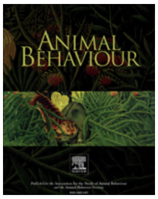
Animal Behaviour 83 (2012) 323–330

Contents lists available at SciVerse ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav



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

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ARTICLE INFO

Article history:
Received 14 August 2011
Initial acceptance 4 October 2011
Final acceptance 4 November 2011
Available online 2 January 2012
MS. number: ARV-11-00652R

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

Keywords:
alarm call
food-associated call
referential signalling
status signalling

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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doi:10.1016/j.anbehav.2011.12.008

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 feeding site (Wilkinson & Boughman 1998). Golden-lion tamarins produce the ‘chuck’ call during feeding but also during intergroup encounters and predator mobbing (Halloy & Kleiman 1994). Toque macaques produce a specific call in response to food; however, they also sometimes produce this call during nonfood contexts associated with elation, such as at the onset of rain following dry periods, or on hot sunny days towards the end of the rainy season (Dittus 1984). Thus, although such calls may be associated with feeding, their production within nonfood contexts indicates that these calls may function more generally in social recruitment and may more accurately reflect the caller’s motivational response to an event rather than the caller’s discovery of food specifically.

WHAT INFORMATION DO FOOD-ASSOCIATED CALLS CONVEY?

Related to the question of acoustic specificity is determining what information may be conveyed by food-associated calls. The arousal-based perspective suggests that food-associated calls most likely relate to the signaller’s level of excitement or arousal in response to the feeding event (e.g. Owren & Rendall 2001). In this sense, receivers may be responding to the signaller’s increased level of excitement, which has been triggered by the presence of food, rather than the specific expectation of a feeding opportunity. However, disentangling motivation from reference is notoriously difficult to address empirically, although it is likely that both may be communicated (Evans 1997). This follows from a series of studies that have shown that even vocal signals with high emotional valence, such as alarm calls, can still simultaneously communicate referential information about an external object or event (see Seyfarth et al. 2010). For instance, recent work on the alarm call responses of meerkats has demonstrated that both emotional and referential information are coded into the same signal and that they develop on different ontogenetic timescales (Hollen & Manser 2007). Furthermore, it can also be the case that a call that, from the signaller’s perspective, is purely arousal based may still provide potentially functionally referential information if the call can be shown to be elicited by a narrow range of stimuli. The issue of disentangling arousal from reference may be less problematic if the question of the information conveyed by a signal is addressed separately from both the signaller’s and receiver’s perspectives (Seyfarth & Cheney 2003).

Therefore, while food-associated calls undoubtedly convey some degree of information of the caller’s level of arousal in response to the presence of food, there is also the potential for food-associated calls to provide other information, including the quantity, quality or divisibility of the food source (see Table 1 for details). For the majority of species, this additional information about the feeding opportunity appears to be conveyed via changes in call rate, rather than changes in the acoustic structure of the calls themselves. For example, tufted capuchins and chimpanzees increase the call rate in response to greater quantities of foods (Hauser et al. 1993; Di Bitetti 2005), while male fowl (Marler et al. 1986), cottontop tamarins, *Saguinus oedipus* (Elowson et al. 1991), red-bellied tamarins, *Saguinus labiatus* (Caine et al. 1995) and spider monkeys (Chapman & Lefebvre 1990) increase their call rates in response to both greater quantities of food and foods of higher quality. Changes in call rate have also been shown to covary with other features relating to the caller’s perception of the feeding event, including food divisibility (Hauser et al. 1993), food accessibility (Bugnyar et al. 2001), the anticipation of food acquisition (Gros-Louis 2006), as well as the caller’s hunger level (Hauser & Marler 1993a; Wauters et al. 1999).

Although changes in call rates may feasibly represent a form of functionally referential communication (e.g. in the waggle dance of the honeybee, *Apis mellifera*, the length of the waggle run varies as a function of distance to the food source; von Frisch 1956), it is relevant to note that there are no examples of functionally referential alarm calls in which information is conveyed via call rates alone (Blumstein 1999). Instead, most animals produce acoustically distinct alarm calls that convey referential information about specific features of the predation event, such as the class of predator or the response urgency (Evans et al. 1993; Blumstein 1999; Zuberbühler 2003). Therefore, although call rate may provide some information about the feeding event, the degree of specificity may be insufficient in the majority of species examined to be classed as functionally referential with regard to the specific characteristics of the feeding opportunity, such as food quality, divisibility or accessibility.

ACOUSTIC VARIATION IN FOOD-ASSOCIATED CALLS

Although variation in call rate is the most common form of acoustic variation in food-associated signalling, some species produce food-associated calls whose acoustic structure covaries with features of the feeding event (golden-lion tamarins: Benz 1993; rhesus macaques: Hauser & Marler, 1993a; ravens: Bugnyar et al. 2001; chimpanzees: Slocombe & Zuberbühler 2006; bonobos: Clay & Zuberbühler 2009). Furthermore, playback experiments in some of these species have also demonstrated that these acoustic variants are meaningful to receivers (Hauser 1998; Slocombe & Zuberbühler 2005; Clay & Zuberbühler 2011).

One striking similarity across studies is that acoustic variation in food-associated calls is typically associated with perceived food quality, rather than other food-specific features such as quantity or divisibility (but see Bugnyar et al. 2001). Chimpanzees, for example, produce graded variants of their food-associated ‘rough grunt’ as a function of food quality (Slocombe & Zuberbühler 2006), whereas bonobos produce an array of different food-associated calls whose production is probabilistically related to the quality of food encountered by the caller (Clay & Zuberbühler 2009). Rhesus macaques produce up to five food-associated calls; three calls (‘warble’, ‘harmonic arch’, ‘chirp’) are given in response to high-quality and rare food items, whilst the other two calls (‘coos’, ‘grunts’) are given to lower-quality foods as well as in nonfood contexts (e.g. group movement, grooming; Hauser & Marler 1993a). In a habituation–dishabituation playback experiment, Hauser (1998) found that rhesus monkeys categorized food-associated calls based upon their referential similarities rather than shared acoustic features, indicating that call perception is based on their functional referents rather than purely on acoustic features.

One obvious question is why this select group of species, but apparently not other species, communicate about food quality via acoustic characteristics instead of by call rate. However, referential alarm calls are not an ideal model for understanding the presence or absence of referentiality in food-associated calling. For instance, while there is compelling evidence that the evolution of referential alarm calls is driven by the incompatibility of escape responses (Macedonia & Evans 1993; but see earlier discussion for cases where escape strategies are not incompatible or not the usual reaction to alarm calls: e.g. Fichtel & Kappeler 2002; Digweed et al. 2005; Wheeler 2008), feeding poses no such incompatibility problem. Perhaps the closest analogy to alarm calls is that seen when a social species encounters divisible versus indivisible food. Yet even here, the trend seems to be to elect to produce or not to produce a food call, rather than to produce variable food-associated calls (e.g. Dahlin et al. 2005; Table 1).

In addition to food quality, acoustic structure can also relate to other, more social features of the feeding event. For instance, ravens produce both short ‘who’ and long ‘haa’ yells during feeding and their differential usage is relative to food availability (Bugnyar et al.

Table 1
Summary of the results of studies of food-associated calls in mammals and birds, from caller and receiver perspectives

Species	Specificity of production (in food context)	Receiver response	Changes in call with food characteristics	Information encoded by food-associated calls	Social group structure	Source
Fowl *Gallus gallus*	Yes	Approach and foraging behaviour	Increased call rate	Quality of food	Stable	Marler et al. 1986; Evans & Evans 1999
House sparrow *Passer domesticus*	Yes	Approach	None	Divisibility of food	Transient	Elgar 1986
Pinyon jay *Gymnorhinus cyanocephalus*	No	Approach	Number of calls and use of call groups vs single calls	Social recruitment: call when alone to attract foragers and call more in presence of mate	Variable, dependent on season	Dahlin et al. 2005
Cliff swallow *Petrocheldion pyrrhonota*	Yes	Approach	None	Quantity of food (insect swarm density)	Transient	Brown et al. 1991
Carolina chickadee *Poecile carolinensis*	Yes (for D call)	Approach	Number of calls	Social recruitment	Transient	Mahurin & Freeberg 2009
Raven *Corvus corvax*	Yes	Approach	Increased call rate ('haa' calls but not 'yells')	Accessibility, caller's hunger level and quality of food	Fission–Fusion	Heinrich 1988; Bugnyar et al. 2001
Greater spear-nosed bat *Phllostomus hastatus*	No	Approach	None	Social recruitment: contact calls used during foraging for coordination	Stable	Wilkinson & Boughman 1998
Bottlenose dolphin *Tursiops truncates*	No	Approach	Not specified in the literature	Food presence, exploit prey sensory system to facilitate capture	Fission–Fusion	Janik 2000
Marmoset *Callithrix geoffroyi*	Yes	Approach and foraging behaviour	Not specified in the literature	Social recruitment	Stable	Kitzmann & Caine 2009
Chimpanzee *Pan troglodytes*	Yes	Approach and foraging behaviour	Increased call rate, distinct sounds ('rough grunts')	Quantity/divisibility/ quality of food, resource ownership	Fission–Fusion	Hauser & Wrangham 1987; Hauser et al. 1993; Slocombe & Zuberbühler 2006
Bonobo *Pan paniscus*	Yes	Approach site previously associated with food	Distinct sounds	Quality of food	Stable	Clay & Zuberbühler 2009, 2011
Tufted capuchin monkey *Cebus apella nigritus*	Yes	Approach	Increased call rate	Quantity/quality of food	Stable	Di Bitetti 2003, 2005
White-faced capuchin monkey *Cebus capucinus*	Yes	Approach	Increased call rate	Caller spacing, resource ownership, anticipation of food acquisition	Stable	Boinski & Campbell 1996; Gros-Louis 2004a, b, 2006
Red-bellied tamarin *Saguinus labiatus*	Yes	Approach implied but not directly tested	Increased call rate	Quantity/quality of food, caller spacing, resource ownership, social recruitment	Stable	Caine et al. 1995
Spider monkey *Ateles geoffroyi*	No	Approach	Increased call rate	Social recruitment, quantity/quality of food	Stable	Chapman & Lefebvre 1990
Cottontop tamarin *Saguinus oedipus*	No	Food call	Increased call rate, call type (C- and D-chirp)	Quantity/quality of food, caller food preference, approaching food, feeding	Stable	Elowson et al. 1991; Roush & Snowdon 2000
Golden-lion tamarin *Leontopithecus rosalia*	No (predator mobbing, intergroup interactions)	Context dependent	Call rate and distinct sounds	Quality of food, caller food preference	Stable	Benz et al. 1992; Benz 1993
Mandrill *Mandrillus sphinx*	Yes	Approach	Not tested	Social recruitment	Stable/male membership changes with season	Laidre 2006
Rhesus macaque *Macaca mulatta*	No (group movement, grooming, mother-infant interactions)	Context dependent	Distinct sounds (chirps, warbles, harmonic arches)	Divisibility of food, caller's hunger level, caller food preference	Stable	Hauser & Marler 1993a, b
Toque macaque *Macaca sinica*	No (rain after drought)	Context dependent	Probability of calling	Quantity/rarity/ quality of food	Stable	Dittus 1984, 1988

2001). ‘Haa’ yells are produced upon sighting the food and appear to provide information about the food itself and its accessibility. However, ‘who’ yells are produced upon approaching the food and appear to convey information about the caller during the feeding event. Carolina chickadees, *Poecile carolinensis*, adjust the acoustic structure of their calls depending on whether another individual has joined them to feed. Playback experiments show that these calls function in social recruitment to a feeding site compared to calls given after other individuals have joined the caller (Mahurin & Freeberg 2009). Food-associated calls may also convey information about the caller themselves, including the caller’s rank (cottontop tamarins: Roush & Snowdon 1999), identity or sex (white-faced capuchins, *Cebus capucinus*: Gros-Louis 2006).

WHAT IS THE FUNCTION OF FOOD-ASSOCIATED CALLS?

Along with the information conveyed by food-associated calls, an important related question concerns the ultimate function of these calls. Although this is a discrete question, logically separate from the meaning of food calls, an integrative Tinbergian approach to understanding the phenomena warrants some discussion of function. Indeed, by understanding the function of these calls, we may evaluate the question of whether there is a unifying explanation for the evolution of functionally referential food calls.

In their original synthesis, Macedonia & Evans (1993) focused only on the putative call ‘meaning’ when developing a unifying hypothesis for functional referential vocalizations. However, incorporating call function can provide insights into cases for acoustically distinct calls (i.e. alarm or food-associated calls) where response strategies are not necessarily incompatible (i.e. predator escape strategies in response to predator-specific alarm calls) or may differ from the typical behavioural reaction to the calls (e.g. Kirchhoff & Hammerschmidt 2006; Furrer & Manser 2009).

Similarly to alarm calls (e.g. Wheeler 2008), there appear to be a diverse array of possible functions to food-associated calls. Several themes have emerged in our review, and although not mutually exclusive, they indicate that the function of food-associated calls is closely tied to the socioecology of a given species. For the majority of species, food-associated calls attract foragers and appear to function in social recruitment (e.g. Dittus 1984; Chapman & Lefebvre 1990; but see Gros-Louis 2004b; Table 1). Although social recruitment to a food source may, at first, appear counterintuitive, there are a number of benefits to attracting other individuals to the food source. This may work at the level of enhancing inclusive fitness via kin selection (e.g. Hauser & Marler 1993a, b; Judd & Sherman 1996) as well as by enhancing fitness directly.

For small-bodied species that are vulnerable to predation, recruiting conspecifics, or even heterospecifics, may function to reduce predation risk, either by dilution or increased vigilance (Sridhar et al. 2009; house sparrows, *Passer domesticus*: Elgar 1986; Newman & Caraco 1989; Elowson et al. 1991; cottontop tamarins: Caine et al. 1995). For flocking bird species, attracting conspecifics may also benefit the forager in terms of manipulation of the food patch. For example, in colonially nesting cliff swallows, *Petrochelidon pyrrhonota*, that feed on insect swarms, attracting more foragers may increase the chance of the insect swarm’s movements being tracked, thus enabling each signaller to exploit the same insect swarm for longer than if these signallers were foraging alone (Brown et al. 1991). In other species, callers may benefit by recruiting foragers that can assist in the cooperative defence of resources (Heinrich & Marzluff 1991; Marzluff & Heinrich 1991; Wilkinson & Boughman 1998).

In addition to functions relating to defence, signallers may receive reproductive rewards by attracting conspecifics to the food source. Male fowl call more often in the presence of females (Marler et al. 1986; Evans & Marler 1994), and females in turn prefer to mate with males that food call more often (Pizzari 2003). Likewise, the production of food-associated calls by male bonobos attract females to a food source, which subsequently engage in copulations with the calling males (Van Krunkelsven et al. 1996). Reproductive benefits may also work at the level of maintaining an association with long-term mating partners. For instance, pinyon jays call more when their long-term mate is present than when nonmates are present (Dahlin et al. 2005). In addition to direct reproductive benefits, signallers may also receive indirect benefits, through kin selection, by alerting kin to a food patch (Hauser & Marler 1993a, b; Judd & Sherman 1996). For example, tufted capuchins call more in the presence of larger audiences of kin than of nonkin (Pollick et al. 2005), and in rhesus macaques, females in larger matrilines call more than those in smaller matrilines (Hauser & Marler 1993a).

The attraction of potential mates indicates that food-associated calls may play a role in enhancing social status or reputation. The communication of social status is also supported by evidence that food calls may also function to attract allies and close social partners (e.g. bonobos: Van Krunkelsven et al. 1996; chimpanzees: Slocombe et al. 2010). This ‘reputation building’ function may be especially relevant in species living in socially stable groups with the chance for repeated interactions between group members (as opposed to transient group formations, such as flocking birds or bats). In a recent study by Slocombe et al. (2010), male chimpanzees were shown to call more in the presence of close social partners, regardless of the audience size or the presence of oestrous females. Furthermore, although the size and divisibility of the food patch influenced calling, the presence of social partners explained most of the variation in calling behaviour, suggesting that food-associated calls may function to enhance affiliation between allies. It is also notable that in chimpanzees and bonobos, there appears to be an association between acoustically variable calls signalling food quality and the suggestion of a ‘reputation’ building function. Such a hypothesis requires further attention.

In contrast to these previous examples in which food-associated calls function in social recruitment, food calls may function to reduce foraging competition in some primate species that forage in large and stable groups (rhesus macaques: Hauser & Marler 1993a, b; cottontop tamarins: Caine et al. 1995; white-faced capuchins: Gros-Louis 2004b; tufted capuchins: Di Bitetti 2005). Conflicts resulting from competition over food are common in social foragers, and thus food calling may provide a clear establishment of resource ownership and the motivational state of the caller to defend the resource, thereby reducing the likelihood of the caller being challenged by another individual.

The best evidence in support of this function for food-associated calling comes from white-faced capuchins (Gros-Louis 2004b) and red-bellied tamarins (Caine et al. 1995). For both species, individuals that called were less likely to have food taken from them than were individuals that remained silent. In white-faced capuchins, call production increases the distance between foragers, thus functioning to regulate forager spacing and reduce competition (Boinski & Campbell 1996; Gros-Louis 2004b). In this species, neither increased quantity nor divisibility of food increases the likelihood of call production (Gros-Louis 2004b). Thus, for these two species, food-associated calling may convey information to potential challengers about the caller’s willingness to defend their resource, thus deterring the challenger, and hence reducing the likelihood of aggression following conflict over ownership (Gros-Louis 2004b).

An alternative explanation to this ‘resource ownership’ hypothesis is that individuals call to avoid aggression from more dominant individuals upon their discovery of food (Hauser et al.

1993). In rhesus macaques, a species with strict dominance hierarchies, Hauser & Marler (1993b) found that individuals that did not call upon finding food were more likely to receive aggression from other group members than those that did vocalize. The possibility that group members call to avoid ‘punishment’ implies the unlikely scenario that monkeys are capable of some degree of mental state attribution, in the sense that the more dominant individual expects to be informed and that they are aware that information has been withheld from them. This kind of hypothesis does not appear likely based on the current evidence for primates, aside from possibly great apes (e.g. Cheney & Seyfarth 1996, 1999; Hare et al. 2001). It may be more parsimonious to conclude that animals may be using more simple associations; for instance: expel from the food patch those subordinates that do not call, but cofeed with those that do call. In either case, the function of food-associated calls in this instance may be to reduce aggression during feeding or to facilitate group cohesion.

With some notable exceptions, the proximate function of food-associated calling may be to attract other individuals to the feeding opportunity. However, the ultimate function varies with the social and ecological pressures faced by the species in question. For groups with stable or semi-stable social foraging groups, the functions include facilitation of group cohesion, consolidation of social alliances, enhancement of social status within the group, as well as increased direct and indirect fitness. However, not all of these functions are present in all species with stable social groups.

In species with more transient group composition, such as flocking birds, the function of food calls may be to reduce predation threat and time spent vigilant and to increase foraging efficiency (Sridhar et al. 2009). However, small-bodied mammals with stable social groups face similar pressures (e.g. red-bellied tamarins: Caine et al. 1995; greater spear-nosed bats: Wilkinson & Boughman 1998). In these species, food calls may share the same function as in species with more fluid group membership.

Based on the evidence detailed above, it seems unlikely that there is a generalized or unified function to food-associated calls. The function of food-associated calls depends on the balance of social and ecological pressures faced by a given species. Yet, social and ecological pressures do not appear to determine which species produce functionally referential food signals (Table 1). There is evidence from many species with stable, semi-stable and completely transient social groups that food-associated calls occur in nonfeeding contexts and therefore do not meet the production criteria for functionally referential calls. The majority of the species in which both the production and perception criteria for functional reference have been examined have stable social groups. However, differences in the experimental methods used create a challenge for conclusively determining whether food-associated calls in a particular species should be classified as functionally referential or only food-associated. Although the majority of the studies have used playback experiments either in wild- or captive-living groups, the control vocalizations selected range from very similar sounds naturally produced by the species in question to no sounds played (silence). In addition, the receiver response criteria used to class a call as functionally referential range from specific food-searching behaviour to approach of the playback speaker. Some standardization of the methods used to evaluate putative functionally referential signal is desirable, although this may be difficult to achieve given the diversity of animals, information content and functions of these signals.

CONCLUSIONS

The widespread evidence of selective food-associated signalling suggests that, compared to other contexts in which functionally referential signals have been identified (i.e. alarm or agonistic interactions), food-associated calls may be produced or withheld in response to the signaller’s own ecological, social and reproductive pressures. The contrast between the production of alarm signals and food-associated calls may reflect the difference in the pressures that would have selected for functionally referential signals. Alarm signals have a critical function in survival, whereas food-associated calls do not. The pressure for alarm calls to convey accurate and actionable information to increase mate or other kin survival has most likely selected for their referential function. Food-associated calling has not been so tightly linked to reproductive success or survival; therefore, there may be less selective pressure for the caller to provide specific information about feeding opportunities.

Evidence from a range of taxa suggests that the variability and specificity of food-associated call production will most likely be linked to the social structure and environmental factors affecting each species. In species that live in stable social groups, which enable repeated interactions over time, the selective use of food-associated calls may be more likely to function to enhance a caller’s social status. However, competition for resources in large stable foraging groups may instead select for food-associated calls that advertise resource ownership and function to reduce antagonistic interactions. Predation risk and resource defence are also factors affecting the use of food-associated calls, and appear most relevant for smaller-bodied species under strong predation pressure. In these instances, food-associated calls function to recruit conspecifics to the food source.

Yet, even species that we might expect to give food calls do not produce them. For instance, macaques often give ‘coo’ calls in response to food (Hauser & Marler 1993a), but no one has ever described or noted analogous ‘food-associated’ calls in vervet monkeys or baboons. This is a puzzle, given these species’ many behavioural similarities and their rather similar ecology. A well-developed theory of food-associated calling should explain both the presence and the absence of food calls.

Taken together, the evidence does not suggest a unifying explanation for functionally referential food-associated signals. Instead, it suggests that a suite of factors affecting each species will determine under what circumstances food-associated calls are produced and what information is conveyed. Signals during feeding may have the potential to convey a considerable amount of useful information to receivers, but the evidence for their status as functionally referential signals is, aside from a few select cases, less convincing.

Acknowledgments

This paper emerged from a meeting, Vocal Communication and Social Cognition, organized by Marta Manser and Simon Townsend, and supported by the Gleichstellung, University of Zurich. Z.C. was supported by The Leverhulme Trust, with many thanks to Prof. K. Zuberbühler. D.T.B. was supported by National Science Foundation grant NSF IDBR-0754247. We thank Dorothy Cheney and two anonymous referees for their particularly insightful comments.

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