The acoustic structure of suricates' alarm calls varies with predator type and the level of response urgency

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The variation in the acoustic structure of alarm calls appears to convey information about the level of response urgency in some species, while in others it seems to denote the type of predator. While theoretical models and studies on species with functionally referential calls have emphasized that any animal signal considered to have an external referent also includes motivational content, to our knowledge, no empirical study has been able to show this. In this paper, I present an example of a graded alarm call system that combines referential information and also information on the level of urgency. Acoustically different alarm calls in the social mongoose *Suricata suricatta* are given in response to different predator types, but their call structure also varies depending on the level of urgency. Low urgency calls tend to be harmonic across all predator types, while high urgency calls are noisier. There was less evidence for consistency in the acoustic parameters assigned to particular predator types across different levels of urgency. This suggests that, while suricates convey information about the level of urgency along a general rule, the referential information about each category of predator type is not encoded in an obvious way.

Keywords: alarm calls; functionally referential; level of response urgency; suricates; social mammals

1. INTRODUCTION

The alarm calls of some species of mammals and birds appear to convey information primarily about predator types, while in others it seems as though alarm calls convey information about the level of response urgency. The acoustic structure of the alarm calls of vervet monkeys (*Cercopithecus aethiops*) (Seyfarth *et al.* 1980), ring-tailed lemurs (*Lemur catta*) (Macedonia 1990), Diana monkeys (*Cercopithecus Diana*) (Zuberbuehler *et al.* 1997), Barbary macaques (*Macaca sylvanus*) (Fischer *et al.* 1995) and chickens (*Gallus domesticus*) (Gyger *et al.* 1987) varies depending on predator type. Aerial predators elicit an acoustically different call from terrestrial predators or snakes, and such calls evoke specific different responses by receivers. Alarm calls denoting predator types have been described as functionally referential signals, meaning that these vocalizations function as though they encode information about specific objects or events in the external environment (for a review see Evans 1997).

On the other hand, different anti-predator calls appear to denote different levels of response urgency in several sciurid species such as ground squirrels (Owings & Virginia 1978; Robinson 1981) and marmots (Blumstein & Arnold 1995; Blumstein & Armitage 1997). Although these species emit acoustically different calls for aerial and terrestrial predators they are not highly predator-type specific. These calls seem to vary with the type of hunting and speed of the approaching animal rather than predator type (Robinson 1981). Individuals run to their burrow in response to any predator type and also to playbacks of all call types (Blumstein & Armitage 1997). Some authors have argued that the alarm calls given by some ground squirrels and marmots are probably more an expression of the signaller's fear at the moment of the predator encounter, which varies depending on the level

of urgency (Marler *et al.* 1992; Blumstein & Armitage 1997). The evolution of functionally referential alarm calls in some species and not in others has been explained by the different hunting strategies of predators and the different adaptive ways of escaping from them (Cheney & Seyfarth 1990; Macedonia & Evans 1993).

Studies of species whose alarm calls are considered to be functionally referential have mainly concentrated on variation in the acoustic structure of these calls depending on predator type. However, several authors have pointed out that these vocal signals probably also convey information about the level of urgency (for a review, see Evans 1997). Nevertheless, with the exception of a study on lemurs (Pereira & Macedonia 1991), none of these studies has ever tested whether the acoustic structure of alarm calls varies simultaneously with predator type and level of urgency. In a theoretical approach, Marler *et al.* (1992), who view alarm calls based on the level of urgency primarily as an expression of motivation, tried to model the relationship between the acoustic structure of calls and the referential and motivational content of signals in general. They suggested that, rather than using the terms 'referential' and 'motivational' in a categorical fashion, the terms should be viewed as varying along a continuum. They argued that some minimal degree of stimulus specificity must be present in even the most prototypical of motivational signals, since variations in motivational state will be associated with different kinds of external stimulation. On the other hand, even words in human speech, as an example of highly referential signals, are always accompanied by some motivational information. While it is difficult to make statements about the motivational state of a caller under natural conditions, it is possible to analyse the variation in the acoustic structure of functionally referential alarm calls depending on the level of urgency by

Figure 1. Spectrograms of the different call types emitted during predator encounters divided according to context.

controlling for predator type and the distance to the caller.

Suricates (*Suricata suricatta*), which are cooperatively breeding mongooses that live in open semi-desert areas, use several structurally different alarm calls for warning other group members when predators approach (Ewer 1963; Moran 1984) (figure 1). Suricates are diurnal and live in groups of three to 33 individuals. They forage for 5–8 h d⁻¹ in the open, digging for invertebrates and small vertebrates in the sand. Foraging animals frequently scan their surroundings for predators. In addition, group members alternate at guarding from a raised position (Clutton-Brock *et al.* 1999). Guards and foraging individuals emit several different alarm calls if they spot a predator. Their main predators are jackals (*Canis mesomelas*), martial eagles (*Polemaetus belliochous*) and, for the pups, pale chanting goshawks (*Melierax canorus*) and snakes. Suricates also emit alarm-like call vocalizations in response to deposits such as faecal, urine or hair samples of predators and foreign suricates. These calls cause a response in other group members similar to that shown

when they encounter snakes. Other group members join the caller in order to investigate deposits in the same way as they join a caller to mob a snake.

In this paper I investigate what kind of alarm calls suricates emit in the context of predator encounters. In particular, I ask whether suricates emit acoustically different alarm calls to different predator types and whether their call structure and call rate depend on the level of response urgency?

2. METHODS

(a) Study site and animals

Data on alarm calls made in response to predators were collected at two study sites in the southern part of the Kalahari desert in South Africa from November 1995 to December 1996, and again from January 1999 to August 1999. Eight groups with a total of 70 adult individuals were followed along the dry riverbed of the Nossob in the Kalahari Gemsbok National Park and another 10 groups with a total of 131 adult individuals were followed on ranch land close to Van Zyl's Rus along the dry

Table 1. Labelling the different alarm calls depending on the most common context in which they were emitted.

call type	calls analysed (<i>n</i>)	predator type	risk	distance (m)
moving animal	23	aerial/terrestrial	low/high	20–50
panic	14	bird alarm	low/high	0–50
alert	25	aerial	low/high	> 100
aerial low	29	aerial	high	200–500
aerial medium	32	aerial	high	100–200
aerial high	15	aerial	high	50–100
terrestrial low	26	terrestrial	high	200–500
terrestrial medium	20	terrestrial	high	20–200
terrestrial high	23	terrestrial	high	5–20
recruitment low	21	deposits	low	0–10
recruitment high	20	snakes	high	0–10

river-bed of the Kuruman (see also Clutton-Brock *et al.* 1998). All individuals at both study sites could be identified and were habituated to a degree that allowed us to follow them within 0.5 m.

(b) Recording methods

In order to determine whether the alarm calls of suricates denote different categories of predators and/or levels of urgency, I analysed alarm calls from recordings during naturally occurring predator encounters and from manipulation experiments. Responses to predators were noted while walking with the group at a distance of only a few metres. Whenever an alarm-like call was recorded the following observations were noted: (i) the identity of the first (usually only) alarmer, (ii) the stimulus eliciting the call, and (iii) the distance of the caller from the stimulus. Because I did not have a big enough sample size for calls made in response to terrestrial predators and deposits, I included calls recorded from manipulation experiments for these contexts. For the terrestrial calls I recorded responses to the approach of a person with a dog on a leash towards the foraging group from as far as 500 m away to as close as 15 m of the group. In order to obtain recordings of calls elicited by deposits, I put out urine and hair samples of a dog in front of foraging individuals.

Alarm calls were recorded on 90 min digital audio tape (DAT) tapes using a Sony DAT Pro II digital audio tape recorder (Sony Corporation, New York City, USA) and a Sennheiser MKH 816 directional microphone (Sennheiser, Old Lyme, CT, USA). The recordings of the calls that I used for the analyses were made within 0.5–10 m of the caller. I was able to record the alarm calls emitted during predator encounters in 615 cases. Two hundred and forty-five of those calls and nine calls from the manipulation experiments were of sufficiently high quality to be acoustically analysed. Recordings were obtained from 102 adults in 18 different groups. The total included multiple vocalizations from identified individuals. In order to ensure that the acoustic analysis was not influenced by individual variation in call production, I included the calls of at least six (average 12 and maximum 15) different subjects for each vocalization type. Only one call per individual per predator encounter event or manipulation experiment was used in the analysis. The dataset did not allow for a comprehensive analysis of individual variation.

(i) Categories of calls depending on context

I divided the calls that were recorded into different context categories depending on predator type, risk and distance

(table 1). I named the call types according to predator type, level of urgency, the behaviour of the predator or the response of the suricates. Although this is not an ideal nomenclature for the calls, it seems a better representation of how the calls were categorized depending on context than trying to label the calls according to their acoustic structure.

Vocalizations were categorized depending on whether they were elicited in response to aerial or terrestrial predators, snakes or deposits. The same calls that were elicited in response to snakes were also given during encounters with foreign suricates that had escaped into boltholes and, on one occasion, a caracal (*Felis caracal*) resting in a bolthole. Other group members joined the caller and then mobbed the animal in all of these cases. Similarly, when the suricates found deposits on the ground, such as faecal, urine or hair samples of other suricates or predators, they emitted alarm-like calls that caused others to approach the caller and investigate the deposit. Since calls in response to snakes and deposits caused the same response in other group members, I categorized them as 'recruitment' calls based on their context. This category does not represent a specific predator type, but rather a specific context in which suricates encounter predators or signs of predators that are more or less stationary on the ground or in boltholes. However, for consistency I will refer to three different predator types in the rest of this paper. Aerial predator type refers to any animal approaching from the air, terrestrial predator type refers to any animal approaching on the ground and recruitment events refer to any animal or deposit that is stationary on the ground or in a bolthole.

The distance categories were only applied to the aerial and terrestrial predator types and not for recruiting events, since vocalizations that were emitted in response to snakes, animals in boltholes and deposits always occurred within a very short distance (0–10 m) of the stimulus. For aerial predators, stimuli as far as 200–500 m away were labelled as far, stimuli 100–200 m away as close and stimuli closer than 100 m as very close. For terrestrial predators, animals at distances greater than 200 m were classified as far, animals between 20 and 200 m as close and animals within 20 m as very close. In order to standardize the level of urgency of a situation for the three different predator types, I labelled aerial and terrestrial predators at a far distance as low urgency, at a close distance as medium urgency and at very close distance as high urgency. For recruitment calls, situations when calls were elicited in response to deposits were of low urgency, while encounters with snakes posed a high urgency situation.

In addition, I distinguished between another three call types depending on context categories that were not specifically related to a single predator type. The first, the alert call, was made in response to non-dangerous birds that were often close by (100–500 m), but also to raptors that were very far away (> 500 m) and, on a few occasions (two out of a total of 114 observations) to terrestrial predators that were far away (> 200 m). Most of the time, this call was elicited just once and repeated one or a few more times with several seconds in between them. I labelled it as an alert call since this call just seemed to alert the other group members. This call looked acoustically similar to calls given by group members when they appeared to have lost contact with the rest of the group and become disorientated. However, no acoustic comparison has been done so far. The second category of calls was given in response to birds emitting alarm calls or when aerial and terrestrial predators in close proximity made a sudden move and seemed to surprise the suricates. The response of the suricates was typically to run to the next bolthole and go below without looking around. This call seemed to express a very high urgency situation. I labelled this category as a panic call. The third category of calls was given to terrestrial and aerial predators and also to non-dangerous animals. The call was only observed when an animal moved, such as a distant terrestrial predator walking towards or away from the suricates, a foreign suricate moving, a perched raptor moving its wings or big birds taking off or landing. This call was also given in response to non-dangerous birds, such as southern yellow-billed hornbills (*Tockus leucomelas*) flying 5–10 m above the suricates. The call was typically only given once in the case of a non-dangerous animal approaching or leaving, but in the case of predators the call was followed by the predator-type specific alarm call. I refer to calls given in these contexts as moving animal calls.

I distinguished between stimuli of high and low risk since suricates not only emitted calls in response to potential predators, but also to non-dangerous animals approaching the group. Vocalizations in the high-risk aerial category included all of the calls elicited in response to raptors, while I considered all of the non-dangerous birds (non-raptors), including vultures, as being of low risk. The high-risk terrestrial predators group contained all of the carnivores, while the low-risk category consisted of herbivore species. The high-risk contexts that elicited recruitment calls consisted of encounters with snakes and other animals in boltholes, whereas encounters with deposits comprised low-risk contexts.

(ii) *Acoustic analysis*

The calls were sampled at 44.8 kHz using a Macintosh power book G3 series and CANARY 1.2.4 software. Spectrograms were then generated using SIGNAL software (Engineering Design, Belmont, MA, USA) by conducting a 1024 short-time Fourier transformation with a time-resolution of 5 ms and a frequency range of 8 kHz. Twenty-eight different acoustic parameters describing the frequency and time dynamics of a call were measured using the LMA 8.7 program (developed by K. Hammerschmidt). A detailed description of the filtering algorithms and the calculation of the acoustic parameters are given in Schrader & Hammerschmidt (1997). In brief, four different categories of measurements were used. First, three dominant frequency bands were determined from a filtered frequency–time spectrum, the signal-to-noise ratio of which had been enhanced by conducting a change-point analysis (Hammerschmidt 1990). Dominant frequency bands are distinguished by

amplitudes that exceed given thresholds in a consecutive number of cells. Several features were calculated on these dominant frequency bands, such as the start, end, peak and mean frequency and also the modulation. Second, the distribution of amplitudes over the frequency range was determined from unfiltered frequency–time spectra. Third, frequency range and frequency peaks were measured from power spectra. Fourth, temporal parameters were calculated, such as the call duration and the temporal location of the maximum and minimum amplitudes. Including so many acoustic parameters allows a comprehensive quantitative description of complex acoustic patterns, without any assumptions about the importance of any of the parameters for discrimination between groups (for a discussion see also Schrader & Hammerschmidt 1997).

(iii) *Statistical analysis*

In order to determine whether alarm calls could be assigned to different contexts according to their acoustic structure, I performed a discriminant function analysis (DFA) using the statistical package SPSS 9.0. The DFA provides a classification procedure that assigns each call to its appropriate group (correct assignment) or to another one (incorrect assignment) by comparing the multivariate patterns resulting from any interaction of the variables. In order to estimate the reliability of the DFA, a subset of the calls are randomly 'selected' for establishing the model. The remaining 'unselected' calls are then used for the test run in order to obtain an estimation of the model's validity. In addition, I conducted a two-way ANOVA testing for the influence of predator type and level of urgency on single acoustic parameters for those parameters that explained most of the variation in the discriminant model using STATVIEW 4.01.

3. RESULTS

(a) *Predation risk*

Suricates live under high predation risk and interrupt their foraging activities frequently. One group member emitted an alarm call or responded to a disturbance by running for shelter every 42 ± 22 min (mean $\pm$ s.e.) ($n = 6$ groups each observed on 10 days) during foraging activities. The suricates not only gave alarm calls in response to potential predators, but also in response to non-dangerous animals such as herbivores and non-raptors. I observed them responding to 69 different species, consisting of 14 herbivore, seven carnivore, eight medium-sized to large non-raptor, 24 small to medium-sized raptor and nine large raptor species (see Manser (1998) for a detailed list of predators). Furthermore, they also responded to the alarm calls emitted by several bird species, including fork-tailed drongos (*Dicrurus adsimilis*) and yellow-billed hornbills. Martial eagles, tawny eagles (*Aquila rapax*) and jackals posed the greatest danger to the suricates. Pups were also vulnerable to pale chanting goshawks. All four species have been observed to prey on suricates (T. H. Clutton-Brock, unpublished data).

(b) *Alarm call production*

(i) *Discriminant function analysis of acoustic structure depending on context*

The DFA confirmed that the acoustic structure of the suricates' alarm calls varied with context. The classification procedure in a model established with 34 acoustic parameters (see table 2) was run 10 times. Ninety per cent

Table 2. Acoustic parameters explaining the variation in calls (Wilk's λ , F -value and p -value) depending on predator type and the level of urgency along different dimensions.

(The rank columns indicate how much influence the different acoustic parameters have in the model for the level of urgency in comparison with predator type (the values in parentheses in the second rank column are the ranks for predator type). Acoustic parameters abbreviations: ampvar, variation in amplitude; ampratio, ratio of the amplitude of dominant frequency band 1 to dominant frequency band 2; DFA1end, frequency at which the energy distribution in the spectrum reaches the first quartile of the total distribution at the end of the call; DFA1min, frequency at which the energy distribution in the spectrum reaches the first quartile of the total distribution at the minimum location; DFA1maloc, location of the maximum frequency in the first quartile of the energy distribution; DFA2min, minimum frequency of the second quartile of the energy distribution; DFB1end, end of the first dominant frequency band; DFB1min, minimum of the first dominant frequency band; DFB1mean, mean of the first dominant frequency band; DFB1maloc, location of the maximum frequency in the first dominant frequency band; DFB1miloc, location of the minimum frequency in the first dominant frequency band; DFB1fretr, number of changes of direction in global modulation of the first dominant frequency band; DFB1mtr, average change of local modulation of the first dominant frequency band; DFB1tradd, overall direction of the modulation of the first dominant frequency band; DFB1trfak, number of times the original curve crosses the average of the first frequency band; DIFFmin, minimum difference between dominant frequency bands 1 and 2; DIFFmean, average difference between dominant frequency bands 1 and 2; duration, duration from the onset to end of a call; noise, percentage of time in which no harmonic structure could be detected; PFend, frequency with the highest amplitude at the end of a call; PFchmea, peak frequency modulation; PFjump, maximum difference in peak frequency in two consecutive time-segments; PFsll, slope of the peak frequency from the start to end; PFmaloc, location of the peak frequency ($1/\text{call duration (ms)} \times \text{location of peak frequency (ms)}$); PFtotmax, frequency with maximum amplitude; PFtrfre, peak frequency modulation, number of changes in direction; tonal, percentage of the time in which harmonic structure could be detected; ranmax, maximum frequency between highest and lowest frequency.)

rank	predator type			rank	level of urgency		
	acoustic parameter	mean F -value	mean p -value		acoustic parameter	mean F -value	mean p -value
1	PFend	30.86	< 0.000	1 (13)	ampvar	97.294	< 0.000
2	DFA1end	27.34	< 0.000	2 (15)	duration	55.091	< 0.000
3	PFtotmax	22.98	< 0.000	3 (4)	noise	49.241	< 0.000
4	noise	21.90	< 0.000	4 (11)	DIFFmin	36.210	< 0.000
5	DFB1maloc	20.97	< 0.000	5 (26)	PFjump	26.454	< 0.000
6	DFB1end	17.92	< 0.000	6 (8)	DFB1min	23.661	< 0.000
7	DFA1min	16.96	< 0.000	7 (24)	DFB1fretr	20.796	< 0.000
8	DFB1min	16.32	< 0.000	8 (25)	PFtrfre	20.556	< 0.000
9	DFB1mean	14.75	< 0.000	9 (28)	PFmaloc	19.127	< 0.000
10	ampratio	14.38	< 0.000	10 (20)	DF1mtr	17.897	< 0.000
11	DIFFmean	13.31	< 0.000	11 (18)	DFB1miloc	14.466	< 0.000
12	DFB1trfak	13.12	< 0.000	12 (27)	PFchmea	13.518	< 0.000
13	ampvar	12.02	< 0.000	13 (11)	DIFFmean	12.491	< 0.000
14	DFA1maloc	11.54	< 0.000	14 (7)	DFA1min	9.673	< 0.000
15	duration	9.89	< 0.000	15 (21)	tonal	9.237	< 0.000
16	PFsll	9.06	< 0.000	16 (6)	DFB1end	9.179	< 0.000
17	DIFFmin	8.24	0.001	17 (14)	DFA1maloc	8.853	< 0.000
18	DFB1miloc	7.60	0.001	18 (2)	DFA1end	8.727	< 0.000
19	DFA2min	7.16	0.002	19 (10)	ampratio	8.050	0.001
20	DFB1mtr	4.71	0.014	20 (1)	PFend	7.093	0.002
21	tonal	4.41	0.016	21 (12)	DFB1trfak	6.079	0.003
22	ranmax	2.69	0.083	22 (22)	ranmax	5.505	0.011
23	DFB1tradd	2.34	0.126	23 (5)	DFB1maloc	4.876	0.011
24	DFB1fretr	2.09	0.141	24 (9)	DFB1mean	4.102	0.022
25	PFtrfre	1.99	0.169	25 (16)	PFsll	3.682	0.031
26	PFjump	0.60	0.563	26 (3)	PFtotmax	1.074	0.355
27	PFchmea	0.43	0.663	27 (19)	DFA2min	0.676	0.554
28	PFmaloc	0.25	0.795	28 (23)	DFB1tradd	0.507	0.625

of the calls were randomly 'selected' each time and the remaining 10% of calls were used for the cross-validation. This yielded $82.1 \pm 6.2\%$ (mean $\pm$ s.d.) ($n = 10$ runs) correct assignment to the proposed context categories with the selected calls. The 10% of unselected calls in the test run showed a $66.4 \pm 8.8\%$ ($n = 10$ test runs) correct assignment versus the expected 9% correct assignment by chance alone (table 3).

Because the DFA analysis suggested that some acoustic parameters might be related to predator type and others to the level of urgency (figure 2a), I performed a second DFA using the calls given in response to only one of the specific predator types. This excluded the panic call and moving animal call from the analysis, because they were given in response to both aerial and terrestrial predators. This also excluded the alert call, because it was not only elicited by

Figure 2. Arrangements of the different call type categories established by the DFA: (a) predator type specific and non-predator type specific call types; (b) only predator type specific call types. Circles are spanned by the mean centroids of the categories $\pm$ s.d. (average standard deviation of the calls to the centroid within a call type) from 10 runs of the DFA for the first two discriminant factors.

predators, but also in response to non-dangerous animals (non-raptors). This analysis indicated that the variation in predator type was explained by different acoustic parameters to those that explained the variation in the level of urgency (figure 2b). While some acoustic measures were important for both, several had no significant effect for the predator type category model, but were important for the urgency model (table 2). The measures that remained in both models differed in their influence in explaining call variation, as the p - and F -values of Wilk's λ suggest.

If the acoustic structure of alarm calls changed along one dimension depending on predator type and along another dimension depending on the level of urgency, then the acoustic parameters that explained the level of urgency for one predator type should also have explained the level of urgency for the other two predator types. Correspondingly, the acoustic parameters that explained the predator type at one level of urgency should still have explained the same predator type at other levels of urgency. In order to test this hypothesis, I took those acoustic parameters that explained the high and low levels of urgency for aerial alarm calls and investigated whether the same acoustic parameters also determined the high and low levels of urgency for terrestrial alarm calls and recruitment calls. This analysis was conducted six times in total, using all possible combinations of the three predator and two urgency types. The classification with the selected dataset yielded an average correct score of $87.3 \pm 3.2\%$ as compared with 50% by chance. The correct assignment in the test run was $77.8 \pm 4.6\%$. I then conducted a similar analysis in which I compared calls to different predator types at low levels of urgency with calls to the same predator types at high levels of urgency (and

vice versa). This analysis yielded a correct assignment for the selected dataset of $85.1 \pm 2.6\%$, but only $38.2 \pm 2.2\%$ for the test set, thereby suggesting an assignment by chance (33%).

(ii) *Univariate analysis on acoustic structure*

Testing the univariate differences for the parameters that explained most of the variation in the discriminant function for predator type and level of urgency showed that single acoustic parameters varied in a different way for these two variables (figure 3a,b). The five acoustic parameters that accounted for the greatest variation in the model of the level of urgency either increased or decreased with urgency level, and this was consistent over the three predator types. The pattern for the five most important parameters for the model on predator type was less clear. Here, each parameter showed a significant difference between predator type for at least one level of urgency. However, the difference between predator type was consistent for only a few parameters over two or three levels of urgency.

(iii) *Call duration, calling rate and call interval*

The suricates' alarm calls not only differed in their acoustic structure, but also in their frequency of occurrence and call rate within bouts (table 4). Calls given in response to distant predators or to non-dangerous animals (herbivores and non-raptors) were usually only given once and were of longer duration than other calls that were given in response to low urgency predator situations. Low urgency calls in response to all predator types were of short duration with relatively long intervals in between them and given repeatedly over long periods. The more urgent the calls became, the shorter the call

Table 3. Classification table of the DFA for the different alarm call types in the category of alert alarm calls depending on context.

(x_1 is the average number of calls selected in the 10 runs establishing the model, and x_2 is the average number of unselected calls in the cross-validation of the 10 test runs. The percentages of correctly classified calls are also the averages of the 10 runs for the selected calls and unselected calls.)

call type	selected		test (unselected)	
	x_1 calls	percentage correctly classified	x_2 calls	percentage correctly classified
panic	12.5	94.4	1.5	75.4
moving animal	20.6	89.9	2.4	82.9
alert	23.2	94.8	1.8	77.1
aerial low	26.9	74.7	2.1	60.2
aerial medium	27.9	76.5	4.1	69.5
aerial high	13.7	83.7	1.3	62.8
recruitment low	23.3	89.5	2.7	66.1
recruitment high	18.5	75.2	1.5	62.1
terrestrial low	21.2	64.8	1.8	51.3
terrestrial medium	18.9	80.6	2.1	61.1
terrestrial high	17.5	79.3	2.5	63.3
overall total	224.2	82.1	23.8	66.4

intervals were in relation to call duration. This was true for the terrestrial alarm calls and recruitment calls, though not for the aerial alarm calls. With aerial alarm calls, the more urgent the situation, the fewer calls an individual emitted. The panic call was usually given once or twice in very short intervals and then individuals ran.

4. DISCUSSION

(a) *The information encoded in suricates' alarm calls*

Alarm calls in suricates convey information about both predator type and level of urgency. The acoustic parameters that encode information about the level of urgency are different from those that vary between predator type. The change in the acoustic structure along the dimension of level of urgency is consistent across predator types, but there is no consistent rule for the acoustic structure along the dimension of predator type across levels of urgency.

The acoustic structure of suricates' alarm calls varies depending on different types of predators, and their calls can be classified into discrete categories. Playback experiments of the different alarm call types, which are described elsewhere (Manser *et al.* 2001), elicited the appropriate different responses corresponding to different predator types. This high production specificity from the signaller's perspective and the high perception specificity from the receiver's side suggest that suricates' alarm calls are functionally referential.

In addition, the acoustic structure of the alarm calls also changed depending on the level of urgency. Calls within a predator type at different levels of urgency showed no clear discrete distinctions, but rather the calls graded from a harmonic into a noisy structure as the level

of urgency increased. This was consistent across all the aerial, terrestrial and recruitment calls.

The level of urgency appeared not only to be reflected in the acoustic structure of the call, but also in the calling rate and the duration of a calling bout. Calls elicited in response to non-dangerous animals (herbivores and non-raptors) or predators that were very far away were typically of longer duration and given only once as compared with calls in low, medium or high urgency situations with predators. The calling rate in a bout within the latter calls increased because the interval between calls decreased substantially and because each single call became shorter with increasing urgency. In the case of aerial calls, fewer calls were emitted in the medium and higher urgency situations than in low urgency situations. This could be because the caller in the case of the aerial predator did not have time to emit more calls, as has been described for ground squirrels (Sherman 1985) and marmots (Blumstein & Armitage 1997). This is also supported by the fact that the panic call, which is emitted in the context of the highest level of urgency, is only given once or twice. This might suggest that the calling rate and the number of calls emitted depend on the time in which an individual has to respond, while the acoustic structure grading along the level of urgency may be a direct expression of the caller's emotional state at the moment of calling (Morton 1977; Marler *et al.* 1992; Evans 1997).

(b) *The relation between motivational and referential information*

Although it has been suggested that most animal calls carry both referential and motivational information, to our knowledge, no study has documented how these two parameters interact. Marler *et al.* (1992) suggested the use of a referential and motivational continuum as a model for the multidimensional relationship between the acoustic structure of a call, the characteristics of the classes of stimuli that elicit the call and the motivational state of the caller at the time of calling. If we assume that the level of response urgency during a predator encounter event directly influences the motivational state of a caller and that this is expressed in the vocalizations that are emitted, we can try to apply the motivational–referential continuum model to the suricates' alarm calls. However, the reduction in the multivariate dimensions of the acoustic structure, i.e. the referential and motivational contents of the call, each of which is represented by one dimension in their model, makes it very difficult to explain the acoustic variation in calls with this model. The referential content in the suricates' alarm calls appears to be encoded in different acoustic parameters from those of the content of the level of urgency.

It might be possible to describe the change in the acoustic structure along a continuum for the dimension of the level of urgency, but it is difficult to place the different call types along a referential continuum. In order to do this, we would have to have a measurement of referentiality. One approach to estimating the degree of referential content in a call might be to use the specificity of an alarm call to a predator type. In the case of the suricates, all of the types of low, medium and high urgency aerial and terrestrial calls were only elicited by aerial and terrestrial predators, respectively. On the other hand, recruitment calls were

Figure 3. Univariate analysis of the acoustic parameters that explain most of the variation in the two models depending on the level of urgency and predator type. (a) First five acoustic parameters that explained most of the variation in the model of the level of urgency. (b) First five acoustic parameters that explained most of the variation in the model of predator type. See the legend to table 3 for the acoustic parameter abbreviations.

typically given in response to snakes, but also in response to other suricates and, on one occasion, a caracal found in a bolthole. We could possibly argue that aerial and terrestrial calls are more predator-type specific than recruitment calls. However, it might be that these calls convey information about the way that predators approach, rather than a specific predator type (Evans 1997). Alternatively, a recruitment call may be an expression of affect in that it is information about what the alarmer wants the receivers to do, in this case group aggregation, as suggested by Owings & Morton's (1998) management view.

The moving animal call represents a similar case to the recruitment call in that this call is also given in response to a variety of different predator types. However, this call type seems to relate to a specific behaviour, i.e. that the

approaching or leaving intruder is moving. If it is a dangerous situation, different alarm calls more specific to the predator type and the urgency of the situation will follow immediately. Although this call in itself does not convey specific information about a predator type, it appears to relate to a specific behaviour. This suggests a high production specificity, but only on the dimension of predator behaviour instead of predator type. However, it could be that the moving animal call is a higher urgency version of the alert call. Based on their acoustic structure, the DFA positioned these two call types along the same dimension as the predator-type specific low/medium urgency calls in relation to the high urgency calls. Playback experiments of these call types will be necessary in order to answer the question as to whether moving

Table 4. Measurements of call duration, duration of the interval between calls, calls per second, number of calls and duration of a call bout depending on alarm call type.

(Values are means $\pm$ s.d.)

call type	individuals (n)	call duration (ms)	call interval (ms)	calls per second	number of calls	call bout duration (s)
panic	8	175 $\pm$ 76	124 $\pm$ 52	3.24 $\pm$ 2.54	2.1 $\pm$ 1.4	0.50 $\pm$ 0.5
moving animal	11	517 $\pm$ 226	—	1.00	1.0	0.52 $\pm$ 0.23
alert	14	166 $\pm$ 57	4957 $\pm$ 4314	0.20 $\pm$ 0.26	1.1 $\pm$ 0.4	0.80 $\pm$ 2.4
aerial low	5	104 $\pm$ 11	701 $\pm$ 625	1.20 $\pm$ 1.32	758.0 $\pm$ 1345	745.00 $\pm$ 965
aerial medium	24	105 $\pm$ 28	388 $\pm$ 275	2.19 $\pm$ 2.36	4.3 $\pm$ 5.3	4.60 $\pm$ 4.6
aerial high	6	247 $\pm$ 145	1349 $\pm$ 1015	0.71 $\pm$ 0.59	3.3 $\pm$ 2.9	4.50 $\pm$ 7.7
terrestrial low	6	70 $\pm$ 27	659 $\pm$ 645	1.26 $\pm$ 1.39	392.0 $\pm$ 842	603.00 $\pm$ 1015
terrestrial medium	8	107 $\pm$ 42	389 $\pm$ 236	2.17 $\pm$ 0.97	1066.0 $\pm$ 701	435.00 $\pm$ 212
terrestrial high	8	367 $\pm$ 109	443 $\pm$ 384	1.92 $\pm$ 1.15	5.80 $\pm$ 4.5	4.40 $\pm$ 4.3
recruitment low	7	72 $\pm$ 16	300 $\pm$ 224	3.36 $\pm$ 1.35	34.0 $\pm$ 32	120.00 $\pm$ 163
recruitment high	9	470 $\pm$ 192	578 $\pm$ 234	1.00 $\pm$ 0.24	10.0 $\pm$ 4	10.00 $\pm$ 4.1

animal and recruitment calls that appear to denote a specific context are the expression of the affective state of the caller or may function referentially in a different dimension to aerial and terrestrial calls.

On the other hand, the panic call, which was mainly elicited in response to birds emitting alarm calls, but also on a few occasions in response to aerial or terrestrial predators very close by, obviously shows a much lower stimulus specificity. This call causes the suricates to just run to the next shelter without looking around and, thus, is probably much more the expression of the great fear of the alarmer, as has been described for some ground squirrels and marmots (Owings & Virginia 1978; Blumstein & Armitage 1997).

Suricates' alarm calls appear to represent a case where both information about predator type and level of urgency are conveyed with varying degree in specific acoustic call structures. While the change in the acoustic structure along the dimension of the level of urgency is consistent in all the different predator types, there is no consistent pattern for the acoustic structure along the dimension of predator type. This suggests that, while suricates convey information about the level of urgency of a specific context along a general rule, the referential information about each category of predator type is not encoded in an obvious way. This might support the idea that referential alarm calls that are elicited in response to different predator classes evolve from affective vocalizations in the repertoire that have very different acoustic structures (Macedonia 1993). It would be interesting to see whether similar patterns of the acoustic structure of referential alarm calls that vary with the level of urgency could be found in other species.

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