A POTENTIAL TOOL FOR SWIFT FOX (*VULPES VELOX*) CONSERVATION: INDIVIDUALITY OF LONG-RANGE BARKING SEQUENCES

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Vocal individuality has been found in a number canid species. This natural variation can have applications in several aspects of species conservation, from behavioral studies to estimating population density or abundance. The swift fox (*Vulpes velox*) is a North American canid listed as endangered in Canada and extirpated, endangered, or threatened in parts of the United States. The barking sequence is a long-range vocalization in the species' vocal repertoire. It consists of a series of barks and is most common during the mating season. We analyzed barking sequences recorded in a standardized context from 20 captive individuals (3 females and 17 males) housed in large, single-pair enclosures at a swift fox breeding facility. Using a discriminant function analysis with 7 temporal and spectral variables measured on barking sequences, we were able to correctly classify 99% of sequences to the correct individual. The most important discriminating variable was the mean spacing of barks in a barking sequence. Potential applications of such vocal individuality are discussed.

Key words: animal communication, Canidae, conservation, individuality, swift fox, vocalization, *Vulpes velox*

Identifying and discriminating among individual animals in a population can have important applications in species conservation. McGregor and Peake (1998) give 3 general reasons for the importance of individual identification in conservation biology: validation of estimates of population size and monitoring techniques, gaining detailed information about life history, and assessing whether certain types of individuals in a population (e.g., females, juveniles, floaters, etc.) have specific needs that should be considerations in determining management priorities. To identify individuals, animals are often captured and marked for later reidentification with radiocollars, ear tags, dyes, fur shaving, and so on. Valu-

able information can be gathered by capturing individual animals, but capture is sometimes not feasible (e.g., protected species, large geographic scale, cost) or could reduce an animal's fitness (Cypher 1997). Naturally occurring individual variation offers an alternative to marking or identification by capture and handling (Gese 2001). Individual discrimination using vocal characteristics is a noninvasive method that has received much attention in bioacoustics and the behavioral sciences and should be especially advantageous in certain situations (e.g., for nocturnal animals).

Spontaneous vocalizations or vocalizations elicited by playback frequently have been used to localize, attract, or survey individuals or species that might otherwise be

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difficult to detect or approach; examples are coyotes (*Canis latrans*) and timber wolves (*C. lupus*—Gaines et al. 1995), odontocete whales (Leaper and Scheidat 1998), lions (*Panthera leo*) and spotted hyenas (*Crocuta crocuta*—Ogutu and Dublin 1998), neotropical bats (O'Farrell and Miller 1999), and forest raptors (Gosse and Montevecchi 2001). It might also be possible to obtain information about individuality, age, reproductive state, sex, and so on, but relatively little research on these applications has been carried out. Individually distinctive vocalizations have been documented frequently in, for example, vocalizations of birds (marbled frogmouth [*Podargus ocellatus*]—Jones and Smith 1997; greater flamingo [*Phoenicopterus ruber*]—Mathevon 1997; corncrake [*Crex crex*]—Peake et al. 1998) and mammals (timber wolf—Tooze et al. 1990; barbary macaque [*Macaca sylvanus*]—Hammerschmidt and Todt 1995; Arctic fox [*Alopex lagopus*]—Frommolt et al. 1997; dhole [*Cuon alpinus*]—Durbin 1998; fallow deer [*Dama dama*]—Reby et al. 1998). Vocalizations used have most often been associated with territoriality, mating, and maintaining intraspecific contact—situations in which it could be beneficial for vocalizing animals to broadcast information about individual identity (Bradbury and Vehrencamp 1998).

The swift fox (*Vulpes velox*) is a small canid native to the grasslands of North America. Due to serious population declines over much of its northern range, the species was reintroduced in Canada beginning in the early 1980s; in Canada it is currently considered endangered by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC, in litt.). In the United States, where the swift fox does not have federal protection, the species' status by state is extirpated, endangered, threatened, or fur bearer (R. Kahn et al., in litt.). Presence-or-absence surveys of distribution have revealed that the swift fox is currently present over about 40% of its historical range in the United States (Clark 2001).

This information is useful, but data on density and abundance are lacking for United States populations, making it difficult to monitor population trends (C. G. Schmitt, in litt.). In their 1999 annual report, the Swift Fox Conservation Team reiterated the need for survey techniques that will improve estimates of densities or counts and to evaluate current techniques (C. G. Schmitt, in litt.). Discrimination among individuals should enable improvements to methods for estimating numbers and densities and benefit the evaluation of survey methods.

Swift foxes of both sexes utter a long-range vocalization, the barking sequence, which also has been termed the mating and territorial call (Avery 1990) and lubricious bay (K. Weagle and C. Smeeton, in litt.). It is comprised of a series of barks (Fig. 1). In captive foxes, observed sequences contain 3–15 barks (6.5 ± 0.43 *SE*) uttered in rapid succession (S. Darden, in litt.) and are used mainly during the mating season (S. Darden, in litt.; K. Weagle and C. Smeeton, in litt.). In the swift fox and other fox species, the barking sequence is thought to be a contact vocalization for members of a social unit and is associated with territoriality and mating (kit fox [*V. velox (macrotis)*] "lone-some call"—Egoscue 1962; red fox [*V. vulpes*] "barking stanza"—Tembrock 1963; swift fox "mating/territorial call"—Avery 1990; Arctic fox "barking-series"—Frafjord 1995). Furthermore, swift foxes in the wild have been observed to respond vocally to barking sequence playback (W. C. Harris and S. M. McAdam, in litt.).

Auditory monitoring of recordings and visual inspection of spectrograms of swift fox barking sequences suggest individuality (Fig. 1). If barking sequences exhibit individuality at the quantitative level, the vocalizations could be used as a tool in swift fox management and research. In this study, we used a multivariate quantitative analysis of barking sequences recorded in a controlled social context to investigate the po-
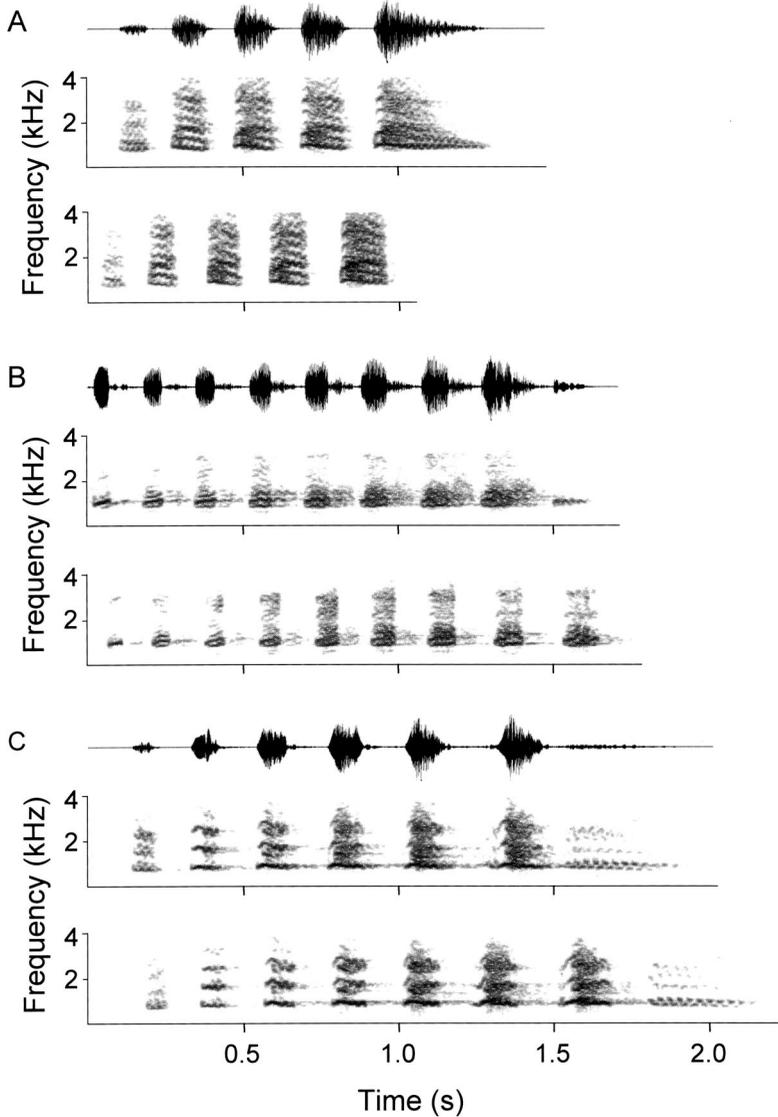
FIG. 1.—A, B, and C) Barking sequences of swift foxes (*Vulpes velox*). Sequences from 3 foxes, 2 sequences each, illustrating within- and between-individual variation (waveform above, spectrogram below, for uppermost sequence of each individual). The lowest and most energy-rich frequencies are represented in the spectrograms (0–4 kHz). (Avisoft SASLab Pro software, version 3.91: Hamming window, 512-point FFT, 100% frame size, 87.5% overlap; 43 Hz and 2.9 ms resolution.)

tential for using the barking sequence as an individual discrimination tool.

MATERIALS AND METHODS

Data collection.—Barking sequences were recorded in February–March 2000 and 2001 at a captive breeding facility near Cochrane, Alberta, Canada (51°12′N, 114°27′W). These periods coincided with the time of year when courtship behavior and fertilization are observed in the captive population (February–April). Recordings were made from a canvas observation hide placed 2–3 m from the perimeter of each fox enclosure between sunset and sunrise (approximately 1600 and 0700 h, respectively), which is

when the foxes were most active and when >90% of the barking sequences were produced in a 24-h period (Darden 2002). Foxes were housed in pairs in each enclosure (15 enclosures, each ~200 m^2 in size) and were visually isolated from adjacent neighbors by a plywood barrier 1 m high. Eleven foxes (8 males and 3 females) observed over the 2 years were included in the study. Recordings were made with a directional microphone (AT815b, Audio-Technica Ltd., Leeds, England) and a digital audio tape recorder (TCD-D8, Sony Corporation, Tokyo, Japan). Recording sessions were initiated on nights with little to no wind or precipitation and temperatures of −25 to +5°C. Additional recordings of 9 foxes in the colony made by the Cochrane Ecological Institute, Alberta, Canada, in 1995 (February–March) were also analyzed. These recordings were made on cassette tapes (ECM-909A microphone and WM-D6C Professional Walkman, Sony Corporation, Tokyo, Japan). The foxes sampled in the study included 3 females and 17 males from 18 mated pairs and were between 1 and 11 years old. There are disproportionately more males in the sample because they called more frequently than females over the course of an observation session and were thus more likely to be recorded. Also, sequences of calling females often overlapped other foxes, making more of their recordings unusable (Darden 2002).

We considered the foxes to be in a controlled social setting because of the way they were housed (pairwise). In this setting, all the pairs had vocal and olfactory contact with other pairs, but there could be no physical intrusions by neighboring foxes, and members of a mated pair were always close enough to maintain visual contact. To further reduce the number of confounding factors, criteria were implemented to select sequences for analysis. Sequences were uttered in 2 general contexts: while facing or approaching the mate (which we termed ''directed at mate'') and while investigating or standing alert and facing the pen's perimeter (''not directed at mate''). Superficially, the sequences in these 2 contexts only differed in overall amplitude (barking sequences in the not-directed-at-mate context were of a noticeably greater amplitude) and in the other vocalizations emitted immediately before or after (close contact calls were often emitted in association with the directed-at-mate barking sequence). Further-

more, the rate of calling appeared to be influenced by female reproductive state (Darden 2002). Therefore, only sequences not directed at the mate and sequences recorded before female conception were used to control for possible motivational and physiological factors.

Sound analysis.—Recordings were filtered with an analog filter (3550, Krohn Hite Inc., Avon, Massachusetts—150–8,000 Hz, 24 dB/octave) and stored as individual wave files sampled at 22,050 Hz. They were then inspected spectrographically for signal-to-noise ratio, overlap from other callers, and blurring by echoes. The first 10 high-quality barking sequences (i.e., high signal-to-noise ratio, low blurring, and no overlap from other callers) from each of 17 individuals were analyzed. Another 3 of the 20 individuals only had 8 sequences that were deemed usable; this gave a total of 194 sequences for use in the study. Each sampled sequence was spaced anywhere from a few minutes to 3 days from the next sequence, which was possible because observed sequences were not emitted in bouts (i.e., there was always a change in behavior between uttered sequences).

Temporal measurements were made from spectrograms. High–time resolution spectrograms (0.73 ms resolution) of each barking sequence were created with Avisoft SASLab Pro software, version 3.91, (R. Specht, http://www.avisoft.de), and temporal measurements were made with spectrograms and waveforms pictured simultaneously for increased accuracy. Element and interelement durations and element cadences were calculated from the measurements (Fig. 2). Sequence-based variables were also computed: sequence duration, total (sum) element duration divided by sequence duration (duty cycle), the number of elements divided by the sum of within-sequence element cadences (rate of barking), and the mean and within-sequence variable pattern (variance) of element parameters in a sequence. This gave a total of 12 temporal parameters. A single observer made all the measurements with a test of measurement consistency over time showing consistency ($r = 0.9997$, $n = 122$, *d.f.* = 120) and small measurement error (0.5 ± 0.12 ms).

Several problems are associated with accurately quantifying spectral parameters of complex mammalian vocalizations, and more commonly used measurements, such as fundamental and dominant frequencies, could not be reliably
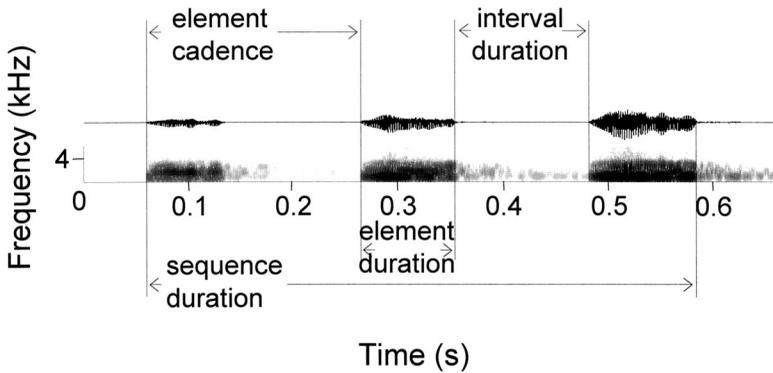
FIG. 2.—Temporal measurements and calculations from the waveform and high–time resolution spectrogram of a swift fox (*Vulpes velox*) barking sequence. (Hamming window, 128-point FFT, 25% frame size, 87.5% overlap; 172 Hz and 0.73 ms resolution.)

quantified for every bark due to the complex acoustic structure of each bark (Darden et al. 2002). Instead, measurements related to global frequency structure were taken in a custom-made program written by S. B. Pedersen in Mathcad 2001 software (Darden et al. 2002). The program generates a smoothed spectrum of the signal's Fourier components with a windowed autocorrelation function and can be used to calculate energy distributions within a frequency range. Measurements from this type of spectrum will not be affected by erratic peaks resulting from the signal's chaotic structure and will represent the entire signal rather than parts of the signal. In the analysis, the spectral variables were measured from the energy density spectrum (Hann, 1,024 points, frequency resolution = 22 Hz) of the windowed autocorrelation function (window width = 3.9 ms) of each element (Fig. 3). Variables were the lower, center, and upper frequency distributions (25th, 50th, and 75th percentile energy distributions, respectively) and lower and upper frequency limits (2.5th and 97.5th percentile energy distributions, respectively). The measurements were made in the 200–8,000 Hz range to include energy at
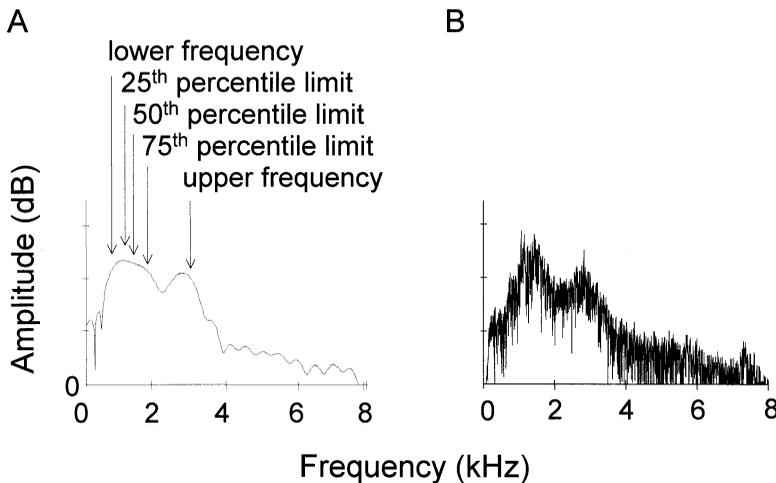

FIG. 3.—A) Smoothed energy–density spectrum created from the windowed autocorrelation function of a base element, illustrating the measurements taken for the spectral description of single elements in a swift fox (*Vulpes velox*) barking sequence (see text). B) Unsmoothed spectrum shown for comparison.

higher frequencies that can result from formant structure and that minimize low-frequency environmental noise. The 25th to 75th percentile frequency distribution bandwidth and frequency distribution range (2.5th to 97.5th percentile) were calculated from these measurements. Sequence variables included the mean and variance of variables within a sequence. This resulted in a total of 21 spectral parameters.

Root mean square values of each element in a sequence were calculated with SIGPRO software, version 2.0 (S. Pedersen). Element amplitudes were then calculated so that each bark received a value relative to the highest amplitude bark in the sequence. There was just one sequence-derived variable (amplitude variance of the elements in a sequence), for a total of 2 amplitude variables.

The barks, or elements, of a sequence are relatively uniform except for barks at the beginning and end of a sequence, which often vary greatly in amplitude and duration compared to the central barks of a sequence (Fig. 1). To standardize our sample of barks, a subset was selected from each sequence according to an objectively defined criterion. Using the single-variable distribution analysis described by Tolkamp and Kyriazakis (1999) for defining bouts, barks from all individuals were pooled and subsampled such that we did not include the following: barks at the beginning of a sequence with an amplitude ≤ -19 dB relative to the bark in the sequence with the highest amplitude and barks at the end of a sequence with a relative amplitude ≤ -12 dB, or a duration ≥ 0.25 s, or both (Darden 2002). All references to ''the sequence'' in the remainder of this section refer to the sequence of subsampled elements.

Statistical analysis.—Discriminant function analysis was used to investigate how, and to what degree, individual barking sequences differed. All variables were transformed (Box–Cox transformation—Sokal and Rohlf 1995) to approach univariate normality and homoscedasticity. One variable was excluded from the analysis because it diverged from a normal distribution. Before the discriminant function analysis was carried out, variables were selected that exhibited greater between- than within-individual variation (univariate analysis of variance, ANOVA) and low data redundancy (<0.7 correlation). The ANOVA (PROC GLM in SAS/Stat, version 6.12) was nested to control for the possible ef-

fects of age, sex, and differing recording conditions in 2000–2001 and 1995 (recordist and equipment).

The selection procedure resulted in 7 variables that were used in the discriminant function analysis, including 4 temporal variables (Fig. 2): sequence duration, mean element cadence of a sequence, element cadence variance of a sequence, and duty cycle. The remaining 3 were spectral variables (Fig. 3): mean element center frequency (50th percentile) of a sequence, mean element 25th to 75th percentile frequency distribution bandwidth of a sequence, and 25th to 75th percentile frequency distribution bandwidth variance within a sequence (Table 1). With the final variables selected, a discriminant function analysis of sequences grouped by individual fox was conducted in SAS/Stat, version 6.12, with a preliminary test for the equality of covariance matrices. Group covariance matrices were not equal ($\chi^2 = 945$, *d.f.* $= 532$, $P < 0.0001$) and the classification of barking sequences in the discriminant function analysis was therefore based on a quadratic classification rule using within-group covariance matrices (McGarigal et al. 2000; Rencher 1995). The discriminant function analysis was then validated by a randomization procedure, in which correct classification due to chance was averaged from discriminant function analyses conducted on 1,000 randomized, within-variable permutations of the data set (McGarigal et al. 2000; Solow 1990).

The importance of variables in discriminating among individuals was investigated using a potency index and a post hoc Tukey means test. With ≥ 1 canonical function, the potency index can be an index of the relative discriminatory power of each variable on the basis of its correlation with each of the canonical functions and the function's eigenvalue (Perreault et al. 1979 in McGarigal et al. 2000). The Tukey means test (PROC GLM, TUKEY MEANS; SAS/Stat, version 6.12) was used with the objective of counting how many pairs of individuals differed in variable measurements in a pairwise comparison of means.

RESULTS

The 7 canonical functions defined in the discriminant function analysis had canonical correlations significantly different from 0 (i.e., significant correlation with the mul-

TABLE 1. Summary statistics by individual (ID) and for the total sample (totals), results of 1-way ANOVAs (R^2, F) across individuals for selected variables ($P < 0.0001$ for each variable), and variable potency index (PI) and total significant differences in Tukey comparisons (Tukey; see text) for variables included in the discriminant function analysis of swift fox (*Vulpes velox*) barking sequences. Identification numbers refer to the same individuals as in Fig. 4.

ID	Cadence[a] (ms) $\bar{X}$	SE	Duty cycle (ms) $\bar{X}$	SE	Center frequency[a] (Hz) $\bar{X}$	SE	Bandwidth[a,b] (Hz) $\bar{X}$	SE	Bandwidth variance[a,b] $\bar{X}$	SE	Sequence duration (ms) $\bar{X}$	SE	Cadence variance[a] $\bar{X}$	SE
1	228	2	608	6	1,460	10	650	20	0.080	0.016	1,118	44	0.0011	0.0002
2	211	4	596	19	1,150	20	400	10	0.001	0.000	936	36	0.0010	0.0002
3	215	3	606	17	1,130	50	730	80	0.023	0.007	1,084	57	0.0008	0.0001
4	229	3	504	9	1,120	40	550	60	0.057	0.025	1,317	47	0.0009	0.0002
5	343	10	603	23	1,540	80	680	50	0.045	0.019	858	88	0.0043	0.0012
6	246	6	521	14	1,100	10	370	10	0.003	0.001	909	72	0.0027	0.0010
7	189	2	468	19	1,140	40	420	10	0.003	0.001	1,049	76	0.0001	0.0000
8	237	5	384	23	880	20	310	10	0.001	0.001	1,341	47	0.0017	0.0004
9	215	3	476	4	880	10	330	10	0.001	0.000	1,166	53	0.0013	0.0003
10	249	6	523	9	1,220	20	440	10	0.003	0.000	964	53	0.0029	0.0005
11	228	5	591	13	1,490	40	540	20	0.004	0.002	990	47	0.0016	0.0005
12	232	5	412	11	1,320	70	580	50	0.031	0.012	1,552	86	0.0011	0.0003
13	229	4	513	24	1,380	50	620	90	0.062	0.026	1,055	68	0.0029	0.0006
14	230	2	564	27	1,360	30	500	40	0.010	0.005	1,055	43	0.0006	0.0001
15	182	2	436	21	1,110	30	340	10	0.002	0.001	1,601	92	0.0004	0.0001
16	243	4	554	7	1,350	50	740	30	0.020	0.004	1,219	55	0.0028	0.0008
17	260	3	376	14	1,170	50	630	40	0.050	0.014	1,357	34	0.0021	0.0005
18	201	5	480	5	1,350	50	470	30	0.015	0.005	1,114	56	0.0014	0.0005
19	216	6	546	20	1,100	60	510	60	0.049	0.011	1,066	58	0.0018	0.008
20	208	3	528	5	1,030	30	370	30	0.003	0.002	1,037	44	0.0013	0.0001
Totals	229	8	513	17	1,210	40	510	30	0.023	0.006	1,146	56	0.0016	0.0016
R^2	0.84		0.71		0.70		0.66		0.58		0.54		0.54	
F[c]	48.03		22.78		22.30		17.60		11.34		11.94		9.96	
PI	0.28		0.14		0.13		0.11		0.07		0.06		0.06	
Tukey	107		94		98		79		68		56		34	

[a] On the basis of measurements from each element of the sequence.
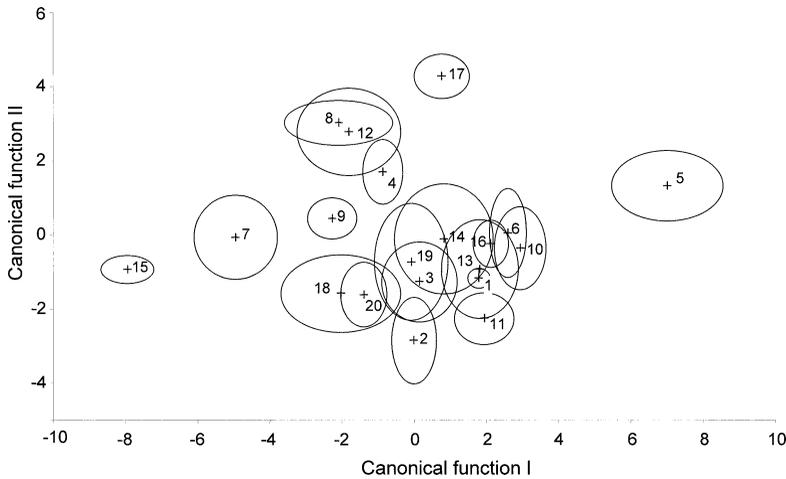[b] 25th to 75th percentile energy distribution.
[c] d.f. = 19, 174.

Fig. 4.—Plot of mean group scores of the first 2 canonical functions (74.8% of the variation described by all 7 functions) of the discriminant function analysis of the individuality of swift fox (*Vulpes velox*) barking sequences with 7 variables and 20 individuals. (+) Centroids; ellipses, mean ± 1 *SD*.

tivariate data set, $P < 0.0001$) and were retained for further analysis. Most (99%) of the barking sequences were classified to the correct individual. Correct classification for each individual was 90%–100%. The randomization procedure revealed a 64.1% ± 0.13% (*SE*) correct classification due to chance. Only 1 of the 1,000 data sets had a correct classification greater than or equal to the original data set, and our results therefore differ from those expected due to chance (64.1%) at $P = 0.001$.

The first 4 canonical functions had an eigenvalue >1 and describe $>90\%$ of variation in the data set described by all 7 functions. The first 2 functions are plotted against each other in Fig. 4. The first function accounts for 55.0% of the described variation and has a correlation of 0.95 with the multivariate data set (canonical correlation). The second canonical function describes 19.8% of the variation and has a canonical correlation of 0.89.

Inspection of calculated potency indexes reveals that the best (''most potent'') discriminating variable is the mean element cadence of a sequence followed by the duty cycle and the mean element center frequency (Table 1). These values can be compared

with the results of the post hoc Tukey means test. There was a total of 190 pairwise Tukey tests for each variable, and the total number of comparisons that showed significant differences ($P < 0.05$) are given in Table 1. The mean element cadence of a sequence, duty cycle, and mean element center frequency variables had the greatest number of significant differences, with more than half the comparisons being significant. The mean element cadence of a sequence was again the best discriminating variable. Some pairs did not differ for some variables, but none was equal for all variables.

DISCUSSION

The barking sequences of swift foxes in this study exhibit high individuality. Among the canids, vocalizations with individual distinctiveness have been documented in timber wolves (Tooze et al. 1990), Arctic foxes (Frommolt et al. 1997), and dholes (Durbin 1998) by quantitative multivariate analysis. Although it is difficult to compare studies directly because of varying techniques, variables and sample sizes, it seems that the degree of individual distinctiveness of the foxes in this study is

relatively high. The same is true if we compare our results with those of mammalian species from other taxonomic groups, including barbary macaques (Hammerschmidt and Todt 1995) and fallow deer (Reby et al. 1998).

The mean cadence of barks in a sequence was the most important discriminating variable in our analysis. A sequence's duty cycle, which is essentially the ratio of sound to silence in the sequence, followed mean cadence in terms of discrimination potency. The mean center frequency of barks in a sequence was likewise important in discriminating among individuals and was the best discriminating spectral variable. Durbin (1998) also found element cadence to be a top discriminating variable in dhole whistle calls and the top temporal variable. The spectral variable describing the most variation among individual dholes was the frequency of greatest amplitude in a whistle (Durbin 1998). Timber wolf howls analyzed by Tooze et al. (1990) were discriminated primarily by spectral variables, as were Arctic fox barking sequences analyzed by Frommolt et al. (1997). In the wolves, spectral variables related to fundamental frequency and frequency variation about a central band were the most important variables (Tooze et al. 1990). We did not use these types of variables in our study because of the problems associated with measuring them reliably in the relatively noisy barks of the foxes. However, they might be important in individual discrimination. For the Arctic foxes, the most potent spectral variables described the distribution of energy within barks (Frommolt et al. 1997).

Use of captive foxes in this type of study has the advantage of recording individuals in a standardized social context and, thus, controls for variation due to certain contextual differences. However, there may be unknown effects of captivity on vocal individuality. The captive foxes are most likely more closely interrelated than individuals in a wild population and are obviously spaced much more closely. If the structure of bark-ing is predominantly genetically determined or if the foxes are imitating neighboring foxes that remain in captivity for several generations, captives should exhibit less vocal individuality than wild foxes. This would make the results of our study conservative. However, an opposite effect of captivity might occur if it is advantageous to be individually distinctive, with foxes actively changing their barking sequences relative to others in the population. The captives would then express greater individuality than wild foxes because they can probably hear more individuals in a given mating season than can wild foxes. In that case, our results would overestimate individuality in the wild.

If individual variation similar to that observed in captivity does occur in wild foxes, it might be possible to use the barking sequence to discriminate reliably among unknown wild individuals, with several considerations. First, the reliability of measured variables needs to be evaluated in terms of the length of time over which within-individual consistency is maintained and in terms of the effects of recording conditions. Barking sequences in this study were sampled over a period of up to 3 days. However, within-individual variation probably increases with increasing recording interval length (Darden 2002). Although swift foxes generally occupy areas of flat to rolling short-grass prairie and pastureland where long-range vocalizations should be minimally attenuated and have limited reverberation (e.g., low absorption, scattering, and reflection from vegetation), distortions will occur, both in the frequency and temporal domain during sound transmission (e.g., boundary effect and turbulence from wind and temperature gradients—Wiley and Richards 1982). Some variables will be more robust to differing conditions than others. For example, due to differential attenuation of frequencies dependent on distance, it is possible that certain temporal measurements, such as cadence, from recordings made under varying field condi-

tions can be more reliably compared than any of the spectral measurements used in our analysis (Embelton 1996). In fact, in our study, certain variables were not considered for analysis because of the potential for high variation due to recording conditions (e.g., frequency range and upper frequency measures). Transmission experiments should be carried out in natural swift fox habitat to quantify barking transmission properties and reliability of measured variables.

Investigation of meaning and context of the swift fox barking sequence should also be carried out before it can be sensibly applied as a tool in conservation research (Gaines et al. 1995; Legare et al. 1999; McGregor et al. 1999). Call and response rates or probabilities might vary seasonally or for different members of the population, which would bias samples. For example, in coyotes, where the howl appears to have a territorial spacing function, howling rates vary with seasonal, spatial, and social factors (Gese and Ruff 1998), and playback of conspecific loud calls to lar gibbons (*Hylobates lar*) elicits different responses from individuals depending upon the receiver's sex, the playback call's location, and the caller's identity (Raemakers and Raemakers 1985). Furthermore, behaviors associated with the vocalization must be investigated to avoid any adverse effects of the playback procedure (Baptista and Gaunt 1997).

From the results of this study, it seems that there is potential for the application of the barking sequence as a tool in swift fox conservation and management. Barking sequences can be used, for example, to add information to behavioral studies where it is not possible or desirable to capture or mark certain or all individuals in a population, to evaluate and supplement survey techniques currently in use for the swift fox that do not involve individual identification (e.g., scent station, track or scat deposition surveys), or to provide an independent method of counting individuals. Several areas of research involving swift fox long-

range communication, barking sequence function, and mating and territorial behavior need to be investigated to provide estimates of the accuracy and usefulness of such applications of the barking sequence. Knowing the potential coding of information in the barking sequence can aid in such studies.

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