

VERVET MONKEY ALARM CALLS: SEMANTIC COMMUNICATION IN A FREE-RANGING PRIMATE

BY ROBERT M. SEYFARTH, DOROTHY L. CHENEY & PETER MARLER

Rockefeller University, Field Research Center, Millbrook, N.Y. 12545

Abstract. Vervet monkeys (*Cercopithecus aethiops*) at Amboseli, Kenya, give acoustically different alarm calls to different predators. Each alarm evokes contrasting, seemingly adaptive, responses. Animals on the ground respond to leopard alarms by running into trees, to eagle alarms by looking up, and to snake alarms by looking down. In a 14-month field study examining the semantic properties of alarm calls, we played tape-recorded alarms to vervets in the absence of actual predators and filmed the monkeys' responses. Playbacks confirmed observations and showed that (1) alarm length, amplitude and alarmist's age/sex class had little effect on response quality, and (2) context was not a systematic determinant of response. We conclude that vervet alarm calls function to designate different classes of external danger.

A central issue in the study of non-human primate communication is that of semantics: has any species other than man evolved the ability to use signs to refer to objects in the external world? It is now generally agreed that captive chimpanzees (*Pan troglodytes*) and gorillas (*Gorilla gorilla*) can be taught a form of communication in which individuals are able to use a number of arbitrary or semi-iconic symbols to represent a variety of objects, even in the absence of contextual cues (Gardner & Gardner 1969; Premack 1970; Rumbaugh et al. 1973; Patterson 1978; Terrace 1979).

For those interested in the evolution and function of primate communication under natural conditions, however, two points complicate the interpretation of these data on captive apes. First, in all of the projects cited above, individual apes became fluent in the use of a particular set of signs only after extensive training by humans. There is as yet no evidence that non-human primates are capable of developing a form of semantic communication in the absence of human training. Second, such training has occurred in environments that differ both socially and physically from the animals' natural habitats. Consequently, although much has been learned about the cognitive and communicative potential of chimpanzees and gorillas, it is not known whether animals exploit this potential under natural conditions. Indeed, the successes of research on the signalling abilities of captive apes serve to emphasize just how little is known about non-human primate communication in general, and in particular about the selective forces that might favour the evolution of semantic signals over other forms of communication.

The aim of this paper is to determine whether the predator alarm calls of free-ranging vervet monkeys (*Cercopithecus aethiops*) serve to designate predators as external referents and, if so, what the role of contextual cues may be in this designation. Struhsaker (1967a) suggested that acoustically different alarm calls were given by vervets in response to different types of predators, and that each call evoked a different and seemingly adaptive response. This paper describes playback experiments designed to replicate and extend Struhsaker's observations, and to determine whether different alarm calls are capable of evoking different responses from the monkeys in the absence of actual predators. Part I of this paper provides observational data on the behaviour of vervet monkeys during encounters with predators. Part II describes experiments in which tape recordings of alarm calls by known individuals were played to groups of vervets in a variety of environmental contexts.

Part I: Observations of Alarm Calls

A. Study Area and Observational Methods

Data on social behaviour and vocalizations of three groups of vervet monkeys were collected between March 1977 and May 1978 in Amboseli National Park, Kenya. The park lies in an area of semi-arid acacia savanna described by Struhsaker (1967b), Altmann & Altmann (1970), and Western & Van Praet (1973). During the study period, the three groups occupied adjacent home ranges with the following age/sex compositions: Group A: seven adult males, eight adult females, seven juveniles (animals over the age of one year but not yet

sexually mature), and eight infants (animals under the age of one year); Group B: two to three adult males, seven adult females, one juvenile, and six infants; Group C: two to four adult males, eight adult females, 11 juveniles, and eight infants. Documented variations in the age/sex composition of each group during the study were due to births, deaths, immigrations and emigrations.

On a typical day, two observers spent approximately 2.5 h with each group. Observation sessions were scheduled to provide similar amounts of data each month on each individual in each group during hourly periods from 0700 to 1800 hours. This protocol dictated the timing of observation sessions with each group. Observation sessions were terminated after each individual in the group had been sampled at least once. During each observation session, both observers sampled behaviour using focal animal and sequence sampling (Altmann 1974). All animals in each group were sampled for at least 170 min each month, for a total of over 1400 contact hours with all three groups. During focal animal sampling, each observer tape-recorded as many vocalizations as possible, noting the individuals involved as well as the behaviour immediately preceding and following each utterance. These data were supplemented, whenever possible, by ad libitum recordings. Recordings were made only from known individuals, and data analysis was limited to those occasions when the behaviours immediately preceding and following the vocalization had been observed. Recordings were made at a distance of 0.5 to 7 m, using either a Nagra III or a Nagra SNN tape recorder at 9.5 cm/s and Sennheiser directional microphones (MKH 804).

Observers were usually alerted to the presence of a predator by the monkeys' alarm calls. On a number of occasions, however, observers sighted an approaching predator before the monkeys gave signs of having done so. At the first indication of a predator, one observer attempted to identify the species involved. Having done so, we scanned the area for other potential predators that might have provoked alarm calls. Meanwhile, the second observer noted the identities of all monkeys calling and tape-recorded as many alarm calls from known individuals as possible. Observations and recording continued until alarming by all individuals had ceased for 15 min. Whenever possible, the time elapsed between each individual's

first and last alarm call was noted, as were the times of onset and termination of alarming by nearby groups of monkeys.

In the following description and analysis of alarm calls, the technical terms unit, phrase, bout, non-tonal unit, tonal unit, compound unit, mixed unit, and distribution of major energy of non-tonal sounds are defined as in Struhsaker (1967a, pp. 282–283). The sound spectrograms presented below (Figs. 1–4) were made with tape at normal speed (9.5 cm/s), using a Kay Sonagraph Model 7029A, with a wide band filter (300 Hz), the FL1 shaping selector, and either 80 to 8000 Hz (Figs 1, 3, 4) or 160 to 16 000 Hz (Fig. 2) frequency scales.

B. Results

1. The predators of vervet monkeys. Over a 14-month period, a variety of animals elicited alarm calls from vervet monkeys (Table I). Predators in Table I have been divided into four general categories. Within each category, animals have been arranged into three subdivisions according to the following criteria: confirmed predators are animals that either prey on vervets or are known from other studies to prey on small monkeys in areas like Amboseli (see references below); potential predators are animals that prey on species the size of vervets but do not attack monkeys as far as is known; and non-predators are animals or objects that were observed to elicit alarm calls but do not prey on monkeys or similarly sized animals. Rows arrange animals or objects according to the type of alarm call they most commonly elicited, including such rare events as a mouse that elicited a snake alarm call and a falling leaf that elicited an eagle alarm call. The acoustical distinctions among alarm call types are discussed below (Section B.2). Examination of Table I indicates that monkeys did make what might be termed 'mistakes', by giving alarms to non-predators that posed no apparent danger to them. Most 'mistakes' of this sort were made by juveniles and infants (Seyfarth & Cheney, in press).

As Table I indicates, vervet monkeys in Amboseli are currently preyed upon by four types of confirmed predators: leopards, martial eagles, pythons, and baboons. No analysis of the responses to them by vervets can be attempted without some reference to the hunting strategies of these predators.

From the little that is known about their behaviour, leopards (*Panthera pardus*) appear

to hunt monkeys primarily by concealing themselves in bushes and pouncing on animals that walk by (Altmann & Altmann 1970; Eisenberg & Lockhart 1972; Muckenhirn 1972). Descriptions of leopards hunting langurs (*Presbytis entellus*) in Sri Lanka support our impression that small monkeys such as langurs and vervets, who spend considerable amounts of time in the terminal branches of trees, are most vulnerable to leopard attacks when they are on the ground (Eisenberg & Lockhart 1972; see also Haddow 1952). In Amboseli, Struhsaker (1967a) and Altmann & Altmann (1970) describe attacks in which leopards concealed in bushes pounced on a vervet or a baboon, and during the present study a leopard killed an adult male vervet monkey in this manner. The apparently greater vulnerability to leopards of vervets when on the ground than when in trees should be borne in mind when considering the adaptiveness of their responses to leopard alarms (see below).

Martial eagles (*Polemaetus bellicosus*) appear to hunt monkeys from the air, attacking from a long stoop at great speed (Brown 1963, 1966; Brown & Amadon 1968). During the present study, a one-year-old juvenile vervet was killed by a martial eagle in this manner while crossing

open ground. Gargett (1971) reports similar predation by a black eagle (*Aquila verreauxi*) on a juvenile vervet in Zimbabwe. Struhsaker (1967a) saw a crowned hawk eagle (*Stephanoaetus coronatus*) feeding on a vervet it had presumably killed, but this raptor has since become rare in Amboseli and was not seen during this study. Martial eagles seem to be equally adept at taking monkeys in trees and on the ground (Haddow 1952; Brown & Amadon 1968; G. R. C. Cunningham Van Someren, personal communication), and in this study martial eagles stooped at vervets in trees on a number of occasions. In response to such attacks, vervets often ran out of the trees and into dense bush on the ground, conforming with the interpretation (Cunningham Van Someren, personal communication) that vervets are safest from eagle attacks when they are on the ground in dense bush, and relatively more vulnerable when they are in trees or open country.

Among snakes, pythons (*Python sebae*) are the species most commonly reported to attack monkeys (e.g. Haddow 1952; Isemonger 1962). In the early weeks of the present study, a group of vervets was observed giving alarm calls to a

Table I. The Animals that Elicited Alarm Calls from Vervet Monkeys

	Confirmed predators	Potential predators	Non-predators
Mammalian carnivore alarms	Leopard (<i>Panthera pardus</i>)	Lion (<i>Panthera leo</i>) Hyaena (<i>Crocuta crocuta</i>) Cheetah (<i>Acinonyx jubatus</i>) Jackal (<i>Canis mesomelas</i>)	Warthog (<i>Phacochoerus aethiopicus</i>)
Avian predator alarms	Martial eagle (<i>Polemaetus bellicosus</i>)	African hawk eagle (<i>Hieraetus spilogaster</i>) Black-chested snake eagle (<i>Circaetus pectoralis</i>) Tawny eagle (<i>Aquila rapax</i>) Verreaux's eagle owl (<i>Bubo lacteus</i>)	African goshawk (<i>Accipiter tachiro</i>) Bateleur (<i>Terathopius ecaudatus</i>) Egyptian goose (<i>Alopochen aegyptiacus</i>) Grey heron (<i>Ardea cinerea</i>) Ground hornbill (<i>Bucorvus leadbeateri</i>) Lilac-breasted roller (<i>Coracias caudata</i>) Marabou stork (<i>Leptoptilos crumeniferus</i>) Pigeon (<i>Streptopelia spp.</i>) Secretary bird (<i>Sagittarius serpentarius</i>) Spoonbill (<i>Platalea alba</i>) Vulture (e.g. <i>Trigonoceps occipitalis</i>) Falling leaf
Snake alarms	Python (<i>Python sebae</i>)	Cobra (<i>Naja spp.</i>) Black mamba (<i>Dendroaspis polylepis</i>) Green mamba (<i>D. angusticeps</i>) Puff adder (<i>Bitis arietans</i>)	Tortoise (fam. <i>Testudinidae</i>) Mouse (? <i>Arvicanthus spp.</i>)
Baboon alarms	Baboon (<i>Papio cynocephalus</i>)		

Animals arranged in rows according to the type of alarm they most commonly elicited. For definitions of confirmed predators, potential predators, and non-predators see text.

python with a large lump in its stomach on the morning following the overnight disappearance of an adult female. There is thus circumstantial evidence that vervets in Amboseli are preyed upon by pythons. Pythons were encountered on two occasions (see below), always when monkeys were on the ground. Vervets also regularly encountered cobras (*Naja* spp.) and mambas (*Dendroaspis* spp.), both on the ground and in trees. No attacks by these snakes were observed, although all have been known to kill animals the size of vervets.

Predation by baboons (*Papio cynocephalus*) on vervets is frequently observed in Amboseli (Hausfater 1976). Between April 1977 and June 1978 two immature vervets from the main study groups were killed by baboons. Vervets are killed primarily by adult male baboons, who isolate juveniles from the rest of their group and then chase and kill them (Hausfater 1976). Vervets seem to be more vulnerable to attacks by baboons when on the ground than when in trees (Hausfater 1976; D. Post, D. Klein, personal communication).

No attacks on vervets by such potential predators as lions, cheetah, hyenas, or species of eagle other than the martial eagle were observed, although all are capable of taking monkey-sized prey (Kruuk & Turner 1967; Brown & Amadon 1968; Schaller 1972). It is likely that when such predators do attack monkeys, their hunting strategy is similar to that of the confirmed predator they most closely resemble. In other words, vervets are probably most vulnerable to mammalian carnivores when on the ground, and most vulnerable to several eagle species when in the open or on the terminal branches of trees.

2. The alarm calls of vervet monkeys. Struhsaker (1967a) found that vervets in Amboseli gave acoustically different alarm calls to large mammalian carnivores, raptors, humans, and snakes. These calls were structurally discrete, and could easily be distinguished by a human listener in the field. Moreover, the calls seemed to be non-iconic, in that the acoustic properties of each call type were unrelated to the predators' physical or vocal attributes.

Figures 1 and 2 illustrate typical alarm calls given to leopards, eagles, and snakes by adult male R (Group C), adult female LB (Group A), and 2.5-year-old juvenile male T (Group C). Only recordings made from encounters in which the predator was positively identified are illustrated. For comparison with Struhsaker's (1967a)

results, the leopard alarm call of adult male R is similar to the 'threat alarm bark' (Plate 16.9b). Those of adult female LB and juvenile male T seem to correspond with Struhsaker's 'chirp' call (Plate 16.9a). The eagle and snake alarms of all individuals are comparable with the 'rraup' call and the 'snake chutter', respectively (Plate 16.1d).

Among adult males, large mammalian carnivore alarms (hereafter called 'leopard' alarms for brevity) consisted of a series of relatively long tonal units formed by a series of rapidly alternating exhalations and inhalations (Struhsaker 1967a). These could contain up to eight units in a phrase (e.g. Fig. 3), with major energy concentrated in relatively tonal 'bands' between 1.5 and 2.0 kHz and around 0.3 kHz. In contrast, the leopard alarms of adult females and juveniles lacked an inhalation phase, typically contained fewer units per phrase, and sounded more shrill and abrupt than those of adult males (Fig. 3, but see below). The major band of energy was concentrated between 0.5 and 1.5 kHz. The eagle alarms of all individuals consisted of short units, grouped closely together to make a relatively short phrase. The major energy was concentrated between 0.2 and 1 kHz. Finally, the snake alarms of all age/sex classes consisted of a series of short, relatively widely separated units. The major energy of these units was consistently concentrated at higher frequencies than in other alarms, often reaching above 16.0 kHz (Fig. 2).

This brief description of the monkeys' alarm calls to three different classes of predator does not include their alarms to baboons or humans. During the present study neither of these species elicited enough alarm calls to permit recording or analysis.

Despite individual differences in call structure, the members of each age/sex class gave acoustically similar types of alarm calls to each class of predator (Fig. 3). Analysis of the responses of vervets to each type of alarm call indicated that the monkeys had no difficulty in discriminating between alarm call types despite individual variation within each call type. Whether responses varied with caller identity was not investigated in this study (but see p. 1086).

While the leopard alarm calls of all individuals were distinct from all other vocalizations, eagle and snake alarms bore some resemblance to certain vocalizations used during social interactions within the group. Statistical analyses were therefore performed to determine

whether, in addition to differing from each other, alarm calls were also distinguishable from other classes of vocalizations that they most closely resembled. Table II presents results of tests on all adults for whom a sample of vocalizations was available. Comparisons were made between eagle alarms and intra-group grunts (Struhsaker's 'woof' or 'progression grunt', 1967a, Plates 16.3b and c), the latter being the vocalization that, both audibly and spectrographically, most closely resembled eagle

alarms. For each animal, eagle alarms were significantly different from grunts in at least one measure, but which measure was significant varied across individuals. Similar comparisons were made between the two vocalizations that were most similar to snake alarms, the inter- and intra-group chutter (Table III; see also Struhsaker 1967a). Here again, results suggest that there was at least the potential for distinguishing alarms from acoustically similar vocalizations. These findings are consistent

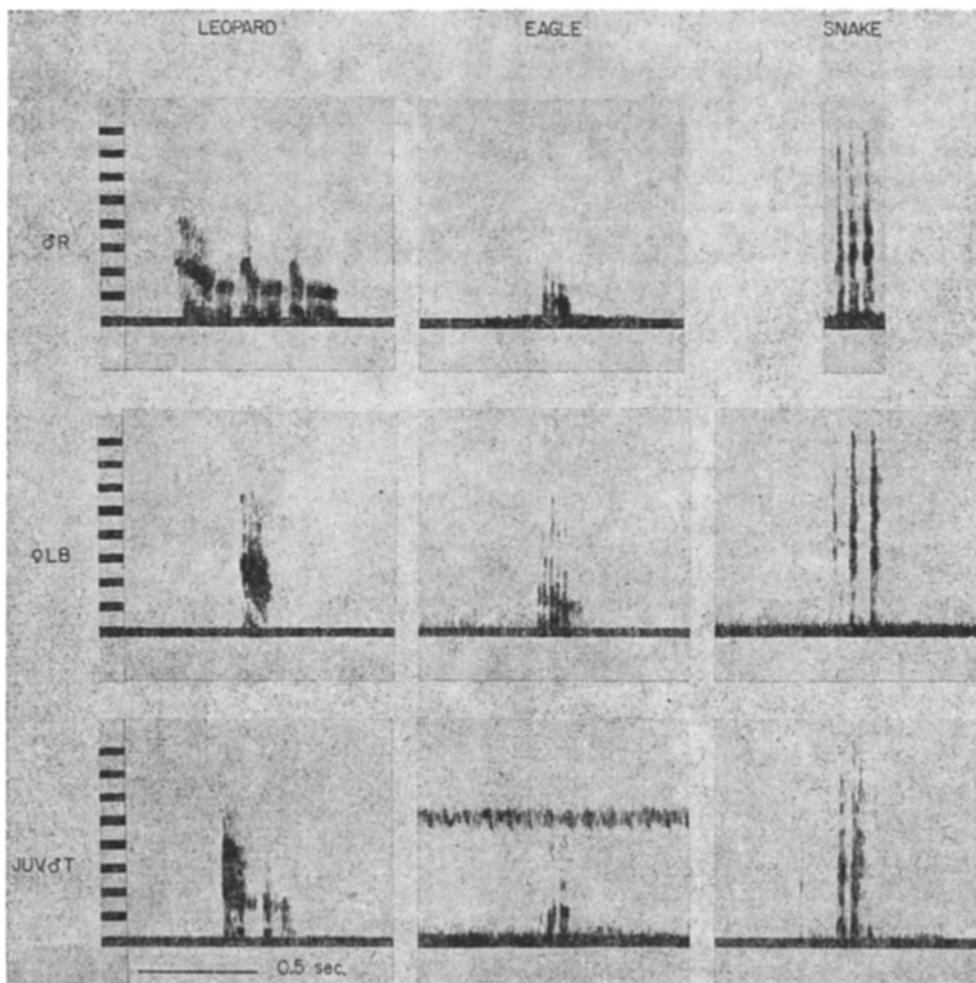


Fig. 1. Examples of the alarms given by three individuals to leopards, martial eagles, and snakes. Top row shows alarms by adult male R (Group C); middle row shows alarms by adult female LB (Group A); and bottom row shows alarms by 2.5 year-old juvenile male T (Group C). X-axis shows time; Y-axis shows frequency in units of 1 kHz. In eagle alarms of juvenile T, noise around 5 kHz is insects.

with the hypothesis that each type of alarm call was represented by a discrete acoustical unit (Green & Marler 1979), unlikely to be confused with any other part of the monkeys' vocal repertoire.

Struhsaker (1967a) found that males over three years of age responded to the presence of a large mammalian carnivore by giving multi-unit alarm barks (similar to those by adult males shown in Figs. 1-3), while females and younger juveniles responding to the same predator gave shrill, abrupt calls (similar to that of female LB in Figs. 1 and 2). Struhsaker also suggested that certain other alarm calls were given exclusively or primarily by members of particular age/sex classes. Adult males, for example, rarely gave snake alarms, and were never observed to alarm at an avian predator. During this study, individuals of all ages and both

sexes were heard on at least one occasion to give appropriate alarms to each of the three types of predator discussed above, although animals of different age and sex alarmed more at some types of predator than others (Cheney & Seyfarth, in press.)

Struhsaker found that the alarm calls of adult males to mammalian carnivores differed acoustically from those of adult females and juveniles. In this study, females and juveniles gave shrill, single-unit alarm calls on 8 of the 12 occasions that leopards were encountered. On all other occasions (33%), however, adult females gave multi-unit alarm barks similar to those of adult males (Fig. 4). It was our impression that adult females were more likely to give multi-unit rather than single-unit alarms if the predator was in close proximity or actually attacking a member of the group. Whether juveniles gave

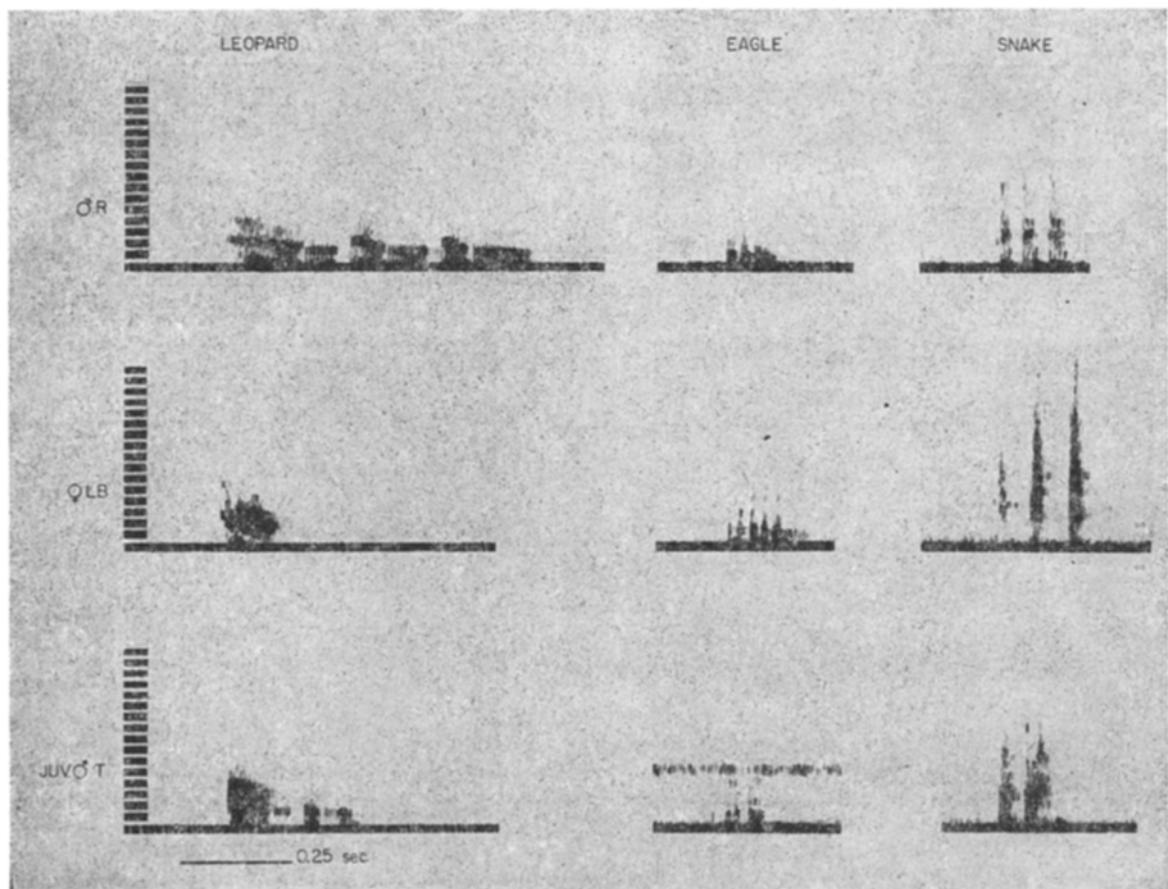


Fig. 2. Legend as in Fig. 1, except Y-axis now runs to 16 kHz.

single- or multi-unit alarms seemed to depend on a number of factors, including age, sex, and the characteristics of a particular interaction with a predator. Older juveniles were more likely than younger juveniles to give multi-unit alarms; juvenile males were more likely to do so than juvenile females; and all juveniles were more likely to do so when predators were nearby or attacking. In Figs 1 and 2, the leopard alarm of juvenile male T is intermediate between a single-unit call (like that of female LB) and a multi-unit alarm (like that of male R). Note that the first unit of T's alarm is similar to female LB's alarm call, whereas subsequent units in T's alarm resemble the later units of male R's alarm call.

Finally, it should be emphasized that, as in Struhsaker's study, each type of alarm call

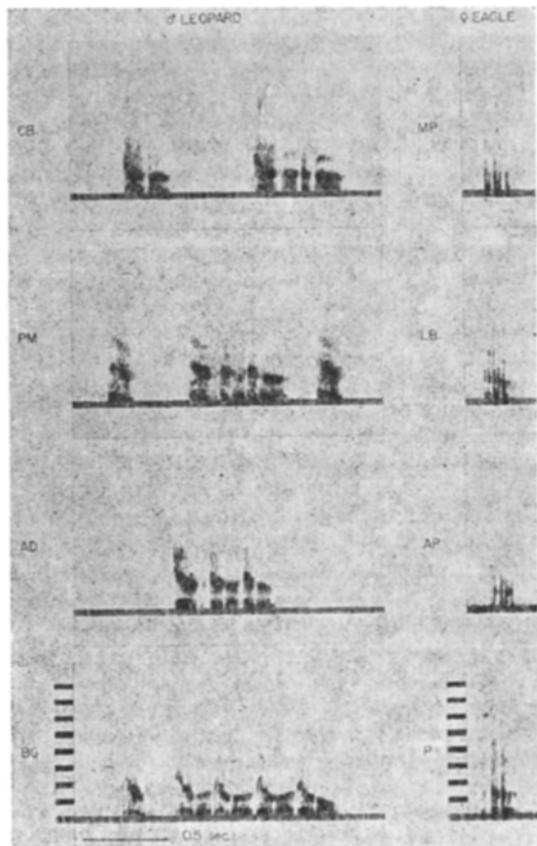


Fig. 3. Representative leopard alarms by four adult males (CB of Group C; PM, AD, and BG of Group A), and representative eagle alarms by four adult females (MP and LB of Group A; AP and P of Group C). Legend as in Fig. 1.

seemed easily distinguishable to the human ear. To test this impression, in the early months of the study we made tape recordings of a number of different alarm calls, classifying each without the benefit of spectrographic analysis. A similar 'blind' classification was made with other types of vocalizations. Sound spectrograms of each of these calls were then prepared and compared with our field classifications. In all cases, classification of alarm calls by ear agreed with their division into three categories by examination of spectrograms. No alarm call was ever confused with another type of vocalization, or vice versa.

3. Responses to alarm calls. When a monkey uttered an alarm call, observers were usually in a position to observe the responses of from 5 to 20 individuals. Taking data only from those cases in which the response(s) of at least one monkey other than the alarmist could be observed, Table IV shows the distribution of responses to leopard, eagle, and snake alarms when monkeys were on the ground and in the trees. These data represent all occasions when a leopard, eagle, or snake alarm was given, regardless of whether or not a predator was actually identified. Two points are worth emphasizing. First, the responses listed are those that were most apparent to the observers, and the list is by no means exhaustive. It is entirely possible, for example, that the monkeys showed subtle responses to alarm calls which we did not observe (see also below). Second, data represent only responses to 'first' alarms; that is, the first alarm to be given in any bout of alarming, where bouts were separated by alarm-free intervals of at least 15 min. By considering only first alarms, we ensure that the data are drawn from independent observations, uncomplicated by responses that may have occurred only after a number of monkeys had alarmed. In 38% of all bouts of alarming initiated by adults or juveniles when a predator could be identified ($N = 245$ bouts), first alarms were followed by alarm calls from other individuals. When such alarmists were adults or juveniles, their alarm calls tended to be of the same type as the first alarm call, so that leopard alarm calls were followed by more leopard alarm calls, eagle alarm calls by more eagle alarm calls, and so on. When infants joined in, however, they sometimes called differently.

Data in Table IV support Struhsaker's (1967a) observation that each type of alarm call evoked a response or set of responses that differed qualitatively from the responses evoked by

other types of alarm calls. When monkeys were on the ground, they responded to leopard alarms by Running into Trees, while the most common response to eagle alarms was to Look Up or Run into Cover. Running into Cover was defined as running into a bush rather than a tree, and remaining either on the ground or less than 1.5 m off the ground while within the bush. Monkeys on the ground commonly responded to snake alarms by looking down and/or approach-

ing the snake. In many cases, monkeys were observed to 'mob' snakes, as described by Struhsaker (1967a, p. 305). Such mobbing seemed to be similar to the mobbing of snakes by ground squirrels, prairie dogs, and other mammals (Coss & Owings 1978; Owings & Owings 1979). When the monkeys were in trees, leopard alarms evoked no apparent response (Table IV, see also below), although on two occasions animals ran higher into the

Table II. Results of Statistical Comparison between Eagle Alarms and Intra-Group Grunts, Using a Number of Acoustical Features

Individual	Group	Significantly different feature(s)	Direction of difference
Ad. δ R	C	1*	Eagle alarm > grunt
Ad. φ LB	A	2** 3**	Eagle alarm > grunt Eagle alarm > grunt
Ad. φ AP	C	1** 5* 6**	Eagle alarm > grunt Eagle alarm > grunt Grunt > eagle alarm
Ad. φ MP	A	3*	Eagle alarm > grunt

Features tested were: 1, frequency of strongest energy band; 2, frequency of highest energy band; 3, frequency of highest energy overall; 4, frequency of lowest energy band; 5, number of units; 6, unit length. * = $P < 0.05$, ** = $P < 0.01$, two-tailed t -test.

Table III. Results of Statistical Comparison between Snake Alarms and Inter-Group Chutters (Left Column) and between Snake Alarms and Intra-Group Chutters (Right Column)

Individual	Group	Snake alarm versus inter-group chutter		Snake alarm versus intra-group chutter	
		Significantly different feature(s)	Direction of difference	Significantly different feature(s)	Direction of difference
Ad. δ R	C	N/A	N/A	2* 3*	alarm > chutter alarm > chutter
Ad. δ W	A	N/A	N/A	3*	alarm > chutter
Ad. φ LB	A	N/A	N/A	1** 2* 3*	alarm > chutter alarm > chutter alarm > chutter
Ad. φ P	C	1** 6**	alarm > chutter alarm > chutter	2*	alarm > chutter
Ad. φ AP	C	1* 2* 3*	alarm > chutter alarm > chutter alarm > chutter	N/A	N/A
Ad. φ L	C	3* 7*	alarm > chutter chutter > alarm	1* 5*	alarm > chutter chutter > alarm

Features tested were: 1, frequency of strongest energy band; 2, frequency of highest energy band; 3, frequency of highest energy overall; 4, frequency of lowest energy band; 5, unit length; 6, inter-unit interval; 7, phrase length. * = $P < 0.05$; ** = $P < 0.01$, two-tailed t -test. N/A = no recordings available.

tree. The most common response to eagle alarms was to look up or to run out of the tree, and the most common response to snake alarms was to look down and/or to approach the predator. There was no indication that the alarm calls of one age/sex class were more or less likely to evoke responses than the alarm calls of other age/sex classes.

C. Discussion

Any consideration of a functionally 'semantic' form of communication by free-ranging apes or monkeys must take into account how such a highly specialized communication system might

be used, and what sorts of selective pressures might favour its evolution over the evolution of other forms of communication. Given what is known about the hunting behaviour of leopards, eagles, and snakes, the qualitatively different responses shown by vervets to each type of alarm call seem to represent an appropriate strategy for escaping from each type of predator. To a degree, these escape strategies are mutually exclusive. For example, vervets seem best able to escape attacks from leopards by running into trees, but this behaviour may increase the monkeys' susceptibility to eagle attacks. Similarly, while running into cover may permit vervets

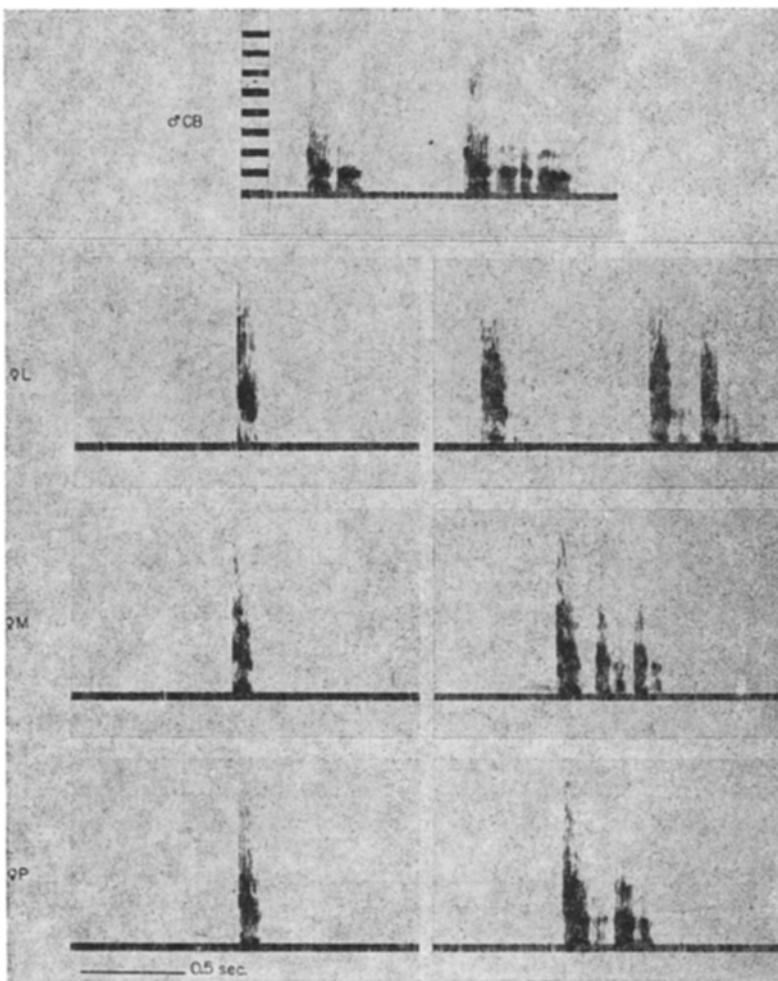


Fig. 4. Leopard alarms of adult male CB (top row), and representative single-unit (left) and multi-unit (right) leopard alarms by adult females L, M, and P (Group C). Legend as in Fig. 1.

to escape eagle attacks, it may expose them to attacks by leopards. Since the different predators of vervets seem to demand different responses, selection should favour an alarm call repertoire with sufficient referential specificity (Marler 1977) to signal unambiguously different types of danger.

The results described above support Struhsaker's earlier observations that vervet monkeys give acoustically distinct alarm calls to different types of predators and seem to respond differently to each type of alarm. However, there are still potential ambiguities in the interpretation of these results. Most serious is the possibility that monkeys who were apparently responding to an alarm call might in fact have seen the predator themselves. Differences in responses might therefore have been due simply to the perception of different predators, in which case acoustic differences between alarm calls would be irrelevant. Moreover, it is also possible that our perception of the monkeys' responses was affected by our expectations of what a 'correct' response should be. In gathering data on responses to alarms, observers were inevitably biased, not only in favour of those responses that to us were more salient than were others, but also in favour of responders as opposed to non-responders. It was our impression that many animals, including

the alarmists themselves, often showed no obvious responses to alarm calls. If this were indeed the case, non-responders would have an important effect on our interpretation of the 'meaning' of each call to the monkeys. Yet the lack of a response is difficult both to observe and to quantify under natural conditions. With these points in mind, we decided to conduct a series of field experiments in which tape-recordings of leopard, eagle, or snake alarms given by known individuals would be played to the monkeys in the absence of actual predators.

Part II: Experimental Playback of Vervet Monkeys' Alarm Calls

A. Experimental Design and Methods

Playbacks of the alarm calls of vervet monkeys were conducted on two groups (A and C) between July 1977 and May 1978. The calls used were tape-recorded from known individuals during actual encounters with leopards, eagles, and snakes (see Part I, A). Playbacks were divided among the alarm calls of adult males, adult females, and juveniles. We set a number of conditions to be met before an experiment could be conducted. Within the limits set by these conditions, experiments were conducted opportunistically. No two trials were ever conducted on the same group within 24 h of each other, and the order in which alarm call types were

Table IV. The Number of Occasions When at Least One Individual Showed a Particular Response to a Given Type of Alarm

Ground		Responses			
Alarm type		Run into tree	Run into cover	Look up	Look down
Leopard	20	1			
<i>N</i> = 29					
Eagle	6	26	64		
<i>N</i> = 108					
Snake	1	2		8	7
<i>N</i> = 16					
Tree		Responses			
Alarm type		Run higher in tree	Run out of tree	Look up	Look down
Leopard	2				
<i>N</i> = 24					
Eagle	1	2	10		
<i>N</i> = 33					
Snake				8	9
<i>N</i> = 10					

N = Number of occasions when each type of alarm was given as a first alarm. Upper table shows responses when monkeys were on the ground; lower table shows responses when monkeys were in a tree.

played to each group was randomized. As much as possible, each call was used only once, and the calls of a given individual were played only to the members of its own social group. No playbacks were ever conducted within 30 min of natural production of alarm calls, either by a member of the study groups or by the members of other vervet groups within earshot.

When conducting an experiment, we first waited until at least one adult male, two adult females, and two juveniles were close enough together that they could be filmed. If an infant was present, it was counted as a subject only if it was off its mother. A speaker (Perma-power half-mile hailer, model S-610) was then concealed behind a bush or tree at a mean distance of 14.7 m ($SD = 9.95$; see below) from the experimental subjects. Speaker orientation relative to the subjects was systematically varied throughout trials, so that animals received a roughly equal number of playbacks from each direction. The speaker was then connected to an Amplivox amplifier (model S702) and a Nagra III tape recorder, controlled by one of the observers at a distance from the speaker of at least 10 m. The monkeys were then filmed using a sound movie camera (Beaulieu model 5008S or Elmo model 350SL) for 10 s before and 60 s after the alarm had been played. This procedure allowed us to record the playback on the film sound track, to establish a base-line probability that the monkeys would show certain behaviours in the absence of an alarm call, and to compare baseline data with the monkeys' behaviour after playback.

Table V illustrates the number of trials in which leopard, eagle, and snake alarms were played to the monkeys in specific environmental contexts. Because of failure to fulfill the conditions placed on the timing of an experiment (see above), over 100 tests were aborted after

we had set up equipment or even begun to film. This occurred, for example, when subjects left the camera's field of view or when an adjacent vervet group began to give alarm calls. In all such cases, the trial was terminated before the alarm call had been played. All results discussed in the following sections derive from trials in which we obtained a complete filmed record.

To control for the possibility that the age or gender of the alarmist might affect the subjects' responses, trials were divided equally among the alarms of adult males, adult females, and juveniles. As noted earlier (p. 1073), leopard alarm calls by adult males, as well as some by adult females and juveniles, were longer and contained more units than other types of alarm calls. To control for the possibility that alarm call length might influence responses, we constructed long and short versions of each call type. Short versions contained a single acoustic unit and had a mean duration of 0.3 s ($SD = 0.21$). Long versions contained a mean of five units and had a mean duration of 3.7 s ($SD = 2.5$). In constructing the different versions of each call type, we exploited naturally occurring variation in calling behaviour. For example, Fig. 3 shows, in the second row, one single-unit and one multi-unit leopard alarm given by adult male PM (Group A). Similarly, Fig. 4 shows, in the bottom row, a single-unit leopard alarm given by adult female P (Group C), and a multi-unit leopard alarm given by the same female. In each case, naturally occurring variation provided material for a 'matched pair' of long and short alarms by the same individual.

Playback tapes were prepared from field recordings, chosen on the basis of their quality and freedom from background noise and distortion. Peak Nagra VU meter readings and distances from observer to alarmist were noted when original recordings were made. The calls

Table V. The Number of Times Each Type of Alarm was Played to Monkeys in Different Contexts

Alarm played	Context		
	Monkeys on the ground	Monkeys in a tree	
Leopard	19		10
Eagle		closed canopy	open canopy
	14	11	10
Snake	tall grass 10	short grass 10	10

were dubbed from one tape recorder to another with the playback level on both machines set to achieve the original VU meter reading. The dubbed tape was then played on the Nagra through the portable amplifier and speaker, in an area similar to the study site but quite separate from it. One observer listened at a standard distance from the speaker of 15 m. Levels on the playback equipment were then adjusted to deliver a sound that was judged by the listener to be normal for that type of alarm. A second listener made a second, independent judgment, and concurrence was reached on a level that was judged to simulate normal production levels.

In both Struhsaker's (1967a) study and our own, alarm call types differed systematically in amplitude: leopard alarms were louder than eagle alarms, which in turn were louder than snake alarms (see below). These natural differences in amplitude among alarm call types were preserved during playback experiments. This procedure was adopted after having prepared some playback tapes of different alarm call types at a standard intensity. While this seemed logical in some respects, it introduced complications. At high amplitudes snake alarms sounded grossly distorted, while at low levels leopard alarms sounded very distant. For these reasons, we decided instead to match natural levels of production as much as possible.

Because of the differences in amplitude among alarm call types, we elected to play eagle alarms at shorter speaker-subject distances than leopard alarms, and snake alarms at shorter distances than eagle alarms (Table VI). The actual amplitude at which the calls were delivered to the subjects was estimated in Millbrook, New York, after the field project had ended. Stimulus recordings were replayed outdoors, at the level setting used in actual experiments, and at the mean distance used during playback trials for each call type (Table VI). Intensities were measured with a General Radio sound-level meter (model 1933), using the 'A' weighting scale. Mean values and ranges of the intensity measurements for each alarm call type were as follows: leopard, $\bar{X} = 56$ dB, range 50–62; eagle, $\bar{X} = 53$ dB, range 46–57; snake, $\bar{X} = 48$ dB, range 46–50. Even at the mean distance at which each alarm call type was played during playback trials, leopard alarms remained significantly louder than eagle alarms, and eagle alarms were significantly louder than snake alarms (Kruskal-Wallis overall

one-way analysis of variance, $H = 20.9$, $P < 0.001$; two-tailed Mann-Whitney U tests, $P < 0.05$ for each paired comparison). Variation in speaker-subject distance across alarm type, however, ensured that a substantial proportion (88%) of alarm calls used as playback stimuli overlapped in amplitude with at least one alarm of another type (see below).

The data from each experiment consisted of: (1) the filmed record; (2) a narrative commentary, spoken into a tape recorder during each trial and transcribed into a written record that evening; and (3) a map, drawn to include the position and identity of each monkey, nearby trees and bushes, the speaker, the movie camera, and all human observers. As noted earlier, the primary aims of the experiment were first, to determine whether it was possible to duplicate, through playbacks, the same set of responses seen during observation; and second, to determine whether the monkeys received any cues other than the alarm itself that might have caused them to show one response rather than another. In analysing filmed records, therefore, it was necessary to define a priori a set of mutually exclusive responses, the scoring of which would be consistent throughout all experiments and conservative with respect to our hypotheses.

The responses scored during film analysis were defined as follows:

1. Run into Tree, Run into Cover, Stand Bipedally (animals on the ground only); Run Higher in Tree, Run Out of Tree (animals in trees only). These responses were unambiguous on film. For animals on the ground, the distinction between Running into a Tree and Running into Cover has already been discussed (p. 1077).

3. Look Up, Look Down, 'Scan' Since our observational results led to specific predictions about when the monkeys would respond to an alarm call by looking up or looking down, we defined these behaviours as conservatively as possible. An animal was said to have Looked Up when its head was tilted back, its face was

Table VI. The Mean Distance at Which the Speaker Was Placed from Subject Animals during Playback of Alarm Calls of Different Types

Alarm played	Mean distance (in metres) \pm SD
Leopard	20.9 \pm 11.9
Eagle	14.4 \pm 7.5
Snake	8.6 \pm 4.8

oriented straight up into the sky, and its chin was pointed into the air. Looking Down occurred when an animal faced straight down toward the ground, with its chin close to or touching its chest. Whenever an animal oriented its face somewhere in between these two extremes, the behaviour was scored as 'Scanning'. Scanning fell into three categories: (a) Look in the Direction of the Speaker, (b) Look in Any Direction Other than the Speaker, and (c) Look at Other Monkeys. 'Looks' were defined as occurring whenever an individual made a head movement that resulted in the orientation of its face directly at the speaker or another monkey (Cheney & Seyfarth 1980). When a monkey looked at others, their identities were recorded.

Some response categories could occur simultaneously. For example, an animal could be scored as 'looking in a direction other than the speaker' and 'looking at individual X' at the same time. Other response categories, however, were mutually exclusive by definition. Because of the difficulty of scoring the gaze of rapidly moving animals, for example, responses entailing locomotion superseded Looking or Scanning. By this scoring procedure, therefore, an individual could not both Run and Look at the same time.

Films were scored independently by two people, one of whom had not participated in the experiments. In cases where the two disagreed on the occurrence of a particular response,

the more conservative score relative to our hypothesis was accepted. Two measures were used to score films. Latency to respond to an alarm was measured by counting the number of frames from the onset of an alarm call on the film sound track to the first indication that an animal had begun to show a particular behaviour. Duration of response was measured by the number of frames, up to a maximum of 180 (10 s), during which an animal showed a given response. Bout lengths were not distinguished in calculating duration. For example, an individual could look up for a total of 60 frames either in one bout of 60 frames or three bouts of 20 frames each.

B. Results

1. Responses to alarm call playbacks. Table VII shows the number of leopard, eagle, or snake alarm playbacks in which at least one subject showed more of a given behaviour in the 10 s after playback than in the 10 s before it. Data on those cases in which alarms caused one or more subjects to show a decrease in the duration of any behaviour listed are not shown because (a) this occurred in less than 5% of all trials, (b) no alarm type significantly decreased the duration of any of the behaviours listed (cf. below, Tables X and XI), and (c) alarm types did not differ significantly in their ability to decrease the duration of any behaviour (cf. below, Table VIII). Two conclusions emerge from the results in Table VII.

Table VII. The Number of Trials involving Playback of Different Alarm Types in Which at Least One Animal showed a Given Response for Longer in the 10 s After Playback than in the 10 s Before Playback

Ground		Responses						
Alarm		Look toward Speaker	Scan	Run into Tree	Run into Cover	Look Up	Stand Bipedally	Look Down
Leopard (19 trials)		10	10	8	2	4	9	1
Eagle (14 trials)		12	11	2	6	7	6	4
Snake (19 trials)		19	19	2	2	2	12	14
Tree		Responses						
Alarm		Look toward Speaker	Scan	Run Higher in Tree	Run Out of Tree	Look Up	Look Down	
Leopard (10 trials)		9	8	4	0	3	4	
Eagle (17 trials)		16	14	4	5	11	12	
Snake (9 trials)		5	6	2	0	5	9	

First, all three types of alarm usually caused one or more individuals to look in the direction of the speaker (or toward what under natural conditions would be the alarmist) and to scan in other directions, for longer after playback than before. Results support Struhsaker's (1967a) impression that all three types of alarm are easily localizable. The monkeys behaved as if they were searching for additional cues, both from the alarmist and elsewhere. It seems likely that, although unrecorded in naturally occurring alarms, both looking in the direction of the alarmist and scanning in other directions also occurred during these alarms.

Second, although two responses were common to all alarm types, some alarm types were also more likely than others to elicit certain responses. For example, when monkeys were on the ground, leopard alarms caused at least one subject to look down for longer in the 10 s after playback than in the 10 s before it in one of 19 trials. Eagle alarms produced similar results in 4 of 14 trials, and snake alarms in 14 of 19 trials. In analysing these results statistically, sample size usually precluded an overall test across all alarm types (e.g. Sokal & Rohlf 1969, p. 565). Fisher Exact Probability Tests

were therefore used to compare responses. In the example cited above, snake alarms were significantly more likely than either leopard or eagle alarms to cause animals on the ground to look down ($P < 0.05$).

Table VIII presents the results of all statistical tests in which responses to alarm types were found to differ significantly. Note that, for most behaviours listed in Tables VII and VIII, one-tailed tests were used. This was because both Struhsaker's (1967a) earlier study and our own observations prior to experimentation (see Part I, B) led to the following *a priori* predictions: (1) when monkeys were on the ground, leopard alarms would be more likely than either eagle or snake alarms to cause animals to Run into Trees, eagle alarms would be more likely to cause animals to Look Up or Run into Cover, and snake alarms would be more likely to cause animals to Look Down; (2) when animals were in trees, leopard alarms would be more likely to cause animals to Run Higher in Trees, eagle alarms would be more likely to cause animals to Look Up or Run Out of the Tree, and snake alarms would be more likely to cause animals to Look Down. In analysing behaviours that occurred during experimentation for which no

Table VIII. Results of Statistical Comparisons of Responses to Playbacks Across Alarm Types

Ground		Responses				
Alarm		Run into Tree	Run into Cover	Look Up	Stand Bipedally	Look Down
Leopard (19 trials)	(E)S*					
Eagle (14 trials)		L S		S (L)		
Snake (19 trials)						L*E*
Tree		Responses				
Alarm		Run Higher in Tree	Run Out of Tree	Look Up	Look Down	
Leopard (10 trials)						
Eagle (17 trials)		(L)(S)		(L)		
Snake (9 trials)						L*(E)

Entries in each cell indicate that the alarm in a given row caused one or more individuals to show a given response in a significantly larger number of trials when compared with one or both other alarm types. Thus for animals on the ground, leopard alarms caused one or more individuals to run into trees in a significantly larger number of trials than did either eagle, E, or snake, S, alarms. See text for method of calculation. Levels of significance indicated as follows: letter in parentheses = $0.05 < P < 0.10$; letter alone = $0.01 < P < 0.05$; starred letter = $P < 0.01$.

explicit prediction had been made (e.g. Look toward Speaker, Scan, Stand Bipedally), two-tailed tests were used.

As results in Table VIII indicate, the predictions outlined above were generally supported by experiments. When animals were on the ground, leopard alarms were more likely than other types of alarm to cause them to Run into Trees, eagle alarms were more likely to cause animals to Run into Cover and/or Look Up, and snake alarms were more likely to cause them to Look Down. When animals were in trees, results were less conclusive. However, eagle alarms were more likely to cause animals to Run Out of the Tree and/or Look Up, and snake alarms were more likely to cause them to Look Down.

The preceding analysis is conservative because it treats each trial as an independent event, and makes no assumptions about the extent to which individuals in any given trial responded independently of one another. The analysis, however, makes no distinctions among individual subjects within each trial. Thus results shown in Table VIII might have occurred, for example, because only infants and juveniles, but not adults, responded differently to each alarm type. If this were so, our analysis would over-emphasize the extent to which different alarms produced different responses. Conversely, by giving equal weight in a given trial to behaviour shown by a single individual and to behaviour shown by many individuals, our analysis might actually blur distinctions among the responses most commonly evoked by each alarm type. With these points in mind, the following sections consider whether subjects responded independently of one another, and whether

results were consistent across individual subjects.

2. Were responses independent? To test whether individuals responded independently of one another, films were re-examined to determine how many animals showed a particular response to an alarm only after first looking at another animal who had already begun that same response. We found this to occur in an average of 25% of all cases (Table IX). By this criterion, responses of individual subjects appeared to be largely independent of the behaviour of other individuals. Interestingly, however, infants were the individuals most likely to look at others before responding (Seyfarth & Cheney, in press).

3. Responses by individuals in different age/sex classes. To test whether results were consistent across individual subjects, the duration of a particular behaviour by a given individual in the 10 s before playback was compared with the duration of the same behaviour by the same individual in the 10 s following playback. If an individual appeared in more than one trial of a given type (e.g. leopard alarm playback on the ground), the mean duration of each behaviour by that individual before and after playback was used for analysis. Each individual thus served as its own control, and the members of each age/sex class could be tested using a matched-pairs signed ranks test. Results are shown in Tables X and XI. As noted earlier, two responses were common to all alarm types: leopard, eagle, and snake alarms consistently caused the members of most age/sex classes to look in the direction of the speaker, and to scan in other directions, for significantly longer after alarms than before (Table X). In addition

Table IX. The Number of Animals in Playback Experiments who Showed a Given Response With or Without First Looking at Another Animal who had Already Begun That Same Response

Responders		Run into Tree	Run into Cover	Run Higher in Tree	Run Out of Tree	Look Up	Look Down	Total
Adult ♂♂	with without	3 5	2 4	0 2	1 1	10 1	1 16	8 38
Adult ♀♀	with without	3 10	3 3	0 1	2 1	6 19	3 26	17 60
Juveniles	with without	7 18	10 9	2 9	6 4	3 18	5 26	33 84
Infants	with without	5 3	1 3	2 6	0 0	1 4	2 6	11 22

to the responses that occurred after all types of alarm, each alarm type also elicited a distinct set of responses (Table XI). Such responses were generally consistent across age/sex classes. When monkeys were on the ground, leopard alarms caused adult males, adult females, and juveniles to Run into Trees. Eagle alarms had no significant effect on adult male behaviour, but caused adult females and juveniles to Look Up and/or Run into Cover. Snake alarms caused adults and juveniles to Look Down and/or Stand Bipedally. When animals were in trees,

leopard alarms had no significant effect on adult behaviour. Juveniles, however, responded by Running Higher in the Tree. Eagle alarms caused adult females to Look Up and juveniles to Look Down. The Look Down response to eagle alarms by juveniles appeared to be related to the manner in which they ran out of the tree upon hearing the alarm. When Running Out of a Tree, juveniles usually did so in spurts: Run, stop and Look Down (perhaps in search of a good hand- or foot-hold), Run, stop and Look Down, and so on.

As Table XI indicates, alarm call playbacks did not significantly alter the behaviour of all individuals. Infants and adult males were particularly likely to show no statistically significant responses (other than Looking at the speaker and Scanning). Three factors could have contributed to this apparent lack of response. First, for adult males and infants, sample size was generally smaller than for adult females and juveniles, and Wilcoxon tests in some cases could not be carried out. Second, the responses of infants to alarm calls of different types tended to be more generalized than those of adults and juveniles (Seyfarth & Cheney, in press). Third, the apparent failure of adult males to respond consistently to alarm calls (particularly eagle alarms) may have been related to the males' relative lack of vulnerability to such predators (Cheney & Seyfarth, in press).

The consistency of results across age/sex classes was also tested by comparing types of alarms against each other, in order to determine whether, for the members of a given age/sex class in a given context, certain alarm types were more likely than others to elicit particular responses. For the purposes of this analysis, only those monkeys who showed a given behaviour for longer after playback than before it were considered to have responded to an alarm. Individuals who participated in more than one trial of a given type were scored as having responded only if the mean duration of a particular behaviour in the 10 s before playback was less than the mean duration of the same behaviour in the 10 s after playback. Table XII presents data on the number of individuals in each age/sex class who responded to a given type of alarm with a given behaviour. Table XIII presents the results of statistical comparisons within each age/sex class and across alarm types, and indicates which responses were significantly more likely to occur when alarms of one type were played, compared with when alarms of

Table X. Results of Wilcoxon Tests on Two Behaviours Shown by Subjects Before and After Playback

Ground		Responses	
Alarm	Responders	Look toward Speaker	Scan
Leopard 19 trials	8♂♂	X*	
	14♀♀	X*	X
	16 Juv.	X	X
	8 Inf.	X	X
Eagle 14 trials	9♂♂	X*	(X)
	13♀♀	X*	
	15 Juv.	X*	
	7 Inf.	(X)	
Snake 19 trials	9♂♂	X*	
	16♀♀	X*	X*
	14 Juv.	X*	
	11 Inf.	(X)	X
Tree			
Leopard 10 trials	4♂♂	Look toward Speaker	Scan
	7♀♀	X	(X)
	11 Juv.	X*	
	1 Inf.		
Eagle 17 trials	7♂♂	(X)	
	15♀♀	X	
	15 Juv.	X*	
	8 Inf.		
Snake 9 trials	4♂♂		
	8♀♀		
	13 Juv.		
	6 Inf.		

Left-hand columns indicate the total number of trials for each alarm type, and the total number of individuals who participated in one or more trials. Entries in each cell indicate that individuals in a given age/sex class showed a given response for significantly longer after playback than before. (X) = $0.05 < P < 0.10$; X = $0.01 < P < 0.05$; X* = $P < 0.01$, Wilcoxon matched-pairs signed-ranks test.

another type were played. When animals were on the ground, leopard alarms were significantly more likely than either eagle or snake alarms to cause animals of all age/sex classes to Run into Trees. Eagle alarms were significantly more likely than leopard or snake alarms to cause adult females and juveniles to Run into Cover and/or Look Up, and snake alarms were significantly more likely than other alarms to cause adult males and juveniles to Look Down. Similar results were obtained from experiments conducted in trees. As in earlier analyses, results were generally consistent across age/sex classes, although the responses of infants were less likely than the responses of others to differ from one alarm type to another.

It should be emphasized that all observed changes in behaviour following playbacks of alarms were non-vocal in nature. In a total of 88 experiments, only once did a monkey (a juvenile) respond to an alarm call by giving an alarm itself. In contrast with the chorusing that occurs in natural predator encounters, playbacks did not increase the probability that monkeys would utter alarms. Under natural conditions, animals other than the first alarmist presumably sight the predator and then call. In doing so, they may be guided by the caller's gaze. Thus visual cues may contribute to natural chorusing, supplementing the first alarm.

4. Response differences due to the age/sex class of the alarmist. Observations of natural

Table XI. Results of Wilcoxon Tests on the Behaviour of Subjects Before and After Playback

Ground		Responses				
Alarm	Responders	Run into Tree	Run into Cover	Look Up	Stand Bipedally	Look Down
Leopard 19 trials	8♂♂ 14♀♀ 16Juv. 8Inf.	X X* X*				
Eagle 14 trials	9♂♂ 13♀♀ 15Juv. 7Inf.		X*	X (X)	X	
Snake 19 trials	9♂♂ 16♀♀ 14Juv. 11Inf.				X* X	(X) X
Tree		Responses				
Alarm	Responders	Run Higher in Tree	Run Out of Tree	Look Up	Look Down	
Leopard 10 trials	4♂♂ 7♀♀ 11Juv. 1Inf.		X			
Eagle 17 trials	7♂♂ 15♀♀ 15Juv. 8Inf.		X	X	X	
Snake 9 trials	4♂♂ 8♀♀ 13Juv. 6Inf.				X	

Legend as in Table X.

encounters with predators indicated that the members of different age/sex classes were not equally likely to alarm at different predators. Adult males, for example, were significantly more likely to alarm at leopards than at eagles or snakes (Cheney & Seyfarth, in press). This raises the possibility that, in playback trials, different alarms produced different responses not because of differences in the acoustic features of different types of alarms but because monkeys responded differently to the alarms of animals of different age and sex. This hypothesis was tested in two ways.

First, comparisons were made among the alarms of adult males, adult females, and juveniles on the null hypothesis that the age/sex

class of the alarmist should have no effect on the number of subjects who showed a particular response to a given type of alarm. All alarm types and responses shown in Tables VII–XIII were tested in this way. Significant differences were found only during leopard alarm playbacks (Table XIV), and no single age/sex class was disproportionately responsible for the differences. Furthermore, although the alarm calls of one age/sex class occasionally caused more subjects to respond than did the alarm calls of another age/sex class, in no case did such differences blur the qualitative distinctions in response shown to different types of alarm.

In a second test to determine whether different alarms produced different responses solely

Table XII. Responses Elicited by Playback of Leopard, Eagle, and Snake Alarms

Ground		Responses						
Alarm	Responders	Look at Speaker	Scan	Run into Tree	Run into Cover	Look Up	Stand Bipedally	Look Down
Leopard 19 trials	8♂♂	8	6	6	0	2	3	0
	14♀♀	10	8	7	0	2	4	2
	16Juv.	9	9	11	3	1	3	0
	8Inf.	7	6	4	1	1	4	0
Eagle 14 trials	9♂♂	7	4	0	2	1	0	1
	13♀♀	13	8	1	4	6	2	2
	15Juv.	12	5	2	9	4	6	1
	7Inf.	5	3	0	3	2	2	1
Snake 19 trials	9♂♂	9	6	1	2	1	2	5
	16♀♀	12	14	0	2	0	8	6
	14Juv.	11	9	3	4	1	6	6
	11Inf.	5	7	0	1	0	4	3
Tree								
Alarm	Responders	Look at Speaker	Scan	Run Higher in Tree	Run Out of Tree	Look Up	Look Down	
Leopard 10 trials	4♂♂	4	2	2	0	1	1	
	7♀♀	6	5	1	0	0	2	
	11Juv.	9	4	6	0	1	3	
	1Inf.	1	0	1	0	1	0	
Eagle 17 trials	7♂♂	5	3	0	2	3	3	
	15♀♀	11	10	0	2	6	8	
	15Juv.	12	4	1	6	5	8	
	8Inf.	5	3	4	1	1	1	
Snake 9 trials	4♂♂	2	1	0	0	2	2	
	8♀♀	4	2	0	0	3	6	
	13Juv.	4	4	0	0	0	6	
	6Inf.	4	4	0	0	0	3	

Legend as in Table X. Numbers in each cell represent the number of individuals who showed a given response for longer after playback than before it.

because of differences in the age/sex class of the alarmist, we rearranged our data according to the age/sex class of the alarmist and without regard to the acoustic properties of each alarm call. As Table XV demonstrates, no significant differences emerged, indicating that experimental results cannot be explained solely in terms of different response biases according to the age or sex of the alarmist.

5. Response differences due to the length of alarm calls. Leopard alarms, particularly those of adult males, were generally longer and contained more units than eagle or snake alarms (see p. 1073). This raises the possibility that different responses to playbacks occurred primarily because of differences in alarm call length,

with differences in acoustic morphology being of only secondary importance. In field playbacks involving ground squirrels (*Spermophilus beecheyi*), an increase in the number of whistle alarms produced qualitatively different responses (Leger et al. 1979).

To test this hypothesis, paired comparisons were made between responses in a given context to the long and short versions of each alarm call type by the members of each age/sex class. Again, all possible combinations of alarm type and response were considered. Of a total of 78 possible paired comparisons, six showed significant differences (Table XVI). In five of the six cases, 'long' alarms were more effective than 'short' alarms in eliciting a given response. It

Table XIII. Results of Statistical Comparisons Within a given Age/Sex Class and Across Alarm Types

Ground		Responses				
Alarm	Responders	Run into Tree	Run into Cover	Look Up	Stand Bipedally	Look Down
Leopard 19 trials	8♂♂	E*S				(E)
	14♀♀	E S*				
	16Juv.	E*S*				
	8Inf.	E S				
Eagle 14 trials	9♂♂					
	13♀♀	L				
	15Juv.	L(S)		(L)S*		
	7Inf.					
Snake 19 trials	9♂♂					L(E)
	16♀♀				(E)	
	14 Juv.					L*E
	11Inf.					
Tree		Responses				
Alarm	Responders	Run Higher in Tree	Run Out of Tree	Look Up	Look Down	
Leopard 10 trials	4♂♂					
	7♀♀					
	11Juv.	E S*				
	1Inf.					
Eagle 17 trials	7♂♂					
	15♀♀					
	15Juv.	L S		(L)		
	8Inf.			S		
Snake 9 trials	4♂♂					
	8♀♀					(L)
	13Juv.					
	6Inf.					

Legend as in Table VIII.

should be emphasized, however, that while long alarms were occasionally more salient than short alarms, differences due to alarm call length occurred in less than 10% of all possible cases; and changes in call length did not blur the qualitative distinctions among the responses evoked by each type of alarm.

6. Differences due to the amplitude of alarm calls. There were significant differences in the amplitude of each type of alarm call, even given the adjustments of distance at which playbacks were conducted (see above, Part II, A). It

might therefore be argued that differences among responses to each type of alarm occurred primarily because of differences in amplitude among the various calls. Leger et al. (1979), for example, found qualitative differences in responses by ground squirrels (*Spermophilus beecheyi*) when the amplitude of whistle alarms was increased.

In order to test whether variation in response was due to differences in amplitude, we first selected a subset of leopard, eagle, and snake alarms, given by adult males, adult females,

Table XIV. Differences in the Effectiveness of Alarms by the Members of Different Age/Sex Classes

Alarm	Context	Difference	Response
Leopard	Ground	♂ > Juvenile	Run into Tree
Leopard	Ground	♀ > Juvenile	Run into Tree
Leopard	Tree	♂ > ♀	Run Higher in Tree
Leopard	Tree	Juvenile > ♀	Run Higher in Tree

Table shows all cases in which, for a particular type of alarm in a given context, alarms by the members of one age-sex class were significantly more likely than alarms by another age-sex class to elicit a particular response. All differences significant at 0.05 level, based on two-tailed χ^2 or Fisher Exact Probability Tests.

Table XV. Relation between the Age/Class of an Alarmist and Responses Elicited by Playback, Regardless of the Acoustic Features of Alarms

Ground		Responses			
Alarmist		Run into Tree	Run into Cover	Look Up	Look Down
Adult male N = 17		6 (3.5)	3 (2.9)	1 (3.8)	6 (5.8)
Adult female N = 15		2 (3.7)	3 (3.1)	5 (4.0)	7 (6.2)
Juvenile N = 17		4 (4.8)	4 (4.0)	7 (5.2)	7 (8.0)
$\chi^2 = 5.9, df = 6, \text{ns}$					

Tree		Responses			
Alarmist		Run Higher In Tree	Run Out of Tree	Look Up	Look Down
Adult male N = 14		4 (3.5)	1 (2.3)	9 (7.3)	9 (10.0)
Adult female N = 10		2 (2.6)	3 (1.7)	5 (5.4)	7 (7.4)
Juvenile N = 11		3 (3.0)	2 (2.0)	5 (6.3)	10 (8.7)
$\chi^2 = 3.0, df = 6, \text{ns}$					

N = number of playbacks involving an alarm by a member of each age-sex class. Numbers in each cell represent the number of experiments in which one or more subjects showed a given response for longer after playback than before. Expected values in parentheses.

and juveniles, that did not differ significantly in amplitude (Kruskal-Wallis one-way analysis of variance, $df = 2$, $H = 3.95$, $P > 0.10$). The experimental trials in which these alarm calls were played were then subjected to the same statistical tests as those shown in Tables VIII, XI, and XIII. An example of one such test is shown in Table XVII. Results indicate that significant qualitative differences in the monkeys' responses to leopard, eagle, and snake alarms still existed even when call types did not differ significantly in amplitude. Experimental results could therefore not have been due solely to differences in the amplitude of each call type.

C. Discussion

1. The semantic attributes of the alarm calls of vervet monkeys.

The qualitatively different

responses elicited by experimental playbacks of leopard, eagle, and snake alarms demonstrate that alarm calls alone, even in the absence of actual predators, provided the monkeys with sufficient information to make distinct and apparently adaptive responses. Variation in the age/sex class of the alarmist, alarm call length, and amplitude—although probably important—did not blur distinctions among major response categories. Variation in the acoustical structure of different alarm call types was the only feature both necessary and sufficient to explain observed differences in response. The monkeys behaved as though each alarm call designated specific objects or events in the external world.

It is, of course, a difficult task to establish the precise meaning to the monkeys of each alarm type: eagle alarms, for example, may have

Table XVI. Results of Paired Comparisons between Long and Short Versions of Each Alarm Call

Alarmist	Alarm	Context	Difference: long versus short	Response
Adult ♂	Leopard	Ground	long > short	Run into Tree
Adult ♀	Leopard	Ground	long > short	Run into Tree
Adult ♂	Eagle	Tree	long > short	Run Out of Tree
Adult ♂	Eagle	Tree	long > short	Look Up
Adult ♀	Eagle	Ground	long > short	Run into Cover
Juvenile	Eagle	Ground	short > long	Run into Cover

Table shows all cases in which, for a particular type of alarm in a given context by members of a given age/sex class, alarms of one length were significantly more likely than alarms of another length to elicit a given response. All differences significant at 0.05 level, based on two-tailed χ^2 or Fisher Exact Probability Tests.

Table XVII. Results of Experimental Playbacks in Which Alarm Amplitude was Controlled

Ground		Responses				
Alarm	Responders	Run into Tree	Run into Cover	Look Up	Stand Bipedally	Look Down
Leopard	5 ♂♂ 5 ♀♀ 6 Juv. 3 Inf.	E*S*				
Eagle	7 ♂♂ 12 ♀♀ 15 Juv. 5 Inf.		L S	S		
Snake	8 ♂♂ 13 ♀♀ 11 Juv. 9 Inf.				(L)E L L E	

Legend as in Table VIII.

referred to a particular species of raptor, a class of avian predator, a certain escape strategy, or all of these designations. There are limits to how far a semantic analysis of signals can be carried when it is based solely on the responses that those signals evoke (Marler 1961). Nevertheless, it seems appropriate to conclude that the alarm calls of vervet monkeys designate particular external referents (see Hockett 1960; Altmann 1967). Certainly the calls are arbitrary and non-iconic, in the sense that 'they do not resemble in physical contours what they denote' (Altmann 1967; Green & Marler 1979). Arbitrariness is accepted as one criterion for differentiating symbols from icons (Saussure 1916; Peirce 1940; Lyons 1977).

This view of alarm calls as a form of semantic signalling, probably involving the formation of internal perceptual concepts, or symbols, contrasts with earlier interpretations. Traditionally, animal signals have been seen as 'affective' or emotional, providing information only about the internal motivational state of the signaller and/or the probability that the signaller will engage in certain sorts of behaviour (Smith 1977, pp. 71, 181; but see also p. 182). For our present purposes, the distinction between 'affective' and 'semantic' signalling is a useful one. It provides a framework within which to assess results from this study, and it highlights the fundamentally different approaches that have been used to investigate communication among captive and free-ranging primates. As noted earlier (see introduction), research involving captive apes has shown that they can learn to use arbitrary signals to represent actions and objects, and that complex cognitive processing is involved. By contrast, studies of the same and related species in the wild (van Lawick Goodall 1968; Fossey 1972) have generally been interpreted as demonstrating that the signalling behaviour of apes reflects only different levels of arousal (e.g. Premack 1975; Savage-Rumbaugh & Rumbaugh 1978; cf. Menzel 1975).

It might also be argued that the alarm calls of vervet monkeys are simply manifestations of different levels of arousal. Differences in responses of vervets to each alarm type might be due, for example, to the fact that alarm calls somehow convey the information that leopards are more frightening than eagles and eagles are more frightening than snakes (see Premack 1975). For instance, leopard alarms were generally louder than eagle alarms, which in

turn were louder than snake alarms (Part II, A). Such amplitude differences might convey information to a listener about levels of caller arousal, thus explaining the differing responses to various alarms. Two points, however, argue cogently against this view. First, the three different types of alarm calls produced qualitatively different responses, even in those trials where amplitude levels across call types were similar (Table XVII). Second, if the alarm calls of vervet monkeys were only manifestations of different degrees of arousal of the alarmist, it might be expected that an increase in the alarmist's arousal level would have been accompanied by an increase, among other things, in the length of the alarm call (e.g. Leger et al. 1979). This in turn should have blurred the qualitative distinctions among responses to different alarm call types. However, while an increase in alarm length did increase responsiveness in some cases (Table XVI), changes in length had no effect on the qualitative distinctions among responses. It therefore seems appropriate to interpret arousal-related properties of alarm calls as ancillary to more specific call features, supplementing and enriching the meaning of calls rather than serving as a primary basis for meaning (Marler 1977).

It might also be argued that the alarm calls of vervets have no external referents, but instead convey information only about the probability of the signaller's subsequent behaviour (Smith 1977, p. 270; see Griffin 1976, p. 29). This view would seem to imply that alarms are manifestations of generalized internal states, inextricably linked physiologically to particular sets of behaviours. Such an hypothesis is difficult to test because, as noted above, it is difficult if not impossible to determine unequivocally all that an alarm 'means' to a listener, or what the physiological correlates of such meaning might be. The fact that each type of predator evoked both a limited set of alarm calls and a limited set of responses inevitably implies that there will be a predictable relationship between alarm call type and subsequent caller behaviour. This correlation does not prove, however, that alarm calls function solely to signal the probability of subsequent caller action. Monkeys were often observed to give alarm calls without exhibiting escape responses. Furthermore, they almost invariably responded to alarm playbacks without uttering alarms themselves (p. 1086). Thus the link between alarm call and escape behaviour, while real, can be severed, as might

be expected if animals were capable of operating in a 'symbolic' mode (Marler 1977).

This is not to suggest that there is no affective component to alarm calls. It is almost certainly true that monkeys responding to alarms use such features as amplitude, length, rate of delivery, and number of individuals alarming when assessing how close a predator is and whether or not it poses immediate danger. It is also entirely possible that, in evolutionary terms, alarms with different acoustical features first appeared as manifestations of different emotional states. Whatever the precise motivational basis or evolutionary history of alarm calls, however, the monkeys are clearly capable of disassociating the production of an alarm from the set of responses that the alarm normally elicits.

A second issue concerns the role of context in determining the 'meaning' of a signal. Smith (1965, 1969, 1977), for example, has argued that most animal signals do not refer to specific narrowly defined external referents. Instead, each signal is presumed to encode as its 'message' one of a small number of very generalized referents, such as 'attack', 'escape', or 'frustration'. The specificity of responses to such general signals is thought to occur largely because signals are given in different contexts. By this interpretation, the 'meaning' of each signal is highly context-dependent (Smith 1977, pp. 181, 270).

In our experiments, context was not a systematic determinant of the responses of vervets to alarm calls. Different alarms evoked different responses in the same context, and responses to some alarms remained constant despite contextual variation. For example, monkeys looked up when they heard eagle alarm calls, regardless of whether they were on the ground or in the trees. Given the variable role of context in determining responses to alarm calls, the most parsimonious explanation would appear to be that, for all those within earshot, each alarm represented a certain class of danger (see above). Individual monkeys then responded according to the nature and degree of their vulnerability to that danger at the time.

2. Are the alarm calls of vervet monkeys unique? Although there are no published reports of any non-human species with as wide an array of alarm calls as that shown by vervet monkeys, there is no reason to believe that the alarms of vervet monkeys are, in principle, unique. Struhsaker (1975), for example, describes dis-

tinct alarm calls given by red colobus monkeys (*Colobus badius*) to birds and potential ground predators. Similarly, several species of ground squirrels (e.g. *Spermophilus beecheyi*) utter different alarm calls to ground and aerial predators, and respond differently to such calls (Melchior 1971; Turner 1973; Sherman 1977; Leger & Owings 1978; Owings & Virginia 1978; see also Smith 1978). Similar predator- or danger-specific alarms are common among birds (e.g. Daanje 1941; Nice 1943; Marler 1956; Ryden 1978; Thielke 1976; Latimer 1977). There are, however, virtually no detailed studies of referential specificity in the alarms of birds or mammals. Almost nothing is known about how alarms develop, how their use may be modified during adulthood to cope with changing environmental circumstances, or how their function compares with the use of vocalizations in other social contexts. In these respects, recent data on alarms by vervet monkeys are of particular interest.

Infant vervet monkeys often make 'mistakes' when giving alarm calls and responding to the alarms of others (Seyfarth & Cheney, in press). As they grow up, infants appear to sharpen the association between specific classes of predators, particular alarm calls, and responses to such calls. Furthermore, there are hints that the monkeys have some ability to change both their alarm calls and their responses depending on the hunting behaviour of their predators. In the Cameroon forests, for example, where vervets are hunted by humans with dogs, their alarms both to humans and to dogs are soft and pitched within a frequency band that matches the ambient background noise. As a result, the calls are difficult to detect (Kavanagh 1978). The monkeys' response to these calls is to flee silently to dense bush, where humans cannot follow. In the nearby savanna, however, where vervets are not hunted by man, the monkeys flee to the tops of trees and utter loud alarms when approached by dogs.

This paper has focused on a relatively narrow and specialized subset of vervet monkey vocalizations. By far the most frequently occurring vocalizations among vervets are a graded series of grunts, uttered during social interactions (Struhsaker 1967a). Such grunts evoke few immediately obvious responses, and seem at first to be simply manifestations of different levels of arousal. On close examination, however, there are suggestions that the vervets' grunts, like their alarm calls, function in a

semantic manner. Preliminary analysis of the non-alarm vocalizations of vervets, as well as more extensive research on such vocalizations in Japanese macaques (*Macaca fuscata*) (Green 1975), indicate that subtle variants within the monkeys' graded vocal repertoire are specific to particular social contexts. At least some vocalizations are also individually distinctive (Cheney & Seyfarth 1980; see also Struhsaker 1967a; Marler & Hobbet 1975; Lillehei & Snowdon 1978). Our current understanding of these signals is in many respects similar to our understanding of alarm calls before we began experimentation. Despite a great deal of correlational data, we do not yet understand how monkeys make use of acoustical differences in those calls that seem to lack clear external referents. Having shown that alarm calls, whatever their motivational basis, can be used to convey information about external events, our next stop is to investigate whether calls used during social interactions function in a similar manner.

Acknowledgments

We thank the Office of the President, Republic of Kenya, for permission to conduct research in Amboseli National Park, and we are especially grateful to J. Kioko, the Warden of Amboseli during our project, for his help. During field work, G. Hausfater, A. Hill, D. Klein, C. Marler, T. Struhsaker, and especially P. Lee provided valuable assistance, and we are grateful to them. We thank R. Denny for the major role she played in analysing films, and A. Huessener for preparing the sonograms. Parts of the manuscript were presented in seminars or at conferences, where we received helpful comments from S. Altmann, M. Baker, C. Beer, R. Dooling, D. R. Griffin, C. Ristau, W. Searcy, and K. Yasukawa. We thank S. Green, C. Hockett, W. Searcy, T. Struhsaker, and K. Yasukawa for detailed comments on earlier drafts. Research supported by NIMH postdoctoral fellowship MHO7446 to Robert M. Seyfarth, a grant from the Wenner-Gren Foundation and a NSF National Needs postdoctoral fellowship to Dorothy L. Cheney, and National Geographic Society grant No. 1767 and NSF grant BNS 16894 to Peter Marler.

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(Received 21 September 1979; revised 31 December 1979; MS. number: A2382)