

Suricate alarm calls signal predator class and urgency

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Human speech encodes both referential and affective information, but evidence for a similar phenomenon in animal vocalizations has been lacking. Recent work on suricates, an African mongoose, shows that animal alarm calls simultaneously encode information about both predator type and the signaler's perception of urgency.

Although Darwin hypothesized that animal signals were primarily manifestations of an individual's motivation or level of arousal [1], research over the past 20 years has shown that some animal vocalizations – particularly alarm calls – can function to designate specific objects or events in the external world [2–5]. Such predator-specific alarm calls have been termed 'functionally referential', because listeners appear to derive specific information about predator type from a call's acoustic features [6] (see Box 1). These signals have often been contrasted with the more general contact, affiliative, and alerting calls that are thought to comprise the majority of animal vocalizations [7].

The dichotomy between reference and affect in animal signals is probably simplistic. Even highly semantic human speech includes information about the speaker's motivation or affect [8]. More recent reviews of animal communication have argued that animal signals inform listeners about both specific external events and the signaler's level of motivation or arousal [9]. Supporting this hypothesis, playback experiments on free-ranging monkeys indicate that the information content of predator-specific alarm calls is not blurred by variation in call rate or context, two features that seem likely to be correlated with urgency or arousal [2,10]. What is unclear, however, is whether animal signals are capable of encoding both referential and affective information in their acoustic structure alone. Here we summarize results from a recent study of suricates (*Suricata suricatta*), a southern African mongoose, which provide the first definitive evidence that animal alarm

calls simultaneously provide listeners with information about both predator type and the level of urgency.

Predator-specific alarm calls

Suricates are diurnal, cooperatively breeding mongooses that inhabit open semi-desert areas in groups of three to 33 individuals. They forage for five to eight hours per day, typically at a distance of 20–50 m from the nearest burrow or shelter [11]. Foraging animals frequently scan their surroundings for predators (Fig. 1). Group members also alternate guarding from a raised sentinel position [12].

Guards and foraging individuals emit several different alarm calls when they spot a predator. Some call types are given to many different predators and appear to be general alerting calls [13]. Other call types are given only to specific classes of predators. Suricates give one alarm call type to mammalian predators, primarily jackals (*Canis mesomelas*), that attack on the ground. They give a second, acoustically distinct alarm call in response to avian predators, primarily martial eagles (*Polemaetus bellicosus*), tawny eagles (*Aquila rapax*) and pale chanting goshawks (*Melierax canorus*) that attack from the air. They give a third

Box 1. Signalers and receivers

David Premack was one of the first to note that a vocalization can provide referential, or semantic, information to listeners even when the signaler has no such goal or intention [a]. If a friend always gives a particular cry of excitement when he finds a strawberry, we rapidly learn to associate the cry with strawberries. The call becomes functionally referential even if the signaler is unaware of the sound–meaning relation and does not intend to provide information to others. This distinction between call meaning from the listener's, as opposed to the signaler's, perspective is particularly relevant in the case of animal vocalizations. For example, baboons give loud 'contact' barks when moving through wooded areas. Because barks are often clumped in time, animals appear to be exchanging information (calling and answering) about their location. Playback experiments, however, indicate that a baboon gives barks primarily when she herself is peripheral or at risk of becoming separated. She rarely answers the contact barks even of close kin when she is in the center of the group and surrounded by others [b,c]. Nevertheless, the calls function to help animals maintain contact with one another because typically more than one individual is separated from the group at any one time. Listeners gain

information as an inadvertent consequence of signaler behavior. Similarly, the predator-specific alarm calls given by vervet monkeys inform listeners about the proximity of particular types of predators, but signalers appear to give alarm calls primarily with reference to their own vulnerability. They do not alter their behavior to alert ignorant individuals, nor do they instruct infants in the correct usage or response to alarms [d]. The asymmetry between signalers and recipients might arise because monkeys lack the ability to represent the mental states of others [e]. Whether this generalization holds for chimpanzees remains an open question [f].

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Fig. 1. *Suricata suricatta*, demonstrating the typical raised position of the adult used to scan the surroundings. (Photograph courtesy of T.H. Clutton-Brock).

alarm call type to snakes, such as the Cape cobra (*Naja nivea*), puff adder (*Bitis arietans*) and the mole snake (*Pseudaspis cana*). Snake alarm calls are also given to fecal, urine or hair samples of predators and/or foreign suricates. Because snake alarm calls to all of these stimuli cause other animals to approach the caller, give alarm calls themselves, and either mob the snake or investigate the deposit, they are collectively termed 'recruitment alarm calls' [13].

During 21 months between November 1995 and August 1999, 615 alarm calls were tape-recorded from known individuals in encounters with known predators. Calls were classified according to the stimulus that elicited them. Mammalian and avian alarm calls were classified according to whether they were given in situations of high, medium or low urgency. For mammalian predators, stimuli more than 200 m away were classified as 'far', from 20–200 m away as 'close', and within 20 m as 'very close'. For avian predators, stimuli 200–500 m away were classified as 'far', from 100–200 m away as 'close', and within 100 m as 'very close'. Mammalian and avian alarm calls given to a predator at far, close and very close distances were labeled 'low', 'medium', and 'high urgency calls', respectively. Recruitment alarm calls were scored as 'high urgency' if elicited by snakes and 'low urgency' if elicited by any other stimulus.

Acoustic analysis

Of the calls recorded, 254 were of sufficiently high quality to permit acoustic analysis. To control for individual variation, calls were drawn from at least six different subjects for each call type (the average number of subjects was 12, and the maximum was 15). Only one call per individual and predator encounter was used in analysis. Canary software [14], Signal software (Engineering Design, Belmont, MA, USA), and LMA software [15] were used to measure 28 different acoustic parameters that described the frequency and time dynamics of each call [13]. Discriminant function analysis (DFA) was used to test whether calls could be assigned to different behavioral contexts according to their acoustic structure.

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DFA confirmed that mammalian, avian and recruitment alarm calls were acoustically different from one another. Within each predator class, high, medium and low urgency calls also showed significant acoustic differences (Fig. 2). The acoustic measures that accounted for variation across alarm call types were, for all but one measure, different from the acoustic measures that accounted for variation across levels of urgency [13]. Along the dimension of urgency, changes in acoustic structure were consistent across alarm call types: low urgency calls tended to be clear and more harmonic, whereas high urgency calls were harsher and noisier. By contrast, when the level of urgency was held constant there was no consistent rule relating acoustic features to the different predator classes [13]. The referential information about each predator type was not coded acoustically in any consistent way.

Call responses

In the field, suricates were played alarm calls in the absence of actual predators and their responses were filmed. Playback of alarm calls given to different predators elicited significantly different responses, duplicating behavior seen under natural conditions. In response to playback of mammalian predator alarm calls, subjects moved rapidly in the direction of the loudspeaker while scanning the area. They typically gathered together 5–10 m away

from the loudspeaker and then retreated toward the nearest large system of burrows. Avian predator alarm calls elicited several, not mutually exclusive responses: freezing and crouching, scanning the sky, and running to the nearest burrow. In response to recruitment alarm calls, subjects raised their tails, approached the loudspeaker slowly, and sniffed the area around the loudspeaker [16].

In addition to these qualitatively different responses, within each predator class subjects responded in quantitatively different ways to the playback of calls that had originally been recorded in circumstances of low, medium or high urgency. Latency to relax and resume foraging behavior increased from low to medium to high levels of urgency following playback of mammalian alarm calls, and from low to high urgency following playback of recruitment calls. Playback of avian predator alarm calls elicited a different pattern of results. Latency to relax and resume feeding increased from low to medium urgency calls, but the shortest latency to resume feeding followed high urgency calls. This occurred, we believe, because high urgency avian alarm calls elicited a unique response – freezing and crouching. When crouching animals detected no predator, they soon resumed foraging. By contrast, the most common response to low and medium urgency avian alarm calls was to run immediately to a burrow; from this underground position the resumption of normal activity required more time [16].

Motivational vocalizations

Acoustically different alarm calls are believed to have evolved in species in which individuals are attacked by a variety of different predators, each of which demands a different escape strategy [17,18]. Because suricates are preyed upon by species with different hunting techniques, selection may have favored an alarm call repertoire that encodes information about predator type in addition to level of urgency. By contrast, many ground squirrels and marmots escape from all predators in the same way, by running to their burrows. In these species, alarm calls are less predator-specific. Instead, they appear to denote low-risk and high-risk situations [19,20].

Suricate alarm calls offer the first indication that animal vocalizations can, through their acoustic features alone,

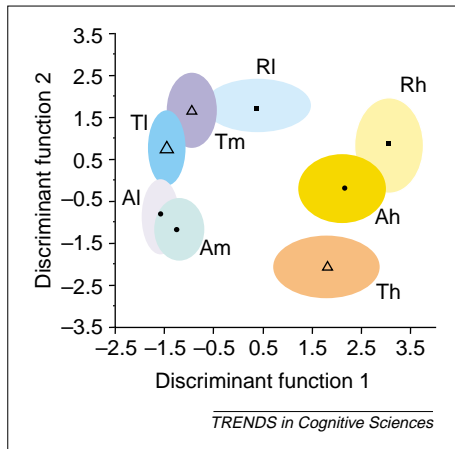


Fig. 2. Arrangement of the alarm calls given in different predator contexts according to their values as established by discriminant function analysis (DFA) of the calls' acoustic properties. Circles are spanned by the mean \pm SD of the first two discriminant functions, with data drawn from 10 runs of the DFA. T, A and R stand for terrestrial predator alarms, aerial predator alarms and recruitment alarms, respectively; l, m and h stand for low-, medium- and high-urgency calls, respectively. (Modified, with permission, from Ref. [13].)

simultaneously provide listeners with information about both a specific external referent and the caller's motivational state. Suricates respond in qualitatively different ways to playbacks of different alarm call types and, within each predator category, in quantitatively different ways to calls that convey different levels of urgency. The acoustic cues used to encode information about different predators are generally different from those used to encode information about response urgency. Presumably, this helps listeners decode the two sorts of information simultaneously. No consistent acoustic change underlies the differences among mammalian, avian and recruitment alarm calls; the mapping of referent class onto acoustic structure

follows no predictable acoustic rule. By contrast, information about urgency is encoded following a specific rule that holds across all alarm call types [21].

Results indicate that a dichotomy between 'referential' and 'motivational' communication is as untenable in animal vocalizations as it is in human speech. Rather than considering animal vocalizations as points that lie along a continuum between reference and affect, it is more accurate to regard them as signals that simultaneously encode both.

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Meeting Report

From corpora to cuttlefish

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The 7th Neural Computation and Psychology Workshop was held at the University of Sussex, Brighton, on 17–19 September 2001. The theme was 'Connectionist Models of Cognition and Perception'.

This workshop enabled the continuing interaction of a core group of mostly

UK-based researchers. As in the past, the issue of the interpretation of connectionist models was to the fore. John Bullinaria (University of Birmingham, UK) has persistently argued that it is too easy to produce apparently convincing simulations of psychological data, given the number of degrees of freedom involved: it is all too

tempting to tinker with a model until it produces a desired interaction, which is then reported. (As an interesting exercise, where more than one simulation is reported in a paper, the reader is invited to try plotting them all on the same axes; the results can be illuminating.) Bullinaria described work on evolving network architectures to