a new paternity guard. Behav Ecol 1:1-6.
- Munn C, 1986. Birds that 'cry wolf.' Nature 319:143-145.
- Rawlins RG, Kessler MJ, 1987. The Cayo Santiago macaques. New York: SUNY Press.