Survivor Signals: The Biology and Psychology of Animal Alarm Calling

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I. Introduction

Many social species produce specific vocalizations when threatened or startled by a predator or some other significant disturbance. These signals are usually termed ''alarm calls'' (from old Italian ''all' arme'' meaning ''to arms'' on the approach of an enemy), but ''distress,'' ''alert,'' or ''mobbing calls'' are also common, usually in cases where the calls are given in conjunction with some specific antipredator behavior. Although many authors treat mobbing calls as functionally distinct from alarm calls, this distinction is not always useful. For example, many forest primates produce acoustically distinct alarm calls to ground predators, such as leopards, but these calls are often accompanied by mobbing behavior (e.g., Zuberbühler et al., 1997). In this chapter, I will therefore treat mobbing calls as a subtype of alarm calls, one that is linked with relatively specific antipredator behavior.

Alarm calls have long been of interest to researchers and they have continued to bewilder and fascinate, for a number of reasons. A first one is merely practical. When working with free-ranging animals, it is often difficult to divide the continuous stream of behavior into discrete and meaningful units that can be studied systematically. Alarm calls are a rare exception. They are structurally and perceptually unique, which facilitates identification and systematic study considerably.

Second, alarm calls are a particularly useful tool for studying cognitive mechanisms, often providing a rare window into an animal's mind. Diurnal life and sociality are strongly associated with whether or not a species produces alarm calls (Shelley and Blumstein, 2005) and individual callers often require a specific audience (Zuberbühler, 2008). Because of these social dimensions, alarm calls are interesting for a number of scientific

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disciplines. Key problems are what features of the event alarm calls convey, whether callers have a targeted audience and are aware of their situation, and whether receiver responses are driven directly by the calls or whether they are linked to specific mental representations that relate to the associated events. In this context, eavesdropping is increasingly recognized as an important process as most species live in relatively complex systems where they share some of their predators with other species (e.g., McGregor and Dabelsteen, 1996). Research on alarm calls has also helped to clarify a number of theoretical concepts, such as the nature of referential signaling, and the relation between animal signals and human communication (Tomasello, 2008; Zuberbühler, 2003).

Third, it has long been recognized that alarm calls pose somewhat of a conundrum to evolutionary theory (Maynard-Smith, 1965). In many species, alarm calls are amongst the most noticeable signals in a species' vocal repertoire, which is paradoxical as this is likely to reveal the presence and location of the caller to the predator. Why is such seemingly maladaptive behavior common in animal communication? What selection processes have provided an advantage to individuals that behave conspicuously in the presence of a predator? Much of the earlier research has focused on the impact of kin selection, but more recent studies emphasize the different ways by which callers can benefit more directly.

The objective of this review is not so much to provide a systematic overview of the alarm calling behavior in the various taxonomic groups, but to generate progress with regard to these theoretical issues, for which studies of the alarm calling have turned out to be particularly useful. A special focus will be on nonhuman primates, simply because much work has been carried out with these species especially with regard to cognitive questions, but various examples from nonprimate species will also be discussed.

II.   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. Firstly, they can provide a selective advantage to the signaler if they increase the survival chances of closely related kin, the kin selection hypothesis (Maynard-Smith, 1965). Calling may be costly to the signaler and increase the predation risk but under this hypothesis this is all outweighed by the benefits of increased survival of recipients who carry a proportion of the caller's genes.

Secondly, alarm calling is beneficial to a signaler if it increases the reproductive success of the caller, the sexual selection hypothesis (Darwin, 1871). This may go by the way of receivers preferring individuals as mating partners that are more willing to produce risky alarm calls in the presence of predators, compared to more reluctant individuals. In some primates, there are considerable sexual dimorphisms in alarm calling: male calls are usually more conspicuous than female calls, suggesting that sexual selection has acted upon male callers (Zuberbühler, 2006).

Thirdly, the alarm calling is directly beneficial for the caller, if it elicits behavior in others that decreases the vulnerability of the caller, the individual selection hypothesis. Here, two main scenarios have been distinguished (Zuberbühler, 2006). A first one draws on the effects of alarm calling on other potential prey animals, usually group members, in terms of their antipredator responses. In many cases, the initial costs of alarm calling are quickly outweighed by other individuals' antipredator responses. A good example is the turmoil caused by escaping birds when hearing an alarm call, creating a cloud of confusion for the predator from which the caller can benefit (the ''prey manipulation hypothesis''; Charnov and Krebs, 1975). Callers also benefit if this initiates a subsequent group effort to get rid of the predator, as for instance, in predator mobbing (the ''cooperative defense hypothesis''; Curio, 1978). However, sometimes animals give alarm calls to a predator in the absence of an 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 and without the intermediate step of other prey behavior (the ''perception advertisement'' hypothesis; Bergstrom and Lachmann, 2001). This is especially the case for predators that depend on surprising their prey, which may give up hunting once detected. In the following, selected empirical findings that support one or several of the proposed selective forces underlying the evolution of alarm calling are discussed.

A.   KIN SELECTION

A first solution to the apparent paradox is that individuals give alarm calls preferentially when close genetic relatives are nearby. Kin selection theory can explain the evolution of conspicuous signaling in the presence of predators, if alarm calling improves the survival of individuals that share a certain proportion of the caller's own genes (Sherman, 1977). Individuals prevented from reproduction should be especially susceptible. Another testable prediction is that the number of close relatives in the audience should impact on an individual's willingness to produce risky alarm calls. 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. In great gerbils (*Rhombomys opimus*), adults alarm call more often when pups are present, while solitary individuals seldom give alarms, suggesting that alarm calls primarily function to warn vulnerable offspring (Randall et al., 2000). In socially living Siberian jays (*Perisoreus infaustus*), alpha females alarm call more frequently when accompanied by offspring than by unrelated immigrants, even if they are already independent. In contrast, alpha males call indiscriminately, suggesting that they are affected by different factors (Griesser and Ekman, 2004). In gray-cheeked mangabeys (*Lophocebus albigena*) of Kibale National Park, Uganda, adult males are most active in defense but also overrepresented in the prey spectrum of crowned eagles, demonstrating the high costs of antipredator behavior. High-ranking males are most likely to alarm call and attack the eagles, suggesting that they are more motivated to secure the survival of offspring (Arlet and Isbell, 2009).

An empirically more challenging endeavor has been to explain alarm calling with the presence of nondescendent kin, such as brothers and sisters. If kin selection operates at this level to provide indirect fitness benefits, then individuals should be willing to engage in risky alarm call behavior if it increases the survival chances of closely related nondescendent kin, following Hamilton's rule (Hamilton, 1963). Considerable empirical effort has been devoted to this topic, particularly in various rodent species, but the overall picture is very inconsistent. Males and females often differ in terms of their alarm calling to the presence of nondescendent kin, suggesting that kin selection has affected individuals in sex-specific ways. For example, in Gunnison's prairie dogs (*Cynomys gunnisoni*), females with nondescendent kin call more often to a ground predator than females without nondescendent kin. Males are also keen alarm callers, but calling is unrelated to kinship of nearby listeners (Hoogland, 1996). A nondescendent kin audience can enhance alarm calling differently to aerial and ground predators. For example, Belding's ground squirrels (*Spermophilus beldingi*) show kin-sensitive responding to terrestrial predators, but in the case of aerial predators the caller's own exposure appears to be the main factor (Sherman, 1977, 1985). A study on Columbian ground squirrels (*Spermophilus columbianus*) found the opposite pattern (Macwhirter, 1992). In this species, females do not behave nepotistically toward other nondescendent kin in the presence of terrestrial predators, but do so in response to aerial predators.

Kin selection has also been put forward as an explanation for the evolution of alarm calls in nonhuman primates, but the overall evidence is even less strong. For example, spider monkeys alter their alarm call behavior as a

function of the number of kin in the vicinity (Chapman et al., 1990) and gibbons produce calls than can be heard in neighboring home ranges, which are often occupied by the callers' close relatives, suggesting that these calls also warn kin (Clarke et al., 2006; Tenaza and Tilson, 1977). In Capuchin monkeys, alarm calling to vipers was consistent with the predictions of the kin selection hypothesis, but callers also benefited from attracting other conspecifics for cooperative defense (Wheeler, 2008).

In sum, alarm calling is probably widely affected by the presence of kin, but the strongest effects are found for descendents, and alarm calling may simply be one aspect of parental care. In some species, kin selection appears to have additionally favored alarm calling to benefit a nondescendent kin audience, but no clear and general patterns are visible. In cases where individuals alarm call to warn nondescendent relatives, kin selection appears to have acted in various idiosyncratic ways. Reviewing over 200 species of rodents, Shelley and Blumstein (2005) concluded that alarm signals evolved primarily to communicate to predators, but that nepotistic benefits can be important for maintaining alarm calling in a species.

B. SEXUAL SELECTION

Animals also give alarm calls when no kin is nearby, and this requires a very different set of evolutionary explanations. One is based on the idea of alarm calls as sexually selected behavior, produced by one sex as part of its attempts to increase reproductive success. Indirect evidence comes from the sexual dimorphisms in alarm call structure and usage seen in a number of species. In domestic chickens, for example, males are more likely to produce alarm calls while in the presence of unrelated females compared to other audiences (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 primates, particularly the forest guenons, adult male alarm calls are structurally different from those of the adult females. The male calls are conspicuous loud signals given in response to predators and other circumstances, and they carry over remarkable distances (Gautier and Gautier, 1977). Research on West African Diana monkeys (Cercopithecus diana) and other forest primates has shown that these calls can function as predator alarm calls (Zuberbühler, 2003). These monkeys live in small stable social groups with one adult male and several adult females with their offspring (Uster and Zuberbühler, 2001). They are hunted by leopards (Panthera pardus) and crowned eagles (Stephanoaetus coronatus), and

both the adult male and the females produce predator-specific alarm calls to these predators (Zuberbühler et al., 1997). However, the vocal behavior of the adult males consists of low-pitched high-amplitude calls given in long sequences, which carry over up to a kilometer through dense tropical forest habitat. Male–male competition is a likely candidate responsible for this structural specialization of male calls. In this case, sexual selection seems to have acted as a secondary evolutionary force on communication systems where alarm calls have already been present.

Polygynous social systems 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 polygynous 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 engage in antipredator behavior, such as producing costly alarm calls in the presence of a predator (Eckardt and Zuberbühler, 2004). 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). Subadult male Diana monkeys go through a phase in which their alarm shows remnants of a female alarm call, but also 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, 2002a), a further sign that sexual selection has acted secondarily on the structure and usage of male monkey alarm calls.

Primates are not the only group of animals where sexual selection appears to have acted on alarm call behavior. In fowls (*Gallus gallus*), mating frequency and rate at which males produced alarm signals are related. Increased calling may result from recent mating success, a form of mate investment, but it is also possible that calling is attractive to females (Wilson and Evans, 2008). In roe deer (*Capreolus capreolus*), solitary individuals alarm call more frequently to predators than deer in groups, suggesting that the calls do not serve to warn conspecifics of potential danger, but to inform any potential predator that it has been identified. However, if a male's alarm calls are played from within a buck's territory, this provokes counter-barking or aggressive behavior, not antipredator behavior, suggesting that the male alarm calls possess a communication function in male–male competition (Reby et al., 1999).

According to Darwin (1859), 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." If alarm calls are unnecessarily conspicuous this could have been favored by the forces of sexual selection.

C. INDIVIDUAL SELECTION

Animals, sometime, give alarm calls in the absence of any apparent audience, suggesting that alarm calling can provide direct benefits to the caller. Two main evolutionary routes have been suggested for alarm calls to be favored by individual selection. Either the caller signals directly to the predator or it affects the behavior of other potential prey in a way that increases its own chances of survival.

1. Prey Manipulation and Cooperative Defense

Alarm calls are usually of great interest to other nearby individuals, especially if they share predators with the caller. If the alarm leads to chaotic movement, it can confuse or disorient a predator (the "prey manipulation" hypothesis, e.g., Charnov and Krebs, 1975). In starlings, for example, alarm calls trigger flock departures, thus reducing the probability of the initial caller being targeted. The alarm calling is more common when visibility is reduced, suggesting that calling has a cost to the producer (Devereux et al., 2008). In some cases, alarm calls attract other individuals to the site and this can lead to mobbing behavior, a phenomenon with its own literature (Curio, 1978). In meerkats (Suricata suricatta), mobbing is performed not only to deter predators but also to gather information and to allow young to learn about predators by observing adults, a hypothesis suggested on other occasions (Curio et al., 1978; Graw and Manser, 2007). In Siberian jays, kin groups mobbed predator models for longer and produced more alarm calls than nonkin groups, but predator type and the social position of the individual had further effects on mobbing behavior (Griesser and Ekman, 2005). Collective antipredator behavior can include multiple species but then this may be related to the degree of familiarity between individuals of the different species (Eckardt and Zuberbühler, 2004; Wolters and Zuberbühler, 2003). Brood parasites, such as cowbirds, can also elicit alarm calling, which then leads to mobbing to the benefit of the caller (e.g., Grim, 2008). In conclusion, if individuals share the same predator alarm calls often lead to joint antipredator behavior from which the caller can benefit in ways that would not be possible with solitary antipredator behavior.

2. *Predator-Directed Signals*

Alarm calls can interfere in various ways with a predator's hunting technique. One interesting example is the distress calls given by individuals when restrained by a predator. These calls often have a startling effect and appear to increase the chances of escape. However, predator-directed signals can also occur at earlier stages of a predation event. For example, if predators depend on unwary prey then alarm calling will signal detection and that further hunting is futile (the ''perception advertisement'' hypothesis, e.g., Bergstrom and Lachmann, 2001). Some primate alarm calls appear to function in this way, particularly to forest leopards (Zuberbühler and Jenny, 2002) and to some degree to crowned eagles (Shultz and Noë, 2002). Crowned eagles and leopards reliably elicited high rates of conspicuous alarm calls in Diana monkeys, while playbacks of two other equally dangerous predators, the chimpanzees (*Pan troglodytes*) and human poachers, never did, a pattern found in a number of species (Zuberbühler, 2003). Monkeys seem to be aware of the respective hunting strategies of these predators, and adjust their alarm calling behavior accordingly.

But are alarm calls effective in deterring predators? Results of a radio-tracking study showed that forest leopards hunt monkeys by approaching unwary groups and hiding in their vicinity, presumably to wait for individuals to descend to the ground (Zuberbühler and Jenny, 2002). The alarm calling monkeys reliably caused the leopard to abandon a hiding spot to move on and leave the area, strong evidence in support of the idea that alarm calling is directly beneficial for monkeys (Zuberbühler et al., 1999a; Fig. 1) and this is typically potentiated by the subsequent mobbing behavior of other prey animals. Bergstrom and Lachmann (2001) have generated a game-theoretical model, the watchful babbler game, aimed to explain why callers can benefit by signaling to a predator that it has been detected. The main finding was that willingness to signal increases with predator density, and increasing pursuit costs to the predator will allow for cheaper signals by the prey.

Perception advertisement is a relatively frequently encountered functional explanation of alarm calls in the recent literature, especially for primates. It has been suggested as a primary function of alarm calls in gray-cheeked mangabeys responding to crowned eagles (Arlet and Isbell, 2009) and in spectral tarsiers responding to snakes (Gursky, 2006). In capuchin monkeys, alarm calls to felids appear to be addressed to both predators and conspecifics; this can leads to cooperative defense behavior, which is also seen after alarm calls to raptors (Wheeler, 2008).

To conclude, individual selection is a powerful and ubiquitous force underlying the evolution of alarm calling in many species, but warning descendent kin and partners can also benefit callers. In many cases, it is
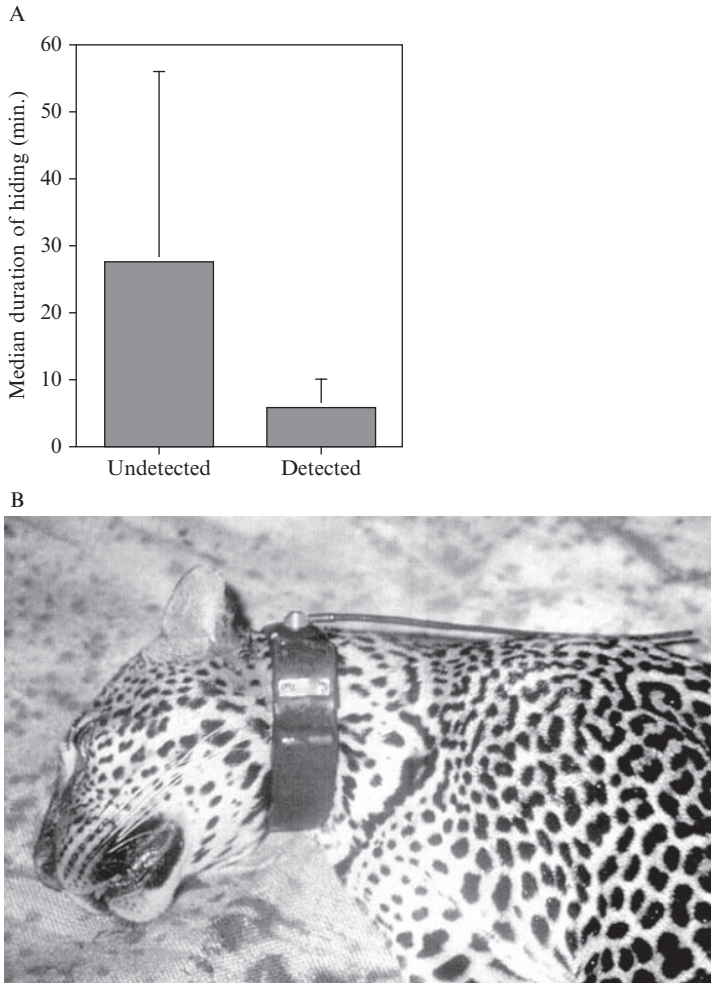
Fig. 1. The hunting behavior of forest leopards in the Taï Forest, Ivory Coast, is influenced by the alarm calling behavior of monkeys: (A) duration of hiding in the vicinity of a monkey group before and after detection; (B) a radio-collar is fitted to an anesthetized forest leopard to study the alarm call responses of forest monkeys to this predator (Zuberbühler et al., 1999b; photo: David Jenny).

difficult to tease apart the various possible functions, perhaps because multiple functions are present. This is well illustrated in cases where alarm calls are directly aimed at the predator. If callers enjoy a reasonable protection from being captured, other prey often joins in, leading to a cooperative effort.

III.   ALARM CALL STRUCTURE

A.   ACOUSTIC DIVERSITY

Many species possess a repertoire of acoustically distinct alarm calls (e.g., mammals and birds: Slobodchikoff et al., 1991; Blumstein and Arnold 1995; primates: Macedonia and Evans, 1993; Ouattara et al., 2009; Struhsaker, 1967; Birds: Gyger et al., 1987; Takahashi and Hasegawa, 2008). The diversity of calls can be the result of variation in temporal, spectral, and sequential call features. In white throated magpie-jays (*Calocitta formosa*), callers vary the temporal features of call production by altering call duration and intercall interval, and both parameters are perceptually salient to receivers (Ellis, 2008). A particularly remarkable example of alarm calling behavior is found in drongos, a family of small passerine tropical birds. In greater racket-tailed drongos (*Dicrurus paradiseus*) of Sri Lankan rainforests, callers learn to mimic alarm calls of other species and include them as part of their own alarm calling behavior (Goodale and Kotagama, 2006).

In primates, there are considerable differences in how species convey information about external events with vocal signals. A common finding is that one acoustically distinct alarm call type is given to a narrow range of aerial threats, while a second type is given to other types of danger, usually terrestrial predators or other disturbances. Capuchin monkeys, *Cebus capucinus*, produce two basic types of alarm calls, which can be separated further into different subtypes (Digweed et al., 2005). For the first call type, three subtypes could be distinguished given to aerial predators, humans (a terrestrial disturbance), and unfamiliar conspecifics. However, the second call type, given to snakes, caimans, terrestrial predators, and during aggressive interactions, revealed no clear context specificity and all acoustic variation appeared to be linked with changes in urgency, although this variable was not measured independently (Fichtel et al., 2005).

Some other primates convey information by assembling a small repertoire of calls into more complex sequences, as discussed later.

Another way to generate acoustic diversity is by modifying some of the acoustic features on a graded continuum. This type of alarm call system has been extensively studied in baboons. Female Chacma baboons (*Papio cynocephalus*) produce loud barks in response to predators but also when individuals seek to reestablish contact with other group members. The barks constitute a graded continuum, ranging from tonal to noisy-harsh. Tonal barks are given to seek contact, while harsh barks are given to mammalian carnivores and crocodiles (Fischer et al., 2001a). In playback experiments, individuals discriminated between the different bark variants, suggesting that they conveyed meaning using a graded calling system

(Fischer et al., 2001b). From about 6 months of age, infants begin to reliably discriminate between alarm and contact barks, demonstrating that call comprehension is learned (Fischer et al., 2000). Similarly, male baboons respond to predators with alarm ''wahoos,'' but the same call type is also produced during male contests, and when a male has become separated from the group. Call variants given in these three contexts differ in a range of features, such as call rate, frequency characteristics, duration, and amplitude (Fischer et al., 2002). In playback experiments, females responded for significantly longer to alarm than to contest ''wahoos'' and only alarm ''wahoos'' caused females to flee (Kitchen et al., 2003). In Thomas langurs, males produce loud calls in a range of contexts, including to predators. The calls differed acoustically depending on context and receiver responses to the different variants suggested that they perceived the differences in loud call characteristics between the various contexts (Wich et al., 2003). In chimpanzees, finally, individuals produce screams when detecting a leopard (SOS scream, Goodall, 1986; Zuberbühler, 2000a; Fig. 2), but they also give screams during agonistic interactions (victim or aggressor screams: Slocombe and Zuberbühler, 2005a, 2007) and during social frustration (tantrum screams). Receivers are able to discriminate between the call variants, suggesting they can infer the most likely associated context (Slocombe et al., 2009; Zuberbühler, 2000a).

B. Receiver Psychology

Animal signals may have largely evolved in relation to the psychology of the targeted receivers, that is, what they find easy to detect, discriminate, and remember (Guilford and Dawkins, 1991; Klump and Shalter, 1984). One classic study is by Klump et al. (1986), who have compared the auditory sensitivity of a small songbird, the great tit, and its primary predator, the European sparrowhawk. To predators, the main demand of alarm calls is to interfere with their hunting technique. If predators spend large amounts of time observing their prey before attacking, alarm calls should be so that they can be detected easily, discriminated from other vocal signals, and remembered as a sign of a failed hunting attempt. In line with this, many species produce highly conspicuous calls to stalking predators. For example, chaffinches produce more alarm signals to models of cats than hawks (Jones and Whittingham, 2008). Many forest primates behave conspicuously to leopards, a ground predator that captures monkeys from concealed locations (Zuberbühler et al., 1999a).

Responses of monkeys to predatory chimpanzees, in contrast, are very different, reflecting the fact that their hunting behavior is not deterred by acoustic signals. To chimpanzees, monkeys escape silently to locations
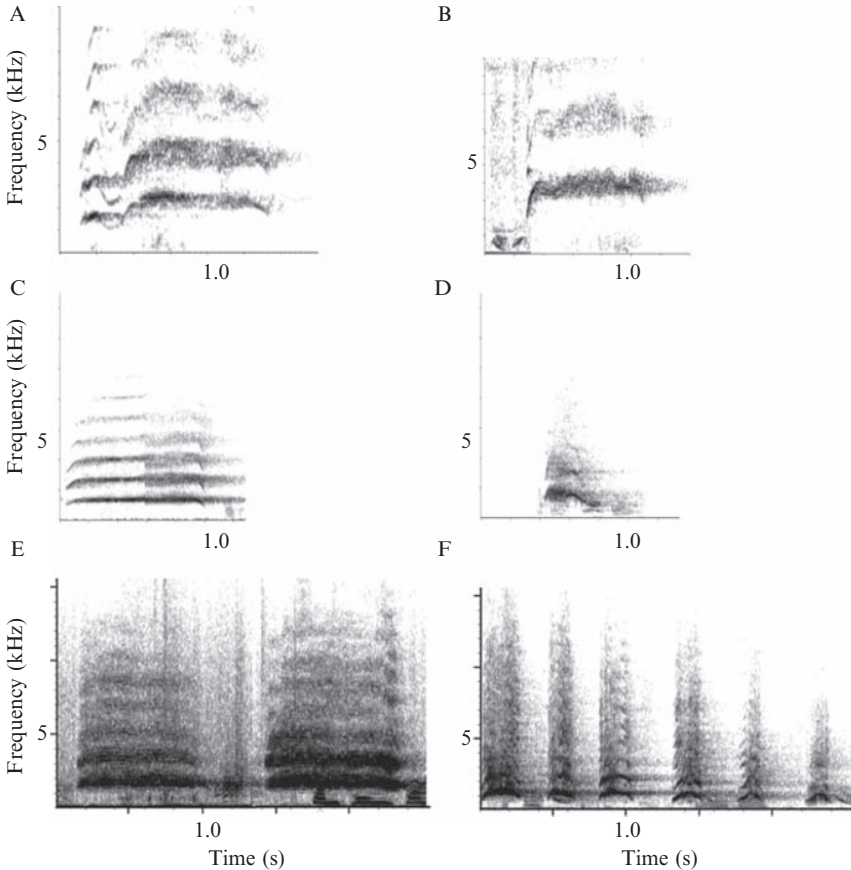
FIG. 2. Acoustically variable screams produced by chimpanzees in a range of social contexts: (A) victims screams, (B) SOS screams given to a leopard; (C) victim screams and (D) aggressor screams given during an agonistic interactions; (E) severe victim screams and (F) mild victim screams given during aggression. Chimpanzees and other primates can discriminate between the different scream variants (Slocombe et al., 2009; Zuberbühler, 2000a).

within the forest canopy where an encounter is less likely. Similarly, bird alarm calls to aerial predators are acoustically different from alarm calls to terrestrial predators, or calls given in distress or during mobbing. Marler (1955) suggested that the aerial alarm calls of birds were acoustically adapted to minimize the costs for the signaler by making localization more difficult for raptors. Many songbirds produce high-frequency "seet" calls when threatened by a raptor, a call that is difficult to locate and that also causes less interest in raptors (Jones and Hill, 2001; Jurisevic and

Sanderson, 1998). Here, natural selection appears to have favored an acoustic structure that makes perception and localization difficult, while keeping response motivation low. Aerial alarm calls are not specifically adapted to the perceptual capacities of raptors; other birds also find them hard to localize (Wood et al., 2000). When comparing the auditory sensitivity of three different songbirds, house sparrows, white-breasted nuthatches, and tufted titmice, all three species exhibited maximum sensitivity from 2.2 to 3.2 kHz, but in the high-frequency range, sensitivity varied with the maximum frequency of species-specific vocalizations (Henry and Lucas, 2008). In white-faced Capuchin monkeys, the acoustic structure of general alert calls are easier to localize than aerial alarm calls, allowing signalers to remain inconspicuous in the presence of raptors (Digweed et al., 2005).

It is very likely that predator-driven effects are modulated by habitat acoustics (see also chapter by Naguib and Brumm). If call production is tuned to receiver psychology, as argued earlier, then natural selection is likely to act on efficient signal transmission, with habitat acoustics as a key variable. In two species of whistling rats (*Parotomys brantsii* and *Parotomys littledalei*), the alarm calls consist of high-pitched vocalizations that are difficult to locate, but the lower pitched calls were produced by the species that lived in a more closed habitat, *P. littledalei*, suggesting that the transmission properties of the habitat have further shaped acoustic differences (le Roux et al., 2002). There was no evidence that alarm calls were adapted to the habitat in marmots (Blumstein, 1999).

C. INDIVIDUAL DIFFERENCES

Individual differences in vocalizations (''signatures'') are reliably found across species and call types, particularly in calls given during social interactions. For example, chimpanzee calls, such as screams, copulation calls, or pant hoots, are individually distinct, allowing bystanders to assess the relevance of an ongoing social event and to locate a socially relevant partner (Slocombe and Zuberbühler, 2007; Townsend et al., 2008). The adaptive function of individual signatures in alarm calls, on the other hand, is more difficult to understand although this has been understand (e.g., Bayly and Evans, 2003; Yorzinski et al., 2006). Individual differences are likely to occur due to size and shape differences of the vocal tract, and the crucial question is whether such inevitable differences can be perceived by conspecifics. Alarm calls are a potentially attractive vehicle for dishonest signaling, suggesting that receivers benefit from an ability to recognize group members by their vocalizations. In mixed species bird flocks, where individuals do not interact repeatedly and probably do not know each other individually, deceptive alarm calling has been reported (Munn, 1986). In vervet monkeys, receivers are reluctant to

respond to the alarm calls of juveniles, which often alarm call to disturbances that are not dangerous to anyone (Hauser, 1993; Seyfarth and Cheney, 1986). However, this age-effect is not universal. In yellow-bellied marmots (*Marmota flaviventris*), alarm calls of juveniles elicit greater vigilance than calls from adult females, suggesting that receivers perceive juveniles as especially vulnerable (Blumstein and Daniel, 2004). Alarm calls of adults are also individually distinct and when calls were broadcast and rerecorded over different distances, the acoustic variables that conveyed the caller's identity persisted (Blumstein and Munos, 2005). Individually distinct alarm calls have also been found in the great gerbil (*Rhombomys opinus*, Randall et al., 2005). In Belding's ground squirrels (*S. beldingi*), individually distinctive alarm calls were linked with the genetic similarity between callers, suggesting that the development of alarm call structure is under genetic control (McCowan and Hooper, 2002). Meerkats (*S. suricatta*) produce individually distinct alarm calls, but surprisingly in playback experiments, receivers failed to distinguish between different callers (Schibler and Manser, 2007). In this species, attending to individual differences may be irrelevant because unreliable callers are uncommon, and predation pressure is high.

Somewhat different results are obtained in primates. In putty-nosed monkeys, pyow (but not hack) alarm calls contain individually distinct acoustic features (Price et al., 2009). In playback experiments, females did not respond to the pyow-hack call sequences, indicating group travel, if they were produced by an unfamiliar male (Arnold and Zuberbühler, 2008), suggesting that this was because they attended to the acoustic features of the pyows. Individual differences in alarm calls have further been reported from baboons (Fischer et al., 2002), Thomas langurs (Wich et al., 2003), or cotton-top tamarins (Sproul et al., 2006).

D. Population Differences

Geographic variation in vocal behavior has been described in a wide range of species, but not normally in alarm calls. In golden-mantled ground squirrels (*Spermophilus laterialis* and *Spermophilus saturatus*), alarm calls to predatory wolves varied geographically, but this was not just due to genetic differences as changes were also observed between years (Eiler and Banack, 2004). Alarm calls of Gunnison's prairie dogs (*C. gunnisoni*) to humans differed between populations, with no differences between neighboring colonies (Slobodchikoff et al., 1998), which suggested that habitat differences could account for some of the effects (Perla and Slobodchikoff, 2002).

E. SEQUENTIAL ORGANIZATION

When responding to predators, many species respond with sequences of calls, and sometimes these calling bouts contain acoustically different call types. In fowls (*G. gallus*), males respond to raptors with distinctive aerial alarm calls, but there are significant changes throughout a sequence (Bayly and Evans, 2003). In Arabian babblers (*Turdoides squamiceps*), the first call is always a short, metallic-sounding ''tzwick.'' In response to cats, babblers continue to use ''tzwicks,'' but switch to long trills in response to owls (Naguib et al., 1999). Black-capped chickadees (*Poecile atricapilla*) produce significantly more chick-a-dee calls to near than distant predators, while the syllable composition also differed between the two conditions (Baker and Becker, 2002). In Carolina chickadees (*Poecile carolinensis*), the average number of note types and categories of note composition in a calling sequence was associated with the proximity of the signaler to the ground, the signaler's flight behavior, and the presence of an avian predator (Freeberg, 2008).

Richardson's ground squirrels (*Spermophilus richardsonii*) produce call sequences that consist of acoustically variable syllables. Sequences begin either with chirps or with a whistle followed by chucks. The production of chucks is related to the proximity to the disturbance and they increase vigilance in recipients (Sloan et al., 2005). Playback experiments showed that altering syllable order affected receiver responses, with the first syllable triggering strong responses regardless of their position within the (artificial) sequence (Swan and Hare, 2008a,b).

In primates, evidence for sequential signaling comes from observational work on Capuchin monkeys (*Cebus olivaceus*) (Robinson, 1984). A fraction of calls were given in sequences although it was not possible to link any of them with specific events. In Campbell's monkeys, males produce sequential signals to discriminate between different types of disturbances. One alarm call type is mainly given to crowned eagles, while another type is mainly given to leopards (Zuberbühler, 2001). If the disturbance is nonimminent, for example, if the caller heard distant alarm calls by other monkeys or if a large branch fell to the ground somewhere in the vicinity, the males reliably introduce loud calls by a pair of low-resounding ''booms,'' followed by a 30 s period of silence, before they produced their loud calls. Playback experiments demonstrated that artificially adding booms to a loud call sequence altered the meaning of the calls for other monkeys. Nearby Diana monkeys largely ignored boom-introduced predator alarms by Campbell's monkeys, despite the fact that they normally responded very strongly if the same calls were played back without the booms (Zuberbühler, 2002a,b). Meaningful call combinations have also been found in Nigerian putty-nosed monkeys. Here, adult males produce two alarm call types to predators, ''pyows'' and ''hacks.'' ''Hacks'' are reliably given to crowned eagles, ''pyows'' are given to leopards, although the match between

predator category and call type is far from perfect (Arnold and Zuberbühler, 2006a), in contrast to other primates' alarm call system such as Diana or vervet monkeys (Seyfarth et al., 1980; Zuberbühler et al., 1997). One other surprising finding was that males often combined the two call types in context-specific ways (Arnold et al., 2008). One combination, some "pyows" followed by some "hacks," was highly specific, in the sense that it is a reliably predicted group movement both in predation and nonpredation situations (Arnold and Zuberbühler, 2006b). Subsequent playback experiments confirmed that it was the syntax of this call sequence, not the acoustic features of the individual components, which carried the crucial information for other group members (Arnold and Zuberbühler, 2008; Fig. 3). Black-and-white colobus monkeys possess an alarm call system that relies on the structural organization of call units, rather than just the acoustic features of individual calls, but this system differs from the ones discussed so far. Across sub-Saharan Africa, black-and-white colobus monkeys produce two basic call types, snorts and acoustically variable roars. In some areas, these calls are given before dawn, usually as part of a chorusing event involving many groups. However, the monkeys use the same basic calls also in response to predators. Field experiments have demonstrated that the syntax of these sequences is largely dependent on the external event, that is, whether callers respond to a neighbor's dawn calls or to the presence of a leopard or eagle (Schel et al., 2009). Similar to the Campbell's monkey calls, it is the sequential information that carries the bulk of the message to receivers (Candiotti et al., in preparation).

Fieldwork with free-ranging lar gibbons produced some evidence that call sequences in apes can also carry meaning. Using predator models, it could be demonstrated that both members of a pair readily produced songs in response to terrestrial predators, such as clouded leopards or tigers. These songs consisted of the same basic units as the duet songs, which are produced regularly in the morning, but the song units were arranged in different ways. Although the relevant playback experiments have yet to be carried out, some natural observations indicated that neighboring individuals (often close relatives of the callers) seemed to understand these syntactic nuances, because they responded with their own matching song type (Clarke et al., 2006).

IV. THE COGNITIVE BASES OF ALARM CALLS

A. ONTOGENY OF COMPETENCE

1. Signalers

An interesting question is whether animals have an experience-independent ability to identify their predators (Blumstein et al., 2008). In meerkats, captive-born individuals produce all alarm calls documented in the wild and
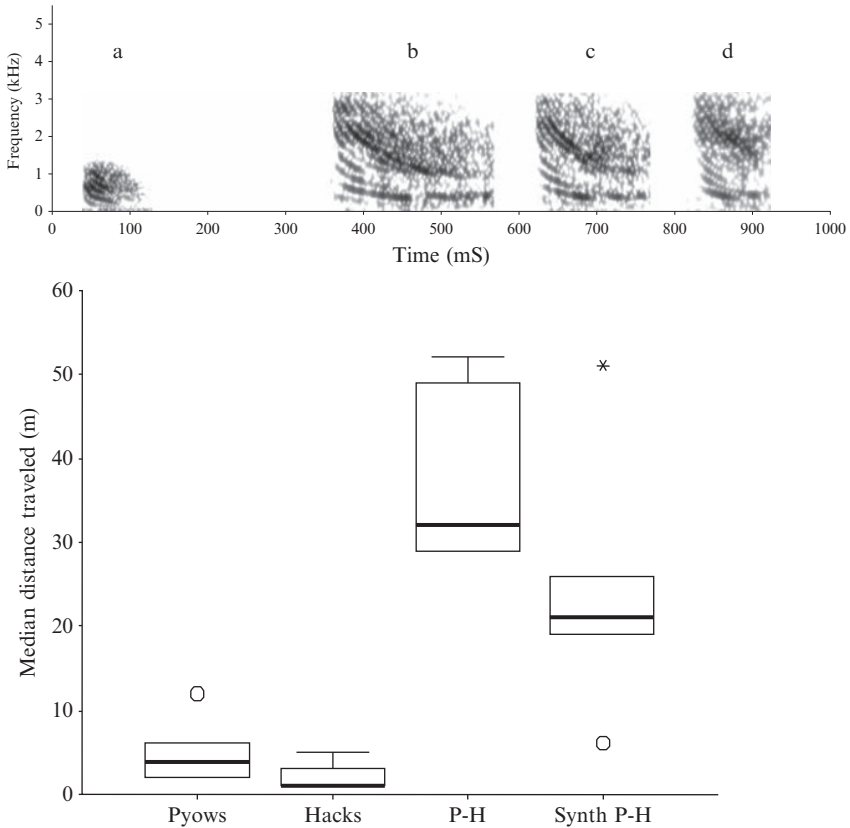
Fig. 3. Putty-nosed monkeys combine two of their loud alarm calls in different sequences in context-specific ways. Responses to crowned eagles typically consist of series of hacks and responses to leopards usually consist of series of pyows, and the two call sequences cause different responses in the group's females. If in addition the calling male is about to leave the area he combines hacks and pyows into a pyow-hack sequence, which triggers progression in listeners (Arnold and Zuberbühler, 2008). (a) hack, (b-d) pyows.

do so in similar contexts. In this species, predator recognition is strongly based on odors, which seems to be largely innate (Hollen and Manser, 2007b). Interactions with a predator, therefore, are not necessary for correct alarm-call usage in these animals. Compared to adults, however, young meerkats were less likely to give alarm calls overall, and more likely to do so to nonthreatening species, suggesting that some learning is necessary (Hollen et al., 2008). Focusing on ontogenetic patterns, one study found that the acoustic features linked to the urgency of the situation underwent developmental modification before the acoustic features linked with predator type (Hollen and Manser, 2007a).

Not much is known about how monkeys learn to use their alarm call repertoire (Janik and Slater, 2000). One core question is how a relationship between a particular alarm call and a corresponding external event is formed. Some observational data are available from free-ranging vervet monkeys. These monkeys come in contact with over 150 species of birds and mammals, and only a small proportion of them are posing a threat to them (Seyfarth and Cheney, 1997). Infant vervet monkeys do not apply their alarm calls randomly, however. Instead, they give eagle alarm calls only to birds and other objects in the air, but never to animals on the ground. Similarly, they give leopard alarm calls to a variety of species on the ground, most of which do not pose any danger to them, but then they learn to focus call usage to the relevant predator classes (Seyfarth and Cheney, 1997). Some studies have compared the alarm calling behavior of populations in which a particular predator was present or absent (e.g., Gil-da-Costa et al., 2003). In a recent one, the alarm calling response to leopards was compared between two populations of Guereza colobus monkeys in Uganda that differed in terms of their histories of leopard predation. Despite the fact that leopards had been locally extinct in one region for decades, colobus groups still responded to leopard models in largely the same way as groups from a neighboring region where leopards were common (Schel and Zuberbühler, in press). In a study on Diana monkeys, experience with leopards determined alarm calling, not in terms of the acoustic structure of alarm calls, but in how calls were produced in sequences (Stephan and Zuberbühler, 2008; Fig. 4).

A largely unexplored area of research is how social learning influences vocal behavior. In spectral tarsiers (*Tarsius spectrum*) on Sulawesi, Indonesia, infants gave alarm calls in response to all potential predator types. Infants and mothers produced a twittering alarm call to raptor models and repeated harsh loud alarm calls to snake models. Infants sometimes gave incorrect alarm calls and then, interestingly, mothers produced alarm calls at lower rates than if the infants gave correct alarm calls (Gursky, 2003).

2. Receivers

At the receiver side, the ontogenetic processes involved in acquiring adult competence are somewhat better understood (Janik and Slater, 2000). Learning appears to play a powerful role in most groups of animals. In white-browed scrubwrens (*Sericornis frontalis*), for example, fledglings respond to their parents' aerial alarm calls whereas nestlings fail to do so (Magrath et al., 2006). In contrast, nestlings responded to ground alarm calls from early on, while the response to aerial alarm calls emerged only toward the end of the nestling stage (Platzen and Magrath, 2005). In another study, nestlings did not show evidence of recognizing alarm
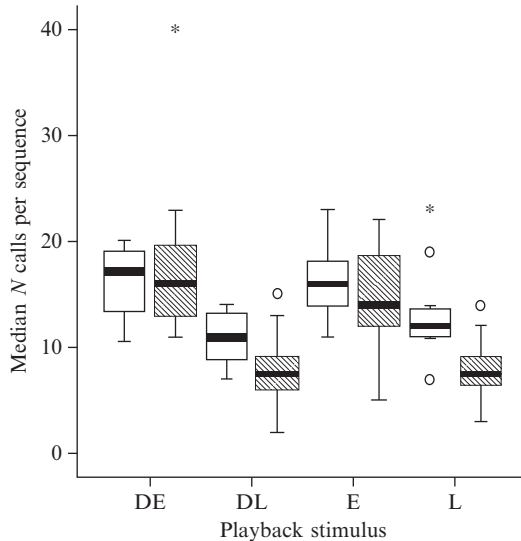
FIG. 4. Diana monkeys on Tiwai Island are not familiar with leopards but are exposed to crowned eagles, while Tai monkeys are hunted by both predators. Playback experiments have revealed differences in how callers of the two populations structure their calling behavior. Box plots indicate the median numbers of calls per sequence in Taï (hatched boxes) and Tiwai (open boxes). Diana monkeys to playbacks of eagle shrieks (E), leopard growls (L), male Diana alarm calls to eagles (DE), and male Diana alarm calls to leopards (DL). Box plots show median values, quartiles, range, and outliers. Circles and asterisks show extreme values, asterisks being more extreme (Stephan and Zuberbühler, 2008).

calls of parents until very late (Maurer et al., 2003). Yellow warblers (*Dendroica petechia*) produce ''seet'' calls to brood-parasitic brown-headed cowbirds (*Molothrus ater*) and ''chip'' calls toward mammalian and avian nest predators. Nestlings remained inactive for longer periods to chip than to seet alarm calls, suggesting that only chip calls were recognized as a source of danger (Gill and Sealy, 2003).

In laboratory rats, individuals produce ultrasonic alarm calls in the 22 kHz range, and naïve individuals are predisposed to associate these calls with aversive stimuli, which is subsequently difficult to extinguish (Endres et al., 2007). In Belding's ground squirrels (*S. beldingi*), responses to alarm calls are similar in free-living and captive juveniles, but captive individuals show more exaggerated and prolonged responses (Mateo and Holmes, 1999). In meerkats, infants initially respond to alarm calls indiscriminately by running to nearby adults. The probability of producing adult-like responses increases with age, with exposure to adult models explaining some of the observed variance in competence (Hollen and

Manser, 2006). Squirrel monkeys (*Saimiri sciureus*) appear to have an innate predisposition in order to respond to alarm peeps but require experience to associate them with the appropriate type of predatory threat (Herzog and Hopf, 1984). Infants, juveniles, and subadults responded more frequently to alarm peeps than adults, and responses changed with age. Adults responded more frequently to the alarm peeps of other adult than infants (McCowan et al., 2001).

Research on interspecies communication is another fruitful area to study how individuals come to understand alarm signals. For example, birds that migrate together respond to each other's alarm calls, but some of these calls are not universally recognized by other birds (Nocera et al., 2008). In Verreaux's sifakas (*Propithecus verreauxi*) of Madagascar, infants from about 6 months no longer run toward an adult but perform predator-specific escape responses to alarm calls of conspecifics and those of other species (Fichtel, 2008). In another study, captive and wild populations of sifakas produced the same acoustically distinct alarm calls to raptors and ground predators, but differences were found in usage and comprehension (Fichtel and van Schaik, 2006).

B. WHAT INFORMATION IS CONVEYED?

The alarm calling has been related to physiological stress responses, according to a study on yellow-bellied marmots (*M. flaviventris*) (Blumstein et al., 2006). What specific aspects of a predator encounter callers respond to (e.g., degree of threat or predator category), however, is a contentious issue.

1. *Predator-Specific Alarm Calls*

The classic study for predator-specific alarm calls was conducted on East African vervet monkeys. In this primate, individuals produce acoustically different alarm calls to at least five different types of predator: large terrestrial carnivores, eagles, snakes, baboons, and unfamiliar humans (Struhsaker, 1967). Some of these calls elicit antipredator responses in other monkeys 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). Similar findings have been reported from other monkey species. In Diana monkeys, 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 (Zuberbühler et al., 1997). Free-ranging saddleback and moustached tamarins (*Saguinus fuscicollis* and *Saguinus mystax*) in Peru each produce acoustically distinct alarm calls to aerial and

terrestrial predators. Playbacks of conspecific and heterospecific alarm calls showed that receivers responded by looking into the direction from where the predator was most likely to be expected. The acoustic features of the calls, in other words, provided sufficient information about the predator type or the appropriate reaction (Kirchhof and Hammerschmidt, 2006). In a study on redfronted lemurs and white sifakas (*P. verreauxi*), gaze and escape directions corresponded to the hunting strategies of the two predator classes, suggesting that the corresponding vocalizations were categorized correctly. The terrestrial alarm call was less specific than the aerial alarm calls because it was also given to a range of other disturbances (Fichtel and Kappeler, 2002).

Birds have long been known to possess acoustically distinct alarm calls, typically in response to raptors and terrestrial predators (Curio, 1969). In pale-winged trumpeters (*Psophia leucoptera*), for example, adults produce a range of vocalizations, including alarm calls to raptors and terrestrial predator, but the terrestrial alarm call is also used for conspecific intruders. Receivers respond to these calls as to the corresponding event, suggesting that they denote meaning to the calls (Seddon et al., 2002). In yellow warblers (*D. petechia*), parents produce a ''seet'' alarm calls in response to brood-parasitic brown-headed cowbirds (*M. ater*) and chip alarm calls to nest predators and other intruders, but not cowbirds. In a population allopatric with cowbirds, seet calls were rarely produced in response to cowbird or avian nest predator models and never to seet playbacks, suggesting that the seet calls can take on a specific meaning (Gill and Sealy, 2004). In black-capped chickadees (*P. atricapilla*), the acoustic features of predator calls vary with the size of the predator, and receivers appear to understand the implications of the acoustic differences (Templeton et al., 2005).

In great gerbils, *R. opinus*, individuals produce acoustically distinct alarm calls to dogs, humans, and monitor lizards, with age, sex, and other individual factors explaining a further proportion of the acoustic variance (Randall et al., 2005). In Gunnison's prairie dogs (*C. gunnisoni*), as discussed earlier, individuals respond to live predators in a relatively specific ways, which are identical to their responses of the corresponding alarm calls (Kiriazis and Slobodchikoff, 2006). In addition, the acoustic structure of alarm calls to terrestrial predators varies as a function of stimulus silhouette (Ackers and Slobodchikoff, 1999), a finding also reported from black-tailed prairie dogs (*Cynomys ludovicianus*) (Frederiksen and Slobodchikoff, 2007).

2. Urgency-Related Alarm Calls

Alarm calls have been interpreted as threat- or urgency-related in a number of species. Empirically, this is mostly based on the finding that some structural aspect of the alarm signal changes with the distance

between the caller and the predator. For example, reed warblers (*Acroce-phalus scirpaceus*) give the same alarm calls to common cuckoos (*Cuculus canorus*, a nest parasite), and sparrow hacks (*Accipiter nisus*, a predator), but call usage varies with distance from the nest (Welbergen and Davies, 2008). In great gerbils (*R. opimus*), three different alarm vocalizations can be discriminated but these calls are related to the distance of the predator and hence signaled urgency, and receiver responses mirrored this distance-related specificity (Randall and Rogovin, 2002). In three species of marmots, Olympic (*Marmota olympus*), hoary (*Marmota caligata*), and Vancouver Island marmots (*Marmota vancouverensis*), call structure also varied as a function of distance to and type of the disturbance. However, callers often changed calls within a calling bout and there were no call-specific responses observed in receivers (Blumstein, 1999). In primates, some studies have interpreted acoustic variables of alarm calls to vary with threat-related variables. In bonnet macaques (*Macaca radiata*), for instance, callers were exposed to models of leopards and pythons, but differences in alarm call structure were explained with the level of perceived threat, not predator type (Coss et al., 2007). In domestic chickens (*G. gallus*), 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, some species of squirrels produce acoustically distinct alarm calls, but they too do not appear to respond to the predator category *per se*, but to the relative distance and threat imposed by the predator (Leger et al., 1980).

Urgency is often expressed in the temporal features of an alarm call sequence. In Brants' whistling rat (*Parotomys branisii*), the duration of alarm calls is related to the threat of the situation, although this parameter did not affect receiver responses (Le Roux et al., 2001b). Richardson's ground squirrels (*S. richardsonii*) produce repetitive calls to predator models and call rates are inversely correlated with the distance between the caller and the disturbance. Receivers respond with increased vigilance as call rate goes up (Warkentin et al., 2001). Richardson's ground squirrels also produce alarm calls in the ultrasonic 48 kHz region; while the ratio of ultrasonic to audible 8 kHz alarm calls increases with increasing distance from the disturbance. Ultrasonic calls do not travel well in space, making them more suitable for close-range communication (Wilson and Hare, 2006).

In a playback study, the effects of call length and variation in intersyllable latency in repetitive alarm calls on the behavior of call recipients were examined and results showed that the length of calls had no significant effect but recipients showed greater vigilance after the playback of monotonous calls than after variable calls (Sloan and Hare, 2004).

The urgency of the situation may also become apparent for a receiver by focusing on the number of individuals producing alarm calls. In Richardson's ground squirrels, repetitive alarm calls of two juvenile callers, played from separate speakers, induced greater vigilance in adults, but not other juveniles than the calls of one juvenile caller only (Sloan and Hare, 2008).

3. Combined Messages

In some species, both predator type and urgency-related features appear to be encoded in the same utterance. For example, white-browed scrubwren (*S. frontalis*) produce a specific aerial trill alarm call, which consists of more elements and higher pitch if the predator is close, something that is recognized by listeners (Leavesley and Magrath, 2005). Meerkats produce acoustically distinct alarm calls to different predator types, but their call structure also varies depending on the level of urgency (Manser, 2001). In playback experiments, receivers responded differently to alarm calls given to snakes, and to aerial or terrestrial predators. Within the aerial alarm calls, however, responses differed depending on the level of urgency encoded in the calls (Manser et al., 2001), suggesting that some of their alarm calls simultaneously encode both predator type and the signaler's perception of urgency (Manser et al., 2002).

In primates, the typical finding is that individuals produce acoustically distinct calls to different types of disturbances, but other factors may also be at work in some species. In squirrel monkey (*S. sciureus*), responses to artificially modified mobbing calls increased with call frequency and amplitude (Fichtel and Hammerschmidt, 2003). Redfronted lemurs (*Eulemur fulvus*) give specific alarm calls only toward raptors, and another alarm call type to terrestrial predators, such as dogs, and during intergroup encounters, which differs in frequency depending on the two contexts. Altering the frequency or amplitude of the calls generated differences in the orienting response of receivers, demonstrating that individuals attended to these features (Fichtel and Hammerschmidt, 2002).

A difficult problem, rarely addressed in field studies, is to separate the effects of predator type from the threat exerted by the predator. In Diana monkeys, callers responded to predator type, while distance (and hence threat) had only minor effects within the different alarm calls

(Zuberbühler, 2000b; Fig. 5). Similar findings have also been reported from Campbell's monkeys, *Cercopithecus campbelli* (Zuberbühler, 2003), suggesting that nonhuman primates generally label the biological class of a predator, regardless of momentary discrepancies in degrees of threat.

4. *The Evolution of Urgency and Predator-Related Signaling*

What exactly has lead to the evolution of predator-related signaling has caused a lively debate. One idea is that the distinction between urgency and predator-related alarm calling has to do with the caller's habitat. For species inhabiting three-dimensional habitats, it may be more adaptive to produce signals that classify predator types, whereas those living in two-dimensional environments may benefit better from signaling the risk associated with a disturbance, especially if individuals rely on only one basic escape strategy. The hypothesis was addressed with a study on Brants' whistling rat (*P. brantsii*). Individuals were exposed to three predator types, human, raptor, and snake. Calls did not differ between predator types, but call duration varied positively with distance (Le Roux et al., 2001a). This hypothesis was challenged by a set of studies on Gunnison's prairie dogs. Here, individuals produced alarm calls to red-tailed hawks (*Buteo jamaicensis*), domestic dogs (*Canis familaris*), and coyotes (*Canis latrans*). Although the alarm calls produced to these predators were composed of the same structures, their relative distribution was predator-dependent (Slobodchikoff and Placer, 2006). Responses to the different alarm calls were compared with responses to the corresponding predators, and this did not reveal any differences (Kiriazis and Slobodchikoff, 2006). The habitat hypothesis also failed to explain the alarm calling behavior in suricates, despite the fact that they only have one escape response, to retreat to bolt holes (Manser et al., 2001).

Another hypothesis is that the range of predators, and the type of adaptive antipredator responses, may be more important than the habitat, as demonstrated in various monkey species. This idea has received support from game-theoretic modeling. It was found that when the number of alarm signals is limited, the evolutionary trend is to group together the situations, which require similar responses (Donaldson et al., 2007).

C. EAVESDROPPING

Eavesdropping is usually defined as the use of signal information by individuals other than the primary target. Who exactly the target of signaling event is can be difficult to decide, unless other species are involved. Eavesdropping, thus, is typically reported from studies on heterospecific interactions (e.g., Templeton and Greene, 2007). A general assumption is
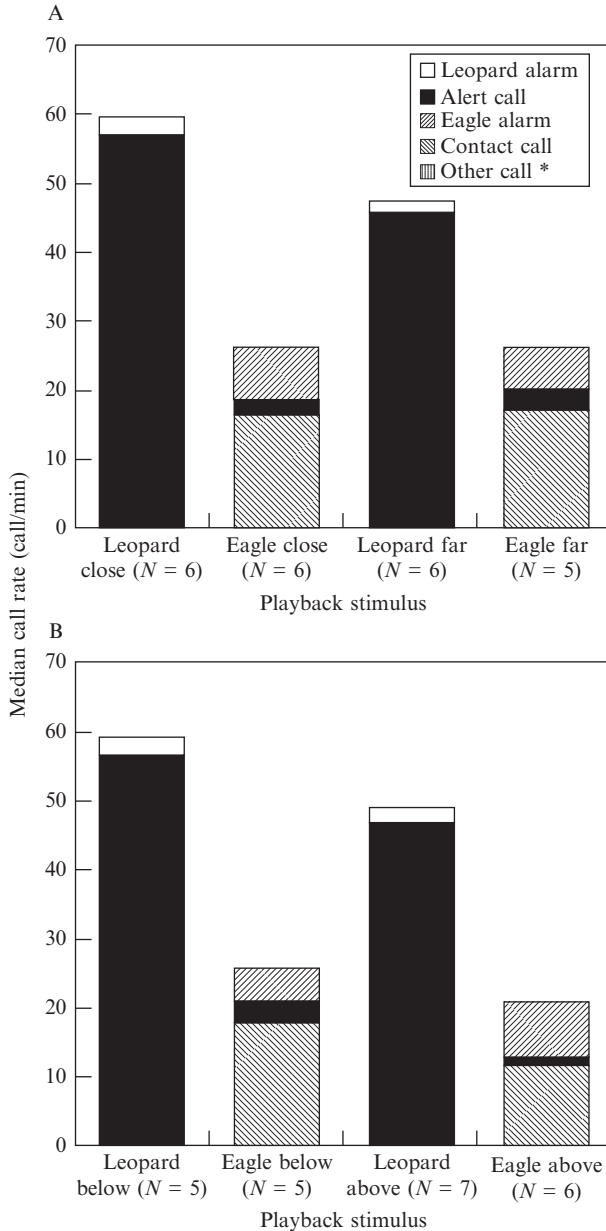
Fig. 5. The acoustic structure of Diana monkey alarm calls is mainly determined by the predator type present, while distance and direction of attack only have minor effects. Box plots depict female vocal behavior in response to leopards and crowned eagles as a function of (A) predator distance and (B) elevation. Bars represent the median number of calls produced in the first minute after onset of the playback stimulus (Zuberbühler, 2000d).

that individuals will benefit most from responding to the alarm signals of another species if they have similar predators, as the case, for instance, in mixed species bird flocks or polyspecific monkey groups.

In the Sri Lankan rainforest, the aerial alarm calls of Orange-billed Babbler (*Turdoides rufescens*) and Greater Racket-tailed Drongos (*D. paradiseus*) cause babblers to move quickly away from the playback speaker after hearing their own species' or drongo alarm calls, but drongos show no difference in response to any treatment (Goodale and Kotagama, 2008). Drongos are known to mimic a variety of sounds associated with danger, including the calls of alarm calls of other species in the forest (Goodale et al., 2008). It is possible, therefore, that they are better than other birds in attending to subtle acoustic differences, and thus recognized the playback stimuli as artificial. In another experiment, the aerial alarm calls of white-browed scrubwrens (*S. frontalis*) and superb fairy-wrens (*Malurus cyaneus*) were used as playback stimuli. The two species co-occur in mixed species flocks during the nonbreeding season, and produce acoustically similar aerial alarm calls. Results showed that both species responded to each other's alarm calls with appropriate antipredator behavior (Magrath et al., 2007). Subsequent research has shown, however, that the ability to eavesdrop on other species' alarm calls is entirely based on learning, even when the two species produce acoustically similar alarm calls to the same predator. Fairy-wrens responded to playback of the acoustically similar scrubwren aerial alarm calls only if the two species lived in sympatry. Moreover, fairy-wrens responded to aerial alarm calls of a honeyeater (*Phylidonyris novaehollandiae*), despite the fact that these calls were acoustically very different. In conclusion, in these birds call similarity is neither sufficient nor necessary for interspecific eavesdropping (Magrath et al., 2009). The idea of learning is further supported by the responses to alarm calls of black-capped chickadees (*Poecile atricapillus*) by resident and migrant birds in Belize. Familiarity with the chickadees alarm calling behavior was a prerequisite for proper responses, even if the calls were broadcast out of context at a novel location (Nocera et al., 2008).

It is possible that much of the observed eavesdropping is the result of simple associative learning. For example, in adult golden-mantled ground squirrels (*Spermophilus lateralis*) it was possible to associate a novel sound with the appearance of a predator, using a classical conditioning protocol. After repeated trials, individuals that experienced the tone paired with the hawk responded with antipredator behavior that was indistinguishable from responses to natural, conspecific alarm calls (Shriner, 1999). It is, therefore, not surprising perhaps that eavesdropping is by no means restricted to operating within particular groups of animals. For example, red squirrels (*Sciurus vulgaris*) and sympatric Eurasian jays (*Garrulus glandarius*) share

the same predators, and red squirrels respond with antipredator behavior to playbacks of jay alarm calls, but not to control sounds (Randler, 2006). Similarly, eastern chipmunks respond to the alarm calls of eastern tufted titmice (Schmidt et al., 2008).

Although alarm calling is a typical feature of sociality, the ability to eavesdrop is not. In Gunther's dik-diks (*Madoqua guentheri*), a monogamous, territorial, and nonsocial miniature antelope with a simple vocal repertoire, individuals responded to playback of white-bellied go-away bird (*Corythaixoides leucogaster*) alarm calls by running to cover, decreasing their foraging activity, increasing their rate of head turning, and increasing their period of vigilance compared to control stimuli (Lea et al., 2008). A similar pattern emerged in a study on highly territorial zenaida doves (*Zenaida aurita*) that have no vocal alarm signals of their own. They often associate with Carib grackles (*Quiscalus lugubris*), which produce conspicuous alarm calls. Zenaida doves suppressed foraging, remained alert, and tail-flicked in response to grackle alarm calls (Griffin et al., 2005). In another study, it was found that a nonvocal reptile, the Galapagos marine iguana (*Amblyrhynchus cristatus*) eavesdrops on the alarm call of the Galapagos mockingbird (*Nesomimus parvulus*) and responds with antipredator behavior despite the fact that iguanas do not produce any acoustic signals themselves (Vitousek et al., 2007).

Primates are also highly attentive to the alarm calls of other species. Vervet monkeys (*C. aethiops*), for example, respond to superb starlings' (*Spreo superbus*) terrestrial and raptor alarm calls, and young vervet monkeys need several months to learn to recognize starling alarm calls (Hauser, 1988). 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 (*P. verreauxi*, Oda and Masataka, 1996). The various monkey species living in the West African forests 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). This ability, however, is not a uniquely primate capacity. Yellow-casqued and black-casqued hornbills readily distinguish between Diana monkey eagle and leopard alarm calls as well (Rainey et al., 2004a,b; Fig. 6).

What exactly receivers are able to extract from heterospecific alarm calls is a more demanding problem. Banded mongooses (*Mungos mungo*) respond to alarm calls of several sympatric plover species (*Vanellus* spp.). Plover alarms mainly encode the level of urgency experienced by the caller, but there was no evidence that the mongooses differentiated between calls given in high and low urgency situations (Muller and Manser, 2008).
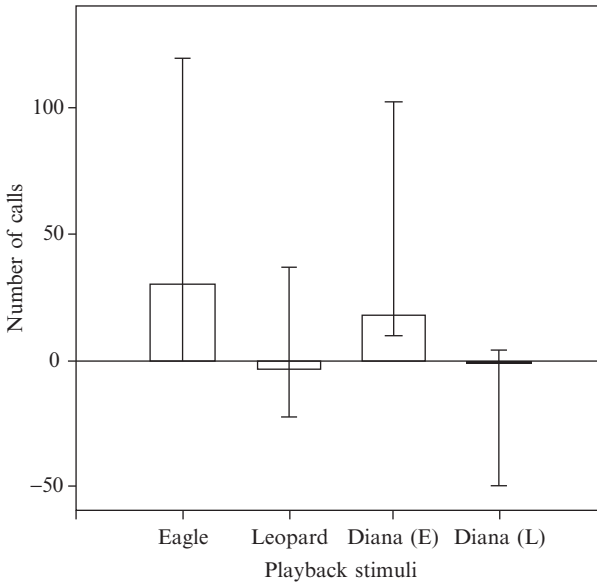
Fig. 6. Hornbills respond to Diana monkey alarm calls, provided they signal the presence of a crowned eagle, a predator shared by both species (Rainey et al., 2004).

D. Cognition of Comprehension

What kinds of mental representations do individuals activate when hearing another individual's alarm calls? A cognitively simple model suggests that responses to alarm calls are based on superficial processing of the calls' physical features. Call comprehension, in this view, does not require any specialist cognitive equipment but can be handled by general associative learning mechanisms (Tomasello, 2008). 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 (Yates and Tule, 1979). Under this model, alarm calls are processed by signalers accessing the meanings potentially associated with the calls, that is, the mental representation associated with the calls.

The notion that animals possess mental concepts, akin to ours, is not universally accepted, despite decades of research (Herrnstein and Loveland, 1964). One parsimonious hypothesis is that animals simply learn to generalize across stimuli, rather than forming mental concepts. For example, an

individual may simply learn, over hundreds of exposures, to attend to the peripheral features common to a training set, rather than accessing the organizing principle. Using extensive conditioning paradigms can be problematic since the training experience itself can interfere with the mental concepts to be investigated. Evolutionary relevant mental concepts should reveal themselves unprompted and during natural acts of communication.

In one such study, Diana monkeys were exposed to typical vocalizations of their predators, crowned eagles or leopards, or the corresponding monkey alarm calls to them (Zuberbühler et al., 1999b). In each trial, the playback speaker was positioned in the vicinity of a Diana monkey group to play two stimuli, a prime and a probe, separated by 5 min of silence. Monkeys were primed with either a predator vocalization followed by the same predator vocalization (baseline condition) or alarm calls followed by the matching or nonmatching predator vocalization (test and control conditions). Results showed that the semantic content of the prime stimuli, not the acoustic features, explained the response patterns of the monkeys: Both eagle shrieks and leopard growls, two normally very powerful stimuli, lost their effectiveness in eliciting alarm calls in the test condition if subjects were primed first with the corresponding male alarm calls (Fig. 7).

In another experiment, the alarm calls of crested guinea fowls (*Guttera pucherani*), a gregarious ground-dwelling forest bird, to ground predators were investigated. When hearing these alarm calls, Diana monkeys respond as if a leopard were present, 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. For Diana monkeys, the best antipredator response to humans is to remain silent to avoid detection. In playback experiments, 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. After a 5-min period of silence, the same group was exposed to playbacks of guinea fowl alarm calls. 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 the type of predator most likely to have caused the birds' alarm calls (Zuberbühler, 2000c).

A similar problem exists when the monkeys are confronted with a nearby group of chimpanzees, a dangerous predator. Chimpanzees are occasionally attacked by leopards themselves (Zuberbühler and Jenny, 2002) and when this happens they give loud and conspicuous ''SOS'' screams (Goodall, 1986). When chimpanzee SOS screams were broadcast to different groups of Diana monkeys about half of all the groups switched from a
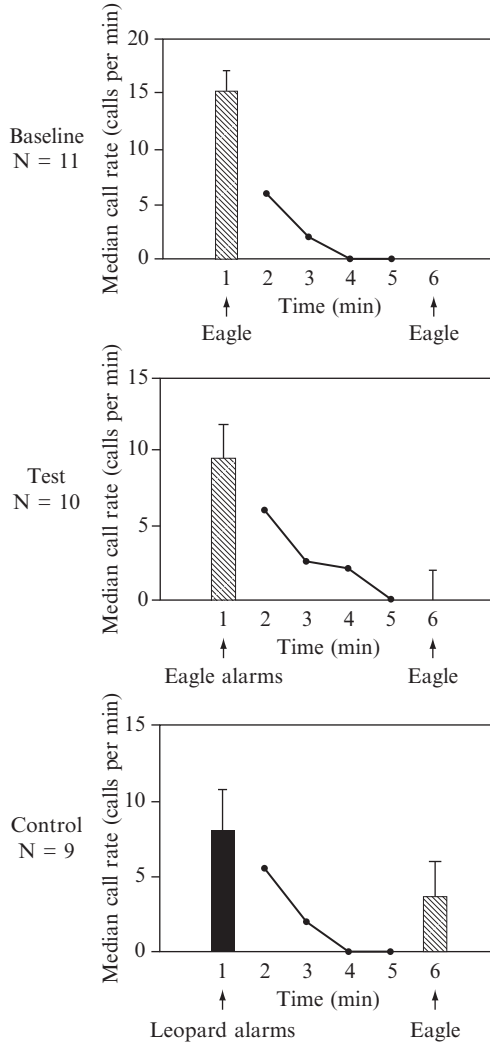
Fig. 7. Diana monkeys no longer respond to predator vocalizations if they have been warned by the corresponding alarm calls 5 min earlier (Zuberbühler et al., 1999a).

chimp-specific cryptic response to a leopard-specific conspicuous response, 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, 2000a).

Primates, in other words, process their own and other species' alarm calls on a conceptual-semantic rather than a perceptual-acoustic level. Whether this is true for other groups of animals is largely unknown.

E. AUDIENCE EFFECTS AND SOCIAL AWARENESS

Humans are generally aware of what their receivers understand and know about a situation, and human communication is heavily influenced by this factor. Meaning is shared between individuals. Human communication, hence, is more than the product of a mere stimulus-response contingency and involves signalers actively assessing receivers' mental states. Whether such social awareness is a uniquely human trait, or whether precursor abilities are also present in nonhuman animals is an open question. The literature on audience effects is relevant to this question. Audience effects have been observed widely, also in studies of alarm calling behavior. For example, the 22 kHz ultrasonic alarm calls of rats are dependent on conspecific presence and the caller's own assessment of safety (Litvin et al., 2007, but see Wohr and Schwarting, 2008). In yellow mongoose, individuals do not produce alarm calls when alone (Le Roux et al., 2008), and in Thomas langurs (*Presbytis thomasi*), males only emit alarm calls if they are with an audience (Wich and Sterck, 2003). Primates are also sensitive to the composition of their audience, particularly the presence of kin or mates (e.g., Cheney and Seyfarth, 1985), but an unresolved issue is whether callers can alter their calling behavior in systematic ways to affect the behavior of nearby individuals. In Thomas langurs, males continued to give alarm calls to a model predator until all other group members had given at least one alarm call themselves, as if the males were trying to keep track of which group members had and had not called (Wich and de Vries, 2006). Similarly, in a study on blue monkey alarm calls, adult mlaes were exposed to playbacks of a neighbor's eagle alarm calls. Results showed that male responded with significantly more eagle alarm calls if group members were close to the calling neighbor (and presumed eagle) compared to when they were further away, regardless of the calling male's own position (Papworth et al., 2008; Fig. 8). Nonhuman primates, and possibly other social mammals, it seems, exhibit a considerable amount of social awareness, although this ability has revealed itself more clearly in other contexts (Slocombe and Zuberbühler, 2007).
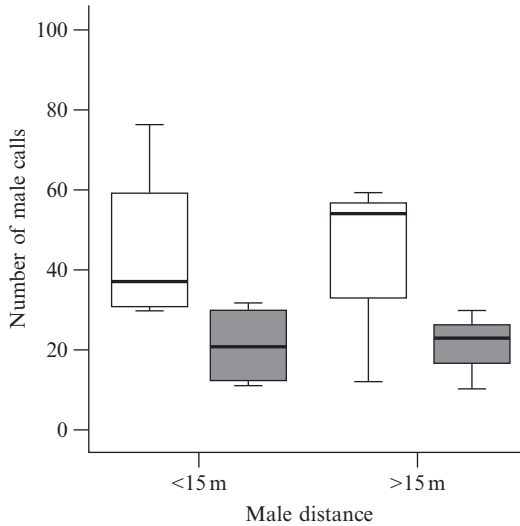
Fɪɢ. 8. Blue monkey males alarm call more if their group is close to a suspected eagle than if they are further away, regardless of their own position relative to the eagle. Box plots indicate male calling effort as a function of females' distance to the speaker. White boxes represent cases when the females were close (<15 m) and gray boxes when they were far from the stimulus (>15 m) (Papworth et al., 2008).

F. Deception

Deceptive use of alarm calling has originally been observed in mixed species flocks of birds (Evans et al., 2004; Munn, 1986). More recently, similar observations have been made in mixed species associations between gork-tailed drongos (*Dicrurus adsimilis*) and pied babblers (*Turdoides bicolor*). When foraging alone drongos remain silent in the face of terrestrial predators, but when foraging with babblers they consistently produce alarm calls. Babblers respond to drongo alarm calls by fleeing to cover, providing drongos with opportunities to steal babbler food items by occasionally giving false alarm calls (Ridley et al., 2007).

Within conspecific social groups, deceptive alarm calling is not common (Wheeler, 2009). One potential strategy to minimize the costs of deception is for receivers to assess signalers in terms of their reliability. In Richardson's ground squirrels, for example, receivers discriminate between reliable and unreliable signalers, which is revealed in terms of their responsiveness (Hare and Atkins, 2001), a finding also reported from vervet monkeys (Cheney and Seyfarth, 1988). In yellow-bellied

marmots (*M. flaviventris*), receivers assess the reliability of a caller based on which they decide how much time to allocate to vigilance (Blumstein et al., 2004).

V. Conceptual Issues

From a biological perspective, human language is just another example of the diverse ways by which mammals can communicate. Although human language is a complex and flexible behavior, it has shared most of its evolutionary past with other mammals. Only very recently, some hundred thousand years according to one theory (Enard et al., 2002), did humans begin to diverge significantly from the rest of the animal world in terms of their communication skills. This process coincided with other important changes, including a rapid increase in brain size, which makes it difficult to decide whether language is a specially adapted behavior, or the by-product of other transitions.

In language, speakers possess two main mechanisms to generate meaning. Either they can produce meaning through the semantic content encoded by an utterance or they generate nonencoded signals, such as pointing, changing the tone of voice, or gestures that are understood by both signaler and recipient (Tomasello, 2008). The compound meaning, therefore, is thus largely determined by the intentions with which speakers produce the utterance in a given context. Grice (1969) has argued that producing a meaningful utterance is thus equivalent with getting the recipient to recognize the intention of the utterance, a crucial feature of human communication. Whether or not the Grician approach has any heuristic value for studying animal communication is controversial, recent research on primate gestural communication has produced considerable progress in relation to the question of animal intentionality (Call and Tomasello, 2007).

A. Reference, Meaning, and Arousal

In the animal literature, referential communication is usually defined as "encoding information about environmental events" (external reference), which is distinguished from encoding individual attributes, such as species, size, or motivational state (internal reference) (Evans, 1997). Macedonia and Evans (1993) have produced a list of criteria required for demonstrating reference, in terms of production and perception criteria. First, a signal only qualifies as "referential" if its eliciting stimuli belong to a common category, for example, "leopard" or "ground predator." The "perception" criterion concerns the receivers. Here, the requirement is that a signal alone

is sufficient to trigger appropriate responses, regardless of context, something that is usually demonstrated with playback experiments. In Macedonia and Evans' view referential and context-dependent signaling are largely equivalent, provided the signaler reliably produces a particular signal in response to a specific event (=context), to which the receiver responds with an appropriate response.

The classic study for Macedonia and Evans-type animal referential communication is the well-known field experiment with free-ranging vervet monkeys (Seyfarth et al., 1980). These monkeys produce a range of alarm calls to different predator types, and listeners respond to these calls in ways that suggest they are linked to mental representations of the corresponding predator categories. A number of other studies have reported similar findings, although the evidence is usually stronger for the perception criterion. For example, chimpanzees produce rough grunts when encountering food, and the acoustic fine structure of these calls corresponds strongly with the perceived value of the food (Slocombe and Zuberbühler, 2005a,b). In playback experiments, it was possible to demonstrate that different rough grunt types conveyed information about food. In this study, the chimpanzees learned that two types of food, apple and bread, were consistently given at two different locations. When hearing the rough grunts given to bread, the subject was more likely to search at the bread location, than when hearing rough grunts to apples.

Although Macedonia and Evans' (1993) production and perception criteria are intuitively straightforward and widely used for referential communication in animal literature, a number of issues have emerged over the years. First, concerning the production criterion, if a signal is not stimulus specific, it must be explained in other terms, such as arousal, motivation, or response urgency. In long-term studies, instances of atypical call production usually accumulate, making it less and less likely that the production criterion can be fulfilled. For instance, putty-nosed monkeys typically give ''hacks'' to crowned eagles, but sometimes males produce the same calls to a falling branch. Of course, it is always possible that there are subtle differences between the hacks given to eagles and falling branches, which are meaningful to listeners, but it is equally possible that there are no unifying principles within the human conceptual system. The ''production'' criterion is anthropomorphic because it depends on finding a mental concept that encompasses all calling events, regardless of the psychological processes that take place in the animal. Concerning the perception criterion, one complication is that some primates are capable of invoking several meanings when hearing a particular call type, and subsequently use context to select among the semantic alternatives. As mentioned before, in the absence of further evidence Diana

monkeys respond to playbacks of guinea fowl alarm calls as if a leopard were present, but they alter their responses if the guinea fowls' alarm calls are caused by human presence (Zuberbühler, 2000c). Strictly speaking, these cases failed the perception criterion because listeners take the ongoing context into account if it is relevant and available.

It is also relevant that the term ''reference'' is used very differently in other literatures. Pointing, for instance, is widely considered to be referential, even though it fails Macedonia and Evans' (1993) production criterion. Pointing merely joins the attention of the signaler and recipient to an external referent, while the emerging meaning depends entirely on the knowledge and conventions shared by signaler and receiver (Tomasello, 2008). For example, by pointing to a snake a signaler can refer to its color, location, biological species, deadness, or request for it to be removed. The referent, in other words, has less to do with the specifics of the object, but with what assumptions signalers and receivers make about each other's intentions and world knowledge. These considerations take the quest for the mammalian origins of human language away from reference as conceptualized by Ogden and Richards (1923) referential triangle, toward an investigation of the biological roots of cooperative motivation and social awareness during the acts of communication.

B. The Evolution of Articulation

Alarm calls have also helped to clarify a number of problems concerning the basic biology of sound production in animals. Humans possess extraordinary motor control over their articulators, the physical basis of speech production, and alarm calls have been somewhat useful for understanding the origins of vocal flexibility. For mammals, the default assumption has long been that animal vocal tracts resemble a uniform tube with no relevant constrictions (Lieberman, 1968; Lieberman et al., 1969). In a uniform vocal tract, the resonance frequencies produced by the larynx will appear as evenly spaced multiples of the first resonance in the spectrogram. Frequency modulation, according to the uniform-tube idea is achieved at the level of the sound source, not due to vocal tract filtering (Riede and Zuberbühler, 2003a,b). Acoustic analyses have revealed that Diana monkey alarm calls contain two main and acoustically modulated formants, something that is not predicted under the uniform-tube hypothesis. Using lateral radiographs and postmortem dissection, Riede et al. (2005) determined the geometry of the Diana monkeys' vocal tract and identified a number of constrictions between vocal folds and lips (Fig. 9). Moreover, when responding to a leopard, forest guenons, such as Campbell's, Diana, or putty-nosed
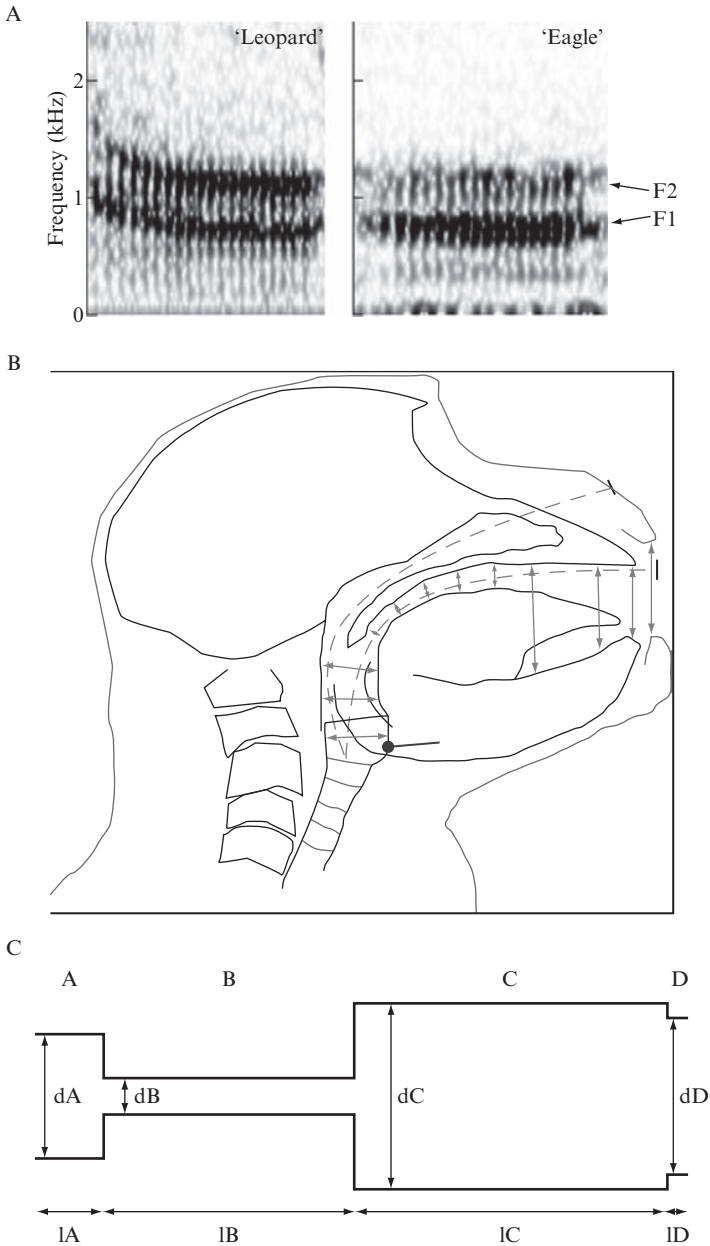
Fig. 9. Diana monkey vocal tracts contain constrictions that enable callers to produce formant frequencies, which can be modulated by mandible, lip, and larynx movements. (A) Male leopard and eagle alarm calls, (B) schematic representation of a Diana monkey vocal tract, and (C) three-tube model of a Diana monkey vocal tract capable of replicating the basic formant frequency patterns seen in natural calls (Riede et al., 2005).

monkeys, produce alarm calls with formants exhibiting a strong decrease in frequency. A study in Diana monkeys has shown that these modulations are not caused by changes at the level of the sound source, since very little variability in the fundamental frequency was observed. In sum, there is good evidence that nonhuman primates are able to constrict the pharynx and other regions of the vocal tract, during alarm call production, to achieve acoustic effects similar to those caused by tongue movements, the principle way of articulation in humans. Although sophisticated tongue movement can be observed in nonhuman primates, this is typically in the context of food transport. To what degree tongue movements play a role during vocal behavior in animals is still largely unknown.

VI.   Conclusions

The alarm calling is found in a large number of species, demonstrating its adaptive value in predation avoidance. There is evidence that alarm calls are or have been under the influence of all major selective forces, that is, individual, kin, and sexual selection. In nonhuman primates, alarm calling is the result of complex cognitive processes. This is interesting because predation is an ecological force often thought to have lead to rather basic behavioral patterns, not higher cognitive abilities. Instead, complex cognitive processes, such as inference making, causal understanding, semantic and syntactic processing, and rapid association learning have also been reported. Alarm call studies have also been useful for addressing problems of how animals generate meaning, although many argue that the resemblance with human language is only superficial, mainly because there is no good evidence that signalers try to communicate their intentions, something that characterizes human language. Instead, callers respond to external events that often have direct survival consequences, and receivers are left on their own to make sense of these contingencies provided by the caller.

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