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Food-associated vocalizations in mammals and birds: what do these calls really mean?

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We dedicate this paper to the memory of Professor Chris Evans, a scholar and friend who thought hard about the meaning of animal signals

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Alarm calls and food-associated calls from a diverse range of species are said to be functionally referential, in that receivers can use these sounds to predict environmental events in the absence of other contextual cues. The evolutionary driver for referential alarm calls has been hypothesized to be the mutually incompatible escape behaviours required to avoid different predators. However, some species produce acoustically distinctive and referential alarm calls but do not show highly referential abilities in other domains. We examined whether food-associated calls in many species are likely to be functionally referential and whether they specifically communicate about characteristic features of food. Food-associated calls are given in both feeding and nonfeeding contexts, and the types of information contained vary greatly. Most species do not produce unique calls for different foods; more common is variation in the call rate, which suggests that call structure reflects the callers' internal state rather than the food type. We also examined the ultimate function of food-associated calls to evaluate whether there is a unifying explanation for the evolution of functionally referential food calls. Based on the literature, there does not appear to be a unifying function. In conclusion, while functionally referential food-associated calls have been convincingly demonstrated in a few species, it is more common for these vocalizations to reflect arousal rather than additionally providing specific referential information about the feeding event. At this point, there is no compelling hypothesis to explain the evolution of functionally referential food-associated calls. Given the multiple functions of food-associated signals, we should not expect a unitary explanation.

A key question in the animal communication literature concerns whether animal signals convey information to receivers about objects or events in the external world (Seyfarth & Cheney 2003; Seyfarth et al. 2010; but see Rendall et al. 2009). These signals, termed 'functionally referential', have been defined as those that enable receivers to predict environmental events in the absence of other visual or contextual cues, to the extent that the signal elicits the same adaptive response in the receivers as if the receivers had actually experienced the eliciting stimuli themselves (Marler et al. 1992; Macedonia & Evans 1993; Evans 1997). The use of the modifier 'functional' acknowledges the fact that, although some animals produce calls that appear to refer to external objects or events, the psychological processes underlying call production and perception are poorly understood (Marler et al. 1992). This definition further takes into account that, at least from the producer's perspective, these calls in nonhuman animals differ substantially from truly referential communication in the linguistic sense. A key difference is that animal signallers appear to lack the flexibility and communicative intentions seen in language, with calls more genetically predetermined (e.g. Zuberbühler 2003; Seyfarth & Cheney 2010). Nevertheless, functionally referential vocalizations continue to arouse considerable interest and debate because of their implications for the evolution of symbolic communication and language (e.g. Scarantino 2010), as well as for indicating that some aspects of animal communication may be conceptually, rather than just affectively or emotionally, driven (Cheney & Seyfarth 1990; Zuberbühler et al. 1999).

Using the original terminology, a signal must meet specific production and perception criteria to be classified as functionally referential (Seyfarth et al. 1980; Marler et al. 1992; Macedonia & Evans 1993; Evans 1997). First, the signal must possess a discrete acoustic structure and be stimulus-class specific (i.e. there must be a tight association between signal production and the eliciting stimuli). Second, the signal must elicit the appropriate receiver response, independent of context (Marler et al. 1992; Evans et al.

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1993; Evans 1997). Following this definitive framework, functionally referential vocalizations have been identified in many, but not all, primate species (see Zuberbühler 2003, 2009), as well as in bird and other mammalian species, such as fowl, *Gallus gallus* (Evans & Marler 1994; Evans & Evans 1999), ravens, *Corvus corvax* (Bugnyar et al. 2001), black-capped chickadees, *Poecile atricapillus* (Templeton et al. 2005) and meerkats, *Suricata suricatta* (Manser et al. 2001). To date, the majority of evidence for functionally referential signals comes from studies of alarm call systems (Zuberbühler 2003, 2009). Using a combination of observational studies and playback experiments, alarm calls have been shown to convey a range of information about the predation event, including the class of predator (e.g. terrestrial or aerial), level of response urgency and the caller's imminent behaviour (Evans 1997; Blumstein 1999; Leavesley & Magrath 2005).

However, although such signals have the potential to provide information about specific events in the environment, a growing body of evidence suggests that most alarm signals do not meet the strict definition for production specificity. For example, evidence from a range of species has shown that alarm calls produced to specific predator types may also be given in other circumstances, including in response to nonpredatory disturbances (i.e. falling trees and nonpredatory animals: Arnold & Zuberbühler 2006; Wheeler 2010), and in response to social disturbances, such as agonistic encounters with other conspecific groups (Fichtel & Kappeler 2002; Digweed et al. 2005; Fichtel & van Schaik 2006), as well as during habitual dawn choruses (Marler 1972). Rather than conveying highly specific information to receivers, these calls may function to attract the attention of the receiver to a particular stimulus (K. Arnold & K. Zuberbühler, unpublished data). This evidence suggests that the many animal signals that convey information have a broader use and may not meet the original definition of functionally referential. This matter will be further discussed in later sections.

In addition to alarm call systems, vocalizations produced during feeding have also been identified as functionally referential in a number of bird and mammal species (e.g. fowl: Evans & Evans 1999; ravens: Bugnyar et al. 2001; tufted capuchins, *Cebus apella*: Di Bitetti 2003; rhesus macaques, *Macaca mulatta*: Hauser & Marler 1993a; chimpanzees: Slocombe & Zuberbühler 2005; Geoffroy's tufted-ear marmosets, *Callithrix geoffroyi*: Kitzmann & Caine 2009). The possibility of referential signals in the feeding context follows from the logic that, in a manner similar to that of alarm calls, food-associated calls are elicited by specific stimuli that occur within the external environment (i.e. the discovery or presence of food).

In this review, we ask whether food-associated calls in a range of species meet the criteria for functional reference and address the question of the potential evolutionary drivers for food-associated calls. The key question is whether, similar to alarm calls, there may be a unifying explanation to food-associated calls. To investigate the possibility of functional reference, we will explore the kinds of information conveyed by food-associated calls, and their referential specificity and underlying functions.

FUNCTIONALLY REFERENTIAL FOOD-ASSOCIATED CALLS?

To date, the most convincing cases of functional reference in the feeding context come from studies of fowl (Evans & Marler 1994; Evans & Evans 1999, 2007). Upon discovery of a food item in the presence of a hen, male fowl produce a specific food-associated vocalization. Consistent with the criteria described above, fowl's food-associated calls are produced specifically within the context of food, have an acoustically distinct structure, and playback experiments have demonstrated that they elicit specific feeding behaviours in receivers, in the absence of other stimuli (Marler et al. 1986; Evans & Marler 1994; Evans & Evans 1999). Beyond fulfilling the production criteria, results from a playback study by Evans & Evans (2007) indicated that receivers perceive these calls as food specific and that these calls appear to create a representation of food in the receiver.

Similarly, a recent study of marmosets (*Callithrix geoffroyi*) showed that receivers increased feeding-related behaviours (foraging and feeding) following playbacks of food-associated calls compared to when they heard control vocalizations (Kitzmann & Caine 2009). Playback experiments with both chimpanzees, *Pan troglodytes*, and bonobos, *Pan paniscus*, have demonstrated that receivers expend greater foraging effort (e.g. time spent foraging, number of inspections of a feeding patch) following playbacks of food-associated calls as opposed to control conditions, where no sounds were played (Slocombe & Zuberbühler 2005; Clay & Zuberbühler 2011). Receivers also exerted a greater foraging effort at the location associated with the specific type of food-vocalization played (i.e. calls associated with high- versus low-quality foods). However, in both studies, the individuals were required to first learn the contingency that food 'could' be available in one of two previously learned feeding locations. Thus, although individuals in both studies increased foraging effort at the location associated with the call, their previous experience makes it difficult to completely rule out the possibility that, upon hearing the calls, individuals were responding to caller arousal rather than to information regarding food presence specifically.

In other playback studies, the perceptual responses of receivers have been measured in terms of approach behaviour and time spent looking towards the speaker playing the food-associated calls (e.g. Di Bitetti 2003; Gros-Louis 2004a). However, while a greater approach response could feasibly result from an expectation of food presence, approach behaviours themselves are not equivalent to feeding behaviours. Approaching the playback speaker may instead indicate that the calls are effective in social recruitment or in communicating the caller's level of excitement, neither of which is necessarily related to food. In this manner, many of the studies claiming functional reference have still not provided conclusive evidence fulfilling the perception criteria that such calls refer to specific feeding opportunities in the environment. And, unlike predator-class-specific alarm calls, in these cases, referential food-associated calls may only communicate that food is present, rather than conveying additional information about the event, such as food type or quantity.

FOOD-ASSOCIATED VERSUS FOOD-SPECIFIC VOCALIZATIONS

Acoustic specificity between stimulus and signal, such as has been demonstrated for fowl food calls, is a key prerequisite for functional reference. The notable problem for a unifying concept of functionally referential food-associated calls is that, for a considerable number of species, calls produced during feeding are also produced in nonfood contexts (e.g. toque macaque, *Macaca sinica*: Dittus 1984; spider monkey, *Ateles geoffroyi*: Chapman & Lefebvre 1990; rhesus macaque, *Macaca mulatta*: Hauser & Marler, 1993a; golden-lion tamarin, *Leontopithecus roaslia*: Halloy & Kleiman 1994; red-bellied tamarin, *Saguinus labiatus*: Roush & Snowdon 2000; bonobo: Clay & Zuberbühler 2009), and in some species, may not even be food-specific at all (greater spear-nosed bat, *Phyllostomus hastatus*: Wilkinson & Boughman 1998; bottlenose dolphin, *Tursiops truncates*: Janik 2000; pinyon jay, *Gymnorhinus cyanocephalus*: Dahlin et al. 2005). For example, spider monkey 'whinnie' calls attract foragers to the food source but also serve other functions in social recruitment that are unrelated to feeding (Chapman & Lefebvre 1990). Greater spear-nosed bats produce contact calls that function, in the feeding context, to recruit conspecifics to the