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Food-associated calls and audience effects in tufted capuchin monkeys, *Cebus apella nigritus*

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Several species of birds and primates produce food-associated vocalizations upon finding or consuming food. Tufted capuchin monkeys produce two food-associated vocalizations (the grgr and the foodassociated whistle series), which are functionally referential. By experimentally placing new food sources (feeding platforms containing half pieces of banana), I explored the factors that affect the production of food-associated calls in a wild group of tufted capuchins. Finders of these platforms called in 81% of the discoveries when the platform contained fruit (N = 57) but in 0% of cases when the platform was empty (N = 5). Males and females of all ages and dominance ranks gave food-associated calls when discovering a platform with fruit. The probability that a finder gave food-associated vocalizations was lower during the period of food scarcity and when the platform contained a small amount of bananas (three pieces as opposed to ≥ 20 pieces). There was an effect of the audience on the latency to give food-associated calls. The time elapsed until the finder gave the first food-associated call decreased with the presence and density of nearby individuals and increased with the distance from other individuals to the platform. The latency to call was longer for females than for males. The audience effect and the effect of the sex of the finder are consistent with the hypothesis that capuchins use these vocalizations deceptively by withholding information about the presence of a food source. By increasing the latency to call, finders of new food sources can obtain a larger amount of food and thus reduce the costs associated with calling.

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Several species of birds and primates give food-associated calls when they discover or consume food (see review in Hauser 1996). In some species, food-associated vocalizations attract other individuals to the food source (Dittus 1984; Elgar 1986a; Marler et al. 1986a; Brown et al. 1991; Roush & Snowdon 2000; Di Bitetti 2003). Thus, foodassociated calls seem to announce the presence of food to conspecifics or groupmates. The attraction of other individuals to the food source may in turn reduce the food intake of the food finder. For example, Di Bitetti & Janson (2001a) showed that, in tufted capuchin monkeys, the longer it takes another group member to arrive at a newly discovered food source, the greater is the finder's share of the resource as well as the total amount it consumes. The time to arrival of other individuals to a newly discovered resource increases if the finder takes longer to give foodassociated calls. It is possible that the cost of reduced food intake is offset by other benefits. For example, Elgar

Correspondence and present address: M. S. Di Bitetti, CONICET and Laboratorio de Investigaciones Ecológicas de las Yungas (LIEY), Universidad Nacional de Tucumán, Av. Córdoba 464, 3370 Puerto Jguazú, Misiones, Argentina (email: dibitetti@yahoo.com.ar). (1986a) provided evidence that solitary house sparrows, Passer domesticus, produce a persistent 'chirrup' call when discovering food, and that this call recruits other house sparrows. He also showed that the probability of calling increases with predation risk (Elgar 1986b). By attracting other individuals to a newly discovered food source, house sparrows may reduce the risk of predation or decrease the time spent in predator vigilance, benefits that may offset the reduced food intake. Similarly, Hauser (1992) and Hauser & Marler (1993) showed that in rhesus macaques, Macaca mulatta, finders that do not give food-associated calls (and are caught 'cheating') receive higher rates of aggression and end up eating less food than animals that give food-associated calls after finding a sharable resource. Food-associated calls may be given to reduce punishment by more dominant animals (Hauser 1992).

One of the differences between animal and human vocal communication was thought to be that nonhuman animals were not capable of using vocal signals voluntarily as in human speech. The production of animal signals was thought to be obligatory and reflexive as opposed to the voluntary control of human words (Hauser 1996). Some empirical evidence suggests that this is not always

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the case. Rhesus monkeys can be trained to produce some vocalizations at a higher rate in an operant conditioning task (Sutton et al. 1973 cited in Jürgens 1995). Voluntary use of vocalizations in animals is also suggested by the audience effects shown by some animals. Audience effects occur when animals modify their calling rate depending on their audience. Audience effects have been demonstrated for the alarm calls of several birds and monkeys (Karakashian et al. 1988; Cheney & Seyfarth 1990; Marler et al. 1991) and for the food-associated calls of chickens, Gallus gallus domesticus (Marler et al. 1986b; Evans & Marler 1994; Wauters et al. 1999) and primates (Caine et al. 1995; Van Krunkelsven et al. 1996). Audience effects have two potential implications. First, some authors have suggested that audience effects are a necessary condition for intentional signalling, and that this is especially the case for signals that have external referents, like alarm calls or food-associated calls (Marler & Mitani 1988; Marler et al. 1991). Second, audience effects have been interpreted by some authors as cases of deception, in which finders withhold information, or nonfinders provide false information. It has been argued that the most frequent form of deception in intraspecific animal communication should be through withholding information and not through active production of incorrect signals, because there is a much lower chance that cheaters will be discovered (and punished) in the first case (Cheney & Seyfarth 1990; Marler et al. 1991).

Tufted capuchin monkeys produce two distinct vocalizations, the grgr and the food-associated whistle series, at higher rates when feeding on fruit (Fig. 1; Di Bitetti 2003).



Figure 1. Two spectrograms of food-associated calls from tufted capuchin monkeys. (a) Two grgrs from an adult female. (b) A food-associated whistle series from a young juvenile. Both vocalizations were produced by animals eating bananas at feeding platforms. Spectrograms were obtained with Avisoft-SASLab Pro program. These vocalizations were digitized with a sampling rate of 16 000 kHz. To obtain the spectrograms, I made a fast Fourier transform using the following spectrogram parameters: FFT length = 256, frame (%) = 100, hamming window, and 50% overlap. The frequency resolution of this call is 81 Hz and the time resolution is 8.0 ms.

These food-associated calls are given by independently locomoting individuals of both sexes and of all ages. Upon hearing food-associated calls played back from a concealed speaker, focal animals (those from which I videotaped and measured their responses) approached the speaker on about 50% of the trials (N = 15). This response was not observed when I played back acoustically similar (but contextually different) vocalizations. Food-associated calls of tufted capuchins meet the two criteria for functional referential signals (Di Bitetti 2003): they are given in a well-defined context (context specificity) and receivers respond to the signal without contextual cues as if food were present (context independence).

In this paper, I address the question of what factors (amount of food, season, time of day, age, sex and dominance rank of finder, and the presence of or distance to other individuals) affect the production of food-associated calls and the time between discovery and calling ('latency') when an individual discovers a food source. By using novel food sources (platforms filled with bananas), I provide empirical evidence that food-associated calls of tufted capuchin monkeys show an audience effect.

METHODS

This study was conducted between August 1997 and August 1998 on a wild group of tufted capuchin monkeys inhabiting a subtropical rainforest at Iguazú National Park, in northeastern Argentina. The study group is the Macuco group, which has been intensively studied since 1991 (see Di Bitetti 2001b; Di Bitetti & Janson 2001b). All individuals in the group (N = 24-26 individuals, variation due to births and one immigration) were easily recognized by their size, pelage, tuft shape, scars, and other natural markings. Tufted capuchins are omnivorous animals, but the bulk of their diet includes fruit and arthropods (Robinson & Janson 1987). They live in multimale–multifemale social groups with a stable and linear dominance hierarchy (Janson 1985; Di Bitetti 1997).

During the study period, the group was followed continuously for periods of 1–4 weeks, with short interruptions of a few hours to a few days (usually as a result of heavy storms), totalling about 2500 h of contact time with the study group. With the aid of two field assistants, I obtained data on ranging patterns, foraging and social behaviour. To describe the capuchins' vocal behaviour, I obtained 57.1 h of focal-animal tape recordings, indicating the context of call production (Di Bitetti 2001a). Recordings of the discovery experiments (see below) and ad libitum recordings added another 29.4 h of monkeys' vocal recordings.

To study the vocal behaviour of capuchins when they discover new and highly preferred food sources, I used feeding platforms containing half pieces of banana. Platforms were wood structures (50×50 cm) with chickenwire bottoms. When the group was engaged in foraging behaviour (moving slowly, usually looking for arthropod prey), I placed one of these platforms at a random location about 200 m ahead of group movement. The group was followed by one or two field assistants who communicated

to me by walkie-talkies the location of the first individuals in the group and the general direction of the group's movement. I placed the platforms 3-12 m above the ground. To place the platform I threw a stone attached to the end of a rope over a horizontal branch or a fork on a tree. I then attached the platform to one end of the rope and raised it to about 50 cm below the branch from which it was hanging. When I raised the platform I made sure that no individual was within 50 m of the platform, a distance large enough to avoid giving unintended cues to the potential discoverers (see Janson & Di Bitetti 1997). If I heard animals nearby (<50 m), I aborted the experiment and made sure that no animals saw the platform and the bananas by covering them with a cloth. I never performed more than one discovery experiment per day and usually only two or three per week. I conducted a total of 65 discovery experiments, evenly spread across the seasons.

When an individual approached to within about 35 m of the platform, I started to tape-record its vocalizations. If the animal found the platform, I also dictated on the tape: (1) the identity of the finder, (2) the time when the animal discovered the platform (as evidenced by a fixed stare to the platform usually followed by a sudden increase in speed of movement directed to the platform), (3) the time when the finder reached the platform, (4) the distance from the finder to its nearest neighbour, (5) the number of individuals within a 10-m radius of the finder, (6) the distance from the next individual (other than the finder) to the platform, and (7) the vocalizations given by the finder. Times, distances and counts were estimated at/ from the moment of the discovery. I also recorded how many half bananas were taken by each individual that entered the platform. I usually estimated distances based on the number of steps that I had taken between previously calibrated points. On a few occasions, distances to the nearest neighbour or distances from the next individual to the platform were roughly estimated with the aid of information provided by my field assistants or assessed by the sounds produced by the foraging animals. I used four different amounts of half bananas in the platforms: 40 (N = 20 discoveries), 20 (N = 20), 3 (N = 20) or 0 pieces (N = 5). The order of presentation of these treatments was randomized. Three discoveries were discarded from the data set because the discovery was confusing (I could not determine a clear discoverer or who was calling in two occasions), and on another occasion the discoverer (a juvenile) could not reach the platform (it was placed in a tree that was difficult to access). On three other occasions, technical reasons prevented me from starting to record on time, and I missed some of the data for those discoveries. Therefore, sample sizes vary slightly from one statistical test to another. For further details on the experimental procedures, see Di Bitetti (2001a), Di Bitetti & Janson (2001a); for similar procedures, see Janson & Di Bitetti (1997).

I used an indirect estimate of hunger level by dividing days into two time intervals: (1) the first 2 h of group activity (from when the group started its activity until 0750–0900 hours, depending on the date of the year) and (2) from the end of the previous interval until the group arrived at their sleeping site. I assumed that the animals

would be hungrier during the first 2 h of activity, after 10-13 h without feeding. These time periods can be used as an indirect estimate of daily hunger variation (Hauser 1992). As an indirect estimate of the opportunity cost of losing access to a resource, I made use of the marked seasonal variation in food availability at Iguazú. I estimated seasonal variation in fruit and insect availability during the period of this study, and during previous years, using fruit traps and insect sampling techniques (Di Bitetti 2001b; Di Bitetti & Janson 2001b). The year was divided into two study periods: (1) a period of relative food scarcity (early May-early September) and (2) a period of relative food abundance (mid-September-April). The opportunity cost indirectly measures the cost of losing access to a resource, which increases as the number of alternative resources available is low.

I made the tape recordings with a directional Sennheiser microphone (MKH815T) covered with a windshield, on CrO₂ tapes (Maxell XLII and Sony UX) using a Marantz cassette recorder (model PMD222). I performed sound analysis and spectrograms of the vocalizations with the program Avisoft-SASLab Pro for IBM compatible PC (McGregor & Holland 1995). Calls were classified into discrete types by visual inspection of spectrograms backed up by discriminant function analysis (Di Bitetti 2001a). The latency to produce the first food-associated call (hereafter latency to call) was measured as the time in seconds starting when the finder discovered the platform until it gave the first food-associated call (either a grgr, a food-associated whistle series or a chihui immediately followed by a food-associated whistle series; for a description of these vocalizations see Di Bitetti 2001a).

The latency to call was used as the dependent variable in most statistical tests (regression, ANOVA, multiple regressions and ANCOVA). Time and distance variables were transformed to their logarithms to base 10. I used the G test (log-likelihood ratio test) and logistic regression to see what factors affected the probability of an individual giving or not giving food-associated calls. I used logistic regression to see how continuous variables affected the probability of the finder calling before or after entering the platform it discovered. I performed the statistical tests with the program JMP (version 3.2, SAS Institute 1996).

RESULTS

The finder gave food-associated calls in 46 of 57 (81%) of the discoveries when the platform contained bananas. Finders did not call when there were no bananas in the platform. Individuals of all age and sex classes (except infants) discovered platforms. Individuals of all age–sex classes gave food-associated calls upon discovering a platform with bananas. In 84% of the discoveries where the finder called (N = 45), the first food-associated call given by the finder was a food-associated whistle series. In the remaining seven discoveries where the finder called, the first food-associated call was a grgr (N = 2), a grgr followed within 10 s by a whistle series (N = 3) or a chihui followed within 10 s by a food-associated whistle series (N = 2).

In two of the 11 discoveries in which the finder of a platform that contained bananas did not call, the platform contained 40 pieces of banana and the finder was an oestrous female. When I excluded the discoveries by oestrous females (see Discussion for a justification), a logistic multiple regression with the probability of calling as the dependent variable showed that finders had a lower probability of calling during the season of relative fruit scarcity (Wald chi-square test: $\chi_1^2 = 6.0485$, P = 0.0139), when more individuals were within 10 m of the finder ($\chi_1^2 = 4.3750$, P = 0.0365) and when the platform contained only three pieces of fruit as opposed to either 20 or 40 pieces ($\chi_1^2 = 3.9132$, P = 0.0479). I obtained similar results when using the distance to the nearest individual of the finder instead of the number of individuals within 10 m of the finder as a continuous variable in the logistic regression. I found no effect of time of day (i.e. hunger level; $\chi_1^2 = 0.4043$, P = 0.5249) or the sex ($\chi_1^2 = 0.0480$, P = 0.8265), age ($\chi_2^2 = 2.3610$, P = 0.3071) or dominance rank ($\chi_1^2 = 0.4918$, P = 0.4831) of the finder on whether it called or not upon finding a platform.

A multiple regression analysis showed that the latency to call increased the farther the next individual (other than the finder) was from the platform at the moment of the discovery ($F_{1,40} = 8.4568$, P = 0.0059; Fig. 2a) and decreased as more individuals were within 10 m of the finder at the moment of the discovery ($F_{1,40} = 6.0276$, P = 0.0185; Fig. 2b). The distance to the finder's nearest neighbour had no effect when the previous two variables were statistically controlled for in a multiple regression model ($F_{1,39} = 0.6955$, P = 0.4094).

To explore the effect of the social variables (sex, age and dominance rank of the finder) and ecological variables (amount of fruit in the platform, time of day, and season) on the latency to call, I performed a series of multiple regression ANCOVA with latency to call as the dependent variable and distance from the next individual to the platform and the social and ecological variables as independent variables. I found no statistically significant effect of the amount of fruit in the platform ($F_{2,38} =$ 0.9213, P = 0.4067), the time of day ($F_{1,39} = 1.4154$, P = 0.2414) or the season ($F_{1,39} = 1.7647$, P = 0.1918) when the other variables were statistically controlled for. Similarly, age and dominance rank showed no statistical effect on the latency to call in multiple regression ANCOVA models when sex and distance from the next individual to the platform were also included as independent variables (effect of age: $F_{2,38} = 1.0921$, P = 0.3458; effect of dominance rank: $F_{1,39} = 1.5355$, P = 0.2227). The sex of the finder and the distance from the next individual to the platform showed a highly significant effect on the latency to call. The latency to call increased with the distance from the next individual to the platform and males had a shorter latency to call than females (Fig. 3). In this study, the sex of the finder was highly correlated with the dominance rank of the finder; male finders were of higher rank than female finders $(F_{1.11} = 22.3305, P = 0.0006, only individuals that dis$ covered platforms and called were included in this analysis). However, there was no effect of dominance



Figure 2. Linear regression of the latency to the first food-associated call (seconds) on (a) the distance from the nearest individual (other than the finder) to the platform, and (b) the number of individuals within 10 m of the finder. These variables were measured at the moment when the finder discovered the platform.

rank within each sex ($F_{2,38} = 0.7481$, P = 0.4801) in a statistical model where dominance rank was nested within sex after controlling for the distance from the next individual to the platform. I obtained similar results to those described above when I included the number of individuals within 10 m of the finder as another independent variable in addition to the distance of next individual to the platform in the statistical tests.

Because different individuals have different probabilities of discovering platforms (Di Bitetti & Janson 2001a), they contributed different and very uneven sample sizes to the pool of data. Thus, the effect of the sex of the finder on the latency to call may be the result of different individuals contributing more than one data point to the data pool, in violation of the assumption of independence of the data (the pooling fallacy, Machlis et al. 1985). Females had an almost significantly longer latency to call in a nested ANCOVA model with distance from next individual to the platform as a continuous variable, sex as the class variable and individual identity as a variable nested within sex (effect of sex: $F_{1,11} = 4.4776$, P = 0.0580). There was statistically significant unexplained variation between individuals (effect of the identity



Figure 3. Linear regression of the latency to the first food-associated call (seconds) on the distance from the nearest individual (other than the finder) to the platform for male (lower regression line) and female (upper regression line) finders. ANCOVA results: whole model test: $R_{adj}^2 = 0.6745$, $F_{2,40} = 44.5202$, P < 0.0001; effect of the distance from next individual to platform: $F_{1,40} = 60.8611$, P < 0.0001; effect of sex: $F_{1,40} = 28.6115$, P < 0.0001. Regression lines for males and females did not differ in slope but had different interceptions at the origin.

of the finder nested within sex: $F_{11,29} = 2.7007$, P = 0.0158). When the number of individuals within 10 m of the finder was included in the model as another variable, the effect of sex reached statistical significance ($F_{1,11} = 5.9187$, P = 0.0332) but there was still some unexplained variation between individuals (effect of the identity of the finder nested within sex: $F_{11,29} = 2.4181$, P = 0.0291). Even though there may be variation between individuals, the effect of the distance from the next individual to the platform on the latency to call was observed in all the individuals for which I had large sample sizes (Fig. 4).

A finder sometimes called almost immediately before arriving at a platform, but on other occasions it called only after entering the platform and securing some banana pieces. The farther the distance from the next individual to the platform, the lower the probability of the finder giving the first food-associated call before arriving at the platform (logistic regression, chi-square test: $\chi_1^2 = 10.22$, P = 0.0014). Similar results were obtained when I used the distance from the finder to its nearest neighbour or the number of individuals within 10 m of the finder as predictor variables. Males had a higher probability of calling before arriving at the platform than females (Wald chi-square test: $\chi_1^2 = 6.468$, P = 0.0110) after controlling for the effect of the distance from the next individual to the platform at the moment of discovery. Dominant individuals had a higher probability of calling before arriving at the platform than did subordinate ones (Wald chi-square test: $\chi_1^2 = 6.5732$, P = 0.0104) after controlling for the effect of the distance of the next individual to the platform. I found no effect of the amount of food ($\chi_2^2 = 3.3038$, P = 0.1917), season ($\chi_1^2 = 0.2199$, P = 0.6391), or time of day ($\chi_1^2 = 2.1084$, P = 0.1465), on whether the finder called before or after arriving at the



Figure 4. Relationship between the latency to give the first foodassociated call (seconds) on the distance from the nearest individual (other than the finder) to the platform for the two individuals that discovered the most platforms: (a) adult immigrant male GE (linear regression: $F_{1,8} = 22.8242$, P = 0.0014); (b) subadult natal male IGU (linear regression: $F_{1,7} = 7.0914$, P = 0.0323).

platform after controlling for the effect of the distance of the next individual to the platform. One particular individual, a subadult male (IGU), discovered nine platforms, and he called before arriving at the platform in eight of his discoveries. The effect of the distance from the next nearest individual to the platform on the probability of calling before arriving at the platform still held when this individual was excluded from the logistic regression, but the effect of sex disappeared.

On three occasions (all with 40 pieces of banana), no individual other than the finder saw the platform. These finders all gave food-associated calls but took a median of 400 s to call (range 354–425 s), significantly longer than the median latency to call for the other discoveries (36 s, interquartile range 7.5–131 s; Wilcoxon two-sample test with the normal approximation: S = 125, Z = 2.6565, $N_1 = 3$, $N_2 = 41$, P = 0.0079). In these discoveries, the mean (\pm SE) distance from the next individual to the platform was 36.7 \pm 7.6 m when the finder discovered the platform (a distance at which animals cannot usually see each other). The mean distance from the finder to its nearest neighbour was 20.0 \pm 5.7 m. On all three occasions, the finder started to call when no individual was

within 35 m of the platform and the group was getting farther away from it. However, no individual was attracted to the platform by the calls. These observations contrast with most other discoveries, in which, if no other animals were nearby (usually within 20 m), the finder started feeding in silence until the sound of an approaching individual triggered the first food-associated call.

DISCUSSION

Tufted capuchin monkeys usually gave food-associated calls when they discovered platforms filled with bananas. Individuals of all ages (excluding small infants), sexes and dominance ranks gave these vocalizations. The first call was usually a food-associated whistle series. This behaviour is not specific to the discovery of the feeding platforms, but is similar to what capuchins do when they feed on or discover natural resources (Di Bitetti 2001a, 2003). The most important factor that determined the time elapsed until a finder of a new food source gave the first food-associated call was the presence of other individuals nearby. The distance from the next individual (other than the finder) to the food source, the distance from the finder to its nearest individual, and the number of individuals within 10 m of the finder at the moment of the discovery affected the latency to call. Animals called sooner if more individuals were nearby or if the next individual was closer to the finder or to the food source. Likewise, the probability of calling before versus after arriving at the platform was strongly affected by the presence of individuals nearby. Females were slower to call than males. There was also variation between individuals in the latency to call that was not explained by their sex. Thus, there is a marked audience effect in the food-associated call system of tufted capuchin monkeys, but the extent of this effect differs between individuals and between the sexes.

In about 20% of the discoveries, the finder did not call. On two occasions, the noncalling finder was an oestrous female. During the 3–6 days of their oestrous cycle, females have a set of particular behaviours: they become very skittish and follow the alpha male (and sometimes other adult males) at short distances almost continuously, they produce an oestrous grimace and an oestrous vocalization for long (up to 3 h) bouts, they rarely forage for insects and they feed on fruits only during short and concentrated bouts (see Janson 1984). Thus, I would not normally expect oestrous females to give food-associated calls when discovering a platform. When excluding the two discoveries by oestrous females, I found that three factors affected the probability of a finder not giving foodassociated calls. First, they had a higher probability of not calling during the season of relative fruit scarcity. This suggests that they tend not to call when the opportunity cost of losing access to a resource is presumably higher. However, with these data I cannot rule out the possibility that this seasonal pattern is due to another factor and not to the opportunity cost since I have only 1 year of data. Data from more seasons (or more than one group) are necessary to test for the effect of the opportunity cost. Second, individuals had a lower probability of giving foodassociated calls if the platform contained a small amount of food (three pieces of banana that could be monopolized by the finder) as opposed to a large amount (20 or 40 pieces). Finally, individuals had a higher probability of not calling when many others were nearby. These last two factors may indicate that finders have a higher probability of not calling if they can monopolize the food source or if nearby animals are already aware of the presence of the food source when the finder arrives at the source.

Audience effects have been observed in the alarm calls of ground sciurids, birds (Sullivan 1985; Karakashian et al. 1988; Evans & Marler 1994) and primates (Cheney & Seyfarth 1985). They have also been studied in the foodassociated calls of chickens (Marler et al. 1986b, 1991; Gyger & Marler 1988; Evans & Marler 1994; Wauters et al. 1999) and primates (Caine et al. 1995; Van Krunkelsven et al. 1996; Roush & Snowdon 2000). Roosters give foodassociated calls at higher rates in the presence of a hen (either his mate or an unknown female) than when no other animal is present. Interestingly, they suppress their calling behaviour if the audience is another male chicken (Marler et al. 1986b, 1991). Broody hens call at higher rates than nonbroody hens. They also call more when food is present and their chicks are in visual contact but isolated, or out of sight but in vocal contact, than when their chicks have free access to the food (Wauters et al. 1999). In captive red-bellied tamarins, Saguinus labiatus, individuals call at higher rates if their cagemates are out of view in an adjacent cage (Caine et al. 1995). However, in a similar captive setting, Roush & Snowdon (2000) did not find any evidence for audience effects in the foodassociated calls of captive cottontop tamarins, Saguinus *oedipus.* It is not clear how to explain these differences although the last authors explain the lack of an audience effect in their study animals as a result of lack of experience with the experimental conditions.

Some authors have found differences in the foodassociated calling rate in relation to the dominance rank, age or sex of the caller. Dominant and adult individuals were more active callers in studies of vagrant ravens, Corvus corax (Heinrich & Marzluff 1991) and cottontop tamarins (Roush & Snowdon 1999). In tufted capuchins, males tend to have shorter latency to give the first foodassociated call when discovering a new food source than females. That females have a longer latency to call when discovering a new food source than males is not surprising; for females, an increase in food intake could make a proportionally higher difference in fitness than for males. It will be necessary to conduct further experiments to disentangle the effects of the finder's sex and dominance rank, since these were highly correlated in my study. Variation between individuals in the latency to call was also important but I was not able to pinpoint this variation to any factor. It would also be important to conduct experiments to evaluate whether the sex or dominance rank of the audience has any effect on the latency to call (or the calling rate) of the finder.

The audience effects observed in the alarm and foodassociated calls of the domestic chicken have been interpreted as having potentially important cognitive implications (Marler et al. 1986b, 1991; Karakashian et al. 1988). First, audience effects suggest that animals are not responding simply to environmental events but that they can modulate their vocal behaviour depending on the presence of an appropriate audience (Marler et al. 1991; Evans 1997). This in turn may suggest that signalling is not a simple reflexive behaviour. Studies on the alarm and food-associated calls of the chicken suggest that the audience effect does not occur simply as a result of an increase in arousal levels or as a reduction in the response threshold of the sender due to the presence of an audience (Karakashian et al. 1988; Evans & Marler 1994; Evans 1997). Second, audience effects are suggestive of a deceptive use of vocalizations. Animals may produce alarm calls (Møller 1990) or food-associated vocalizations (Gyger & Marler 1988) in 'inappropriate' contexts when by doing so they obtain some benefit (e.g. attract mates or guard paternity). Alternatively, animals may withhold vocalizations under conditions where they would usually produce them if by doing so they obtain some gain (e.g. larger amount of food, Hauser 1992). In tufted capuchin monkeys, the finder's share of a newly discovered resource, as well as the total amount of it consumed by the finder, increases with the time elapsed until other individuals join the finder. The time it takes other individuals to join the finder increases with the distance from those individuals to the platform and with the time it takes the finder to give the first food-associated call (Di Bitetti & Janson 2001a). Thus, all other things being equal, capuchins that delay (or avoid) the production of food-associated signals obtain more food than those that call immediately upon finding food.

The idea that audience effects in alarm or food-associated calls suggest an intentional or deceptive use of these signals relies on the critical assumption that these vocalizations are referential or semantic signals (Marler et al. 1991, 1992; Evans 1997). I show elsewhere (Di Bitetti 2003) that the food-associated calls of tufted capuchins are functionally referential signals. The audience effects observed in the food-associated calls of tufted capuchins suggest an intentional or deceptive use of these vocalizations. It is not just the presence or absence of an appropriate audience that triggers the production of foodassociated calls but the distance between the finder and its potential audience. Food-associated calls can be heard from distances of more than 100 m under normal environmental conditions (personal observation). Thus, it is not simply the presence or absence of an audience (like in the chicken experiments) that affects the latency to call, because during the experiments, other animals were usually within auditory range of the finder at the moment of the discovery. It is the presence of individuals within visual range that usually triggers these calls. In the arboreal environment where capuchins live, visibility is highly limited by the network of leaves, branches and epiphytes. The median distance at which individual capuchins discovered a feeding platform in these experiments was 12 m (see also Janson & Di Bitetti 1997) but the median distance from the next individual to the platform was 22 m. Capuchin monkeys are very noisy when foraging for arthropods and they produce contact notes at high rates (Di Bitetti 2001a). Strikingly, individuals discovering platforms when no other individuals are nearby stop giving contact notes and producing noises, as if trying to remain cryptic (personal observation). All these observations are consistent with the idea that tufted capuchins' food-associated calls are functionally referential signals that are used in a deceptive manner (see also Hauser 1992). Capuchins took longer to call when no other animals were within visual range and, by doing so, extended the time of arrival of other individuals to the food source and increased their total food intake. Thus, finders seem to withhold the production of food-associated calls under certain conditions in a functionally deceptive way.

In tufted capuchin monkeys, the audience effect contradicts the hypothesis that food-associated calls provide predation risk benefits to callers. If finders that produce food-associated calls obtain reduced predation benefits, we should expect them to have shorter latencies to call when the distance to their nearest neighbours is large in order to recruit group members to the newly discovered food source (see Elgar 1986a, b).

If tufted capuchins obtain more food when delaying the production of food-associated calls (Di Bitetti & Janson 2001a), why do they call at all? A hypothesis consistent with the audience effect of tufted capuchins is that animals are punished by other group members if they fail to 'cooperate' by providing information about food to their groupmates (Clutton-Brock & Parker 1995). Hauser (1992; see also Hauser & Marler 1993) proposed that rhesus macaques give food-associated calls to avoid being punished and this also may be the case with tufted capuchins. The costs of punishment may outweigh the costs of reduced food intake and this may explain the maintenance of food-associated calls. However, the punishment-enforced cooperation hypothesis fails to explain why food-associated calls evolved in the first place. A mechanism based on trait-group selection (Wilson 1983), group augmentation (Kokko et al. 2001), biological market (Noë et al. 1991; Noë & Hammerstein 1994) or reciprocity (Maynard Smith 1982; Roberts 1998) may explain how food-associated calls evolved in the first place, but punishment-enforced cooperation may be a more recent force that keeps the system working, by increasing the costs to nonaltruistic individuals. However, I found no evidence that noncallers are punished, probably because capuchins are very aware of the presence of nearby individuals and will rarely be found cheating. It is even possible that punishment may take the form of lack of cooperation or a reduction in the frequency of affiliative behaviours received by nonaltruistic individuals, instead of actual aggression towards them. This may create a system where animals may compete for being the major providers of altruistic acts or other group benefits (Stambach 1988; Roberts 1998).

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