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STRUCTURE AND FUNCTION OF RED FOX *VULPES VULPES* VOCALISATIONS

NICK NEWTON-FISHER, STEPHEN HARRIS*, PIRAN WHITE & GARETH JONES

Department of Zoology, University of Bristol, Woodland Road, Bristol BS8 1UG, UK

ABSTRACT

A sonagraphic analysis of the structure of fox vocalisations, based on 512 adult and 73 cub vocalisations obtained from archive recordings, was combined with field data on the vocal behaviour of an urban fox population. Calls were described quantitatively by six variables: duration, lowest and second lowest frequency bands (from sonagrams), highest and second highest peak frequencies (from power spectra) and the number of components. They were separated into 20 call types, eight of which were cub vocalisations. Call types were used singly or in combination, and some gradation between particular call types was apparent. Hypotheses regarding call function were generated based on the matching of acoustic properties with their seasonal occurrence and the socioecological pressures acting on foxes at different times of the year. Calls that were structurally suited to agonistic and contact functions were found to be significantly more common during the winter, the time of mating and dispersal, when foxes move over greater areas.

INTRODUCTION

For animals which are social, yet spend a considerable amount of their time alone, vocalisations provide the only means of communicating instantaneously over long distances and in conditions of poor visibility, such as in dense vegetation or at night (Cohen and Fox 1976). Since foxes *Vulpes vulpes* are largely nocturnal and live in social groups, but on average only meet another fox twice a night (White 1992), it is not surprising that they produce a wide variety of vocalisations. However, the importance of these vocalisations in fox social biology is not understood.

Relatively little work has been done on either the sonagraphic structure or function of canid vocalisations. Most work has been carried out on the wolf *Canis lupus*, for which the role of howling has been investigated experimentally (e.g. Harrington and Mech 1979, 1983, Harrington 1986), and a recent structural analysis of wolf pup vocalisations has been undertaken by Coscia et al. (1991). Cohen and Fox

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*Correspondence author.

(1976) and Tembrock (1976) have analysed the structure of general canid vocalisations, coyote *Canis latrans* vocalisations have been documented by McCarley (1975) and Lehner (1978), and red wolf *Canis rufus* vocalisations by McCarley (1978). Fox vocalisations are poorly documented. Tembrock (1957) divided them into 28 groups and 40 call types, but his classification was based on captive animals and was mostly subjective, being produced before the widespread use of sonagraphic analysis. The dearth of clear, quantitative descriptions of fox vocalisations has resulted in a variety of onomatopoeic call names (e.g. Burrows 1968, Macdonald 1987), which make comparisons between studies difficult. The confusion is exacerbated by the lack of consistency in the descriptive names used and a lack of clear definition as to which calls are grouped together.

Various 'functions' have been proposed for fox vocalisations (e.g. Burrows 1968, Tembrock 1976, Lloyd 1980, Macdonald 1987), but none have been validated by field experiments. To understand what the different vocalisations may mean to foxes, and indeed which vocalisations should be regarded as distinct, call types first need to be identified quantitatively, with no *a priori* consideration of their 'meaning'. Possible call functions can then be deduced by matching seasonal behavioural data collected in the field with the structural characteristics of the various calls. This approach can then lead to the formulation of specific hypotheses which can subsequently be tested using controlled manipulative playback experiments (McComb 1992).

In this paper, a sonagraphic analysis of prerecorded fox vocalisations is combined with field data collected from the fox population in urban Bristol, to examine the structural properties and seasonal patterns of vocalisations in the light of the socioecological pressures acting on the foxes at different times of the year, and to discuss the possible function of each call type.

MATERIALS AND METHODS

Sources of fox calls

An extensive and exhaustive search was made of all archive material, both commercially available and library recordings (Ranft 1990). Additional recordings were obtained from individual recordists (see Appendix for a detailed list). This yielded a large number of calls recorded in a wide range of habitats and situations. Because archive material was used for the analysis, it was not possible to control for sex and social status of the foxes or for environmental conditions. Thus all calls were assumed to be independent data. Because the recordings analysed came from several sources, recording techniques varied between tapes. However, variation in recording quality probably made only a small contribution to the total variation in signal characteristics, since the call types classified by multivariate analysis were usually recognisable on several different tapes. All recordings had a good signal:noise ratio.

The vocalisations produced by adult foxes, and to a lesser extent by cubs, showed a high degree of variation. Most calls occurred in groups; only rarely were calls uttered singly. Within these sequences, a number of combination calls occurred where two different call types would be mixed. In order to establish a classification of the basic call types, all identified combinations were excluded from the analysis.

Data analysis

The calls were analysed using a Kay DSP Sona-Graph Model 5500, after replay on a Sony WM-D6C cassette recorder, and viewed in real time on the Kay Sona-Graph. Each sequence of calls (each 'track') was checked to ascertain the most appropriate input frequencies. Quantitative data were collected for calls randomly selected from each track. Input frequency, time and frequency resolution were altered to achieve an adequate display of the structure of each call. Measurements of frequency and duration were taken from the screen display using line cursors. Quantitative data were collected for five continuous and one discrete variable. These were: call duration, lowest and second lowest frequency bands (from sonagrams), highest and second highest peak frequencies (from power spectra) and the number of components. These six variables were chosen because they were measurable in every call, conceptually distinct, and unambiguous. Frequencies of highest and second highest peak energies were determined from both the colour scaling of intensity on the sonagraph display and the power spectrum of the entire call. The number of components was defined as the number of temporally discrete elements on the sonagraph display, where the inter-element distance (time) was less than that between any two 'blocks' of elements, and less than the call duration.

245 adult and 73 cub calls were subjected separately to hierarchical cluster analysis to define call types objectively. The agglomerative 'average linkage between groups' clustering method, using Euclidean distance between calls (de Ghett 1978, Norusis 1985) was used, and the groups produced from the analysis of adult calls were used to generate canonical discriminant functions (Norusis 1985). These were then used to classify the remaining 267 adult calls to produce the phonetic classification. This procedure was used because the cluster analysis could not classify the entire adult data set sensibly. However, the entire cub data set was classified by the clustering procedure and the groupings

subsequently checked with discriminant analysis. Cluster and discriminant analyses were run on SPSS^x.

Field data

Capture, handling and radio-tracking of foxes were conducted as described in Harris (1980) and Saunders et al. (1993). Foxes from seven neighbouring social groups were radio-tracked between May 1990 and August 1991, and all vocalisations heard were recorded. Hence all calls and not just those made by the focal animal were included, since when more than one animal was present it was often difficult to determine which was vocalising. To ensure unambiguous and comparable interpretation by several different field workers, only eight call types were identified in the field, based on the descriptions of Macdonald (1987). These call types were then re-defined to correspond with call types subsequently identified by the sonagraphic analyses. To enable direct comparisons, the frequency of the different vocalisations heard was standardised between seasons, being expressed per 400 hours of total radio-tracking time, which was approximately the average total radio-tracking time in each season. Thus this figure does not represent the frequency of vocalisations per individual animal, which would be lower. Comparisons were made using χ^2 and an *a posteriori* Tukey-type multiple comparison test (Zar 1984). Seasons were defined as: winter December–February; spring March–May; summer June–August; autumn September–November.

RESULTS

The cluster and discriminant analyses separated the calls into 12 adult and 8 cub call types. A number of cub calls were qualitatively indistinct from their adult counterparts. Table 1 gives the mean values of the six measured variables for each call type. Figure 1 shows the relative distance between each call type, and the coefficients of similarity produced by the hierarchical cluster analysis are shown in Table 2.

Description of call types

1. ADULT CALLS

Type 1: *barks* (Figure 2)
This call was recognisable by its rapid onset and concentration of energy primarily into two constant frequency bands. With the exception of the

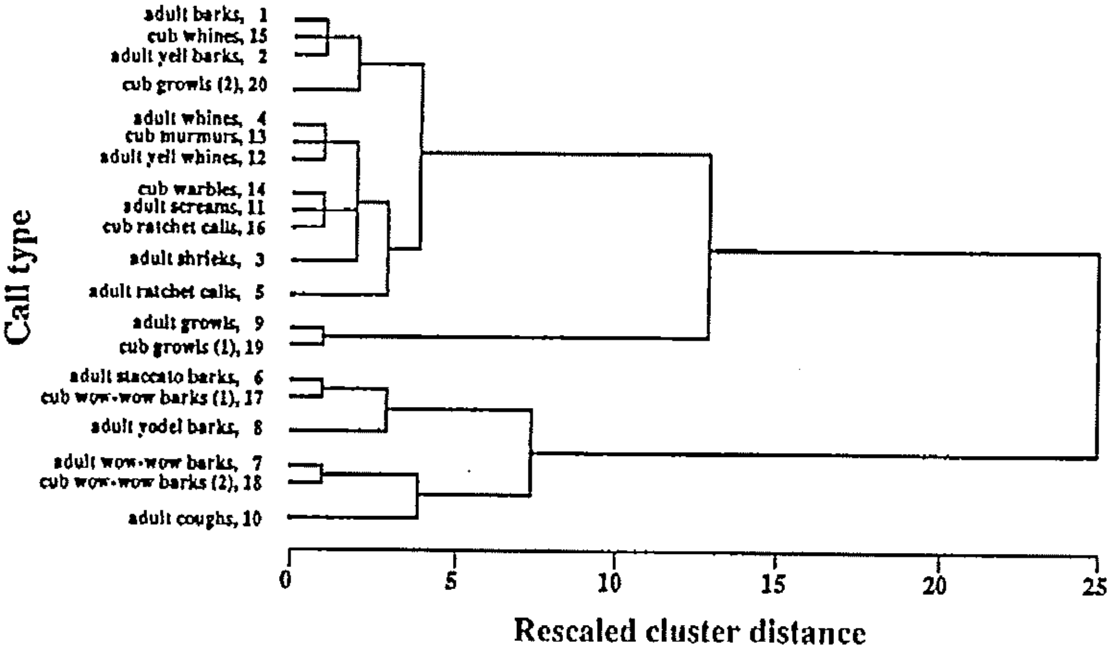


Figure 1. Dendrogram produced by hierarchical cluster analysis using mean values for each call type, showing the relative distance, and thus degree of similarity, between each call type. Details of the call types are given in text.

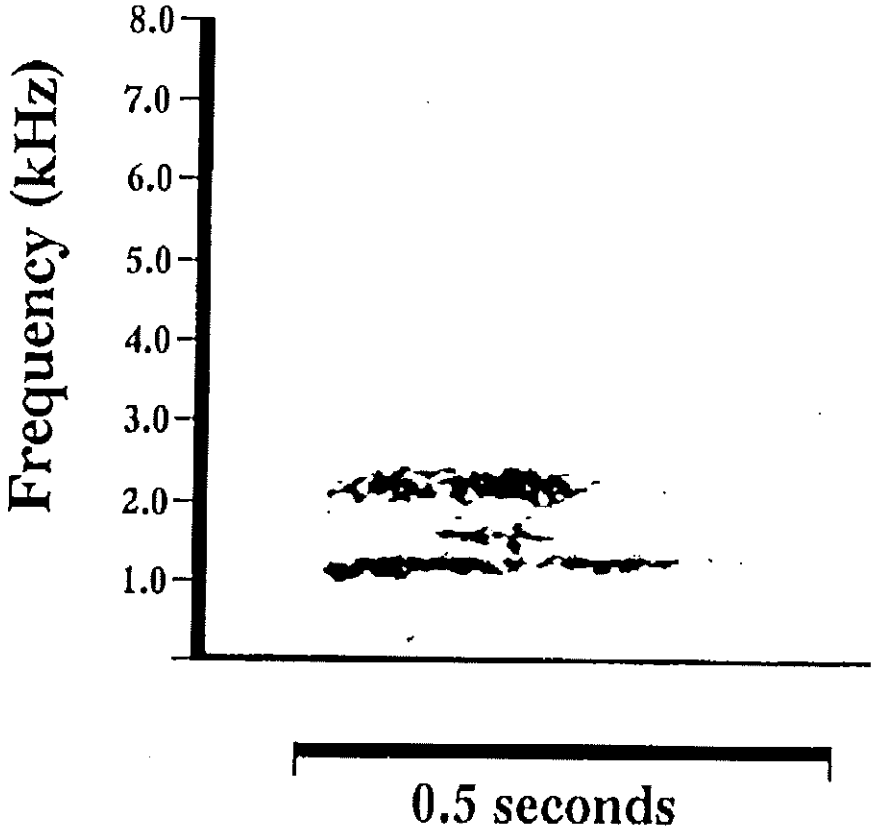
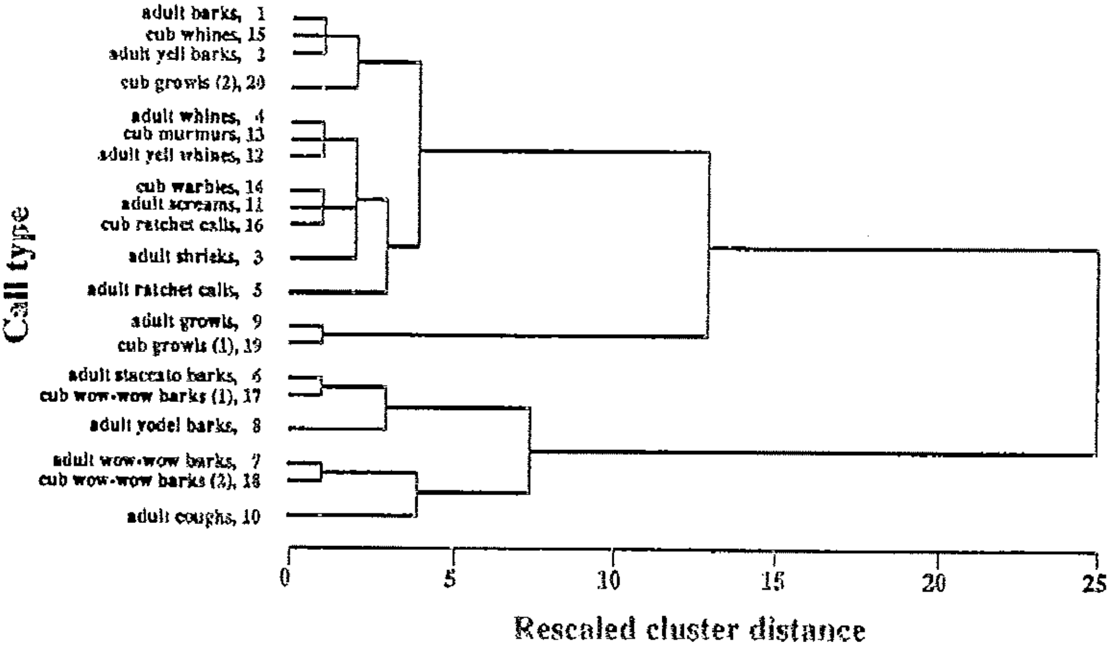


Figure 2. Sonagram showing acoustic structure of call type 1 (barks).



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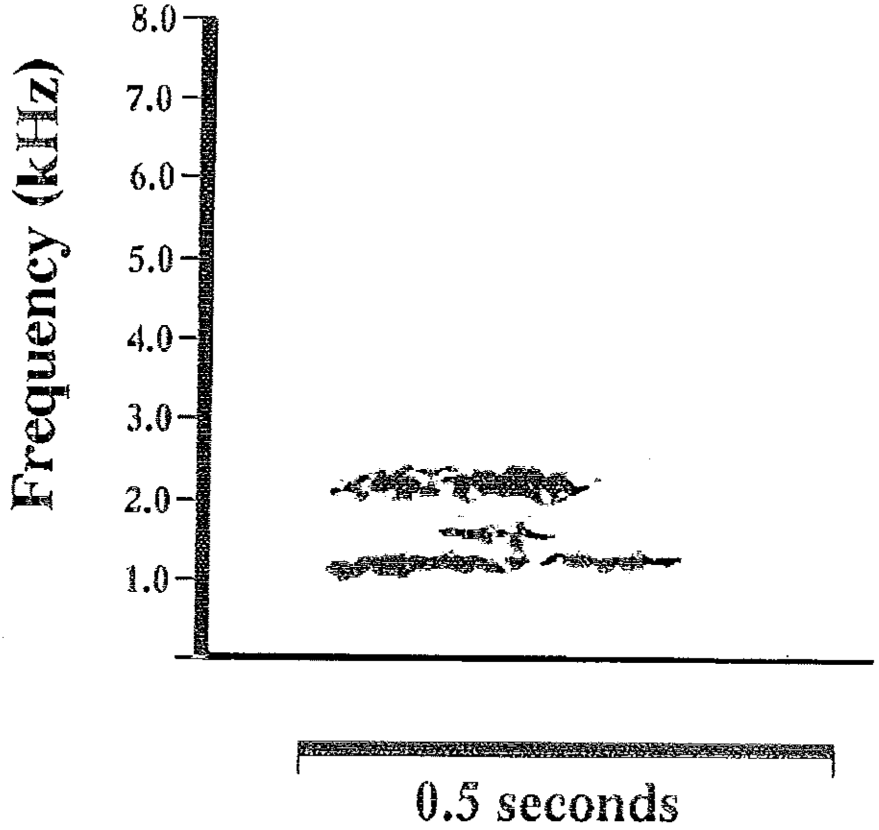

Figure 2. Sonagram showing acoustic structure of call type 1 (barks).

TABLE 1

Summary statistics for each call type. See text for descriptions of the calls.

		Parameters					
		Duration (s)	Lowest frequency band (kHz)	Second lowest frequency band (kHz)	Highest peak frequency (kHz)	Second highest peak frequency (kHz)	Number of components
Adult calls							
1. Barks	$\bar{x}$	0.827	0.948	1.369	1.019	1.464	1.000
	S.D.	0.357	0.133	0.218	0.150	0.301	0.000
2. Yell barks	$\bar{x}$	0.757	0.916	1.428	1.482	1.165	1.000
	S.D.	0.236	0.106	0.153	0.170	0.324	0.000
3. Shrieks	$\bar{x}$	0.674	0.858	1.356	1.547	2.510	1.000
	S.D.	0.184	0.141	0.231	0.384	1.385	0.000
4. Whines	$\bar{x}$	0.652	1.061	2.048	1.066	2.032	1.000
	S.D.	0.352	0.147	0.277	0.158	0.294	0.000
5. Ratchet calls	$\bar{x}$	0.169	1.849	2.443	2.190	2.305	1.000
	S.D.	0.073	0.471	0.513	0.528	0.699	0.000
6. Staccato barks	$\bar{x}$	0.928	0.729	1.114	0.820	1.097	3.541
	S.D.	0.210	0.078	0.301	0.239	0.355	0.787
7. Wow-wow barks	$\bar{x}$	1.237	0.532	1.037	0.755	1.210	5.773
	S.D.	0.250	0.203	0.377	0.152	0.278	1.631
8. Yodel barks	$\bar{x}$	1.137	0.775	1.504	0.780	1.489	4.364
	S.D.	0.469	0.087	0.220	0.852	0.271	1.814
9. Growls	$\bar{x}$	1.167	0.120	0.274	0.191	0.203	1.000
	S.D.	0.213	0.013	0.018	0.090	0.787	0.000
10. Coughs	$\bar{x}$	0.590	0.363	0.579	0.411	0.547	5.667
	S.D.	0.633	0.263	0.264	0.309	0.285	3.082
11. Screams	$\bar{x}$	0.731	1.448	2.103	1.840	2.016	1.000
	S.D.	0.281	0.330	0.439	0.428	0.431	0.000
12. Yell whines	$\bar{x}$	0.861	0.972	1.764	2.268	2.324	1.000
	S.D.	0.384	0.321	0.402	0.417	0.359	0.000

Cub calls							
13. Murmurs	$\overline{x}$	1.113	1.050	2.193	1.072	2.209	1.000
	S.D.	0.301	0.164	0.223	0.141	0.238	0.000
14. Warbles	$\overline{x}$	0.682	0.886	1.510	0.939	1.613	1.000
	S.D.	0.393	0.189	0.251	0.231	0.257	0.000
15. Whines	$\overline{x}$	0.569	1.311	2.149	1.509	2.427	1.000
	S.D.	0.329	0.317	0.540	0.240	0.168	0.000
16. Ratchet calls	$\overline{x}$	0.115	0.913	1.817	2.350	2.370	1.000
	S.D.	0.066	0.241	0.283	0.477	0.436	0.000
17. Wow-wow barks 1	$\overline{x}$	0.618	0.831	1.235	0.831	1.272	2.800
	S.D.	0.260	0.384	0.406	0.384	0.382	1.398
18. Wow-wow barks 2	$\overline{x}$	1.364	0.998	1.465	0.998	1.470	5.250
	S.D.	0.383	0.133	0.189	0.133	0.248	0.463
19. Growls 1	$\overline{x}$	0.730	0.153	0.311	0.153	0.401	1.000
	S.D.	0.255	0.031	0.105	0.031	0.344	0.000
20. Growls 2	$\overline{x}$	0.214	0.480	0.995	1.444	0.845	1.000
	S.D.	0.139	0.309	0.431	0.396	0.284	0.000

TABLE 2

Agglomeration schedule for cluster analysis on call type means. The coefficients show the degree of similarity between the clusters being combined. The results are displayed graphically in Figure 1.

Stage	Clusters combined		Coefficient of similarity
1	1	15	0.0731
2	9	19	0.2332
3	4	13	0.2660
4	1	3	0.4102
5	12	14	0.4157
6	11	16	0.5702
7	4	12	0.6569
8	6	17	0.7010
9	7	18	0.8167
10	2	11	0.9805
11	1	20	1.1894
12	2	4	1.3483
13	2	5	1.8755
14	6	8	1.9356
15	7	10	2.1919
16	1	2	2.6525
17	6	7	5.2346
18	1	9	8.6369
19	1	6	16.9248

initial portion of the call, few other bands were present. The mean duration was 830 ms, but the category included both brief 'yaps' and more extended barks. The call had only one component but appeared to be used in calling sequences, often linking into other calls.

Type 2: *yell barks* (Figure 3)
This call was similar to type 1, having the same three main frequency bands. However, it could be distinguished from type 1 calls by the concentration of most energy in the central band and the gradual drop in frequency of this band through the second half of the call. Many of the calls described as 'alarm barks' by sound recordists were of this type, although some were classified as type 1 calls.

Type 3: *shrieks* (Figure 4)
Although highly distinctive, with multiple frequency bands persisting for at least half the call, a few were similar to some of the calls allocated to type 2. Unlike type 1, all were very similar and did not grade into other call types. The energy of the call was more equally invested, although two bands again dominated (on average 1.5 and 2.5 kHz).

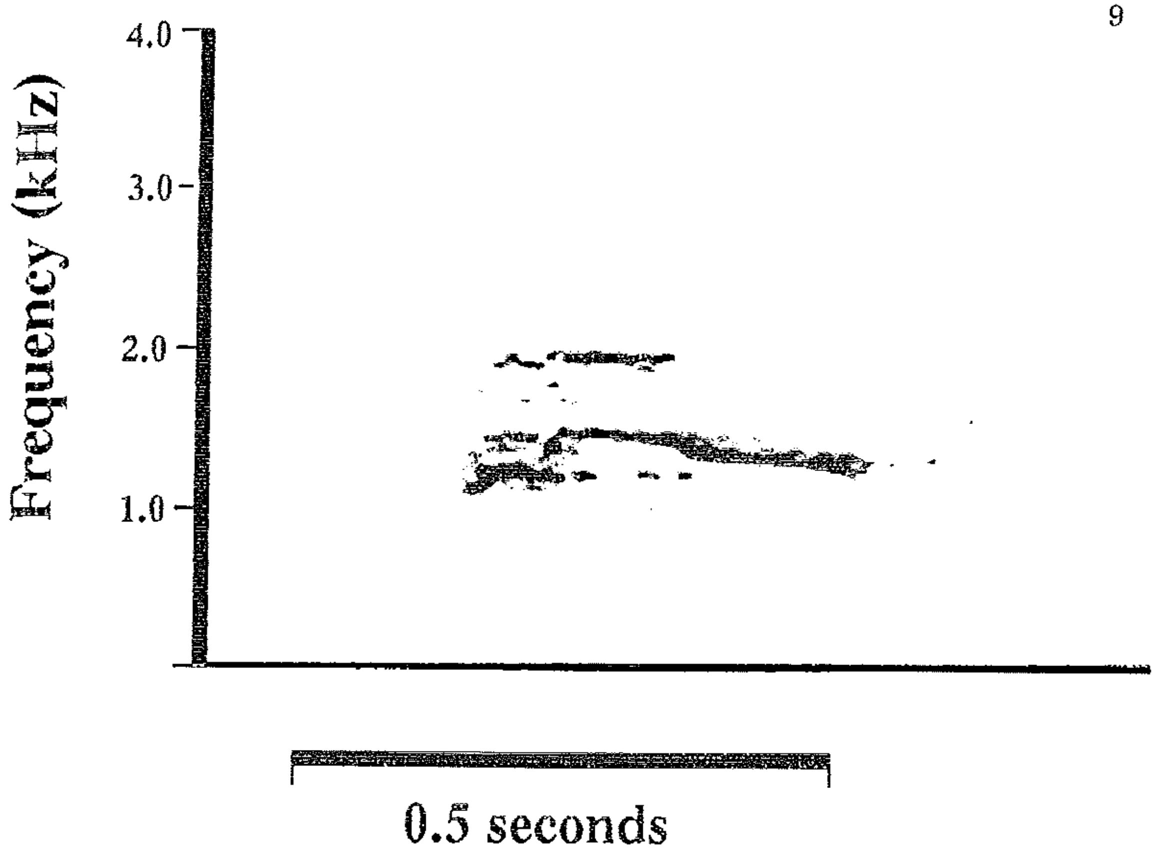

Figure 3. Sonagram showing acoustic structure of call type 2 (yell barks).

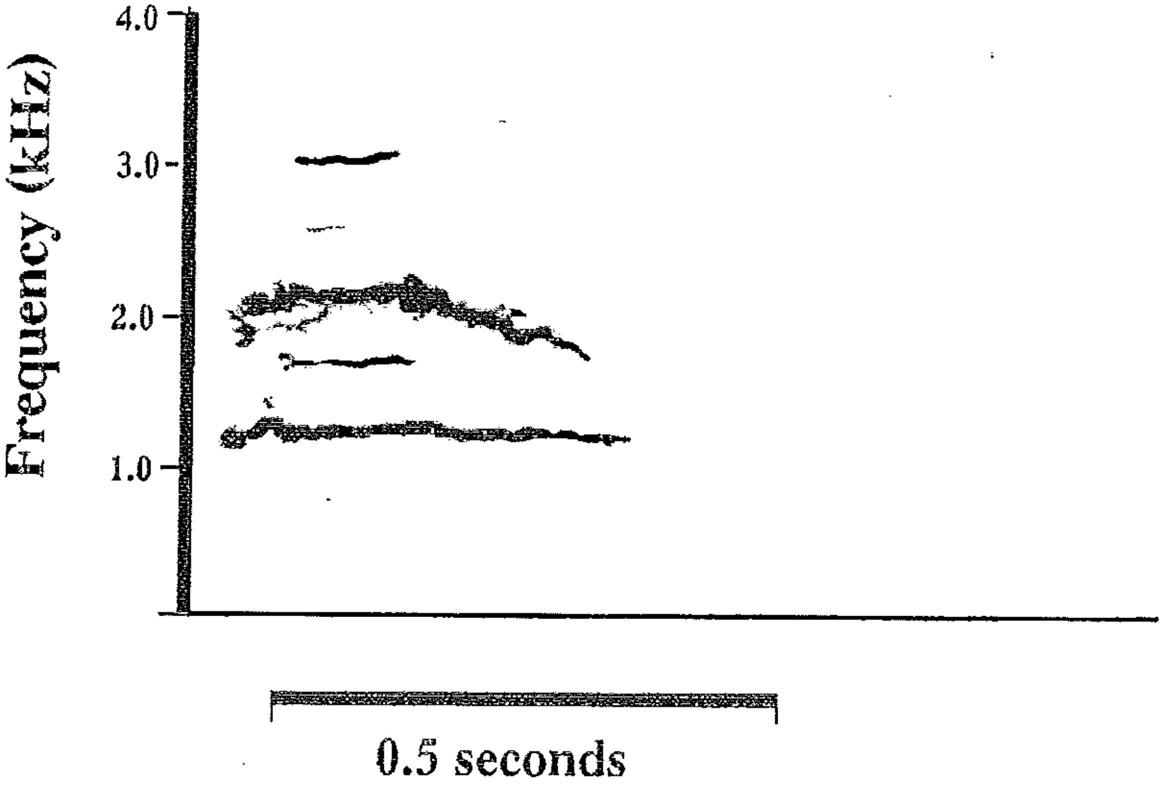

Figure 4. Sonagram showing acoustic structure of call type 3 (shrieks).

Type 4: *whines* (Figures 5 and 6)
These were single component calls, and often followed in sequence from type 1 or 2 calls. They consisted primarily of very distinctive 'high whines'. These had a single frequency band containing nearly all the energy (averaging 1.07 kHz) and two higher, fainter bands, possibly natural harmonics. Whilst the majority of the call was at this frequency, the beginning and end were frequency modulated, rising at the start and dropping at the end. The drop was often trilled. The analyses also grouped whimpers (Figure 6) in this group, although they were qualitatively distinct. Whining as such was not included in this category, because it appeared to be a quality superimposed onto other call types, rather than a basic call type.

Type 5: *ratchet calls* (Figure 7)
This call type has been referred to as 'keckern' (Tembrock 1957), 'clickerting' (Margoschis and Burrows 1978), 'clicketing' (Macdonald 1987) or 'gekkering' (Macdonald 1987). Ratchet calls occurred most commonly as a burst with a highly variable number of components. This variability meant that it was not possible to define clearly call duration or the number of components. However, individual components used alone ('snirks', Macdonald 1987) were structurally identical to those occurring in a sequence, and quantitative data therefore were taken from these. Each component was of short duration (average 170 ms), and covered a

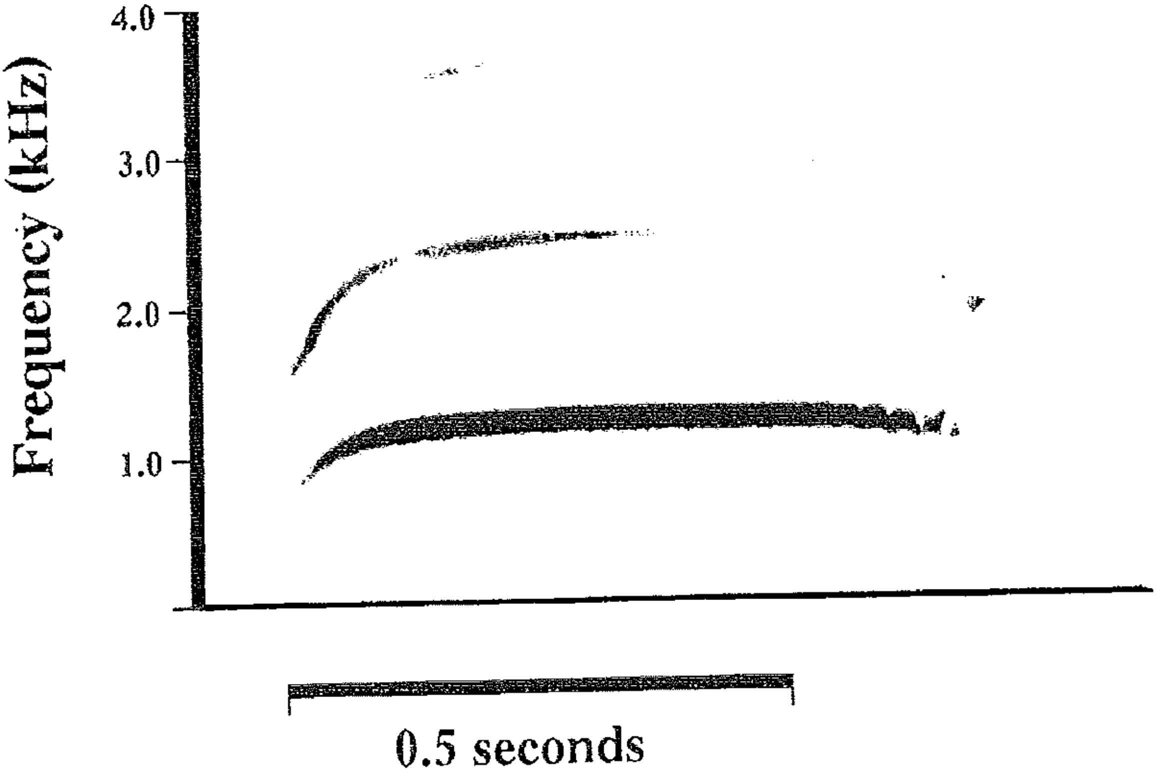

Figure 5. Sonagram showing acoustic structure of call type 4 (high whines).

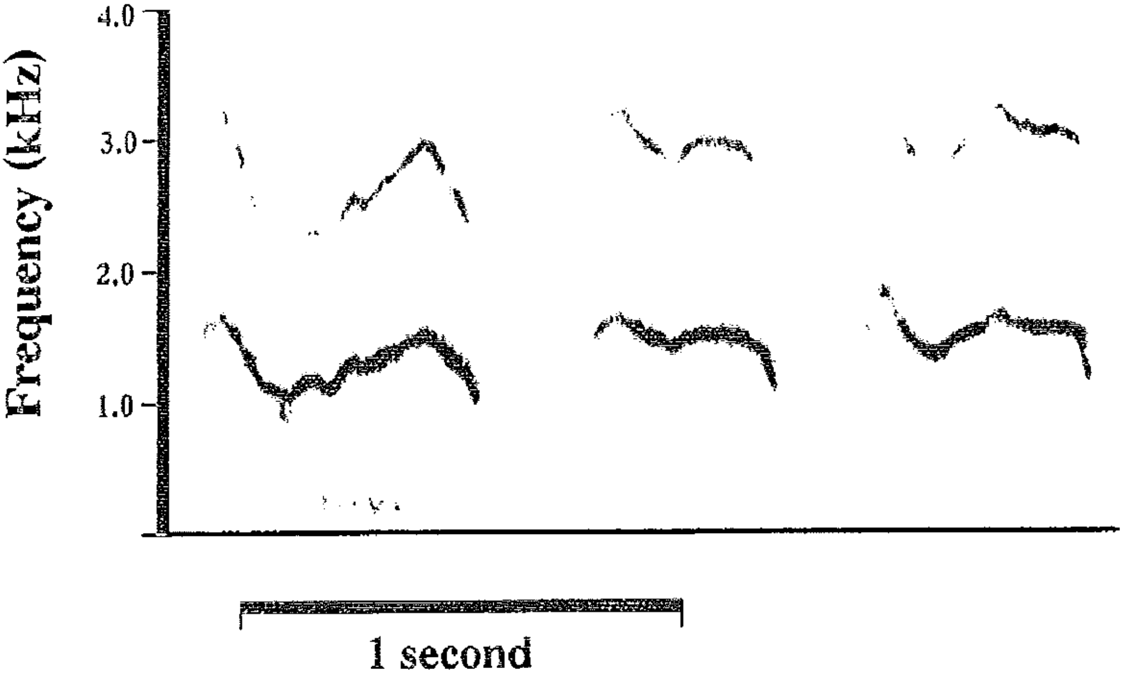

Figure 6. Sonagram showing acoustic structure of call type 4 (whimpers).

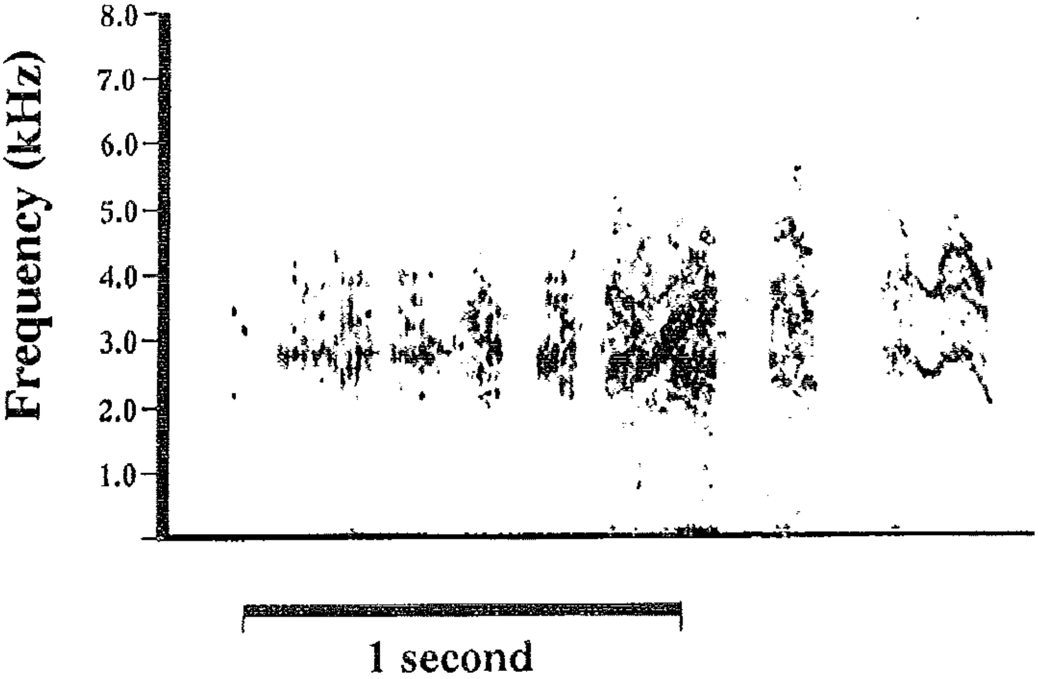

Figure 7. Sonagram showing acoustic structure of call type 5 (ratchet calls).

wide range of frequencies, mainly 2-3 kHz. Clear frequency bands were not readily distinguishable, although the distribution of energy was uneven.

Type 6: *staccato barks* (Figure 8)
Call types 6 and 7 were the two main examples of long range multiple component barking. For type 6, each component was brief (75-300 ms) but distinct, covering a range of frequencies. The frequency range increased throughout the call. There was no clear frequency banding, but energy was invested into frequencies between 600 Hz and 1 kHz.

Type 7: *wow-wow barks* (Figure 9)
These multiple component barks had brief components (up to around 250 ms), typically linked. Each call covered a broad range of frequencies (250 Hz-1.5 kHz), and two clear but wide frequency bands (approximately 755 Hz and 1.21 kHz) were apparent, where the majority of the energy was concentrated. This type of call tended to have more components than type 6 (a mean of 5.8 compared to 3.5).

Type 8: *yodel barks* (Figure 10)
These were much softer calls than types 6 and 7, and consisted of single and linked components, occupying a single, narrow frequency (approxi-

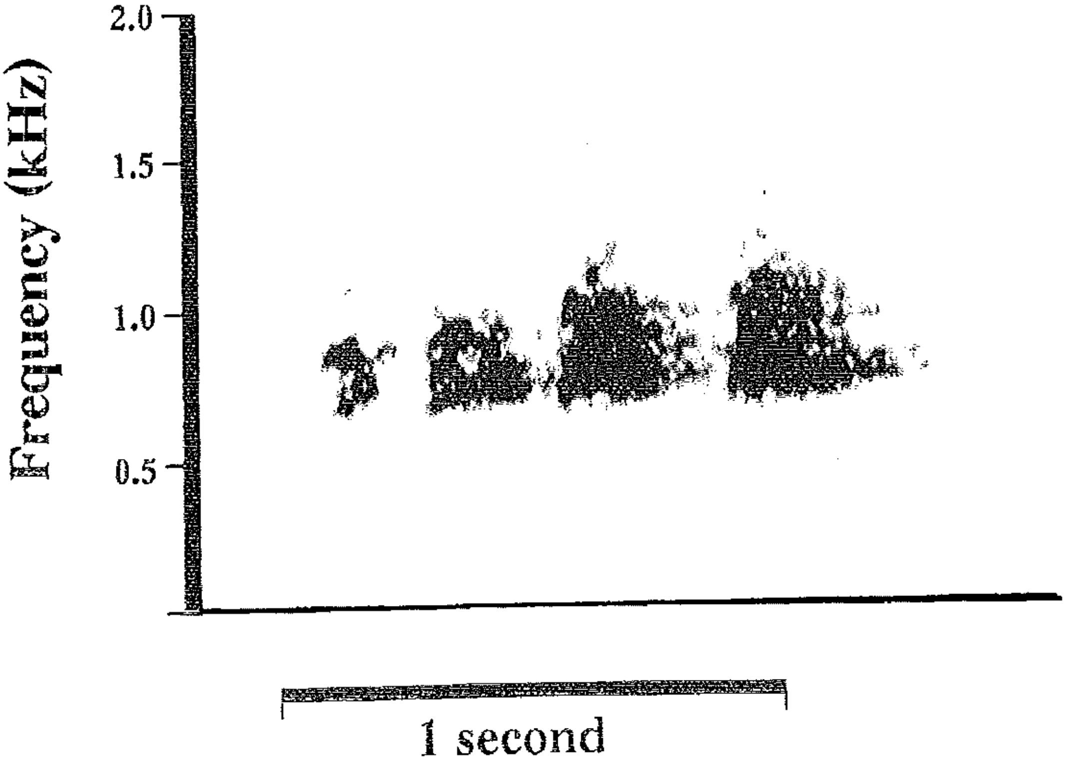

Figure 8. Sonagram showing acoustic structure of call type 6 (staccato barks).

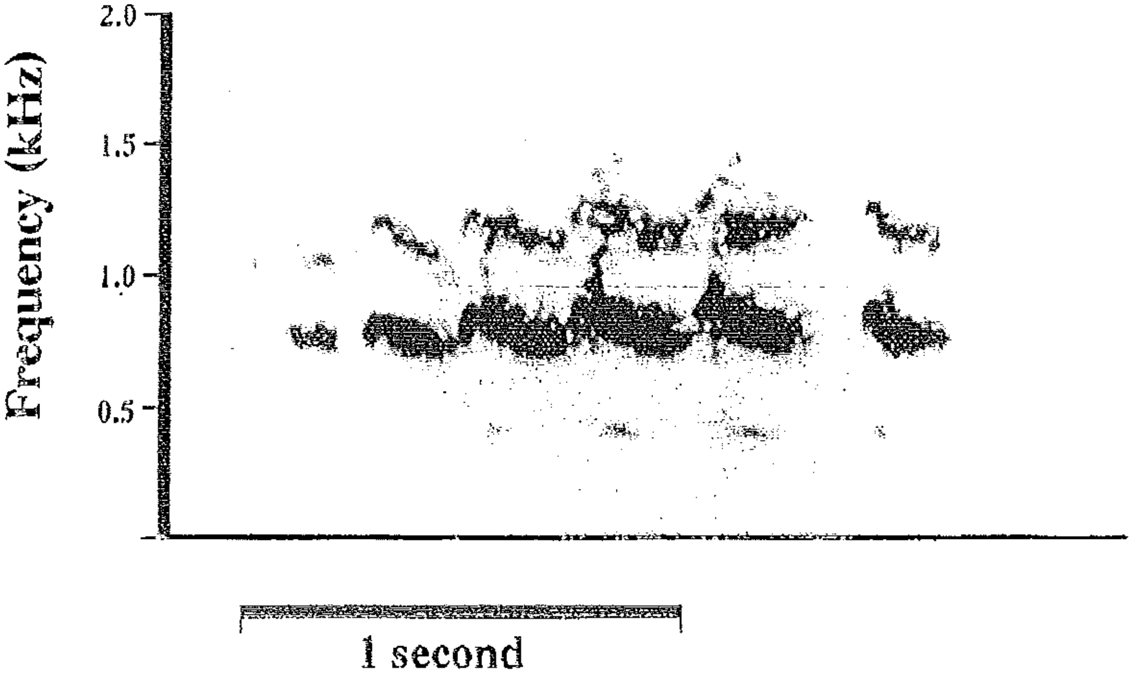

Figure 9. Sonagram showing acoustic structure of call type 7 (wow-wow barks).

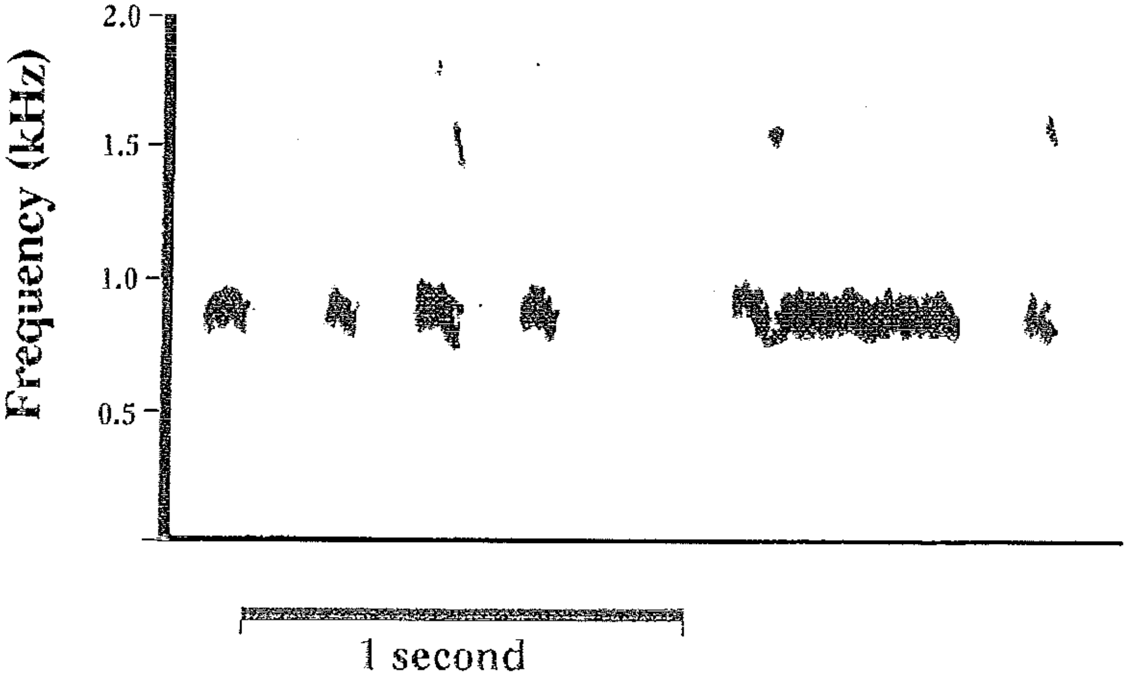

Figure 10. Sonagram showing acoustic structure of call type 8 (yodel barks).

mately 780 Hz). The energy of the call was invested in a frequency band which rose and fell rapidly, producing a yodel effect. This call seems to be that referred to as a 'warble' (Macdonald 1987), and is possibly the same as the 'coo' call, one form of which has been described as trilled (Cohen and Fox 1976).

Type 9: *growls* (Figure 11)
Type 9 calls were highly distinctive and qualitatively similar to the growls of other canids. Almost all the call energy was concentrated below 375 Hz, with two broad bands being distinguished (on average 190 and 200 Hz). Call duration averaged 1.17 s.

Type 10: *coughs* (Figure 12)
These were highly distinctive, low frequency calls. They almost always consisted of a number of nearly identical components (mean of 5.7), although occasionally a single component would be uttered. The energy was spread over a range of frequencies (250 Hz–1 kHz), but concentrated between 250 and 750 Hz, with some division into bands apparent. The last component of the call often dropped in frequency.

Type 11: *screams* (Figure 13)
Calls within this group showed only very slight frequency banding. The

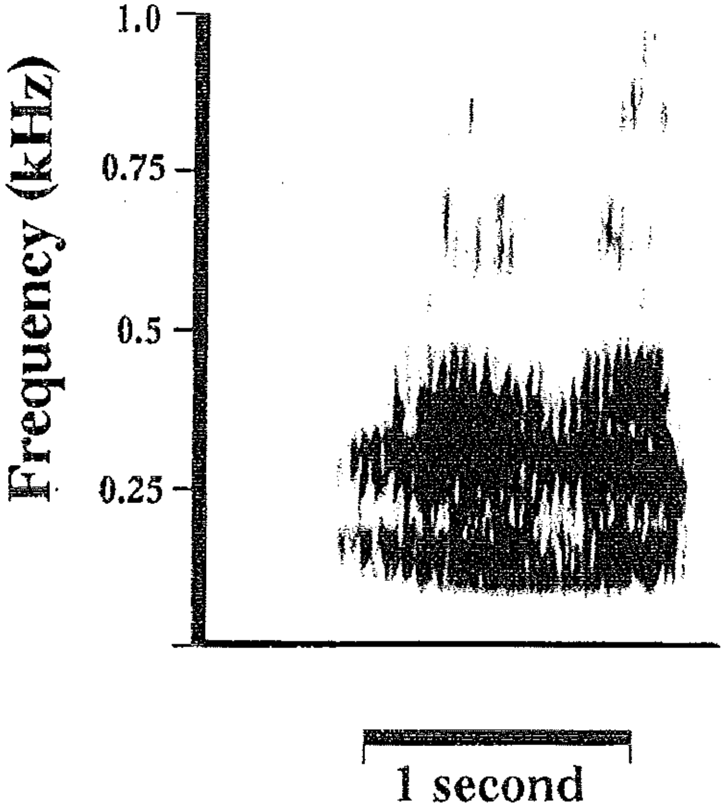

Figure 11. Sonagram showing acoustic structure of call type 9 (growls).

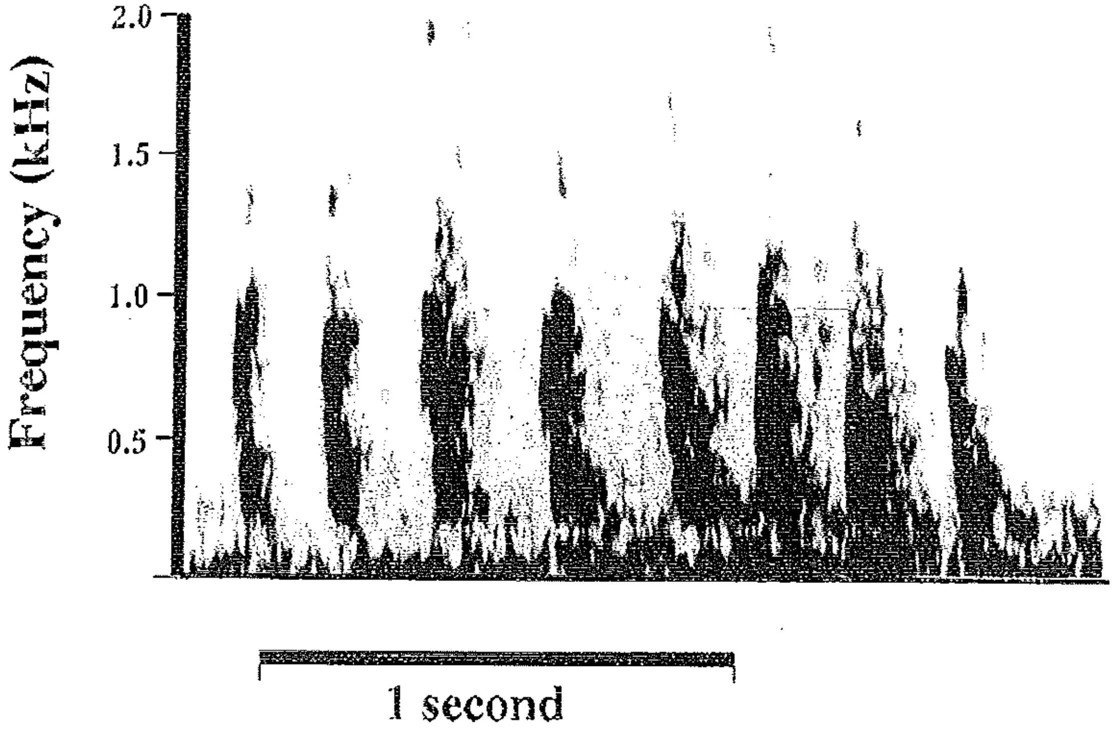

Figure 12. Sonagram showing acoustic structure of call type 10 (coughs). The low frequency noise is caused by foxes walking on gravel.

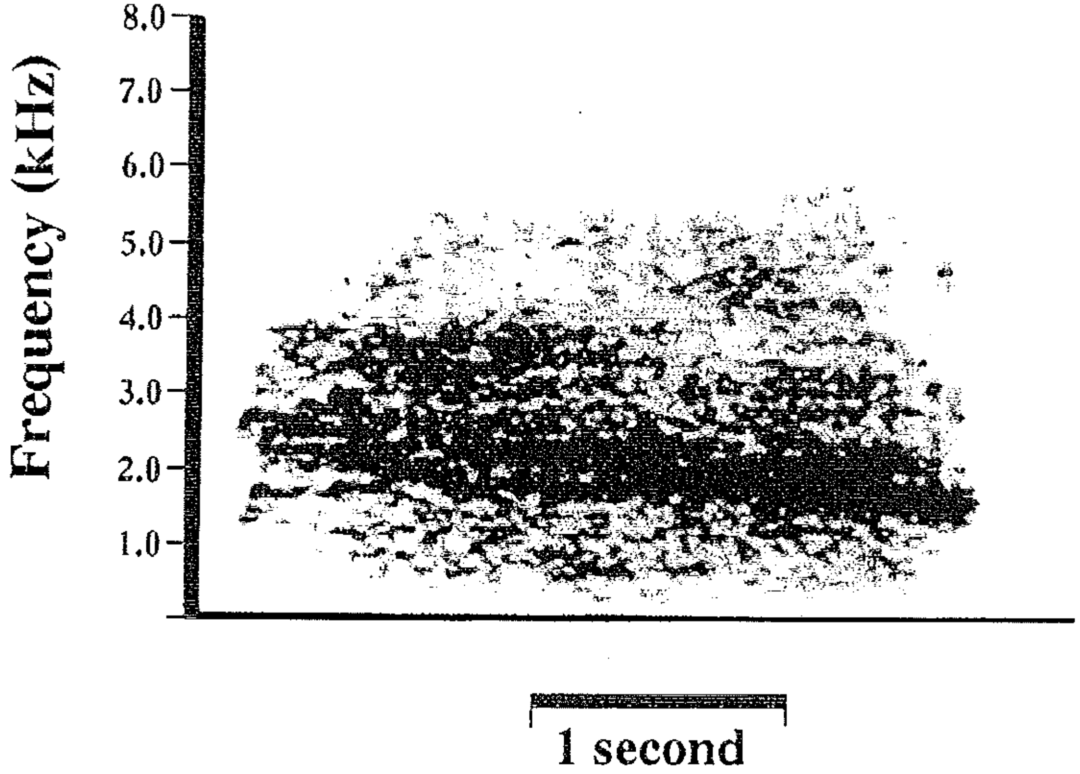

Figure 13. Sonagram showing acoustic structure of call type 11 (screams).

energy of the call was spread over a range of some 5 kHz, but most was concentrated at 1.84 kHz. Average duration was 730 ms, and there was no division into components.

Type 12: *yell whines* (Figure 14)
These were 'noisy' calls with clear frequency banding. The characteristic feature was the change in frequency of the highest energy; this rose about 1 kHz during the first third of the call and subsequently fell with increasing rapidity. The value for the frequency of highest energy in Table 1 is a mean for the whole call.

2. CUB CALLS

With many of the cub vocalisations, two distinct groups of qualitatively similar calls were produced. These differences may be functional, or simply idiosyncratic variation, but there is a strong possibility that the separation represents ontogenetic changes, as appears to be the case for types 13 and 14.

Type 13: *murmurs* (Figure 15)
These calls were characteristic of newborn cubs, but seem to be retained in the vocal repertoire throughout life, having clear similarities with

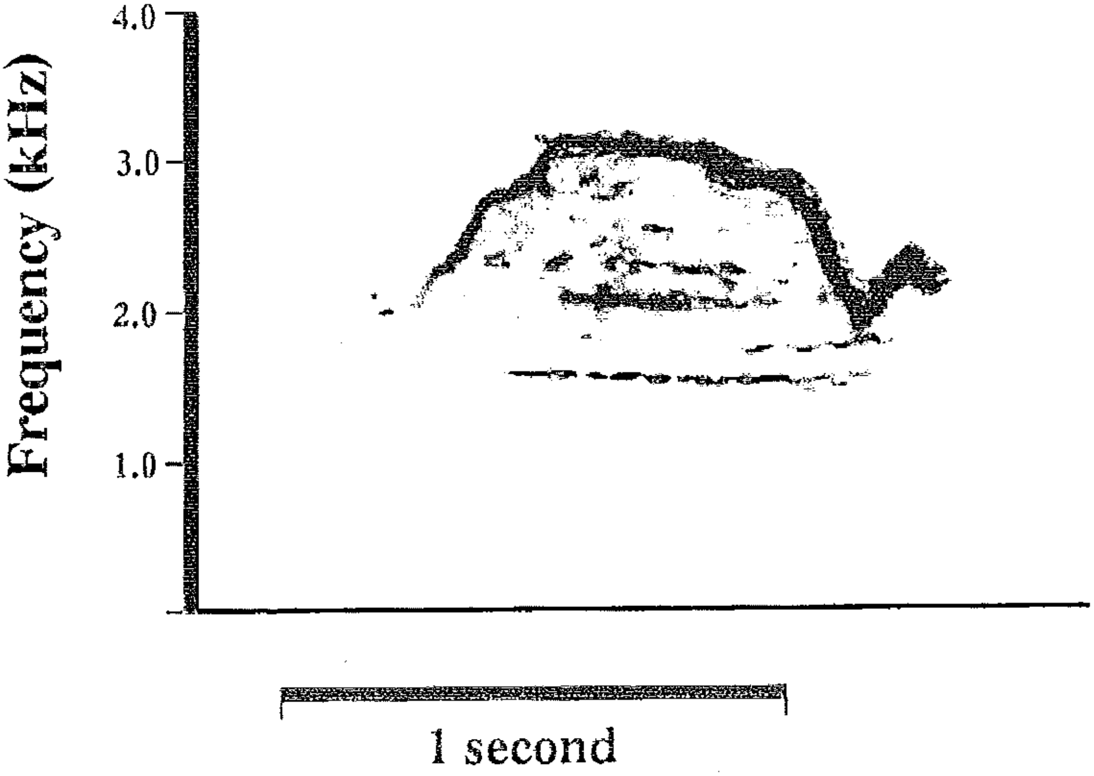

Figure 14. Sonagram showing acoustic structure of call type 12 (yell whines).

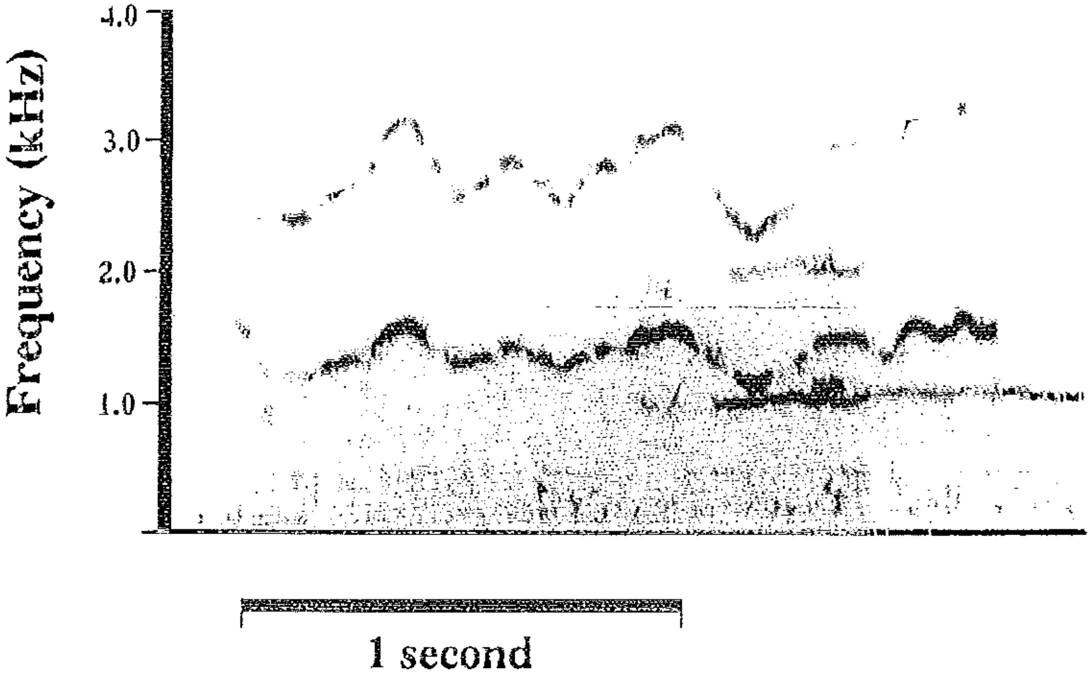

Figure 15. Sonagram showing acoustic structure of call type 13 (cub murmurs).

adult whimpers (Figure 6). The call consisted of two frequency bands, the fundamental frequency and first harmonic, which rose and fell in frequency in what appeared to be a random pattern. The duration was variable (mean of 1.11 s) and the majority of the energy at a mean frequency of 1.07 kHz.

Type 14: *warbles* (Figure 16)
These were a second form of murmuring, produced as the cubs reach two to three weeks of age. Although separated by the analytical procedure, there was a fair degree of overlap between these and type 13 calls. The call shows clear ontogenetic development, becoming more warbled and increasingly separated into a number of components, reaching the characteristic warble by about two weeks. This process continues with division into components taking precedence over warbling, until the wow-wow bark (types 17 and 18) develops.

Type 15: *whines* (Figure 17)
These are very common in young cubs, appearing prior to warbles (type 14). They could be distinguished by a general lack of frequency change through the call, and sonagraphically by their "clean" structure. The fundamental frequency was 1.51 kHz on average, with first and second

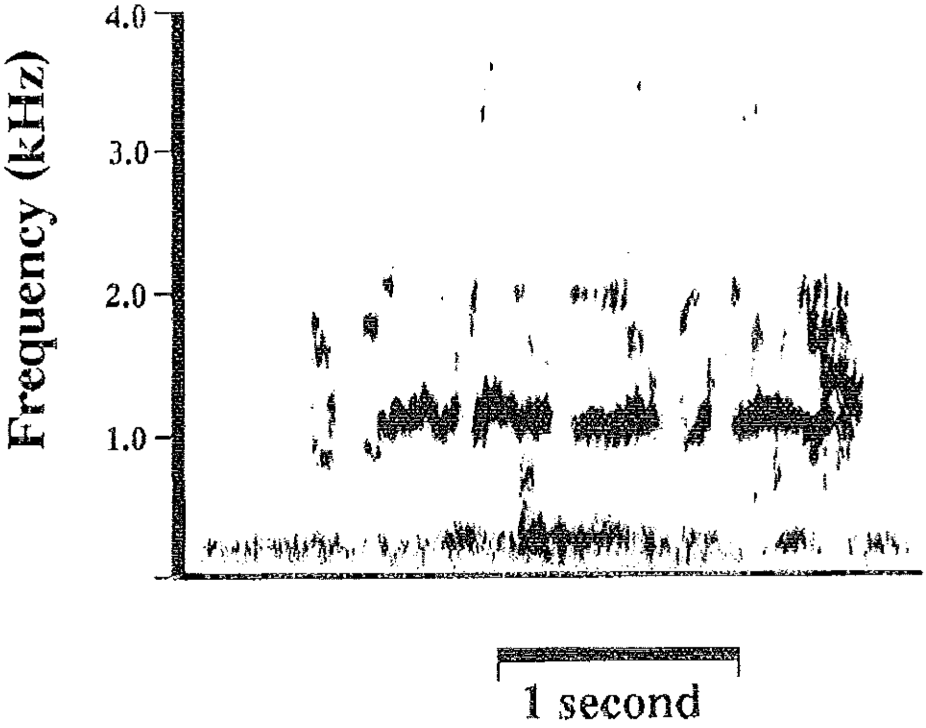

Figure 16. Sonagram showing acoustic structure of call type 14 (cub warbles).

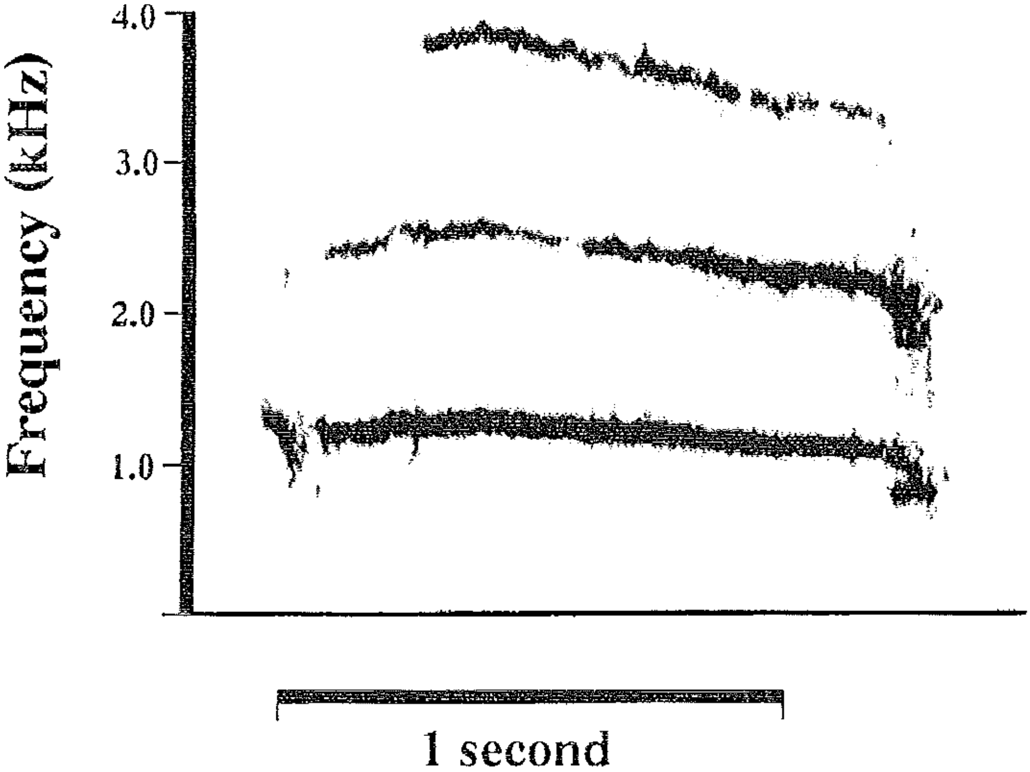

Figure 17. Sonagram showing acoustic structure of call type 15 (cub whines).

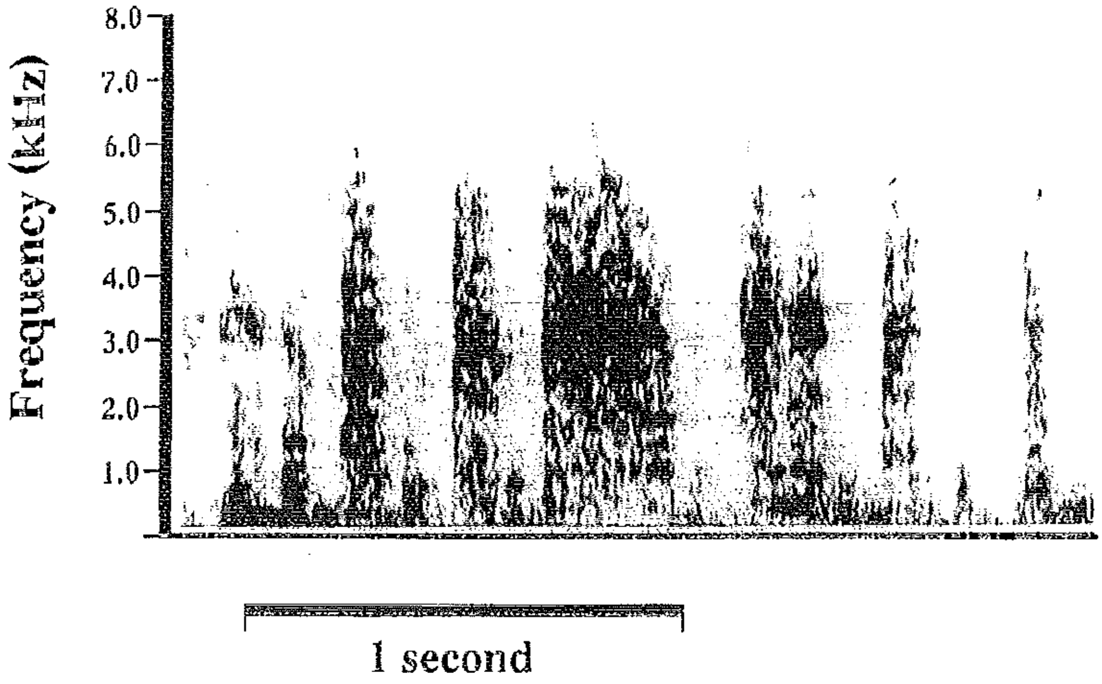

Figure 18. Sonagram showing acoustic structure of call type 16 (cub ratchet calls).

harmonics. Duration was variable, but averaged 570 ms for each whine. These calls were always found in sequences, often as long as the sample recording.

Type 16: *ratchet calls* (Figure 18)
These calls were very similar to the equivalent adult vocalisation (type 5), although the calls differed quantitatively, with the cub version carrying most energy at a higher frequency than that of the adult. This difference in frequency structure is probably due to differences in body size.

Types 17 and 18: *wow-wow barks* (Figures 19 and 20)
The analysis separated these multiple component barks into two separate groups, with type 17 being shorter and of a lower pitch than type 18. Both were higher pitched than either of the comparative adult calls (types 6 and 7). As with the ratchet calls (types 5 and 16), this juvenile quality was probably due to the difference in body size.

Type 19 and 20: *growls* (Figures 21 and 22)
Both groups of growls were shorter and higher pitched than their adult equivalent (type 9), but were qualitatively similar. Type 19 growls were longer than type 20 growls (mean of 730 ms compared to 210 ms) and of a lower pitch (mean lowest frequency of 150 Hz compared with 480 Hz, and

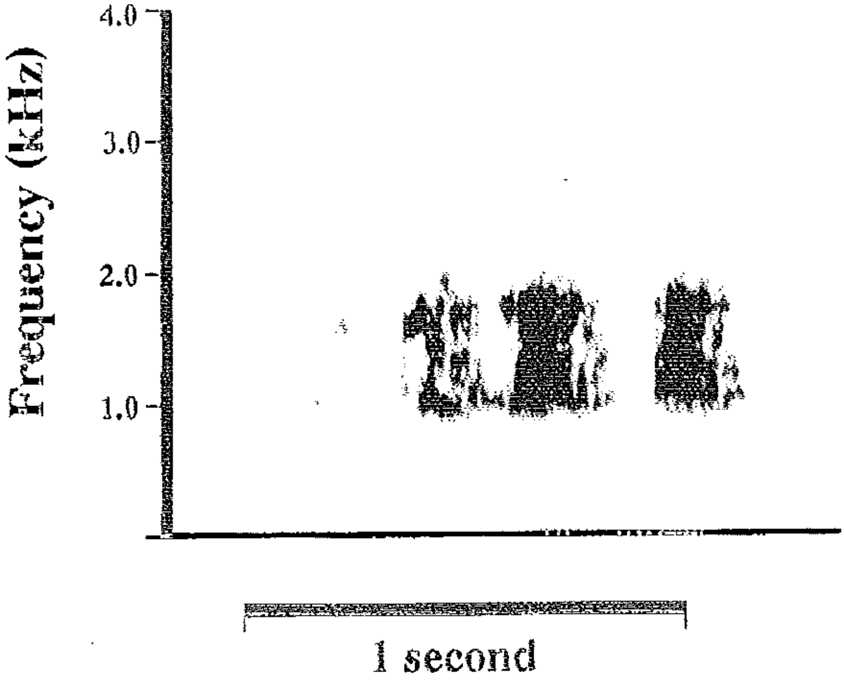

Figure 19. Sonagram showing acoustic structure of call type 17 (cub wow-wow barks 1).

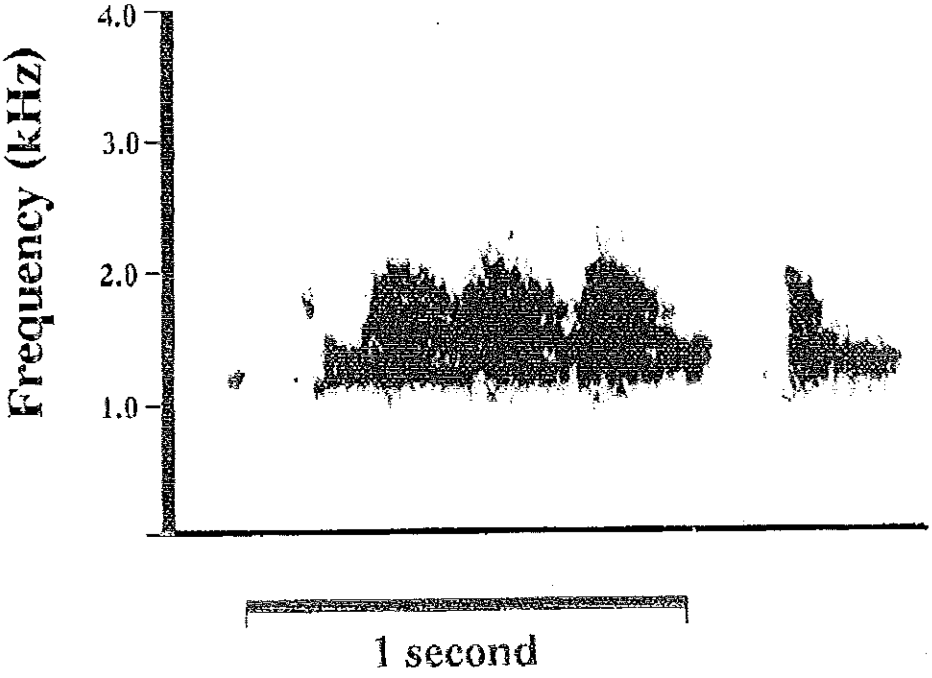

Figure 20. Sonagram showing acoustic structure of call type 18 (cub wow-wow barks 2).

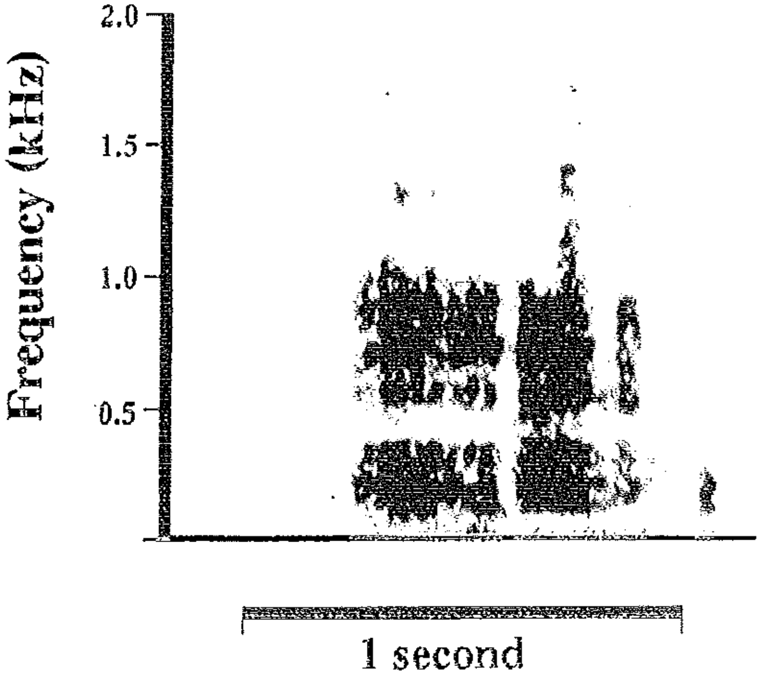

Figure 21. Sonagram showing acoustic structure of call type 19 (cub growls 1).

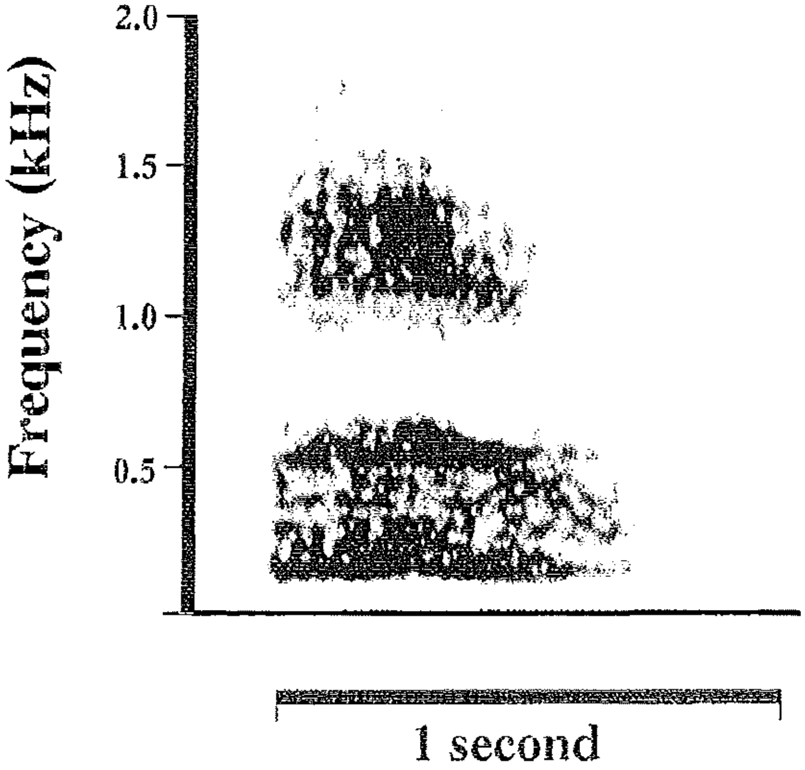

Figure 22. Sonagram showing acoustic structure of call type 20 (cub growls 2).

mean highest frequency of 153 Hz compared with 1.44 kHz). It was not possible to examine for age-related differences in these calls because precise ages of the vocalising animals were not known.

Discriminant analysis

The accuracy of the grouping of adult calls was 85.0%, while that for the cub calls was 93.2%. The null hypothesis that the group means are equal can be rejected for each variable (Table 3). The only significant correlation between each of the variables was between the lowest and second lowest frequencies ($r = 0.74$).

TABLE 3

Results of discriminant analysis, giving Wilks' lambda, F statistic and level of significance for each of the discriminating variables.

	λ	F	p
Adult calls			
Duration	0.677	21.4	< 0.0001
Lowest frequency band	0.257	129.2	< 0.0001
Second lowest frequency band	0.269	121.8	< 0.0001
Highest peak frequency	0.231	149.0	< 0.0001
Second highest peak frequency	0.461	52.5	< 0.0001
Number of components	0.266	123.7	< 0.0001
Cub calls			
Duration	0.355	16.11	< 0.0001
Lowest frequency band	0.334	17.69	< 0.0001
Second lowest frequency band	0.222	31.12	< 0.0001
Highest peak frequency	0.193	37.02	< 0.0001
Second highest peak frequency	0.148	50.92	< 0.0001
Number of components	0.121	64.12	< 0.0001

For the adult calls, the first five of the discriminant functions contributed significantly to the division into groups ($p < 0.001$). Three measures (highest peak frequency and lowest and second lowest frequency bands) contributed to the first discriminant function, with the number of components contributing most to the second function. The highest peak frequency, or fundamental frequency, was the single most important variable in classifying the calls (Table 4). For cub calls, the first four discriminant functions were responsible for the division into groups, while the remaining function reflected only random variability (Table 5).

TABLE 4

Pooled within-group correlation between discriminating variables and canonical discriminant functions for adult calls, together with the percentage of variance accounted for by, and level of significance of, each discriminant function.

	Discriminant function 1	Discriminant function 2	Discriminant function 3	Discriminant function 4	Discriminant function 5
Duration	–0.222	–0.065	0.111	0.156	–0.099
Lowest frequency band	0.654	0.438	–0.411	–0.383	0.149
Second lowest frequency band	0.600	0.415	–0.587	0.299	–0.014
Highest peak frequency	0.733	0.433	0.445	–0.156	–0.225
Second highest peak frequency	0.366	0.201	–0.067	0.384	0.816
Number of components	–0.615	0.671	0.099	0.103	0.012
% variance accounted for	48.42	19.24	15.48	10.72	4.13
χ^2	2493.2	1618.7	1086.9	623.34	262.22
d.f.	66	50	36	24	14
p	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001

TABLE 5

Cub calls. Pooled within-group correlation between discriminating variables and canonical discriminant functions for cub calls, together with the percentage of variance accounted for by, and level of significance of, each discriminant function.

	Discriminant function 1	Discriminant function 2	Discriminant function 3	Discriminant function 4
Duration	-0.127	0.415	0.002	0.612
Lowest frequency band	0.165	0.297	0.476	-0.279
Second lowest frequency band	0.332	0.336	0.547	0.197
Highest peak frequency	0.294	-0.275	0.823	-0.012
Second highest peak frequency	0.456	0.357	0.741	-0.146
Number of components	-0.598	0.311	0.690	0.030
% variance accounted for	52.53	29.64	14.13	2.78
χ^2	439.98	274.65	141.56	46.92
d.f.	42	30	20	12
p	< 0.0001	< 0.0001	< 0.0001	< 0.0001

Field data

The field data were categorised into the following call-type groups—barks/yell barks, shrieks, whines, ratchet calls, wow-wow barks (including staccato barks), growls, screams and yell whines. It was not possible for different field workers consistently to distinguish adult from cub vocalisations in general, or yell from normal barks or staccato from wow-wow barks. Yodel barks and coughs were not included, since they are quiet calls, unlikely to be heard in the field unless the fox is in close proximity. Figure 23 shows the seasonal occurrence of these different vocalisations. The paucity of all vocalisations is immediately apparent. Total rates of vocalisations varied significantly with season ($\chi^2 = 24.93$, d.f. = 3, $p < 0.001$), being higher in winter than in spring, summer and autumn, and higher in spring than in autumn. This was largely because of a significant increase in agonistic vocalisations (ratchet calls, screams and yell whines) in the winter ($\chi^2 = 14.18$, d.f. = 3, $p < 0.01$).

The most common vocalisations were the barks/yell barks, but even these were heard an average of only 20 times per 400 hours of radio-tracking. However, they were significantly more common in winter than in the other seasons ($\chi^2 = 19.27$, d.f. = 3, $p < 0.001$). Of 77 sequences of barks/yell barks heard, 67 were separate from other sounds, three immediately followed an agnostic interaction, three were interspersed with wow-wow barks, and five were part of a communication between two or more individuals. In one of these instances, the communication was inter-

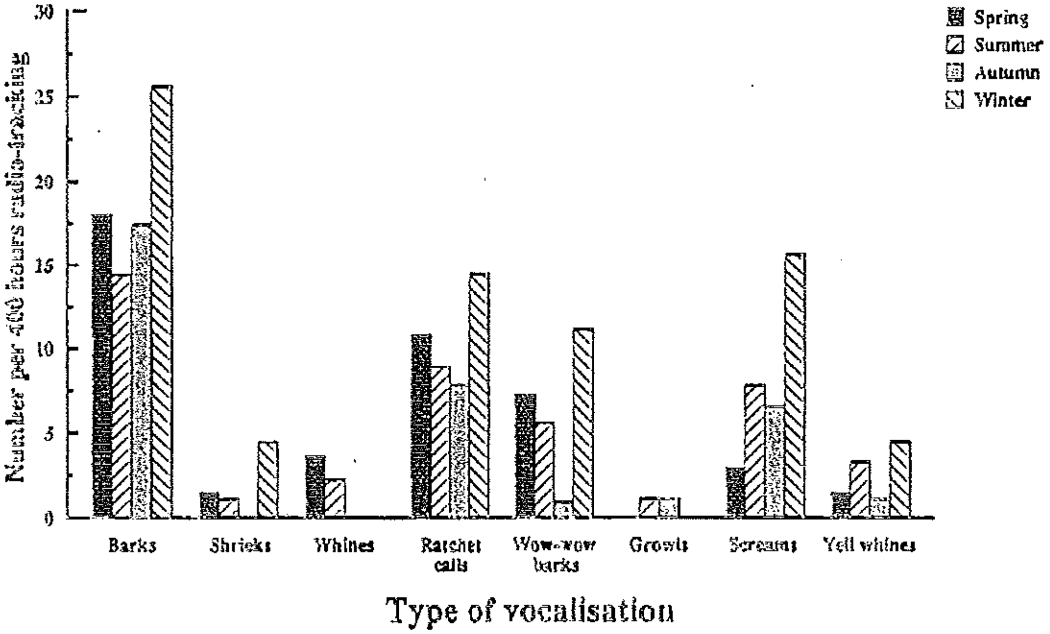

Figure 23. Incidence of vocalisations heard in different seasons, expressed as the number of occurrences per 400 hours radio-tracking. For details of the types of calls recognised in the field, and the definitions of seasons, see text. Total number of hours radio tracking: spring 556, summer 360, autumn 368, winter 360.

group, and in three it was intra-group. Wow-wow barks were significantly more common in the winter than the other three seasons ($\chi^2 = 10.95$, d.f. = 3, $p < 0.05$), and significantly more common in both spring and summer than in autumn. Of the 26 sequences of wow-wow barks heard, five were separate from other calls, two immediately followed an agnostic interaction and four were part of a communication, all intra-group. On one occasion, a wow-wow bark, probably from a cub, had a beckoning effect on a dog fox. Shrieks also showed significant seasonal differences in occurrence, again being significantly more common in winter than in the other three seasons ($\chi^2 = 8.24$, d.f. = 3, $p < 0.05$).

DISCUSSION

The sonagraphic analysis produced 20 quantitatively distinct call groups, eight of which were cub calls. Three of the four frequency variables were critical in assigning the calls to groups. This is in agreement with earlier work identifying frequency as a key information parameter (Tembrock 1976, Movchan and Orlova 1990). All the basic canid vocalisations identified by Cohen and Fox (1976), except 'pants', are present, and further categories, particularly different types of barks, have been identified. It should be noted that, although all available fox recordings were investigated, this list is not intended to be an exhaustive catalogue of fox vocalisations. Combination calls were excluded from the analysis, and a few other call types were also heard but were too rare to be analysed. These included four examples from the same fox of a 'trill bark' that bore a close qualitative resemblance to wow-wow barks, but were structurally more similar to a yodel bark, and various other sounds associated with feeding. However, all the main vocalisations have been described, and the extensive source of material suggests that any calls not included will be rare.

Total vocalisations were at their most frequent during winter, which correlates with both peak dispersal and the mating period. At this time, the normally strict territorial system is disrupted by dispersing foxes crossing occupied ranges, and by changes in the movements of the resident foxes themselves. Male foxes will trespass into adjacent ranges in search of extra-group mating opportunities, and females will move closer to the boundary of the group ranges, perhaps scent marking to attract neighbouring males (White 1992). Because of these wider-ranging movements in the winter, encounter rates between members of the same group are at a minimum (White 1992), and intra-group communication is therefore most difficult. Another consequence of the ranging behaviour of the males is that territory defence will also be most active. Thus, both intra- and inter-group vocal communication are at their highest levels. The call types that are best suited to intra-group long-distance communication are those that have the potential to convey information and are therefore structurally complex. The frequency banding of wow-wow barks has the potential to convey information about identity, and their gradual onset, with the full frequency banding not apparent until 500 ms into the call, also implies a relatively 'friendly' use. The frequency of the call is also adapted for distance, the lowest frequency band being 550 Hz. The higher occurrence of this call in the winter also supports this role, which was suggested by Macdonald (1987). Staccato barks have a simpler structure and, being energetically cheaper, may serve simply to establish or maintain contact.

In contrast to intra-group contact calls, inter-group ones would be expected to start in an abrupt 'hostile' manner, best suited to a warning function, yet also be able to convey some information. Normal and yell barks both start abruptly, have three principal easily discernible frequencies between 1 and 2 kHz, and are relatively stereotyped. They show redundancy and are structurally more complex than staccato barks, though less so than wow-wow barks. They have previously been ascribed an inter-group territorial function, and both their structure and their peak frequency in winter suggest this may be the case. The concentration of energy in a few main frequency bands is especially suitable for conveying information (Movchan and Orlova 1990). The explosive start to the calls may derive from a sudden expiration, which is characteristic of agonistic canid calls (Tembrock 1976). Normal barks are perhaps a more general warning call, and may correspond to an intra-group alarm bark. The frequency banding will theoretically assist location, but this is compensated for by the rapid onset and short duration (Marler 1955).

Agonistic vocalisations reach a peak in winter, when aggressive encounters are at their most frequent (White 1992). Ratchet calls are very ritualised, being both highly stereotyped and redundant. The ambiguous call length indicates that the call is context-specific and may be backed up with olfactory or visual signals, and that all the information is conveyed within each component. Each component is short, relatively instantaneous, and with a minimal ascent time and frequency spread. The wide frequency spread of screams, over 5 kHz, is characteristic of defensive sounds (Tembrock 1976) and carries little information, there being very little in the way of discrete frequency bands. This, together with the rapid onset and high amplitude, gives the sound an explosive quality, and suits it to the role of a threat call (Tembrock 1976). The frequency banding of yell whines would allow the encoding of identity, and these calls seem to signify intense submission. They may therefore be used on both an inter- and intra-group basis, and may coincide with either agonistic or affiliative behaviour respectively. Growls are characteristic threat calls in many canids. Their low amplitude means that they are only able to operate over short distances. It is possible that differences in frequency would emphasise differences in the size of two aggressors, hence representing some ritualisation of aggression. Coughs are similar to growls in their low frequency, but are less harsh, and are commonly emitted by the dog fox or vixen in close proximity to the cubs. They will alert the cubs to potential danger, but will be difficult to locate.

Whilst shrieks were most common in winter, they do not appear to be structurally suited to aggression. They have a relatively gradual onset, are highly complex and of long duration, and the vocaliser is therefore easy to locate. The majority of energy is concentrated at a lower frequency than in the yell and normal barks and will therefore travel further. The call is highly stereotyped and redundant, suggesting an interactive function. It has long been thought to be a call made by vixens to attract dog foxes (Lloyd 1980, Macdonald 1987) and its greater use in winter would lend support to this. However, dog foxes have been observed to make the call (Macdonald 1987), and in the present study it was heard on several occasions outside the mating season. The precise function or functions remain unclear.

The only call type that showed any marked seasonal trend, other than an increase in winter, was whimpers. This category was grouped with high whines by the structural analyses, but is a much quieter, smoother sound, and seems to correspond with the 'mew' described by Cohen and Fox (1976). It is similar to the murmuring of cubs and may function as a contact seeking vocalisation at close quarters, such as between adults and cubs close to the breeding earth. Its greater occurrence in spring and summer, and its absence in autumn and winter, supports such a hypothesis.

The different cub vocalisations identified in the structural analyses are sufficiently similar to their adult equivalents to fulfil the same function, or at least represent earlier ontogenetic versions of these calls. However, the juvenile quality in the call structure would allow any fox hearing the call to identify the signaller as a cub.

This work has supported previous qualitative observations made by Burrows (1968) and Lloyd (1980) that fox calls are more common in the winter months, with a clear correspondence between the increases in certain types of call and the social pressures existing at that time of year. Winter conditions (cold, clear nights) are also most conducive to vocal communication (Wiley and Richards 1978) and least so for scenting, and this may also encourage the greater use of vocalisations at this time of year. The results presented here have also lent support to some earlier suggestions concerning the function of certain vocalisations, and the coupling of structural analyses with seasonal field data has led to the development of specific hypotheses that can be tested experimentally. It is only by conducting controlled playback experiments in the field that the precise functions of the calls can be proved conclusively.

However, this study has also raised more general questions about canid vocal behaviour. Fox vocalisations have been shown to be more than just an 'emotional language' (Cohen and Fox 1976). Distinct calls occur, which appear to be able to convey information about identity and location, as well as motivational state. Yet the single most striking result from the field data is the general rarity of vocalisations. It is possible that in an urban environment, where group home ranges are small, averaging 26 ha for the study groups (White 1992), distance communication is largely unnecessary because of the relatively high density of scent marks per unit area. Another reason may be that the complex structure and background noise of the urban environment make vocal communication less effective. However, Burrows (1968) found that vocalisations in a rural fox population were also mostly rare. Vocalisations are likely to have only minimal impact on time and energy budgets in foxes (Montgomery 1974), but it appears that scent marking is generally preferred as a means of indirect communication, with vocalisations perhaps being used only in circumstances where instantaneous communication is required.

ACKNOWLEDGEMENTS

We would like to thank Rob Berry for his assistance, Paul Duck for providing access to fox recordings in the British Library of Wildlife Sounds (National Sound Archive), Nigel Tucker for access to BBC recordings, and Ray Goodwin and Richard Margoschis for providing otherwise unavailable recordings. We would like to thank Glen Saunders for help in collecting the field data, and Warren Cresswell and Stephanie Wray for advice on statistics. Piran White is grateful to the Ministry of Agriculture, Fisheries and Food for a postgraduate studentship.

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APPENDIX

Sources of fox calls

1. BBC Sound Archives. All recordings not examined at the British Library of Wildlife Sounds were listened to and three tracks selected and analysed.
2. BBC Video Archive. CNH21901 *Foxwatch*—four twenty minute programmes, recorded from live broadcasts of young cubs in an earth, and CNH19325 *Wildlife on One: Foxwatch*—compilation from live broadcasts, including many calls not on CNH21901.
3. British Library of Wildlife Sounds. Entire catalogue of fox calls listened to, except some BBC recordings available from BBC archive. Following tracks selected and analysed: 00051, 00053, 00054, 01546,

02288, 02369, 02819, 02820, 04380, 06660, 06680, 06681, 06682, 09580, 11258, 15455, 15457, 20941, 20943, 20949, 20952, 23703, 27049, 27251, BBC MP15062-Fr2, MP25014-Bk1, MP25245-Bk1, MP25275-Fr1, MP25493-Bk2, MP25493-Bk3, MP25493-Fr3, MP25493-Fr4, MP25494-Bk1.

4. Goodwin, R. Unreleased material. One cassette of 14 tracks.
5. Macdonald, D. & Jackson, K. (1989). *Running with the Fox.* One cassette, SN856. Sounds Natural, Fulbrook, Oxford.
6. Margoschis, R. & Burrows, R. (1978). *British Wildlife Habitats no. 3. The Fox.* One cassette. R. Margoschis, Atherstone, Warwickshire.
7. Margoschis, R. Unreleased material. Tracks: 51MF1-4, 52MF1-4, 53MF1-5, 53MF6-19.

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Since the acceptance of this paper for publication, Schassburger (1993) has published a major review of the structure and function of wolf vocalisations. As in this paper, he grouped vocalisations on the basis of their structural affinities, which were then related to the corresponding meanings and functions of the various sounds. Schassburger (1993) concluded that the wolf's vocal repertoire is a bipartite system, with two major types of call: harmonic (frequency 380-680 Hz) and noisy (frequency 70-170 Hz). The information contained in the harmonic portion of the system is more clear-cut and unambiguous, whilst that contained within the noisy repertoire is more elaborate and therefore more expressive of subtle motivational functions. In the wolf, harmonic vocalisations are non-aggressive, amiable and submissive, whereas noisy ones are aggressive or dominant. Complexity within the wolf's vocal repertoire, and therefore the enhancement of communicative value, is achieved by the use of mixed sounds, transitions and gradations. Schassburger (1993) attempted to draw comparisons between wolves, coyotes and red foxes, but was limited by the lack of structural information on the various types of canid vocalisation. A preliminary comparison between his study and ours suggests that adult fox vocalisations are generally higher in frequency than those of wolves, and that in foxes both aggressive and non-aggressive vocalisations appear to differ more in structural complexity than in frequency. These two studies, on species exhibiting very different patterns of social organisation (Fox 1975), thus provide a structural basis on which to develop a functional classification of canid vocalisations.

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