

The evolution of functionally referential alarm communication

Multiple adaptations; multiple constraints*

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Many species produce specific alarm vocalizations when they encounter predators. There is considerable interest in the degree to which bird, ground-dwelling sciurid rodent, and primate alarm calls denote the species or type of predator that elicited the vocalization. When there is a tight association between the type or species of predator eliciting an alarm call, and when a played-back alarm call elicits antipredator responses qualitatively similar to those seen when individuals personally encounter a predator, the alarm calls are said to be functionally referential. In this essay I aim to make two simple points about the evolution of functionally referential alarm communication. Firstly, functionally referential communication is likely to be present only when a species produces acoustically distinct alarm vocalizations. Thus, to understand its evolution we must study factors that influence the evolution of alarm call repertoire size. Secondly, and potentially decoupled from the ability to produce acoustically distinctive alarm vocalizations, species must have the perceptual and motor abilities to respond differently to acoustically-distinct alarm vocalizations. Thus, to understand the evolution of functionally referential communication we also must study factors that influence the evolution of context-independent perception. While some factors may select for functionally referential alarm communication, constraints on production or perception may prevent its evolution.

Keywords: evolution, referential communication, context, habitat acoustics, social structure, alarm calls

1. Introduction

Human language is notable in the degree to which we can assign arbitrary acoustic labels to types of stimuli (Hockett 1960). While labeling is but one of many characteristics of language, it is one of the more suitable characteristics for broadly comparative study. There is considerable interest in describing the degree to which species that do not meet most of the criteria of language produce and perceive referential signals (e.g., Cheney & Seyfarth 1990; Macedonia 1990; Evans & Marler 1995; Evans 1997). Referential signals communicate information about environmental events or objects (or perhaps actions — Cheney & Seyfarth 1990). Why do some species have the ability to label objects while many do not?

Because the word referential has specific cognitive and philosophical implications (Evans & Marler 1995; Evans 1997), the term ‘functionally referential’ has been created (Marler *et al.* 1992). Signals are said to be functionally referential if they meet the following two criteria. First, signals must be stimulus-class specific. When alarmed by predators many species emit specific vocalizations referred to as alarm calls (Klump & Shalter 1984). To be stimulus-class specific, alarming aerial stimuli must elicit ‘aerial alarm calls’ and alarming terrestrial stimuli must elicit ‘terrestrial alarm calls’. If there is a high degree of ‘production specificity’, the stimulus class eliciting calls will be relatively narrow. For instance, eagles, but not corvids may elicit ‘dangerous raptor alarm calls’, and foxes but not weasels may elicit ‘dangerous mammal calls’. Second, signals must be ‘contextually independent’ (Marler *et al.* 1992; Evans *et al.* 1993; Evans 1997). That is, in the absence of the stimulus that normally elicited them, alarms must produce appropriate antipredator responses in individuals hearing them.

Many alarm calls are situationally specific in that call structure varies according to the conditions of production. Interestingly, some species that produce calls with a degree of production specificity do not respond differently to played-back variants. I suggest the ability to produce stimulus-class specific signals is not necessarily related to the ability to have contextually independent perception. By separating factors responsible for the evolution of functionally referential signals, we may identify factors that constrain or favor their evolution. Below I illustrate these two points by considering a hypothetical alarm call system, such as that commonly found in some ground-dwelling sciurid rodents and primates (Owings & Hennessy 1984; Macedonia & Evans 1993).

Marmots (*Marmota*: Rodentia) are large, alpine ground squirrels found

throughout the Northern Hemisphere. Marmots are preyed upon by a variety of terrestrial and aerial predators; all 14 species emit alarm calls in response to predators. I studied production specificity and contextual independence in the alarm calls of seven marmot species (Blumstein 1995a, b, Blumstein & Arnold 1995; Blumstein & Armitage 1997a; Blumstein 1999; Blumstein unpublished observations). Species vary in the number of call types (whistles, chirps, trills), and the mechanisms by which they encode situational variation. Despite previous suggestions in the literature (Heard 1977; Lenti Boreo 1992), no species appears to have functionally referential alarm calls. There is, however, considerable variation between species in the degree of production specificity and in the degree of contextual independence. Thus, I believe this system is appropriate to ask questions about factors that select for the evolution of production specificity and the evolution of contextually independent communication.

For instance, the rate at which yellow-bellied marmots (*Marmota flaviventris*) emitted their most common type of alarm call covaried with the degree of risk (proximity to predator and predator type) a caller experienced. Calls played back at different rates elicited different postures and levels of vigilance in perceivers (Blumstein & Armitage 1997a). In contrast, golden marmots (*M. caudata aurea*) produced a single type of alarm call and ‘packaged’ their calls to create multiple-note alarm calls. While golden marmots varied the number of notes per call as a function of risk, playbacks of calls with different numbers of notes did not elicit response differences (Blumstein 1995a, b). The closely-related Olympic (*M. olympus*) hoary (*M. caligata*) and Vancouver Island marmots (*M. vancouverensis*) shared four different call types; the Vancouver Island marmot had a unique fifth call type. In none of the species did call type uniquely covary with the stimulus class (aerial/terrestrial) eliciting the calls. While the call type did not covary, microstructural components of hoary and Vancouver Island marmot calls covaried with stimulus class more than the microstructure of Olympic marmot calls (Blumstein 1999). While hoary marmots did not respond differently to alarm call playbacks, Vancouver Island marmots responded differently to microstructural variants, and Olympic marmots varied the number of calls they uttered according to perceived risk and responded accordingly.

Macedonia (1990) studied alarm communication in ring-tailed lemurs (*Lemur catta*) and black-and-white ruffed lemurs (*Varecia variegata variegata*) in large semi-natural field cages at the Duke University Primate Center. Both species were subject to similar experimental manipulations. Ring-tailed lemur alarm calls met both criteria of functional reference; ruffed lemur calls did not.

Ruffed lemur aerial predator calls ('abrupt roars') were also used in social contexts and therefore did not meet the production specificity criterion. Ruffed lemur terrestrial predator calls ('pulsed squawks') had a reasonably high degree of production specificity, but call structure formed an acoustic continuum with 'wails' — a potential group aggregation vocalization usually emitted after social conflict. Thus, rather than narrowly defining environmental stimuli, the squawk-wail continuum seems to be associated with general arousal. Macedonia found no strong evidence of contextual independence: adult ruffed lemurs did not reliably respond to pulsed squawks as they would if there was a terrestrial predator present. Interestingly, when adult ruffed lemurs had their vision obstructed (e.g., they were in deep vegetation), they tended to respond to squawks as though they communicated the presence of a terrestrial predator (J.M. Macedonia, personal communication). If the degree of functional reference is viewed along a continuum (Evans 1997), it is possible that ruffed lemur calls, despite their limited contextual independence, are near the threshold where we would classify them as having functionally referential alarm communication. Subsequent experiments may tease apart factors influencing how lemurs respond to terrestrial alarm calls (J.M. Macedonia, personal communication).

I realize that negative findings are difficult to interpret, and that different experimental protocols might generate different results. However, current results suggest that the processes generating production specificity and context independence may be de-coupled. I also realize that motor theories of perception link the production and perception of acoustic signals in human and non-human systems (e.g., Liberman & Mattingly 1985; Williams & Nottebohm 1985). However, I believe it is important to envision each process, to some degree, subject to unique selective pressures and to unique constraints. Recent work suggests that note evolution and song evolution, two components of bird song typically thought to be subject to similar selective pressures, are subject instead to unique selective pressures and constraints (van Buskirk 1997). The evolution of functionally referential communication can be viewed along a continuum: it is useful to study the degree of functional reference rather than simply classifying species as referential or not (Evans 1997). A model of decoupled evolution might explain cases where a species seems to be on the threshold of functional reference and is thus consistent with a more continuous view of referential communication.

2. The evolution of production specificity

Functional reference requires that individuals of a species produce stimulus-class specific calls. Animals can vary the structure of their calls in different ways but only one of these ways seems to preadapt a system for functionally referential communication. There are at least three ways to produce a potentially referential alarm call (Blumstein & Armitage 1997a).

First, animals may vary the rate or number of times a single call type is produced. Morse-code is a referential system that uses the number/duration of simple pulses to encode referential information. Honey bee (*Apis mellifera*) dances predict the presence of food and the length of the waggle run varies as a function of the distance to the food source (von Frisch 1967). However, I am aware of no natural functionally-referential alarm calling system in which a number/rate based mechanism actually communicates the presence of a specific predator species.

Second, call type may predictably co-vary with call intensity. Animals could vary the amplitude of a single call specifically to communicate information about predator species. Although speculative, varying call intensity may be used to communicate more affective aspects of call meaning, such as the degree of risk a caller faces (Scherer 1985; Marler *et al.* 1992). Since sound intensity attenuates with distance, conspecifics might have difficulty determining predator species based only on the perceived volume of a call. If signals degrade predictably with distance, sound intensity may be used to estimate distance between a perceiver and a signaler (Morton 1982). However, it seems unlikely that an intensity mechanism alone would be an efficient way to encode functionally referential information.

Third, animals could produce acoustically distinctive call types. This mechanism seems to be an apparent precursor to functionally referential communication and several species vary alarm call type to encode referential information (e.g., vervet monkeys (*Cercopithecus aethiops*) — Seyfarth *et al.* 1980; ring-tailed lemurs — Macedonia 1990; and chickens (*Gallus gallus*) — Evans *et al.* 1993). To understand the evolution of referential communication, we need to understand factors that select for meaningful repertoire size. By emphasizing meaningful repertoire size, I note that while some songbirds have huge vocal repertoires (e.g., Kroodsma 1982, 1988), each 'song type' in no sense refers to a particular object or event. With the possible exception of matched countersinging in birds where individuals sing the same song type in response to their neighbor's song (e.g., Catchpole & Slater 1995), songbird repertoires do

not typically refer to external objects or events. Categorical perception (e.g., Harnad 1987) further increases the challenge of defining meaningful repertoire size: calls that appear continuously graded may be categorically perceived (Snowdon 1987). To date, evidence of functional reference in an alarm calling is restricted to systems with unique call types.

To study functional reference we need to look for evidence of acoustically distinctive, stimulus-class-specific signals. There are factors that might be responsible for the desirability of producing stimulus-class-specific signals. Additionally, there are factors that may influence the ability of a species to produce different call types.

First, all sounds must be transmitted through space during which time they attenuate and may degrade in several ways (Morton 1975; Wiley & Richards 1978; Brown & Waser 1988; Forrest 1994). In particularly destructive environments, or for species that communicate over long distances, effective communication about predator type may have to be simple. Variable signals may not be transmitted with a high degree of fidelity and may not be distinguishable at a distance (Blumstein & Daniel 1997). Empirically, acoustics must be studied at a biologically meaningful scales: call transmission fidelity should be measured at realistic communication distances. Some species live in environments with potentially poor acoustics but may overcome degradational problems by clumping together and communicating over relatively short distances (e.g., red junglefowl (*Gallus gallus*) — Collias 1987; Collias & Collias 1996).

Species may be limited in the types of signals they can produce. If habitat structure precludes the differentiation of sounds a species can produce from each other at a distance over which they must communicate, the physical habitat has effectively selected for relatively simple communication. Low transmission fidelity over meaningful communication distances may select against the production of acoustically distinctive call types and may select for a number or rate based communication mechanism. By doing so, habitat acoustics may interact with production constraints to further constrain the evolution of functionally referential alarm calls.

Second, because vocal tract morphology influences call production (Hauser *et al.* 1993; Fitch & Hauser 1995), and vocal tract morphology may be associated with a particular behavior or posture (Andrew 1963), the production of variable signals may be partly a function of the performance of certain behaviors or postures (Owings & Hennessy 1984). If concomitant postures or escape behaviors constrain or otherwise influence the production of variable vocalizations, 'production-related postural changes' may favor or constrain the evolu-

tion of production specificity.

Third, some species' alarm calls are directed to predators (Hasson 1991). Signaling to different predators may select for stimulus-class specific signals. For instance, signals associated with mobbing behaviors (e.g., Curio 1975) are designed to be obvious to the predator: they are loud, broad spectrum, repeated signals (e.g., Marler 1957). Species who communicate to multiple predators may have multiple call types if each is best suited to communicate with a predator. For instance California ground squirrels (*Spermophilus beecheyi*) produce primarily acoustic signals when they encounter a mammalian or avian predator (i.e., they alarm call), and primarily visual and tactile signals when they encounter a rattlesnake (i.e., they tail flag). Modality may be related to what the predators best perceive: acoustically-oriented predators can hear alarm calls, while snakes can see a tail-flagging squirrel (e.g., Owings & Hennessy 1984; Hersek & Owings 1993). The converse may also be true: call structure may vary to increase crypsis to predators (e.g., Marler 1955, 1957; but see Klump *et al.* 1986). If call type or structure is predictably associated with a predator-class, calls have the potential to be functionally referential to conspecific perceivers. Indeed, it would be surprising if a species had distinctive predator-specific alarm calls that were not salient to conspecifics.

3. The evolution of contextual independence

Just because a species produces stimulus-class-specific vocalizations, it does not necessarily follow that call types communicate information about stimulus-class type or are in any sense 'referential' (Evans 1997). Functionally referential calls characteristically evoke responses that are contextually independent: perceivers must respond to a variable call much as they would to the eliciting stimulus, even when no other cues are available. Typically, contextual independence is studied using playback procedures where exemplars are played back to subjects after controlling for many potential contextual cues (Cheney & Seyfarth 1990; Evans *et al.* 1993; Blumstein & Armitage 1997a; but see Smith 1991). Playback techniques, by depriving perceivers of natural contextual cues, thus provide a very conservative test of functional reference.

Context is considered crucial for meaningful communication (e.g., Smith 1965, 1977, 1990, 1991; Leger 1993). Relevant context may exist on a variety of temporal domains and take a variety of forms. For instance, signal meaning may, on an immediate time scale, be a function of location (e.g., Lenti Boero

1992) or, on a longer time scale, be a function of previous experience with the signal and its environmental correlates (Smith 1991; Leger 1993).

Context may also be embedded in call structure. Juvenile vervet monkeys produce alarm calls to a variety of stimuli, only some of which are dangerous to adults, and some adults produce calls when there are no predators around (Cheney & Seyfarth 1990). Thus knowledge of the individual producing a call is an important contextual variable that modifies a perceiver's response (e.g., Cheney & Seyfarth 1990).

For the purpose of this discussion, I lump all contextual cues. In general, whenever a signal has a less-than-perfectly-reliable relationship with classes of eliciting stimuli, or when an optimal response depends on the perceiver's situation, supplemental contextual cues (e.g., nonvocal responses such as the signaller's escape behavior) may clarify the relationship. What specific factors might select for the ability to respond to signal variation without requiring the rich contextual information usually associated with a signal?

First, time constraints or costs of assessment (Real 1990; Dawkins & Guilford 1991; Briggs *et al.* 1996) may influence whether a perceiver can or will use additional contextual information to interpret a signal's meaning. If messages (such as alarm calls) have to be interpreted immediately, there may be limited time to assess and process additional contextual cues. Of course, there may be several contextual cues incorporated in a signal's structure and these cues may be useful in interpreting its meaning (e.g., call volume — Blumstein & Armitage 1997a; caller identification — Cheney & Seyfarth 1990). But for signals designed to be interpreted immediately, context may be relatively less important.

Second, the costs of responding to a call emitted when there is no predator may influence the degree to which additional contextual cues are useful in interpreting a signal's meaning. If the adaptive response to a particular predator is to descend into a burrow and remain there during which time an individual could not forage or engage in other required activities, it would behave the individual to know with certainty that the predator was present. In contrast, fewer contextual cues might be required if the appropriate antipredator response had limited costs or did not involve substantial trade-offs.

Third, species living in areas with predictable acoustics may be better able to 'predict' how a signal may change and therefore be able to usefully employ additional acoustic cues. Ranging (Morton 1982) requires an individual to estimate a signal's degree of acoustic degradation and is only possible when acoustic degradation is predictable. Alarm signals may suffer substantial

degradation or have to function over a range of distances. For instance, alarm calling marmots may have to communicate to individuals scattered throughout their > 3 ha home ranges; in consequence, their alarm calls are very loud. By the time the alarm call reaches a target individual, calls may have degraded to such a degree that certain microstructural differences are not distinguishable (Blumstein & Daniel 1997).

Fourth, the presence of predictable individuals (e.g., stable neighbors, stable group mates, etc.) may influence whether additional contextual cues are used to interpret a calls' meaning. If there is individual variation in how signal structure maps onto predator type, individuals in stable social groups can learn these associations and caller identity may be an important contextual cue. In less stable groups, individuals may not learn these individual-specific associations; thus, other cues might be more important for interpreting a call's meaning.

4. The evolution of functional reference

In conclusion, I suggest that the evolution of functional reference requires multiple adaptations. Several factors may select for functionally referential alarm communication systems. For instance, Macedonia & Evans (1993) suggested that incompatible escape strategies may be responsible for the evolution of some predator-class specific alarm calls. They noted that primates with functionally referential alarm calls have unique and apparently optimal escape strategies for different predators (e.g., flee up a tree and move to peripheral branches when exposed to mammalian carnivores versus flee to the inner branches to avoid raptors). In contrast, squirrels and marmots primarily use their burrows as refugia for terrestrial mammalian and avian predators; selection for predator specific responses may be relatively less intense and therefore communication may not be functionally referential.

Social complexity may drive the evolution of communicative complexity (e.g., Marler 1977). For instance, Kroodsma noted an association between population density and song repertoire size in some birds (Kroodsma 1983, 1988). Functional reference might be favored in more complex social aggregations (Blumstein & Armitage 1997b) where there are both direct and indirect fitness benefits (Brown 1987) from reliable signalling. A comparative study of ground-dwelling sciurid rodents illustrates that social complexity is an important factor responsible for the evolution of alarm call repertoire size (Blumstein & Armitage 1997b).

While these broad factors might select for functionally referential communication systems, both stimulus-class specific production and contextually independent perception have their own unique set of selective factors which may constrain or favor their evolution. To understand the evolution of functional reference, we need to study both the broad factors responsible for the evolution of functionally referential communication, as well as those factors that may constrain production specificity and perception.

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