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

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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.

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;

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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 ± 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
Coula	72	33	13
Klainedoxa)	30	22	11
Nauclea	68	46	20
Parinari	62	38	13
Sacoglottis	65	42	11
Total	297	181	68