Food-associated calls in chimpanzees: responses to food types or food preferences?

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Chimpanzees produce specific vocalizations, ‘rough grunts’, when encountering food, and it has been suggested that these calls vary acoustically depending on the food type discovered by the caller. Nearby listeners often behave as if the calls are meaningful to them, indicating that the calls may function as referential labels for particular foods. We investigated whether rough grunt variants are the result of callers responding to specific food types or relative food preferences. We recorded calls from captive individuals in response to nine different food items, which could be ranked as high, medium or low preference. Individuals consistently produced three acoustically distinct grunt variants to the three food preference classes. There was no evidence that chimpanzees produced individual labels for food types of low and medium preference. However, calls to high-preference food types differed significantly in their acoustic structure. These acoustic patterns remained stable over trials, suggesting that rough grunts have the potential to serve as semantic labels for individual high-preference food types. We were unable to replicate these findings with a set of recordings from the wild, although most other aspects of calling behaviour remained identical. We discuss these discrepancies between the wild and captivity and suggest that the emergence of referential labels for food items may be a by-product of the special circumstances found in captive settings.

Various bird and primate species produce acoustic signals when encountering food. These signals typically attract others to the feeding site, suggesting that callers must benefit in some way from their seemingly altruistic behaviour. It has been suggested that callers profit from the resulting increase in group size, if it reduces the costs of vigilance (Elgar 1986), it increases foraging efficiency (Brown et al. 1991), or it defends the food source from competing species (Bugynar et al. 2001). Finally, callers may benefit from attracting and helping relevant conspecifics, such as genetic relatives or potential mates (Trivers 1972).

Food-associated calls are also interesting from a comparative psychology perspective, as they sometimes provide a window into the mental processes underlying call production. In domestic chickens, *Gallus gallus domesticus*, for example, males produce food-associated calls, and calling is mediated by the nature and composition of the audience (Marler et al. 1986a, b; Gyger & Marler 1988; Evans & Marler 1994). These calls elicit anticipatory feeding behaviour in recipients, suggesting that the calls are meaningful to them in the sense that they predict the presence of food (Evans & Evans 1999).

Food-associated calls are also documented in nonhuman primates, and the underlying cognitive processes have been explored in some detail (e.g. Toque macaque, *Macaca sinica*: Dittus 1984; spider monkey, *Ateles geoffroyi*: Chapman & Lefebvre 1990; tufted capuchin, *Cebus apella*: Di Bitetti 2005; white-faced capuchin, *Cebus capucinus*: Boinski & Campbell 1996; Gros-Louis 2003), although little is known about the kind of information conveyed by these calls. In domestic chickens, males are able to adjust their calling rate as a function of the quality of a food source, perhaps the result of different levels of arousal. This may provide useful information for recipients, which goes beyond merely signalling the presence of food (Marler et al. 1986b; Gyger & Marler 1988). A number of New World monkeys appear to follow the same principle: cottontop tamarins, *Saguinus oedipus*, and white-faced capuchins increase call rates to food they prefer, independent of quantity (Elowson et al. 1991; Roush &

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Snowdon 2000; Gros-Louis 2003). In rhesus macaques, *Macaca mulatta*, however, the calling rate is not related to food preference but apparently varies with hunger level (Hauser & Marler 1993a, b). Instead, differences in preference are reflected in changes in the acoustic structure of the calls (Hauser & Marler 1993a) and listeners appear able to gain information about the quality of the discovered food source from these calls (Hauser 1998).

Chimpanzees, *Pan troglodytes*, also vocalize when eating or approaching food (Goodall 1965, 1968, 1986; Reynolds 1965). Others sometimes orient towards or approach the calling animal (Goodall 1968, 1986), suggesting that they extract some information from the calls. Acoustically, these food-associated calls grade from soft grunts to high-pitched shrieks, typically described under the umbrella term 'rough grunts' (Marler & Tenaza 1977, page 987).

The mechanisms underlying call production are not well described and the reasons why chimpanzees produce these calls remain uncertain. However, we do know that captive chimpanzees are more likely to give rough grunts when discovering a large and divisible food source compared to a small or indivisible one (Hauser et al. 1993) and that callers may adjust call production depending on the audience present (*P. troglodytes*: Hauser & Wrangham 1987; *P. paniscus*: Van Krunkelsven et al. 1996).

There is some controversy concerning the nature of the information encoded by chimpanzee rough grunts. One study suggested that individuals produce acoustically distinct rough grunt variants to different food types and that these signals served as referential labels for recipients (Hallberg et al. 2003). In another study, individuals were allowed to search for either apples or bread at two different locations, after a playback of a group member's rough grunts given to either apples or bread. The focal animal's foraging behaviour was guided by the type of grunts played back, demonstrating that rough grunt variants informed recipients about the nature of a food source encountered by the caller (Slocombe & Zuberbühler 2005). Both studies are consistent with the idea that chimpanzee rough grunts inform recipients about the type of food encountered by the caller. If chimpanzees were labelling specific food types, then this would represent a rather sophisticated type of functionally referential communication, requiring substantial degrees of social learning by both the signaller and recipient. Alternatively, a more parsimonious hypothesis suggests that the results of these previous studies can also be explained by calls reflecting an individual's assessment of the relative preference of the food encountered. To test the two hypotheses, we examined data collected from a captive group of chimpanzees housed at Edinburgh Zoo, U.K., and from wild chimpanzees of the Sonso community in Budongo Forest, Uganda.

METHODS

Study Sites

Edinburgh

K.S. collected data for 4 months between May and September 2004 from a captive group of chimpanzees housed at Edinburgh Zoo, U.K. The group consisted of three adult, one subadult and two juvenile males and four adult and one subadult females, 5–43 years old, and was housed in an outdoor area (1452 m^2) connected by a tunnel to a 90-m^2 indoor area. All individuals had free access to both areas through the tunnel at all times except during cleaning. They were fed up to eight times each day at irregular intervals. The chimpanzees were regularly fed over 20 different types of food and they received the nine foods used in this study at least twice a week in routine feeds during the study period. Data were collected during feeding events in the outdoor enclosure, when food was scattered over the enclosure by a caretaker.

Budongo

K.S. collected data for a total of 6 months, during the dry seasons (January–March) of 2003 and 2004 from the Sonso community of the Budongo Forest Reserve, Uganda (Reynolds 1992, 2005). Budongo Forest covers an area of 428 km^2 of moist, semideciduous tropical forest, between 1°35′ and 1°55′N and between 31°08′ and 31°42′E (Eggeling 1947). The study site is at an altitude of 1100 m and has an annual rainfall of about 1600 mm. Habituation to humans started in 1990. Provisioning has never been used. At the time of the study, the Sonso community consisted of 53 individuals with nine adult males and 17 adult females, four subadult males and two subadult females, and 21 juveniles and infants.

Data Collection

Food preference hierarchy

Edinburgh. To determine the food preferences of the captive study animals, we systematically tested nine food types (bread, banana, mango, grape, plum, chow, apple, greens and carrot) in pairwise comparisons. During these events, a caretaker scattered two types of foods in roughly equal amounts throughout the outdoor enclosure. The feeding events were filmed and the first choice of each individual was recorded. The chimpanzees were habituated to the presence of the observer and the video camera before data collection began. We recorded the choices of four individuals (Louis, Quafzeh, Emma, Kilimi) from a total of 55 feeding events ($N_{\text{Louis}} = 52$; $N_{\text{Quafzeh}} = 49$; $N_{\text{Emma}} = 43$; $N_{\text{Kilimi}} = 46$). For each individual, we determined a food preference hierarchy based on his or her choices, by counting how many times a particular food item was chosen relative to the other eight food types. These scores were then converted to percentages, ranging from 100% (i.e. always chosen above all other eight foods) to 0% (i.e. never chosen in comparison to the other eight foods). The foods were then ranked for each individual on the basis of the percentage scores.

Budongo. We identified the three most highly preferred food items during the dry season study period, based on the proportions of the chimpanzees' feeding time spent consuming these items: 30.9% *Cynometra alexandri* (CYN), 24.3% *Ficus exasperata* (Fe), 15.6% *Ficus sur* (FSu) (data from Bates 2005). It was not possible to determine food preferences objectively in the wild population, in a comparable way to the captive population. However, based on the feeding time data we were confident that the three foods chosen could be ranked as medium–highly preferred foods. We recorded the rough grunts produced by four adult males in response to these three foods.

Recording Rough Grunts

For the Edinburgh chimpanzees, rough grunts were recorded from individuals feeding exclusively on one type of food in the outdoor enclosure. Vocalizations were recorded from a range of 5–20 m. For the Budongo chimpanzees, K.S. tried to follow a focal individual all day to record rough grunts while the individual was feeding from the three selected species. Recording distances varied from 5 to 30 m. All recordings were made with a Sennheiser directional microphone (wild: ME67/K6; captive: MKH816) and a Sony TCD-D8 portable DAT recorder. Recordings were transferred digitally from the DAT recorder on to a PC (Toshiba, Celeron 1.8 GHz) with a sampling rate of 44.1 kHz, 16 bits accuracy using Cool Edit Pro LE (Syntrillium software Corporation, Phoenix, AZ, U.S.A.).

Selection of Calls for Analysis

Edinburgh

We excluded all calling bouts that suffered from heavy interference, from either other chimpanzee calls or extraneous background noise such as other zoo animals or visitors. This resulted in a set of 76 calling bouts, which were suitable for acoustic analysis (range 1–3 bouts/individual per food type). We selected the first 15 s of each bout starting from when the focal chimpanzee first made physical contact with the food. Within these segments, we selected the first three calls that were free from other chimpanzee calls or masking noise. We analysed calls from four chimpanzees, one from each of four age–sex classes (Louis, adult male; Emma, adult female; Quafzeh, subadult male; Kilimi, subadult female).

Budongo

We recorded calls from four adult males (Black, Maani, Nick and Zefa). As with the captive individuals, we selected the first 15 s of a calling bout once the chimpanzee was collecting food or feeding. We then measured the first three calls per bout that were free from other chimpanzee calls and other masking noise. This resulted in a total of 38 bouts from the four males (range 1–6 bouts/individual per tree species).

Acoustic Analyses

For acoustic analyses, we used Praat Version 4.2.23 (www.praat.org) with the following settings: window length: 0.005 s; dynamic range: 70 dB. Rough grunts consisted of both voiced and unvoiced calls. For unvoiced calls, it was impossible to determine the fundamental frequency, so we excluded from further analyses all measures related to this otherwise commonly used parameter. The following four measures could be reliably taken from all calls: (1) temporal parameters: duration of call (s): duration from beginning to end of main acoustic energy; intercall duration (s): time from the end of the measured call to the beginning of the next call in the call sequence; (2) spectral parameters: peak frequency (Hz): frequency at which most acoustic energy was present in the call; first formant frequency (F1) (Hz): mean frequency of the first formant across the call for which the first formant was present (M.J. Owren, unpublished software). There is an important difference between these two spectral measurements. In primates and other mammals, the larynx is the main acoustic production device from where sound passes through the supralaryngeal vocal tract. Depending on its constrictions, the vocal tract has differing resonant modes that selectively allow specific frequencies to pass and radiate through the mouth or nostrils into the environment. These vocal tract resonances have been termed ’formants’ (Fant 1960). While ‘peak frequency’ simply refers to the overall location of acoustic energy in the signal, ‘formant frequency’ refers specifically to the filtering properties of the vocal tract only. Unequivocal identification of formants requires an analysis technique that separates the effect of the glottal source from the effect of the vocal tract (Owren & Bernacki 1998).

Statistical Analyses

Call structure and food preferences

To establish whether there was any relation between the acoustic structure of the rough grunts and individual food preferences, we analysed a sample of 108 calls from captive animals (4 individuals × 3 preference categories × 3 bouts × 3 calls). Each individual contributed an equal number of bouts from each quality category, but the food types within those categories were chosen randomly. We then ran an analysis of covariance (ANCOVA) on the 108 calls with peak frequency, call rate, duration and first formant frequency entered as covariates and individual entered as a fixed factor. These independent variables were used to predict the percentage preference rating of the food that elicited the calls.

Call structure and food types

To examine whether call structure varied systematically with food type, we investigated whether chimpanzees were able to encode information about particular food types within each preference category. We analysed high-, medium- and low-preference food types separately in this way, to minimize the confounding effects of preference. First, rough grunts given to the highly preferred foods, bread, mango and banana, were analysed to investigate whether calls varied reliably with type of food. Each of the four captive individuals contributed one bout (containing three calls) to each food type. Thus a total of 36 calls were analysed, with each food type represented by 12 calls. For the rough grunts given to the medium-preferred foods, grapes, plums and chow, each of the four individuals contributed one bout (containing three calls) to each food type. Two exceptions to this were the calling bouts given to plums by Kilimi and Quafzeh, which contained only two measurable calls each. Thus a total of 34 calls were analysed, with grapes and chow represented by 12 calls each and plums represented by ten calls. Finally, we analysed rough grunts given to the least preferred foods, apples, greens and carrots. The two female chimpanzees were never observed giving rough grunts to greens or carrots; therefore, this analysis was based only upon the data from the two males. A total of 18 calls were analysed, with each food type represented by six calls. If an individual had more than one suitable calling bout for each food type, we randomly selected the bout to be used (range 1–3).

We conducted mixed-design analyses of variance (ANOVA) to investigate whether the four acoustic variables varied reliably with the type of food that elicited the calls. The type of food was entered as the within-subjects variable (three conditions) and individual was entered as the between-subjects variable. We then conducted direct discriminant function analyses to assess how well the four acoustic variables, when taken together (providing a quantitative description of the sound), could discriminate between the food types associated with the call.

To obtain a more representative view of the larger available data set, we generated three randomly chosen data sets for each food type analysis. This allowed us to run three iterations for each food type analysis, thereby using a wider selection of randomly chosen calls than a single iteration permitted.

The data sets used in the food type analyses were smaller than those used in the first food preference analysis and were therefore associated with lower levels of statistical power. To provide a fair and direct comparison of the two competing hypotheses, matching food preference data sets were produced for each of the nine food type analyses (3×3 iterations). These data sets contained the same number of calls from each individual as each of the ‘type’ analyses. This meant that the statistical tests carried out to test each hypothesis had identical levels of statistical power. The calls in each of the matching ‘preference’ data sets were randomly selected in the same way as reported for the first preference analysis.

RESULTS

Food Preference Hierarchy

For the Edinburgh chimpanzees, we tested preferences to all nine foods in all possible combinations, i.e. 36 pairwise comparisons. Some pairings were tested multiple times. There was high consistency in individual choices over time, suggesting that individual preferences were stable. The four study animals showed a high degree of agreement on preference, with differences appearing between individuals only for the high-preference foods (Table 1). On the basis of the mean group ratings, these nine food items were divided into three broad group preference categories: high (67–100%), medium (34–66%) and low (0–33%).

Do Rough Grunts Label Food Preference?

Rough grunts produced in response to foods of different preference categories had subtly different acoustic structures (Fig. 1). Visual examination of the spectrograms indicated that high-preference foods elicited calls with a clear harmonic structure, a high peak frequency and a long duration (Fig. 1a), whereas low-preference foods elicited noisy signals with no clear harmonic structure, a low peak frequency and a short duration (Fig. 1c). Medium-preference foods elicited calls with structures that were intermediate to these two variants (Fig. 1b).

Figure 2 illustrates the graded nature of the acoustic structure of the rough grunts. Peak frequency increased as preference increased ($R^2 = 0.3925$, $P < 0.001$). Duration ($R^2 = 0.0794$, $P = 0.003$) and first formant frequency ($R^2 = 0.0692$, $P = 0.005$) also produced positive relations with preference. There was no obvious relation between the intercall duration and preference ($R^2 = 0.0005$; $P = 0.964$).

Table 1. The individual food preferences of the four focal captive chimpanzees and the average preferences of this group of four animals

		Individual									
		Emma		Kilimi		Louis		Quafzeh		Group mean	
Food preference	Food type	%	Rank	%	Rank	%	Rank	%	Rank	%	Rank
High	Bread	100.0	1	100.0	1	81.3	2	100.0	1	95.3	1
	Mangos	75.0	3	87.5	2	100.0	1	87.5	2	87.5	2
	Bananas	81.3	2	75.0	3	75.0	3	75.0	3	76.6	3
Medium	Grapes	68.8	4	56.3	4	62.5	4	62.5	4	62.5	4
	Plums	50.0	5	50.0	5	56.3	5	50.0	5	51.6	5
	Chow	37.5	6	37.5	6	37.5	6	37.5	6	37.5	6
Low	Apples	25.0	7	31.3	7	25.0	7	25.0	7	26.6	7
	Greens	12.5	8	12.5	8	12.5	8	12.5	8	12.5	8
	Carrots	0.0	9	0.0	9	0.0	9	0.0	9	0.0	9

The percentage associated with each food represents the number of times that food was chosen over the other eight foods in pairwise comparisons. The ranks are assigned on the basis of the percentages for each individual.

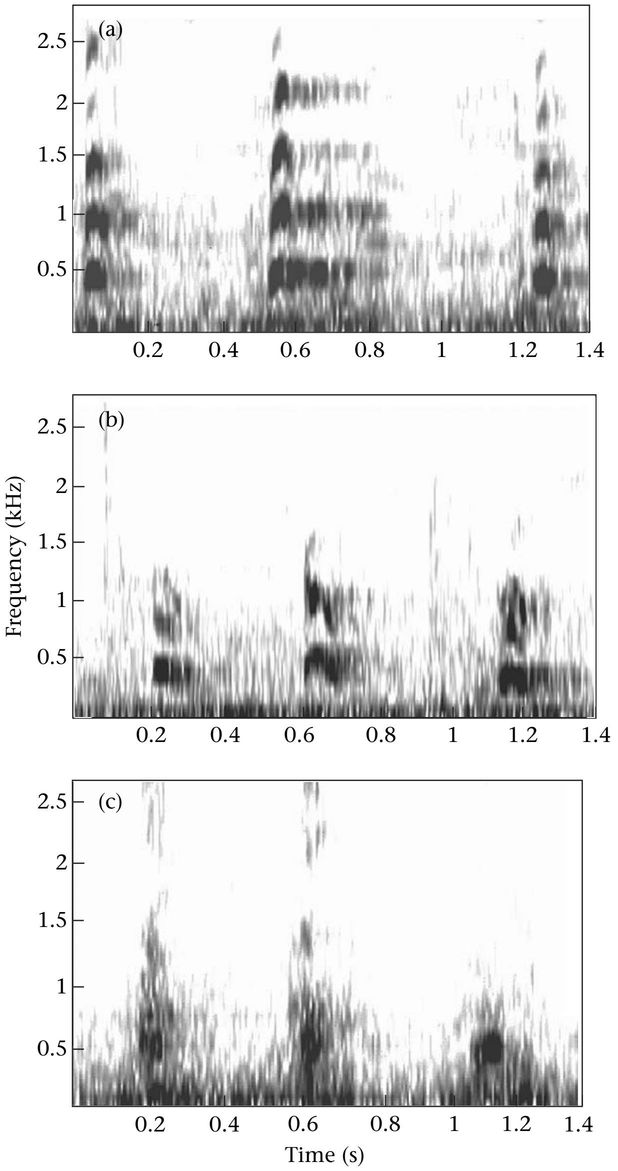

Figure 1. Example time–frequency spectrograms illustrating rough grunts given by captive adult male Louis in response to (a) bread, (b) chow and (c) carrots. Bread is a high-preference food, chow a medium-preference food and carrots a low-preference food. The spectrograms depict a representative 1.4-s section of a 15-s calling bout given to bread, chow and carrots, respectively. Acoustic energy is depicted by the darkness of the image. These calling bouts were selected on the basis of their clarity and freedom from interference from other sources of noise such as other chimpanzee calls.

An ANCOVA was run on 108 calls with peak frequency, intercall duration, duration and first formant frequency entered as covariates and individual as a fixed factor. The variance inflation factors (VIF) of the independent variables were less than 1.5, indicating that colinearity was not a problem. When combined in one model the variables successfully predicted the individuals' preference ratings for the food that elicited the grunts ($F_{7,100} = 11.70$, $P < 0.001$, $R^2_{\text{adj}} = 0.452$), indicating that the acoustic structure of the rough grunts varied significantly with individual preferences. Peak frequency made the most important contribution ($F_{1,100} = 58.73$, $P < 0.001$), followed by call duration ($F_{1,100} = 3.29$, $P = 0.073$). Intercall duration and first formant frequency did not vary significantly with preference (intercall duration: $F_{1,100} = 1.09$, $P = 0.304$; first formant frequency: $F_{1,100} = 0.02$, $P = 0.948$), consistent with the patterns observed in Fig. 2. Any systematic individual variation was controlled for in this analysis and individual did not make a significant contribution to the model ($F_{3,100} = 1.793$, $P = 0.153$).

These patterns remained consistent with the smaller preference data sets provided to match the food type analyses. More specifically, calls given to foods of the three different preference categories differed significantly in peak frequency (Table 2). In addition, more than half the analyses revealed significant differences in duration and intercall duration between the calls given to foods of different preference categories (Table 2). All the discriminant functions, derived from the four variables describing the acoustic structure of rough grunts given to high-, medium- and low-preference foods, explained a significant amount of variation between grunts given in response to foods from the three different preference categories (Table 3). The functions all correctly classified calls, according to the preference category of food that had elicited them, at a level significantly above that expected by chance (Table 3). This confirms that rough grunts given to foods of different preferences have consistently and significantly different acoustic structures.

Do Rough Grunts Label Food Type?

Results so far are consistent with the 'preference' hypothesis in demonstrating that the acoustic structure of rough grunts could be explained by individuals responding to low-, medium- or high-preference foods. However, it is also possible that the chimpanzees were producing acoustically distinct grunts to individual food types. Given the high correlation observed between food type and preference rating (Table 1), we had to control for preference to investigate whether rough grunts labelled specific food types. We therefore examined grunts given to food types within the high-, medium- and low-preference categories separately.

We found that different types of high-preference foods elicited rough grunts that differed subtly, but significantly, in their acoustic structures. The mixed-design ANOVAs revealed that the acoustic structure of bread, banana and mango calls varied significantly, especially with regard to the first formant frequencies and call durations (Table 2). This variation was sufficient for all of the discriminant function analyses to classify correctly the calls according to the type of food that elicited them at a level above that expected by chance (Table 3).

In contrast, there was no evidence that the rough grunts given to different types of medium- or low-preference foods differed in their acoustic structures. The mixed-design ANOVAs revealed that the grunts given to medium-preference foods, chow, plums and grapes, did not differ on any of the four acoustic variables (Table 2). This pattern

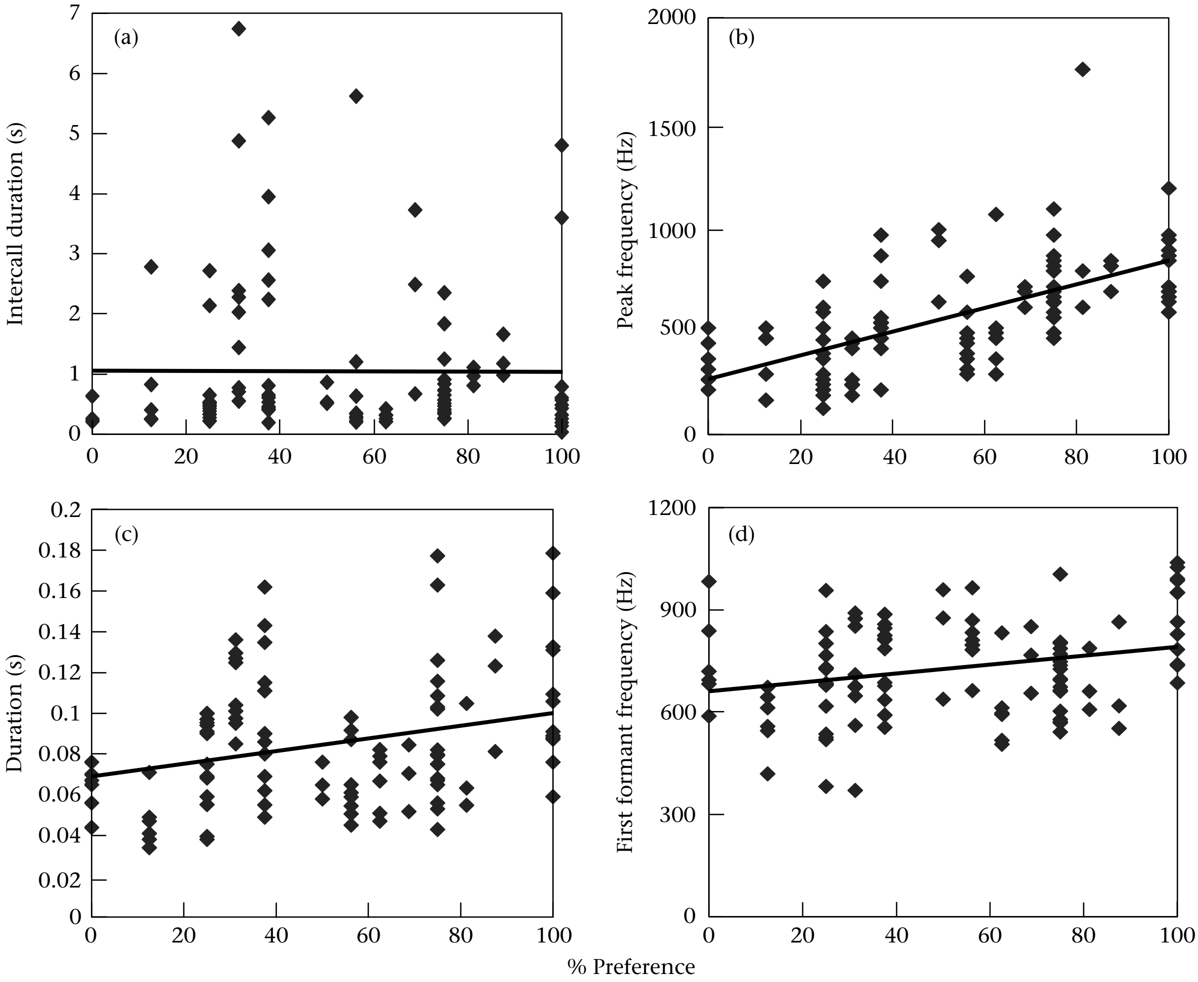

Figure 2. Scatterplots showing four acoustic measures that describe the calls elicited by different foods, plotted against the individual preference ratings for each food. Each data point represents a single call (108 calls in total). Each of the four individuals contributed nine bouts each containing three calls. (a) Intercall duration, $R^2 = 0.0005$, (b) peak frequency, $R^2 = 0.3925$, (c) duration, $R^2 = 0.0794$, (d) first formant frequency, $R^2 = 0.0692$.

remained stable across all three iterations we ran. Similarly, no significant acoustic differences were found between the grunts given to low-preference foods, apples, carrots and greens (Table 2). Discriminant function analyses were unable to discriminate correctly between calls given to plums, chow and grapes or between calls given to carrots, greens and apples (Table 3).

The results obtained so far indicate that chimpanzees, despite having a preference-driven calling system, can effectively label specific food types, at least within the highly preferred food class (bread, banana, mango). For this to be of theoretical importance (i.e. whether calls function as labels for food items), however, acoustic structures need to be consistent from one feeding event to the next. We thus compared the calls produced by three individuals, Emma, Louis and Quafzeh, to bananas and bread on 3 separate days (27 calls to bread and 27 calls to bananas, respectively: 3 individuals × 3 feeding events × 3 calls/bout). If the chimpanzees were labelling food types, then there should be no difference between the calls given in response to the three different feeding events. Consistent with this hypothesis, our mixed-design ANOVAs failed to reveal any significant differences in the acoustic structure of calls given to banana on the 3 days. The calls given to bread varied only in terms of the intercall duration ($F_{1,7} = 8.47$, $P < 0.05$). Cross-validated discriminant function analyses were equally unable to account for a significant amount of variance between the calls given to 'bread' or 'banana' in the three feeding events (bananas: Wilk's $\lambda = 0.808$; $\chi^2_8 = 4.792$; 22.2% correctly classified; binomial (0.33), two-tailed, $P = 0.324$; bread: Wilk's $\lambda = 0.453$; $\chi^2_8 = 17.810$; 48.1% correctly classified; binomial (0.33), two-tailed, $P = 0.148$).

Food-Associated Calls in Wild Chimpanzees

The data set composition for the wild chimpanzees was identical to the high-preference food type data set from the captive individuals ($N = 36$: 4 individuals × 3 foods × 3 calls/bout), which enabled us to make some direct comparisons. Rough grunts recorded from the wild chimpanzees, in response to the top three food species during the study period, were acoustically very similar to

Table 2. The results of mixed-design analyses of variance conducted to test differences between the acoustic structure of rough grunts given to foods of different types and foods of different preference categories

Data set	Iteration	Acoustic variable (*F* values)			
		Formant frequency	Peak frequency	Call duration	Intercall duration
High type (*N*=36)	1	6.38**	5.00* (1,9)	16.27***	4.20 (1,3)
Bread, mangoes, bananas	2	4.93*	0.24 (1,10)	1.76 (1,9)	1.76
	3	11.04**	1.45	5.31*	5.20* (1,3)
Mean		7.45	2.23	7.78	3.72
SD		3.19	2.47	7.56	1.77
Matched preference (*N*=36)	1	4.76	8.89*	5.86*	3.74 (1,3)
High, medium, low	2	11.25**	58.93*** (1,9)	4.96*	5.99* (1,3)
	3	1.96	15.17***	7.13*	8.97* (1,3)
Mean		5.99	27.66	5.98	6.23
SD		4.77	27.26	1.09	2.62
Medium type (*N*=34)	1	1.034	0.01	2.73	2.52
Grapes, plums, chow	2	1.85	2.06	0.28	0.06
	3	0.39	2.97	1.94	2.07
Mean		1.09	1.68	1.65	1.55
SD		0.73	1.52	1.25	1.31
Matched preference (*N*=34)	1	2.99	6.87*	6.12*	2.46 (1,3)
High, medium, low	2	4.37*	17.71***	1.29 (1,6)	5.14*
	3	2.93	18.75** (1,7)	0.98 (1,6)	5.16*
Mean		3.43	14.44	2.80	4.25
SD		0.81	6.58	2.88	1.55
Low type (*N*=18)	1	2.25	0.12	2.95	2.39
Apples, greens, carrots	2	2.03	0.72	3.82	2.44
	3	1.57	0.34	4.19	2.74
Mean		1.95	0.39	3.65	2.52
SD		0.35	0.30	0.64	0.19
Matched preference (*N*=18)	1	1.77	3.82	2.86	4.94*
High, medium, low	2	1.14	20.06**	40.75***	8.69* (1,1)
	3	12.69**	10.06* (1,4)	10.07**	1.27
Mean		5.20	11.31	17.89	4.97
SD		6.49	8.19	20.12	3.71

Food type or preference: within-subjects variable; individual: between-subjects variable; systematic effects of individual on acoustic measures were controlled by entering individual as a between-subjects variable, but this variable is not reported as it is not considered further. Degrees of freedom: High = 2,16; Medium = 2,12; Low = 2,10. If the assumption of sphericity was not met then Greenhouse–Geisser values were reported and the degrees of freedom associated with those analyses are shown in the table.
$^*P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$.

the ones given by captive chimpanzees to high- or medium-preference foods (Figs 1, 3, Table 4). The mean peak frequency and duration of the wild calls were intermediate to the mean values of high- and medium-preference foods in the captive individuals. Wild chimpanzees also gave rough grunts with intercall periods and first formant frequencies similar to those given by captive chimpanzees to high- and medium-preference types of food.

Our previous analyses showed that captive chimpanzees gave acoustically distinct rough grunt calls to three highly preferred food types. However, a mixed-design ANOVA revealed that the rough grunts elicited by CYN, Fe and FSu fruits did not differ in peak frequency ($F_{2,16} = 2.53$, $P = 0.111$), duration ($F_{1.0,8.2} = 2.04$, $P = 0.191$) or first formant frequency ($F_{2,16} = 0.39$, $P = 0.685$). The only parameter that differed significantly between the grunts given to the three wild food types was intercall duration ($F_{1.2,9.4} = 9.12$, $P = 0.012$). A discriminant function analysis was unable to account for a significant amount of variance between calls given to the three food types (Wilk's $\lambda = 0.705$, $\chi^2_8 = 11.00$, $P = 0.201$). The function correctly classified only 41.7% calls (cross-validated) according to the type of food that elicited them, a level expected by chance (binomial (0.33), $P = 0.252$, two-tailed).

DISCUSSION

This study has shown that chimpanzees produce rough grunt calls with different acoustic structures that vary according to the relative preference of the food encountered. Our analyses showed that chimpanzee rough grunts are a graded acoustic signal, in which differences in food preference have direct effects on the calls' acoustic structure (Fig. 2). Effects were primarily observed on the peak frequency and duration of calls, with highly preferred food eliciting long signals with high peak frequencies, whereas least preferred food elicited short signals with low peak frequencies. Medium-preference foods elicited calls with an acoustic structure intermediate

Table 3. The results of discriminant function analyses conducted to test whether the acoustic structure of rough grunts could determine which type or preference of food elicited the grunts

	Iteration	Wilk's λ	χ^2	% Correctly classified	*P*†
High type (*N*=36)	1	0.550	20.47**	50.0	0.048
Bread, mangoes, bananas	2	0.650	13.60	50.0	0.048
	3	0.420	27.35**	61.1	0.001
Mean		0.54	20.47	53.7	0.032
SD		0.12	6.88	6.41	0.027
Matched preference (*N*=36)	1	0.42	27.06**	66.7	0.001
High, medium, low	2	0.25	43.98***	66.7	0.001
	3	0.38	30.12***	61.1	0.001
Mean		0.35	33.72	64.8	0.001
SD		0.09	9.02	3.23	0.001
Medium type (*N*=34)	1	0.630	13.60	47.1	0.104
Grapes, plums, chow	2	0.810	6.29	30.6	0.540
	3	0.720	9.59	41.2	0.402
Mean		0.72	9.83	39.6	0.348
SD		0.09	3.66	8.36	0.223
Matched preference (*N*=34)	1	0.36	30.15***	67.6	0.001
High, medium, low	2	0.47	22.62**	52.9	0.026
	3	0.5	20.28**	52.9	0.026
Mean		0.44	24.35	57.8	0.018
SD		0.07	5.16	8.49	0.014
Low type (*N*=18)	1	0.320	15.47	55.6	0.082
Apples, greens, carrots	2	0.450	10.74	44.4	0.428
	3	0.390	12.57	55.6	0.082
Mean		0.39	12.93	51.9	0.197
SD		0.07	2.39	6.47	0.020
Matched preference (*N*=18)	1	0.17	24.07**	77.8	0.001
High, medium, low	2	0.10	30.58***	77.8	0.001
	3	0.19	22.22**	61.1	0.026
Mean		0.15	25.62	72.2	0.009
SD		0.05	4.39	9.64	0.014

Chi-square $df = 8$ (uncorrected for individual); cross-validated classification.
†Binomial test (0.33), two tailed.
$^{**}P < 0.01$; $^{***}P < 0.001$.

to these two call variants. Although rough grunts varied systematically with food preference, which consistently accounted for more of the variance in the acoustic structure of the calls than the type of food, our subsequent analyses showed that this vocal system is capable of incorporating more than just three preference categories. Within the highly preferred category, calls could potentially function as labels for individual food items: discriminant function analyses were able to classify correctly a significant number of rough grunts to bananas, bread and mangoes and these patterns remained stable over time. Rough grunts given by members of the free-ranging community at Budongo Forest in response to three preferred foods were acoustically very similar to the ones given by the captive individuals to medium- or high-preference foods. More complex comparisons were not possible because of the difficulties in accurately assessing food quality or preference in the wild.

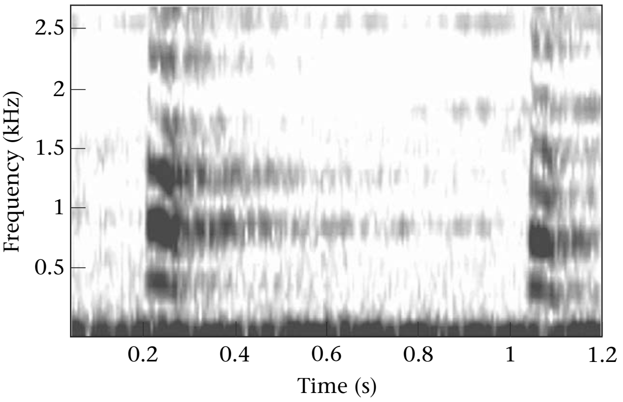

Figure 3. Example time–frequency spectrograms illustrating rough grunts given by wild adult male Black in response to *Ficus exasperata*. The spectrograms depict a representative 1.2-s section of a 15-s calling bout given while feeding on *F. exasperata*. Acoustic energy is depicted by the darkness of the image.

Psychological Mechanisms

The psychological mechanisms underlying call production in chimpanzees are not well understood. In chickens and some New World primates, differences in food preference affect calling rates, that is, the duration of intercall intervals. Chimpanzee rough grunting did not follow this pattern because intercall intervals were unaffected by our measures of food preference. Chimpanzee rough grunts may thus be more analogous to the calling behaviour of rhesus macaques in which call types vary acoustically with food preference, whereas call rate is merely mediated by hunger. In chimpanzees, social factors are also likely to be important for call production, a virtually unexplored topic that deserves more systematic attention.

Observations such as the ones reported in chickens are usually taken to argue that calling behaviour is driven by the caller's level of 'excitement', an explanation that makes intuitive sense. Although widespread in the animal communication literature, this and related terminology ('affect', 'motivation', 'emotion' or 'arousal') are usually not further specified, and it is rarely made explicit what sets of behavioural parameters or physiological processes they describe, apart from the vocal behaviour they are seeking to explain. Nevertheless, the notion of 'affective signals' is widespread and typically pitted against what is conceived as the less parsimonious alternatives, 'referential signalling', 'mental representation', 'cognitive processing' or the like. We prefer to remain agnostic about how best to conceptualize the psychological mechanisms underlying chimpanzee rough grunts. Currently, there is

Table 4. The acoustic structure of rough grunts recorded from captive and wild chimpanzees

Food	Formant frequency (Hz)	Peak frequency (Hz)	Call duration (s)	Intercall duration (s)
Captive				
Bread	813.35	1085.50	0.13	0.63
Mango	688.18	743.50	0.09	0.53
Banana	715.18	763.42	0.13	0.81
High preference mean	738.91	864.14	0.12	0.66
Grapes	699.98	569.50	0.06	0.99
Plums	788.10	624.20	0.07	1.45
Chow	747.92	579.83	0.10	1.34
Medium preference mean	745.33	591.18	0.08	1.26
Low preference mean	643.15	358.72	0.06	0.70
Wild				
Ficus sur	788.92	789.42	0.16	0.57
Ficus exasperata	753.33	698.58	0.10	0.40
Cynometra alexandri	759.50	683.25	0.07	0.96
Wild mean	767.25	723.75	0.11	0.64

Mean values of the four acoustic variables taken from calls given to the three wild food types and the six captive high- and medium-preference food types are given, together with the mean of all preference categories in the captive population and the mean of the wild food types combined.

insufficient evidence to make any assumptions about the mechanisms driving call production. This includes whether chimpanzees are intentionally producing grunts that can provide listening individuals with information about the nature of discovered food sources. What can be said with some certainty is that call production must be the result of the individuals' prior experiences with the particular foods, as well as the social effects of call production. Whether this should be called an 'affective' response does not really increase our understanding in relevant ways (Seyfarth & Cheney 2003).

Another line of reasoning, often invoked in this context, concerns the question of how signal structure relates to biological function. Morton (1977) has been particularly influential in this debate and other more recent approaches have also sought to understand the effect of receiver psychology on the evolution of signal design (Guilford & Dawkins 1993). It may be of relevance that the preferred foods in our study tended to elicit rough grunts with higher frequencies, rather than the other way around. For example, callers may be more likely to experience agonistic interactions in the presence of highly preferred foods, and it may be this social dimension that ultimately drives their vocal behaviour. Morton's (1977) law states that higher-pitched calls are typically produced by fearful animals or individuals seeking to appease others.

Variation with Food Preference or Food Type?

Our results also show that captive chimpanzees produce acoustically distinct rough grunts to different types of high-preference food, suggesting a process of vocal individuation for food items. Comparable findings were not available for rough grunts given to medium- or low-preference foods, suggesting that individuals make fine-grained distinctions only between highly preferred foods. Calls produced to the highly preferred foods bread and bananas were structurally consistent across feeding events, suggesting that these calls could provide recipients with reliable labels for specific food types. The fact that rough grunts are graded signals does not preclude them a priori from serving as referential signals. Research on baboons, *Papio cynocephalus ursinus*, has shown that individuals perceive acoustically graded calls as discrete units (e.g. Fischer et al. 2001).

Our findings thus seem to provide some support for the hypothesis that rough grunts can function as labels for particular food items (Hallberg et al. 2003), although ecologically valid playback studies are still needed to elucidate the exact information content of these calls from the listener's perspective. However, we were unable to replicate this finding with data from the wild. There was no evidence that the Budongo chimpanzees used acoustically distinct labels for different types of highly preferred foods. What can explain the differences between the results obtained for the wild and captive populations? We can think of at least three explanations.

First, our preference judgments for the three foods in the wild might have been inaccurate. We had no way of objectively testing food preferences in the wild and although proportion of time spent eating certain items is accepted as a good index of preference, it has limitations. It cannot be used to determine relative preferences of common and rare foods, or the preference of foods eaten in the study period compared with those available at other times of the year. The categorization of the three species of food as 'high preference' might therefore have been an overestimate. Rough grunts produced to these three foods fell somewhere in between the grunts given by captive individuals to high- and medium-preference foods (Table 4), supporting this view. If the three foods were in fact only of medium preference then, in line with the captive findings, we would not expect to see any differentiation between food types.

A second, and perhaps more parsimonious, explanation suggests that the previously proposed process of vocal individuation of food items is an unlikely event in the wild because of the immense variation in food sources encountered by individuals. The situation in captivity is very different because food availability, quality and quantity are predictable. During the study period the captive population regularly received 20 different foods in sufficient quantities for all individuals to be able to obtain some. They received four food types every day, 11 other foods at least once a week and five other foods at least once every month. The food was always of high quality (ripe, fresh) and the quantity varied only trivially. In addition, individuals in captivity could always see all other group members and observe their choices and calling behaviour closely. In contrast, in the wild the quality, quantity and availability of food are highly variable. The quality of a food source is reliant on the ripeness of the fruit or the age of the leaves. The quantity of the food source is determined by the size of the tree or food patch and also its state of depletion. Foods are usually highly seasonal (e.g. *Cynometra alexandri*) or follow unpredictable fruiting patterns (e.g. *Ficus* species). This means that the probability of obtaining a certain food has to be tracked over seasons, not just a few weeks, or it is highly unpredictable. In addition, wild chimpanzees forage over a large home range, often in a low-visibility habitat, in a fission–fusion social system; it is therefore not possible for individuals to observe all the feeding choices and calling behaviour of all community members, as it is in captivity. This limits the opportunity for signallers to monitor the reactions of others to call variants and for listeners to learn the contingencies between individual call variants and the eliciting contexts; both processes are proposed to be important factors in the development of an effective communication system (Owings & Morton 1998). The scale of variation that wild chimpanzees are confronted with in terms of number of food types (e.g. tree species, fruits, leaves, flowers), quality (e.g. ripeness), quantity (e.g. patch size, depletion state) and availability (e.g. seasonal variation) is enormous. In light of these factors the emergence of individualized food labels seems to be a rather unlikely event. In contrast, for captive animals food type automatically becomes the key factor in determining the relative value of a food source, since all other variables remain fairly constant. This may explain why we were able to associate some rough grunt variants with particular food types (Table 2).

Third, it may not be necessary for individuals in the wild to provide individual labels for particular food types. It has repeatedly been suggested that wild chimpanzees possess sophisticated knowledge of the distribution of key food trees throughout their home range (Goodall 1986; Boesch & Boesch-Achermann 2000; Bates 2005). A communication system capable of encoding the relative value of a food source, rather than the actual food type, may thus be sufficient since experienced listeners can infer the type of food from the location of the caller. A recent playback study describing responses to grunts produced to apples and bread corroborates this view (Slocombe & Zuberbühler 2005).

In sum, our findings are most compatible with the idea that captive chimpanzees can converge on idiosyncratic semantic conventions, in which particular rough grunt types become meaningful labels by referring to specific food items, such as bread or bananas. However, this may be possible only in a setting where most aspects of feeding events are predictable and regular and the type of food becomes the principal determinant of food value. When the differences in the relative preferences for foods are sufficiently large, as bread, mango and banana were in our study group, a preference-driven calling system can differentiate between them. Equally, these differences in calling can become meaningful to listeners in captivity because individuals usually eat in sight of one another and can observe individual food choices and calling behaviours. It may therefore be possible for listeners to infer the type of food referenced by a call, although it is still essentially a marker of relative food value.

In conclusion, chimpanzees produce rough grunts with acoustic structures that vary as a function of preference for the food they discover. In the restricted setting of captivity this system can obtain naming functions, in which calls may refer to particular types of foods. Data from the wild show a broad similarity between the calling behaviour of wild and captive chimpanzees, providing the captive results with ecological validity. However, unlike the captive chimpanzees, there is no evidence that wild chimpanzees produce acoustically distinct calls to different food types. In the wild, the exact meaning of calls may be the product of call type and context (e.g. Smith 1977).

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References

Bates, L. 2005. Cognitive aspects of food location and travel behaviour in chimpanzees of the Budongo Forest, Uganda. Ph.D., thesis, University of St Andrews.

Boesch, C. & Boesch-Achermann, H. 2000. *The Chimpanzees of the Taï Forest. Behavioural Ecology and Evolution.* Oxford: Oxford University Press.

Boinski, S. & Campbell, A. F. 1996. The huh vocalization of white-faced capuchins: a spacing call disguised as a food call? *Ethology*, **102**, 826–840.

Brown, C. R., Brown, M. B. & Shaffer, M. L. 1991. Food-sharing signals among socially foraging cliff swallows. *Animal Behaviour*, **42**, 551–564.

Bugnyar, T., Kijne, M. & Kotrschal, K. 2001. Food calling in ravens: are yells referential signals? *Animal Behaviour*, **61**, 949–958.

Chapman, C. A. & Lefebvre, L. 1990. Manipulating foraging group size: spider monkey food calls at fruiting trees. *Animal Behaviour*, **39**, 891–896.

Di Bitetti, M. S. 2005. Food-associated calls and audience effects in tufted capuchin monkeys, *Cebus apella nigritus*. *Animal Behaviour*, **69**, 911–919.

Dittus, W. P. J. 1984. Toque macaque food calls: semantic communication concerning food distribution in the environment. *Animal Behaviour*, **32**, 470–477.

Eggeling, W. J. 1947. Observations on the ecology of the Budongo Rain Forest, Uganda. *Journal of Ecology*, **34**, 20–87.

Elgar, M. K. 1986. The establishment of foraging flocks in house sparrows: risk of predation and daily temperature. *Behavioral Ecology and Sociobiology*, **19**, 433–438.

Elowson, A. M., Tannenbaum, P. L. & Snowdon, C. T. 1991. Food associated calls correlate with food preferences in cotton-top tamarins. *Animal Behaviour*, **42**, 931–937.

Evans, C. S. & Evans, L. 1999. Chicken food calls are functionally referential. *Animal Behaviour*, **58**, 307–319.

Evans, C. S. & Marler, P. 1994. Food calling and audience effects in male chickens, *Gallus gallus*: their relationships to food availability, courtship and social facilitation. *Animal Behaviour*, **47**, 1159–1170.

Fant, G. 1960. *Acoustic Theory of Speech Production*. The Hague: Mouton.

Fischer, J., Metz, M., Cheney, D. L. & Seyfarth, R. M. 2001. Baboon responses to graded bark variants. *Animal Behaviour*, **61**, 925–931.

Goodall, J. 1965. Chimpanzees of the Gombe Stream Reserve. In: *Primate Behavior: Field Studies of Monkeys and Apes* (Ed. by I. DeVore), pp. 425–473. New York: Holt, Rinehart & Winston.

Goodall, J. 1968. A preliminary report on expressive movements and communication in the Gombe Stream chimpanzees. In: *Primate Studies in Adaptation and Variability* (Ed. by P. C. Jay), pp. 313–374. New York: Holt, Rinehart & Winston.

Goodall, J. 1986. *The Chimpanzees of Gombe: Patterns of Behavior*. Boston, Massachusetts: Belknap Press of the Harvard University Press.

Gros-Louis, J. 2003. The function of food-associated calls in white-faced capuchin monkeys, *Cebus capucinus*, from the perspective of the signaller. *Animal Behaviour*, **140**, 565–592.

Guilford, T. & Dawkins, M. S. 1993. Receiver psychology and the design of animal signals. *Trends in Neuroscience*, **16**, 430–436.

Gyger, M. & Marler, P. 1988. Food calling in the domestic fowl, *Gallus gallus*: the role of external referents and deception. *Animal Behaviour*, **36**, 358–365.

Hallberg, K. I., Nelson, D. A. & Boysen, S. T. 2003. Representational vocal signalling in the chimpanzee. In: *Animal Social Complexity* (Ed. by F. B. M. de Waal & P. L. Tyack), pp. 317–322. London: Harvard University Press.

Hauser, M. D. 1998. Functional referents and acoustic similarity: field playback experiments with rhesus monkeys. *Animal Behaviour*, **55**, 1647–1658.

Hauser, M. D. & Marler, P. 1993a. Food-associated calls in rhesus macaques (*Macaca mulatta*). 1. Socioecological factors. *Behavioral Ecology*, **4**, 194–205.

Hauser, M. D. & Marler, P. 1993b. Food-associated calls in rhesus macaques (*Macaca mulatta*). 2. Costs and benefits of call production and suppression. *Behavioral Ecology*, **4**, 206–212.

Hauser, M. D. & Wrangham, R. W. 1987. Manipulation of food calls in captive chimpanzees: a preliminary report. *Folia Primatologica*, **48**, 207–210.

Hauser, M. D., Teixidor, P., Fields, L. & Flaherty, R. 1993. Food-elicited calls in chimpanzees: effects of food quantity and divisibility. *Animal Behaviour*, **45**, 817–819.

Marler, P. & Tenaza, R. 1977. Signalling behavior of apes with special reference to vocalisation. In: *How Animals Communicate* (Ed. by T. A. Sebeok), pp. 965–1033. Bloomington: Indiana University Press.

Marler, P., Dufty, A. & Pickert, R. 1986a. Vocal communication in the domestic chicken: I. Does a sender communicate information about the quality of a food referent to a receiver? *Animal Behaviour*, **34**, 188–193.

Marler, P., Dufty, A. & Pickert, R. 1986b. Vocal communication in the domestic chicken: II. Is a sender sensitive to the presence and nature of a receiver? *Animal Behaviour*, **34**, 194–198.

Morton, E. S. 1977. On the occurrence and significance of motivational-structural rules in some bird and mammal sounds. *American Naturalist*, **111**, 855–869.

Owings, D. H. & Morton, E. S. 1998. *Animal Vocal Communication: a New Approach*. Cambridge: Cambridge University Press.

Owren, M. J. & Bernacki, R. H. 1998. Applying Linear Predictive Coding (LPC) to frequency-spectrum analysis of animal acoustic signals. In: *Animals' Acoustic Communication* (Ed. by S. L. Hopp, M. J. Owren & C. S. Evans), pp. 129–162. Berlin: Springer Verlag.

Reynolds, V. 1965. Chimpanzees of the Budongo Forest. In: *Primate Behavior: Field Studies of Monkeys and Apes* (Ed. by I. DeVore), pp. 368–424. New York: Holt, Rinehart & Winston.

Reynolds, V. 1992. Chimpanzees in the Budongo Forest, 1962–1992. *Journal of Zoology*, **228**, 695–699.

Reynolds, V. 2005. *The Chimpanzees of the Budongo Forest*. Oxford: Oxford University Press.

Roush, R. S. & Snowdon, C. T. 2000. Quality, quantity, distribution and audience effects on food calling in cotton-top tamarins. *Ethology*, **106**, 673–690.

Seyfarth, R. M. & Cheney, D. L. 2003. Signalers and receivers in animal communication. *Annual Review of Psychology*, **54**, 145–173.

Slocombe, K. E. & Zuberbühler, K. 2005. Functionally referential communication in a chimpanzee. *Current Biology*, **15**, 1779–1784.

Smith, W. J. 1977. *The Behavior of Communicating: An Ethological Approach*. Cambridge, Massachusetts: Harvard University Press.

Trivers, R. L. 1972. Parental investment and sexual selection. In: *Sexual Selection and the Descent of Man* (Ed. by B. Campbell), pp. 136–179. Chicago: Aldine.

Van Krunkelsven, E., Dupain, J., Van Elsacker, L. & Verheyen, R. F. 1996. Food calling by captive bonobos (*Pan paniscus*): an experiment. *International Journal of Primatology*, **17**, 207–217.