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Variation among Mammalian Alarm Call Systems and the Problem of Meaning in Animal Signals

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Abstract

Understanding the information conveyed by animal signals requires studies of both production and perception. It is important to determine the relationship between signal morphology and the circumstances of production, the way signaller behavior varies with motivational state and the role of context in mediating responses to signals. Alarm calls are well-suited to research of this type because they are widespread in birds and mammals and typically evoke unambiguous responses. We review studies of alarm calling in primates and ground-dwelling sciurid rodents, concentrating especially on whether these signal systems may be viewed as 'functionally referential', that is, as conveying sufficient information about an event for receivers to select appropriate responses. Comparisons of the physical, behavioral and habitat characteristics of these species suggest that incompatibility of the escape responses required to avoid different classes of predators may have been an important factor in the evolution of functionally referential alarm calls.

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Introduction

Many species of mammals and birds emit vocal signals in response to predators. Often, one type of 'alarm' call is elicited by aerial predators whereas a different call type is evoked by terrestrial predators (e.g., MARLER 1957; KLUMP & CURIO 1983). The adaptive significance of structural differences between aerial and terrestrial predator alarm calls has been discussed extensively (e.g., MARLER 1955, 1957; CURIO 1978; BROWN 1982; KLUMP & CURIO 1983; KLUMP & SHALTER 1984). In this review, we focus instead on another aspect of alarm calling, namely what these vocalizations may mean to the animals using them. We assess signal

meaning from the standpoint of usage, or the relationship between signal structure and eliciting stimulus, as well as from the responses of conspecific receivers.

Calls evoked by predators have several properties that make them particularly well-suited for addressing questions about signal meaning. First, the eliciting stimulus often can be identified with confidence. Second, responses to alarm calls typically contrast conspicuously with behavior engaged in immediately prior to the call. Third, the differences in hunting style characteristic of different types of predator give rise to qualitatively different escape tactics. This variation in response type provides sensitive assays for playback experiments designed to explore the effects of alarm calls on conspecific receivers.

The study of vocal antipredator behavior also provides insights into the way nonhuman animals classify objects and events in the world around them (CHENEY & SEYFARTH 1990). Such work is thus logically complementary to laboratory studies of stimulus categorization (e.g., HERRNSTEIN et al. 1976; HERRNSTEIN 1984, 1985, 1991) and concept formation (e.g., LEA 1984; PEPPERBERG 1987a, b). We will argue, as well, that comparative studies of alarm call systems have the potential to identify the factors responsible for the observed variation in antipredator behavior.

Considerable controversy has arisen about the information conveyed by alarm calls (e.g., OWINGS & HENNESSY 1984; GOUZOULES et al. 1985; MARLER 1985; MARLER et al. 1992; SMITH 1991). One view suggests that, in at least some animals, these vocalizations serve as 'referential signals' that denote different classes of predators (e.g., SEYFARTH & CHENEY 1980; SEYFARTH et al. 1980a, b). To those unfamiliar with the details of this argument, it may seem self-evident that an animal emitting an alarm call in response to an approaching raptor is communicating something about aerial predators to conspecifics. This need not be the case. Such a vocalization could, for example, be a manifestation of the fear or panic associated with the threat of predation. Alternatively, it could reflect a desire for the dispersal or aggregation of group members.

Another possibility is that different types of alarm call do not denote predator classes, but rather, reflect a differential in 'response urgency' associated with the time constraints that different types of predators impose on their prey (e.g., ROBINSON 1980; OWINGS & HENNESSY 1984). Because the immediacy of threat posed by aerial and terrestrial predators may differ in a relatively consistent fashion, alarm calls could indicate how rapidly evasive behavior must be enacted. One call type might convey that time is available to gather information about predator type, location, and behavior before responding, whereas another call type could indicate that an immediate response is necessary.

This review has three principal components. We begin by discussing the issue of external reference in animal signals and develop a set of criteria for recognizing call systems with this property. We then review observations and experiments involving primates and ground-dwelling sciurid rodents (ground squirrels, marmots, and prairie dogs), the two taxa in which alarm calling has received the most study. Finally, we compare the antipredator behavior of these mammals with the goal of identifying selective forces that may underlie the evolution of particular types of call systems.

Many believe that a fundamental difference between language and the communication of animals lies in the ability of humans to communicate about objects and events in the external world (e.g., PREMACK 1975; LURIA 1982; BICKERTON 1990; reviewed by MARLER 1985). This property of language has been variously labelled 'semantic communication', 'representational signalling', 'symbolic representation', and 'referential signalling'. In contrast to language, animal signals are often seen as being limited to expression of motivation or 'affect'.

The term 'referent' has not been used consistently in analyses of animal communication. SMITH (1981, 1991: 214) suggested a relatively broad definition in which signals are considered to have multiple referents including "(a) several kinds of behavior (plus their probabilities and other variables), (b) physical characteristics of the signaller (e.g., its species and other identities), and (c) for some signals, external stimuli to which the signaller is responding." Other authors (e.g., SEYFARTH et al. 1980b; MARLER 1985; MARLER et al. 1992) favor a more restrictive definition, (approximating SMITH's third category) in which 'referent' is reserved for objects or events *external* to the signaller.

In this review, we adopt the latter usage because we are concentrating on the issue of whether animals communicate about phenomena external to themselves. However, we do not intend to imply that referential signals encode information *only* about the eliciting event. Abundant and compelling evidence indicates that information is also encoded about species, individual identity (e.g., CHENEY & SEYFARTH 1988, 1990), affective state (JÜRGENS 1979; SEYFARTH et al. 1980b) and, at least probabilistically, about the subsequent behavior of the signaller (EVANS et al. 1993).

Criteria for Demonstrating 'External Reference' in Animal Signals

Recent theoretical papers have assessed whether animal signals have external referents by applying criteria that require examination both of the signaller's behavior and of the effects of the signal on conspecifics (MARLER et al. 1992). That is, by examining both production and perception.

The 'production' criterion is that referential signals should exhibit a degree of stimulus specificity. This requires that all eliciting stimuli must belong to a common category, although the size of this category (and hence the absolute level of specificity) could vary considerably. Taking signals elicited by aerial predators as an example, alarm calls in one species might be evoked only by red-tailed hawks (a high degree of specificity), while another species might call in response to all raptors and also to other birds with similar silhouettes (much less specificity). Variation in specificity, however, is also a characteristic of human speech, which is the paradigmatic example of referential signalling. The expressions 'aircraft', 'commercial jet' and 'Boeing 747' form a continuum of increasing specificity (i.e., they correspond to successively smaller stimulus categories) but all are unambiguously referential.

One clear correlate of the 'production specificity' criterion is that referential signals should not occur at appreciable rates in inappropriate contexts. We therefore would not expect them to be produced in the absence of the putative referent. Similarly, the link between signal type and stimulus category should be

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maintained over the whole range of variation in the nonvocal behavior of the signaller. If the putative referent of a call is 'aerial predator', then airborne raptors should evoke the same call type whether the calling animal is simply orienting toward them or fleeing toward a refuge.

The 'perception' criterion requires that referential signals should be sufficient, in the absence of the eliciting stimulus and of other normally available cues, to allow receivers to select appropriate responses. We shall refer to this property as 'context independence'. This test establishes that cues provided by the nonvocal antipredator behavior of the signaller are not essential. It does not imply that such cues are not salient to conspecifics, or that they do not mediate the response to vocalizations when they are available. Indeed, contextual information probably often plays an important role, perhaps especially in species that have stable social groups (Marler et al. 1992; Evans et al. 1993).

We refer to signals that meet both the production criterion and the perception criterion as 'functionally referential' (Marler et al. 1992). This term acknowledges the power of philosophical arguments on the problem of 'meaning' (e.g., Grice 1957; Quine 1973; Dretske 1988) and the constraints inherent in the study of alien communication systems, including those of nonhuman animals and of pre-verbal human infants. For example, it is particularly difficult to determine whether animal signals should be thought of as denotative (i.e., as labels for stimulus categories) or imperative (i.e., as instructions describing appropriate responses) (e.g., Cheney & Seyfarth 1990, 1992; Baron-Cohen 1992).

Animal signals may be viewed as falling along a continuum. Those principally reflecting motivational state, such as the 'distress' and 'contentment' calls of precocial birds (Collias & Joos 1953; Abraham 1974), lie at one end. Those that reliably correspond to particular stimulus categories, and are relatively unaffected by affective response, lie at the other. The production and perception criteria for functional reference described above effectively define a threshold value on such a continuum (Marler et al. 1992).

Case Studies of Vocal Antipredator Communication

Vervet Monkeys: Alarm Calls as Referents for Different Predator Classes

The best-known example of alarm call usage in primates comes from work on the vervet monkey (e.g., Struhsaker 1967; Seyfarth et al. 1980a, b; Seyfarth & Cheney 1980, 1986, 1990; Cheney & Seyfarth 1981, 1985; Owren & Bernacki 1988; Owren 1990a, b). Tom Struhsaker (1967) first described the vervet alarm call system and demonstrated that different kinds of predators elicited different call types. Robert Seyfarth, Dorothy Cheney and Peter Marler then conducted a series of observational and experimental studies designed to determine whether vervet alarm calls referred to predators in the way that human words can denote objects and events.

Struhsaker (1967) had observed that when vervets on the ground detect a large carnivore nearby they produce 'leopard' alarms that cause conspecifics to run high up into trees. The 'eagle' alarm, given when dangerous raptors were

seen, elicited skyward scanning, descent from tree canopies and movement into the cover provided by dense thickets. Pythons and venomous snakes evoked 'snake' alarms that other vervets responded to by standing bipedally and scanning the ground around them. The reactions of other vervets to the alarm calls of a group member were thus well matched to the hunting tactics of each of the three types of predator. However, these observational data could not exclude the possibility that the apparent responses to calls might, in fact, have been mediated principally by other cues, such as those provided by the caller's nonvocal behavior (e.g., SMITH 1981, 1991). It therefore was crucial to design an experiment that isolated the information provided by alarm calls and excluded the contextual cues that normally would accompany call production.

Vervet alarm calls that had been recorded during natural encounters with predators were subsequently played back to the monkeys in the absence both of predators and of the caller. This technique eliminated all potential information about the eliciting stimulus other than that provided by call structure (SEYFARTH et al. 1980 a, b). The playback exemplars were selected to include calls from several different individuals and variation in acoustic properties thought to be influenced by motivational state, such as call duration and amplitude.

The overall pattern of vervet responses in these playback experiments revealed that they (a) looked upward, ran out of trees, and ran into cover more often in response to eagle than to leopard or snake alarm playbacks, (b) ran into trees more often in response to leopard than to eagle or snake alarm playbacks, and (c) stood bipedally and/or scanned the ground more often in response to snake than to eagle or leopard alarm playbacks (SEYFARTH et al. 1980b). Presentations of tape-recorded alarm calls were thus sufficient to elicit the pattern of antipredator behavior that was normally evoked by the predators themselves. The results of this playback experiment are consistent with the idea that different vervet alarm calls refer to different classes of predator (SEYFARTH et al. 1980b).

If vervet alarm calls are indeed referential then we might expect that the response evoked by playbacks would be mediated principally by the external referent of the call presented (i.e., by the environmental events normally associated with it), rather than simply by acoustic morphology, as in the case of more arbitrary stimuli (e.g., HULSE et al. 1990).

In a series of recent experiments, CHENEY & SEYFARTH employed a habituation/dishabituation technique to examine this issue directly (CHENEY & SEYFARTH 1988; SEYFARTH & CHENEY 1990). Subjects were first played one type of call to establish a baseline level of response. They then received eight presentations either of the same call type or of a different call type. During these habituation trials calls either were from the same individual as the baseline stimulus or from a different group member. Finally, the first stimulus was presented again (test) and baseline and test-trial response durations were compared.

In the first experiment (CHENEY & SEYFARTH 1988), playback exemplars consisted of eagle and leopard alarm calls and of three call types ('wrrs', 'grunts', and 'chutters') typically emitted during interactions with another vervet group. Eagle and leopard alarms clearly are elicited by different external stimuli (SEYFARTH et al. 1980b), whereas the intergroup-context calls have more similar

eliciting conditions. The subjects transferred habituation across wrrs, grunts, and chutters (i.e., responses on the test trial were significantly briefer than on the baseline trial), but only when the calls presented had all been recorded from the same individual. Subjects did not, however, transfer habituation between eagle and leopard alarms, regardless of the caller's identity (CHENEY & SEYFARTH 1988).

Acoustic analyses revealed reliable differences, in both spectral and temporal characteristics, between all of the call types compared (see CHENEY & SEYFARTH 1988; Table IV), suggesting that the transfer of habituation obtained in wrr and chutter playbacks was not attributable to an inability to discriminate the habituation and test exemplars. Subsequent laboratory experiments have demonstrated that vervets discriminate readily between their eagle and snake alarms (OWREN 1990a), which appear to be more similar acoustically than the eagle and leopard alarms used in the field habituation experiments. Vervets also appear to discriminate among various types of grunt (CHENEY & SEYFARTH 1982), even though the acoustic differences are subtle (SEYFARTH & CHENEY 1984). Taken together, this evidence supports CHENEY & SEYFARTH's (1988) proposal that acoustic differences among vervet call types are unlikely to explain the results obtained.

In a second experiment using the habituation/dishabituation technique (SEYFARTH & CHENEY 1990), vervets were presented with eagle and leopard alarms in combination with alarm calls of a sympatric bird, the superb starling (*Spreo superbus*), evoked by avian and by terrestrial predators. Starling 'raptor' alarms were elicited by several species of avian predator, including falcons, kestrels, goshawks and martial eagles. Though less specific than vervet eagle alarms, starling raptor alarms are sometimes associated with the approach of a vervet predator.

The vervets transferred habituation between playbacks of vervet eagle alarms and starling raptor alarms despite the qualitative differences between these two stimuli in acoustic structure. In contrast, habituation was not transferred between vervet leopard alarms and starling raptor alarms (SEYFARTH & CHENEY 1990).

These results suggest that the vervets' responses to starling alarm calls were based on the correlations between call type and the characteristics of probable eliciting stimuli. Starling raptor alarms and vervet eagle alarms are associated with similar environmental events whereas vervet leopard alarms and starling raptor alarms are not. As in the earlier experiment, the duration of test trial responses was better predicted by the information conveyed by the playback stimuli than by their acoustic characteristics.

Differentials in the Production Specificity of Vervet Alarm Calls

The results of playback experiments with vervets (SEYFARTH et al. 1980b; SEYFARTH & CHENEY 1988, 1990) invite comparisons of the production specificity of their alarm calls with that of human words. Words vary greatly in degree of referential specificity (e.g., MARLER 1977) and current evidence from studies of call usage suggests that vervet alarm calls share this property.

On rare occasions, leopard alarms seem to be elicited by other types of predator. For example, vervets occasionally produce leopard alarms in response to attacking snakes (R. SEYFARTH, pers. comm.). In one case, where a large

python dropped from a tree onto an impala, vervets not only responded with leopard alarms but continued to call for more than an hour as the python slowly ingested its victim (M. HAUSER, pers. comm.). CHENEY & SEYFARTH (1990) also reported that leopard alarms were given at a low rate (less than 1 % of over 1000 encounters) to eagles. In these cases, leopard alarms were emitted by adult males in response to stooping raptors.

Leopard alarms also are produced occasionally by vervets engaged in agonistic social interactions (STRUHSAKER 1967; CHENEY & SEYFARTH 1990). Descriptions of this behavior suggest that, just as with eagle-evoked calls, the eliciting circumstances were specific (CHENEY & SEYFARTH 1990: 108): male vervets produced leopard alarms "when their own group was being driven back toward the center of the territory (by another group), and hence losing the encounter, and when a new migrant male was attempting to approach their group". Most of these recordings, however, were obtained from a single male whose behavior may not be representative.

Taken together, these descriptions of 'inappropriate' leopard alarm usage are consistent with the idea that variation in affective state plays a more important role in production of leopard alarms than snake and eagle alarms, because these latter two call types do not appear to be produced in the absence of the predators with which they are normally associated. Thus, the level of production specificity varies as a characteristic of each of the vervet alarm calls. Leopard alarms are less specific and hence might be placed further from the referential pole of a 'motivational-to-referential continuum' (MARLER et al. 1992) than eagle and snake alarms.

Ground-Dwelling Sciurids:
Alarm Calls as Indicators of 'Response Urgency'

The alarm calling behavior of ground-dwelling sciurids probably has been studied more extensively than that of any other animal group (chipmunks: BURKE DA SILVA & KRAMER, pers. comm.; ground squirrels: e.g., MELCHIOR 1971; TURNER 1973; BETTS 1976; OWINGS & COSS 1977; OWINGS et al. 1977; LEGER & OWINGS 1978; OWINGS & VIRGINIA 1978; LEGER et al. 1979, 1980; OWINGS & LEGER 1980; ROBINSON 1980, 1981; SCHWAGMEYER & BROWN 1981; HARRIS et al. 1983; DAVIS 1984; LEGER et al. 1984; SHERMAN 1985; OWINGS et al. 1986; MACWHIRTER 1992; marmots: e.g., WARING 1966; DAVIS 1991; prairie dogs: e.g., WARING 1970; SMITH et al. 1977; SLOBODCHIKOFF & COAST 1980; OWINGS & LOUGHRY 1985; LOUGHRY & MCDONOUGH 1988; SLOBODCHIKOFF et al. 1991). Vocal responses to predators also have been examined in several arboreal sciurids (e.g., EMMONS 1978; C. C. SMITH 1978; S. F. SMITH 1978; see BETTS 1976 for citations prior to that year).

For example, the alarm call system of California ground squirrels (*Spermophilus beecheyi*) resembles that of vervet monkeys in that different types of predator are responded to with acoustically different alarm calls. 'Whistles' are elicited principally by aerial predators, whereas 'chats' and 'chatters' usually are evoked by ground predators (OWINGS & VIRGINIA 1978).

A number of exceptions to this pattern of usage occur, however, revealing a reduced degree of production specificity. California ground squirrels being

chased at high speeds by carnivores sometimes produce whistles. Similarly, raptors that have been detected at a distance, and hence present no immediate threat, sometimes elicit chatters (OWINGS & VIRGINIA 1978; LEGER et al. 1980; OWINGS & LEGER 1980; LEGER et al. 1984; SHERMAN 1985).

A similar pattern of alarm call usage has been described in Belding's ground squirrels (S. beldingi; ROBINSON 1980, 1981; SHERMAN 1985). In 21 of the 31 occasions when Belding's ground squirrels produced trills in response to hawks, the hawks either were perched or walking on the ground and were therefore unlikely to attack. Similarly, in 12 of the 14 instances when squirrels gave whistles to carnivores they were being closely pursued.

All of these findings are consistent with the idea that ground squirrel alarm calls do not denote different predator classes in the same way as some vervet alarms but instead reflect differences in response urgency perceived by the caller (e.g., BETTS 1976; ROBINSON 1981; OWINGS & HENNESSY 1984; SHERMAN 1985). Raptors frequently hunt ground squirrels by flying low, hugging the contours of the ground to conceal their approach. They consequently often go undetected until they are close to the burrow, which allows little time for escape. By comparison, carnivores must stalk ground squirrels slowly until the final rush, which increases the probability of being detected while still beyond attack range. Carnivores therefore typically present a less urgent threat than do raptors (OWINGS & HENNESSY 1984). Hawks that have been detected at a sufficient distance such that attack is not imminent elicit the same response as slow-moving carnivores, whereas squirrels that have been surprised by a carnivore give the call type normally associated with a rapidly approaching raptor. Ground squirrel alarm calls thus provide only probabilistic information about predator identity and cannot be considered functionally referential. Nevertheless, this call system likely allows accurate assessment of the time available for response and thus is well matched to the hunting tactics of sciurid predators and to squirrel antipredator behavior.

Comparison of Ground Squirrel and Vervet Alarm Calls

Vervet leopard alarms and ground squirrel whistles share some general similarities in usage. Both calls are primarily evoked by a particular predator class, but they are also occasionally produced in response to other types of predator as well as in social contexts when aggression is likely. Whether vervet leopard alarms elicited by predators have subtly different acoustic properties from those produced in agonistic interactions, as is apparent for ground squirrel whistles, is unknown.

Other characteristics of vervet leopard alarms and ground squirrel whistles are different. Unlike ground squirrels, vervets do not appear to vary call type with the level of response urgency presented by a carnivore. Leopards that are hunting, sleeping, attacking, or even moving in a direction away from the monkeys all elicit leopard alarms, rather than eagle or snake alarms. Similarly, eagle and snake alarms are almost always produced during encounters with eagles and snakes, respectively, despite considerable apparent variation in the immediacy of the threat (CHENEY & SEYFARTH 1990). This suggests that while response

urgency appears to play an important role in determining the type of alarm call produced by ground squirrels, it seldom influences usage of vervet alarms.

Contrasts also exist in the structural relationships among alarm calls in vervets and ground squirrels. California ground squirrel whistles are single-unit, tonal, narrow-band vocalizations. Chats are compound calls made up of a short whistle and an appended frequency upsweep. Chatters comprise a series of chat variants (Fig. 1 in OWINGS & VIRGINIA 1978; Fig. 3 in OWINGS & LEGER 1980). Calls with acoustic structures intermediate between whistles and chats also occur. The alarm calls produced by California ground squirrels thus form an acoustic continuum whereas those of vervets seem to be more discrete. We cannot exclude the possibility, however, that ground squirrel calls are perceived categorically (e.g., EHRET 1987; SNOWDON 1987).

In marked contrast to the results obtained in a long-term study of free-ranging vervets (CHENEY & SEYFARTH 1990), a recent laboratory experiment suggests that calls with characteristics intermediate between those of the recognized categories might occur. Silhouettes simulating predators were presented to both wild-caught and first-generation captive-born vervets. The calls elicited appeared to grade among vervet alarm call types (BROWN et al., in press). Moreover, production of these apparent acoustic intermediates was not restricted to a particular class of eliciting stimuli. A playback experiment that paired these variants with 'typical' vervet alarms might reveal the extent to which the acoustic variation is perceptually salient and the way calls with intermediate characteristics are categorized. These findings suggest that experiments under controlled laboratory conditions are likely to complement field observations for understanding fully the relationships between vervet alarm call structure and the characteristics of eliciting stimuli.

To address quantitatively the apparent differences in signal meaning between the alarm calls of ground squirrels and those of vervets, we have summarized published data on 'cross-taxon calling' (i.e., alarm calls evoked by a predator class other than the usual one; Table 1). Vervets exhibited little overlap in which call type was elicited by which predator class whereas California ground squirrels exhibited a greater degree of cross-taxon calling — particularly in the case of carnivores eliciting whistles (Table 1). In Belding's ground squirrels (ROBINSON 1980; LEGER et al. 1984) this trend is more pronounced: avian predators often elicited calls typically associated with carnivores.

Data from studies of two other ground squirrel species, the arctic ground squirrel (*C. undulatus:* MELCHIOR 1971) and Richardson's ground squirrel (*S. richardsoni:* DAVIS 1984), suggest a level of alarm call production specificity equivalent to that of vervets (Table 1). Therefore, different ground squirrel species may have undergone different selective regimes resulting in urgency-based alarm call systems for some species and referential systems for others (e.g., LEGER et al. 1984). However, the differences between *C. undulatus* and *S. richardsoni*, on the one hand, and *S. beecheyi* and *S. beldingi*, on the other, may only be an artifact of the more limited data available for the former two species. For example, an initial study of *S. beldingi* (TURNER 1973) suggested predator-class-specificity in alarm calling, whereas additional data have revealed a pattern of call

Table 1: Proportions of acoustically distinct antipredator calls elicited by mammalian and avian predators in some studies of ground squirrels and primates

Study	Species	Mammalian predators		Avian predators	
		Type A call	Type B call	Type A call	Type B call
A. Ground squirrels					
1. OWINGS & VIRGINIA 1978	*Spermophilus beecheyi*	50 (93 %)	4 (7 %)	1 (1 %)	64 (99 %)
2. OWINGS & LEGER 1980/LEGER et al. 1980	*S. beecheyi*	109 (87 %)	17 (13 %)	5 (2 %)	209 (98 %)
3. TURNER 1973	*S. beldingi*	17 (94 %)	1 (6 %)	0 (0 %)	19 (100 %)
4. ROBINSON 1980	*S. beldingi*	45 (92 %)	4 (8 %)	11 (16 %)	39 (78 %)
5. LEGER et al. 1984	*S. beldingi*	58 (98 %)	1 (2 %)	18 (53 %)	16 (47 %)
6. SHERMAN 1985	*S. beldingi*	139 (91 %)	14 (9 %)	31 (11 %)	240 (89 %)
7. DAVIS 1984	*S. richardsonii*	63 (100 %)	0 (0 %)	0 (0 %)	25 (100 %)
8. MELCHIOR 1971	*Citellus undulatus*	16 (100 %)	0 (0 %)	1 (2 %)	54 (98 %)
B. Primates					
9. SEYFARTH & CHENEY 1980	*Cercopithecus aethiops*	69 (100 %)	0 (0 %)	3 (2 %)	137 (98 %)
10. MACEDONIA & POLAK 1989	*Lemur catta*	>30**	1	0 (0 %)	23 (100 %)

Call types A and B refer, respectively, to those termed by authors "terrestrial/mammalian" (cf. snake) or "aerial/avian" predator alarms; in some cases, alarm calls may have been elicited by innocuous mammals and birds; 2. responses from two studies combined (each study examined only one call type); 6. nos. refer to focal animals, several of which were observed during each experimental squirrel/(aerial) predator interaction; 10. estimated**: pers. obs.

usage more consistent with a response-urgency-based system (ROBINSON 1980; LEGER et al. 1984; SHERMAN 1985; Table 1).

A recent study of alarm calling in Gunnison's prairie dogs (*Cynomys gunnisoni*) suggests that call morphology may reflect relatively subtle variation in stimulus characteristics (SLOBODCHIKOFF et al. 1991). The structure of alarm barks elicited by each of four humans walking through the colony was quantified using 12 measures of spectral and temporal characteristics. Between 70 % and 94 % of the calls were correctly classified (i.e., matched to the eliciting human) by discriminative function analysis. Playback experiments have not yet been conducted, so the perceptual significance of this acoustic variation currently is unclear.

In summary, current evidence indicates that external reference plays a larger role in the alarm calls of the vervet monkey than in those of ground-dwelling sciurids. For both kinds of mammals, however, these vocalizations evidently have been shaped by functional requirements. The evolution of externally referential alarm calls might be expected to occur only in taxa where vocal differentiation of predator classes yields a significant advantage in reproductive success. Some understanding of how physical and environmental factors might generate selection for such vocal signals can be gained by comparative studies of related species with different behavior and ecology.

Lemurs: Interspecific Variation in Alarm Call Meaning

Aerial and terrestrial predators elicit structurally distinct alarm calls in many species of lemurs (see MACEDONIA 1990). Long-term comparative studies of alarm calling in forest-living ringtailed lemurs (*Lemur catta*) and black-and-white ruffed lemurs (*Varecia variegata variegata*) at the Duke University Primate Center (Durham, NC) have included observations of natural encounters with potential predators as well as presentations of simulated predators and playback experiments (e.g., MACEDONIA & POLAK 1989; MACEDONIA 1990; MACEDONIA & YOUNT 1991; PEREIRA & MACEDONIA 1991). Most responses of the semi-captive ringtailed and ruffed lemurs to predators match closely those reported for free-ranging conspecifics (e.g., JOLLY 1966; SAUTHER 1989; H. MORLAND, pers. comm.).

These two lemur species differ in physical characteristics, behavior and ecology. Ringtailed lemurs weigh approximately 2 kg as adults, are the most terrestrial of the extant lemurs and live in an open arid/semi-arid habitat (e.g., JOLLY 1966; TATTERSALL 1982). In contrast, ruffed lemurs weigh about 75 % more than ringtails (roughly 3.5 kg), are highly arboreal and live in closed-canopy rainforest (e.g., PEREIRA et al. 1988; MORLAND 1990).

Alarm Call Usage in Ringtailed Lemurs

When ringtailed lemurs first detect a potentially threatening aerial object they respond with 'gulps' (Fig. 1a). Gulps are low-amplitude calls that are evoked by a broad range of startling visual and auditory stimuli (including mammalian predators); they seem to function as general 'group alert' signals. Aerial predators also elicit two much more specific vocalizations: 'rasps' (Fig. 1b,
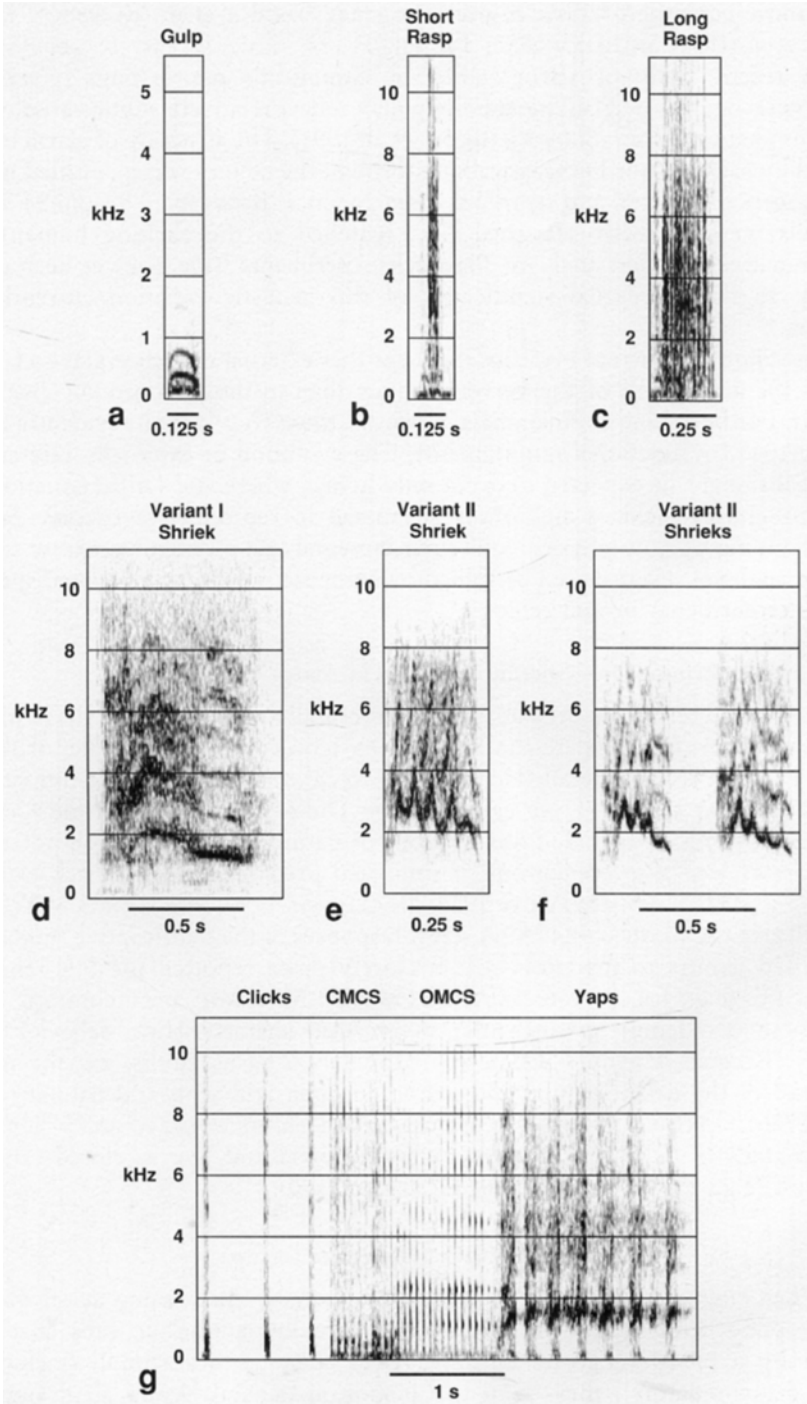
Fig. 1: Vocalizations emitted by the ringtailed lemur (*Lemur catta*) in response to predators.
g: CMCS = closed mouth click series; OMCS = open mouth click series

c) and 'shrieks' (Fig. 1 d). The rasp is a brief, noisy sound given by one to several group members when sighting airborne raptors. Shrieks characteristically are produced when a raptor has approached to within attack range. Unlike gulps and rasps, shrieks are high-amplitude calls that appear to be predator-directed (MACEDONIA & POLAK 1989; MACEDONIA, in press), although conspecifics within earshot likely benefit from hearing them as well. Also, the acoustic structure of shrieks appears to covary with the severity of the raptor encounter. For example, responses to a stooping raptor model elicited shrieks with a strikingly different structure (Fig. 1 e, f) than those elicited typically by actual or simulated raptor flyovers (Fig. 1 d). Systematic investigation of this issue, however, remains to be conducted. Both rasps and shrieks are referred to as 'aerial alarm calls' for brevity.

Frequently, the initial vocal response of ringtailed lemurs to carnivores, like that to aerial predators, is gulps. These soon are followed by several types of 'location indicating' calls ('clicks' and 'click series') and 'yaps' (Fig. 1 g), which are used as carnivore-mobbing calls. Yaps are referred to here as 'ground alarm calls'.

Extensive recordings of the vocal responses of ringtailed lemurs to predators demonstrate a high degree of production specificity. Except for a single instance that appeared to be a 'mistake' (MACEDONIA, in press), aerial alarm calls were elicited only by aerial stimuli and ground alarm calls were elicited exclusively by mammalian stimuli (JOLLY 1966; MACEDONIA & POLAK 1989; SAUTHER 1989; MACEDONIA 1990; PEREIRA & MACEDONIA 1991).

The importance of response urgency was examined directly in a series of experiments with both aerial and terrestrial predators (PEREIRA & MACEDONIA 1991). A representative carnivore (large dog; Canis familiaris) was presented both at a distance of 30—50 m (low urgency) and at 7—11 m (simulating a high-urgency ambush). Similarly, lemurs were tested with a museum specimen of a red-shouldered hawk (Buteo lineatus) and a great-horned owl (Bubo virginianus) as representative aerial predators. These birds were presented 2—3 m above the ground (low response urgency). A high-urgency aerial predator stimulus was created using a technique similar to that employed in the classic experiments of LORENZ and TINBERGEN (SCHLEIDT 1961): a raptor-shaped silhouette was sus-pended from a wire and 'flown' toward the subjects in apparent stoop. Despite this variation in immediacy of threat, cross-taxon calling was absent (PEREIRA & MACEDONIA 1991).

No aerial alarms were given to the perched raptors, although those stimuli did elicit all of the other vocal and nonvocal behavior normally associated with aerial predators (i.e., bipedal locomotion, emission of 'chirps' and 'plosive barks': MACEDONIA 1990; MACEDONIA & YOUNT 1991; PEREIRA & MACEDONIA 1991). Possibly, a live raptor in the same position would have been a more effective stimulus. However, an alternative interpretation is that ringtailed lemur aerial alarm calls may denote airborne raptors only, in contrast with vervet eagle alarms, which are produced in response to aerial predators regardless of spatial location (STRUHSAKER 1967).

Ringtailed lemur ground alarm calls were evoked principally by carnivores and were unaffected by whether the predator or the lemurs were on the ground or

in trees (MACEDONIA, in press). However, like vervet leopard alarms, ground alarm calls of ringtailed lemurs are also, although rarely, produced during social interactions. This only occurred when males were engaged in long high-rate bouts of 'howling' (an advertisement call; e.g., ANDREW 1963; JOLLY 1966; MACEDONIA, in press).

In sum, ringtailed lemurs and vervets share similar stimulus specificity in alarm call production. For both species, a narrower range of stimuli elicit aerial alarms than ground alarms.
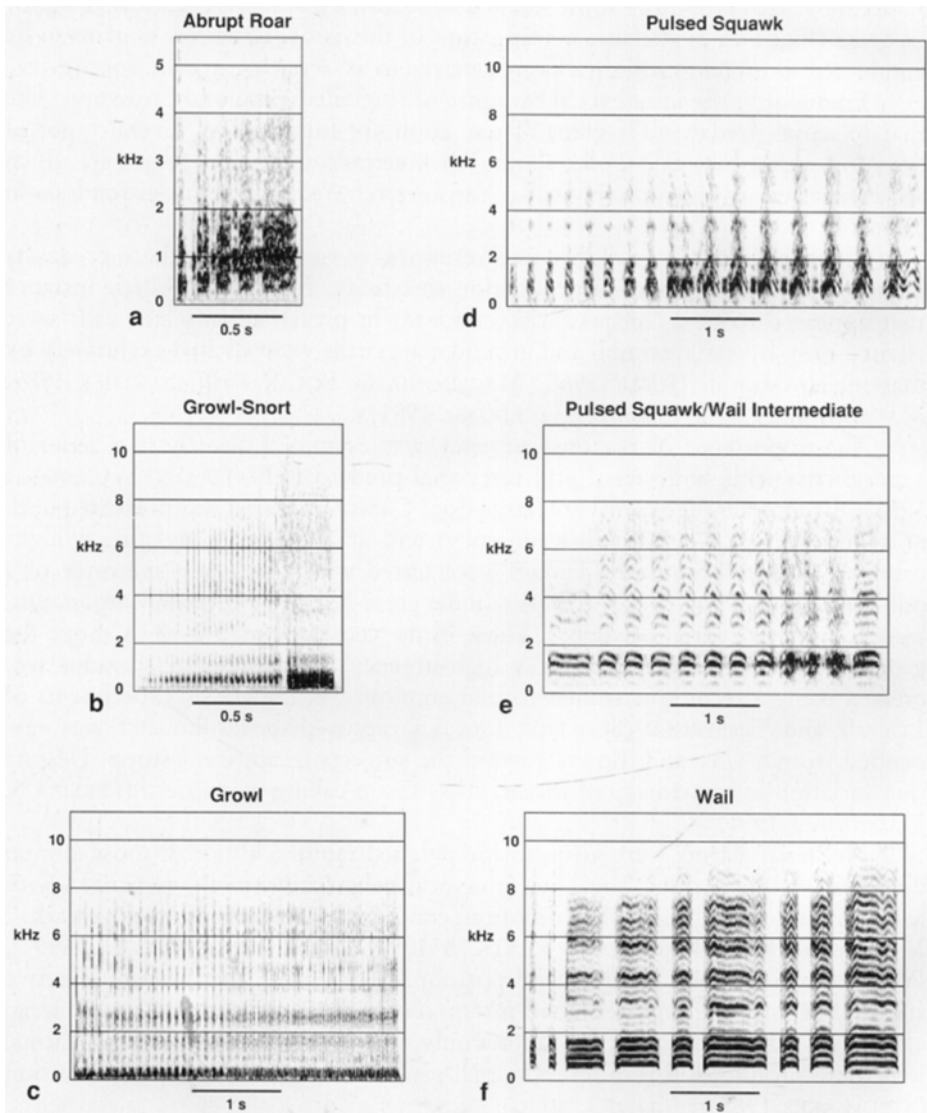
Fig. 2: Vocalizations emitted by the black-and-white ruffed lemur (*Varecia variegata variegata*) in response to predators

Alarm Call Usage in Ruffed Lemurs

Ruffed lemurs respond to the sight or call of a nearby raptor by emitting 'abrupt roars' (aerial alarm calls; Fig. 2a) at irregular intervals. In response to carnivores they typically produce disturbance vocalizations ('growl-snorts' and/or 'growls': Fig. 2b, c) followed by mobbing calls ('pulsed squawks': Fig. 2d). Pulsed squawks are referred to here as 'ground alarm calls'.

Although raptors usually elicited aerial alarm calls and terrestrial predators usually elicited ground alarm calls, some cross-taxon calling occurred. Ground alarm calls sometimes were produced during bouts of calling in response to an aerial predator. In addition, ground alarm calls were emitted in response to the same calls of nearby groups and in contexts where no eliciting stimulus could be identified.

Ground alarm calls of ruffed lemurs also intergrade structurally with another vocalization, the 'wail' (Fig. 2f). Wails are contact calls that seem to serve an 'all clear' function following major disturbances (including responses to predators). They also elicit leisurely group reaggregation in these and other contexts (PEREIRA et al. 1988; IWANO 1989). Wails emitted in the context of terrestrial and aerial predators typically grade into ground alarm call/wail intermediates (Fig. 2e) and back again many times.

Considering the structural and functional relationship between ground alarm calls and wails, ground alarm calls may act as a high-urgency summons for group reaggregation (i.e., a 'rally cry'), although such usage may be restricted largely to mammalian-predator threat (PEREIRA et al. 1988; MACEDONIA 1990). If so, then ground alarm calls of ruffed lemurs, like those of ground squirrels, likely permit only a 'best bet' identification of the eliciting stimulus because of their probabilistic association with carnivores.

Aerial alarm calls also occurred commonly in agonistic social interactions. In this context they seem to be employed as a high-intensity, intergroup threat vocalization (PEREIRA et al. 1988). Both types of ruffed lemur alarm calls thus have a significantly lower level of production specificity than ringtailed lemur alarm calls.

Playback Experiments with Ringtailed Lemurs

Playbacks of ringtailed lemur aerial and ground alarm calls elicited responses that did not differ qualitatively from those evoked by actual predators (MACEDONIA 1990). Presentations of aerial alarm calls evoked downward movement if the ringtails were in trees and looking upward if they were on the ground. Playbacks of ground alarm calls caused ringtails to run into trees if they were on the ground and to stay in trees if they were already in them. The responses elicited by alarm call playbacks to ringtailed lemurs thus resemble closely the behavior of vervets in analogous experiments (e.g., SEYFARTH et al. 1980b).

Playback Experiments with Ruffed Lemurs

Responses to playbacks do not suggest that ruffed lemur alarm calls provide sufficient information about eliciting conditions for conspecifics to select an appropriate antipredator response (MACEDONIA 1990). Presentations of their

aerial alarm calls did not evoke looking upward if the subjects were on the ground, or moving downward if they were in trees, at significantly higher rates than playbacks of their ground alarm calls. Similarly, ruffed lemurs did not run into trees more often following playbacks of ground alarm calls than after playbacks of aerial alarm calls.

Thus, the degree to which alarm calls of ringtailed lemurs and ruffed lemurs can be considered functionally referential are markedly different. Ringtailed lemur alarms meet both production and perception criteria. Their eliciting conditions are specific, and playbacks are sufficient to evoke appropriate antipredator responses. In contrast, ruffed lemur alarms have relatively low production specificity and do not elicit qualitatively different responses in playback experiments. Ruffed lemur alarms therefore do not qualify as functionally referential, although they likely provide receivers with a probabilistic estimate of predator type, particularly when contextual cues are available.

The Evolution of Externally Referential Antipredator Calls

The vocal and nonvocal antipredator behavior of the ringtailed lemur more closely resembles that of the vervet monkey than it does that of the ruffed lemur. Ringtails and vervets have several highly specific alarm calls to which they respond in comparably specific ways, whereas the ruffed lemur's vocal and nonvocal responses to predators are less specific. Several other attributes shared by vervets and ringtails, that are not shared with the ruffed lemur, may have influenced selection for external reference in their alarm calls.

First, vervets and ringtails are relatively small-bodied in comparison to their primary avian and mammalian predators. In contrast, adult ruffed lemurs are likely to be invulnerable to predation by any extant Malagasy raptors, although the large viverrid carnivore *Cryptoprocta ferox* (7—12 kg, ALBIGNAC 1972) must pose a potentially lethal threat (MACEDONIA, in press).

Second, both vervets (e.g., KINGDON 1988) and ringtailed lemurs (e.g., WARD & SUSSMAN 1979) are highly terrestrial, compared with their close relatives. Because the locomotor (i.e., grasping) advantage that primates hold over clawed carnivores when both are in the trees is lost when on the ground, increased time spent on the ground is likely to produce a commensurate increase in the probability of being killed by a carnivore (e.g., SEYFARTH et al. 1980b; GOUZOULES et al. 1985). The highly-arboreal lifestyle of the ruffed lemur reduces considerably the likelihood of facing a carnivore on the ground.

Third, vervets and ringtails both live in open habitats where carnivores could block escape routes to trees. By comparison, ruffed lemurs inhabit closed-canopy rainforest where the probability of access to trees being blocked by a carnivore is low.

Ground-dwelling sciurids share with vervets and ringtailed lemurs the attributes of being relatively small-bodied, terrestrial and living in an open habitat, but they do not appear to have functionally referential alarm calls. Thus, although they may be important, these factors are not sufficient to explain the evolution of referential alarm calls.

We therefore suggest that the *incompatibility of responses required by different predator classes* may have been the major selective force in the evolution of predator-class-specific alarm calls. For ground-dwelling sciurids, responses to all types of predators occur on a single plane (the ground) where the burrow represents the primary retreat (though bushes also serve as refuges from raptors: SHERMAN 1985). In contrast, vervets and ringtails must respond to raptors and carnivores in two planes (ground and trees), and in ways that frequently are diametrically opposed (e.g., flee the branch network in response to raptors; enter the branch network in response to carnivores). The importance of 'conflicting escape tactics' would seem to have had only a minor impact on ruffed lemurs, who, at least as adults, may be invulnerable to predation by Malagasy raptors and who maintain a nearly perpetual advantage over carnivores by spending most of their time in the trees.

Summary and Conclusions

We have reviewed research on the alarm call systems of primates and ground-dwelling sciurids to illustrate the variation in call meaning that exists both between and within species.

Observations of encounters between free-ranging vervets and different types of potential predator, together with experimental playbacks of their alarm calls, support the view that these vocalizations function to denote predator class. Nevertheless, production specificity does vary. 'Leopard' alarms are occasionally emitted in response to approaching raptors and during agonistic social interactions. 'Inappropriate' usage of this type has not been described for eagle and snake alarms. Variation in a caller's motivational state evidently plays a larger role in controlling production of leopard alarms than in other vervet alarm calls.

Ground squirrels and their terrestrial relatives have qualitatively similar behavioral responses to all potential predators. Both carnivores and raptors evoke running toward a burrow, although the speed of this response, and the probability of entering the burrow once there, may vary. Ground squirrel alarm calls also lack a high level of production specificity. It is likely, however, that correlations between eliciting stimulus and response urgency, together with contextual cues, such as the number of calling individuals, permit a probabilistic identification of predator type. An urgency-based alarm call system of this kind is adaptive for burrowing mammals, like ground squirrels, whose responses to different predator classes are qualitatively similar and which principally require information about the necessary speed of response.

Observational and experimental work with ringtailed and ruffed lemurs suggests that antipredator calls of ringtailed lemurs denote predator classes whereas those of ruffed lemurs do not. Being relatively small-bodied, terrestrial, and living in an open habitat likely has increased predator pressure in ringtails and vervets over that of their respective arboreal ancestors (e.g., GOUZOULES et al. 1985; MACEDONIA, in press). Comparison to ground squirrels demonstrates, however, that although these characteristics may be necessary to evolve functionally referential alarm calls, they are not sufficient. We propose instead that the

primary force underlying the evolution of referentially specific alarm calls is the use of fundamentally incompatible escape responses to evade different classes of predators.

Acknowledgments

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