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Audience effects on food calls in captive brown capuchin monkeys, *Cebus apella*

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Brown capuchins give distinct calls upon encountering food. Based on studies on other species that point at divisibility of food and audience as critical variables, we predicted that capuchins would adjust their food calling for both the amount of food and the nature of their audience. We predicted that the food-associated call serves to attract conspecifics in certain conditions. Twelve female capuchins were tested in two food-quantity conditions (large and small) and four audience conditions with a control (higher-ranking female, lower-ranking female, high-ranking male, entire group and alone). All subjects called more for larger than smaller amounts and the highest-ranking females called less than others. Subjects called more in the presence of a group than for any other audience, and this applied most strikingly to high-ranking subjects. This result may be related to the presence of kin rather than group size. We also analysed the acoustic parameters of the calls, predicting that, under conditions where call production rose, those acoustic variables associated with heightened arousal would rise in value. However, call production and those acoustic features were not always correlated. These results suggest that food calls in this species do not solely reflect arousal caused by food and are influenced by multiple audience effects.

A key issue in vocal communication research concerns the extent to which calls are influenced by an audience (Cheney & Seyfarth 1990; Evans 1997). Audience effects, which occur when a caller uses a signal differently depending on the composition of its audience (Marler et al. 1986; Tomasello & Call 1997), can elucidate the complex ways that external factors influence calling behaviour, although the question of voluntary control is still unanswered (Tomasello & Call 1997).

The audience effect is important to study in a communicative context because it suggests that call production may depend not only on food itself but also on the social environment and the caller's social status (Roush & Snowdon 1999). Audience effects on signalling behaviour exist in many taxa, including vervet monkeys, *Cercopithecus aethiops* (Cheney & Seyfarth 1990), chickens, *Gallus gallus domesticus* (Gyger et al. 1986; Evans & Marler 1994), budgerigars, *Melopsittacus undulatus* (Striedter et al. 2003), chimpanzees, *Pan troglodytes* (Hauser & Wrangham 1987), fish, *Betta splendens* (Matos et al. 2003), ground squirrels, *Spermophilus beldingi* (Sherman 1977), marmots, *Marmota flaviventris* (Blumstein & Armitage 1997) and woodpeckers, *Picoides pubescens* (Sullivan 1985). Many of these studies have focused on food or food-associated calls, because they are particularly suitable for studying audience effects as a result of a variety of influencing factors.

Variation in production is suggested by the way that food-associated calling depends on food quantity (Hauser & Wrangham 1987; Caine et al. 1995; Brosnan & de Waal 2003a), quality (Chapman & LeFebvre 1990; Elowson et al. 1991; Benz 1993), divisibility (Elgar 1986; Hauser et al. 1993) and the social environment in which the food is discovered (Chapman & LeFebvre 1990; Hauser & Marler 1993a, b; Evans & Marler 1994; Caine et al. 1995; Roush & Snowdon 2000). This evidence suggests that food calling is not solely an emotional response elicited by the discovery of food, but can also be a form of communication that is sensitive to social conditions and provides information about both the signaller and the nature of its discovery. For example, female rhesus macaques, *Macaca mulatta*, who belong to larger matrilines give more calls than do females of smaller matrilines, suggesting an inclination to call more in the presence of kin than unrelated individuals if members of larger matrilines more often find themselves in the proximity of kin (Hauser & Marler 1993b). Evans & Marler (1994) found that the presence of females potentiated food calls in

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males, thus demonstrating an audience effect of sex. The presence of an appropriate audience acts specifically to increase call production, and this effect is independent of other nonsignalling behaviour.

The brown capuchin is a highly social New World monkey that engages in food sharing and has a flexible dominance hierarchy (de Waal 1997a). This species produces a distinct, tonal vocalization when expecting, encountering or consuming food, which is characterized by an average frequency of 1100 Hz (Izawa 1979; van Schaik & van Noordwijk 1989; Visalberghi & Addessi 2000; Fig. 1). Di Bitetti (2001, 2003), based on extensive playback experiments, suggested that this call is functionally referential. In an experimental field setting, subjects responded to the playback of food-associated calls with a rapid and direct movement to the speaker in almost 50% of the trials, but did not show this response to the playback of similar-sounding control stimuli. We do not know whether any other socioecological context is associated with this call, but the initial evidence suggests that it is predominantly and reliably a food-associated call.

Female capuchins in particular may be more discriminating in their food-calling behaviour. Di Bitetti (2005) found that female brown capuchins took longer to call than did males in the presence of food, depending on the proximity of the audience, and female white-faced capuchins, *C. capucinus*, are more likely to call and at higher rates than are males in the presence of food (Gros-Louis 2004). Female brown capuchins may also be more sensitive to reciprocal exchange involving food (Brosnan & de Waal 2003b). In a series of experiments investigating value perception and exchange in front of an audience who received differential rewards, females paid more attention to their partners' behaviour than did males and were more consistent in their exchange behaviour, suggesting that females may be more sensitive to audience effects.

There are at least two hypotheses for why a social primate calls in the presence of food. One, the food announcement hypothesis, is that food calls serve to attract other members of the group, alerting them to feeding opportunities (Dittus 1984; Chapman & LeFebvre 1990; Hauser et al. 1993). These calls would thus not only serve to announce the presence of food but also to attract conspecifics. One prediction that follows is that all individuals would call at higher rates for an audience than when they are alone.

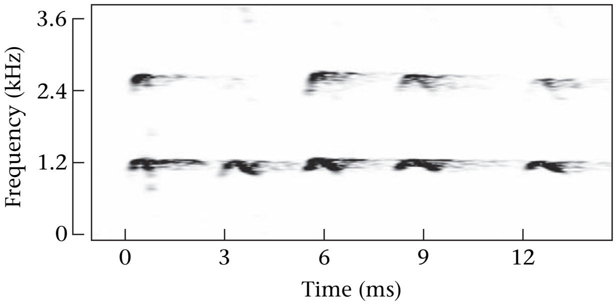

Figure 1. Spectrogram of five brown capuchin food calls. The food call is tonal with an average fundamental frequency of approximately 1100 Hz.

Another possibility, the food ownership hypothesis, is that food calls serve to announce possession of food and not necessarily to inform others of a willingness to share. Gros-Louis (2004) found that white-faced capuchins who produced the 'huh' vocalization more often upon discovering food in the presence of a higher-ranking animal received less aggression than those who did not call. Thus, announcing food ownership with higher rates of calling led to more successful foraging by way of better-regulated interindividual spacing, particularly in the presence of dominant individuals. This result supports a conclusion by Boinski & Campbell (1996) that the food call in this species may be a spacing mechanism and not necessarily a signal to share food. Additional support for the food ownership hypothesis is that brown capuchins decrease the latency to call when a larger group of conspecifics is nearby (Di Bitetti 2005). A prediction based on this hypothesis is that low-ranking individuals will call more than high-ranking individuals, because they will have more difficulty in keeping others away from the food source. Although the food-associated calls of white-faced and brown capuchins may not be completely analogous in usage and function, the comparison is nevertheless useful for informing hypotheses.

Studies on audience effects on calls typically look for differences in call production; that is, how many times the call is produced in a defined period of time. It is unknown, however, whether variation in acoustic structure for the same class of calls is affected by differences in the social environment. Much less is known about the factors responsible for variation in signal structure within call type than about call rate (Marler 1992; Evans 1997). There is no comprehensive model of the relation between stimulus category and signal structure, apart from Morton's (1977) broadly based motivation-structural rules (Evans 1997), so it is difficult to predict how the acoustic structure of a single type of call will vary with audience effects. In the present study, however, we expected that trends in call production and acoustic structure would reflect the same condition. For example, if a female capuchin produces more calls for a higher-ranking audience than for a lower-ranking one because she is more aroused (i.e. more fearful) in the former's presence, then those acoustic parameters typically associated with heightened arousal, such as frequency (kHz) and jitter (the short-term perturbation in the fundamental frequency; Mitani & Brandt 1994), should also increase in value. Furthermore, and in accordance with Morton's (1977) motivation-structural rules, acoustic features of calls characteristic of more aggressive, less fearful dominant individuals, such as lower frequency, should also be evident.

This study focused on underlying variation in the food call and the different ways that an audience could affect it in a controlled experimental setting. We manipulated audience and food quantity to determine whether female brown capuchins gave food calls differentially depending on the caller's position in the hierarchy, the composition of its audience and audience size. We predicted that low-ranking individuals would call more than would high-ranking individuals, according to the food ownership hypothesis, to keep others away, and that female capuchins would call more for larger amounts of food, as reported in other species.

METHODS

Subjects and Housing

Subjects were 10 adult and two subadult females from two social groups of brown capuchins, the Nuts and the Bolts, housed at the Yerkes National Primate Research Center since 1991. For the duration of testing (June–December 2001), each group consisted of two adult males and four adult females, totalling 12 adult subjects in both groups. There were also eight subadults, seven juveniles and two infants, for a total of 29 animals in both colonies. Audience monkeys included both females and dominant males. Adults and subadults were used.

The groups were housed in two indoor–outdoor pens, with total areas of 25 m^2 (the Bolts) and 31 m^2 (the Nuts). During normal hours and in most weather conditions, the monkeys had free access to the indoor and outdoor spaces. Each indoor space was further divided into two sections by a chain-link fence, with two small doorways and one door for human access. The two groups had auditory but not visual contact because of an opaque screen. The adjacent office had windows through which researchers could monitor the monkey area. The floors in each indoor area were covered with sawdust. Subjects received Purina small primate chow twice a day at approximately 0930 and 1730 hours. Water was available ad libitum and subjects received trays of fruit, vegetables and bread with a protein solution each day in the midafternoon. Experimental pairs and group conditions consisted solely of individuals from the same group.

Experimental Set-up

A mobile test chamber (144 × 60 × 60 cm) was attached to the front of the indoor enclosure of the group. We removed individuals in pairs from their social group using a trained capture process: the subject entered a transport box and from there was moved to the test chamber. The subject occupied the left side of the chamber and the audience monkey or group remained in the home enclosure, in front of which was the test chamber. For the duration of testing, an opaque plastic panel prevented movement back into the indoor enclosure. The home enclosure, however, was fully visible through mesh from the subject's area in the test chamber. The rest of the subject's and audience's group, as well as the neighbouring group, were locked in the outside enclosures for all testing procedures to ensure, to the best of our abilities, that the test subject and audience were visually and audibly separated from all other individuals. This control reduced but did not eliminate the potential for sound interference from others, thereby facilitating more accurate data collection and reducing the possible influence of confounding factors. Testing was not conducted on days when inclement weather prevented animals from being locked outside. A food tray (152 × 35.5 cm) was placed in front of the test chamber, on which food was presented to the subject in a small plastic bowl.

A microphone (Audio Technica ATR55) was placed directly above the subject's compartment via a metal stand, approximately 15 cm above the chamber. The microphone was directly connected to a Dell Pentium II 566 mHz computer running a sound analysis program (described below), which recorded the vocalizations. Although the microphone was closer to the subject than to the audience, the program occasionally recorded the audience's vocalizations in the background. The amplitude of the subject's vocalizations was much greater than that of any background noise or calls, so we were able to distinguish between individual calls and eliminate these from the spectrograms.

Design and Procedures

Each of 12 female capuchins underwent five audience conditions. Each subject was tested alone, which served as the baseline condition. Then she was tested with three audiences consisting of one other monkey: a higher-ranking female, a lower-ranking female and a high-ranking male. Finally, she was tested with the rest of her group present. The neighbouring group was locked outside for all conditions. There were some exceptions within the one-monkey audiences for certain subjects: the two highest-ranking females could not be tested with a higher-ranking female, so they were tested only with a lower-ranking female and the dominant male. Two of the four low-ranking monkeys were not tested with females lower in rank than themselves. Therefore, we took these considerations into account in statistical analyses, and examined relative rank in the data. Female–female dyads excluded kin; neither mothers and daughters nor sisters were tested.

Each audience condition was paired with two food conditions: high quantity, which consisted of 10 banana slices (approximately one whole banana) and 20 grape halves, and low quantity, which consisted of two banana slices and two grape halves. Grapes are a highly favoured food of these capuchins (de Waal 2000), so we were assured of a consistent desire for this food.

Monkeys were not tested within 2 h of receiving chow in the morning, but on certain days they were tested immediately after the morning cleaning. In this case chow was withheld until after testing, which never took place more than 1 h after their normal morning feeding time. Testing took place at various times during the day, but not within 2 h of morning chow and always before they received their afternoon trays of food. There was no difference in call production rates between the morning and afternoon tests (paired t test: $t_{145} = 0.645$, two-tailed, $P = 0.520$). Monkeys were given 5 min to acclimate to the test chamber (with which most subjects were already familiar; de Waal 1997a; Mendres & de Waal 2000; Brosnan & de Waal 2004). The test began with the presentation of the food in a clear plastic container. In addition to recording subjects' vocalizations, all tests were videorecorded with a Canon GL1 digital video recorder. Test sessions lasted 5 min. Data on food calling were collected from examining video and digital audio recordings of each test. To minimize the effects of conditioned food calling in the presence of humans, we attempted to minimize and standardize the time spent in the testing area for each test. Experimenters were not present immediately before the test, and only one experimenter entered the animal area to start the video recorder and left immediately afterwards.

Each subject repeated each combination of conditions twice, with the exception of low-food trials, which were tested once to avoid what we originally believed would lead to habituation. Thus, each subject underwent 15 tests, for a total of 180 trials.

Acoustic Analyses

Calls were digitized using Cool Edit Pro version 1.2a (Syntrillium Software Corp., Phoenix, Arizona, U.S.A.; sampling rate = 44.1 kHz using a 1024-point fast Fourier transform (FFT) with a Blackmann filter). We counted a single, continuous vocalization as a call. Others have considered this to be a syllable in a whistle series, which collectively is considered one call (Di Bitetti 2001). Calls for analysis were selected in the following manner: a sample consisted of 15 calls from each trial: five from the first 30 s, five from the middle of the trial (as close to 2 min and 30 s as possible), and five from the last 30 s. The first five calls were chosen within each section. If a call was not easily distinguished, we picked the next call that was appropriate. Calls were almost always taken from within a bout, defined as a series of the same class of calls separated with intercall intervals of not more than 1 s. Sometimes we were unable to obtain 15 calls because some subjects did not make that many calls for some trials.

The spectrograms included low-level noise (usually below 500 Hz), so a high-pass filter was applied to remove it for cleaner analyses. Approximately 50% of the recorded calls also included some echo, and these were edited manually for each call to capture the accurate duration and end frequency of each call. All calls were counted to calculate call production in different conditions.

A.S.P. identified all units for acoustical analysis. Fellow laboratory members independently confirmed and verified the selection and analyses of a subset of the calls (approximately 15%). Analyses were performed using Signal Analysis macros (McCowan 1995), which take 60 equidistant measurements of time and frequency at maximum amplitude from within each identified call. This technique measures at the fundamental frequency ($F0$), which is normally the highest amplitude section of a call, although it allows variance from the $F0$ when maximum amplitude is elsewhere, such as in the harmonics. To ensure consistent sampling, harmonics were removed so that only the $F0$ was selected for analysis. Acoustical measurements taken on each call included peak frequency (Hz), frequency range (Hz), duration (ms), jitter factor (a weighted measure of the amount of frequency modulation; Mitani & Brandt 1994), peak amplitude (dB), and amplitude range (dB; Table 1).

Statistical Analyses

Analyses focused on two levels: the group of 12 subjects as a whole and each of the three rank classes: high ($N = 2$), middle ($N = 4$) and low ($N = 6$). Kolmogorov–Smirnov one-sample tests were performed on each set of acoustic data to check for normal distribution, given the small sample sizes. The frequency range, duration, jitter factor and amplitude range data were skewed, so the data were log-transformed to perform appropriate parametric tests. After log transformation, the amplitude range and jitter factor values were more normally distributed but the frequency range and duration values remained moderately skewed. P values were Bonferroni-adjusted in the multivariate ANOVA post hoc tests to conservatively correct for multiple comparisons. Means and standard errors (SEs) given are of untransformed data.

RESULTS

Call Production

We recorded 8266 calls, of which we analysed a subset of 1042 (see Methods) for acoustic parameters. All 8266 calls were included to determine individual and average counts of call production. The data were first examined for production differences between food quantities. All subjects called more for larger amounts of food ($\bar{X} \pm SE = 52.87 \pm 12.33$) than for smaller amounts across all conditions, including alone (28.48 ± 7.51; paired t test: $t_{11} = 3.68$, one-tailed, $P = 0.004$). The number of calls an individual produced was dependent on her own rank within the hierarchy, classified as high, middle, or

Table 1. List of acoustic variables and their definitions

Acoustic parameter	Description
Mean frequency (Hz)	Average frequency across call
Frequency range (Hz)	Peak frequency minus minimum frequency
Duration (ms)	Temporal distance of call
Jitter factor	Calculated variable that represents a weighted measure of the amount of frequency modulation, by calculating the sum of the absolute value of the difference between two sequential frequencies divided by the mean frequency. The sum result is then divided by the total number of points measured −1 and the final value is obtained by multiplying it by 100 (Mitani & Brandt 1994)
Mean amplitude (dB)	Calculated as average amplitude across call
Amplitude range (dB)	Calculated as peak amplitude minus minimum amplitude

low (one-way ANOVA, Brown–Forsythe corrected: $F_{2,168} = 709.31$, $P < 0.001$). Higher-ranking subjects called less ($\overline{X} \pm SE = 15.57 \pm 4.10$) than did either mid-ranking (50.36 ± 5.07; Bonferroni post hoc test: $P = 0.002$) or low-ranking subjects (50.05 ± 7.30; $P = 0.005$; Fig. 2).

To assess whether audience composition had an effect on calling, we conducted a three-way mixed repeated measures ANOVA. Audience condition (alone, low-ranking female, high-ranking female, high-ranking male, group) and food quantity (large, small) were the within-subjects factors, and caller rank (high, middle, low) was the between-subjects factor. There was a significant main effect only for food quantity (Greenhouse–Geisser corrected: $F_{1,7} = 8.97$, $P = 0.015$).

To evaluate differences between rank classes and how audience size affected calling behaviour, we performed a three-way mixed repeated measures ANOVA, with audience size (none, partner, group) rather than audience condition, and food quantity (small, large) as the within-subjects factors, and caller rank (high, middle, low) as the between-subjects factor. There was a main effect for food quantity ($F_{1,7} = 9.01$, $P = 0.038$ and audience size ($F_{2,18} = 3.94$, $P = 0.038$) as well as a significant interaction between audience size and food ($F_{2,14} = 5.80$, $P = 0.011$).

Post hoc tests revealed that subjects generally called more for larger audiences (Fig. 3). High-ranking subjects tended to call more for a group audience ($\overline{X} \pm SE = 64.25 \pm 13.25$) than for either the partner audience (9.09 ± 5.09) or when they were alone (4.25 ± 3.75). Due to small sample size in the high-rank group, these post hoc tests were not significant.

Acoustic Parameters

We analysed the following acoustic characteristics of the subjects' calls: mean frequency, frequency range, duration, jitter factor, mean amplitude and amplitude range. We compared the acoustic characteristics of the subjects' calls under the same conditions used to examine call production to evaluate whether the two sets of measurements reflected similar trends. For example, if a low-ranking subject produced more calls in the presence of a dominant animal, did her mean frequency or jitter factor increase in value as well?

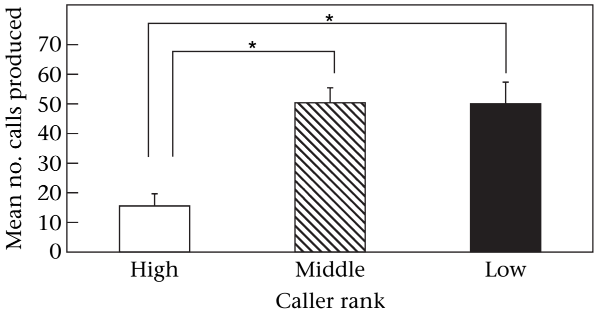

Figure 2. Comparison of mean number of calls produced in the presence of food, averaged across all quantities. *$P < 0.05$.

An overall multivariate ANOVA showed that caller rank had an effect on all dependent variables (mean frequency: $F_{2,1013} = 4.65$, $P = 0.01$; frequency range: $F_{2,1013} = 7.99$, $P < 0.0001$; duration: $F_{2,1013} = 6.77$, $P < 0.001$; jitter factor: $F_{2,1013} = 58.79$, $P < 0.0001$; mean amplitude: $F_{2,1013} = 18.99$, $P < 0.0001$; amplitude range: $F_{2,1013} = 3.51$, $P = 0.03$; Table 2). Audience composition (alone, low-ranking female, high-ranking female, high-ranking male, group) had an effect on mean frequency ($F_{4,1013} = 7.96$, $P < 0.0001$), frequency range ($F_{4,1013} = 3.46$, $P = 0.008$) and jitter factor ($F_{4,1013} = 2.81$, $P = 0.024$), but not on duration ($F_{4,1013} = 0.616$, $P = 0.651$), mean amplitude ($F_{4,1013} = 1.81$, $P = 0.124$), or amplitude range ($F_{4,1013} = 1.02$, $P = 0.393$).

Just as we had examined call production data for subject rank effects, we also did so for the acoustic data. Bonferroni post hoc tests from the original multivariate ANOVA revealed that for all acoustic parameters except amplitude range, the high-ranking subjects generally had lower values than did the middle- or low-ranking subjects (Table 2).

Based on these differences, it was logical to conduct the rest of our tests within each rank class. The high-ranking subjects did not modify their calls along any acoustic variable for different audiences. The mid-ranking subjects changed along five variables as a function of audience: mean frequency ($F_{4,551} = 3.57$, $P = 0.007$), frequency range ($F_{4,551} = 6.31$, $P < 0.0001$), jitter factor ($F_{4,551} = 2.92$, $P = 0.021$) and mean amplitude ($F_{4,551} = 3.81$, $P = 0.005$). The largest differences were found in the jitter factor and mean amplitude of their calls, which were highest when they were alone (Table 3).

Audience had an effect on all acoustic parameters except amplitude range in the low-ranking subjects: (mean frequency: $F_{4,337} = 13.99$, $P < 0.001$; frequency range: $F_{4,337} = 5.50$, $P < 0.00$; duration: $F_{4,337} = 6.43$, $P < 0.001$; jitter factor: $F_{4,337} = 2.48$, $P = 0.044$; mean amplitude: $F_{4,337} = 6.53$, $P < 0.00$). Post hoc tests revealed a particularly strong increase in value for mean frequency, frequency range and mean amplitude: these were highest when the audience consisted of another low-ranking animal (Table 4).

A correlational analysis was performed to determine whether call production and acoustic parameters similarly measure the subjects' behaviour. Number of calls produced was positively correlated with call duration (Pearson's correlation: $r_{106} = 0.33$, $P < 0.05$) and mean amplitude ($r_{106} = 0.32$, $P < 0.05$) only. Call production did not significantly correlate with mean frequency ($r_{106} = 0.07$, $P = 0.464$), frequency range ($r_{106} = 0.009$, $P = 0.923$), jitter factor ($r_{106} = 0.129$, $P = 0.184$), or amplitude range ($r_{106} = 0.100$, $P = 0.304$).

DISCUSSION

Brown capuchin monkeys' vocalizations varied according to the composition of their audience. These data generally support the findings of numerous studies (Sherman 1977; Gyger et al. 1986; Evans & Marler 1994; Caine et al 1995; Blumstein & Armitage 1997; Brosnan & de Waal 2003a; Matos et al. 2003; Striedter et al. 2003) in that

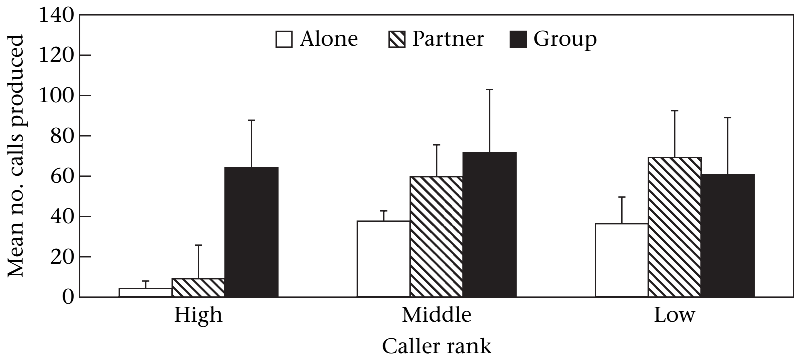

Figure 3. Effect of audience size on call production.

the presence or absence of a conspecific audience affected call production. This study goes further, however, in two respects: the audience varied in controlled ways and acoustical components of calls were investigated.

Call Production

Female capuchins called more in the presence of greater amounts of food, as do many other species (Hauser & Wrangham 1987; Evans & Marler 1994; Caine et al. 1995; Wauters & Richards-Yris 2003). This result is contrary to what Di Bitetti (2005) found in wild brown capuchins; food quantity differences did not affect calling rates, only latency to call. This difference may be due to experimental constraints, such that in a captive situation, variable latency is nonexistent because of an ever-present, constantly visible audience.

Brown capuchins may become more aroused by an abundance of food and vocalize to reflect this arousal. It is also possible that a more abundant food source elicits more calling to attract conspecifics, as Di Bitetti (2001) found in brown capuchins in the wild. The variation observed in our experiment may not be the result of a conscious awareness of an audience and full control over calling behaviour, but is probably the result of learning. Functionally, however, these calls could announce the presence of food to group members at a distance. Through playback experiments, Di Bitetti (2003) found that upon hearing food-associated calls given by an individual at a food source, group members moved towards the caller, but they did not do so when they heard similar but nonfood types of calls. It remains less clear what benefits signallers receive by attracting others to a food source and partially sacrificing their own share, but signallers may obtain indirect benefits by alerting relatives to the presence of food (Hauser & Marler 1993a; Judd & Sherman 1996). More direct benefits include decreased predation (Elgar 1986) or foraging benefits if call recipients cooperatively defend resources (Heinrich & Marzluff 1991; Wilkinson & Boughman 1998). Reciprocal exchange is also a possibility, which has been found in a grooming context in this species (Parr et al. 1997). Experimental work with food-associated calls and audience effects in the wild (Di Bitetti 2003) has revealed that this food-associated call does attract others instead of repelling them, as does the huh vocalization during foraging in white-faced capuchins. Further studies with controlled audience reactions will help to clarify why these animals call variably depending on the social environment.

That the females called most for a group audience may be attributable to the group size, but we did not exclude kin from this group, which leaves open the possibility that females call preferentially to kin, as Hauser & Marler (1993a, b) suggested for rhesus macaques. This last possibility needs to be formally tested in capuchins, but the results from the highest-ranking females in our study lend support to this idea because they rarely called for any audience other than the one including their kin. Even though this audience also contained dominant males, kin may still be a potential influence, as suggested by Hauser & Marler's (1993a, b) finding that when feeding, females call more in the presence of kin than in the presence of nonkin. The cost associated with calling can be

Table 2. Mean ± SE values for all acoustic variables, by rank class, and results of post hoc comparisons for each variable

	Subject rank			Comparison *P* value	
Acoustic variable	High	Middle	Low	High < middle	High < low
Mean frequency (Hz)	1081.55±13.03	1125.43±5.96	1115.81±9.00	0.011	0.155
Frequency range (Hz)	126.16±9.76	155.84±5.43	163.82±6.54	0.095	0.002
Duration (ms)	128.93±3.64	145.26±3.13	161.24±3.32	0.342	0.000
Jitter factor	0.79±0.04	0.94±0.03	1.34±0.38	0.077	0.000
Mean amplitude (dB)	−36.09±0.48	−32.54±0.34	−34.67±0.33	0.000	0.517
Amplitude range (dB)	24.85±1.08	28.44±0.53	15.33±2.99	0.630	1.000

Table 3. Selected acoustic post hoc comparisons for mid-ranking subjects

Acoustic variable	Comparison groups	*P*
Jitter factor	Alone > group	0.014
	Alone > high rank	0.002
	Alone > low rank	0.004
Mean amplitude	Alone > group	0.002
	Alone > high rank	0.002
	Alone > low rank	0.022

P values for Bonferroni post hoc comparisons are shown.

high, especially in the presence of a dominant individual who will claim the food from the caller (Di Bitetti & Janson 2001). The ultimate benefits of calling in the presence of desirable food for a dominant audience and for kin are different, however, although the proximate cost, loss of food, is the same.

These results also lend partial support to the food ownership hypothesis, in that lower-ranking animals called more often than did higher-ranking ones, possibly to avoid aggressive theft attempts by the latter. Although direct evidence for the costs of calling, or lack thereof, has been scant, Gros-Louis (2004) suggested that low-ranking white-faced capuchins learn over time to call more in the presence of food because they receive less aggression from dominant individuals and experience fewer stolen food attempts, a hypothesis that is echoed for brown capuchins by Di Bitetti (2001). The fact remains, however, that low-ranking individuals in our study did call at high rates upon food discovery, potentially alerting others and attracting group members to food, even if the primary aim was to avoid stealing and aggression. Food ownership and food announcement thus do not have to be mutually exclusive.

Acoustic Parameters

Morton's (1977) motivation-structural rules suggest that as an animal becomes aroused its vocalizations will reflect that emotional state. If the animal enters a state of increased fear or anxiety, the acoustic frequency of its calls tends to increase. Other acoustic characteristics such as jitter would also be expected to increase in a heightened emotional state (Scherer 1989). We thus predicted that if a monkey experienced anxiety while eating in the presence of a particular audience, then some acoustic features of its calling behaviour would reflect this change in state. Thus, if call production rose for one condition, we expected to see an increase in value for mean frequency and jitter. The results did not wholly support this prediction and were inconsistent (probably because of strong individual differences, given the sample sizes within each rank class). Call production and two of the six acoustic features, duration and mean amplitude, were positively correlated, such that if call production rose under any condition, the length and loudness of the calls tended to increase as well.

Table 4. Selected acoustic post hoc comparisons for low-ranking subjects

Acoustic variable	Comparison groups	*P*
Mean frequency	Low rank > alone	0.000
	Low rank > group	0.000
	Low rank > high rank	0.000
Frequency range	Low rank > alone	0.001
	Low rank > group	0.020
	Low rank > high rank	0.000
Mean amplitude	Low rank > alone	0.029
	Low rank > group	0.206
	Low rank > high rank	0.003

P values for Bonferroni post hoc comparisons are shown.

Capuchins may be able to control some aspects of their calling behaviour, which would help explain the mid-ranking females' behaviour. These females produced fewer calls when they were alone, but these calls had higher amplitudes than in any other condition. A proximate explanation for this result is that the female might be less inclined to produce many calls while alone because it would attract unwanted attention (e.g. from neighbouring troops or predators). Although she may produce fewer calls, they may be louder to ensure that they are sufficiently salient for attracting groupmates.

The high-ranking females, on the other hand, modified calling rate only. They may not have expended as much acoustic energy (i.e. decibel level, number of calls) as did females of lower rank and relied mainly on calling rate to communicate information about the presence of food. This result supports the food ownership hypothesis in that the calls of high-ranking individuals do not need to be as frequent or as acoustically salient as those of lower-ranking individuals, because they are at low risk for aggressive approaches.

The calls of the lower-ranking subjects were most salient (i.e. mean frequency, frequency range and mean amplitude were highest) when they were with audiences that were also of low rank. The food ownership hypothesis would explain these results; if the call signals a willingness to be approached (Di Bitetti 2003), then perhaps these subjects felt more comfortable with those close to their own rank and signalled more strongly to them than to others. It is also possible that the audience's behaviour affected the subjects' calling. Although the audience was never able to physically approach the caller, they could see each other at all times, and if the audience called or made threatening gestures, this could have affected the characteristics of call production as well as acoustic structure. This aspect of behaviour was beyond the scope of our study but remains an important effect to experimentally investigate in this species, given what we know about wild brown capuchin behaviour (Di Bitetti & Janson 2001; Di Bitetti 2003).

An additional problem with interpreting our results is that calls were recorded and analysed from the entire 5-min testing session, regardless of whether subjects took the entire time to finish eating the food. Thus, calls produced during the high-food condition may have been more frequent because the monkeys spent more time eating in the high-food condition than in the low-food condition.

Call production and acoustic characteristics do not reflect the same pattern, so determining which aspect more accurately indicates the animals' motivation is difficult. Most other studies of food calling have examined rates of calling and not acoustic structure. Although Morton's (1977) motivation-structural rules do not indicate that higher values for frequency (or other acoustic variables) require an increase in call production, it is logical to hypothesize that the two might be correlated. Perhaps, then, the animals have greater voluntary control over call production than they do over the acoustic nature of their calls. The reverse could also be argued, that acoustic modification is more amenable to control than is call production. This study did not allow us to determine the extent of control over either, but this issue is a ripe topic for future work in this area.

Current work with brown capuchins and a value exchange paradigm (Brosnan & de Waal 2003b, 2004) suggests that females of this species are more discriminating with food than are males and are better able to track what is being exchanged and who is getting how much. Repeating this experiment with males as subjects may similarly show that males are more indiscriminate with food calling than are females and call less consistently according to their own rank and the nature of their audience. Females, as the 'ecological sex' (Wrangham 1980), compete over access to food rather than to mates and influence the dynamics of reproduction through mate choice. Females are thus more likely to food-call preferentially to kin, because females are certain which offspring are theirs, whereas males, because of ambiguous paternity, share more widely with juveniles (de Waal 1997b).

Capuchins, then, are capable of modifying their calls in various ways depending on the nature of their audience. Whether they have more control over the production or acoustic nature of their calling remains to be determined. Despite this ambiguity, the monkeys' consistent differences in calling based on their place in the hierarchy, and the composition and size of their audience provide strong evidence for an audience effect on food calls in this species.

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