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The assessment by vervet monkeys of their own and another species' alarm calls

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Abstract. In Amboseli National Park, Kenya, both superb starlings, *Spreo superbus*, and vervet monkeys, *Cercopithecus aethiops*, give acoustically different alarm calls to different classes of predators. The 'raptor alarms' of starlings and vervet monkeys are so called because they are given exclusively to avian species that attack from the air. In contrast, while vervets give 'leopard alarms' to a narrow array of terrestrial predators, starlings give terrestrial predator alarms to a wide variety of species, including some birds. Habituation experiments demonstrate that monkeys compare vocalizations according to their referents, not just their acoustic properties: vervets who learned to ignore playback of a starling's raptor alarm subsequently also ignored playback of a vervet's eagle alarm. Experiments also demonstrate that vervets are sensitive to the breadth of referential specificity exhibited by different calls. Subjects who learned to ignore playback of a starling terrestrial predator alarm subsequently also ignored playback of both vervet leopard and vervet raptor alarms.

Free-ranging vervet monkeys, *Cercopithecus aethiops*, who have learned to ignore one type of call given by an unreliable signaller will subsequently also ignore an acoustically different call given by the same signaller, but only if the calls have similar referents (Cheney & Seyfarth 1988). After repeatedly being played an intergroup 'chutter' in the absence of other groups, vervets not only habituate to this chutter but also ignore an intergroup 'wrr' (a call with consistently different acoustic features) given by the same individual. Such transfer of habituation from one call to another does not occur, however, if the two calls have different referents. Vervets who have habituated to another monkey's leopard alarm call played repeatedly in the absence of leopards, for example, nevertheless still respond to the same signaller's eagle alarm call. Thus, vervet monkeys (and probably other non-human primates) appear to compare calls according to their meaning, not just their acoustic properties.

In this paper, we describe playback experiments designed to investigate further the criteria used by vervet monkeys when comparing vocalizations that have consistently different acoustic properties. Using the same habituation/dishabituation technique employed earlier (Cheney & Seyfarth 1988), vervets were presented with their own species' predator alarm calls and the alarm calls given by a sympatric bird, the superb starling, *Spreo superbus*.

Both vervet monkeys (Struhsaker 1967; Seyfarth et al. 1980) and starlings (Cheney & Seyfarth 1985) give alarm calls with consistently different acoustic properties to raptors and to terrestrial predators, and vervets respond to both their own alarm calls and the alarm calls of starlings as if the calls denote specific types of danger. Vervets respond to both their own and starlings' raptor alarm calls, for example, by looking up into the air or running into dense bush (see below). If monkeys compare not only their own but also other species' vocalizations according to the referents of the calls, habituation to one species' raptor (or terrestrial) predator alarm should generalize to the corresponding alarm call of the other species.

If monkeys respond to vocalizations according to the objects and events they denote, we should also expect them to be sensitive to the breadth of referential specificity exhibited by different calls. In English, for example, we use words with very specific meanings (or narrowly defined referents) like 'praying mantis' or 'banana'. We also use words like 'insect' or 'food' that denote a much broader class of objects and have, as a result, meanings that are more general. In making judgments about synonymy we take these differences into account. Sometimes praying mantis and insect can be used interchangeably; more often they cannot, because the meaning of insect is too broad.

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Vervet monkeys face similar problems when responding to the alarm calls of other species. As we describe below, the predator species that elicit alarm calls from vervet monkeys and superb starlings sometimes coincide; in other cases, however, the alarm calls differ in their degree of referential specificity. Both starlings and vervets, for example, give raptor alarm calls exclusively to avian species that attack from the air. The referents of these two calls are therefore relatively similar. In contrast, while vervets give terrestrial predator alarm calls to only a few species of carnivores, starlings give terrestrial predator alarm calls to a wide variety of species, including some birds and even occasionally vervet monkeys. As a result, the starlings' terrestrial predator alarm call is less restricted than the vervets' own leopard alarm call in the types of predators it denotes.

If vervets do indeed compare vocalizations according to their referents and are sensitive to the specificity of each call's referent, they should transfer habituation more readily when the starling/vervet comparison involves raptor, rather than terrestrial, predator alarm calls. Below, we describe a series of playback experiments by which we attempted to compare the responses of vervet monkeys to their own alarm calls and the alarm calls of superb starlings.

METHODS

Playback Experiments

Experiments were conducted over a 3-month period in 1988 on three groups of vervet monkeys (B, C and 6) living in Amboseli National Park, Kenya. Two of the groups had been observed without interruption since 1977, and one had been observed since 1983 (Cheney & Seyfarth 1987). All groups were composed of individuals of known age, sex and maternal relatedness. All monkeys were habituated to observers on foot.

We conducted two types of experiments using vervet and starling alarm calls: in the first we used alarm calls given to the same class of predators (either terrestrial predators or raptors, termed 'same referent' alarm calls); in the second we used alarm calls given to different classes of predators ('different referent' alarm calls). In all the experiments we used the same habituation/dishabituation technique employed in earlier experiments using the vervets' own intergroup and alarm vocalizations (Cheney & Seyfarth 1988).

In the same referent experiments we used alarm calls that had all originally been given to the same class of predator, either a raptor or a terrestrial predator. We began on day 1 by playing a vervet's (or a starling's) alarm call to a previously designated subject, to establish the duration of the subject's response to that call in the absence of any other prior alarm calls (the control condition). On day 2, we played a starling's (or a vervet's) alarm call to the same subject eight times (the habituation series). Playback of each alarm call was separated by a mean interval of 10 min. Then, approximately 10 min after presentation of the eighth alarm call, we played the vervet's (or starling's) alarm call (the test condition) again. In eight of the same referent experiments we used vervet and starling raptor alarm calls, while six involved the two species' terrestrial predator alarms.

In the different referent experiments, the alarm calls used in the habituating series had originally been given to a different class of predator than had the control and test alarm calls. So, for example, if a vervet's (or starling's) raptor alarm call was used in the control and test trials, a starling's (or vervet's) terrestrial predator alarm call was played in the habituation series. Conversely, when a vervet's (or starling's) terrestrial predator alarm call was used in the control and test trials, a starling's (or vervet's) raptor alarm call was played in the habituation series. Seven of the different referent experiments used raptor calls as control and test stimuli, and seven used terrestrial predator alarm calls as control and test stimuli.

Starling alarm calls were used as habituating stimuli more often than vervet alarm calls. Starling raptor alarm calls were used in 11 of the 15 experiments in which a raptor alarm call served as the habituating stimulus, and starling terrestrial predator alarm calls were used in nine of the 13 experiments in which a terrestrial predator alarm call was used as the habituating stimulus. This bias was deliberate, because we wished to avoid overexposing the monkeys to repeated playbacks of their own alarm calls. Since starling alarm calls occurred naturally at a higher rate than vervet alarm calls, frequent playback of starling alarm calls was less anomalous than frequent playback of vervet alarm calls.

The vervet alarm calls used as stimuli had all been recorded from adults of known age, dominance rank and matrilineal kinship, who had been under continuous behavioural observation for at least 4 years and who were living in our study groups at the time tests were conducted. Calls were recorded either during regular focal animal samples (Altmann 1974) on each group member, or on an ad libitum basis when other group members were being sampled. Calls were selected for use as playback stimuli on the basis of recording quality and freedom from background noise.

We used recordings from as many different individuals as possible. When vervet calls were used as habituating stimuli, we played as many different alarm calls from the same individual as possible (in all cases, alarm calls that had been recorded on different days). Control and test presentations, however, always involved exactly the same call. The starling alarm calls used as stimuli came from a large pool of calls recorded from birds in the study area (not known individually) over the past 5 years. In a habituation series of eight calls, four different calls were used. Control and test presentations, however, always involved exactly the same call.

No experiments were conducted if a natural vervet alarm call had been given on the same day. Because starlings gave alarm calls at high rates, it was not always possible to conduct trials on a day when there had been no naturally occurring starling alarms. However, in no case did we begin an experiment when starlings were already alarm calling, or within 15 min of a starling alarm. In addition, starlings often gave alarm calls (especially terrestrial predator alarm calls) in long bouts; for example, when they were mobbing a snake, monkey or lilac-breasted roller that was approaching their nest. No experiments were conducted in conjunction with such alarm call bouts. In any case, because all experiments were similarly confounded by occasional starling alarm calls, comparison of responses across different types of playback experiments should still be valid.

Our behavioural measurements of responses to calls were the same as those used in previous experiments (see e.g. Seyfarth et al. 1980; Cheney & Seyfarth 1982, 1985, 1988). Responses included looking toward the speaker, running to trees, and looking up in the air. The behaviour of subjects during the habituation series was timed with a stop watch; the behaviour of subjects during control and test presentations was filmed with a video camera. To determine whether habituation across the two species' alarm calls had occurred, we compared the duration of subjects' responses during control trials with the duration of their responses during test trials. As in our previous experiments, the magnitude of the decrement in response between control and test trials were taken to measure the extent to which habituating and test stimuli were judged to be the same (for one of the earliest examples of how this technique is used, see Eimas et al. 1971).

All subjects were at least 3 years old. To control for individual differences in the strength of responses, we used the same subjects in same referent and different referent experiments whenever possible. Given the small sample of potential subjects and signallers in each group, however, this was not always practical.

Species that Elicit Alarm Calls

Data on the species that elicit alarm calls from vervet monkeys in Amboseli have already been presented (Seyfarth & Cheney 1980, 1986). To obtain comparable data from starlings we noted, whenever possible during 8 months of observation in 1985–1986 (October to May) and 3 months of observation in 1988 (May to July), those species that elicited alarm calls from these birds. It should be emphasized that the resulting list is by no means exhaustive, since starlings were not being observed systematically. To our knowledge, there are no published descriptions of the superb starling's alarm calls or the species that evoke alarm calls from starlings.

Acoustic Analysis

Data on the acoustic features of alarm calls given by vervet monkeys have been documented elsewhere (Seyfarth et al. 1980; Cheney & Seyfarth 1988; Owren & Bernacki 1988). The acoustic features of alarm calls given by starlings were analysed using a Kay Electric digital sonagraph (model DSP 5500) and the Personal Acoustics Lab (PAL) system of computer hardware and software, which draws upon ILS version 6.1 for waveform editing, display and analysis. Calls were first displayed on spectrograms using a frequency range of 80–8000 Hz and a wide band (300 Hz) filter. To check for energy above 8000 Hz, spectrograms were also made using a frequency scale of 160–16 000 Hz. Spectrograms allowed measurement of call length, unit length and the length of inter-unit intervals. A unit was defined as any continuous burst of signal energy; if a number of acoustically similar units was repeated in rapid succession, the units were called

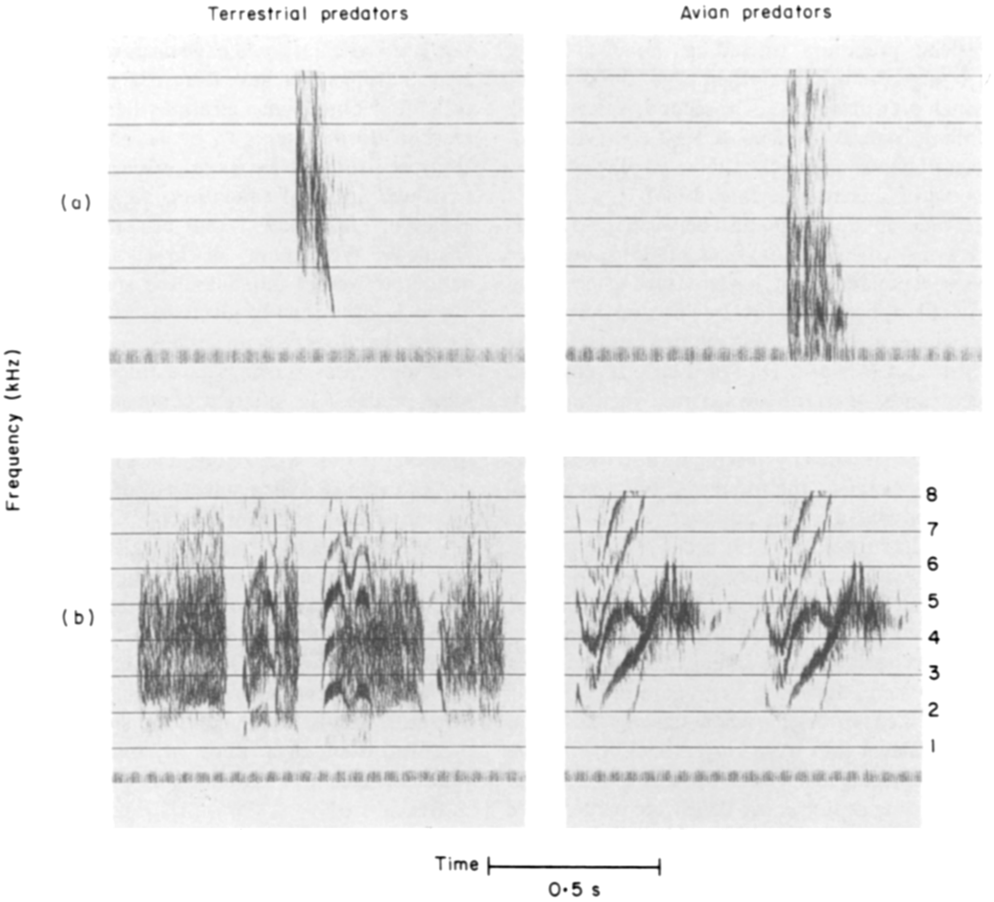

Figure 1. Spectrograms of alarm calls given by adult female vervet monkeys (a) and superb starlings (b) in response to terrestrial and avian predators. The vervet and starling terrestrial predator alarm calls were originally given in response to a leopard and a slender mongoose, respectively. The vervet and starling avian predator alarm calls were given in response to a martial eagle and a pale chanting goshawk, *Melierax poliopterus*, respectively.

iterations (Cheney & Seyfarth 1988; Owren & Bernacki 1988). A call was defined as a group of units (or iterations) separated from other similar groups by a time interval greater than that separating units (or iterations) within a call. For vervet vocalizations, examination of regular striations in spectrograms also revealed whether a call was voiced or unvoiced. Generally speaking, calls that are voiced are relatively tonal, with one or more bands of concentrated energy, while unvoiced calls are acoustically noisy, with energy spread in roughly equal amounts across a wide frequency range. In analysing starling vocalizations, where the mechanisms of sound production are different from those found in vervets, calls were classified simply as tonal or noisy.

After calls had been displayed on spectrograms, every unit (or iteration) in each call was digitized using ILS software with a sampling rate of 16 000 Hz, a step size of 12·5 ms and an analysis window of 6·25 ms. The ILS subroutine FFT (fast Fourier transformation) was then used to locate frequency peaks throughout the call and to measure spectral frequency changes over time.

RESULTS

The Alarm Calls of Superb Starlings

Superb starlings give two different alarm calls to predators, neither of which bears any acoustic resemblance to the vervets' own alarm calls (Fig. 1).

The first, a harsh, noisy call, is given to various terrestrial predators (including vervets), all of which prey on starlings or their eggs but only some of which prey on vervets. The second, a clear rising or falling tone, is given to at least eight different species of hawks and eagles, only two of which prey on vervets (Cheney & Seyfarth 1985).

Vervet monkeys distinguish between these different alarms. Cheney & Seyfarth (1985) found that vervets responded to playback of starling terrestrial alarm calls by becoming vigilant, looking toward the area where a speaker was hidden and running toward trees (see also Hauser 1988). In contrast, vervets almost never ran toward trees when the starling's raptor alarm call was played. Instead, subjects responded to this call by looking up into the sky.

The responses of the monkeys to the starlings' two alarm calls are not, however, as clear cut as these results suggest, possibly because the starlings' alarm calls are not equally precise in the information they convey. In our original experiments, few subjects looked up when they were played a starling terrestrial alarm call. In the experiments described here, however, two of eight subjects (25%) looked up briefly when starling terrestrial predator alarm calls were played in control trials. (By contrast, subjects looked up in 72% of trials in which starling raptor alarm calls were played.) We suspect that the more extreme results in our original experiments were due to the inclusion of juvenile subjects, who were more likely than adults to run to trees, and to the fact that all experiments were conducted when subjects were on the ground. By contrast, the 1988 sample included only adult females and males, more than half of whom were already in a tree when the terrestrial predator alarm was played. Adults in trees were more likely than juveniles on the ground to remain seated and simply scan the area around them.

Data on the stimuli that elicited alarm calls from starlings also suggest that starling terrestrial predator alarms refer to a broader array of predators (and hence are associated with a wider variety of escape strategies) than are starling raptor alarms. In 1986, we observed starlings giving terrestrial predator alarm calls to a wide variety of species (Table I), including not only carnivores like leopards and servals, but also two species of mongoose, at least three species of snake, and birds like fiscal shrikes and lilac-breasted rollers that hunt not by diving from above but by locating the starlings' nests and stalking them from a nearby branch. Starlings also gave terrestrial predator alarms to vervets, particularly when the birds were incubating eggs. Starlings even gave terrestrial predator alarm calls to elephants and giraffes when these species reached up into trees to break off branches. In contrast, starlings gave raptor alarms to a much narrower array of predators, all of which were eagles or small hawks that attack from the air (Table I). While many of these raptors pose no danger to vervet monkeys, the starling's raptor alarm is occasionally given to martial eagles, a species that does prey on vervets.

In some cases, starlings gave different calls to the same predator in different contexts. This is illustrated by the starlings' interactions with two avian species, the Verreaux's eagle owl and the marabou stork (Table I). When starlings were in a tree and encountered an eagle owl perched there, they gave terrestrial predator alarm calls and often approached the owl to mob it. When the eagle owl flew away, however, or when eagle owls were encountered in flight, starlings gave raptor alarms. Similarly, when starlings encountered a marabou stork foraging on the ground, they gave terrestrial predator alarms. If the marabou stork was flying overhead, they gave raptor alarms. These observations suggest that, rather than denoting different classes of predators, starling alarm calls signal different escape strategies (see Owings & Hennessy 1984 for a similar interpretation of alarm calls in California ground squirrels, *Spermophilus beecheyi*).

From the vervets' perspective, starling terrestrial predator alarms are rather general in the information they potentially convey: terrestrial predator alarms reliably indicate that something is nearby, but not whether it is harmful or which escape strategy the monkeys should pursue. Unlike the vervets' own alarm calls, starling terrestrial predator alarms do not reliably distinguish between different classes of predator. For example, vervets give acoustically different alarm calls and respond differently to snakes and leopards (Struhsaker 1967; Seyfarth et al. 1980) whereas these animals elicit acoustically similar alarm calls and responses from starlings. Starling raptor alarms, however, provide vervets with more specific information than do starling terrestrial predator alarms. While starling raptor alarm calls may be imprecise about the magnitude of danger, they nevertheless, like the vervets' own eagle alarm, denote a specific class of predator, its location and an appropriate escape strategy.

Table I. Species that were observed to elicit terrestrial predator and raptor alarm calls from superb starlings

	Eliciting species	
Call	Mammals and reptiles	Birds
Starling terrestrial predator alarms	Leopard, *Panthera pardus*	Fiscal shrike, *Lanius collaris*
	Serval, *Felis serval*	Lilac-breasted roller, *Coracias caudata*
	Caracal, *Felis caracal*	Verreaux's eagle owl, *Bubo lecteus**
	Black-backed jackal, *Canis mesomelas*	Marabou stork, *Leptoptilos crumeniferus**
	Spotted hyena, *Crocuta crocuta*	
	Slender mongoose, *Herpestris sanguineus*	
	Bat-eared fox, *Otocyon megalotis*	
	Dwarf mongoose, *Helogale parvula*	
	Genet, *Genatta genatta*	
	Elephant, *Loxodonta africana*	
	Giraffe, *Giraffa cameleopardis*	
	Vervet monkey, *Cercopithecus aethiops*	
	Baboon, *Papio cynocephalus*	
	Human, *Homo sapiens*	
	Green mamba, *Dendroaspis angusticeps*	
	Black mamba, *Dendroaspis polylepis*	
	Python, *Python sebae*	
Starling raptor alarms		Pygmy falcon, *Poliohierax semitorquatus*
		Kestrel, e.g. *Falco rupicoloides*
		Goshawk, e.g. *Melierax poliopterus*
		Bateleur, *Terathopius ecaudatus*
		African hawk eagle, *Hieraaetus spilogaster*
		Black-chested snake eagle, *Circaetus pectoralis*
		Tawny eagle, *Aquila rapax*
		Martial eagle, *Polemaetus bellicosus*†
		Verreux's eagle owl, *Bubo lacteus**
		Marabou stork, *Leptoptilos crumeniferus**
		Vulture, e.g. *Trigonoceps occipitalis*

*Starlings give terrestrial predator alarms to these species when they encounter them on the ground or roosting in trees, and raptor alarms when they encounter them in flight.

†Martial eagles are the only avian species in this list known to prey on vervet monkeys. Starlings doubtless also give raptor alarm calls to the other avian species that preys on vervets in Amboseli, the crowned eagle, *Stephanoaetus coronatus*. During 1986 and 1988, however, no crowned eagles were sighted.

Given these observations, the playback experiments described below examine two related issues: first, whether vervet monkeys recognize the similarity between their own eagle and leopard alarm calls and the raptor and terrestrial predator alarm calls of starlings; and second, whether vervet monkeys are sensitive to the relative lack of precision in starling terrestrial predator alarm calls compared with starling raptor alarm calls.

Vervets' Responses to their Own and to Starling Alarm Calls in Habituation/Dishabituation Tests

Both in same referent and different referent tests, subjects habituated to the repeated presentation of one species' alarm call. In the same referent series, the mean duration of response to the first alarm call in the series was 3·7 s, compared with 0·1 s for the eighth alarm call ($r_s = -0{\cdot}786$, $P < 0{\cdot}05$, one-tailed test). In the different referent series, the mean duration to the first alarm call was 2·8 s, compared with 0·4 to the eighth call ($r_s = -0{\cdot}952$, $P < 0{\cdot}01$).

In Tables II and III, results for each trial are presented separately. Statistical analysis, however, indicated no difference between trials that used starling, as opposed to vervet, alarm calls as either the habituating or test stimuli. In the Figures and the analysis, therefore, we combine data from both types of trial.

Table II. Results of control and test trials comparing same referent alarm calls given by vervet monkeys and superb starlings

Group	Subject	Habituation alarm call	Test and control alarm calls	Difference between control and test trials
Trials using starling raptor alarm calls				
B	CC	Starling raptor	AF eagle	−4·0
B	AF	Starling raptor	CC eagle	−2·3
B	NU	Starling raptor	AF eagle	−3·4
B	MA	Starling raptor	CC eagle	−4·2
C	PA	Starling raptor	CY eagle	−2·1
C	BH	Starling raptor	TS eagle	−5·3
B	GY*	CC eagle	Starling raptor	−3·5
B	NU	CC eagle	Starling raptor	−2·6
Trials using starling terrestrial predator alarm calls				
C	DE*	Starling terrestrial	CY leopard	−1·3
C	PA	Starling terrestrial	DE* leopard	−0·4
6	AA	Starling terrestrial	KA* leopard	−1·5
6	BU	Starling terrestrial	CY leopard	−2·0
C	PA	CY leopard	Starling terrestrial	+0·7
C	CY	DE* leopard	Starling terrestrial	−10·0

Responses defined as the duration that subjects looked towards the speaker in the 10 s following playback compared with the 10 s preceding playback. A negative number indicates a decrease in the duration of response from control to test trials; a positive number indicates an increase.
*Adult male subject or signaller; all other subjects and signallers were adult females.

Comparison of the monkeys' responses in test and control trials supports the view that vervets treated starling raptor alarms as similar in meaning to vervet eagle alarm calls, but different from leopard alarm calls. In tests in which we compared starling raptor alarms with vervet eagle alarms, all eight subjects transferred habituation from one species' alarm call to the other's (two-tailed Wilcoxon matched-pairs test, $T=0$, $P<0{\cdot}01$). As a result, there was a large decrement between control and test trials (Table II; Fig. 2a). The monkeys behaved as if the two types of alarm calls denoted similar referents despite having markedly different acoustic properties (see Fig. 1).

Conversely, for the different referent series in which we compared starling raptor alarm calls with vervet leopard alarm calls, subjects showed no transfer of habituation from control to test trials. In these experiments, only two of seven subjects showed any decrement in response from control to test trials ($T=6$; $P=0{\cdot}177$; Table III; Fig. 2b). Overall the mean decrement in subjects' responses between control and test trials when starling raptor alarm calls were compared with vervet eagle alarm calls was significantly greater than when starling raptor alarm calls were compared with vervet leopard alarm calls (two-tailed Mann–Whitney *U*-test, $N_1=7$, $N_2=8$, $U=2{\cdot}5$, $P<0{\cdot}01$). Vervets therefore responded to starling raptor alarms as if these calls were similar to their own eagle alarms and different from their own leopard alarms.

When starling terrestrial predator alarms were paired with vervet leopard and eagle alarm calls, however, different results were obtained. In tests that compared starling terrestrial predator alarms with vervet leopard alarms, five of six subjects transferred habituation from one species' alarm call to the other's ($T=2$, $P=0{\cdot}075$; Table II; Fig. 2c). The mean decrement between control and test trials, however, was significantly less than it was for the comparison between the two species' raptor alarms ($N_1=6$, $N_2=8$, $U=8$, $P<0{\cdot}05$).

Moreover, six of seven subjects ($T=5$, $P=0{\cdot}129$; Table III; Fig. 2d) also transferred habituation between starling terrestrial alarm calls and vervet eagle alarm calls, supporting the hypothesis that the meaning of starling terrestrial alarm calls was broader than that of starling raptor alarm calls. Thus, while there was no decrement in response between control and test trials when subjects were asked to compare starling raptor calls with vervet leopard alarm calls, there was an overall decrement

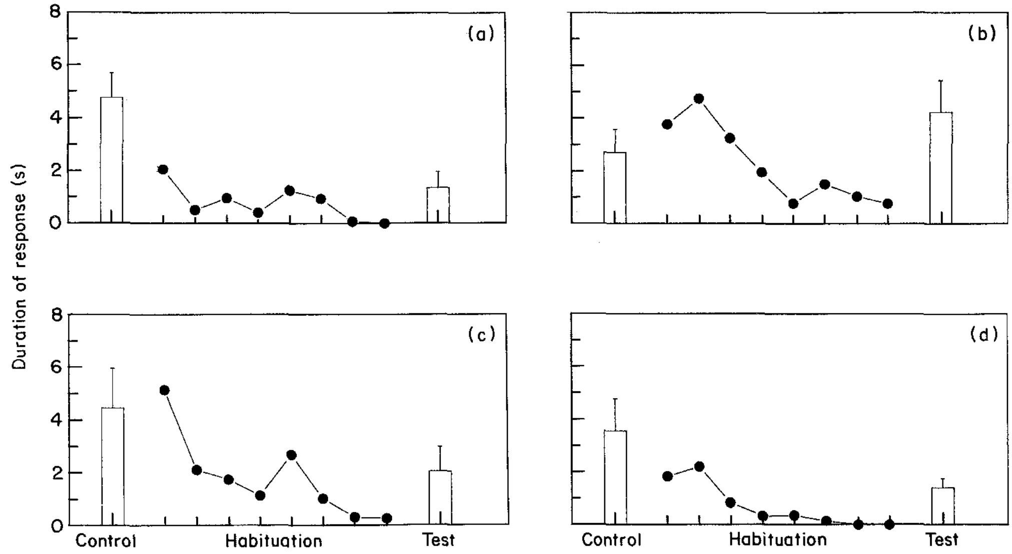

Figure 2. Results of habituation tests comparing vervet and starling alarm calls. Histograms show $\bar{X}$+SE for the duration of eight subjects' responses to playback of a vervet (or starling) alarm following repeated exposure to a starling (or vervet) alarm (test), compared with subjects' responses to the same alarm call in the absence of such exposure (control). Mean duration of subjects' responses during the eight habituation trials is also shown. In (a) vervet eagle and starling raptor alarms were used as stimuli; in (b) vervet leopard and starling raptor alarms; in (c) vervet leopard and starling terrestrial predator alarms; in (d) vervet raptor and starling terrestrial predator alarms.

Table III. Results of control and test trials comparing different referent alarm calls given by vervet monkeys and superb starlings

Group	Subject	Habituation alarm call	Test and control alarm calls	Difference between control and test trials
Trials using starling raptor alarm calls				
C	DE*	Starling raptor	CY leopard	+2·7
C	ET	Starling raptor	CY leopard	+0·3
6	BU	Starling raptor	AA leopard	+6·1
6	TS	Starling raptor	AA leopard	−0·5
6	AA	Starling raptor	KA* leopard	−2·6
C	CY	DE* leopard	Starling raptor	+3·1
6	BU	KA* leopard	Starling raptor	+1·7
Trials using starling terrestrial predator alarm calls				
B	NU	Starling terrestrial	AF eagle	−1·4
B	CC	Starling terrestrial	AF eagle	+1·9
B	AF	Starling terrestrial	CC eagle	−1·3
B	MA	Starling terrestrial	CC eagle	−6·9
C	BH	Starling terrestrial	TS eagle	−4·2
B	MA	CC eagle	Starling terrestrial	−1·4
C	BH	CY eagle	Starling terrestrial	−1·8

Legend as in Table II.

in response when subjects were asked to compare starling terrestrial alarm calls with vervet eagle alarm calls ($N_1=7, N_2=7, U=8, P<0{\cdot}05$). Vervets, in other words, behaved as if starling terrestrial predator alarm calls could have been directed at a raptor.

Table IV. Results of an analysis of the acoustic features of alarm calls given by vervet monkeys and superb starlings to terrestrial and avian predators*

	Vocalizations			
	Vervet monkeys		Superb starlings	
Acoustic features	Leopard alarms	Eagle alarms	Terrestrial predators	Avian predators
Call length (ms)	128·9 (15·8)	141·3 (16·7)	1123·8 (80·3)	1137·1 (48·7)
No. units per call	1·22 (0·15)	3·0 (0·5)	5·0 (0·36)	3·1 (0·13)
Unit length (ms)	103·9 (12·0)	37·7 (7·13)	189·7 (19·4)	324·3 (30·4)
Inter-unit length (ms)	55·0 (11·8)	23·2 (2·27)	46·9 (2·27)	55·5 (4·63)
Per cent of signal energy†	93·0 (4·7)	70·1 (3·43)	89·1 (2·19)	92·1 (2·23)
Tonal quality	Voiced	Mixed	Mixed	Tonal
Strongest frequency at start (Hz)	3417 (280·3)	1289 (243·0)	3222 (121·7)	3900 (294·7)
Strongest frequency at end (Hz)	3211 (356·3)	2000 (551·7)	3017 (112·2)	4216 (146·7)
Frequency change‡	8/9f	6/9f	7/17s	5/9r
No. calls with secondary peaks	5/9	7/9	16/17	5/9

*Values shown represent means, with SE in parentheses, for 17 starling terrestrial predator alarms and nine starling raptor alarms. Data for nine vervet leopard alarms and nine vervet eagle alarms taken from Cheney & Seyfarth 1988, Table IV.

†The proportion of a signal that contains acoustic energy as opposed to intervals of silence.

‡Change in peak frequency over the duration of the call (s: stable; f: falling; r: rising).

Acoustic Analysis

We have suggested that vervet monkeys compare vocalizations according to the meaning of the calls (Cheney & Seyfarth 1988). An alternative hypothesis, however, is that the monkeys compare calls on the basis of their acoustic properties; for example, two calls that are similar in length, dominant frequency or frequency modulation might be judged as similar regardless of the objects or events they denote.

To determine whether the responses of vervet monkeys were affected more by the physical properties of calls than by the referents with which they were associated, we made a number of measurements of the acoustic properties of each call used in playback experiments (Table IV). In presenting these data we should emphasize the different conditions under which vervet monkey and starling calls were recorded. In the case of vervet monkeys, each call was given by a single individual of known age and sex. For starlings, though we tried to use as playback stimuli only the calls of one individual, it was not always possible to determine from the original field recordings how many individuals were calling at any one time. In analysing starling calls, therefore, we could only estimate call length, the number of units per call, inter-unit length and the proportion of a signal that contained acoustic energy as opposed to intervals of silence.

Vervet monkey leopard alarms were voiced, and consisted of one (or occasionally two) units with a rapidly falling frequency over the duration of the call. Starling terrestrial predator alarms contained energy within roughly the same frequency range (3000–3500 Hz) but were longer, noisier and showed little or no frequency change over the duration of a call.

Vervet eagle alarms showed some evidence of voicing, but this was not always apparent (see also Owren & Bernacki 1988). They contained on average three iterations, and generally had a stable frequency falling between 1200 and 2000 Hz. By contrast, starling raptor alarms (like many other hawk alarms given by birds; Marler 1955) were highly tonal and consisted of rapid frequency upsweeps or downsweeps in the range of 3900–4300 Hz.

In short, there was no indication that calls treated as similar by the monkeys in habituation experiments (for example, vervet eagle and starling raptor alarms) were consistently more similar to one another acoustically than were calls treated as different (for example, vervet leopard and starling raptor alarms). The vervet monkeys' responses in playback trials cannot simply be explained by differences in the acoustic features of the different call types used in each comparison.

DISCUSSION

Two conclusions emerge from these results. First, the experiments described here support the hypothesis (Cheney & Seyfarth 1988) that vervet monkeys compare vocalizations (that is, make a same/different judgment between two calls) not just according to acoustic features of the calls but also according to the objects or events that the calls denote under normal circumstances. Vervet monkeys responded to the superb starling's raptor alarm as if it denoted an avian predator. In addition, when comparing this vocalization with two vocalizations of their own, they judged the starling's raptor alarm call as similar to their own eagle alarm and different from their own leopard alarm. After habituating to repeated playback of a starling's raptor alarm call, vervets also ceased responding to a vervet's eagle alarm call. Habituation to a starling's raptor alarm, however, produced no habituation to a vervet's leopard alarm. Vervets, therefore, appeared to treat the starling's raptor alarm as if it referred to a relatively specific class of predators, a class whose membership overlaps considerably the class of predators denoted by the vervets' own eagle alarms.

This is not to say that information about external referents is the only information conveyed by vocalizations. As we have argued earlier (Seyfarth et al. 1980, page 1092), features such as alarm call amplitude, length, rate of delivery and the number of individuals calling almost certainly provide listeners with information about how close a predator is and whether it poses an immediate threat (see e.g. Owings & Hennessy 1984). Nevertheless, results presented here and elsewhere (Cheney & Seyfarth 1988) demonstrate that, for vervet monkeys, the meaning of their own and other species' vocalizations derives in large part from the objects and events that such calls denote.

Second, vervets are apparently sensitive to the array of objects denoted by a given call. In Amboseli, starlings give terrestrial predator alarms to a broad array of predators. Starling raptor alarm calls, in contrast, are given to a much narrower array of stimuli, all birds that attack from the air. Perhaps as a result, vervets in our habituation experiments judged starling terrestrial predator alarms as similar to both vervet leopard and vervet eagle alarms. While starling and vervet eagle alarm calls were treated as essentially interchangeable, starling terrestrial alarm calls were treated as if they were far less precise and denoted a relatively broader array of predators. The monkeys behaved as if they regarded their own terrestrial predator alarm call as more referentially distinct than that of the superb starling, which, indeed, it is.

In our earlier study, vervet monkeys compared vocalizations not only according to their referents but also according to the identity of the signaller. In this study, however, when the comparison involved the calls of two different species, the monkeys' judgment of call meaning was less affected by caller identity. Subjects who had habituated to repeated presentation of a starling raptor alarm, for example, transferred their habituation to a vervet eagle alarm even though the calls obviously came from two different individuals. Apparently, when vervet monkeys compare two of their own species' vocalizations, caller identity plays an important role in their assessment of call meaning. When the monkeys are making a comparison that involves the calls of another species, however, caller identity seems to be less important.

In our early research on vervet alarm calls (Seyfarth et al. 1980) and grunts (Cheney & Seyfarth 1982) we tested each vocalization separately, in effect asking the monkeys to tell us, by their response, what information had been conveyed. We argued that the monkeys' vocalizations function as semantic signals because each call by itself elicited the same response as the object to which it was originally given. Vervets responded to playback of leopard alarms by running into trees even when leopards were not present; they responded to playback of grunts to another group by looking toward the border of their group's range. By contrast, later experiments, including those described here, have attempted to probe further, asking the monkeys to compare the information conveyed by two vocalizations and to reveal the criteria they use in making such comparisons. The results of these tests are difficult to explain without assuming that vervets have some representation of the objects and events denoted by different call types, and that they compare and respond to vocalizations on the basis of these representations.

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