USDA National Wildlife Research Center - Staff Publications

U.S. Department of Agriculture: Animal and Plant Health Inspection Service

August 2006

INFORMATION CONTENT OF COYOTE BARKS HOWLS

Brian R. Mitchell
University of California, Berkeley

Maja M. Makagon
University of California, Berkeley

Michael M. Jaeger
Utah State Uniueraity, Logan, Utah

Reginald H. Barrett
University of California, Berkeley

INFORMATION CONTENT OF COYOTE BARKS AND HOWLS

BRIAN R. MITCHELL[*1], MAJA M. MAKAGON[1], MICHAEL M. JAEGER[2] AND REGINALD H. BARRETT[1]

[1] *Department of Environmental Science, Policy and Management, University of California, Berkeley, 151 Hilgard Hall #3110, Berkeley, CA 94720-3110, USA.*
[2] *National Wildlife Research Center, Department of Forestry, Range, and Wildlife Sciences, Utah State University, Logan, Utah 84322-5295, USA.*

ABSTRACT

The information content of coyote (*Canis latrans*)vocalizations is poorly understood, but has important implications for understanding coyote behaviour. Coyotes probably use information present in barks or howls to recognize individuals, but the presence of individually-specific information has not been demonstrated. We found that coyote barks and howls contained individually specific characteristics: discriminant analysis correctly classified barks of five coyotes 69% of the time and howls of six coyotes 83% of the time. We also investigated the stability of vocalization characteristics at multiple distances from the source. Recordings were played back and re-recorded at 10 m, 500 m, and 1,000 m. Vocalization features were measured at each distance and analyzed to determine whether characteristics were stable. Most howl characteristics did not change with distance, and regardless of the distance discriminant analysis was 81% accurate at assigning howls among six individuals. Bark characteristics, however, were less stable and it is unlikely that barks could be used for individual recognition over long distances. The disparate results for the two vocalization types suggest that howls and barks serve separate functions. Howls appear optimized to convey information (i.e. data), while barks seem more suitable for attracting attention and acoustic ranging.

Keywords: bark, *Canis latrans*, Canidae, communication, coyote, distance effect, howl, individual differences, ranging

INTRODUCTION

Despite decades of interest in using real or imitated coyote (*Canis latrans*) vocalizations for research and management (Alcorn 1946;

*Correspondence and present address: B. Mitchell, Rubenstein School of Environment and Natural Resources, University of Vermont, 81 Carrigan Drive, Burlington, Vermont 05405-0088, USA. Email: brian.mitchell@uvm.edu

Fulmer 1990; Beaudette 1996), there are no detailed studies of the potential information content of coyote vocalizations. "Information" in this context refers to any data that a listener can obtain about a vocalizing individual. Coyote long-range vocalizations are hypothesized to contain cues to the caller's identity, and may have characteristics useful for helping listeners localize a call's source (Lehner 1978). The ability to recognize individuals and determine their location based on vocalizations would allow coyotes to use auditory cues to coordinate social activities (ranging from cooperative foraging to territorial defense) when conditions do not allow for visual communication.

Coyotes in unexploited populations are generally crepuscular or nocturnal and they often live in social groups (packs) that consist of an alpha breeding pair and their offspring (Camenzind 1978; Andelt & Gipson 1979). These groups can range in size from two to seven individuals (Camenzind 1978), although we have observed up to nine individuals in one social group (B. R. Mitchell, personal observation). Coyotes within a pack are often separated by hundreds of meters; field observations indicate a median distance between alphas of 402 m (N = 275 for five alpha pairs), between betas of 543 m (N = 99 for 5 beta pairs), and between alphas and betas of 895 m (N = 378 for 13 pairs; B. R. Mitchell, unpublished data). Because coyotes are often separated and active at night, vocal communication may be even more important than visual communication in many circumstances. Showing that barks and howls include individually specific cues is the first step towards devising field playback experiments that will test whether coyotes actively distinguish individuals based on their vocalizations and whether vocal signals convey additional information that could be used by receivers to coordinate their activities with signallers.

Individual vocal characteristics have been documented in a variety of taxa, from birds (Peake et al. 1998; Walcott et al. 1999) to various mammalian orders including primates (Dallmann & Geissmann 2001), ungulates (Reby et al. 1999), rodents (McCowan & Hooper 2002), elephants (McComb et al. 2000), whales (McCowan & Reiss 2001), seals (Phillips & Stirling 2000), and carnivores (McShane et al. 1995; Holekamp et al. 1999). Numerous studies have taken the additional step of showing that individuals actually do discriminate between different conspecifics. Examples of animals using individual vocal cues can be found in birds (Jouventin et al. 1999), primates (Cheney & Seyfarth 1980; Weiss et al. 2001), elephants (McComb et al. 2003), whales (Sayigh et al. 1999), and seals (Charrier et al. 2002). Within the wild canids, individual differences have been documented in swift foxes (Darden et al. 2003), African wild dogs (Hartwig 2005), wolves (Theberge & Falls 1967; Tooze et al. 1990), and dholes (Durbin 1998). Frommolt et al. (2003) documented

individuality in barks of a territorial population of arctic foxes and also showed that foxes respond differently to barks from members of their own social group than they do to other foxes.

Very few studies have tested whether individually specific characteristics of long-range vocalizations are stable over distance. Instead, most researchers assume that discriminating features carry as far as the sound can be perceived. The problem with this assumption is illustrated by elephant vocalizations. The infrasonic component of elephant calls can carry up to 10 km, but useful discrimination does not occur over these distances – elephants typically only recognize individuals that are less than 1.5 km away. This is because elephants recognize individuals based on higher frequency components of vocalizations that degrade much more quickly than infrasound (McComb et al. 2003).

Coyote signallers should benefit from producing vocalizations that allow members of their social group who are out of visual contact to identify and locate them, because this would facilitate the coordination of territory defence, cooperative foraging, and group social activities. Receivers should pay attention to these cues, because a missed or misinterpreted signal could decrease foraging opportunities or even lead to the death of siblings or offspring (e.g., Camenzind (1978) noted 2 occasions of territorial intrusions resulting in the death of pups). Vocal characteristics that show strong reliability regardless of distance should be preferred by receivers interested in determining the identity of a vocalizing animal (Naguib & Wiley 2001). Recognition based on features that are stable over distance would allow receivers to develop a simple, general purpose perceptual template that could be used for matching vocalizations. If individually specific features of vocalizations degrade or are altered with distance, animals attempting to identify the source of a call would be required to estimate the distance to the source and then factor in an understanding of how acoustic features change with distance. Only then would they be able to match the vocalization to a mental template that had been formed by listening to the sender at close range.

If, however, the signaller is using a long-distance vocalization to provide location information to receivers, then characteristics that degrade with distance are preferred. Humans and birds have been shown to estimate distance to sounds (or "range") using three techniques: amount of reverberation, absolute magnitude, and relative intensity of high-frequency components (Naguib & Wiley 2001). Reverberation is rarely present in animal vocalizations; it is created as sounds reflect off of features in the environment. Therefore increased reverberation in a sound almost always indicates a greater distance to the source. The other types of ranging rely on learned knowledge of the amplitude and general characteristics of the sound

at its source. Distance estimation based on absolute magnitude takes advantage of the tendency for more distant sounds to have lower amplitudes, while ranging based on relative intensity involves judging the ratio of high to low frequencies in vocalizations. Because high frequencies are attenuated more rapidly than low frequencies, a low ratio indicates a distant sound (Naguib & Wiley 2001).

There is therefore a trade-off between vocalization characteristics useful for information transfer and qualities useful for ranging. Vocalization types or components used for long-range communication of content should be stable over distances used by the species, while vocalizations used for ranging should degrade relatively quickly.

We tested whether coyote barks and howls contain individually specific cues by measuring and analyzing multiple vocalizations recorded from known individuals. We predicted that discriminant analysis would demonstrate the presence of individually specific cues by successfully classifying vocalizations to the correct individual. We also tested whether individual information in coyote barks and howls is conserved when transmitted over distances up to 1 km, and we addressed the possible presence of characteristics useful for ranging. We predicted that howls, with their long duration, widely spaced harmonics, and potential for frequency modulation, would be better suited than barks for conveying individually specific cues over biologically relevant distances. We predicted that barks, with their short duration and broad frequency distribution, would be more suitable for ranging.

METHODS

Recordings

Recordings were collected from captive-reared coyotes at the US Department of Agriculture, Wildlife Services, National Wildlife Research Center (NWRC) field station in Logan, Utah, between 8 July 1998 and 27 July 1998. We used a Tascam DA-P1 digital tape recorder (DAT) and a tripod-mounted Sennheiser MKH 70 shotgun microphone.

Subject animals were all housed as breeding pairs in 0.1-ha pens. The coyotes had been housed in these pens for over 6 months, and had never been involved in behavioural research. Details about the seven study coyotes are presented in Table 1. Because the microphone was positioned outside of the pens, recording distances ranged from 5 to 35 m. There were typically two recording sessions per day (morning and evening), during times when the coyotes vocalized regularly and were visually identifiable. Vocalizations

TABLE 1

Sample sizes, sex, age, weight, and relationships for coyotes at the NWRC Logan
Field Station, July, 1998

Coyote	Barks[1]	Howls[1]	Sex	Age	Weight (kg)	Mate	Sibling(s)
F-5414	—	23	F	3	11.0	M-5320	M-5416
F-5438	26	19	F	3	9.1	M-5429	
F-5471	96	—	F	2	8.4	M-5416	
M-5320	91	55	M	5	15.0	F-5414	
M-5416	52	61	M	3	14.4	F-5471	F-5414
M-5429	28	39	M	3	14.8	F-5438	M-5430
M-5430	—	83	M	3	12.5	N/A	M-5429

[1]Sample sizes used in discriminant analyses. Dashes indicate fewer than 15
vocalizations and exclusion from analyses.

always occurred in response to other coyote vocalizations (either other
captive animals or wild individuals in the surrounding hills), and
were presumed to be agonistic. On any given day, only one pair of
coyotes was recorded. During recording sessions we recorded all
vocalizations while making observations about which coyote of the
subject pair was vocalizing.

Recordings were digitized using DiskRec 1.0 (Engineering
Design, Massachusetts, USA) and a 50 kHz Dart Digital Signal
Processor card (Engineering Design). We isolated and saved
vocalizations along with the identity of the vocalizing subject when
that could be determined. Of the 1,754 vocalizations we recorded, 573
contained single vocalizations from known individuals that
contributed at least 15 vocalizations. The final data set had 293 barks
(from 2 females and 3 males) and 280 howls (from two females and
four males).

We used Sound Forge 4.5 (Sonic Foundry, Wisconsin, USA) with
Sonic Foundry Noise Reduction 2.0 to remove excessive background
noise. We then peak-normalized the resulting sounds and produced an
audio playback CD containing each vocalization separated by 4
seconds of silence. Recordings were played using a timer-controlled
playback unit with a 25-watt Johnny Stewart long-range predator
calling speaker (Hunter's Specialties, Iowa, USA). Speaker height was
50 cm, oriented parallel to the ground, and the sound pressure level
was similar to pressure levels produced by vocalizing coyotes
(approximately 105 dB at 1 m). We selected this speaker because it
was portable and powerful, and the trade-off was an uneven frequency
response. Comparing 15 barks sent to the speaker and re-recorded at
10 m revealed that the speaker overemphasized sound at 4 kHz by
about 15 dB-volts relative to sound at 1 kHz. The playback device was
set in open annual grassland at the Gray Davis Dye Creek Preserve
(DCP), in Tehama County, northern California. The DCP had been

the site of extensive playback experiments with coyotes over the previous 2 years (Mitchell 2004). The specific playback site was selected with the help of GIS software to be isolated and flat. We used a tripod-mounted microphone (1.2 m) to record the playback CD at distances of 10 m, 500 m, and 1,000 m. Recordings were made near dawn, when wind speed was minimal.

The recordings from each distance were digitized and isolated. The final vocalization library contained four sets of 573 vocalizations: raw or initial recordings, 10-m recordings, 500-m recordings, and 1,000-m recordings. All recordings were digitized at 25 kHz. The analysis of individual differences was based on the raw recordings, while the distance analysis used only the 10-m, 500-m, and 1,000-m recordings. We expected recordings measured at 10-m to differ from the raw vocalizations due to processing and playback effects (e.g., noise reduction and the speaker's frequency response), but we felt that the 10-m recordings adequately incorporated the characteristics of coyote vocalizations observed at close range. Our distance analysis therefore assumes that the 10-m recordings are similar to actual coyote vocalizations and behave the same way when recorded at greater distances.

Bark measurements and variables

A spectrogram of each bark was displayed in Signal 3.1 (Engineering Design), using 512-point Fast Fourier Transforms (FFTs), a 0.25 ms increment between FFTs, a maximum frequency of 4 kHz, and a Hanning window. The resolution of the cursor used to record measurements was 0.43 ms and 17 Hz. For each bark spectrogram, one observer (M. M. Makagon) recorded the start and end time of the bark based on when the vocalization was within 40 dB of the maximum amplitude of the recording (Figure 1). She also recorded the bark structure (chaotic/noisy, intermediate, or harmonic), and the harmonic structure (frequency contour shape). In this paper, the terms "chaotic" or "noisy" refer to the presence of broadband sound energy produced by the subject animal, and not to background environmental noise. The frequency contour shape was rated on a 5-point scale based on measurements of the lowest (fundamental) harmonic: "1" if the fundamental could not be detected; "2" if the frequency increase across the fundamental was less than 100 Hz; "3" if the frequency increase was more than 100 Hz; "4" if the middle of the fundamental was more than 100 Hz higher than both ends; and "5" if the middle of the fundamental was more than 200 Hz higher than both ends. The measurement thresholds (e.g. 100 Hz) chosen for this and other vocal characteristics are arbitrary, based primarily on differences that could be easily distinguished audibly by human
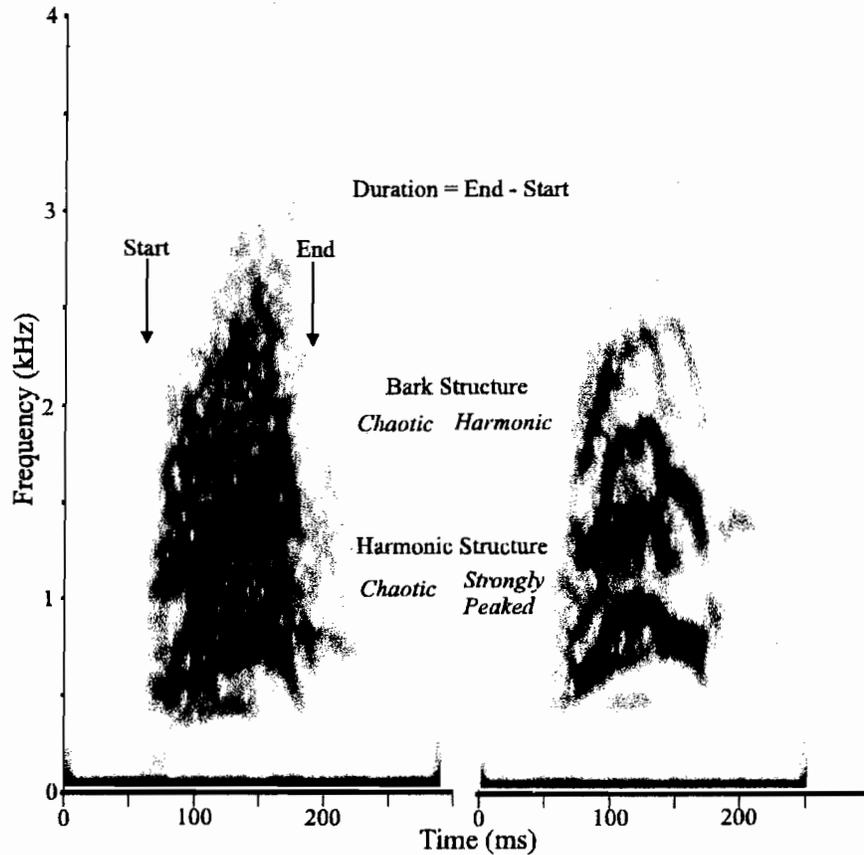
Figure 1. Bark spectrogram measurements and their corresponding variables. Note the presence of echoes in both spectrograms; these were ignored for determining the end of the bark.

observers. The purpose of this analysis is to demonstrate that coyote vocalizations have characteristics that are individually specific. We do not address whether coyotes actually use these characteristics, and we cannot be certain that the thresholds chosen have biological significance for coyotes.

We wrote a program for Signal 3.1 that used the methods of Forrest et al. (1988) to calculate the first four spectral moments (mean, standard deviation, skewness, and kurtosis) of each bark. We also calculated an estimate of the Spectral Harmonic-to-Noise Ratio (HNR) of the barks using methods described in Riede et al. (2005), and we recorded the frequency where HNR was measured. A final Signal 3.1 program generated power spectra for each bark using a 16-k FFT and a 100-Hz moving average for smoothing, and recorded the

maximum dB level and the frequency where the maximum dB level occurred.

Kurtosis and the frequency of the maximum dB were not important in the analyses reported here, and were excluded from data tables to save space. Readers interested in the full tables can find them in Mitchell (2004).

Howl measurements and variables

Spectrograms were displayed in Signal 3.1 using a 5-ms step between successive FFTs, a 1,024-point FFT size, and a Hanning window. Spectrograms were zoomed to approximately 1 second by 1 kHz for measurement, and measurement resolution was at or better than 1.7 ms and 5.0 Hz. Spectrogram measurements were made by two observers (M. M. Makagon and B. R. Mitchell).

Time and frequency measurements were taken at five points along the fundamental for each howl: the howl's start, the end of the howl's rising portion, the point of maximum frequency, the start of the howl's falling portion, and the end of the howl (Figure 2). The howl's start and end were defined at the points where the vocalization was visibly different from background noise. If one of the five points was not visible on the fundamental at one or more distances, then the point was measured on the lowest usable harmonic (almost always the first harmonic) and the frequency measurement was divided to yield the equivalent fundamental measurement.
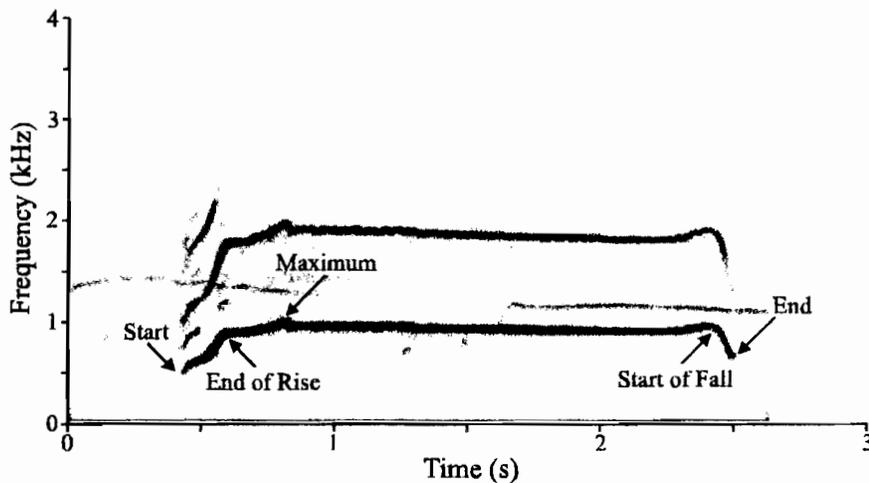

Figure 2. Locations of howl frequency and time measurements.

The frequency and time measurements were converted into duration (measured in ms) and slope (measured in Hz/ms) variables: 1) of the rising portion; 2) from the start of the middle portion to the maximum frequency; 3) from the maximum frequency to the end of the middle portion; and 4) of the falling portion. These eight variables were used along with the frequency measurements in the statistical analyses.

Each howl was assigned a howl type based on the three frequency measurements from the middle of the howl: "1" for howls that increased more than 100 Hz, "2" when the howl peaked in the second half at a value more than 100 Hz above the ends, "3" for a howl showing less than 100 Hz of change in the midsection, "4" when the howl peaked in the first half at a value more than 100 Hz above both ends, and "5" for howls with a midsection that decreased more than 100 Hz. We also documented nonlinear phenomena of howl spectrograms, specifically subharmonics and chaotic sections (i.e., "deterministic chaos" [Fitch et al. 2002]). If one type of nonlinear phenomenon graded directly into another type (such as a segment of deterministic chaos transitioning into a section with subharmonics), we counted two features rather than one. We recorded the number of nonlinear phenomena in the rising, middle, and falling portions of each howl.

We measured frequency modulation of howls by documenting frequency shifting and wavering. Frequency shifts were found in the middle section of a howl and were fairly abrupt changes in the average frequency. Wavers were short frequency-modulated sections that often gave coyote howls a distinctive "warbling" sound. Frequency shifts had to be at least 50 Hz, could not be part of a waver, and could not return to the original frequency for at least 400 ms. Wavers had to be less than 400-ms long, and had to show a frequency drop of at least 50 Hz relative to the start and end of the waver. For each howl, we recorded the number of frequency shifts between 50 and 100 Hz, and the number of shifts greater than 100 Hz. Wavers were classified according to location (rising portion or middle of the howl) and size (50 to 100 Hz, 100 to 200 Hz, or greater than 200 Hz). Wavers in the rising portion of the howl were also counted if they were between 0 Hz and 50 Hz.

Maximum frequency, fall nonlinearities, frequency shifts, rise wavers less than 50 Hz or greater than 200 Hz, and middle wavers greater than 200 Hz were not important in the analyses reported here. These variables were excluded from data tables to save space, but readers interested in the full tables can find them in Mitchell (2004).

Data analysis

We used linear discriminant analysis to examine whether bark and howl variables from our original recordings could be used to tell individuals apart. Many researchers suggest excluding variables that are highly correlated with other variables in the analysis (e.g. Gouzoules & Gouzoules 2000; Kazial et al. 2001); we used a threshold of 0.8. Discriminant analysis also performs poorly when there is no variability within a group (Klecka 1980), so variables were excluded if multiple individuals showed no variation. In addition, the number of variables in a discriminant analysis should be less than 0.33 times the number of observations (Kazial et al. 2001). When this situation occurred, we chose a subset of variables based on the significance of univariate t-tests.

Discriminant analysis is an inferential technique based on sample data, and model validation is based on the data used to create the model. Therefore the classification accuracy overstates the discriminant analysis' true success (Klecka 1980). This bias can be countered with split-sample validation, so we randomly excluded 25% of each individual's vocalizations for use as "test" data to check the discriminant model built using the remainder of the data. All discriminant analyses were conducted using SAS 9.1 (SAS Institute, North Carolina, USA). We used PROC STEPDISC's stepwise variable selection process, followed by PROC DISCRIM with proportional priors.

We computed kappa and its associated 95% confidence interval for each classification according to the procedure in Titus et al. (1984). Kappa adjusts the percentage accuracy of discriminant analyses to account for chance and the effect of unequal group sizes. In other words, kappa corrects for the number of individuals used in the analysis and the distribution of the data. As with raw classification accuracies, kappa is only unbiased with test data that were not used to develop the classification model (McGarigal et al. 2000). However, estimates of kappa were less precise for the test data because of smaller sample sizes, and this led to occasional instances where kappa was lower for the training data.

We used discriminant analysis to classify the original bark and howl recordings to the individual that produced them. Because the presence of sex-specific information in vocalizations can change classification accuracy and alter the importance of different variables (Bachorowski & Owren 1999), we also used discriminant analysis to classify individuals within each gender.

We then used repeated measures MANOVA (in JMP IN 4.0, SAS Institute) to investigate how bark and howl variables changed with distance. We investigated whether measurements at 10, 500, and 1,000 meters differed by individual, whether measurements differed

over distance, and whether individual and distance interacted. The MANOVA results were used to generate a list of variables with minimal distance effects that could be incorporated into a discriminant analysis. Variables were selected if the F-ratio for an individual effect was more than double the F-ratio for the distance effect, which indicated that individual differences outweighed differences due to distance. Variables were also selected if the F-test for a distance effect was non-significant given a Bonferroni-corrected alpha of $0.05/n$, where n equalled the number of bark or howl variables tested. The shortened variable list was used in accordance with the previously described methods to generate a discriminant model based on the 10-m training data. The resulting discriminant functions were checked against the 10-m, 500-m, and 1,000-m test data. These results were also compared to results from analyses where there was no attempt to filter out variables with strong distance effects.

RESULTS

Analysis of original bark recordings

Table 2 lists mean measurements, by individual, for the original bark recordings. The final discriminant model contained duration, harmonic structure, mean, standard deviation, HNR, and HNR frequency. Skewness and kurtosis were excluded because of high correlations with each other and with mean frequency. The squared canonical correlations for the four canonical functions were 0.53, 0.35, 0.14, and 0.08; these values indicate the proportion of variability in each function that is explained by the identity of the barking individual. The discriminating power of the first 2 functions was primarily due to bark duration and mean frequency, the third function was most influenced by bark harmonic structure, and the power of the final function was most affected by HNR (Table 3).

The classification accuracy of the training data was good, with an overall 70% accuracy that ranged between 42% and 89% for each individual (Table 4). The most common mistake was confusion of mated coyotes M-5416 and F-5471 (22 out of 65 total mistakes). The test data classification showed a similar overall accuracy (69%), and more variability in individual success rates (29% to 92%). The corresponding kappa estimates were 0.59 ± 0.08 ($x \pm 95\%$ CI) for the training data and 0.57 ± 0.15 for the test data, indicating a classification success about 60% better than chance.

Analyzing the three males and two females separately led to models with high raw accuracy scores, but similar chance-corrected test model accuracies. The male-only model included duration, bark

TABLE 2

Bark data for coyotes recorded at the NWRC Logan Field Station, July, 1998. [1]

Variable	F-5438	F-5471	M-5320	M-5416	M-5429
Duration (ms)	135 ± 3.3	109 ± 1.7	129 ± 1.7	116 ± 2.3	139 ± 3.2
Bark Structure	2.23 ± 0.12	1.91 ± 0.06	1.70 ± 0.07	2.00 ± 0.09	1.07 ± 0.12
Bark Harmonic Structure	3.46 ± 0.25	2.75 ± 0.13	2.52 ± 0.14	3.25 ± 0.18	1.14 ± 0.25
Max Db (dB-volts)	-42.6 ± 1.12	-43.1 ± 0.58	-42.6 ± 0.60	-46.2 ± 0.79	-47.2 ± 1.08
Mean (Hz)	1,220 ± 22	1,295 ± 11	1,108 ± 12	1,328 ± 16	1,380 ± 21
Standard Deviation (Hz)	624 ± 14	705 ± 7.2	594 ± 7.4	681 ± 9.8	658 ± 13
Skewness	1.67 ± 0.07	1.28 ± 0.04	2.01 ± 0.04	1.25 ± 0.05	1.19 ± 0.07
HNR (volts)	10.57 ± 0.76	8.67 ± 0.40	8.35 ± 0.41	6.49 ± 0.54	3.13 ± 0.73
HNR Frequency (Hz)	806 ± 56	719 ± 29	709 ± 30	728 ± 39	867 ± 54

[1]Values are mean ± standard error. Sample sizes: 26 from F-5438, 96 from F-5471, 91 from M-5320, 52 from M-5416, and 28 from M-5429.

TABLE 3

Standardized canonical coefficients for discriminant analysis of individual differences in barks, based on original recordings of 5 individuals.

Variable	Function 1	Function 2	Function 3	Function 4
Duration	-0.735	0.769	0.265	0.159
Bark Harmonic Structure	0.346	-0.330	0.733	-0.736
Mean	0.856	0.969	0.577	0.145
Standard Deviation	0.321	-0.167	-0.469	0.270
HNR	0.094	-0.144	0.416	1.113
HNR Frequency	-0.159	-0.001	0.318	0.421

TABLE 4

Training data classification matrix from analysis of individual differences in barks, based on original recordings

	M-5320	M-5416	M-5429	F-5438	F-5471	Percent Correct
M-5320	50	2	5	1	10	74
M-5416	4	17	1	0	17	44
M-5429	2	0	15	2	2	71
F-5438	5	1	1	8	4	42
F-5471	0	5	1	2	64	89
Total	61	25	23	13	97	70

structure, harmonic structure, and mean, while the female-only model included duration, bark structure, mean, standard deviation, and HNR. Both skewness and kurtosis were excluded from the males-only model because of high correlations with other variables, and skewness was excluded from the female model. The male-only model was 78% accurate classifying 128 training barks and 72% accurate classifying 43 test barks, with kappas of 0.64 ± 0.12 ($x \pm$ 95% CI) and 0.51 ± 0.24, respectively. The female-only model was 93% accurate classifying 91 training barks and 87% accurate classifying 31 test barks, with corresponding kappa estimates of 0.81 ± 0.15 ($x \pm$ 95% CI) and 0.59 ± 0.38.

Analysis of original howl recordings

Table 5 lists mean measurements, by individual, for the original howl recordings. The final discriminant model contained all frequency measurements except the maximum frequency, all durations except for the rising portion of the howl, all slope measurements, nonlinearities in the rise, 50 and 100 Hz wavers in the rise, and 50

TABLE 5

Howl data for coyotes recorded at the NWRC Logan Field Station, July, 1998. [1]

Variable	F-5414	F-5438	M-5320	M-5416	M-5429	M-5430
Start Frequency (Hz)	394 ± 9.0	446 ± 9.9	380 ± 5.8	392 ± 5.5	370 ± 6.9	374 ± 4.7
End Rise Frequency (Hz)	936 ± 32	1,028 ± 35	1,141 ± 21	1,072 ± 20	673 ± 24	808 ± 17
Start Fall Frequency (Hz)	978 ± 29	1,001 ± 32	1,172 ± 19	1,116 ± 18	671 ± 22	865 ± 15
End Frequency (Hz)	559 ± 34	646 ± 37	1,023 ± 22	504 ± 21	361 ± 26	480 ± 18
Rise Duration (ms)	241 ± 23	234 ± 25	216 ± 15	262 ± 14	191 ± 17	267 ± 12
End Rise to Max Duration (ms)	442 ± 69	312 ± 76	450 ± 45	318 ± 43	397 ± 53	370 ± 37
Max to Start Fall Duration (ms)	440 ± 105	846 ± 115	989 ± 68	631 ± 64	780 ± 81	376 ± 55
Fall Duration (ms)	68 ± 11	73 ± 12	70 ± 7.3	72 ± 6.9	156 ± 8.6	74 ± 5.9
Rise Slope (Hz/ms)	2.67 ± 0.27	2.69 ± 0.29	4.15 ± 0.17	2.84 ± 0.16	2.16 ± 0.20	1.82 ± 0.14
End Rise to Max Slope (Hz/ms)	0.30 ± 0.08	0.52 ± 0.09	0.53 ± 0.05	0.47 ± 0.05	0.44 ± 0.06	0.57 ± 0.04
Max to Start Fall Slope (Hz/ms)	-0.34 ± 0.08	-0.19 ± 0.09	-0.23 ± 0.05	-0.23 ± 0.05	-0.27 ± 0.06	-0.62 ± 0.04
Fall Slope (Hz/ms)	-6.60 ± 0.58	-5.13 ± 0.64	-2.08 ± 0.38	-10.49 ± 0.36	-2.54 ± 0.45	-5.74 ± 0.31
Rise Nonlinearity	0.48 ± 0.12	0.42 ± 0.13	0.82 ± 0.07	0.51 ± 0.07	0.64 ± 0.09	1.01 ± 0.06
Middle Nonlinearity	0.00 ± 0.00	0.21 ± 0.17	0.00 ± 0.00	0.02 ± 0.09	0.46 ± 0.12	0.92 ± 0.08
50 to 100 Hz Rise Wavers	0.09 ± 0.07	0.32 ± 0.07	0.16 ± 0.04	0.08 ± 0.04	0.05 ± 0.05	0.08 ± 0.04
100 to 200 Hz Rise Wavers	0.17 ± 0.06	0.05 ± 0.06	0.09 ± 0.04	0.11 ± 0.04	0.08 ± 0.04	0.04 ± 0.03
50 to 100 Hz Middle Wavers	0.17 ± 0.15	0.21 ± 0.17	0.42 ± 0.10	0.10 ± 0.09	0.21 ± 0.12	0.64 ± 0.08
100 to 200 Hz Middle Wavers	0.09 ± 0.12	0.00 ± 0.00	0.04 ± 0.08	0.00 ± 0.00	0.33 ± 0.09	0.48 ± 0.06
Howl Type	2.65 ± 0.30	3.37 ± 0.33	3.22 ± 0.20	3.00 ± 0.19	3.38 ± 0.23	2.67 ± 0.16

[1]Values are mean ±standard error. Sample sizes: 23 from F-5414, 19 from F-5438, 55 from M-5320, 61 from M-5416, 39 from M-5429, and 83 from M-5430.

Hz wavers in the middle. The maximum frequency was excluded from this analysis because of high correlations with the end of rise and start of fall frequencies. Nonlinear features of the midsection and end, frequency shifts between 50 and 100 Hz, and 100 to 200 Hz wavers in the midsection were excluded because multiple individuals lacked variability for these variables.

The discriminant analysis of howls from six individuals had high squared canonical correlations for the first three canonical functions (0.75, 0.60, and 0.39), suggesting that they would be very successful at classifying individuals. The remaining functions had squared correlations of only 0.18 and 0.07. The variables contributing most strongly to the first function were the end rise, start fall, and end frequencies. The second function was most strongly affected by fall slope, with help from the frequency at the start of the fall. The third function was most influenced by the slope of the rise and the frequency at the end of the rise (Table 6). In other words, the first function favored frequency characteristics, the second was most influenced by the end of the howl, and the third was most affected by the beginning of the howl.

Classification accuracy for the training data was good, with an overall 83% accuracy and a chance-corrected accuracy of 0.79 ± 0.07 ($x \pm 95\%$ CI). Accuracy for specific individuals varied from 47% to 92% (Table 7); the 47% accuracy corresponded to the coyote with the second-lowest number of howls – only 17 were used in the training data. The next-lowest individual accuracy was 71%. The most common classification errors involved the females: 13 of 36 errors involved a

TABLE 6

Standardized canonical coefficients for discriminant analysis of individual differences in howls, based on original recordings of 6 individuals.

Variable	Function 1	Function 2	Function 3	Function 4	Function 5
Start Frequency	-0.198	0.064	0.206	0.894	0.094
End Rise Frequency	0.684	-0.237	-0.601	0.507	0.206
Start Fall Frequency	0.541	-0.539	-0.209	0.001	-0.003
End Frequency	0.695	0.245	-0.083	-0.462	0.121
End Rise to Max Duration	0.411	0.051	0.102	0.016	0.099
Max to Start Fall Duration	0.393	-0.082	0.265	-0.259	0.655
Fall Duration	0.206	-0.378	0.453	-0.548	0.363
Rise Slope	0.396	0.187	0.584	-0.472	-0.469
End Rise to Max Slope	0.187	0.115	-0.155	0.186	0.615
Max to Start Fall Slope	-0.232	-0.312	0.453	0.016	-0.089
Fall Slope	0.433	1.105	0.043	0.774	-0.309
Rise Nonlinearity	-0.170	0.368	-0.322	-0.285	0.112
50 to 100 Hz Rise Wavers	0.327	0.091	0.149	0.023	-0.047
100 to 200 Hz Rise Wavers	0.196	-0.102	0.100	-0.190	-0.561
50 to 100 Hz Middle Wavers	-0.058	0.385	-0.464	-0.057	0.001

TABLE 7

Training data classification matrix from analysis of individual differences in howls, based on original recordings.

	M-5320	F-5414	M-5416	M-5429	M-5430	F-5438	Percent Correct
M-5320	50	2	5	1	10	74	
M-5320	34	1	4	0	2	0	83
F-5414	0	8	3	0	5	1	47
M-5416	0	1	39	3	1	1	87
M-5429	0	0	0	24	5	0	83
M-5430	0	0	2	2	57	1	92
F-5438	1	2	1	0	0	10	71
Total	35	12	49	29	70	13	83

female being classified as one of the other animals. The analysis probably included too few howls from the females (14 from F-5438 and 17 from F-5414) for discriminant analysis to fully model their variability.

The discriminant analysis incorporating all individuals yielded similar results with the test data. Overall accuracy was 83% – with a corresponding kappa of 0.79 ± 0.11 ($x \pm 95\%$ CI) – and individual accuracies varied between 33% and 100%. Out of 12 classification errors for the test data, seven involved a female's howls being classified as belonging to another individual.

The discriminant model that was limited to the four males had a higher estimated kappa than the model incorporating all individuals. The training accuracy was 88% and the test classification accuracy was 93%, with corresponding kappas of 0.84 ± 0.07 ($x \pm 95\%$ CI) and 0.91 ± 0.08. The maximum frequency was excluded from the analysis because of high correlations with other frequency measurements, and the number of nonlinearities in the end of the howl was excluded due to lack of variability for multiple individuals. The final model included the remaining frequency variables (except start frequency), the duration variables (except start duration), the slope measurements, the remaining nonlinearity measurements, 50 to 100 Hz wavers in the beginning and middle of the howl, and 100 Hz wavers in the middle of the howl.

The model based on the two females had lower estimated kappas than the other models. The 87% training and 82% test accuracies compared favourably to the model for all individuals, but because there were only two females and a small sample size (31 training howls) the kappa estimates were lower and had large confidence intervals: 0.74 ± 0.24 ($x \pm 95\%$ CI) for the training data and 0.62 ± 0.48 for the test data. Because of the small sample size for this analysis, it was limited to the 8 variables that showed significant

t-tests (at $\alpha = 0.05$) for differences between the females. The final model included the frequency of the howl's start, the duration between the maximum frequency and the start of the howl's fall, wavers up to 50 Hz in the rising portion of the howl, and the howl type.

Distance effects on coyote vocalizations

Means of bark variables for each distance are provided in Table 8. Most of these variables had similar values at 500 m and 1,000 m that differed from the values recorded at 10 m. The exceptions were bark duration (similar at all distances), HNR frequency (increased with distance), and skewness and the frequency of the peak dB level (both varied erratically). The repeated measures MANOVAs of bark variables showed significant individual, distance, and interaction effects for all variables, except that duration lacked distance and interaction effects (Table 9). For every variable except duration, the distance effect was approximately equal to or larger than the individual effect, indicating that the effect of distance matched or exceeded any differences due to the individuals. Bark duration was the only variable suitable for inclusion in the discriminant analysis of barks recorded at different distances, and classification accuracy based on this variable was poor. Accuracy was 50% for the 10-m training data, 50% for the 10-m test data, 47% for the 500-m test data, and 49% for the 1,000-m test data. This corresponded to a chance-corrected accuracy estimate of 0.27 ± 0.10 ($x \pm$ 95% CI) for the 10-m training data, 0.28 ± 0.16 for the 10-m test data, 0.24 ± 0.16 for the 500-m test data, and 0.25 ± 0.17 for the 1,000-m test data.

TABLE 8

Bark data at 5 different distances for coyotes recorded at the NWRC Logan Field Station and re-recorded at the Dye Creek Preserve.[1]

Variable	10 meters	500 meters	1,000 meters
Duration (ms)	134 ± 1	135 ± 1	132 ± 1
Bark Structure	1.96 ± 0.05	1.72 ± 0.04	1.75 ± 0.04
Bark Harmonic Structure	2.62 ± 0.08	2.14 ± 0.07	2.20 ± 0.07
Max dB (dB-volts)	-41.0 ± 0.1	-51.0 ± 0.3	-54.3 ± 0.4
Mean (kHz)	$1,492 \pm 5$	$1,275 \pm 8$	$1,299 \pm 8$
Standard Deviation (Hz)	679 ± 4	609 ± 3	591 ± 6
Skewness	0.98 ± 0.01	1.25 ± 0.02	1.03 ± 0.03
HNR (volts)	6.56 ± 0.25	6.92 ± 0.22	5.34 ± 0.17
HNR Frequency (Hz)	744 ± 16	824 ± 25	957 ± 31

[1]Values are mean $\pm$ standard error for 293 barks from 5 coyotes.

TABLE 9

Repeated measures MANOVA results for barks recorded at 10, 500, and 1,000 meters.

Variable	Individual		Distance		Interaction	
	$F_{4, 288}$	$p(F)^1$	$F_{2, 287}$	$p(F)^1$	$F^2_{8, 576}$	$p(F)^1$
Duration	25.3	< 0.0001	3.1	0.0463	1.2	0.3229
Bark Structure	16.0	< 0.0001	19.5	< 0.0001	6.0	< 0.0001
Harmonic Structure	19.5	< 0.0001	24.2	< 0.0001	5.9	< 0.0001
Max dB	10.7	< 0.0001	1,340.8	< 0.0001	24.0	< 0.0001
Mean	23.1	< 0.0001	809.1	< 0.0001	4.3	< 0.0001
Standard Deviation	13.7	< 0.0001	143.6	< 0.0001	11.3	< 0.0001
Skewness	18.6	< 0.0001	34.6	< 0.0001	11.7	< 0.0001
HNR	10.3	< 0.0001	23.6	< 0.0001	4.6	< 0.0001
HNR Frequency	10.0	< 0.0001	39.3	< 0.0001	6.5	< 0.0001

[1]α equals 0.0045
[2]F-test is Pillai's Trace

Discriminant analysis results were less consistent when variables with distance effects were allowed into the bark model. For a model containing duration, bark structure, harmonic structure, mean, standard deviation, skewness, and HNR, the training data was classified with a 63% accuracy rate (kappa of 0.49 ± 0.09). Accuracy was 50% for the 10-m test data, 35% for the 500-m test data, and 57% for the 1,000-m test data (with chance corrected accuracies of 0.31 ± 0.16, 0.17 ± 0.14, and 0.42 ± 0.15, respectively).

Means of howl variables for each distance are provided in Table 10. For most variables, the means at each distance were nearly identical. The exceptions are start and end frequency (both increased with distance) and rise duration and rise nonlinearities (both decreased with distance). The repeated measures MANOVA results for the 26 howl variables showed considerably fewer distance and interaction effects (Table 11) than the comparable results for bark measurements. Twenty-one variables had no distance or interaction effect, and 11 of these had significant individual effects. Of the five variables with significant distance or interaction effects, only end frequency had a distance effect F-ratio that was less than half the individual effect F-ratio. In this case we felt that the individual effect outweighed any potential distance effect enough that discriminant analysis would still be stable. The remaining four variables – start frequency, rise and fall duration, and the number of rise nonlinearities – were excluded from the distance-independent discriminant analysis. All of these variables showed significant distance effects with magnitudes similar to or greater than the individual effects.

The accuracy of discrimination among the six individuals was slightly reduced in the final model, but this model was still successful:

TABLE 10

Howl data at 5 different distances for coyotes recorded at the NWRC Logan Field
Station and re-recorded at the Dye Creek Preserve. [1]

Variable	10 meters	500 meters	1,000 meters
Start Frequency (Hz)	484 ± 3	495 ± 3	506 ± 3
End Rise Frequency (Hz)	939 ± 13	938 ± 13	939 ± 13
Start Fall Frequency (Hz)	974 ± 13	974 ± 13	974 ± 13
End Frequency (Hz)	655 ± 16	665 ± 16	671 ± 15
Rise Duration (ms)	191 ± 6	186 ± 6	180 ± 6
End Rise to Max Duration (ms)	379 ± 20	380 ± 20	380 ± 20
Max to Start Fall Duration (ms)	645 ± 33	645 ± 33	645 ± 33
Fall Duration (ms)	73 ± 4	71 ± 3	70 ± 3
Rise Slope (Hz/ms)	2.76 ± 0.10	2.72 ± 0.09	2.80 ± 0.10
End Rise to Max Slope (Hz/ms)	0.51 ± 0.02	0.52 ± 0.02	0.51 ± 0.02
Max to Start Fall Slope (Hz/ms)	-0.36 ± 0.03	-0.36 ± 0.03	-0.36 ± 0.03
Fall Slope (Hz/ms)	-5.35 ± 0.23	-5.43 ± 0.25	-5.28 ± 0.23
Rise Nonlinearity	0.55 ± 0.04	0.49 ± 0.04	0.44 ± 0.03
Middle Nonlinearity	0.32 ± 0.05	0.27 ± 0.04	0.31 ± 0.05
50 to 100 Hz Rise Wavers	0.09 ± 0.02	0.09 ± 0.02	0.10 ± 0.02
100 to 200 Hz Rise Wavers	0.08 ± 0.02	0.08 ± 0.02	0.08 ± 0.02
50 to 100 Hz Middle Wavers	0.34 ± 0.04	0.33 ± 0.04	0.34 ± 0.04
100 to 200 Hz Middle Wavers	0.21 ± 0.04	0.22 ± 0.04	0.21 ± 0.04
Howl Type	3.01 ± 0.09	3.01 ± 0.09	2.98 ± 0.09

[1]Values are mean ± standard error for 280 howls from 6 coyotes.

classification accuracy was 76% for the 10-m training data, 81% for
the 10-m test data, 81% for the 500-m test data, and 81% for the
1,000-m test data. This corresponded to a chance-corrected accuracy
estimate of 0.70 ± 0.07 (x ± 95% CI) for the 10-m training data, 0.72
± 0.12 for the 10-m test data, 0.75 ± 0.12 for the 500-m test data, and
0.76 ± 0.12 for the 1,000-m test data.

Allowing the inclusion of howl variables with distance effects
into the discriminant analysis increased the variability of the results,
although accuracy was still high in all of the test data sets. The
classification accuracy was 81% (kappa of 0.76 ± 0.07) for the training
data, 88% (0.84 ± 0.10) for the 10-m test data, 86% (0.82 ± 0.10) for
the 500-m test data, and 81% (0.76 ± 0.11) for the 1,000-m test data.

DISCUSSION

Individually specific cues in coyote barks and howls

Animal sounds often contain cues that are individually specific. One
source of these cues stems from the physiology of sound production.
The source-filter model of animal acoustics says that the fundamental

TABLE 11

Repeated measures MANOVA results for howls recorded at 10, 500, and 1,000 meters.

Variable	Individual		Distance		Interaction	
	$F_{5, 274}$	$p(F)^1$	$F_{2, 273}$	$p(F)^1$	$F^2_{10, 548}$	$p(F)^1$
Start Frequency	14.13	< 0.0001	39.21	< 0.0001	3.65	< 0.0001
End Rise Frequency	66.27	< 0.0001	6.39	0.0019	0.79	0.6378
Start Fall Frequency	81.24	< 0.0001	0.08	0.9193	1.58	0.1074
End Frequency	103.50	< 0.0001	29.78	< 0.0001	2.06	0.0263
Rise Duration	4.35	0.0008	16.88	< 0.0001	2.57	0.0048
End Rise to Max Duration	1.27	0.2772	1.75	0.1764	0.77	0.6550
Max to Start Fall Duration	12.04	< 0.0001	0.48	0.6169	1.02	0.4257
Fall Duration	12.24	< 0.0001	7.94	0.0004	3.43	0.0002
Rise Slope	18.39	< 0.0001	4.55	0.0113	1.72	0.0733
End Rise to Max Slope	2.20	0.0550	1.63	0.1973	1.51	0.1307
Max to Start Fall Slope	8.64	< 0.0001	0.16	0.8500	0.81	0.6218
Fall Slope	53.08	< 0.0001	1.17	0.3128	1.44	0.1597
Rise Nonlinearity	8.60	< 0.0001	6.92	0.0012	1.50	0.1368
Middle Nonlinearity	15.34	< 0.0001	1.52	0.2200	2.12	0.0215
50 to 100 Hz Rise Wavers	3.71	0.0029	2.03	0.1339	1.12	0.3460
100 to 200 Hz Rise Wavers	1.37	0.2360	0.27	0.7613	0.40	0.9445
50 to 100 Hz Middle Wavers	5.74	< 0.0001	0.82	0.4415	1.03	0.4191
100 to 200 Hz Middle Wavers	7.66	< 0.0001	0.92	0.3985	0.84	0.5919
Howl Type	2.23	0.0515	3.38	0.0356	1.67	0.0854

$^1\alpha = 0.0019$
[2]F-test is Pillai's Trace

frequency of animal vocalizations is determined by characteristics of the sound's source – the larynx. The acoustic energy generated by the larynx is then modified by an acoustic filter whose properties are determined partly by the length, shape, and volume of the supralaryngeal vocal tract. Certain frequencies (the formants) are passed with minimal filtering, while other frequencies are strongly curtailed (Rubin & Vatikiotis-Bateson 1998).

Vocalizations with cues to identity should be the rule rather than the exception, but the reality is that not all calls are useful for detecting morphological differences. Calls with low fundamental frequencies and calls with low-amplitude wideband noise are best for revealing body size and individuality (Owren & Rendall 2001). Although minimum fundamental frequency is constrained by physiology, many mammals can produce a broad range of fundamental frequencies by varying the rate of vocal fold vibration. When they use a high fundamental frequency or sound amplitude, aspects of the individually-specific acoustic filter are more difficult to detect (Owren & Rendall 2001). Canid growls contain highly specific cues to size (Riede & Fitch 1999) and probably identity, but barks (with their high sound amplitudes) and howls (with their high

fundamental frequencies) are less likely to obviously encode this information.

Nevertheless, coyote vocalizations clearly contained individually specific characteristics. The barks of five individuals were correctly classified about 70% of the time (a 58% chance-corrected accuracy), and the howls of six individuals were correctly classified 83% of the time (a 78% chance-corrected accuracy). Individual vocal tract morphology was not expected to leave a large imprint on barks because their high amplitude should mask much of the morphological influence (Owren & Rendall 2001). Some of this influence should remain, though, and we suspect that many of the individual differences in spectral moments were due to differences in vocal tract morphology and sound filtering. The differences among the remaining bark variables were likely due to individual preference. For example, duration of barks could be controlled by decisions about the volume and expulsion rate of air used to form the vocalization.

Howls should be less affected than barks by individual variation in vocal tract morphology because of their relatively high fundamental frequency (Owren & Rendall 2001). Frequency measurements could have been loosely related to individual differences in larynx morphology by representing the range over which each individual was able to comfortably vocalize, and nonlinear phenomena might have a physical basis if the threshold controlling the transition to nonlinear features varies in different coyotes. However, the majority of howl features that were important for discriminating individuals should be under voluntary control. These include the duration of the fall, various slope measurements, and the presence of wavers.

Our results confirm other studies indicating that individuality is a general feature of canid bark and howl vocalizations. Studies of swift foxes (Darden et al. 2003), arctic foxes (Frommolt & Gebler 2004), and domestic dogs (Yin & McCowan 2004) used characteristics of bark sequences in addition to spectral characteristics of individual barks, and were generally able to obtain higher overall classification accuracies than we found for coyote barks. The exception is Yin and McCowan (2004), where they only obtained an average 53% accuracy (a kappa of approximately 0.50) classifying the barks of 10 individuals. Of the intra-bark measurements made in other studies, variables relating to duration and the width and shape of the power spectrum were most important, as they were for this study. For howls, Tooze et al.'s (1990) wolf study reports a lower accuracy (75%) for the same number of individuals. Their analysis used many variables that were similar to the ones we chose, including maximum and end frequencies, howl duration, nonlinearities, and measures of frequency modulation of the fundamental. As with our study, they reported frequency characteristics (e.g. maximum frequency) as being most important for classifying individuals.

The effect of distance

Barks and howls contain individually specific cues, but characteristics of these two vocalization types differ in their stability over biologically relevant distances. Bark features, with the exception of duration, all had significant distance effects that equalled or exceeded the individual effect in repeated measures MANOVA. Discriminant analysis was surprisingly robust to these differences, and was moderately successful at classifying barks even when variables with distance effects were included. Nevertheless, the overall discriminant analysis accuracy for howl characteristics was higher than the accuracy for bark classifications.

The bark characteristics we chose contained less individually-specific information and were less stable over distance than the howl characteristics. While barks may be less suitable for stable information transmission than howls, they are appropriate for other purposes, including acoustic ranging. Barks are short, noisy vocalizations that cover a broad frequency range – from below 500 Hz to over 2.5 kHz. This type of sound has some distinct advantages when used in the context of agonistic interactions or as an alarm call. Barks are likely to trigger the acoustic-startle reflex in nearby animals, which causes them to increase their alertness and orient towards the sound source (Owren & Rendall 2001). This would be a useful response for a coyote that is challenging a conspecific or trying to alert its pack of danger.

Barks are also well structured for use in distance assessment. Broadband noisy vocalizations are ideal for determination of distance via relative intensity changes, and the frequency range of barks is only slightly lower than the 1-kHz to 4-kHz range needed for maximum sound transmission distance in most environments (Wiley & Richards 1978). The abrupt nature of barks, with their sudden onset and offset, also makes these vocalizations suitable for ranging based on reverberation (Naguib & Wiley 2001).

Howls are structurally different from barks; they are tonal, relatively long, frequency modulated vocalizations with a dominant frequency near 1 kHz. Wiley and Richards (1978) predicted that optimal information transmission over long distances would be obtained by tonal, frequency modulated vocalizations with frequencies between 1 kHz and 4 kHz. Howls therefore meet the criteria for an optimum information-containing long-distance vocalization. Despite marked intra-individual variability, each coyote used a particular combination of howl features in a specific way, which allowed the howls to be correctly classified to the vocalizing animal over 80% of the time. When a few variables that showed distance effects were excluded, a discriminant model based on vocalizations recorded at

10 m classified test howls recorded at 10 m, 500 m, and 1,000 m with an 81% accuracy rate.

Howls contain a number of individually specific cues that are transmitted to distances of at least 1,000 m without any noticeable degradation of information content (Table 10). There was no change in most howl characteristics with distance, and it is likely that howls are individually identifiable at even greater distances. The exceptions to the rule, specifically the features of the start of the howl, may also be important. It is possible that there are physiological constraints (e.g., a need to vocally "ramp up" to a full howl) that create the low amplitude ascending portion of coyote howls, but it is also possible that coyotes intentionally maintain this rising portion to attract the attention of receivers and provide them with additional distance information (F. Harrington, personal communication).

In addition to individually specific information, howls conceivably contain information about the sex of the howling individual (Mitchell 2004), plus howls may include more detailed information about the signaller's motivational and physical state. Theberge and Falls (1967) noted that information in howls could be universal (species-wide) or restricted (limited to a social group). Restricted communication does not require a private language; it only requires that individuals alter their vocalizations in consistent ways depending on context, and that close companions are able to associate the context with the vocal variation.

Barks and howls probably serve complementary purposes: the acoustic structure of barks is well suited to ranging, while howls are better suited to transmitting information over long distances. Coyote vocal bouts almost universally feature both calls, indicating that the overall bout may help conspecifics locate and identify the signaller, and potentially extract additional information about the signaller's activities and motivational state.

REFERENCES

Alcorn, J. R. (1946). On the decoying of coyotes. *Journal of Mammalogy*, **27**, 122-126.

Andelt, W. F. & Gipson, P. S. (1979). Home range, activity, and daily movements of coyotes. *Journal of Wildlife Management*, **43**, 944-951.

Bachorowski, J. A. & Owren, M. J. (1999). Acoustic correlates of talker sex and individual talker identity are present in a short vowel segment produced in running speech. *Journal of the Acoustical Society of America*, **106**, 1054-1063.

Beaudette, T. (1996). Calling coyotes. *Wildlife Control Technology*, Sep 1996, 46-49.

Camenzind, F. J. (1978). Behavioral ecology of coyotes on the National Elk Refuge, Jackson, Wyoming. In: *Coyotes: Biology, Behavior, and Management* (Ed. by M. Bekoff), pp. 267-294. New York: Academic Press.

Charrier, I., Mathevon, N. & Jouventin, P. (2002). How does a fur seal mother recognize the voice of her pup? An experimental study of *Arctocephalus tropicalis*. *Journal of Experimental Biology*, **205**, 603-612.

Cheney, D. L. & Seyfarth, R. M. (1980). Vocal recognition in free-ranging vervet monkeys. *Animal Behaviour*, **28**, 362-367.

Dallmann, R. & Geissmann, T. (2001). Different levels of variability in the female song of wild silvery gibbons (*Hylobates moloch*). *Behaviour*, **138**, 629-648.

Darden, S. K., Dabelsteen, T. & Pedersen, S. B. (2003). A potential tool for swift fox (*Vulpes velox*) conservation: Individuality of long-range barking sequences. *Journal of Mammalogy*, **84**, 1417-1427.

Durbin, L. S. (1998). Individuality in the whistle call of the Asiatic wild dog *Cuon alpinus*. *Bioacoustics*, **9**, 197-206.

Fitch, W. T., Neubauer, J. & Herzel, H. (2002). Calls out of chaos: The adaptive significance of nonlinear phenomena in mammalian vocal production. *Animal Behaviour*, **63**, 407-418.

Forrest, K., Weismer, G., Milenkovic, P. & Dougall, R. N. (1988). Statistical-analysis of word-initial voiceless obstruents - preliminary data. *Journal of the Acoustical Society of America*, **84**, 115-123.

Frommolt, K.-H. & Gebler, A. (2004). Directionality of dog vocalizations. *Journal of the Acoustical Society of America*, **116**, 561-565.

Frommolt, K.-H., Goltsman, M. E. & Macdonald, D. W. (2003). Barking foxes, *Alopex lagopus*: field experiments in individual recognition in a territorial mammal. *Animal Behaviour*, **65**, 509-518.

Fulmer, K. F. (1990). Characterizing the functions of coyote vocalizations through the use of playback. Thesis, University of Idaho, Moscow, Idaho.

Gouzoules, H. & Gouzoules, S. (2000). Agonistic screams differ among four species of macaques: The significance of motivation-structural rules. *Animal Behaviour*, **59**, 501-512.

Hartwig, S. (2005). Individual acoustic identification as a non-invasive conservation tool: an approach to the conservation of the African wild dog *Lycaon pictus* (Temminck, 1820). *Bioacoustics*, **15**, 35-50.

Holekamp, K. E., Boydston, E. E., Szykman, M., Graham, I., Nutt, K. J., Birch, S., Piskiel, A. & Singh, M. (1999). Vocal recognition in the spotted hyaena and its possible implications regarding the evolution of intelligence. *Animal Behaviour*, **58**, 383-395.

Jouventin, P., Aubin, T. & Lengagne, T. (1999). Finding a parent in a king penguin colony: The acoustic system of individual recognition. *Animal Behaviour*, **57**, 1175-1183.

Kazial, K. A., Burnett, S. C. & Masters, W. M. (2001). Individual and group variation in echolocation calls of big brown bats, *Eptesicus fuscus* (Chiroptera: Vespertilionidae). *Journal of Mammalogy*, **82**, 339-351.

Klecka, W. R. (1980). *Discriminant Analysis*. Newbury Park: Sage.

Lehner, P. N. (1978). Coyote vocalizations: A lexicon and comparisons with other canids. *Animal Behaviour*, **26**, 712-722.

McComb, K., Moss, C., Sayialel, S. & Baker, L. (2000). Unusually extensive networks of vocal recognition in African elephants. *Animal Behaviour*, **59**, 1103-1109.

McComb, K., Reby, D., Baker, L., Moss, C. & Sayialel, S. (2003). Long-distance communication of acoustic cues to social identity in African elephants. *Animal Behaviour*, **65**, 317-329.

McCowan, B. & Hooper, S. L. (2002). Individual acoustic variation in Belding's ground squirrel alarm chirps in the High Sierra Nevada. *Journal of the Acoustical Society of America*, 111, 1157-1160.

McCowan, B. & Reiss, D. (2001). The fallacy of 'signature whistles' in bottlenose dolphins: A comparative perspective of 'signature information' in animal vocalizations. *Animal Behaviour*, **62**, 1151-1162.

McGarigal, K., Cushman, S. & Stafford, S. (2000). *Multivariate Statistics for Wildlife and Ecology Research*. New York: Springer.

McShane, L. J., Estes, J. A., Riedman, M. L. & Staedler, M. M. (1995). Repertoire, structure, and individual variation of vocalizations in the sea otter. *Journal of Mammalogy*, **76**, 414-427.

Mitchell, B. R. (2004). Coyote vocal communication and its application to the selective management of problem individuals. Dissertation, University of California, Berkeley, Berkeley, California.

Naguib, M. & Wiley, R. H. (2001). Estimating the distance to a source of sound: mechanisms and adaptations for long-range communication. *Animal Behaviour*, **62**, 825-837.

Owren, M. J. & Rendall, D. (2001). Sound on the rebound: Bringing form and function back to the forefront in understanding nonhuman primate vocal signaling. *Evolutionary Anthropology*, **10**, 58-71.

Peake, T. M., McGregor, P. K., Smith, K. W., Tyler, G., Gilbert, G. & Green, R. E. (1998). Individuality in corncrake *Crex crex* vocalizations. *Ibis*, **140**, 120-127.

Phillips, A. V. & Stirling, I. (2000). Vocal individuality in mother and pup South American fur seals, *Arctocephalus australis*. *Marine Mammal Science*, **16**, 592-616.

Reby, D., Cargnelutti, B., Joachim, E. & Aulagnier, S. (1999). Spectral acoustic structure of barking in roe deer (*Capreolus capreolus*). Sex-, age- and individual-related variations. *Comptes Rendus de l'Académie des Sciences Serie III - Sciences de la Vie*, **322**, 271-279.

Riede, T. & Fitch, T. (1999). Vocal tract length and acoustics of vocalization in the domestic dog (*Canis familiaris*). *Journal of Experimental Biology*, **202**, 2859-2867.

Riede, T., Mitchell, B. R., Tokuda, I. & Owren, M. J. (2005). Characterizing noise in nonhuman vocalizations: Acoustic analysis and human perception of barks by coyotes and dogs. *Journal of the Acoustical Society of America*, **118**, 514-522.

Rubin, P. & Vatikiotis-Bateson, E. (1998). Measuring and modeling speech production. In: *Animal Acoustic Communication* (Ed. by S. L. Hopp, M. J. Owren & C. S. Evans). New York: Springer-Verlag.

Sayigh, L. S., Tyack, P. L., Wells, R. S., Solow, A. R., Scott, M. D. & Irvine, A. B. (1999). Individual recognition in wild bottlenose dolphins: A field test using playback experiments. *Animal Behaviour*, **57**, 41-50.

Theberge, J. B. & Falls, J. B. (1967). Howling as a means of communication in timber wolves. *American Zoologist*, **7**, 331-338.

Titus, K., Mosher, J. A. & Williams, B. K. (1984). Chance-corrected classification for use in discriminant analysis: ecological applications. *American Midland Naturalist*, 111, 1-7.

Tooze, Z. J., Harrington, F. H. & Fentress, J. C. (1990). Individually distinct vocalizations in timber wolves, *Canis lupus*. *Animal Behaviour*, **40**, 723-730.

314

Walcott, C., Evers, D., Froehler, M. & Krakauer, A. (1999). Individuality in "yodel" calls recorded from a banded population of common loons, *Gavia immer*. *Bioacoustics*, **10**, 101-114.

Weiss, D. J., Garibaldi, B. T. & Hauser, M. D. (2001). The production and perception of long calls by cotton-top tamarins (*Saguinus oedipus*): Acoustic analyses and playback experiments. *Journal of Comparative Psychology*, **115**, 258-271.

Wiley, R. H. & Richards, D. G. (1978). Physical constraints on acoustic communication in the atmosphere: Implications for the evolution of animal vocalizations. *Behavioral Ecology and Sociobiology*, **3**, 69-94.

Yin, S. & McCowan, B. (2004). Barking in domestic dogs: context specificity and individual identification. *Animal Behaviour*, **68**, 343-355.