

## Alarm Calls

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### Introduction

Animals commonly vocalize when threatened by a predator. These signals, usually termed alarm calls (from old Italian *all arme* ‘to arms’ on the approach of an enemy), have continued to bewilder and fascinate for a number of reasons, the first of which is mainly practical. In animal research, it is often difficult to break down the continuous behavioral stream into discrete and meaningful units, which can be studied systematically. Alarm calls are a rare and noticeable exception. They are highly discrete and easy to identify, making it possible to systematically study both the causes and consequences of behavior. A second motivation, related to the previous one and significant for the evolution of linguistic abilities, relates to the fact that alarm calls provide a unique tool for accessing the cognitive mechanisms underlying an animal’s behavior. Finally, alarm calls are interesting because they seem to pose a problem for evolutionary theory. They are often among the most prominent and noticeable signals in a species’ repertoire, and it seems paradoxical for individuals to behave conspicuously in the presence of a predator, thereby revealing their presence and location (e.g., Shalter, 1978).

Following these considerations, this article has the following objectives. First, it summarizes research that has dealt with the problem of why animals produce seemingly maladaptive behavior in the presence of a predator. What are the evolutionary processes that have provided a selective advantage to individuals who behave this way? Second, from a cognitive–linguistic perspective, the article seeks to seize the

unique opportunity that alarm calls offer, that is, to try to describe the cognitive processes that underlie call production. Several empirical studies are discussed that have aimed to investigate the relationship between the occurrence of an external event (i.e., the appearance of a predator) and the production and comprehension of these signals, particularly in the nonhuman primates. No attempt is made to provide a systematic overview of alarm calling in the various taxonomic groups, however. Instead, a handful of empirical studies have been selected, particularly those that are likely to inform the linguistically interested reader about core cognitive phenomena in nonhumans and their potential relevance for the evolution of linguistic capacities in humans.

### The Evolution of Alarm Calls

Three main groups of evolutionary hypotheses have been put forward to explain why animals produce conspicuous vocalizations in the presence of a predator. First, attention-grabbing behavior in the presence of a predator can provide a selective advantage to the signaler if it increases the survival chances of closely related kin (Maynard Smith, 1965). Calling may be risky, but under this hypothesis, the costs are outweighed by the benefits of increased survival of recipients who carry a proportion of the caller’s genes (the kin selection hypothesis). Second, alarm calling is beneficial to a signaler if it increases the reproductive success of the caller (the sexual selection hypothesis). Third, alarm calling is beneficial if it elicits behavior in others that decreases the vulnerability of the caller directly (the individual selection hypothesis). Within this third hypothesis, two scenarios have been proposed. The first one considers the effects of alarm calling on conspecific recipients (the prey manipulation hypothesis). Here, calling is costly at the beginning of a predator–prey interaction, but quickly

becomes outweighed by the benefits accrued by other individuals' antipredator responses. A good example is the turmoil caused by individuals escaping when hearing an alarm call, creating a cloud of confusion for the predator from which the caller can benefit. However, in some cases animals give alarm calls in the absence of a conspecific audience, suggesting that the behavior has evolved for other purposes. A popular idea here is that some predators are affected by the alarm calls directly, without the intermediate step of other prey behavior (the perception advertisement hypothesis). This is especially the case for predators who depend on unprepared prey. Particularly in the bird literature, the term 'mobbing call' is sometimes used, mainly to refer to cases where alarm calls are part of more elaborate displays, involving conspicuous locomotory behavior in the presence of the predator.

It is important to point out that the three hypotheses are not mutually exclusive but may operate alongside each other in various ways. In the following sections, selected empirical findings that support one or several of the selective forces underlying the evolution of alarm calling are discussed.

#### **Alarm Calls Favored by Kin Selection**

One recurrent finding is that alarm callers are susceptible to the type of audience present (e.g., Karakashian *et al.*, 1988). A first solution to the apparent alarm call paradox is, therefore, that individuals call preferentially when close genetic relatives are nearby. Under such circumstances kin selection theory can explain the evolution of conspicuous signaling in the presence of predators. The reasoning is that costly alarm calling can still be beneficial if it improves the survival of individuals that share a certain proportion of the caller's own genes. One testable prediction is that individuals produce alarm calls as a function of the number of close relatives in the audience. The empirical evidence for the kin selection hypothesis is strongest for the parent-offspring relation (e.g., Blumstein *et al.*, 1997), and alarm calling in this context may be conceptualized as a form of altruistic parental care.

A related but empirically more challenging endeavor is based on the assumption that callers inevitably share high degrees of genetic relatedness with some other nondescendent kin, such as brothers and sisters. If kin selection operates as a selective force, then individuals should be just as willing to engage in risky alarm call behavior if it increases the survival chances of closely related nondescendent kin, apart from that of their own offspring, as long as they are sufficiently closely related to one another. Much empirical effort has been devoted to this topic, particu-

larly in various rodent species, but the overall picture is incoherent. Males and females often differ in their alarm calling in the presence of nondescendent kin, suggesting that kin selection may have affected individuals in sex-specific ways. For example, in Gunnison's prairie dogs, *Cynomys gunnisoni*, females with nearby nondescendent kin call more often to a ground predator than females without nondescendent kin. Males commonly produce alarm calls, but calling is unrelated to kinship of nearby listeners (Hoogland, 1996). A nondescendent kin audience may enhance alarm calling to particular predator types only, but patterns vary from one species to the next. For example, Belding's ground squirrels, *Spermophilus beldingi*, show kin-sensitive response to terrestrial but not to aerial predators, where the caller's own exposure appears to be the main factor (Sherman, 1977, 1985). Conversely, the opposite pattern was found in Columbian ground squirrels (*Spermophilus columbianus*) (Macwhirter, 1992). In this species, females with offspring were more likely than other females to give alarm calls in response to a ground predator, but females did not behave nepotistically toward other nondescendent kin. However, females were more likely to emit alarm calls in response to aerial predators if close nondescendent kin were in the colony.

Kin selection has also been put forward as an explanation for the evolution of alarm calls in non-human primates, although the overall evidence is weak, at least for benefiting nondescendent kin. For example, spider monkeys alter their alarm call behavior as a function of the number of kin in the vicinity (Chapman *et al.*, 1990). Similarly, Kloss's gibbons produce alarm calls that can be heard in neighboring home ranges, which are often occupied by the callers' close relatives, suggesting that these calls may warn not only members of the immediate family, but also neighboring relatives (Tenaza and Tilson, 1977).

The emerging picture of the role of kin selection is that (a) alarm calling is clearly affected by the presence of descendent kin, and as such is a common aspect of parental care, and (b) in some species, kin selection may have additionally favored alarm calling to benefit a nondescendent kin audience, but no general patterns have emerged. In cases in which individuals' alarm calls appear to warn nondescendent relatives, kin selection seems to have acted in various idiosyncratic ways.

#### **Alarm Calls Favored by Sexual Selection**

Animals often give alarm calls when no kin are nearby, requiring a different set of evolutionary explanations. One set is built on the idea that alarm calls are sexually selected signals produced by males as part of

their attempts to increase their reproductive success (Zuberbühler, 2002). According to Darwin (1871), sexual selection "... depends, not on the struggle for existence, but on a struggle between the males for possession of the females; the result is not death of the unsuccessful competitor, but few or no offspring." In these cases, however, sexual selection must have acted as a secondary evolutionary force on communication systems in which alarm calls have already been present.

The sexual selection hypothesis is currently supported by a number of observations relating to alarm call structure and usage. In some species, males are more likely to produce alarm calls while in the presence of unrelated females than to other audiences (e.g., Evans *et al.*, 1994), suggesting that alarm calls may be part of a mating strategy to enhance the caller's reproductive success. Similarly, male vervet monkeys (*Cercopithecus aethiops*) alarm call at higher rates in the presence of adult females than adult males (Cheney and Seyfarth, 1990). In some species, not only do adult males differ from other age/sex classes in terms of call usage, but their alarm calls are also structurally different from those of the adult females. For example, it has long been known that the adult males in many forest monkey species produce conspicuous loud calls in response to predators, which carry over remarkable distances (e.g., Gautier and Gautier, 1977). Recent research on West African Diana monkeys, *Cercopithecus diana*, and other forest primates has shown that these calls function as predator alarm calls (Zuberbühler, 2002, 2003). Diana monkeys live in small but stable social groups with one adult male and several adult females with their offspring (Uster and Zuberbühler, 2001). The monkeys are hunted by leopards (*Panthera pardus*) and crowned eagles (*Stephanoaetus coronatus*), and both the adult male and the females produce conspicuous alarm calls to these two predators. However, the calls of the males are structurally different from those of the females. They are low-pitched, high-amplitude signals given in repeated bursts, which carry over long distances through dense tropical forest habitat, sometimes up to one kilometer (Zuberbühler, 2003) (Figure 1).

A number of observations support the hypothesis that these male alarm calls have been under pressure by sexual selection. Polygynous social systems, in which one adult male mates with several adult females, are notorious for sexually selected conspicuous male traits, including vocalizations (Clutton-Brock and Albon, 1979). In these social systems, male competition over females is especially high, which typically leads to the evolution of male traits that are useful in male–male competition or that females find attractive (Anderson, 1994). In polygy-

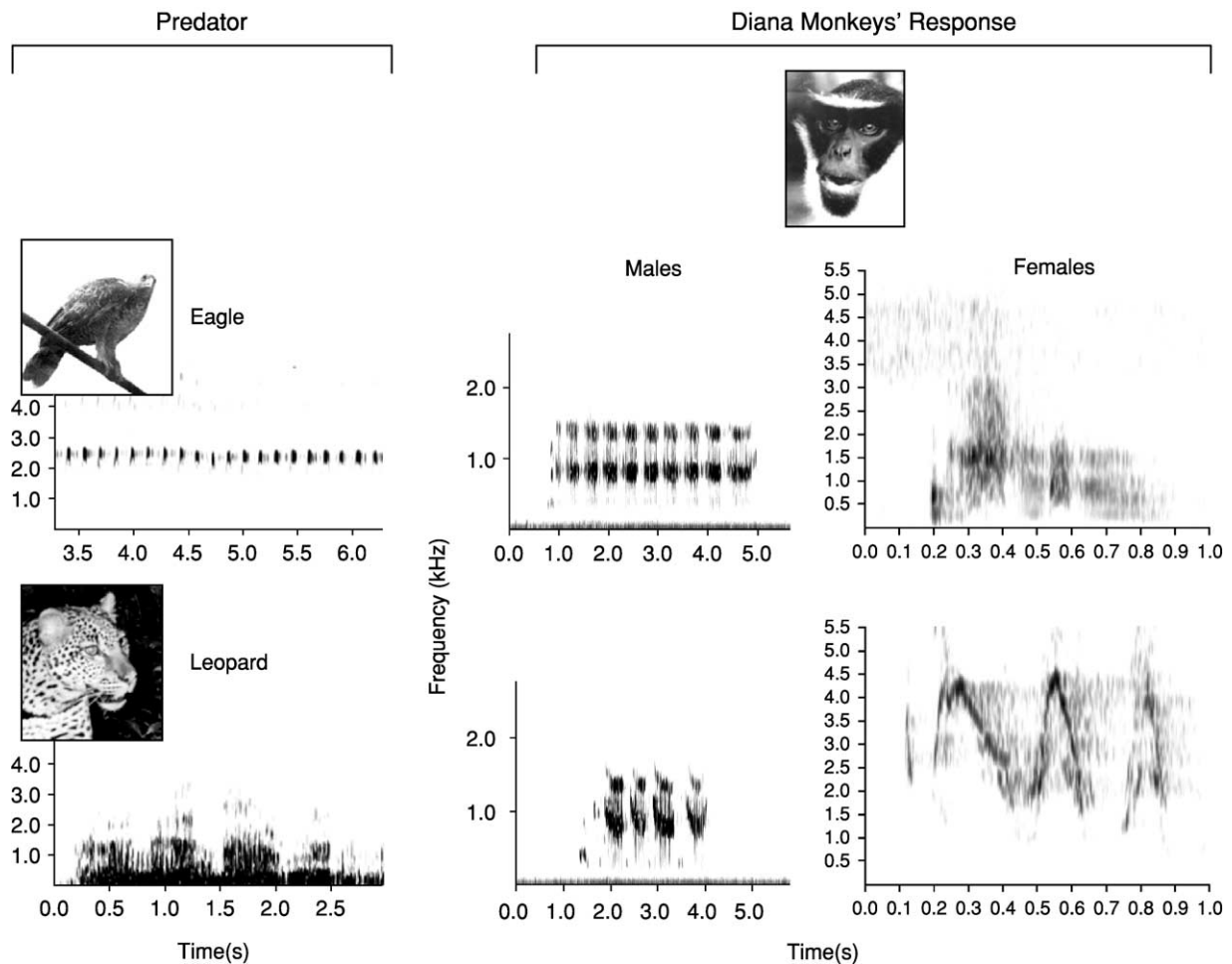
nous monkeys, such as the Diana monkey, males typically try to take over a group of females and mate with them for some time until replaced by another male. If females are able to exert some choice over tenure length of a particular male, then one might expect to see a relation between female tolerance toward the male and how committed he is to engaging in antipredator behavior, such as producing costly alarm calls in the presence of a predator (Eckardt and Zuberbühler, 2004). An alternative explanation is that sexual selection has usurped male alarm calls and transformed them into signals effective in male–male competition. The fact that the male alarm calls carry over very long distances suggests that the intended recipients are not just the male's own group members (which are usually within about 100 m), but also single males roving through the forest or subadult males in neighboring groups. By making their presence and vigor known, tenured males may avoid costly encounters with these males in search of a group of females.

It is interesting to note that during puberty several developmental changes occur in the vocal behavior of male Diana monkeys and other guenons, specifically a drop in pitch and the loss of some of the juvenile vocal repertoire (Gautier and Gautier, 1977). In the Taï forest, Ivory Coast, subadult male Diana monkeys go through a phase in which their alarm shows remnants of a female alarm call as well as the first emerging elements of a fully developed male loud call, suggesting that males go through a transition phase when their calls develop from female alarm calls to male loud calls (Zuberbühler, 2002), a further sign that sexual selection has acted secondarily on the structure and usage of male monkey alarm calls.

Strong evidence for the sexual selection hypothesis is not yet available, although the hypothesis makes various testable predictions. For example, for females to be able to exert a choice, male alarm calls must be individually distinctive, perhaps more so than their own calls. In Diana monkeys, this is certainly the impression one gets after listening to various recordings. Another prediction might be that after a new male takes over, he ought to be especially eager to demonstrate his commitment to antipredator defense by producing large numbers of alarm calls. One such case has been documented in putty-nosed monkeys (*Cercopithecus nictitans*; Eckardt and Zuberbühler, 2004).

#### **Alarm Calls Favored by Individual Selection**

Both kin selection and sexual selection suggest that alarm calling provides a net benefit to the caller because it increases the survival chances of close genetic relatives or the reproductive success of the caller. However, in some cases callers may also



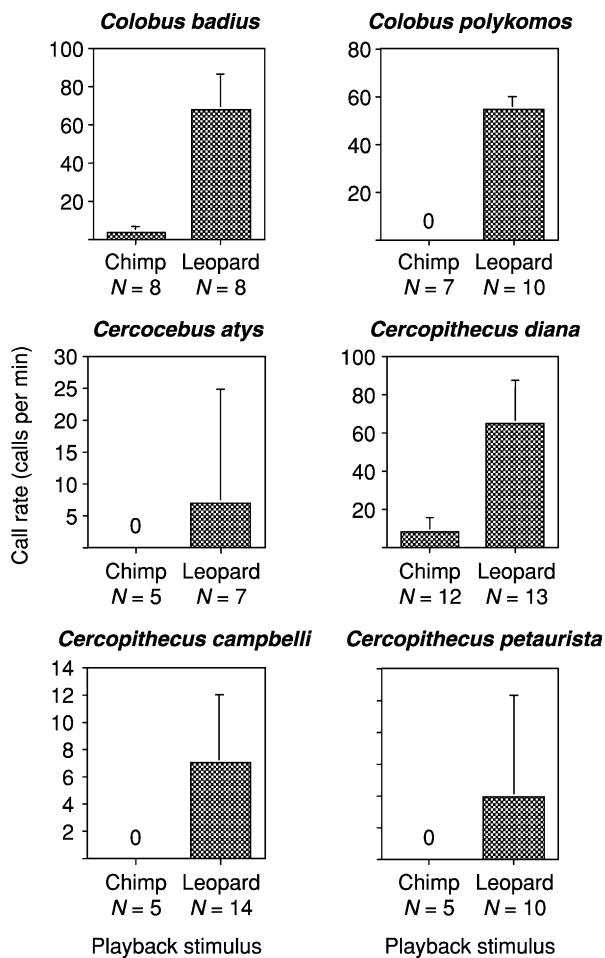
**Figure 1** Spectrographic representations of the predator alarm calls of male and female Diana monkeys in the Tai Forest, Ivory Coast. Reprinted from Zuberbühler K, Cheney D L & Seyfarth R M (1999). *Journal of Comparative Psychology* 113, p. 33–42. Copyright 1999 by the American Psychological Association. Reproduced with permission.

enjoy direct benefits from their actions in terms of their own survival. This is the case if alarm calls elicit collective antipredator behavior in nearby recipients, which confuses or disorients the predator (the prey manipulation hypothesis) (e.g., Charnov and Krebs, 1975).

An alternative idea is that alarm calls directly interfere with the predator's hunting tactic, for example, if predators depend on unwary prey (the perception-advertisement hypothesis), (e.g., Bergstrom and Lachmann, 2001). Recently, this version of the individual selection hypothesis has received some empirical attention. Work on free-ranging Diana monkeys has shown that some primate alarm calls function to advertise perception to predators that rely on unprepared prey, such as leopards (Zuberbühler and Jenny, 2002) and crowned eagles (Shultz and Noë, 2002). Playback experiments have demonstrated that the presence of crowned eagles and leopards reliably elicited high rates of conspicuous alarm calls in Diana monkeys, whereas playbacks of two other equally

dangerous predators, chimpanzees (*Pan troglodytes*) and human poachers, never did (Zuberbühler, 2003). The most likely explanation for these striking differences in alarm call usage is that chimpanzees and humans, but not leopards or eagles, are able to pursue monkeys in the trees, which greatly increases the costs of conspicuous alarm calling. A follow-up study involving most other primate species in the Tai Forest indicated that the pattern described for the Diana monkeys is also accurate for other monkey species (Zuberbühler, 2003; Figure 2).

But are these alarm calls really effective in deterring monkey-hunting leopards? To investigate whether or not this is the case, the hunting behavior of a number of wild leopards in the Tai forest has been monitored with the help of radio-tracking equipment (Zuberbühler, 2003; Zuberbühler and Jenny, 2002). Results have shown that forest leopards hunt monkeys by approaching unwary groups and hiding in their vicinity, presumably to wait for individuals to descend to the ground. Once the monkeys detected a

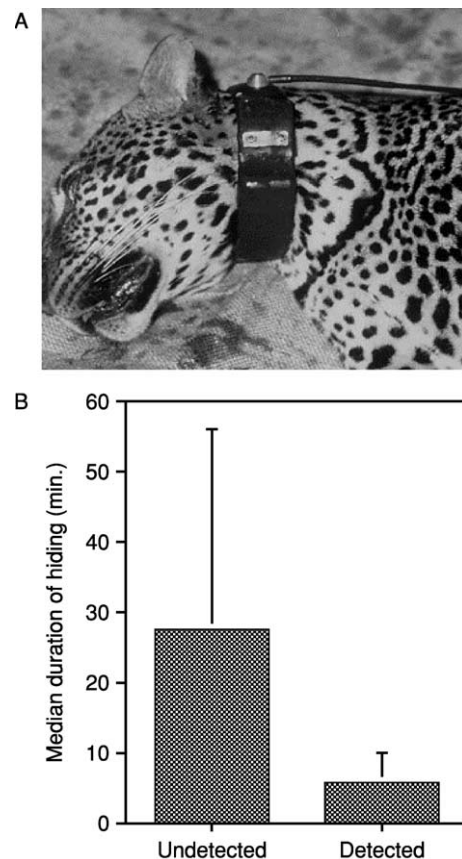


**Figure 2** Alarm call behavior of six Taï monkeys in response to chimpanzee pant hoots and leopard growls. Reprinted from Zuberbuhler K, Jenny D & Bshary R (1999). *Ethology* 105, 477–490. Blackwell Publishing Ltd. Reproduced with permission.

hiding leopard, however, they invariably began to produce alarm calls at very high rates, which typically caused the leopard to leave the area (Figure 3), showing that these alarm calls function to advertise perception and to deter the stalking leopards.

### The Cognitive Bases of Alarm Calls

The previous section addressed the problem of why animals produce conspicuous alarm calls in the presence of a predator; the remainder of the article deals with the cognitive processes involved in alarm call production and perception. The focus is on empirical evidence that is perhaps most relevant for the linguistically interested reader: the kinds of cognitive abilities nonhuman primates recruit when processing their own vocalizations. Results are relevant to assess whether or not these abilities are akin to those involved in speech processing in humans. Theories of language origins have to explain how the highly complex and sophisticated cognitive capacity required



**Figure 3** (A) Immobilized forest leopard is being equipped with a radio-tracking collar. (B) Average duration of hiding behavior of Taï leopards before and after detection by a group of monkeys. Reprinted from Zuberbuhler K, Jenny D & Bshary R (1999). *Ethology* 105, 477–490. Blackwell Publishing Ltd. Reproduced with permission.

for language processing has evolved in an extremely short period of time. Several lines of evidence suggest that humans did not have the anatomical and neural prerequisites to produce modern speech until very recently (Lieberman, 2000; Enard *et al.*, 2002). One implication is that many of the cognitive capacities required for language are phylogenetically much older, having evolved in the primate lineage long before the advent of modern humans and for reasons other than language production. An empirical investigation of the cognitive capacities of our closest living relatives, the nonhuman primates, is therefore of particular interest, because they may shed light on the evolutionary origins of cognitive processes underlying speech. Of particular interest are semantic and syntactic abilities, as they are central to virtually every definition of language (Crystal, 1997). Three aspects are dealt with: (a) the structure of alarm calls, (b) how they are being used in particular circumstances, and (c) the kinds of mental processes that recipients activate when responding to them.

### Alarm Call Structure

The fact that an animal produces different types of alarm calls alone is not a particularly exciting finding; it has been demonstrated in many groups of animals, primates and nonprimates alike (e.g., *nonprimates*: Slobodchikoff *et al.*, 1991; Blumstein and Arnold, 1995; Gyger *et al.*, 1987; e.g., *primates*: Struhsaker, 1967; Macedonia and Evans, 1993; Fichtel and Kappeler, 2002; Eckardt and Zuberbühler, 2004). In primates, and probably most other groups, alarm call production appears to be under relatively tight genetic control, with callers having little flexibility for structural modification (see Blumstein, 1999). For example, infant vervet monkeys rarely produce alarm calls, but if they do, their alarm calls are acoustically similar to those of adult animals (Seyfarth and Cheney, 1997). Their vocal stiffness is the product of very limited control over the articulators, particularly the tongue (Riede *et al.*, 2005). Although some flexibility is possible, nonhuman primates simply do not have sufficient command over the geometry of their vocal tracts to deliver the extensive array of phonemes that bring about human speech.

How exactly the different acoustic structures emerge in the different animal species may not be a random affair. Marler (1955) has argued that some animals have evolved alarm calls with acoustic features that make it hard for predators to detect the caller. The classic example is a passerine aerial predator alarm, the “seeet” call, which humans find hard to locate. However, experimental work has shown that several raptors are able to accurately orient toward the source of playback recordings of passerine “seeet” calls, although the response rates were somewhat lower compared to other alarm call types (Shalter, 1978). Whether this was a result of the raptors’ experiencing perceptual difficulties, as Marler argued, or whether the raptors were simply less motivated to orient toward “seeet” calls because they indicated that the prey was alert, as Shalter argued, is an unresolved issue.

Another line of reasoning refers to the idea that there is an inherent relation between an individual’s psychological state and the acoustic structure of the vocalizations it produces, the so-called motivational-structural rules (Morton, 1977). Here, the proposition is that individuals give low-frequency atonal vocalizations when prepared to assail an opponent. High-frequency tonal vocalizations, in turn, are more likely to be linked with an intention to withdraw. As predators differ in the kinds of threat they pose, and the most adaptive strategies to counteract them, this line of reasoning may also explain some acoustic patterns in alarm calls (see following discussion).

### Alarm Call Usage

From a comparative cognitive perspective, studies of call usage are of some interest because it is sometimes possible to determine what aspects of the environment an individual responds to when giving alarm calls. Particularly enlightening work has been conducted on domestic chickens (*Gallus domesticus*). Cockerels produce acoustically distinct alarms to raptors and ground predators, suggesting that these alarm calls might function as labels for certain predator classes. However, experiments have shown that callers mainly respond to a predator’s direction of attack, regardless of its biological class. For example, when a picture of a raccoon, a typical ground predator, is moved across an overhead video screen, cockerels respond with aerial alarm calls, which they normally give to raptors (Evans *et al.*, 1994). Similarly, although some species of squirrels produce acoustically distinct alarm calls, they also appear not to respond to the predator category *per se*, but instead to the relative distance and threat imposed by the predator (e.g., Leger *et al.*, 1980). The squirrels’ alarm call system is hence capable of encoding the degree of urgency that a caller assigns to a particular event. Similar findings have been reported from other species, such as Arabian babblers (*Turdoides squamiceps*; Naguib *et al.*, 1999) and yellow-bellied marmots (*Marmota flaviventris*; Blumstein and Armitage, 1997), both of which produce acoustically distinct alarm calls but do not assign them systematically to particular types of predators.

This naturally raises the question of whether or not it is appropriate to assume that monkey alarm calls are labels for different types of predators, in the sense that they encode the biological class of predators. Similar to chickens or marmots, monkeys may simply respond to the momentary threat imposed by a predator, regardless of its biological class. Here, alarm calls may be reflections of a caller’s momentary perceived threat, rather than true labels of external events. To distinguish between the two hypotheses, the following playback experiment was conducted with Diana monkeys. Recordings of eagle shrieks or leopard growls were broadcast from a concealed speaker to various wild groups throughout the Tai forest. The position of the speaker was altered systematically such that groups differed in how they encountered the alleged predator. In some cases, the predator vocalizations, either eagle shrieks or leopard growls, were either close or far, or played from below or from above, resulting in eight different playback conditions. Monkeys consistently responded to the predator category represented by the playback stimuli, regardless of immediate threat or direction of

attack. Similar findings were later reported from closely related Campbell's monkeys, *Cercopithecus campbelli*, suggesting that nonhuman primates generally label the biological class of a predator, regardless of momentary discrepancies in degrees of threat (Zuberbühler, 2003).

How does an individual monkey learn to use the leopard alarm call to leopards, but not to snakes? Not much is known about how monkeys learn to use their alarm call repertoire. Some observational data are available from free-ranging vervet monkeys. Although monkeys come in contact with over 150 species of birds and mammals, only a small proportion of these species pose a threat (Seyfarth and Cheney, 1997). One intriguing observation has been that infant vervet monkeys do not appear to apply their innately encoded set of alarm calls randomly to these various groups of animals. Instead, infants give eagle alarm calls only to birds and objects in the air, but never to terrestrial animals (Cheney and Seyfarth, 1990). Similarly, infants initially give leopard alarm calls to a variety of species on the ground, most of which do not pose any danger to them. One interpretation has been that primates are predisposed from birth to divide other animals into a few main groups and then learn to restrict call usage to a small number of relevant predator classes (Seyfarth and Cheney, 1997). Thus, alarm calls appear to be the output of certain psychological states, which are invoked by certain types of events. During maturation monkeys learn to restrict call use to those few species that pose a threat to them. This may also explain why alarm call production is so uniform across various populations in a given species.

In this sense, alarm call production might be analogous to nonlinguistic human utterances, such as laughing. Whether or not an event is perceived as amusing is the result of a cognitive process that draws on various memories. Once it qualifies, people will inadvertently experience amusement, and laughing will be difficult to suppress.

The following observation may illustrate the point. In a group of Campbell's monkeys, housed at the Paimpont Primate Research Station of the University of Rennes, a captive-born adult male was observed to produce eagle alarm calls during an aggressive interaction with a group of DeBrazza's monkeys (*Cercopithecus neglectus*), housed in the adjacent cage (Zuberbühler, unpublished data). During the interaction, the male was vigorously shaking the fence, trying to assault the neighboring individuals, a behavior regularly seen in free-ranging males interacting with predatory crowned eagles. Eagle alarm calls, in other words, may be the vocal manifestation of an extremely aggressive

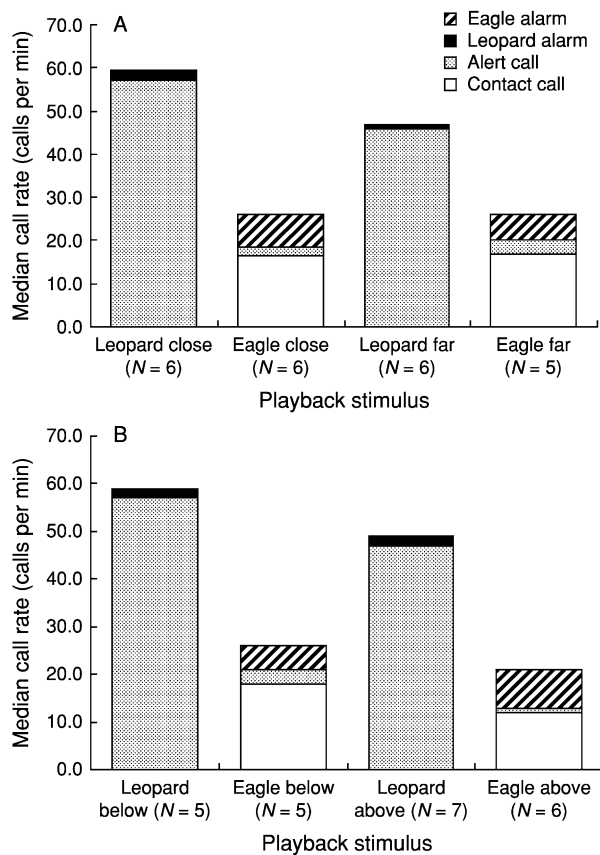
motivation on behalf of the male, which in the wild is typically elicited by the appearance of a crowned eagle. The captive male, having never had the opportunity to interact with an eagle, produced the calls during an aggressive interaction with another monkey species.

### **Alarm Call Comprehension: Conspecific Calls**

What kinds of mental representations do individuals activate as recipients of alarm calls, that is, when hearing another individual's calls? One answer comes from a classic study conducted on East African vervet monkeys. In this species, individuals produce acoustically different alarm calls to at least five different types of predators: large terrestrial carnivores, eagles, snakes, baboons, and unfamiliar humans (Seyfarth and Cheney, 1997; Struhsaker, 1967). Playback experiments have demonstrated that some of these calls elicit in other monkeys anti-predator responses that resemble their natural response to the corresponding predators. For example, playbacks of eagle alarm calls cause monkeys to look up into the air or run into a bush (Seyfarth *et al.*, 1980; Struhsaker, 1967). In the meantime, similar findings have been reported from other monkey species. As mentioned previously, Diana monkey males and females produce acoustically different alarm calls to crowned eagles and leopards. When hearing a male's alarm calls, nearby females respond with their own corresponding alarm calls, suggesting that the calls contain information about the type of predator present (Figure 4).

What kinds of mental representations are responsible for the monkeys' behavior? A cognitively simple model might suggest that the females' response is based on rather superficial processing: individuals respond to the physical features of alarm calls without accessing any of their potential associated meanings. Alternatively, alarm call processing might be more akin to that of linguistic information processing. In human language, speech sounds are not just processed at the peripheral acoustic level, but in relation to the types of cognitive structures they refer to, which are shared by both the signaler and the recipient (e.g., Yates and Tule, 1979).

Under field conditions, questions concerning mental processes are difficult to address, mainly because the choice of experimental techniques is so limited. One paradigm has turned out to be of significant value: the prime-probe technique. It is a variant of the habituation-dishabituation procedure initially developed for prelinguistic children (Eimas *et al.*, 1971), but differs from it because it does not have a long habituation phase. Instead, animals are provided with a one-time exposure to some critical information



**Figure 4** Diana monkey responses to playbacks of predator vocalizations presented with varying degrees of threat: (A) distance, (B) direction of attack. Reproduced from Zuberbühler K (2000). *Animal Behaviour* 59(5), 917–927, with permission of Elsevier.

and then tested on the effect of this manipulation of their subsequent response to an experimental probe stimulus. Figure 5 illustrates the design used to investigate whether Diana monkeys process alarm calls by accessing mental representations of associated predator classes.

In each trial, the playback speaker was positioned in the vicinity of a monkey group. Monkeys were primed with either predator vocalizations (baseline) or alarm calls (test and control). After a five-minute period of silence, the probe stimulus was broadcast. Baseline, test, and control conditions differed in the types of changes between prime and probe stimulus. In the baseline condition, both the acoustic and semantic features were alike. The prediction was that subjects would produce many alarm calls to the prime stimulus but only few calls to the probe stimulus because both the acoustic and the semantic information were repeated. In the test condition, subjects heard alarm calls followed by vocalizations of the *corresponding* predator. In this condition, the semantic features remained the same, whereas the acoustic features changed. Subjects were expected

to respond to the probe by producing (a) many alarm calls (if they attended to the acoustic-perceptual features) or (b) few alarm calls (if they attended to the semantic-conceptual information). Finally, in the control condition, both the acoustic and the semantic features changed. Subjects heard an alarm call followed by the call of the *noncorresponding* predator. Because both the acoustic and the semantic features changed, subjects were expected to produce many alarm calls to both the prime and the probe stimuli, regardless of how they processed the calls.

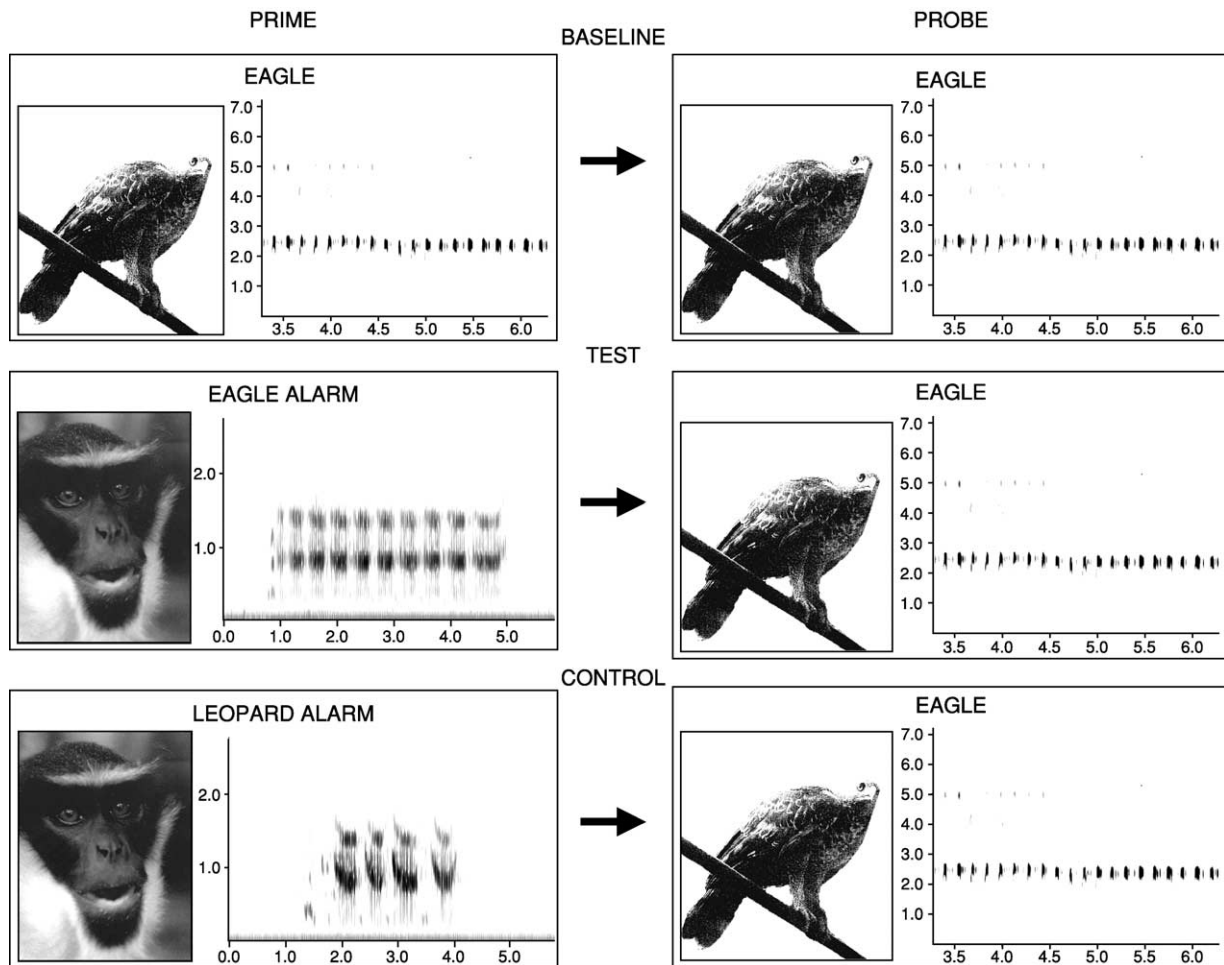
Results showed that the semantic content of the prime stimuli, not their acoustic features alone, explained the response patterns of the monkeys to the probe stimuli (Zuberbühler, 2003). That is, both eagle shrieks and leopard growls, two very powerful stimuli, lost their effectiveness in eliciting alarm calls when subjects were primed with the corresponding male alarm calls. Figure 6 illustrates the effect in response to the crowned eagle.

In conclusion, this experiment suggests that only variation in the semantic properties mattered to the monkeys when reacting to the vocalizations. Primates, in other words, appear to be able to process alarm calls on a conceptual-semantic rather than a perceptual-acoustic level (Cheney and Seyfarth, 1990).

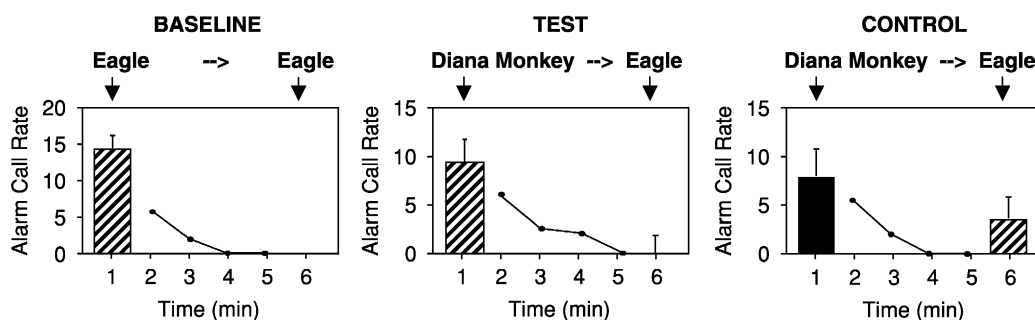
#### Alarm Call Comprehension: Eavesdropping

Primates are highly attentive to the alarm calls of other species. Vervet monkeys (*Cercopithecus aethiops*), for example, respond to superb starlings' (*Spreo superbus*) terrestrial and raptor alarm calls as a function of the calls' referential space – the natural range of predators that typically elicit the alarm calls. Young vervet monkeys need several months to learn to fully interpret starling alarm calls (Cheney and Seyfarth, 1990). Tai forest monkeys respond to the alarm calls of several nonprimate species that are hunted by leopards, such as various species of squirrels and duikers. One interpretation is that the monkeys have a fairly sophisticated understanding of the causes that determine another species' alarm call behavior. Interspecies communication, in other words, may provide additional valuable opportunities to investigate the cognitive mechanisms underlying monkey alarm call processing.

To investigate whether monkeys are able to attend to the most likely cause of an alarm call, as opposed to responding directly to the alarm call itself, the following experiment was conducted. Crested guinea fowls (*Guttera pucherani*), a gregarious ground-dwelling forest bird, produce alarm calls to a series of ground predators, including humans and leopards. When hearing guinea fowl alarm calls, Diana monkeys typically respond with leopard alarm calls,



**Figure 5** Design of the playback study: Monkey groups are primed with eagle- or leopard-related stimuli and then tested with eagle shrieks. Baseline, test, and control condition differ in the acoustic and semantic similarity of the prime and probe stimuli. X-axes of spectrograms represent time(s), y-axes represent frequencies (kHz). Reprinted from Zuberbuhler K, Cheney D L & Seyfarth R M (1999). *Journal of Comparative Psychology* 113, 33–42. Copyright 1999 by the American Psychological Association. Reproduced with permission.



**Figure 6** Results of the prime-probe experiments using eagle shrieks as probe stimuli. Histograms represent the median number of eagle alarm calls (hatched) or leopard alarm calls (solid) given in the first minute after a playback stimulus. Error bars indicate the values of the third quartile of the data set. The points connected by lines between them represent the median alarm call rate during the five-minute period of silence in between two playback stimuli. Using leopard growls as a probe stimulus yielded analogous results. Reprinted from Zuberbuhler K, Cheney D L & Seyfarth R M (1999). *Journal of Comparative Psychology* 113, 33–42. Copyright 1999 by the American Psychological Association. Reproduced with permission.

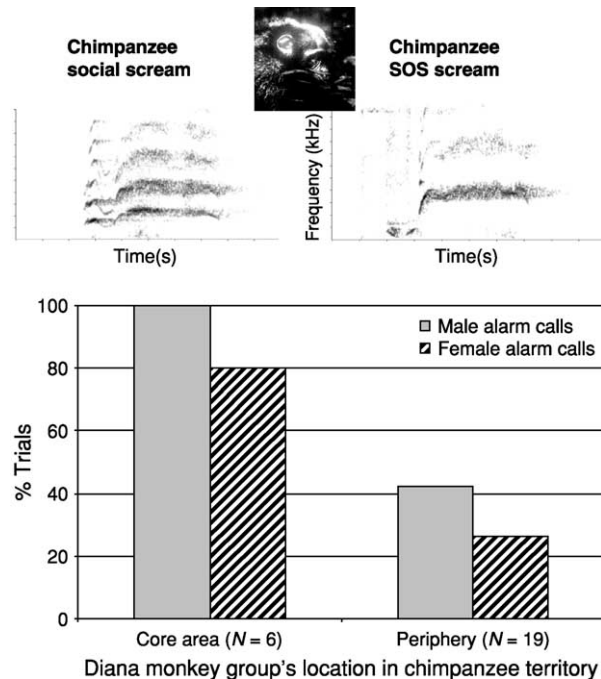
suggesting that the monkeys associate guinea fowl alarm calls with the presence of a leopard. However, crested guinea fowls sometimes give the same alarm calls to humans, which appears to place the monkey in

a behavioral dilemma: the best antipredator response to humans is to remain silent to avoid detection, whereas the best response to leopards is produce a large number of alarm calls to advertise perception.

To make the appropriate decision, Diana monkeys have to be able to draw some inferences about the possible causes of the birds' alarm calls. To investigate the monkeys' level of causal understanding, different groups of Diana monkeys were primed to the presence of a leopard or a human poacher by playing back brief recordings of either leopard growls or human speech in the vicinity of a monkey group. Then, after a five-minute period of silence, the same group was exposed to playbacks of guinea fowl alarm calls. If the monkeys are able to draw inferences about the potential causes of guinea fowl alarm calls, then they should respond with alarm calls after being primed with leopard growls, but not after being primed with human speech. However, if the monkeys have simply learned to associate guinea fowl alarm calls with the presence of a leopard (as their natural response seems to suggest), then their response to guinea fowl alarm calls should not differ between the two conditions. Results revealed significant differences in the way leopard-primed and human-primed Diana monkey groups responded to guinea fowl alarm calls, suggesting that the monkeys' response was not driven by the guinea fowl alarm calls themselves, but by their momentary beliefs of the type of predator most likely to have caused the birds to give alarm calls (Zuberbühler, 2003).

A similar problem exists when the monkeys are confronted with a nearby group of chimpanzees, a dangerous predator (Boesch and Boesch-Achermann, 2000). But chimpanzees are occasionally attacked and preyed upon by leopards themselves (Boesch and Boesch-Achermann, 2000; Zuberbühler and Jenny, 2002). When this happens they give loud and conspicuous alarm calls, the 'SOS' screams (Goodall, 1986). When chimpanzee SOS screams were broadcast to different groups of Diana monkeys, about half of all the groups tested switched to a chimpanzee-specific cryptic response to a leopard-specific conspicuous response (see Figure 2), suggesting that in some groups individuals assumed the presence of a leopard when hearing the chimpanzee alarm screams. Interestingly, Diana monkey groups with a home range in the core area of a resident chimpanzee community were significantly more likely to do so than peripheral groups, which were more likely to respond cryptically, suggesting that Diana monkey groups differ in semantic knowledge of chimpanzee vocal behavior (Zuberbühler, 2003; Figure 7).

Interspecies communication not only occurs between predator and prey but also between different species of primates. For example, ring-tailed lemurs (*Lemur catta*) respond appropriately not only to their own alarm calls but also to playbacks of the alarm calls of sympatric sifakas (*Propithecus verreauxi*; Oda



**Figure 7** Relationship between a Diana monkey group's tendency to respond with leopard alarm calls to chimpanzees' SOS screams and the location of their home range within the resident chimpanzees' territory. Chimpanzee social screams did not elicit any alarm calls. Reproduced from Zuberbühler K (2000). *Animal Behaviour* 59(5), 917–927, with permission from Elsevier.

and Masataka, 1996). The Taï monkeys regularly forage in mixed species groups to improve their protection against predation, and it is therefore not surprising that individuals of mixed species groups respond to each other's alarm calls, such as in the case of the Diana monkey–Campbell's monkey association (Wolters and Zuberbühler, 2003). Male Campbell's monkeys produce two acoustically different alarm calls to crowned eagles and leopards. Playbacks of Diana monkey alarm calls to Campbell's monkeys and vice versa reliably elicited the appropriate alarm responses in the other species (Zuberbühler, 2003). This ability, however, may not be a uniquely primate capacity. Recent playback experiments with yellow-casqued and black-casqued hornbills showed that these birds readily distinguish between Diana monkey eagle and leopard alarm calls (Rainey *et al.*, 2004).

However, primates may be unique in their abilities to attend to the semantic properties of other species' alarm calls. For example, in a prime-probe experiment similar to the one presented earlier (Figure 5), Diana monkeys have been shown to process the semantic features of the Campbell's alarm calls analogous to how they process their own calls (Zuberbühler, 2003). Further work on the Campbell's–Diana monkey system showed that alarm calls undergo semantic adjustments in the minds of the recipients, depending on the sequencing of alarm

calls. As mentioned earlier, Campbell's monkey males give acoustically distinct alarm calls to leopards and crowned eagles, and Diana monkeys respond to these calls with their own corresponding alarm calls. However, in less-dangerous situations, Campbell's males often emit a pair of low, resounding 'boom' calls before their alarm calls. Playbacks of boom-introduced Campbell's eagle or leopard alarm calls no longer elicited alarm calls in Diana monkeys, indicating that the booms have affected the semantic specificity of the subsequent alarm calls, suggesting that monkeys are able to attend to simple syntactic cues when responding to each other's alarm calls (Zuberbühler, 2003).

Is it reasonable, therefore, to liken these animal signals to human words? After all, they share one of the most fundamental properties, the ability to transmit accurate acoustic information about an external event, which is subsequently decoded by insightful recipients. Still, most researchers have remained cautious when interpreting these kinds of data, even in the case of primates. The reason for that stems from a fundamental discrepancy between the cognitive processes driving alarm call production and those governing their perception. There is simply no evidence that, when producing an alarm call, nonhumans are actively trying to inform each other about the events they have just witnessed. Instead, primate behavior appears to be the result of a caller's egocentric interaction with the world, although in some cases the signals happen to reliably and uniquely denote an external event. For this reason, it has been argued that animal alarm calls are merely functionally referential (or semantic), in contrast to true or intentional referentiality, which presumably underlies human speech. Nevertheless, it would be interesting to know how ubiquitously human speech production is intentionally guided, as opposed to speakers' simply knowing which bits of language are used appropriately in which circumstances.

## Conclusions

Alarm calling is found in a large number of species, demonstrating its adaptive value in predation avoidance. It is also intriguingly absent in others, such as some nocturnal prosimians (E. Bramley, personal communication), suggesting that alarm calls are a product of sociality. There is evidence that alarm calls are or have been under the influence of all major selective forces (i.e., individual, kin, and sexual selection), although it is difficult to identify general patterns concerning the importance of these forces.

In nonhuman primates, alarm calling is the result of complex cognitive processes, particularly in the mind of the recipient. Nonhuman primates are highly

attentive to stimuli that predict the presence of a predator, and they have demonstrated astonishing skills in solving predation-related problems. This is interesting because predation is an ecological force usually thought to have led rather basic and rigid behavioral patterns, but not to higher cognitive abilities (Humphrey, 1976). For nonhuman primates, this might have been a misconception because in many of the experiments discussed here, monkeys were showing behavior that resulted from seemingly higher cognitive processes, such as inference making, causal understanding, semantic and syntactic processing, and rapid association learning. Predation, in other words, might have provided a strong selection pressure to favor the evolution of higher intellectual faculties in nonhuman primates. The way they produce, use, and interpret their own and other species' alarm calls is a clear manifestation of this intelligence.

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*See also:* Animal Communication: Deception and Honest Signaling; Animal Communication: Long-Distance Signaling; Animal Communication Networks; Animal Communication: Overview; Animal Communication: Signal Detection; Animal Communication: Vocal Learning; Categorical Perception in Animals; Cognitive Basis for Language Evolution in Non-human Primates; Communication in Grey Parrots; Development of Communication in Animals; Individual Recognition in Animal Species; Non-human Primate Communication; Production of Vocalizations in Mammals; Traditions in Animals.

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