



## Barking in domestic dogs: context specificity and individual identification

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In this study we sought to determine whether dog barks could be divided into subtypes based on context. We recorded barking from 10 adult dogs, *Canis familiaris*, of six breeds in three different test situations: (1) a disturbance situation in which a stranger rang the doorbell, (2) an isolation situation in which the dog was locked outside or in a room isolated from its owner and (3) a play situation in which either two dogs or a human and a dog played together. We analysed spectrograms of 4672 barks using macros that took 60 sequential frequency measurements and 60 sequential amplitude measurements along the length of the call. Statistical analyses revealed that barks are graded vocalizations that range from harsh, low-frequency, unmodulated calls to harmonically rich, higher-frequency, modulated calls. The harsh, low-frequency, unmodulated barks were more commonly given in the disturbance situation, and the more tonal, higher-pitch, modulated barks were more commonly given in the isolation and play situations. Disturbance barks were also longer in duration with more rapid repetition than the barks given in other contexts. Discriminant analysis revealed that dog barks can be divided into different subtypes based on context even within individual dogs, and that dogs can be identified by their bark spectrograms despite the context of the bark.

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With 62 million pet dogs in the U.S.A. alone (Center for Information Management 2002), and a multi-billion-dollar pet industry focused largely on dogs, *Canis familiaris*, is an integral part of family life in America. In spite of domestic dogs' popularity, only a handful of studies have addressed their vocal behaviour (Bleicher 1963; Scott & Fuller 1965; Cohen & Fox 1976; Tembrock 1976; Ohl 1996; Feddersen-Pedersen 2000). Of these studies, only two (Ohl 1996; Feddersen-Petersen 2000) focused primarily on vocal communication.

One reason for the lack of research in this area stems from the idea that the hallmark vocalization of dogs, the bark, seems hypertrophied and occurs in a much wider variety of contexts than for the dog's wolf-like ancestor (Fox 1971; Cohen & Fox 1976; Coppinger & Feinstein 1991; but see Yin 2002). In fact, barking in dogs is so frequent that it is often considered a nuisance behaviour. Many counties in the U.S.A. have adopted ordinances that

address noise from barking dogs (Senn & Lewin 1975); barking is a major source of noise pollution in dog kennels (Sales et al. 1997), and inappropriate barking is one of the most common behaviour problems reported by dog owners in dog behaviour surveys (Beaver 1994, 1999), with up to 35% of owners listing this as a complaint.

This high level of barking, as well as the large variation in contextual use of barks, has led some investigators to conclude that barks are primarily an attention-seeking vocalization rather than a context-specific form of communication (Fox 1971; Coppinger & Feinstein 1991; Bradshaw & Nott 1995). In the case of nondomesticated animals, variation in contextual use of a single vocalization has encouraged many studies. Researchers have examined this variation in a number of species, including Barbary macaques, *Macaca sylvanus* (Fischer et al. 1995; Fischer 1998), gorillas, *Gorilla gorilla* (Seyfarth et al. 1994), chacma baboons, *Papio cynocephalus ursinus* (Fischer et al. 2001), pigtailed macaques, *Macaca nemestrina* (Gouzoules & Gouzoules 1989), sciurid rodents such as squirrels and prairie dogs (Owings & Hennessy 1984) and domesticated cats, *Felis catus* (Nicastro & Owren 2003).

Owings & Hennessy (1984) also point out that, while many early studies have stressed call similarity, variability in both temporal and structural aspects of a call is

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important. Calls should vary with the demands of the situation, which in turn should influence motivational state. For instance, California ground squirrels, *Spermophilus beecheyi*, produce alarm calls that vary based on urgency (Owings & Hennessy 1984), vervet monkeys, *Cercopithecus aethiops*, produce alarm calls that elicit different escape patterns (Seyfarth et al., 1980), and domestic cats produce meows that vary in their emotional effect on humans, and that also may vary acoustically based on the intensity of a cat's need to influence humans to respond (Nicastro & Owren 2003). Furthermore, in cases where one variable call type is used in many different contexts, closer evaluation frequently reveals that the call can be divided into subtypes based on a combination of acoustic parameters (Owings & Leger 1980; Gouzoules & Gouzoules 1989; Slobodchikoff et al. 1991; Fischer et al. 1995, 2001; Ackers & Slobodchikoff 1999). Habituation–dishabituation studies reveal that individuals within a species can distinguish between these subtypes (Cheney & Seyfarth 1988; Fischer 1998; Fischer et al. 2000), and other playback studies show that the subtypes elicit different behavioural responses (Leger & Owings 1978; Cheney & Seyfarth 1982; Gouzoules & Gouzoules 1989; Fischer et al. 1995; Rendall et al. 1999). The latter case indicates that the calls have different functions. These calls could be functionally referential in that they could denote a specific stimulus class or specific type of response, or they may indicate the urgency at which a response should occur (Macedonia & Evans 1993).

Variation between individuals of the same species has also been a topic of many studies examining individual recognition or individual 'signatures'. Vocal signatures have been found in a variety of taxa, including primates (Barbary macaques: Hammerschmidt & Todt 1995; chacma baboons: Fischer et al. 2001; ringtailed lemurs, *Lemur catti*: Macedonia 1986; chimpanzees, *Pan troglodytes*: Mitani et al. 1996), marine mammals (fur seals, *Callorhinus ursinus*: Insley 2001; bottlenose dolphins, *Tursiops truncatus*: McCowan & Reiss 2001) and birds (domestic chicks, *Gallus gallus domesticus*: Kent 1987; mallard ducks, *Anas platyrhynchos*: Gottlieb 1988; barnacle geese, *Branta leucopsis*: Hausberger et al. 1994), among others. Although evidence for individual recognition in Barbary macaques and chacma baboons is based on analyses of bark vocalizations, other factors that may affect acoustic individuality, such as body size (Gouzoules & Gouzoules 1990) and social and

ecological conditions (Medvin & Beecher 1986), also need to be examined.

In light of the findings mentioned above, the discovery of variation in contextual usage of barks in dogs should encourage interest in dogs as study subjects. Such findings could contribute to our understanding of why distinct vocalizations exist in animals, as well as how and why these vocalizations covary with context. Dogs are a particularly good candidate for study of vocal communication because, in contrast to many other animal species, domestic dogs are readily available, vocalize frequently, and we can investigate the current sources of selection as well as the developmental factors that influence their barking habits both within breeds and within individual dogs. Additionally, by understanding the communicative aspects of barking, dog owners can gain a better appreciation of their dogs' communicative abilities and may be more successful at modifying barking-related problem behaviours.

In this study, we used both univariate and multivariate analyses of bark vocal parameters to examine the following three questions about barking. First, can dog barks be classified into subtypes based on context? Second, if so, then what acoustic variables covary with context? And, third, can individual dogs be identified by their barks?

## METHODS

### Study Animals

Subjects were 10 privately owned dogs of various breeds: two Australian cattle dogs, two Australian shepherds, one Dachshund, one English springer spaniel, one Labrador retriever mix, and three German shorthair pointers (see Table 1). Dogs ranged from 3 to 13 years of age. All were neutered, two were females, and all were pets living in households.

We chose individuals of varying breeds because, while using individuals of one breed, sex and size would have increased the internal validity, such a choice would have decreased our ability to make a generalization about dogs. The individual dogs in this study were selected because their owners indicated that they readily barked in a variety of situations. They were recorded during a 3-month period between July and September 2000.

**Table 1.** Names and characteristics of study animals

	Dog	Breed	Weight (kg)	Age (years)	Sex
1	Farley	Australian shepherd	25	3	Male
2	Freidrich	Dachshund	6	5	Male
3	Keri	Labrador mix	34	4	Female
4	Louie	Springer spaniel	19	2	Male
5	Luke	Australian shepherd	25	5	Male
6	Mac	German shorthair pointer	34	5	Male
7	Roodie	Australian cattle dog	18	12	Male
8	Rudy	German shorthair pointer	32	11	Male
9	Siggy	German shorthair pointer	36	11	Male
10	Zoe	Australian cattle dog	16	7	Female

## Data Collection

Dogs were recorded in three contexts: (1) a disturbance situation in which a stranger rang the doorbell, (2) an isolation situation in which the dog was locked outside or in a room isolated from its owner and (3) a play situation in which either two dogs or a human and a dog played together. We chose these contexts because they were relatively discrete and easy to set up. Furthermore, many other studies of vocal communication involve similar contexts. For instance, Fischer et al. (1995) defined 'disturbance calls' in Barbary macaques as calls given in response to disturbances in the external environment that elicit attention but do not elicit an escape reaction. They differentiated these from alarm calls by the distinction that alarm calls elicit an escape reaction. Disturbance barks in dogs in this experiment are analogous to disturbance calls in Barbary macaques. Fischer et al. (2001) defined contact calls in chacma baboons as calls that are produced when an animal is separated from its mother or group. Isolation calls in this study on dogs are analogous to contact calls in chacma baboons. In the play context, we combined barks that were produced during play with humans and during play with other dogs, because dogs in this study barked either while playing with people, or while playing with other dogs, but not in both situations; thus, barks given in these situations should be more similar to each other than those given in the other two contexts.

We set up each situation at least five times for each dog for a total of at least 15 sessions per dog. Up to three data collection sessions were held on a given day, but only one session of each bark context was collected on a given day. Thus, each disturbance session was collected on a separate day, but a disturbance session, isolation session and play session could all occur on the same day. We attempted to collect a minimum of 10 barks per session and a total of at least 150 barks per dog. For contexts for which we recorded fewer than 10 barks per session, we recorded additional sessions to obtain a minimum of 50 barks per context. Two dogs, Freidrich and Rudy, barked in only the disturbance and play situations, so we did not collect any isolation barks for them.

## Vocal Recording

We recorded vocalizations using a DCR VX2000 digital video recorder and its built-in omni-directional microphone with a 48-kHz frequency response. All barks were digitized at a 16-bit, 48-kHz sampling rate, and audio levels were adjusted manually using the audiometer to prevent audio clipping. Dogs were between 1 and 6 m from the microphone during recordings and, in the case of the play barks and disturbance barks, were often moving rapidly, either running from the door to the owner or running back and forth while playing with another dog. Because we were interested in measuring relative amplitudes within each bark rather than absolute amplitudes, and because dog barks are relatively brief (38–137 ms), the movements of the dogs during the recordings probably did not affect the measurements taken.

We included barks in the analysis when the context and dog identity were clear and when the barks were not obscured by ambient or background noise (other dogs barking or people talking). Over 95% of the barks collected were used in the analysis.

## Acoustic Analysis

We analysed 4672 barks (Table 2) in Cool-Edit Pro (Syntrillium Software, Phoenix, Arizona) using a modified version of McCowan's method (McCowan 1995; McCowan & Reiss 2001) with computer macro designed by B. McCowan. We took 60 sequential frequency measurements and 60 sequential amplitude measurements of the maximum amplitude band (the frequency band where the most energy is concentrated) across the duration of each bark. We generated spectrograms using a 512 fast Fourier transformation (FFT) with a Hanning window and generated spectrums at 1024 FFT with a Hanning window.

A number of structural parameters were measured or calculated from these 120 points (Tables 3, 4). They included measurements for evaluating individual barks (inrabark measurements) as well as measurements between barks (interbark measurements).

**Table 2.** Number of barks recorded per individual in each context

	Dog	Disturbance	Isolation	Play	Total	% Total barks across dogs
1	Farley	110	136	251	497	11
2	Freidrich	304	0	184	488	10
3	Keri	180	90	128	398	9
4	Louie	166	423	225	814	17
5	Luke	59	111	61	231	5
6	Mac	259	162	339	760	16
7	Roodie	78	123	404	605	13
8	Rudy	81	0	85	166	4
9	Siggy	88	216	73	377	8
10	Zoe	89	84	163	336	7
	Total	1414	1345	1913	4672	—
	% Total	30	29	41	—	100

**Table 3.** Intraintrabark measurements on maximum amplitude band

Measurement	Code	Description
Start frequency	SF	The frequency at the beginning of the bark
Finish frequency	FF	The frequency at the end of the bark
Minimum frequency	Min	The lowest frequency of the bark
Maximum frequency	Max	The highest frequency of the bark
Mean frequency	Mean	The average of all the frequency measurements in the bark
Frequency at minimum amplitude	MAF	The frequency measurement for the softest portion of the bark
Frequency at maximum amplitude	PAF	The frequency measurement for the loudest portion of the bark
Frequency range	FR	The highest frequency minus the lowest frequency of the maximum amplitude band (i.e. max – min)
Duration	Dur	Bark duration
Location of minimum amplitude	MAL	Onset of minimum amplitude relative to call duration (100%)
Location of maximum amplitude	PAL	Onset of maximum amplitude relative to call duration (100%)
Location of minimum frequency	MinL	Onset of minimum frequency relative to call duration (100%)
Location of maximum frequency	MaxL	Onset of maximum frequency relative to call duration (100%)
Initial frequency slope	SSL	Slope at the beginning of the bark
Middle frequency slope	MSL	Slope in the middle of the bark
Final frequency slope	FSL	Slope at the end of the bark
Coefficient of frequency modulation	COFM	A measure of frequency modulation (McCowan & Reiss 1995b)
Coefficient of variation	CV	A measure of how often the frequency differs from the mean frequency and how big the difference is
Inflection factor	IF	A measure of how often the point before and after the measured point are both lower or higher than the measured point (i.e. a measure of how often the slope of the frequency changes direction)
Minimum amplitude	MAmp	A measurement of the smallest amplitude
Maximum amplitude	PAmp	The largest amplitude
Mean amplitude	Mean Amp	The average amplitude as determined by adding the 60 amplitude measurements and dividing by 60
Amplitude range	AmpR	The loudest amplitude minus the softest amplitude within a bark
Start frequency difference	SFD	How amplitude changes at the start of the bark
Finish frequency difference	FFD	How amplitude changes at the end of the bark
Minimum frequency difference	MinFD	The minimum difference in frequency between two points
Maximum frequency difference	MaxFD	The maximum difference in frequency between two points

We measured harshness or the harmonics-to-noise ratio on 3922 barks using Praat 4.0.4 (Boersma & Weenik 2001), a software program developed for speech analysis.

**Table 4.** Interbark measurements on maximum amplitude band using Cool-Edit Pro macros

Measurement	Code	Description
Intersignal interval	ISI	Interval between barks
Interminimum interval	IMinI	Minimum interval between barks
Intermaximum interval	IMaxI	Maximum interval between barks
Location of minimum amplitude difference	MALD	Difference between location of minimum amplitude between adjacent barks
Location of maximum amplitude difference	PALD	Difference between location of maximum amplitude between adjacent barks
Location of minimum frequency difference	MinLD	Difference between location of minimum frequency between adjacent barks
Location of maximum frequency difference	MaxLD	Difference between location of maximum frequency between adjacent barks

## Statistical Analysis

### Multivariate analysis

We used discriminant function analysis (DFA) to determine which acoustic variables could be used to discriminate between barks used in different contexts. Multivariate analysis is useful when one variable alone is not sufficient for categorizing data, or when the parameters vary in their usefulness for categorizing call types or distinguishing between individuals (Hammerschmidt & Todt 1995). For example, you may be able to distinguish individual 1 from individual 2 based on mean frequency and frequency modulation, whereas to distinguish individual 1 from individual 3 you might need to rely more on bark duration and range of amplitude. Multivariate analysis compensates for these differences.

Discriminant analysis has been useful in analysing both human and nonhuman primate calls (Gouzoules & Gouzoules 1989; Hammerschmidt & Todt 1995; Fischer et al. 2001), as well as calls in other animals such as geese (Hausberger et al. 1994), squirrels (Owings & Leger 1980) and dolphins (McCowan & Reiss 1995a, 2001; McCowan et al. 1998).

Discriminant function analysis determines the combination of independent variables that best discriminates groups from each other (which variables or set of variables can best be used to separate disturbance barks, isolation barks and play barks). Once the variables that best

discriminate between groups are determined, cross validation should be performed by taking additional data and determining whether they fall into the correct categories. We used leave-one-out cross validation to estimate the error rate conditioned on the training data (Hair et al. 1998; Johnson & Wichern 1998). In this technique, each observation is systematically dropped, the discriminant function is re-estimated and then the excluded observation is classified (Mathsoft 1999). Although barks were collected in sessions ranging from 1 to 60 barks and because preliminary nested mixed-effects ANOVA showed no difference in bark characteristics with respect to session, we defined each observation as one bark. Additionally, while one might assume that barks recorded in one session would be more similar to each other than barks recorded during another session, barks in one session might actually be more variable due to a change in the status of the stimulus (e.g. a dog's initial response to the doorbell may differ from its continued response after 5 s). Thus, there may be more variability within a session than between sessions. We did however also run a DFA on the mean values for barks from each dog in each context, as recommended by Slobodchikoff et al. (1991).

To determine which variables significantly contributed to the discriminant functions, we first ran a test for contributing rank in discriminant analysis (BMDP Statistical Software; Dixon et al. 1990). Thirteen variables contributed significantly to context. We then used these variables to run the cross validation discriminant function analysis in S-Plus (Mathsoft 1999). Since individuals were repeatedly measured (in addition to running the DFA on mean values as described earlier), we also ran a discriminant analysis on each individual to see whether the same variables could be used to categorize each individual's barks into separate contexts.

Next we determined which variables were needed to discriminate barks made by specific individuals using similar techniques. Fourteen variables contributed to the discriminant function for dog identity. Since contexts were repeatedly measured for each dog, we then ran a discriminant analysis on each context to see whether the same variables could identify the individual barking within that context. Additionally, we ran a DFA on the mean values for barks from each context for each dog.

### Univariate analysis

Since discriminant analysis categorizes data into different groups but does not tell how each individual variable differs, we ran mixed-effects ANOVA in SAS (SAS Institute 1999) to determine how individual variables change with context. Mixed-effects ANOVAs address pseudoreplication issues that arise when multiple observations are taken for each subject by adjusting the degrees of freedom and thereby adjusting the *P* values. We initially conducted nested mixed-effects ANOVAs with 'session within dog identity' as the nested random effect (or repeated measure). However, because the effect of 'session' was non-significant, we removed it from the models and conducted mixed-effects ANOVAs with 'dog identity' as the random effect (or repeated measure) for the final set of analyses.

Therefore, in these models, dog identity was the random effect and context was the fixed effect.

When our ANOVA results revealed significant differences, we made pairwise comparisons using least-squares means test to determine which contexts differed significantly for each variable. We used the Bonferroni corrections factor at an alpha of 0.05 to account for the number of pairwise comparisons made.

We also used mixed-effects ANOVA to compare standard deviations of individual variables within different contexts. This was used as a measure of stereotypy in the vocalizations.

## RESULTS

### Categorizing Barks by Context

Discriminant analysis using 'context' as the grouping variable showed that variables contributed to the analysis in the following rank order (Table 5). Amplitude range, minimum frequency, duration and mean frequency were the top four variables that contributed to the analysis, accounting for 82% of the variation in the data set.

We pooled data from all animals and subsequently categorized the barks into the three contexts using discriminant function analysis. On average, leave-one-out cross validation showed an average correct assignment of 63% (Pearson's chi-squared test:  $\chi^2_9 = 1788$ ,  $P < 0.0001$ ; Table 6); correct assignment by chance was 33%.

Similarly, analysis on the means for each animal in each context (Table 7) showed that 80% of disturbance barks ( $P < 0.002$ ), 75% of isolation barks ( $P < 0.007$ ) and 60% of play barks ( $P < 0.017$ ) were correctly classified compared with 33% correct assignment by chance alone. This finding demonstrates that pooling in the DFA did not lead to a type I error.

**Table 5.** Ranking of the variables that contributed most to the discriminant analysis on context (ranked from highest contribution to the lowest contribution)

Rank	Acoustic variable
1	Amplitude range (AmpR)
2	Minimum frequency (Min)
3	Duration (Dur)
4	Mean frequency (Mean)
5	Location of minimum frequency (MinL)
6	Coefficient of variation (CV)
7	Finish slope (FSL)
8	Coefficient of frequency modulation (COFM)
9	Location of peak amplitude (PAL)
10	Location of minimum amplitude (MAL)
11	Frequency range (FR)
12	Frequency at maximum amplitude (MAF)
13	Location of maximum frequency (MaxL)

**Table 6.** Percentage of each individual's bark vocalizations and that of all bark vocalizations combined that were correctly classified to context using discriminant function analysis with the cross-validation technique

Dog	% Correct classification of barks				$\chi^2_2$
	Between contexts (33% expected)	Within context			
		Disturbance	Isolation	Play	
Farley	79	74	75	86	494
Freidrich*	88	86	—	89	646
Keri	72	75	67	74	279
Louie	63	54	74	61	403
Luke	77	80	85	66	213
Mac	74	85	64	73	604
Roodie	71	77	62	74	406
Rudy*	94	91	—	97	288
Siggy	64	85	42	65	90
Zoe	83	75	91	83	364
Average	77	78	70	77	
Pooled	63	70	55	62	1788

\*The individual barked in only two contexts, so we expected that 50% of their barks would be correctly categorized by chance alone.

Additionally, when each dog was analysed individually, barks were assigned to the correct context significantly more often than would be expected by chance ( $P < 0.0001$  for each dog; Table 6). These findings indicate that barks can be correctly categorized into separate contexts even within individual dogs.

### Individual Identification

Discriminant analysis using 'dog identity' as the grouping variable showed that 14 variables contributed to the analysis in the following rank order (Table 8). Mean frequency, location of minimum frequency, minimum frequency and location of maximum frequency were the top four variables that contributed to the analysis, accounting for 85% of the variation in the data set. This order of contribution was different from the rank order of contribution for context.

We pooled all animals together, then categorized the barks by individual. Leave-one-out cross validation showed an average correct assignment of 40% (Pearson's chi-squared test:  $\chi^2_2 = 4243$ ,  $P < 0.0001$  in all cases; Table 9). That is, 40% of calls that belonged to a specific dog were

**Table 8.** Variables used for discriminant analysis on individual identity and comparison with rank for context (ranked from highest contribution to lowest contribution)

Rank for dog ID	Acoustic variable	Rank for context
1	Mean frequency (Mean)	4
2	Location of minimum frequency (MinL)	5
3	Minimum frequency (Min)	2
4	Location of minimum amplitude (MAL)	10
5	Coefficient of frequency modulation (COFM)	8
6	Frequency range (FR)	11
7	Duration (Dur)	3
8	Location of peak amplitude (PAL)	9
9	Amplitude range (AmpR)	1
10	Finish slope (FSL)	7
11	Start slope (SSL)	—
12	Location of maximum frequency (MaxL)	12
13	Frequency at peak amplitude (PAF)	—
14	Coefficient of variation (CV)	6

classified as belonging to that dog regardless of context. The assignment expected by chance is 10%. Analysis on the means (across sessions) for each dog in each context showed a much higher average correct classification of 84% (range 16–100%) compared with 10% correct assignment by chance. This finding again demonstrates that pooling in the DFA did not lead to a type I error.

Additionally, when each context was analysed separately, barks were still correctly assigned to the correct individual a significantly higher proportion of the time than would be expected by chance (Table 10). These findings indicate that dogs can be identified by their barks even when only one context is analysed.

### Acoustic Characteristics of Barks in Different Contexts

In addition to finding that barks could be classified into subtypes based on context, univariate analysis revealed that individual structural parameters varied predictably with context (Table 11).

Harshness of barks varied widely both within and between dogs. Mixed-effects ANOVA and pairwise

**Table 7.** Percentage of individuals whose averaged bark vocalizations in a given context were correctly classified to context using discriminant function analysis with the cross-validation technique

Bark context	Classification of barks by DFA			Total	% Correct classification	<i>P</i>
	Disturbance	Isolation	Play			
Disturbance	8	1	1	10	80	<0.0002
Isolation	0	6	2	8	75	<0.006
Play	2	2	6	10	60	<0.017

**Table 9.** Mean percentage of bark vocalizations that were correctly classified to individual regardless of context using discriminant analysis with cross validation

Context	% Mean correct classification of barks		
	Across all individuals*	Range	$\chi^2$
Disturbance	48	21–69	2040
Isolation	55	38–85	1383
Play	56	22–78	3494
Average	53	27–75	—
Pooled	40	21–68	4243

\*Ten per cent correct classification expected by chance ( $P < 0.0001$  for all chi-square values).

comparisons using the least-squares means test indicated that disturbance barks were significantly harsher than isolation and play barks; however, there was no significant difference between isolation and play barks (Fig. 1).

Average minimum frequency, maximum frequency and mean frequency were lower in disturbance barks than in isolation and play barks (ANOVA:  $P < 0.0001$ ; Table 11), and the frequency range was smaller in disturbance barks than in isolation and play barks (Table 11). Coefficient of variation (CV) for frequency was higher in disturbance barks than in isolation and play barks (Table 11). Amplitude range was significantly lower in disturbance barks than in isolation barks and was significantly higher in play barks than in isolation barks (Table 11).

Disturbance barks were significantly longer in duration than isolation and play barks (Tables 11); however, play and isolation barks were not significantly different. Interbark interval was longer in the isolation situation than in the play and disturbance situations (Table 11).

The disturbance context contained clusters of barks whose interbark intervals were too short to determine because the barks were fused or overlapped. These barks, which we label 'superbarks' (Fig. 2), increased the average bark duration in the disturbance context.

A comparison of standard deviations of the same variables indicated that there was more variability in minimum frequency, maximum frequency, mean frequency, frequency range, start slope and interbark interval in the isolation and play contexts than in the disturbance context (Table 12). Standard deviation of coefficient of variation, duration and amplitude range varied more between barks in the disturbance context than in the isolation and play situations.

## DISCUSSION

### Acoustic Characteristics of Barks in Different Contexts

Dog barks are graded vocalizations that range from harsh, low-frequency calls to harmonically rich, higher-frequency calls. Disturbance barks are harsh, low-pitched barks with little amplitude modulation and little pitch modulation. They are also relatively long in duration due in part to fused barks ('superbarks'). Isolation and play barks on the other hand are more tonal, higher-frequency calls with more modulation in both pitch and amplitude. While both disturbance and play barks were characterized by short interbark intervals, isolation barks occurred singly rather than in clusters, thus isolation barks were separated by large intervals. These acoustic findings are consistent with many other vocal communication studies.

The changes in harshness and frequency with context are consistent with Morton's motivation-structural rules, which state that birds and mammals use harsh, relatively low-frequency sounds when they are being hostile and higher-frequency, more tonal sounds when they are approaching in an appeasing or friendly manner, or when they are frightened (Morton 1977; Owings & Morton 1998). In addition to being higher pitched, barks in the play and isolation situations had a larger frequency range and were thus more frequency modulated. A second measure of frequency modulation however, CV, indicated that disturbance barks were more modulated than isolation barks and play barks. The difference between these two measurements of frequency modulation is that frequency range marks the difference between the highest and lowest frequency within the maximum amplitude band of a bark, whereas CV is a measure of the magnitude as well as how often any point of a bark is different from the mean (McCowan et al. 1998). Thus, a bark could have a small frequency range but a large CV if the pitch at each measured point often differs from the mean, even if it differs only slightly from the mean frequency of the bark. Because dog barks are relatively noisy vocalizations and CV was highest when harshness was greatest and lowest when barks were more tonal, the large CV could have been caused by wider maximum amplitude bands or increased noise around the maximum amplitude band of the disturbance barks. As a result, frequency range may be a better measure of pitch modulation for barking in dogs.

In addition to being more modulated in frequency, isolation and play barks were more modulated in

**Table 10.** Percentage of bark vocalizations that were correctly classified to individual within each context and for all contexts combined using discriminant analysis with cross validation

Context	Dog										Total
	Farley	Freidrich	Keri	Louie	Luke	Mac	Roodie	Rudy	Siggy	Zoe	
Disturbance	54	49	28	42	21	42	69	47	42	67	48
Isolation	78	—	58	43	41	48	38	—	46	85	55
Play	78	68	59	61	53	22	28	57	58	78	56
Pooled	68	40	36	30	21	23	44	41	41	63	40

**Table 11.** Results of least-squares means tests comparing acoustic parameters of bark vocalizations ( $\bar{X} \pm SE$ ) that varied significantly between contexts ( $N = 10$  dogs)

Variable	Context			$F_{2,17}$	$P$	Pairwise comparison*
	Disturbance	Isolation	Play			
Harmonic:noise (dB)†	5.05 ± 0.89	10.43 ± 1.82	8.30 ± 1.25	0.1354	<0.0001	D < I, P
Minimum frequency	390 ± 26	484 ± 26	476 ± 24	19.34	<0.0001	D < I, P
Maximum frequency	1156 ± 8.2	1472 ± 9.2	1501.8 ± 7.8	8.46	0.0028	D < I, P
Mean frequency	686 ± 44	860 ± 80	840 ± 50	12.12	0.0005	D < I, P
Frequency range (FR)	766 ± 52	989 ± 102	1025 ± 87	4.82	0.0220	D < I, P
Coefficient of variation (CV)	4.3 ± 0.64	1.9 ± 0.48	1.2 ± 0.13	13.24	0.0003	D > I, P
Amplitude range (AmpR)	33 ± 0.31	37 ± 1.4	39 ± 1.4	4.59	0.0255	D < I < P
Duration (Dur)	346 ± 24	248 ± 8.6	272 ± 16	8.76	0.0024	D > I, P
Interbark interval	1.1 ± 0.2	3.5 ± 0.76	1.1 ± 0.18	13.11	0.0004	I > D, P

\*D = disturbance; I = isolation; P = play.

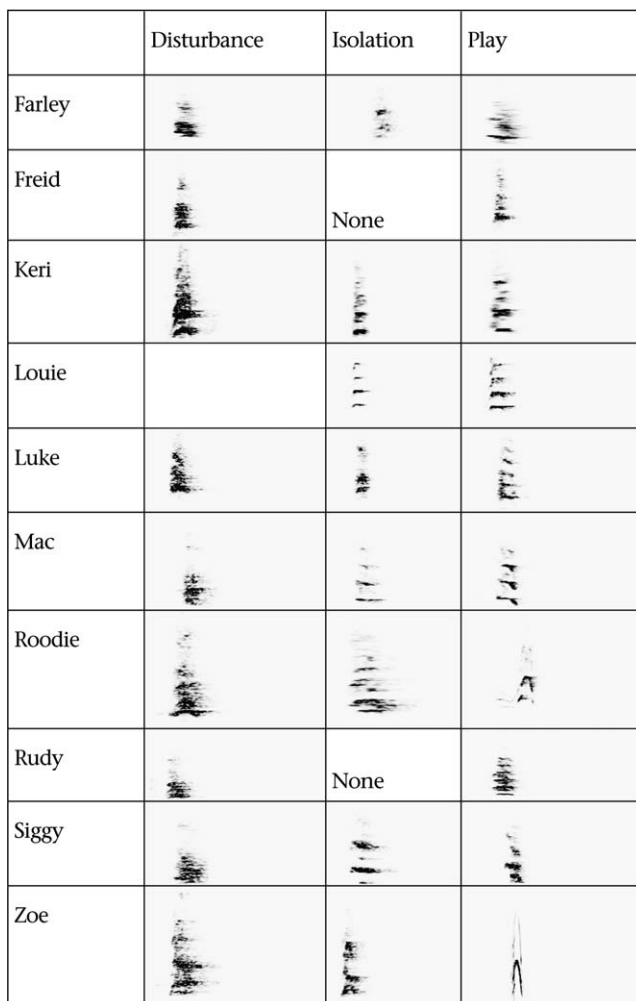
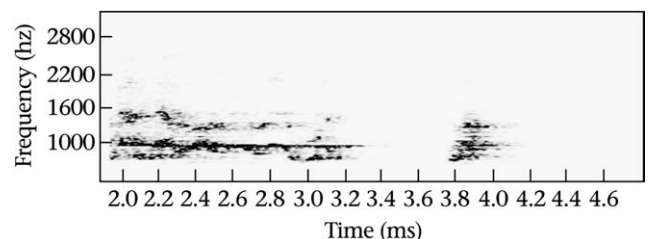
†For harmonic:noise (a measure of harshness or tonicity),  $df = 1, 37$ .

amplitude than disturbance barks. Because the distances at which we recorded the dogs varied, we could not measure absolute amplitude, but disturbance barks were subjectively louder than play and isolation barks. Based on this observation, we propose that disturbance barks were

less amplitude modulated than play and isolation barks because in the disturbance situation, dogs were barking full force throughout the bark.

The differences we found are also consistent with the idea that particular sounds routinely affect listeners by altering their attention and/or arousal. Harsh, high-amplitude sounds increase arousal (Owren & Rendall 2001) and rapidly repeated sounds correlate with increased motor activity and may even elicit higher arousal in the receiver (McConnell & Baylis 1985; McConnell 1990). One mechanism for this increased arousal is that the repeated vocalizations may achieve a cumulative or tonic effect by improving the signal-to-noise ratio and consequently achieve a critical threshold that maintains a behavioural state in the perceiver (Schleidt 1973). Owings & Virginia (1978) found that in California ground squirrels, the rate of calling, as well as the number of notes per call and the duration of calls correlated positively with, and possibly signalled, arousal level in the caller. Similarly, other studies have shown that increased call duration is associated with increased urgency (Manser 2001; Manser et al. 2002) and increased call duration can alter salience of the vocalization by making it sound louder. For humans, the loudness of the sound increases as duration increases for up to several hundred milliseconds (Geldard 1972 cited in Owings & Virginia 1978).

In our study, we expected the most urgent context, the disturbance context, to lead to the most arousal. As expected, disturbance barks were more rapidly repeated than isolation barks, so rapidly that they were fused into superbarks. This rapidity was not manifest in the interbark

**Figure 1.** Sample spectrograms from each dog in three contexts.**Figure 2.** Spectrogram of a fused bark (superbark) followed by a nonfused single bark.

**Table 12.** Results of least-squares means tests comparing acoustic parameters of bark vocalizations in which the standard deviation from the mean differed significantly between contexts ( $N = 10$  dogs)

Variable	Disturbance	Isolation	Play	$F_{2, 16}$	$P$	Pairwise comparison*
Minimum frequency	84 ± 7.5	132 ± 14	144 ± 21	6.95	0.0067	D < I, P
Maximum frequency	373 ± 81	556 ± 146	733 ± 134	3.74	0.0466	D < I, P
Mean frequency	94 ± 9.5	158 ± 23	128 ± 18	3.37	0.0602	D < P < I
Frequency range (FR)	387 ± 81	568 ± 142	758 ± 135	3.69	0.0481	D < I, P
Coefficient of variation (CV)	6.72 ± 1.2	2.26 ± 1.2	1.38 ± 0.24	17.86	< 0.0001	D > I, P
Start slope (SSL)	0.39 ± 0.06	0.73 ± 0.12	0.86 ± 0.2	5.59	0.0144	D < I, P
Duration (Dur)	137 ± 34	39 ± 2.2	38 ± 4.5	12.61	0.0005	D > I, P
Interbark interval	1.1 ± 0.13	2.1 ± 0.18	1.5 ± 0.27	9.71	0.0017	D < P < I
Amplitude range (AmpR)	6.0 ± 0.34	4.9 ± 0.25	4.7 ± 0.24	5.69	0.0136	D > I, P

\*D = disturbance; I = isolation; P = play.

interval, which was similar in both the play and disturbance situations; however, if we had been able to separate fused barks, the interbark interval would have been shorter for the disturbance context than for the play context. Disturbance barks were also longer in duration, in part due to the superbarks, than both isolation and play barks. Although we were unable to measure absolute amplitude of the barks, the repetitive quality and longer duration of the disturbance barks should give the perception of louder barks.

Just as repetition and increased duration can make a call more salient, a third quality, stereotypy, can increase perceived signal detectability. In a noisy environment, stereotypy may facilitate detection over long distances (Wiley 1994) and should increase the perception of loudness. Consequently, we should expect disturbance barks to be more stereotyped than the other types of barks. Disturbance barks were indeed more stereotyped (less deviation between barks) in terms of frequency, frequency modulation, start slope and interbark interval than isolation and play barks. They were, on the other hand, more variable in amplitude range (some disturbance barks were extremely loud whereas others were relatively soft) and in duration. However, this variability most likely occurred because dogs barked full force and with more superbarks when they initially heard the doorbell stimulus but frequently gave softer barks with less rapid repetition when they were looking for the person associated with the stimulus.

#### Classification of barks

Overall, many individual bark parameters covaried with context; however, while individual parameters could often separate barks into two categories, they could not separate barks into the three categories. Multivariate analysis was needed to reveal the three distinct subtypes based on context. The 63% correct classification using cross validation for all of the barks pooled (33% correct classification expected by chance) was lower than that obtained for the 82.2% correct classification in chacma baboons (Fischer et al. 2001); however, in that case there were only two contextual categories of barks. Consequently, the correct classification by chance was higher (50%). A comparison of the ratios between actual correct classification and correct classification expected by chance shows that the

results in dogs are similar to the findings in chacma baboons. When we classified each individual's barks by context, individuals that barked only in two of the three contexts had the highest correct classification scores (88 and 94%).

Although the discriminant function analysis for context yielded robust results, a number of factors could contribute to variation. One is that dogs are more morphologically variable in both size and shape than adult macaques and many other adult animals. The dogs in this study ranged from 5.5 to 36.4 kg, and thus the size of the vocal apparatus varied as well. Riede & Fitch (1999) found that regardless of dog breed and size, the larger the dog, the longer the vocal tract and the closer together the harmonic bands.

The variation could also be attributed to differences in affective state and learning in the different dogs. For instance, to some dogs the doorbell ring may have been perceived as an agonistic situation whereas to other dogs the doorbell may predict the approach of social reinforcement by the person visiting the house. In the isolation situation, dogs may have had different isolation experiences resulting in different thresholds and levels of arousal or frustration. In the play situation, dogs may have perceived play with other dogs to be different from play with humans. Additionally, arousal level and emotional state may have varied depending on the social rank of the play partner.

One way to increase the percentage of correctly assigned barks would have been to use additional acoustic parameters (Hammerschmidt & Todt 1995) that included variables such as bandwidth or interband distance. Regardless, the analysis indicated that barks can be classified into subtypes based on context. An ability to evaluate a cluster or string of barks in a given context would probably have increased the ability to assign the barks to the correct context.

#### Individual identification

Within an animal's vocal repertoire, some calls are better suited for individual identification than others. For instance, in chimpanzees, the long-distance pant-hoot call can be used to discriminate among individuals, but the close-range pant-grunt cannot (Mitani et al. 1996). In

general, narrowband, modulated calls are easier to distinguish (Wiley & Richards 1978, cited in Macedonia 1986) and consequently more likely to be used for individual identification. For example, the ringtailed lemur has an intermediate, narrowband, frequency-modulated call that propagates well, is easy to localize, and has high-information content; consequently it is more likely to fall under Beecher's signature-matching model (Macedonia 1986). Barks, on the other hand, are relatively broadband, harsh vocalizations, which makes them more difficult to encode for subtle differences.

None the less, the results of the present study reveal that dogs can be identified by their barks and that the same acoustic parameters can be used to identify individuals within a given context. Overall correct classification for the pooled total was 40% for the 10 dogs (10% correct classification by chance), which is comparable to the 69.3% correct classification in chacma baboons (Fischer et al. 2001) and 81% in Barbary macaques (Hammerschmidt & Todt 1995) where five individuals were used (20% correct classification by chance). Another study by Fischer et al. (1995) used nocturnal barks in nine adult macaques and showed a much higher correct classification of 89% (11.1% correct classification expected by chance). When 15 individuals were used, correct classification dropped slightly to 86%.

As in the case of classification by context, the percentage correct classification by dog identity might have increased if different parameters such as harshness, bandwidth or interband distance had been used in the DFA. It is also possible that as in chimpanzees, where long-distance pant-hoots were better for individual identification, barks collected in long-distance communication situations rather than those elicited by close-range stimuli might be better for identification purposes. Additionally, although this study focused on dog barks, other canid vocalizations such as howls, which are long, tonal and modulated, might be better for distinguishing between individuals. When howls were used for individual identification of six wolves, correct classification was 75% for the cross-validation set (16.7% correct classification by chance) (Tooze et al. 1990).

Other factors can lead to differences in the ability to identify individuals of a species based on vocalizations. Some species have a stronger need to identify individuals by their vocalizations. This need is influenced by social or ecological factors. For instance, both group size and nature of parental care can influence the need for individually distinct vocalizations. Individuals that live in large groups such as barn swallows, *Hirundo rustica* (Beecher et al. 1986), cliff swallows, *H. pyrrhonota* (Medvin et al. 1993), and pinnipeds (Insley 2001) have more individually distinctive acoustic characteristics than individuals that live in smaller groups. One reason that individual identification is important in large groups is that mother and offspring must be able to find each other in order to stay in contact. This is important in both precocial animals, such as chickens and sheep, that must learn to follow and find their mother at a young age, and in some altricial animals, such as primates, that rely on their mothers for extended periods.

Feral dogs typically do not live in large groups like colony-living birds and pinnipeds. Instead, they live in loose, relatively small, territorial groups near or within villages where they scavenge for food (Boitani et al. 1995; MacDonald & Carr 1995; Coppinger & Coppinger 2002). Because of this structure, few litters are born in close proximity to each other; thus, vocal recognition of individual puppies between and within litters may not be as crucial, but as with other altricial species, one would expect that vocal recognition might be highest during the first several months when puppies rely most on their mothers. Consequently, looking at vocal identification in younger dogs might lead to higher correct classification. In macaques, recognition is stronger in infants than in yearlings (Hammerschmidt & Todt 1995). Mothers can recognize infant calls using only a few parameters, but require twice as many parameters to obtain the same level of identification of yearling calls.

Another aspect of group living that favours vocal recognition is the formation of alliances where individuals selectively recruit support from allies (Gouzoules & Gouzoules 1989; Mitani et al. 1996). Those species with complex alliances should have more distinct long-distance vocalizations. Because feral dogs live in loose groups rather than cohesive packs, selection for individual recognition may be relaxed. Use of vocal communication in individual recognition may be further relaxed if dogs reared as companions for humans are isolated from conspecifics or have contact with only a limited number of dogs.

Despite myriad potential confounding factors and sources of variation, discriminant function analysis did robustly classify barks to specific individuals. Ten dogs were included in this study, and it is possible that some of the dogs had unusual vocal characteristics, such as unusually large variation in their barks or less individually distinct barks. Thus, a larger sample size in future studies could actually lead to better classification by individuals. Furthermore, in most cases, dog barks occur in bouts rather than as single barks. Consequently, using a cluster of barks could increase the ability to identify individual dogs by their barks.

#### *Variables that distinguish context and individual identity*

Although barks could be correctly classified to context and to individual, the variables that contributed the most to each correct classification differed. Mean frequency, minimum frequency and location of the minimum frequency were the most important variables for discriminating the identity of the barking dog, whereas amplitude range, minimum frequency and duration were the most important variables for discriminating the context. These differences can be explained by the motivational structural rules and by anatomic differences. Because the main difference between canids of different sizes is vocal tract length, which directly affects vocal pitch, frequency parameters should be the most important parameters in discriminating barks from dogs of different size. In the case of context, different contexts should be associated with different affective states. Morton's motivation-structural rules, as well as rules on tonic communication,

suggest that harshness, frequency and call duration or repetitiveness vary with affective state. Consequently, one would expect a wider range of parameters to contribute significantly to the discriminant analysis of context.

## Conclusion

This study shows that dog barks can be divided into subtypes based on context even within individual dogs, and that dogs can be identified by their barks despite the context of the bark. Covariation between context and bark structure suggests that dogs may perceive meaningful differences between contexts and adjust their barks accordingly. However, finding subtypes that vary with context does not confirm that subtypes have different functions. Variation in call structure may be attributable to affective state alone without leading to a statistically predictable response in the perceiver. Additionally, finding individually distinctive barks or finding covariation between context and bark structure does not confirm that dogs perceive these differences. To determine whether subtypes have different functions or meanings or whether barks can be used to identify individuals, one has to perform playbacks to determine whether receivers can perceive these differences and whether these differences lead to different responses in the perceiver. As dogs are often dependent on humans for many of their resources, such playback studies should be carried out on both dogs and humans.

In addition to playback studies, further context studies should be performed. While the present study succeeded in identifying three bark subtypes, we might find more bark subtypes if contexts were further divided into subcontexts. For instance, acoustic characteristics may vary based on the status and species (dog or human) of the play partners or on whether the disturbance stimulus is a stranger versus a family member. One might expect that vocalizations could vary based on the affective state associated with these variations in stimuli; consequently, further studies should also assess dog body postures to look for correlations between visual signals, acoustic structure and context.

Lastly, because this study used only 10 dogs of six breeds, it is possible that there are breed differences in the role that barks play in the communication of dogs and in selection for characteristics of barks; however, the fact that barks were context specific for different dogs, even though these dogs came from diverse developmental environments, adds strength to the general findings of this study.

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## References

- Ackers, S. H. & Slobodchikoff, C. N. 1999. Communication of stimulus size and shape in alarm calls of Gunnison's prairie dogs, *Cynomys gunnisoni*. *Ethology*, **105**, 149–162.
- Beaver, B. 1994. Owner complaints about canine behavior. *Journal of the American Veterinary Medical Association*, **204**, 1953–1955.
- Beaver, B. 1999. *Canine Behavior: a Guide for Veterinarians*. Philadelphia: W.B. Saunders.
- Beecher, M. D., Medvin, M. B., Stoddard, P. & Loesche, P. 1986. Acoustic adaptations for parent–offspring recognition in swallows. *Experimental Biology*, **45**, 179–193.
- Bleicher, N. 1963. Physical and behavioral analysis of dog vocalizations. *American Journal of Veterinary Research*, **24**, 415–427.
- Boersma, P. & Weenik, D. 2001. *Praat*. Version 4.0.4. Amsterdam: Institute of Phonetic Sciences, University of Amsterdam.
- Boitani, L., Francisci, F., Ciucci, P. & Andreoli, G. 1995. Population biology and ecology of feral dogs in central Italy. In: *The Domestic Dog: Its Evolution, Behaviour and Interactions with People* (Ed. by J. Serpell), pp. 217–244. Cambridge: Cambridge University Press.
- Bradshaw, J. W. S. & Nott, H. M. R. 1995. Social and communication behaviour of companion dogs. In: *The Domestic Dog: Its Evolution, Behaviour and Interactions with People* (Ed. by J. Serpell), pp. 116–130. Cambridge: Cambridge University Press.
- Center for Information Management (CIM). 2002. *U.S. Pet Ownership and Demographics Sourcebook*. Schaumburg, Illinois: American Veterinary Medical Association.
- Cheney, D. L. & Seyfarth, R. M. 1982. How vervet monkeys perceive their grunts: field playback experiments. *Animal Behaviour*, **30**, 739–751.
- Cheney, D. L. & Seyfarth, R. M. 1988. Assessment of meaning and the detection of unreliable signals by vervet monkeys. *Animal Behaviour*, **36**, 477–486.
- Cohen, J. A. & Fox, M. W. 1976. Vocalizations in wild canids and possible effects of domestication. *Behavioural Processes*, **1**, 77–92.
- Coppinger, R. & Coppinger, L. 2002. *Dogs: a New Understanding of Canine Origin, Behavior and Evolution*. New York: C. Scribner.
- Coppinger, R. & Feinstein, M. 1991. Hark! Hark! The dogs do bark and bark. *Smithsonian*, **21**, 119–129.
- Dixon, W., Brown, M. B., Engelman, L. & Jennrich, R. I. 1990. *BMDP Statistical Software Manual*. Berkeley: University of California Press.
- Fedderson-Petersen, D. U. 2000. Vocalization of European wolves (*Canis lupus lupus* L.) and various dog breeds (*Canis lupus* f. fam.). *Archiv für Tierzucht*, **43**, 387–397.
- Fischer, J. 1998. Barbary macaques categorize shrill barks into two types. *Animal Behaviour*, **55**, 799–807.
- Fischer, J., Hammerschmidt, K. & Todt, D. 1995. Factors affecting acoustic variation in Barbary macaque (*Macaca sylvanus*) disturbance calls. *Ethology*, **101**, 51–66.
- Fischer, J., Cheney, D. L. & Seyfarth, R. M. 2000. Discrimination of call types by free-ranging chacma baboons (*Papio cynocephalus ursinus*). *Folia Primatologica*, **71**, 189–248.
- Fischer, J., Hammerschmidt, K., Cheney, D. L. & Seyfarth, R. M. 2001. Acoustic features of female chacma baboon barks. *Ethology*, **107**, 33–54.
- Fox, M. W. 1971. *Behaviour of Wolves, Dogs, and Related Canids*. Malabar: Krieger.

- Gottlieb, G.** 1988. Development of species identification in ducklings: XV. Individual auditory recognition. *Developmental Psychobiology*, **21**, 509–522.
- Gouzoules, H. & Gouzoules, S.** 1989. Design features and developmental modification of pigtail macaque, *Macaca nemestrina*, agonistic screams. *Animal Behaviour*, **37**, 383–401.
- Gouzoules, H. & Gouzoules, S.** 1990. Body size effects on the acoustic structure of pigtail macaque (*Macaca nemestrina*) screams. *Ethology*, **85**, 324–334.
- Hair, J. F. J., Anderson, R. E., Tathan, R. L. & Black, W. C.** 1998. *Multivariate Data Analysis*. Upper Saddle River, New Jersey: Prentice Hall.
- Hammerschmidt, K. & Todt, D.** 1995. Individual differences in vocalisations of young Barbary macaques (*Macaca sylvanus*): a multi-parametric analysis to identify critical cues in acoustic signaling. *Behaviour*, **132**, 381–399.
- Hausberger, M., Richard, J. P., Black, J. M. & Quris, R.** 1994. A quantitative analysis of individuality in barnacle goose loud calls. *Bioacoustics*, **5**, 247–260.
- Innsley, S.** 2001. Mother–offspring vocal recognition in northern fur seals is mutual but asymmetrical. *Animal Behaviour*, **61**, 129–137.
- Johnson, R. A. & Wichern, D. W.** 1998. *Applied Multivariate Statistical Analysis*. Upper Saddle River, New Jersey: Prentice Hall.
- Kent, J. P.** 1987. Experiments on the relationship between the hen and chick (*Gallus gallus*): the role of the auditory mode in recognition and the effects of maternal separation. *Behaviour*, **102**, 1–14.
- Leger, D. W. & Owings, D. H.** 1978. Responses to alarm calls by California ground squirrels: effects of call structure and maternal status. *Behavioral Ecology and Sociobiology*, **3**, 177–186.
- McConnell, P. B.** 1990. Acoustic structure and receiver response in domestic dogs, *Canis familiaris*. *Animal Behaviour*, **39**, 897–904.
- McConnell, P. B. & Baylis, J. R.** 1985. Interspecific communication in cooperative herding: acoustic and visual signals from human shepherds and herding dogs. *Zeitschrift für Tierpsychologie*, **67**, 302–328.
- McCowan, B.** 1995. A new quantitative technique for categorizing whistles using simulated signals and whistles from captive bottlenose dolphins (Delphinidae, *Tursiops truncatus*). *Ethology*, **100**, 177–193.
- McCowan, B. & Reiss, D.** 1995a. Quantitative comparison of whistle repertoires from captive adult bottlenose dolphins (Delphinidae, *Tursiops truncatus*): a re-evaluation of the signature whistle hypothesis. *Ethology*, **100**, 194–209.
- McCowan, B. & Reiss, D.** 1995b. Whistle contour development in captive-born infant bottlenose dolphins (*Tursiops truncatus*): role of learning. *Journal of Comparative Psychology*, **109**, 242–260.
- McCowan, B. & Reiss, D.** 2001. The fallacy of ‘signature whistles’ in bottlenose dolphins: a comparative perspective of ‘signature information’ in animal vocalizations. *Animal Behaviour*, **6**, 1151–1162.
- McCowan, B., Reiss, D. & Gubbins, C.** 1998. Social familiarity influences whistle acoustic structure in adult female bottlenose dolphins (*Tursiops truncatus*). *Aquatic Mammals*, **24**, 27–40.
- MacDonald, D. W. & Carr, G. M.** 1995. Variation in dog society: between resource dispersion and social flux. In: *The Domestic Dog: Its Evolution, Behaviour and Interactions with People* (Ed. by J. Serpell), pp. 199–216. Cambridge: Cambridge University Press.
- Macedonia, J. M.** 1986. Individuality in a contact call of the ringtailed lemur (*Lemur catti*). *American Journal of Primatology*, **11**, 163–179.
- Macedonia, J. M. & Evans, C. S.** 1993. Variation among mammalian alarm call systems and the problem of meaning in animal signals. *Ethology*, **93**, 177–197.
- Manser, M. B.** 2001. The acoustic structure of suricates’ alarm calls varies with predator type and the level of response urgency. *Proceedings of the Royal Society of London*, **268**, 2315–2324.
- Manser, M. B., Seyfarth, R. M. & Cheney, D. L.** 2002. Suricate alarm calls signal predator class and urgency. *Trends in Cognitive Sciences*, **6**, 55–57.
- Mathsoft.** 1999. *S-Plus 2000 Guide to Statistics*. Seattle, Washington: Data Analysis Products Division, Mathsoft.
- Medvin, M. B. & Beecher, M. D.** 1986. Parent–offspring recognition in the barn swallow (*Hirundo rustica*). *Animal Behaviour*, **34**, 1627–1639.
- Medvin, M. B., Stoddard, P. & Beecher, M. D.** 1993. Signals for parent–offspring recognition: a comparative analysis of the begging calls of cliff swallows and barn swallows. *Animal Behaviour*, **45**, 841–850.
- Mitani, J. C., Gros-Louis, J. & Macedonia, J. M.** 1996. Selection for acoustic individuality within the vocal repertoire of wild chimpanzees. *International Journal of Primatology*, **17**, 569–583.
- Morton, E. S.** 1977. On the occurrence and significance of motivation-structural rules in some bird and mammal sounds. *American Naturalist*, **111**, 855–869.
- Nicastro, N. & Owren, M. J.** 2003. Classification of domestic cat (*Felis catus*) vocalizations by naïve and experienced human listeners. *Journal of Comparative Psychology*, **117**, 44–52.
- Ohl, F.** 1996. Ontogeny of vocalizations of domestic dogs, breed standard-poodle. *Zoologische Beiträge*, **37**, 199–215.
- Owings, D. H. & Hennessy, D. F.** 1984. The importance of variation in sciurid visual and vocal communication. In: *The Biology of Ground-dwelling Squirrels* (Ed. by J. O. Murie & G. R. Michener), pp. 169–200. Lincoln: University of Nebraska Press.
- Owings, D. H. & Leger, D. W.** 1980. Chatter vocalizations of California ground squirrels: predator- and social-role specificity. *Zeitschrift für Tierpsychologie*, **54**, 163–184.
- Owings, D. H. & Morton, E. S.** 1998. *Animal Vocal Communication: a New Approach*. New York: Cambridge University Press.
- Owings, D. H. & Virginia, R. A.** 1978. Alarm calls of California ground squirrels (*Spermophilus beecheyi*). *Zeitschrift für Tierpsychologie*, **36**, 58–70.
- Owren, M. J. & Rendall, D.** 2001. Sound on the rebound: bringing form and function back to the forefront of understanding non-human primate vocal signaling. *Evolutionary Anthropology*, **10**, 58–71.
- Rendall, D., Seyfarth, R. M., Cheney, D. L. & Owren, M. J.** 1999. The meaning and function of grunt variants in baboons. *Animal Behaviour*, **57**, 583–592.
- Riede, T. & Fitch, T.** 1999. Vocal tract length and acoustics of vocalization in the domestic dog. *Journal of Experimental Biology*, **202**, 2859–2867.
- Sales, G., Hubrecht, R., Peyvandi, A., Milligan, S. & Shield, B.** 1997. Noise in dog kenneling: is barking a welfare problem for dogs? *Applied Animal Behaviour Science*, **52**, 321–329.
- SAS Institute.** 1999. *SAS/STAT*. Version 8.2. Cary, North Carolina: SAS Institute.
- Schleidt, W. M.** 1973. Tonic communication: continual effects of discrete signs in animal communication systems. *Theoretical Biology*, **42**, 359–386.
- Scott, J. P. & Fuller, J. L.** 1965. *Genetics and the Social Behavior of the Dog*. Chicago: University of Chicago Press.
- Senn, C. L. & Lewin, J. D.** 1975. Barking dogs as an environmental problem. *Journal of the American Veterinary Medicine Association*, **166**, 1065–1068.
- Seyfarth, R. M., Cheney, D. L. & Marler, P.** 1980. Monkey responses to three different alarm calls: evidence of predator classification and semantic communication. *Science*, **210**, 801–803.

- Seyfarth, R. M., Cheney, D. L., Harcourt, A. H. & Stewart, K. J. 1994. The acoustic features of gorilla double grunts and their relation to behaviour. *American Journal of Primatology*, **33**, 31–50.
- Slobodchikoff, C. N., Kiriazis, J., Fischer, C. & Creef, E. 1991. Semantic information distinguishing individual predators in the alarm calls of Gunnison's prairie dogs. *Animal Behaviour*, **42**, 713–719.
- Tembrock, G. 1976. Canid vocalizations. *Behavioural Processes*, **1**, 57–75.
- Tooze, Z. J., Harrington, F. H. & Fentress, J. C. 1990. Individually distinct vocalizations in timber wolves, *Canis lupus*. *Animal Behaviour*, **40**, 723–730.
- Wiley, R. H. 1994. Errors, exaggeration and deception in animal communication. In: *Behavioral Mechanisms in Evolutionary Ecology* (Ed. by L. Real), pp. 157–189. Chicago: University of Chicago Press.
- Yin, S. 2002. A new perspective on barking in dogs. *Journal of Comparative Psychology*, **116**, 189–193.