

Costs of deception: Cheaters are punished in rhesus monkeys (*Macaca mulatta*)

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ABSTRACT From a functional perspective, deception can evolve in animal populations but should be constrained by the costs associated with detection. It then follows that withholding information should be more prevalent as a form of deception than active falsification of information because of the relative difficulties associated with detecting cheaters. Empirical studies of deception have focused on the benefits of cheating but have provided no data on the costs associated with being detected as a cheater. I present results from field experiments on rhesus monkeys (*Macaca mulatta*) which show that individuals discovering food announce their discoveries by calling on 45% of all trials. Discoverers who failed to call, but were detected with food by other group members, received significantly more aggression than vocal discoverers. Moreover, silent female discoverers ate significantly less food than vocal females. This demonstrates that there are significant costs to withholding information. Such costs may constrain the frequency with which deception occurs in this and other populations.

Theoretical treatments of animal communication (e.g., refs. 1–4) suggest that withholding information from other group members can lead to substantial fitness gains. This form of deception, it is claimed, should occur more frequently than active falsification because it is more difficult to detect cheaters. However, studies of deception in nonhuman animals (5–10) have not provided evidence of the costs associated with cheating. Consequently, we have little understanding of the factors that constrain the frequency of deception. This paper provides experimental data on the costs of deception in a free-ranging monkey.

Under nonexperimental conditions, rhesus monkeys (*Macaca mulatta*) on Cayo Santiago, Puerto Rico, produce a complex of five acoustically distinct calls upon discovering food (Fig. 1). Call production, however, is not a necessary consequence of encountering food. Rather, production or suppression of food-associated calls is affected by gender and the number of closely related kin: females call more (mean = 0.10 call per hr) than males (mean = 0.03 call per hr; $t = 3.78$, $df = 20$, $P < 0.001$), and females with large matriline call more than females with small matriline ($\rho = 0.81$, $n = 6$, $P < 0.05$).

Experiments were conducted on a group (L) of free-ranging rhesus macaques on Cayo Santiago. Over 50% of the diet comes from provisioning (i.e., chow). The remaining portion of the diet is made up of natural foliage, fruits (e.g., coconut), insects, and soil (12). Within the confines of the island (15 ha), movement is unrestricted and, consequently, males transfer between groups. There are no predators on the island (12).

Experiments were conducted on 28 adult males and 21 adult females, including high-, middle-, and low-ranking individuals; only one trial was conducted per individual. Three observers were involved in each experiment. One

observer, positioned ≈ 10 m away from the discoverer, was responsible for videotaping the trial. A second observer positioned herself at a 90° angle between the discoverer and the video camera and was responsible for dropping one of the food or control stimuli in front of the discoverer and then moving 10 m away. Both the second and third observers provided data on interactions occurring outside of the camera's range. The trial started with a 30-sec baseline period and continued for 20 min thereafter. The presentation of stimuli alternated between trials. Individuals were tested when they were > 10 m from other group members and, from our perspective, hidden from view; on Cayo Santiago, individuals often forage at a distance of 10 m from other group members and this is particularly the case prior to the dispensation of chow and in the late afternoon. All trials were transcribed to quantify the behavioral response.

Three variables were explicitly examined for their effects on call production: time of day, food quality, and gender. Trials were conducted either between 0600 and 0700 or between 1300 and 1500. The first time block precedes the strongest peak in feeding activity and the delivery of chow into the dispensers. Consequently, individuals tested during this period were unlikely to have eaten during the previous 10–12 hr. The second time block occurs after $\approx 80\%$ of the day's feeding has been completed and, in general, a majority of the chow has been depleted from the dispensers.

The two food items were chow and coconut. 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 dropped from an opaque bag, ≈ 5 m from the targeted discoverer; each piece of food was approximately the same size and standardized to an average piece of chow (i.e., $3 \times 6 \times 2$ cm). As a control, 15 sticks of wood were presented, each piece approximating the dimensions of a piece of chow.

Upon seeing the sticks drop, discoverers ($n = 9$) never called nor did they approach the drop area. When discoverers noticed either chow ($n = 20$) or coconut ($n = 20$), they typically scanned the area around them for ≈ 2.0 sec (range, 0.0–5.5), apparently to assess the social composition of nearby individuals, and then moved toward the food. On average, discoverers ate 4.9 pieces of food ($SD = 2.3$; range, 0.25–9.0). Time of day, food type, gender, and dominance rank did not have a statistically significant effect on the amount of food consumed.

On 18 of the 40 food trials (45%), the discoverer produced at least one food-associated call. Females called ($n = 15$ trials) significantly more often than males ($n = 3$ trials; $\chi^2 = 14.34$, $P < 0.0002$); calls were given in response to chow on 8 trials and to coconut on 10 trials. Results from a two-factor ANOVA revealed that call rate was significantly higher in the morning (mean = 2.5, $n = 7$) than in the afternoon (mean = 1.2, $n = 11$; $F = 5.87$, $P < 0.03$) and significantly higher to

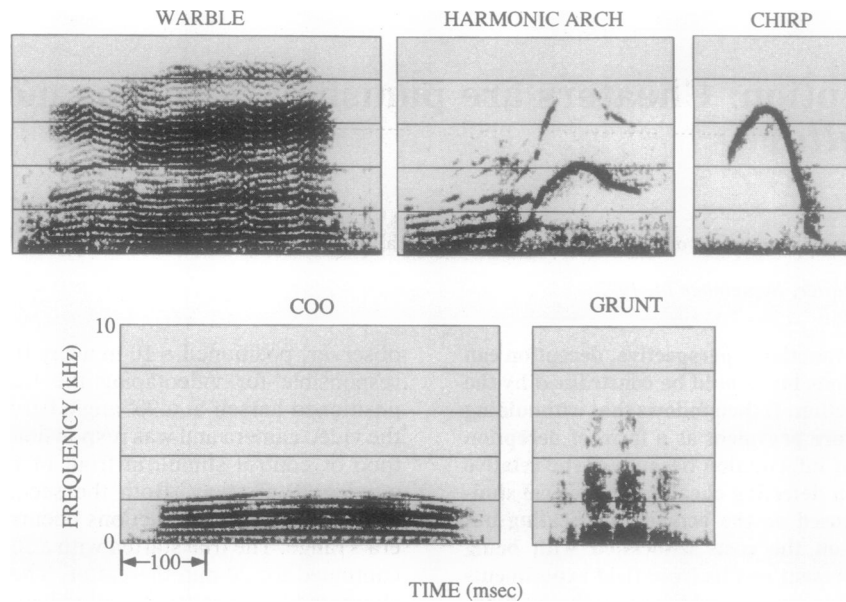


FIG. 1. Audiospectrograms of food-associated calls produced by adult rhesus monkeys on Cayo Santiago; the x-axis represents time in milliseconds and the y axis represents frequency in kilohertz. Warbles, harmonic arches, and chirps are given by individuals who are in possession of food, and typically, when the food item is rare and highly preferred within the diet (e.g., coconut or corn). Coos and grunts are given in both food and nonfood contexts. For coos, there are no acoustically significant differences between exemplars produced in food and nonfood contexts, whereas for grunts, significant differences exist (11).

coconut (mean = 16.1) than to chow (mean = 3.3; data log transformed: $F = 4.98$, $P < 0.04$); the interaction term was not statistically significant. With female discoverers, dominance rank had no statistically significant effect on either the probability of calling or call rate.

The discoverer was detected (i.e., seen at the food drop area) by at least one other group member in 37 out of 40 food trials. Among the first individuals to detect the discoverer, 24 were higher ranking and 11 were lower ranking. Discoverers were detected, on average, within 40.4 sec (SD = 8.4) of the food drop. The mean number of individuals detecting the discoverer was 3.0 (range, 1–17). Vocal discoverers were not detected more rapidly (mean = 39.9 sec) than silent discoverers (mean = 34.2 sec; $t = 0.50$, $P > 0.05$), but a greater number of individuals (mean = 4.8) approached vocal discoverers than silent discoverers (mean = 3.1; $t = 2.43$, $P < 0.05$). Because females with large matriline call at a higher rate to naturally discovered food than females with smaller matriline (see above), one might expect vocal discoverers to recruit more kin than non-kin. However, results from these experiments reveal that vocal discoverers were approached by a greater number of non-kin (mean = 4.1) than kin (mean = 0.7; $t = 5.00$, $P < 0.0001$).

When the first detectors were lower ranking than the discoverer, they either sat near the food area ($n = 6$ trials) or recruited coalition support against the discoverer by scream-

ing ($n = 5$ trials). In cases where coalition support was obtained, discoverers were chased away. When first detectors were higher ranking, they supplanted the discoverer on 18 of 24 trials and were physically aggressive toward the discoverer on 5 trials; such aggression typically involved a chase and, on 2 trials, 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.

Why did some discoverers receive aggression whereas others did not? Neither the discoverer's gender nor the time of day had statistically significant effects on the duration of aggressive behavior or the number of severe aggressive acts (e.g., biting, hitting, rolling). High-ranking male discoverers ($n = 4$) in the top 10% of the hierarchy received no aggression, and the other rank classes did not differ statistically.

The calling behavior of discoverers was the most significant predictor of the probability and intensity of aggression received (Fig. 2). Specifically, discoverers who gave at least one food-elicited call received less aggression than those who did not call. This relationship was statistically significant for the total amount of time receiving aggression ($t = 2.84$, $df = 38$, $P < 0.007$) and the total number of severe acts of aggression ($t = 2.55$, $df = 38$, $P < 0.02$). If the data are restricted to females, one finds that vocal discoverers, in contrast to silent discoverers, received significantly less

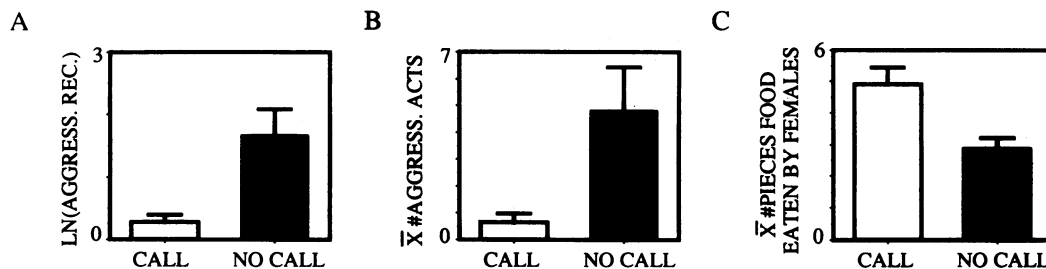


FIG. 2. (A) Logarithmic transform of the amount of time vocal and silent discoverers received aggression from group members. (B) Average number of aggressive acts (i.e., bites, hits, grab and shake, and chases) received by vocal and silent discoverers. (C) Average number of pieces of food obtained by female discoverers. Standard deviations are shown in A–C, where the open bars represent discoverers who called, and the solid bars represent silent discoverers.

aggression ($t = 5.85$, $df = 17$, $P < 0.0001$) and fewer severe aggressive acts ($t = 4.46$, $df = 17$, $P < 0.0003$). The differences in aggression are especially striking given the previously described observation that more individuals approached vocal discoverers than silent discoverers. For females, differences in calling behavior had a significant effect on food consumption. Specifically, vocal females ate more food (mean = 4.9 pieces) than silent females (mean = 2.8 pieces; $t = 3.07$, $P < 0.05$) because silent females often dropped pieces of chow or coconut while they were being chased. Females who were being chased sometimes ($n = 3$ trials) pulled food out of their cheek pouches and dropped it in front of the higher-ranking animal in pursuit. Apparently as a result, the aggressor stopped chasing the discoverer.

Although a significant amount of aggression was directed at silent discoverers, subsequent individuals who obtained food, but did not call, received little aggression. In fact, only three nondiscoverers gave food-associated calls and only four cases of aggression to nondiscoverers were observed. The difference in aggression was not due to differences in the number of individuals who were in close proximity to the discoverer as opposed to nondiscoverers. Thus, individuals appeared capable of detecting the discoverer amidst a group of individuals with food.

One interpretation of the results presented is that within the rhesus population observed, there are "callers" and "non-callers." However, observations revealed that during naturally occurring encounters with food, all but one adult male failed to produce at least one food-associated call. Consequently, it seems unlikely that individuals can be classified *a priori* as vocal or silent. Repeated trials with the same individual will be necessary to test this hypothesis more directly.

In conclusion, both natural observations and field experiments reveal that adult rhesus monkeys on Cayo Santiago often call when discovering a rich food source, and females are more likely to call than males. Because vocal discoverers receive less aggression than silent discoverers, calling in the context of food may represent an announcement of "ownership," a convention which is generally upheld in the population. Ultimately, however, whether an individual calls or not appears to be based on a relatively complex assess-

ment of the costs and benefits of obtaining food as opposed to receiving aggression from group members. From an evolutionary perspective, the costs associated with the failure to call are likely to constrain the frequency of this form of deception. Future research will need to establish (i) how factors such as food quality and quantity affect the probability of calling and (ii) which members of the population, if any, are responsible for "policing" those who attempt to cheat (13) by carrying out silent discoveries.

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