



## Wild chimpanzees modify food call structure with respect to tree size for a particular fruit species



Ammie K. Kalan<sup>\*</sup>, Roger Mundry, Christophe Boesch

Max Planck Institute for Evolutionary Anthropology, Department of Primatology, Leipzig, Germany

### ARTICLE INFO

#### Article history:

Received 22 May 2014

Initial acceptance 9 July 2014

Final acceptance 19 November 2014

Available online 10 January 2015

MS. number: 14-00421R

#### Keywords:

feeding ecology

food calls

functionally referential

*Pan troglodytes*

primate communication

The extent to which animal vocalizations are referential has long been debated since it reflects on the evolution of language. Our closest living relative, the chimpanzee, has been shown to have functionally referential food calls in captivity but evidence for such capabilities in the wild is lacking. We investigated the context specificity and function of West African chimpanzee, *Pan troglodytes verus*, food calls in the wild using all day focal follows of adult males and females of one habituated group in the Taï forest, Côte d'Ivoire. We collected over 750 h of observation and analysed 379 food calls produced for five different food species and found that higher pitched calls were produced for a single fruit species. Additionally, within this species, chimpanzees modified calls according to tree size, whereby smaller trees elicited higher pitched calls. Our results suggest that chimpanzees subtly vary the acoustic structure of food calls with respect to food patch size for a putatively highly valued fruit species, and we propose that arousal alone cannot sufficiently explain the patterns observed. Further work is needed to determine whether variation in food call pitch can influence receiver foraging behaviour. However, in light of our results, we propose that understanding the information content encoded by acoustic variation in chimpanzee food calls requires receiver knowledge about the natural ecological context, specifically spatial memory of tree locations. Therefore, this study highlights the potential significance of feeding ecology in the evolution of flexibly modulated vocal communication.

© 2014 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Context-specific vocalizations, and their potential for referentiality, are particularly interesting because of their implications for an evolutionary continuity between animal communication and human language (Fitch, 2005; Tomasello, 2008). For a vocalization to be classified as functionally referential it must exhibit call production that is stimulus specific, as well as elicit appropriate responses in the audience upon hearing the call alone (Macedonia & Evans, 1993; Seyfarth, Cheney, & Marler, 1980). However, recent criticisms on the use of information theory and linguistic constructs in studies of animal communication (Rendall, Owren, & Ryan, 2009; but see Seyfarth et al., 2010) have sparked a debate on the conceptual benefit of functional reference with respect to animal cognition (Townsend & Manser, 2013; Wheeler & Fischer, 2012). For example, functionally referential vocalizations among animals do not necessitate invoking higher order cognitive mechanisms if the calls are largely produced involuntarily and elicit preconditioned behavioural responses (Owings & Morton, 1998; Owren &

Rendall, 1997). Instead other researchers, namely Wheeler and Fischer (2012), have stressed the importance of pragmatics, specifically how context contributes to meaning attribution of a call, which has been traditionally undervalued in animal communication although it may be indicative of complex, underlying cognitive processing. In baboons, *Papio cynocephalus*, for instance, males will come to the aid of a screaming lactating female only if they have a close friendship with that individual and only if there is a clear threat of infanticide, meaning that they take into account the immediate social context to differentiate between female screams (Palombit, Seyfarth, & Cheney, 1997).

Studies on nonhuman primates, such as the one above, have been valuable in illuminating the cognitive preadaptations that may have already existed in the primate lineage before the advent of language (Zuberbühler, 2003). In fact, there is mounting evidence, largely from investigations of alarm and food calls, that nonhuman primates can produce and use vocalizations flexibly depending on context and the audience (Cäsar & Zuberbühler, 2012; Clay, Pika, Gruber, & Zuberbühler, 2011; Crockford, Wittig, Mundry, & Zuberbühler, 2012; Di Bitetti, 2005; Fischer, Metz, Cheney, & Seyfarth, 2001; Schel, Townsend, Machanda, Zuberbühler, & Slocombe, 2013; Slocombe & Zuberbühler, 2007;

<sup>\*</sup> Correspondence: A. K. Kalan, Max Planck Institute for Evolutionary Anthropology, Department of Primatology, Deutscher Platz 6, 04103 Leipzig, Germany.  
E-mail address: [ammie\\_kalan@eva.mpg.de](mailto:ammie_kalan@eva.mpg.de) (A. K. Kalan).

Townsend, Deschner, & Zuberbühler, 2008; Zuberbühler, 2003). Rather strikingly, however, there is only limited evidence for context-specific vocalizations among our closest living relatives, the great apes. There is some support for context-specific calls in wild chimpanzees, *Pan troglodytes*, but it is not known whether listeners also extract information from these calls (Crockford & Boesch, 2003; Notman & Rendall, 2005). In captivity, though, both chimpanzees and bonobos, *Pan paniscus*, have been shown to use functionally referential food calls (Clay & Zuberbühler, 2011; Slocombe & Zuberbühler, 2005).

Hence, despite criticisms, functionally referential communication continues to be evolutionarily relevant because referentiality is a hallmark of human language (Tomasello, 2008; Zuberbühler, 2003). Since the seminal study of vervet monkey, *Chlorocebus pygerythrus*, alarm calls (Seyfarth et al., 1980), many mammals and birds have demonstrated the capacity for functional reference and meaningful call combinations (Bugnyar, Kijne, & Kotrschal, 2001; Clay, Smith, & Blumstein, 2012; Ouattara, Lemasson, & Zuberbühler, 2009; Townsend & Manser, 2013; Zuberbühler, 2000, 2003). However, the functionally referential alarm and food calls of these species are often produced in other contexts too, thereby violating the production specificity requisite (Clay et al., 2012; Townsend & Manser, 2013). Therefore, it is of particular interest that chimpanzee food calls, although highly graded in acoustic structure, are none the less context specific and produced solely when approaching, gathering or eating food (Goodall, 1986; Marler, 1976; Marler & Tenaza, 1977), unlike food calls produced by most other nonhuman primates, including bonobos (Clay & Zuberbühler, 2011). Notably, graded vocalizations are prevalent among all primates (Marler & Mitani, 1988), and it has been shown that graded acoustic variants, also characteristic of food calls, can still be categorized as distinct call types by the primates themselves (Fischer, 1998; Gouzoules, Gouzoules, & Marler, 1984).

Food calls represent a particularly puzzling form of vocal signalling. From an evolutionary standpoint it is clearly advantageous for group-living animals to have predator-specific alarm calls (Townsend & Manser, 2013); however, it is less clear why animals have food-specific vocalizations. There is a clear benefit to a receiver who is alerted to the presence of food but at what cost to the signaller who then has to share? In fact, socioecological studies have clearly shown that nonhuman primates suffer reduced food intake as party size increases at a food patch (Chapman, Chapman, & Wrangham, 1995; Sterck, Watts, & van Schaik, 1997). It has been hypothesized that this cost is offset by the benefit of enhanced predator detection, or the collective defence of food patches from other groups or competitors (Sterck et al., 1997) and could also offer other advantages such as attracting mates and allies (Mitani & Nishida, 1993) or reinforcing social bonds among individuals (Wittig et al., 2014). Generally, chimpanzee food calls attract nearby individuals to a food patch who then also join in feeding (Goodall, 1986; Marler & Tenaza, 1977; Slocombe & Zuberbühler, 2005). However, the extensive acoustic variation present in chimpanzee food calls remains to be examined with respect to relevant ecological factors and how it might serve to attract others to a food patch.

Recently, wild chimpanzees have been shown to use a sophisticated spatial memory of tree locations and botanical knowledge to find ripe fruits in the forest (Janmaat, Ban, & Boesch, 2013a, 2013b; Normand, Ban, & Boesch, 2009; Normand & Boesch, 2009). Finding mature fruits in the rain forest is a primary challenge for frugivorous primates and is made all the more difficult by seasonality, competition and irregularities in fruit production (Zuberbühler & Janmaat, 2010). Consequently, it may be adaptive for chimpanzee food calls to encode more detailed information about fruits and trees other than simply alerting others to the

presence of food, provided wild chimpanzees know where trees of different species are located in their territory (Janmaat et al., 2013a).

In this study we therefore investigated whether food species, tree size and fruit count influenced food call structure and whether any variation present selectively attracted nearby chimpanzees to a food patch. Previous studies in captivity have found that chimpanzees produced food calls with a longer duration and higher fundamental and peak frequencies for more preferred food items (Slocombe & Zuberbühler, 2005, 2006) and more calls were produced when greater quantities of food were present (Hauser, Teixidor, Fields, & Flaherty, 1993; Hauser & Wrangham, 1987). Based on these findings, we predicted that acoustic structure of food calls would also differ with respect to the amount of food available and species eaten. Specifically, we expected larger quantities to elicit calls with higher dominant frequencies and a longer duration. Similarly, we expected differences in food species, based on their perceived value to chimpanzees, to also elicit differences in dominant frequencies and call duration. In addition, we were interested in addressing to what degree food calls could be considered functionally referential in the wild by investigating whether variants in food call structure differentially attracted nearby chimpanzees to food patches.

## METHODS

### Data Collection

Data were collected between July 2011 and May 2012 at Taï National Park, Côte d'Ivoire on one habituated group of chimpanzees, *P. troglodytes verus*, the South Group, totalling 19 individuals and five dependent offspring (Boesch, 2009; Boesch & Boesch-Achermann, 2000). Focal follows were conducted on five male and four adult female chimpanzees for a total of 754.5 h of observation (average duration:  $8.88 \pm 2.9$  h per day; Appendix Table A1). Whenever a focal individual began eating or collecting food items this marked the start of a feeding event. The feeding event lasted until the focal individual stopped eating and did not resume eating at the same patch. We restricted our analysis to food species that chimpanzees ate naturally on the ground (which facilitated recordings of vocalizations), namely *Nauclea diderichi*, *Coula edulis*, *Klainedoxa gabonensis*, *Parinari excelsa*, *Sacoglottis gabonensis* (Table 1). For all these food species, chimpanzees were observed first to search for ripe fruits or nuts and then to sit at least 1 m from any other individual and feed peacefully on their own collected pile of fruits. The chimpanzees ate other foods on the ground during the study period but only species with at least 10 feeding events with good-quality recordings were used in this analysis. For all feeding events, the food species was noted and diameter at breast height (dbh) of the tree trunk was measured for all trees with a dbh >20 cm by A.K. or her assistant. A.K. counted the edible-looking fruits on the ground and observed which fruits the chimpanzees ate and rejected in order to gauge what an edible fruit looked like

**Table 1**

Summary of the number of feeding events for each species where food calls were produced and recordings were of sufficient quality for analysis

	Total feeding events observed	Feeding events with food calls	Events with measurable calls
<i>Coula</i>	72	33	13
<i>Klainedoxa</i> )	30	22	11
<i>Nauclea</i>	68	46	20
<i>Parinari</i>	62	38	13
<i>Sacoglottis</i>	65	42	11
Total	297	181	68

(e.g. decomposing fruits were ignored). The number of edible fruits was counted within a 1 m strip radiating from the base of the tree then multiplied by the area covered with fruits under the tree. We monitored party composition continuously where a party was defined as all individuals over the age of 5 years present with the focal individual, within a maximum visual detection distance of 25–50 m in Taï forest. The time of arrival of any other individual to a food patch was always noted. A.K. continuously recorded all vocalizations of the focal individual and collected vocalizations of other target individuals ad libitum if they were present in the party. Recordings were made using a Sennheiser ME66/K6 directional microphone with windshield and a Marantz PMD661 solid state recorder using a 44 kHz sampling frequency at 24 bits/s. All recordings were made within 3–10 m from the caller. Only calls for which the identity of the caller was certain were used in the analyses.

### Value of Food Species

Determining the relative value of naturally occurring food species for wild animals is notoriously difficult. Here we report two components that have been used to reflect food choice in animals: the energy content and the time spent feeding on each species. From a previous study on Taï chimpanzees we have the nutritional content of all five food species analysed in this study (Hohmann et al., 2010). We specifically report the energy content since research suggests that primates principally guide their food choice by maximizing energy intake (Zuberbühler & Janmaat, 2010). Originally, we aimed at including all species for which we recorded feeding events with food calls. However, owing to the low numbers of feeding events (less than five) from which only low numbers of good-quality food call recordings were collected (1–25 calls) we could not include the majority in the analysis (17 species excluded). Across the remaining five species there was limited variation in nutritional quality. Therefore, to complement our assessment of the value of these food species for wild chimpanzees, we calculated the total proportion of time chimpanzees were observed feeding on each of the five species, during this study period. A previous study on chimpanzee food calls used the proportion of feeding time by chimpanzees as a measure of preference for food items since food preference cannot be directly tested in the wild as it can in captivity (Slocombe & Zuberbühler, 2006). We report the same here but stress that this is only a proxy for the level of preference since it does not control for the distribution and availability of these species at any given point in time. Hence, we report the energy content and time spent feeding for the five species as crude measures for the perceived value of a food item for wild chimpanzees (Table 2).

### Acoustic Analysis

Vocalization recordings were analysed using Avisoft SASLab Pro v.5.2.06 (R. Sprecht, Berlin, Germany) and the sound analysis

**Table 2**  
Energy content and percentage of total time observed feeding by chimpanzees during the study period for the five species in the analysis

	Part consumed	Energy content (kJ/g dry matter)	Percentage of feeding time
<i>Coula</i>	Nut	24.54	4.92
<i>Klainedoxa</i>	Mesocarp	15.90	9.02
<i>Nauclea</i>	Mesocarp	19.38	10.84
<i>Parinari</i>	Mesocarp	19.15	7.34
<i>Sacoglottis</i>	Mesocarp	18.63	6.00

Energy content was measured by burning a sample of the consumed food item in pure oxygen atmosphere using a bomb calorimeter whereby the heat produced is measured in kJ/g dry matter (details in Hohmann et al., 2010).

software LMA v.2012.10 (Fischer, Noser, & Hammerschmidt, 2013). Spectrograms were created in Avisoft (FFT-length: 1024; window: Hamming; overlap: 96%) after down sampling recordings to 5500 Hz and also used as input files for LMA. In LMA an interactive macro was used to obtain measurements after applying a high-pass filter of 50 Hz. Our analysis only included food calls that were recorded while individuals peacefully ate food items on their own. Any food calls produced while an individual was feeding or foraging but simultaneously engaged in behaviour with, or directed towards, another were excluded. Chimpanzee food calls are generally referred to as ‘rough grunts’ as well as ‘food aaa’ calls, but this distinction has only been qualitatively described (Goodall, 1986; Marler, 1976). We find this distinction misleading since food calls can be highly variable, grading from soft grunts to loud barks, and noisy to tonal; hence, to avoid confusion, we use the term ‘food calls’ hereafter. Importantly, this study does not include pant hoots which do occur in a feeding context but are not restricted to it (Clark & Wrangham, 1993). Food calls were often produced in a series of repeated calls termed a bout. Since we were particularly interested in call structure variation we focused our analysis on individual calls while controlling for bout in our statistical analysis (see Appendix Table A2). Moreover, we did not a priori exclude certain food calls on the basis of tonality; therefore, we measured acoustic parameters that could be obtained from all calls, whether rough or tonal. Six frequency (Hz) variables were measured from all calls: the minimum, maximum and mean of the first dominant frequency band (DF1), the mean and maximum of the second dominant frequency band (DF2) and the maximum peak frequency (Fischer et al., 2013). Three additional acoustic variables were derived from these: the frequency range of DF1 and the minimum and maximum difference between DF1 and DF2. Additionally call duration (ms) was measured for all calls.

### Statistical Analysis

All statistical tests were run in R v.3.0.2 (The R Foundation for Statistical Computing, Vienna, Austria, <http://www.r-project.org>). Inspections of acoustic variables revealed they were highly correlated. Therefore, we conducted a factor analysis (FA) with varimax rotation using the function ‘factanal’. Variables were transformed if necessary to obtain symmetrical distributions, and the relations between variables were visually verified to be more or less linear. The Kaiser–Meyer–Olkin measure (0.89) and Bartlett’s test of sphericity ( $P < 0.001$ ) indicated that an FA was justified (McGregor, 1992). Call duration loaded separately from all frequency variables and was therefore excluded from the FA and tested separately as a response. Thus the nine frequency variables, which were all positively correlated with one another, were combined into a single factor which explained 0.868 of their total variation (loadings: 0.643–0.998; Appendix Table A3). This factor was then used as a response variable, hereafter referred to as ‘call pitch’.

Although we expected species, tree size and fruit count to all affect call structure we were not able to test them together and with their interactions in a single model owing to a complex random effects structure in our data set and the necessity to include random slopes in addition to random intercepts, when conducting general linear mixed models (GLMM; Barr, Levy, Scheepers, & Tily, 2013; Forstmeier & Schielzeth, 2011). Moreover, dbh and fruit count were not correlated across feeding events and therefore had to be tested separately (Appendix Table A4). To test for context specificity in call structure we therefore conducted six main effects models, one for each combination of the three test predictors (food species, tree dbh and fruit count) with the two response variables call duration and call pitch ( $N = 379$  for all models). This was required in order to have a stable model from which robust inference could be

made about the effects of species, tree size or fruit count while controlling for the critical random effects and random slopes terms. The results of the main effects models justified additional GLMMs to investigate the effects of dbh and fruit count while controlling for species. However, only the species *N. diderichi* had a sufficient sample size ( $N = 148$ ) to fit stable GLMMs from which robust results could be obtained. The *Nauclea* only GLMMs were identical to the GLMMs described above except that the nonsignificant predictors latency and sequence in bout (see below) were dropped. All GLMMs were implemented using a Gaussian error structure and identity link function, using the function 'lmer' of the package 'lme4' (Bates, Maechler, & Matrix, 2011). Both tree size and fruit count measurements were standardized within species to a range from zero to one to allow for comparisons across all species and avoid collinearity (Quinn & Keough, 2002). Sex, party size, latency to call from arrival and sequence of the call extracted in the bout were included as control predictors. Random intercepts for individual ( $N = 9$ ), call bout ( $N = 239$ ) and feeding event ( $N = 68$ ) were included, together with the random slope for the test predictor within individual. The distributions of quantitative predictors were verified to be symmetrical and transformed if needed. All quantitative predictors were then z-transformed to a mean of zero and a standard deviation of one before running the model. For all GLMMs we checked for normality and homogeneity of residuals, stability of models, as well as absence of collinearity among predictors, to ensure their reliability and robustness (for details see Appendix Table A2). To establish the significance of a test predictor, a full versus null model comparison was conducted (Forstmeier & Schielzeth, 2011) using a likelihood ratio test with the function 'anova' (Dobson & Barnett, 2008) with significance levels set at 0.05.

To test whether group members were attracted to food patches depending on call structure, we ran an additional GLMM to determine whether nearby chimpanzees arrived according to call pitch variation in *Nauclea* food calls. This model had a negative binomial error structure and log link function and was implemented using the R package 'glmmADMB' (Bolker, Skaug, Magnusson, & Nielsen, 2012). The response was the total number of nearby chimpanzees to arrive at the food patch. Here, 'nearby' means not present when the individual produced the call and therefore not in the focal individual's party. We estimate that food calls can travel up to 300 m in this forest (Eckhardt, Polansky, & Boesch, 2014). The pitch of the first call recorded after arriving at the food patch was used as the critical predictor ( $N = 17$  *Nauclea* feeding events) and the duration (log-transformed) of the feeding event was included as an offset term (McCullagh & Nelder, 1989) to control for time spent at the patch. Events where the whole group was present were not included, and sex and party size were included in the model as control predictors. The random intercept for the calling individual ( $N = 7$ ) as well as the random slope of call pitch within individuals were controlled for in the model. Assessment of stability and significance was done as described above.

## RESULTS

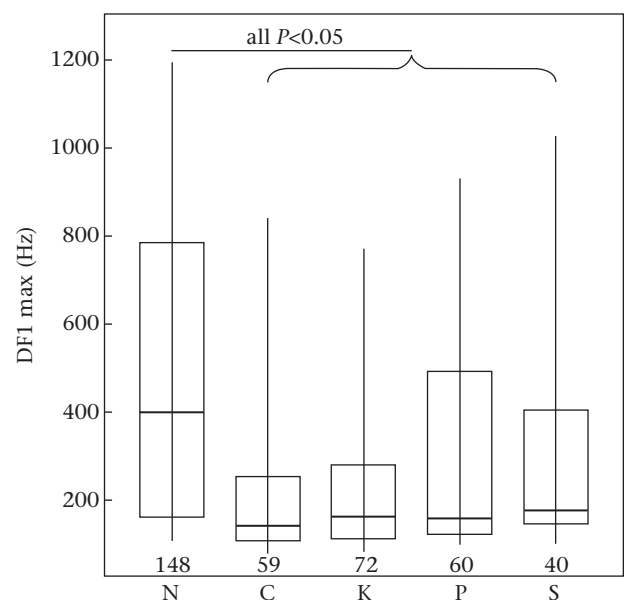
Chimpanzees were observed to feed on 43 fruit species, 17 species of leaves, three species of nuts, five species of seeds, six species of herbaceous pith, five different insects and two species of monkey during the study period. These species constituted a total of 890 feeding events, together lasting for 18 582 min with most of this time spent feeding on fruit species (70.25%), then leaves (14.50%), followed by nuts (5.37%). *Coula edulis* accounted for most of the time spent feeding on nuts. Of the 297 feeding events observed for the five food species regularly eaten on the ground by chimpanzees and for which we had large enough sample sizes for acoustic analysis, only 60% of events elicited food calls by individuals (Table 1).

Call pitch varied with respect to food species ( $\chi^2_4 = 12.35$ ,  $P = 0.015$ ) but not tree size ( $\chi^2_1 = 0.77$ ,  $P = 0.38$ ) or fruit count ( $\chi^2_1 = 0.21$ ,  $P = 0.65$ ). Call duration was nonsignificant for all test predictors (species:  $\chi^2_4 = 1.54$ ,  $P = 0.82$ ; dbh:  $\chi^2_1 = 0.83$ ,  $P = 0.36$ ; count:  $\chi^2_1 = 0.13$ ,  $P = 0.71$ ). *Nauclea* drove the species difference: calls elicited by *Nauclea* were on average of higher pitch than the others (Fig. 1). Interestingly, we observed particularly extensive call variation within *Nauclea* calls. Therefore we conducted two further GLMMs to test for the effects of dbh and fruit count, separately, within *Nauclea* calls only. Tree size was a significant predictor of call pitch within *Nauclea* calls ( $\chi^2_1 = 5.57$ ,  $P = 0.018$ ) but not fruit count ( $\chi^2_1 = 0.77$ ,  $P = 0.38$ ). In fact, larger *Nauclea* trees elicited lower pitched calls (estimate  $\pm$  SE:  $-0.44 \pm 0.14$ ; Fig. 2), meaning that for small trees food calls had high dominant and peak frequencies and the opposite for large *Nauclea* trees (Fig. 3a, b).

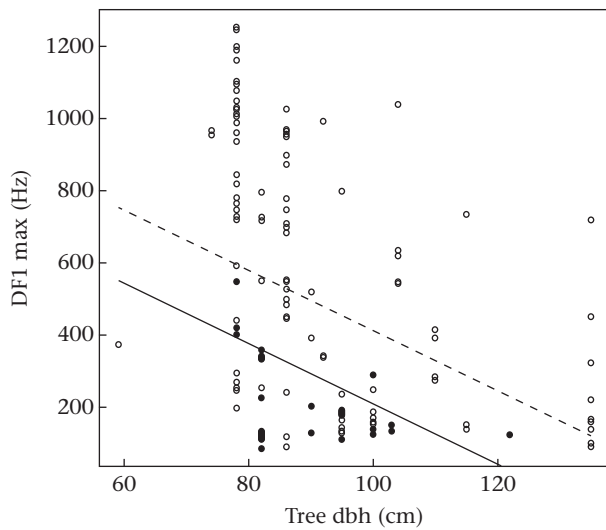
To determine whether nearby individuals were attracted to a food patch depending on call structure, and since *Nauclea* call structure appeared to vary with respect to tree size, we analysed the number of individuals arriving at *Nauclea* feeding events. The number of individuals arriving at the fruit tree tended to decrease as food call pitch produced for *Nauclea* increased (estimate  $\pm$  SE:  $-0.92 \pm 0.52$ ,  $\chi^2_1 = 2.95$ ,  $P = 0.086$ ; Fig. 4). Moreover, for *Nauclea* feeding events during which no food calls were produced, the number of individuals to arrive at the patch was much lower (median (quartiles): 0.00 (0–0) individuals/event) and these feeding events were also shorter (median (quartiles): 14.50 (4.25–19) min,  $N = 22$ ) than those *Nauclea* events at which food calls had been produced (2.00 (0–8.50) individuals/event; 28.00 (15.25–50) min,  $N = 42$ ).

## DISCUSSION

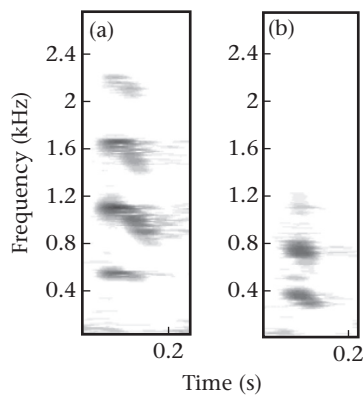
Our results demonstrate that wild chimpanzees modify their call structure with respect to external referents under natural foraging conditions. On average, chimpanzees produced higher



**Figure 1.** Variation in food call pitch for five food species eaten by the Tai chimpanzees ( $N = 379$ ; see also Appendix Table A5). Horizontal lines in the box plot show medians, boxes show quartiles, vertical lines represent percentiles (2.5 and 97.5%), and numbers indicate number of calls analysed. Food species were *Nauclea* (N), *Coula* (C), *Klainedoxa* (K), *Parinari* (P) and *Sacoglottis* (S). For ease of interpretation the y-axis displays the maximum of the first dominant frequency band (DF1 max) which is one of nine variables that loaded onto the factor call pitch (0.976; Table A4).

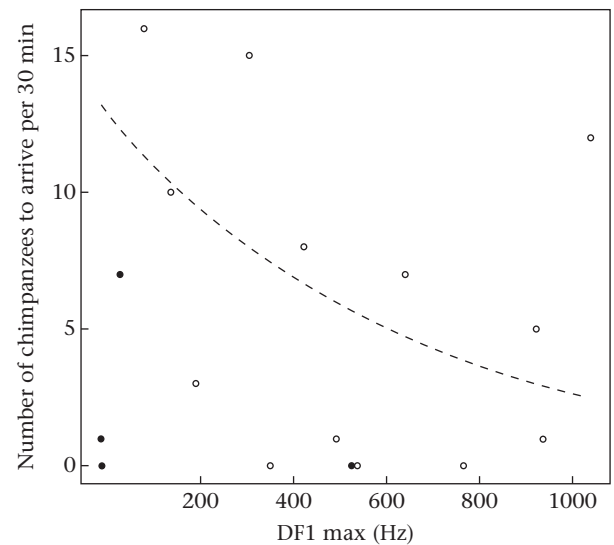


**Figure 2.** Variation in pitch for *Nauclea* food calls ( $N = 148$ ) according to tree size (dbh). As tree size increased, the call pitch of *Nauclea* calls decreased. For ease of interpretation we show DF1 max on the y-axis (see Fig. 1). The regression lines are shown separately for males (open circles, dashed line) and females (filled circles, solid line) because male calls were generally higher pitched than female calls.



**Figure 3.** Spectrograms of two *Nauclea* food calls made by Kuba, an adult male chimpanzee, (a) at a small *Nauclea* tree (dbh = 82 cm) and (b) at a large tree (135 cm).

pitched calls for *N. diderichi* than any of the other species. Food calls produced for the other four species were generally low in pitch and, importantly, did not vary much acoustically and therefore did not appear to encode any specific information. *Nauclea* had the highest energy of the fruit species considered in this study (Table 2). Therefore it may elicit the greatest arousal and feeding competition. Generally, increased physiological arousal is associated with an increase in pitch in animal vocalizations (Morton, 1977) as well as the human voice (Frick, 1985; Hammerschmidt & Jürgens, 2007). This might explain why *Nauclea* fruits elicited higher pitched calls. However, *Nauclea* fruits were only slightly richer in energy than the other three fruit species and were lower in energy than *Coula* nuts; therefore this effect on call pitch could have additionally be driven by a specific preference for *Nauclea* fruits. In fact, chimpanzees were observed to spend the greatest amount of time feeding on *Nauclea* fruits, even when considering all the food species chimpanzees were observed to eat during the study period. Hence, *Nauclea* fruits could be of particularly high value for the chimpanzees. However, our measure of value does not control for availability; thus, this conclusion must be treated cautiously. Still, our result is in line with findings from captivity where high-



**Figure 4.** Number of individuals joining a caller at a food patch, as a function of the pitch of the first food call produced during *Nauclea* feeding events ( $N = 17$ ). The common regression line for both sexes (dashed) shows that more chimpanzees tended to arrive at a *Nauclea* food patch for lower pitched calls. Open and filled circles indicate male and female callers, respectively. For ease of interpretation we show DF1 max (see Fig. 1).

preference food items were associated with higher fundamental and peak frequencies (Slocombe & Zuberbühler, 2005). More importantly, it also supports previous findings from wild chimpanzees where highly preferred food species, also indexed by proportion of time spent feeding, elicited calls with a higher dominant frequency (Slocombe & Zuberbühler, 2006). However, the authors did not find significant differences between high- and medium-preferred food species, which may have just been a consequence of the limited number of species being considered owing to the short study period. Also, more sophisticated measures of food preference are needed to assess its effect on food call variation.

Curiously, *Coula* nuts had the highest energy content of all the species considered (Table 2) and could therefore have been expected to elicit the greatest excitement for chimpanzees. However, *Coula* differs from the other species in this study in several aspects. First, *Coula* nuts are highly seasonal, available for only a few months during the dry season in Tai forest. Second, *Coula* trees are small in comparison to the other four species and do not vary much in size (Appendix Fig. A1). Moreover, chimpanzees must use tools to extract the *Coula* nut, and the process of nut cracking itself produces a redundant acoustic signal in the environment. In summary, these traits set *Coula* apart from the other species in this analysis and may explain why no acoustic variation was found with respect to food calls made for *Coula*. Surprisingly, no call variation was found with respect to the number of fruits present but this may be due to patches having been depleted to some extent or a lack of sufficient variation in our fruit count measurements.

In addition to food calls elicited by *Nauclea* being particularly high pitched, they also exhibited the highest degree of variation in pitch, which was driven by variation in tree size. Chimpanzees eat these fruits on the ground, in an area directly beneath the crown of the tree; therefore, crown size (assessed using dbh) directly reflects patch size (Symington, 1988). Moreover, tree dbh has been shown to be the best predictor of fruit biomass and patch size (Chapman et al., 1992; Symington, 1988) which may be why tree size appeared to be the most salient feature to chimpanzees. Furthermore, it may be adaptive to enrich *Nauclea* food calls by adding

information regarding tree size since recent studies have shown that wild chimpanzees are familiar with the locations of numerous feeding trees in their territory (Janmaat et al., 2013a, 2013b; Normand et al., 2009; Normand & Boesch, 2009). This may explain why a previous study of wild chimpanzees also did not find food-specific call variation (Slocombe & Zuberbühler, 2006). Interestingly, although louder calls are expected to be higher pitched (Frick, 1985), low-frequency calls may travel further in a dense environment such as a tropical forest (Waser & Waser, 1977); hence it is unclear which end of this continuum should be favoured in order to communicate with nearby conspecifics.

A large tree is expected to incite greater arousal which physiologically would result in high-pitched vocalizations (Frick, 1985; Morton, 1977); our results do not support this explanation, however, because food call pitch was lower for larger *Nauclea* trees. Socioecological theory predicts that intraparty feeding competition increases at small patches (Chapman et al., 1995) which may be why chimpanzees produced higher pitched calls for small *Nauclea* trees. However, if feeding competition was motivating signallers to produce high-pitched food calls it would be dependent on the number of individuals in the party. In our GLMM analysis party size was controlled for and, to the contrary, it had a significant negative effect on food call pitch, meaning that when party size was large, the pitch of the call was low (estimate  $\pm$  SE:  $-0.18 \pm 0.069$ ,  $\chi^2_1 = 5.89$ ,  $P = 0.015$ ). Although one may argue that signallers could also become more excited when in smaller parties, because feeding competition is relaxed, and thereby produce higher pitched calls, this does not account for the observed call pitch variation with respect to tree size. Consequently, feeding competition cannot explain why chimpanzees produced higher pitched calls for smaller *Nauclea* trees. Instead, our results suggest that critical ecological information is being encoded by call pitch variation when communicating about a potentially high-value fruit species. Additionally, chimpanzees must be exerting some degree of control over call production in order to modify the pitch of food calls according to tree size. Whether signallers are intentionally modifying their calls to share information with others remains to be seen, but it would be in line with recent evidence from the wild supporting intentional vocal communication in wild chimpanzees (Crockford et al., 2012; Schel, Machanda, Townsend, Zuberbühler, & Slocombe, 2013; Schel, Townsend, et al., 2013).

From the receiver's perspective, nearby chimpanzees had a tendency to join a feeding event when callers made low-pitched calls as compared to when they made high-pitched calls for *Nauclea* trees. Hence, receivers may be inferring specific information regarding food patch size from food calls which to some extent supports previous claims of functional reference, although food quantity was not specifically investigated (Slocombe & Zuberbühler, 2005). To respond specifically to *Nauclea* food call pitch would require chimpanzees to have spatial knowledge about the locations of trees in their territory, for which there is empirical support (Janmaat et al., 2013a; Normand et al., 2009). We suspect that when chimpanzees heard a high-pitched food call coming from the location of a *Nauclea* tree (and *Nauclea* fruits were in season), they might have obtained information regarding the size of the tree, specifically that the patch size was small. Conversely, a low-pitched call from the direction of a *Nauclea* tree meant signallers were feeding at a large patch. Hence, listeners could have been attracted more to larger trees (low-pitched *Nauclea* calls) than small trees (high-pitched *Nauclea* calls) because a larger patch can support more individuals (Chapman et al., 1995; Symington, 1988). This would be in line with recent proposals highlighting the significance of pragmatics in animal communication, namely how receivers use contextual information to decode the meaning of a signal rather than relying on the vocal cue alone (Wheeler &

Fischer, 2012; Wheeler et al., 2011). However, we caution that our results on the receiver's responses are preliminary. Whether chimpanzees really understand variation in food call pitch as encoding information about patch size, specifically for a putatively high-value fruit species, should be tested using playback experiments in the field.

Our results suggest that food calls may attract out-of-sight individuals to a food patch by the use of food call variation. Ultimately, chimpanzee food calls could serve multiple functions: recruiting others to a patch, but once recruited, keeping individuals foraging together (Fedurek & Slocombe, 2013). Both social factors, such as the strength of social and dominance relationships (Schel, Machanda, et al., 2013; Slocombe et al., 2010), and alternative foraging options would be crucial in determining whether a particular chimpanzee decides to join an ongoing feeding event. There could also be additional, not necessarily mutually exclusive, motivations behind food call signalling, such as announcing food ownership (Gros-Louis, 2004) or regulating interindividual spacing (Boinski & Campbell, 1996). However, to tease apart the roles of these other factors and hypotheses with respect to chimpanzee food calls will require further investigations.

Although our study was limited to only five food species, we expect that chimpanzee food calls may be similarly modulated with respect to patch characteristics for other putatively high-value fruit species as observed for *Nauclea*. A complex ecological environment, coupled with a fission–fusion social structure as is found in chimpanzees, may favour the development of simple forms of call modulation, such as pitch, as observed in this study. It is conceivable that subtle modifications in acoustic structure allow for a greater depth of information transmission in a foraging context and thus provide a selective advantage. We suggest that feeding ecology may have been a driving force in the evolution of flexibly modulated vocal communication within the hominoid lineage. In fact, a leading theory for the origins of language suggests foraging to be the initial context in which a form of protolanguage would have first conferred a selective advantage for early *Homo* (Bickerton, 2002). To better understand the impact of ecological selection pressures on communication systems more generally, we encourage future studies to address how ecological complexity can promote, or facilitate, the development of vocal complexity among animals.

## Acknowledgments

We thank the Ministère de la Recherche Scientifique and the Ministère de l'Environnement et des Eaux et Forêts of Côte d'Ivoire, and Office Ivoirien des Parcs et Réserves for permissions to work in the country. We also thank the Centre Suisse de Recherche Scientifique and Tai Chimpanzee Project, especially the TCP assistants and Roman Wittig for logistical support, and the Max Planck Society for funding. Special thanks to Kurt Hammerschmidt for help with the acoustic analysis and Cathy Crockford for helpful discussions. We also thank three anonymous referees for comments that greatly improved the manuscript.

## References

- Barr, D. J., Levy, R., Scheepers, C., & Tily, H. J. (2013). Random effects structure for confirmatory hypothesis testing: keep it maximal. *Journal of Memory and Language*, 68(3), 255–278. <http://dx.doi.org/10.1016/j.jml.2012.11.001>.
- Bates, D., Maechler, M., & Matrix, L. T. (2011). *Package 'lme4'*. Retrieved from <http://cran.r-project.org/web/packages/lme4/lme4.pdf>.
- Bickerton, D. (2002). Foraging versus social intelligence in the evolution of protolanguage. In A. Wray (Ed.), *The transition to language* (pp. 207–225). Oxford, U.K.: Oxford University Press.
- Boesch, C. (2009). *The real chimpanzee: Sex strategies in the forest*. Cambridge, U.K.: Cambridge University Press.

- Boesch, C., & Boesch-Achermann, H. (2000). *The chimpanzees of the Tai Forest: Behavioural ecology and evolution*. Oxford, U.K.: 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(6), 826–840. <http://dx.doi.org/10.1111/j.1439-0310.1996.tb01204.x>.
- Bolker, B., Skaug, H., Magnusson, A., & Nielsen, A. (2012). *Getting started with the glmmADMB package*. Retrieved from <http://glmmadmb.r-forge.r-project.org/glmmADMB.pdf>.
- Bugnyar, T., Kijine, M., & Kotrschal, K. (2001). Food calling in ravens: are yells referential signals? *Animal Behaviour*, 61(5), 949–958. <http://dx.doi.org/10.1006/anbe.2000.1668>.
- Cázar, C., & Zuberbühler, K. (2012). Referential alarm calling behaviour in New World primates. *Current Zoology*, 58, 680–697.
- Chapman, C. A., Chapman, L. J., Wangham, R., Hunt, K., Gebo, D., & Gardner, L. (1992). Estimators of fruit abundance of tropical trees. *Biotropica*, 24(4), 527. <http://dx.doi.org/10.2307/2389015>.
- Chapman, C. A., Chapman, L. J., & Wrangham, R. W. (1995). Ecological constraints on group size: an analysis of spider monkey and chimpanzee subgroups. *Behavioral Ecology and Sociobiology*, 36(1), 59–70. <http://dx.doi.org/10.1007/BF00175729>.
- Clark, A. P., & Wrangham, R. W. (1993). Acoustic analysis of wild chimpanzee pant hoots: do the Kibale Forest chimpanzees have an acoustically distinct food arrival pant hoot? *American Journal of Primatology*, 31(2), 99–109.
- Clay, Z., Pika, S., Gruber, T., & Zuberbühler, K. (2011). Female bonobos use copulation calls as social signals. *Biology Letters*, 7(4), 513–516. <http://dx.doi.org/10.1098/rsbl.2010.1227>.
- Clay, Z., Smith, C. L., & Blumstein, D. T. (2012). Food-associated vocalizations in mammals and birds: what do these calls really mean? *Animal Behaviour*, 83(2), 323–330. <http://dx.doi.org/10.1016/j.anbehav.2011.12.008>.
- Clay, Z., & Zuberbühler, K. (2011). Bonobos extract meaning from call sequences. *PLoS One*, 6(4), e18786. <http://dx.doi.org/10.1371/journal.pone.0018786>.
- Crockford, C., & Boesch, C. (2003). Context-specific calls in wild chimpanzees, *Pan troglodytes verus*: analysis of barks. *Animal Behaviour*, 66(1), 115–125. <http://dx.doi.org/10.1006/anbe.2003.2166>.
- Crockford, C., Wittig, R. M., Mundry, R., & Zuberbühler, K. (2012). Wild chimpanzees inform ignorant group members of danger. *Current Biology*, 22(2), 142–146. <http://dx.doi.org/10.1016/j.cub.2011.11.053>.
- Di Bitetti, M. S. (2005). Food-associated calls and audience effects in tufted capuchin monkeys. *Animal Behaviour*, 69(4), 911–919. <http://dx.doi.org/10.1016/j.anbehav.2004.05.021>.
- Dobson, A. J., & Barnett, A. G. (2008). *An introduction to generalized linear models*. Boca Raton, FL: Chapman & Hall/CRC.
- Eckhardt, N., Polansky, L., & Boesch, C. (2014). Spatial cohesion of adult male chimpanzees (*Pan troglodytes verus*) in Tai National Park, Côte d'Ivoire. *American Journal of Primatology*. <http://dx.doi.org/10.1002/ajp.22316>.
- Fedurek, P., & Slocombe, K. E. (2013). The social function of food-associated calls in male chimpanzees. *American Journal of Primatology*, 75(7), 726–739. <http://dx.doi.org/10.1002/ajp.22122>.
- Fischer, J. (1998). Barbary macaques categorize shrill barks into two call types. *Animal Behaviour*, 55(4), 799–807. <http://dx.doi.org/10.1006/anbe.1997.0663>.
- Fischer, J., Metz, M., Cheney, D. L., & Seyfarth, R. M. (2001). Baboon responses to graded bark variants. *Animal Behaviour*, 61(5), 925–931. <http://dx.doi.org/10.1006/anbe.2000.1687>.
- Fischer, J., Noser, R., & Hammerschmidt, K. (2013). Bioacoustic field research: a primer to acoustic analyses and playback experiments with primates. *American Journal of Primatology*, 75(7), 643–663. <http://dx.doi.org/10.1002/ajp.22153>.
- Fitch, W. T. (2005). The evolution of language: a comparative review. *Biology and Philosophy*, 20(2–3), 193–203. <http://dx.doi.org/10.1007/s10539-005-5597-1>.
- Forstmeier, W., & Schielzeth, H. (2011). Cryptic multiple hypotheses testing in linear models: overestimated effect sizes and the winner's curse. *Behavioral Ecology and Sociobiology*, 65(1), 47–55. <http://dx.doi.org/10.1007/s00265-010-1038-5>.
- Fox, J., Weisberg, S., Bates, D., & Fox, M. J. (2012). *Package "car"*. Retrieved from <http://cran.r-project.org/web/packages/car/car.pdf>.
- Frick, R. W. (1985). Communicating emotion: the role of prosodic features. *Psychological Bulletin*, 97(3), 412–429. <http://dx.doi.org/10.1037/0033-2909.97.3.412>.
- Goodall, J. (1986). *The chimpanzees of Gombe: Patterns of behavior*. Cambridge, MA: Belknap Press of the Harvard University Press.
- Gouzoules, S., Gouzoules, H., & Marler, P. (1984). Rhesus monkey (*Macaca mulatta*) screams: Representational signalling in the recruitment of agonistic aid. *Animal Behaviour*, 32(1), 182–193. [http://dx.doi.org/10.1016/S0003-3472\(84\)80336-X](http://dx.doi.org/10.1016/S0003-3472(84)80336-X).
- Gros-Louis, J. (2004). The function of food-associated calls in white-faced capuchin monkeys, *Cebus capucinus*, from the perspective of the signaller. *Animal Behaviour*, 67(3), 431–440. <http://dx.doi.org/10.1016/j.anbehav.2003.04.009>.
- Hammerschmidt, K., & Jürgens, U. (2007). Acoustical correlates of affective prosody. *Journal of Voice*, 21(5), 531–540. <http://dx.doi.org/10.1016/j.jvoice.2006.03.002>.
- 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.
- Hauser, M. D., & Wrangham, R. W. (1987). Manipulation of food calls in captive chimpanzees. *Folia Primatologica*, 48(3–4), 207–210. <http://dx.doi.org/10.1159/000156298>.
- Hohmann, G., Potts, K., N'Guessan, A., Fowler, A., Mundry, R., Ganzhorn, J. U., et al. (2010). Plant foods consumed by *Pan*: exploring the variation of nutritional ecology across Africa. *American Journal of Physical Anthropology*, 141(3), 476–485. <http://dx.doi.org/10.1002/ajpa.21168>.
- Janmaat, K. R. L., Ban, S. D., & Boesch, C. (2013a). Chimpanzees use long-term spatial memory to monitor large fruit trees and remember feeding experiences across seasons. *Animal Behaviour*, 86(6), 1183–1205. <http://dx.doi.org/10.1016/j.anbehav.2013.09.021>.
- Janmaat, K. R. L., Ban, S. D., & Boesch, C. (2013b). Tai chimpanzees use botanical skills to discover fruit: what we can learn from their mistakes. *Animal Cognition*, 16(6), 851–860. <http://dx.doi.org/10.1007/s10071-013-0617-z>.
- Macedonia, J. M., & Evans, C. S. (1993). Variation among mammalian alarm call systems and the problem of meaning in animal signals. *Ethology*, 93(3), 177–197. <http://dx.doi.org/10.1111/j.1439-0310.1993.tb00988.x>.
- Marler, P. (1976). Social organization, communication and graded signals: the chimpanzee and the gorilla. In P. P. Bateson, & R. A. Hinde (Eds.), *Growing points in ethology*. Cambridge, U.K.: Cambridge University Press.
- Marler, P., & Mitani, J. (1988). Vocal communication in primates and birds: parallels and contrasts. In P. D. D. Todd, D. P. Goedeke, & D. D. Symmes (Eds.), *Primate vocal communication* (pp. 3–14). Berlin, Germany: Springer.
- Marler, P., & Tenaza, R. R. (1977). Signaling behavior of apes with special reference to vocalization. In T. A. Sebeok (Ed.), *How animals communicate* (pp. 965–1033). Bloomington, IN: Indiana University Press.
- McCullagh, P., & Nelder, J. A. (1989). *Generalized linear models* (2nd ed.). London, U.K.: Chapman and Hall/CRC.
- McGregor, P. (1992). Quantifying responses to playback: one, many, or composite multivariate measures? In P. K. McGregor (Ed.), *Playback and studies of animal communication* (pp. 79–96). New York, NY: Plenum Press.
- Mitani, J. C., & Nishida, T. (1993). Contexts and social correlates of long-distance calling by male chimpanzees. *Animal Behaviour*, 45(4), 735–746. <http://dx.doi.org/10.1006/anbe.1993.1088>.
- Morton, E. S. (1977). On the occurrence and significance of motivation-structural rules in some bird and mammal sounds. *American Naturalist*, 111(981), 855–869.
- Normand, E., Ban, S. D., & Boesch, C. (2009). Forest chimpanzees (*Pan troglodytes verus*) remember the location of numerous fruit trees. *Animal Cognition*, 12(6), 797–807. <http://dx.doi.org/10.1007/s10071-009-0239-7>.
- Normand, E., & Boesch, C. (2009). Sophisticated Euclidean maps in forest chimpanzees. *Animal Behaviour*, 77(5), 1195–1201. <http://dx.doi.org/10.1016/j.anbehav.2009.01.025>.
- Notman, H., & Rendall, D. (2005). Contextual variation in chimpanzee pant hoots and its implications for referential communication. *Animal Behaviour*, 70(1), 177–190. <http://dx.doi.org/10.1016/j.anbehav.2004.08.024>.
- Ouattara, K., Lemasson, A., & Zuberbühler, K. (2009). Campbell's monkeys concatenate vocalizations into context-specific call sequences. *Proceedings of the National Academy of Sciences of the United States of America*, 106(51), 22026–22031. <http://dx.doi.org/10.1073/pnas.0908118106>.
- Owings, D. H., & Morton, E. S. (1998). *Animal vocal communication: A new approach*. Cambridge, U.K.: Cambridge University Press.
- Owren, M. J., & Rendall, D. (1997). An affect-conditioning model of nonhuman primate vocal signaling. In Vol. 12. *Perspectives in ethology: Communication* (pp. 299–342). New York, NY: Plenum Press.
- Palombit, R. A., Seyfarth, R. M., & Cheney, D. L. (1997). The adaptive value of 'friendships' to female baboons: experimental and observational evidence. *Animal Behaviour*, 54(3), 599–614. <http://dx.doi.org/10.1006/anbe.1996.0457>.
- Quinn, G. P., & Keough, M. J. (2002). *Experimental design and data analysis for biologists*. Cambridge, U.K.: Cambridge University Press.
- Rendall, D., Owren, M. J., & Ryan, M. J. (2009). What do animal signals mean? *Animal Behaviour*, 78(2), 233–240. <http://dx.doi.org/10.1016/j.anbehav.2009.06.007>.
- Schel, A. M., Machanda, Z., Townsend, S. W., Zuberbühler, K., & Slocombe, K. E. (2013). Chimpanzee food calls are directed at specific individuals. *Animal Behaviour*, 86(5), 955–965. <http://dx.doi.org/10.1016/j.anbehav.2013.08.013>.
- Schel, A. M., Townsend, S. W., Machanda, Z., Zuberbühler, K., & Slocombe, K. E. (2013). Chimpanzee alarm call production meets key criteria for intentionality. *PLoS One*, 8(10), e76674. <http://dx.doi.org/10.1371/journal.pone.0076674>.
- Seyfarth, R. M., Cheney, D. L., Bergman, T., Fischer, J., Zuberbühler, K., & Hammerschmidt, K. (2010). The central importance of information in studies of animal communication. *Animal Behaviour*, 80(1), 3–8. <http://dx.doi.org/10.1016/j.anbehav.2010.04.012>.
- Seyfarth, R. M., Cheney, D. L., & Marler, P. (1980). Vervet monkey alarm calls: semantic communication in a free-ranging primate. *Animal Behaviour*, 28(4), 1070–1094. [http://dx.doi.org/10.1016/S0003-3472\(80\)80097-2](http://dx.doi.org/10.1016/S0003-3472(80)80097-2).
- Slocombe, K. E., Kaller, T., Turman, L., Townsend, S. W., Papworth, S., Squibbs, P., et al. (2010). Production of food-associated calls in wild male chimpanzees is dependent on the composition of the audience. *Behavioral Ecology and Sociobiology*, 64(12), 1959–1966. <http://dx.doi.org/10.1007/s00265-010-1006-0>.
- Slocombe, K. E., & Zuberbühler, K. (2005). Functionally referential communication in a chimpanzee. *Current Biology*, 15(19), 1779–1784. <http://dx.doi.org/10.1016/j.cub.2005.08.068>.
- Slocombe, K. E., & Zuberbühler, K. (2006). Food-associated calls in chimpanzees: responses to food types or food preferences? *Animal Behaviour*, 72(5), 989–999. <http://dx.doi.org/10.1016/j.anbehav.2006.01.030>.
- Slocombe, K. E., & Zuberbühler, K. (2007). Chimpanzees modify recruitment screams as a function of audience composition. *Proceedings of the National Academy of Sciences of the United States of America*, 104(43), 17228–17233. <http://dx.doi.org/10.1073/pnas.0706741104>.

- Sterck, E. H. M., Watts, D. P., & van Schaik, C. P. (1997). The evolution of female social relationships in nonhuman primates. *Behavioral Ecology and Sociobiology*, 41, 291–309. <http://dx.doi.org/10.1007/s002650050390>.
- Symington, M. M. (1988). Food competition and foraging party size in the black spider monkey (*Ateles Paniscus Chamek*). *Behaviour*, 105(1), 117–134. <http://dx.doi.org/10.1163/156853988X00476>.
- Tomasello, M. (2008). *Origins of human communication*. Cambridge, MA: MIT Press.
- Townsend, S. W., Deschner, T., & Zuberbühler, K. (2008). Female chimpanzees use copulation calls flexibly to prevent social competition. *PLoS One*, 3(6), e2431. <http://dx.doi.org/10.1371/journal.pone.0002431>.
- Townsend, S. W., & Manser, M. B. (2013). Functionally referential communication in mammals: the past, present and the future. *Ethology*, 119(1), 1–11. <http://dx.doi.org/10.1111/eth.12015>.
- Waser, P. M., & Waser, M. S. (1977). Experimental studies of primate vocalization: specializations for long-distance propagation. *Zeitschrift für Tierpsychologie*, 43(3), 239–263. <http://dx.doi.org/10.1111/j.1439-0310.1977.tb00073.x>.
- Wheeler, B. C., & Fischer, J. (2012). Functionally referential signals: a promising paradigm whose time has passed. *Evolutionary Anthropology*, 21(5), 195–205. <http://dx.doi.org/10.1002/evan.21319>.
- Wheeler, B. C., Searcy, W. A., Christiansen, M. H., Corballis, M. C., Fischer, J., Grueter, C., et al. (2011). Communication. In R. Menzel, & J. Fischer (Eds.), *Animal thinking: Contemporary issues in comparative cognition* (pp. 187–205). Cambridge, MA: MIT Press.
- Wittig, R. M., Crockford, C., Deschner, T., Langergraber, K. E., Ziegler, T. E., & Zuberbühler, K. (2014). Food sharing is linked to urinary oxytocin levels and bonding in related and unrelated wild chimpanzees. *Proceedings of the Royal Society B: Biological Sciences*, 281(1778), 20133096. <http://dx.doi.org/10.1098/rspb.2013.3096>.
- Zuberbühler, K. (2000). Referential labelling in Diana monkeys. *Animal Behaviour*, 59(5), 917–927. <http://dx.doi.org/10.1006/anbe.1999.1317>.
- Zuberbühler, K. (2003). Referential signaling in non-human primates: cognitive precursors and limitations for the evolution of language. *Advances in the Study of Behavior*, 33, 265–307.
- Zuberbühler, K., & Janmaat, K. (2010). Foraging cognition in nonhuman primates. In M. Platt, & A. Ghazanfar (Eds.), *Primate neuroethology* (pp. 64–83). Oxford, U.K.: Oxford University Press.

## Appendix

**Table A1**

Name abbreviation, age of individual at the end of the study period given in parentheses and observation hours per individual.

	Observation hours
<b>Males</b>	
Woo (18)	137.50
Uta (18)	75.00
Kub (16)	145.25
Jac (13)	23.00
Rom (13)	65.25
<b>Females</b>	
Sum (47)	78.75
Jul (42)	59.25
Ish (42)	94.00
Kin (22)	76.50
Total	754.50

All individuals were 15 years of age or older, except for two subadult males (both aged 13 at the end of the study) who were included owing to the low number of adult males present in the group, and because one adult male disappeared halfway through the study period (Uta). This group had recently suffered from a disease outbreak, and the subadult males included were the third- and fourth-ranked males of the group by the end of the study period. Hence they held important social roles within the group and were physically comparable in development to all other males, of which none were over the age of 18.

**Table A2**

Variables and their transformations that were included in the six production GLMMs (every test predictor was tested separately for the two response variables) and the single response GLMM

	Variables	Transformations	Mean±SD (for transformed predictors)
<b>Production models</b>			
Response	Call duration	Log	
	Call pitch	None	
Test predictors	Food species	Dummy coded for five levels	
	Dbh	None	
Control variables	Fruit count	Square root	−11.09±7.05
	Party size	Square root	−2.76±0.96
	Latency to call from arrival	Square root	−3.98±0.96
	Position in sequence of bout	None	
Random effects	Sex of caller	None	
	Caller ID	None	
Random slopes	Feeding event ID	None	
	Call bout ID	None	
	Food species within caller ID	None	
	Dbh within caller ID	None	
Response model	Fruit count within caller ID	None	
	Response	Total number of arrivals	None
Test predictors	Call pitch	Square root	−1.03±0.51
	Control predictors	Sex of caller	None
Party size		Square root	−2.71±1.20
Random effects	Caller ID	None	
	Random slopes	Call pitch within caller ID	None

We checked for the presence of temporal autocorrelation of the residuals within individual chimpanzees in the original production model but the term was subsequently dropped because the estimate was negative (see the main text for details of how each model was implemented). For the production models with Gaussian error structure, homogeneity and normality of residuals were verified using a qqplot and residuals plotted against the fitted values. For all models we checked for the absence of collinearity (Quinn & Keough, 2002) among predictors using the function 'vif' from the 'car' package (Fox, Weisberg, Bates, & Fox, 2012) applied to standard linear models excluding the random effects. All vifs were below 2.0 and therefore collinearity was not an issue. Stability of all models was evaluated by excluding the levels of the random effects one at a time to ensure no particular level was too influential and model estimates were robust.

**Table A3**

Loadings of the nine acoustic variables on the factor derived through a factor analysis which constituted the variable call pitch in the analyses

Acoustic variable	Loading on the factor 'call pitch'
DF1 max	0.976
DF1 min	0.962
DF1 mean	0.977
DF2 max	0.998
DF2 mean	0.998
Range of DF1	0.643
Minimum difference DF1 and DF2	0.953
Maximum difference DF1 and DF2	0.968
PF max	0.856



**Table A4**

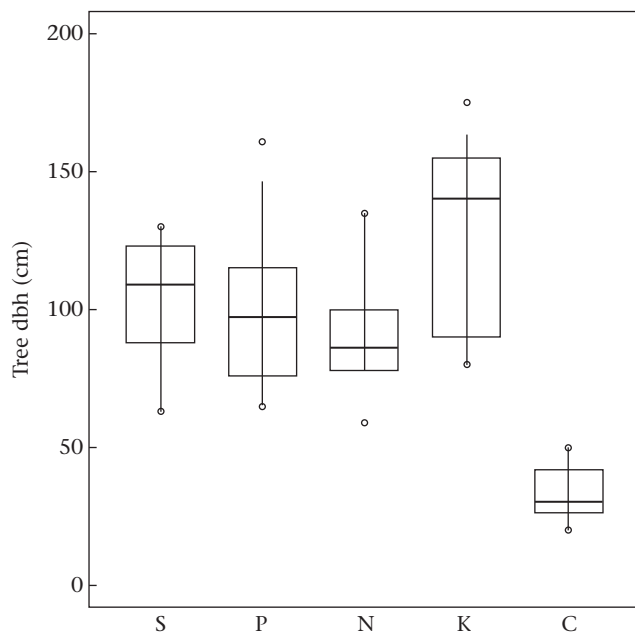
Spearman rank correlations for each species between tree size (dbh) and fruit count measurements of feeding events

Species	$r_s$	No. of trees	$P$
<i>Coula edulis</i>	0.13	37	0.45
<i>Klainedoxa gabonensis</i>	0.17	27	0.39
<i>Nauclea diderichi</i>	0.19	53	0.17
<i>Parinari excelsa</i>	0.15	48	0.30
<i>Sacoglottis gabonensis</i>	0.26	42	0.10

**Table A5**

Average DF1 mean, DF2 mean, PF max and call duration for food calls of each food species with sample size for each indicated in parentheses

	DF1 mean $\pm$ SE (Hz)	DF2 mean $\pm$ SE (Hz)	PF max $\pm$ SE (Hz)	Duration $\pm$ SE (ms)
<i>Coula</i> (59)	186.36 $\pm$ 22.12	396.13 $\pm$ 47.01	295.67 $\pm$ 35.09	204.07 $\pm$ 24.22
<i>Klainedoxa</i> (72)	171.74 $\pm$ 17.90	344.28 $\pm$ 35.89	329.85 $\pm$ 34.39	173.77 $\pm$ 18.12
<i>Nauclea</i> (148)	330.76 $\pm$ 26.31	663.08 $\pm$ 52.75	402.81 $\pm$ 32.05	187.04 $\pm$ 14.88
<i>Parinari</i> (60)	257.46 $\pm$ 32.70	503.37 $\pm$ 63.93	316.17 $\pm$ 40.15	290.54 $\pm$ 36.90
<i>Sacoglottis</i> (40)	163.19 $\pm$ 18.13	344.44 $\pm$ 38.27	261.67 $\pm$ 29.07	210.25 $\pm$ 23.36



**Figure A1.** Variation in tree size (dbh) for each species from all feeding events observed. *Coula* trees are significantly smaller (Kruskal–Wallis test:  $\chi^2_4 = 103.46, P < 0.001$ ). Horizontal lines show medians, boxes show quartiles, vertical lines represent percentiles (2.5 and 97.5%) with minimum and maximum values for each species represented by a circle. For species abbreviations see Fig. 1.