

BRIEF REPORT

Who Cares Who Calls? Selective Responses to the Lost Calls of Socially Dominant Group Members in the White-Faced Capuchin (*Cebus Capucinus*)

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In many social mammals and birds, soft vocalizations are habitually produced during dispersed moving and foraging, the function being to maintain contact and regulate spacing between group members. In some species, much louder calls are given sporadically by specific individuals when they become separated from the group, or 'lost'. The function of these calls has seldom been specifically tested, particularly among social primates, but is often assumed to involve regaining contact with the group based on a combination of individually distinctive calls and antiphonal responses to them from within the group. To test these assumptions, we conducted research on two groups of white-faced capuchins (*Cebus capucinus*) in Costa Rica. We analyzed 82 bouts of 'lost' calls given by 13 different adult individuals when separated from the group and the antiphonal responses they elicited. Lost calls were individually distinctive and were answered in 35% of calling episodes. Answers were selective: dominant males and females were answered more than were subordinate callers of either sex. As a result, dominant callers relocated and returned to the group more quickly than did subordinate callers. We discuss the potential proximate motivations for, and ultimate benefits of, such selective answering of dominant group members. *Am. J. Primatol.* 69:1–9, 2007. © 2007 Wiley-Liss, Inc.

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INTRODUCTION

Vocalizations that researchers frequently label *contact* calls are found in many species of mammals. In primates, they include relatively soft, harmonically structured vocalizations produced at high rates by all group members while

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moving and foraging, often through dense vegetation where there is some risk of becoming separated from the main body of the group [e.g., Hauser, 1991; Palombit, 1992]. They also include loud and sometimes harsh calls that are given less frequently by specific individuals when they actually become separated from the group, or 'lost', and that are often referred to more specifically as lost calls [e.g., Fischer et al., 2001]. Both types of call are hypothesized to serve a contact function, either by maintaining general group cohesion and spacing while moving and foraging, or by facilitating the return of lost individuals to the main body of the group. The proximate mechanisms subserving the contact function in each case are not entirely clear [Cheney et al., 1996; Rendall et al., 2000]. However, given the strongly individualized social relationships that characterize many primate groups, it is generally proposed that a contact function is facilitated in both situations by vocalizations that are individually distinctive: such calls would allow others nearby to modulate their tendency either to approach or to avoid unseen others while foraging, depending on their social relationships with the caller, and thereby minimize resource competition [Boinski, 1993]. Individually distinctive calls also would potentially allow others to respond selectively to the calls of particular group members who are lost [Cheney et al., 1996; Rendall et al., 2000].

Consistent with this proposal, individual differences have been documented in the structure or patterning of both variants of contact vocalization in a number of primate species [Hauser, 1991; Macedonia, 1986; Mitani et al., 1996; Rendall et al., 1998], and several studies have shown that listeners can discriminate among the calls of different individuals, responding more strongly to those of close kin and offspring, for example [Fischer et al., 2000; Rendall et al., 1996, 2000]. There are also a small number of reports of antiphonal calling, cases in which the contact calls of lost individuals elicit answering calls from other members of the group [Biben, 1993; Snowdon et al., 1983; Waser, 1977]. However, such reports are rare.

In this brief report, we present a study of a loud variant of contact call produced by white-faced capuchins (*Cebus capucinus*). Previous studies of capuchins have confirmed that these monkeys produce a "loud arrawh" or "lost whistle" vocalization when they lose sight of the group [Di Bitetti, 2001; Oppenheimer, 1968; Robinson, 1982]. In this report, we focus on the potential cues to individual identity in these calls (hereafter referred to as lost calls) and we test a number of social effects both on calling behavior and on antiphonal responses.

MATERIALS AND METHODS

Study Site and Observations

Data were collected in Santa Rosa National Park, Costa Rica from May to July 2002 and from January to June 2003. The park is located within a larger conservation area known as the Area de Conservacion Guanacaste and consists of 108 km² of tropical dry rainforest located 35 km Northwest of Liberia, Guanacaste [Fedigan & Jack, 2004]. Research was conducted on two habituated groups of white-faced capuchins that are part of a long-term study. The two groups, Cerco de Piedra Group (CP) and Los Valles (LV), each had 18 members. Data collection focused on lost calls produced by adults in both groups ($N = 19$).

Data collection involved making high-quality recordings of all vocalizations and collecting continuous data on associated behaviors using the sequence sample method [Lehner, 1996]. Vocalizations were recorded using a Sony

WM-D6C (Sony Canada, Inc.) recorder and a Sennheiser (Sennheiser Canada, Inc.) ME66 directional microphone. Recordings were subsequently digitized to a Macintosh iBook computer with 16-bit accuracy at a sampling rate of 44.1 kHz.

Acoustic and Behavioral Analysis

Lost call recordings were analyzed using the PRAAT[©] acoustic analysis software [Version 4.1.9, Boersma & Weenink, 2005]. We measured the duration of each recorded bout of calling and of each call within a bout as well as the intensity envelope of each call. For each call, we made a qualitative assessment of its relative harshness or tonality from spectrogram displays (256-point fast Fourier transform) using a five-point scale (1 = harsh to 5 = tonal). We also used linear predictive coding (LPC) [see, Owren & Bernacki, 1998, for an introduction to LPC] to identify broad spectral peaks in each call. (See Digweed et al. [2005] for more detailed descriptions of acoustic analysis methods.)

We then used discriminant function analysis [Klecka, 1980] to test for consistent differentiation in the features of lost calls as a function of the caller's individual identity, sex, and social rank. We used χ^2 and analysis of variance statistics to test for potential effects of caller sex and social rank on several aspects of calling behavior and its functional consequences. We also examined the likelihood that calls would elicit antiphonal responses, operationalized in the field as an answering call from an individual in the main body of the group during the course of a calling episode from a focal animal separated from its group. We defined separation as being more than 100 m from the main body of the group and out of visual contact. In both types of analysis, social rank was operationalized categorically with α and β individuals of each sex defined as 'dominants' and all other individuals defined as 'subordinates' reflecting the clear delineation of α and β rank positions in these capuchins but the comparatively loose and dynamic nature of dominance relationships below the β rank. Dominance relationships were quantified using the pattern of approach-retreat interactions and the direction of submissive signals in other dyadic interactions. The dominant females in both study groups had occupied these positions for 5–15 years and the dominant males for 2–10 years (Fedigan, unpublished).

RESULTS

We recorded 155 lost calls from 13 adults that represented 82 separate bouts of calling from 73 different episodes in which an individual became separated from the group and called. Bouts contained from one to seven calls (mean = 1.89; SD = +1.27). Individual calls had an average duration of 601 ms (SD = 246 ms). Most calls were atonal and covered a broad frequency range. Many also showed a strong peak in the frequency spectrum at approximately 1,100 Hz that appeared to represent a high-frequency, quasi-periodic voice fundamental (see Fig. 1).

Discriminant analysis on the complete set of 155 calls revealed clear cues to caller identity. The overall Wilks' λ (0.01) summarizing individual differentiation in lost call structure was close to zero and statistically significant when evaluated using the χ^2 distribution ($\chi^2 = 322.57$, $P < 0.01$). It was also associated with an eigenvalue of 3.46, considerably exceeding the threshold value of 1.0 that indicates greater variation between than within individuals [Klecka, 1980]. Furthermore, the discriminant functions successfully classified 63.4% of the calls in the sample, which was a considerable improvement over chance (8%). Discriminant analyses based on caller sex and social rank also revealed statistically significant variation at both levels (caller sex, Wilks' $\lambda = 0.58$,

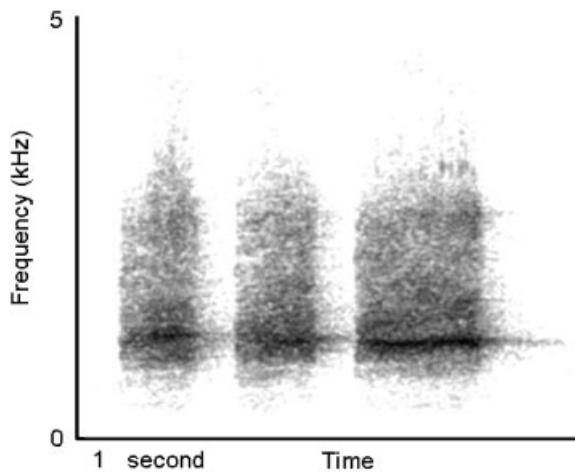


Fig. 1. Spectrogram of a bout of three lost calls from a white-faced capuchin. Spectrogram produced from successive 1,024-point FFT frames (90% frame overlap and hanging window).

TABLE I. Summary of Capuchin Lost Call Production and Consequences

Lost call behaviors	Dominant (<i>N</i>)	Subordinate (<i>N</i>)
Individuals producing lost calls	5	8
Number of lost call episodes	19	54
Number of lost call episodes answered	15	10
Number returned within 20 min	19	10

$\chi^2 = 40.12$, $P < 0.01$; caller rank, Wilks' $\lambda = 0.61$, $\chi^2 = 37.05$, $P < 0.01$). However, the Wilks' λ test statistics were relatively high (close to 1.0) and the eigenvalues associated with them were below one in each case (0.72 and 0.65) indicating greater variation within than between individuals. Classification success by caller sex and by caller rank were 78 and 81.7%, respectively, which represented a relatively modest improvement over chance in each case (50%).

There was no difference in the occurrence of lost call episodes between adult males and females ($\chi^2 = 0.00$, $P > 0.95$), nor were lost call episodes more common among subordinate or dominant individuals ($\chi^2 = 0.14$, $P > 0.75$; see Table I). Lost calls elicited an 'answering' response in 35% of lost-calling episodes (25 of 73 episodes). In these cases, compared to those that elicited no reply, the calling individual was more likely to return to the group within 20 min ($\chi^2 = 28.38$, $df = 1$, $P < 0.01$). For both sexes, the calls of dominant individuals elicited a reply more often than did the calls of subordinate individuals (males: $\chi^2 = 7.91$, $df = 1$, $P < 0.01$; females: $\chi^2 = 6.42$, $df = 1$, $P = 0.01$). As a result, dominant callers were also more likely than subordinate callers to return to the group within 20 min ($\chi^2 = 35.64$, $df = 1$, $P < 0.01$) and, when lost, subordinate callers remained separated from the group for longer than did dominant callers ($F = 5.18$, $df = 1$, $P = 0.03$) and called for a longer time (i.e., longer bout durations; $F = 6.49$, $df = 1$, $P = 0.01$), although they did not produce more calls per bout than did dominants ($F = 1.98$, $df = 1$, $P = 0.16$).

DISCUSSION

Our results indicate that the lost calls of white-faced capuchins are individually distinctive. This outcome is consistent with studies on several other primate species that have likewise reported individual differences in loud, long-distance calls produced when physically separated from other group members [e.g., Fischer et al., 2001; Mitani et al., 1996]. In addition, our results indicate that such vocal differences are also salient to the capuchins, who use them to respond selectively to the calls of certain group members, preferentially answering the calls of dominant individuals separated from the group over those of subordinate individuals. This response asymmetry appeared to have important functional consequences for the monkeys. Because dominant callers were answered more frequently than subordinate callers, dominant individuals also relocated the group and returned to it more quickly. In contrast, subordinate callers remained lost and continued to call for longer periods, which likely increased their exposure to any costs associated with being separated from the group (e.g., increased predation risk; increased intergroup hostility) and to exaggerate further this exposure by drawing attention to their vulnerable status via prolonged, conspicuous calling.

Given the stratified nature of many primate societies, which yields myriad rank-sensitive behavior patterns, the rank-based asymmetry in vocal responses in capuchins is, in the broad sense, not wholly unanticipated. However, to our knowledge, the phenomenon of selectively answering the lost calls of dominant individuals is without specific precedent in the literature on primate communication and raises an important question for future research: if primate social groups benefit from being cohesive (e.g., to reduce predator pressure and improve between-group resource competition), and if answering the vocalizations of lost group members is largely a cost-free act for individuals safely within the core of the group, then why not answer the lost calls of all group members so as to facilitate their return to the group? Why selectively answer dominant callers?

One possible explanation is that what we operationalized as ‘answering’ calls from other group members were not truly answers. That is, they might not have been produced intentionally [*sensu* Dennett, 1983] to selectively assist dominant but not subordinate individuals return to the group. Broader research on primate social cognition suggests that monkeys may not possess developed perspective-taking abilities [Tomasello, 2000], which in this case might be needed to fully appreciate the plight of other individuals who are lost and calling (whether they are dominant or subordinate individuals) and so to answer their calls and provide them with the information they need on the groups’ whereabouts. Indeed, at least two similar studies on baboons that experimentally tested whether group members truly answer each others’ lost calls invoked this “social cognitive constraint” explanation to account for the animals’ general failure to provide answering calls to other group members regardless of their identity or social rank [Cheney et al., 1996; Rendall et al., 2000].

If this explanation has any merit, then the selective ‘answering’ of dominant callers that we observed in capuchins might be, from a mechanistic standpoint, simply an extension of the greater social influence and valence that dominant individuals have compared with subordinate individuals. By definition, socially dominant group members exert greater social influence within primate groups than do subordinate individuals. Hence, their behavior, including their vocal and non-vocal signals, may have greater salience for others and thus garner greater attention and response generally [cf. Boinski, 1993; Cheney & Seyfarth, 1982;

Gros-Louis, 2004]. Thus, it is possible that the preferential vocal responses to dominant callers in capuchins simply represented a generalization of the greater attention and response afforded to those individuals more broadly.

An alternative, non-mutually exclusive explanation is that there are, from an ultimate standpoint, differential benefits associated with having dominant versus subordinate individuals return to the group. For example, in white-faced capuchins, dominant males have been found to provide more protection against potential predators and extra-group invaders than do females or subordinate males [Rose & Fedigan, 1995]. Dominant males are more vigilant, give more predator alarm calls, and approach or mob predators more often than do other group members [Digweed et al., 2005; Perry, 1998; Rose & Fedigan, 1995]. They also participate in more alliances or cooperative relationships that are vital to defending the group against extra-group invaders [Fedigan & Jack, 2004; Perry et al., 2004]. Similarly, α females more often lead group movement to new or clumped food sources and dominant males and females together often lead the group overall [Boinski, 1993]. Furthermore, individual relationships with dominant individuals can also provide a variety of specific benefits that do not flow from relationships with subordinate individuals [Fragaszy et al., 2004]. Taken together, there may be multiple benefits to facilitating the return of dominant individuals to the group, which might represent part of the ultimate rationale for the greater proximate attention given to them generally, including to their vocalizations when they are lost.

This account of the potential proximate motivations for, and ultimate benefits of, selective answering of dominant callers in white-faced capuchins is necessarily somewhat speculative. However, it represents a useful hypothesis for future research aimed at disentangling the various cognitive and social influences on primate communication and their functional consequences for different group members.

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