

Individually distinct vocalizations in timber wolves, *Canis lupus*

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Abstract. Howls were recorded from seven captive wolves temporarily individually isolated from their pack-mates. Sound spectrograms of these recordings were then digitized and 14 variables were measured and subjected to multivariate statistical analyses. Both principal components analysis and discriminant analysis indicated that individuals could be reliably discriminated primarily on the basis of the fundamental frequency of howls and the variability of frequency within howls. The significance of the presence of vocal signatures in this long distance vocalization is discussed in the context of wolf social organization.

Individually distinct vocalizations, or vocal signatures, have been identified in many social mammals (Symmes et al. 1979; Gould 1983; Conner 1985). Although few studies of other mammals have addressed the question of vocal signatures and the functional significance of such among adults, many studies have examined this relationship between mother and young. The importance of vocal recognition, particularly in colony breeding mammals such as elephant seals, *Miroungua angustirostris* (Petrinovich 1974), and bats (Thomson et al. 1985; Gelfland & McCracken 1986), and those in which mother and young are frequently separated, such as reindeer, *Rangifer tarandus* (Espmark 1975), is widely recognized. Recently, vocal recognition between mother and infant has also been demonstrated in racoons, *Procyon lotor*, a solitary living species (Sieber 1986). Vocal signatures among adults have been demonstrated in several species of primates (Cheney & Seyfarth 1980; Snowdon & Cleveland 1980; Macedonia 1986), pikas, *Ochotona princeps* (Conner 1985) and marine mammals (Shiple et al. 1986; Tyack 1986).

Wolf howls function both to decrease and increase distance between communicating individuals (Mech 1970) and, as such, might be expected to provide information on individual identity. They can be broadly described as loud, continuous, tonal sounds with a fundamental frequency of between 150 and 780 Hz (Theberge & Falls 1967; Harrington & Mech 1978). Authors disagree, however, on the presence of vocal signatures in wolf howls (presence: Theberge & Falls 1967; Klinghammer

& Laidlaw 1979; absence: Kolenosky & Johnson 1967) and howls of related canids (absence: Lehner 1978). This controversy is primarily due to the highly variable nature of these long distance vocalizations, both within and between individuals. In this study we provide evidence for the presence of signature information in howls of timber wolves.

METHODS

Study Animals

We recorded three male and three female timber wolves, located at the Dalhousie (Atlantic Provinces) Animal Behaviour Research Facility, Shubenacadie, Nova Scotia, and one female timber wolf at Carlos Avery Game Farm, Forest Lake, Minnesota. All animals were housed outside all year round and maintained on a diet of road-killed white-tailed deer, *Odocoileus virginianus*, supplemented with commercial dog food and a vitamin–mineral supplement.

Equipment

Original audio recordings were made on Sony or TDK SX90 cassette tapes using a Sony Walkman Pro (WM-D6; flat audio frequency response 40 Hz–15 kHz) or a Sony TCM-5000 sound-activated cassette recorder (flat audio frequency response in sound-activated mode 300 Hz–5 kHz; otherwise 90 Hz–9 kHz). Either a Sennheiser MKH 816T or a JVC M510 shotgun unidirectional microphone was used. Individuals were isolated from their pack-mates and recorded between November 1986 and February 1987 and between June and July 1987. Isolation ensured a large sample of high-quality

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Table I. List and description of variables used in sound analysis

Modifier variables	Harm	Maximum number of harmonics to 2000 Hz
	Dside	Duration (s) of non-harmonically related frequency sidebands
Pitch variables	Meanf	Mean frequency of the fundamental as calculated from frequency at 0.05-s intervals over the duration
	Maxf	Maximum frequency of the fundamental
	Minf	Minimum frequency of the fundamental
	Endf	Frequency at the end of the fundamental
	Range	Range of the fundamental (Maxf-Minf)
Shape variables	Cofm	Coefficient of frequency modulation of the fundamental*
	Cofv	Coefficient of frequency variation of the mean frequency†
	Changf	Number of rises and falls in pitch of the fundamental (excluding the initial rise)
	Abrupt	Number of abrupt changes in pitch of the fundamental (> 25 Hz)
	Posmax	Position in the howl at which the maximum frequency occurs, (time of Maxf)/Dur
	Posmin	Position in the howl at which the minimum frequency occurs, (time of Minf)/Dur
	Dur	Duration of the howl (measured at the fundamental)

*The average per cent change in frequency every 0.05 s.

†See Fig. 1.

recordings from individuals in a similar context. No recordings were made during heavy rain or snow, or if wind velocity was greater than 5 m per second.

Sound Analysis

All high-quality recordings were copied from cassette to 6.4-mm tape for sound analysis using a Kay Digital Sona-graph Model 7800. We determined that a range of 2000 Hz and an effective band-filter width of 37.5 Hz provided the best temporal and frequency resolution for analysis. Only one of 25 randomly selected spectrographs contained detectable harmonics above 2000 Hz.

We chose a random sample of numbered spectrographs from each individual using a random number generator (Systat), except for small samples ($N < 30$) when we used the entire sample. We recorded two 'modifier', four 'pitch' and seven 'shape' variables on each howl (Table I, Fig. 1). Continuous variables were measured using a Hipad digitizing tablet and stylist pen interfaced with a Compaq microcomputer. To minimize measurement error, we sampled time and frequency (Hz) from the highest harmonic that was clearly visible along the length of the howl, and divided by the appropriate factor to yield the value of the fundamental. We sampled at intervals of 0.05 along the entire length of the vocalization, beginning at 0.05 s. We tested the precision of this digitizing method both on very flat and highly modulated

howls and found it to be precise on an average of 3.5% (average coefficient of variation for repeated measures ($N = 10$) of all continuous variables on three different howls).

Statistical Analysis

All analyses were computed using the Systat statistical package. We used principal components analysis to reduce the original variable set to a smaller set of uncorrelated variables (Hair et al. 1978), followed by discriminant function analysis using the component scores from the principal components analysis as the raw data (Martindale 1980). We used an eigenvalue of 0.90 (6.5% of the variation in these data) as the cut-off for considering a component. Because discriminant function analysis is appropriate for analysis of two or more predefined groups (categorical variables) and several metrically scaled independent variables (Hair et al. 1978; Martindale 1980), we used it to determine whether there were significant differences between individual wolves (groups) that would allow discrimination, and to identify which characteristics, if any, were most important to this discrimination. While we are aware that the use of more than one howl per individual ('pseudoreplication') may weaken the statistical validity of the overall test, we feel that the use of an independent hold-back sample to test the robustness of our classification more than compensates for any such loss.

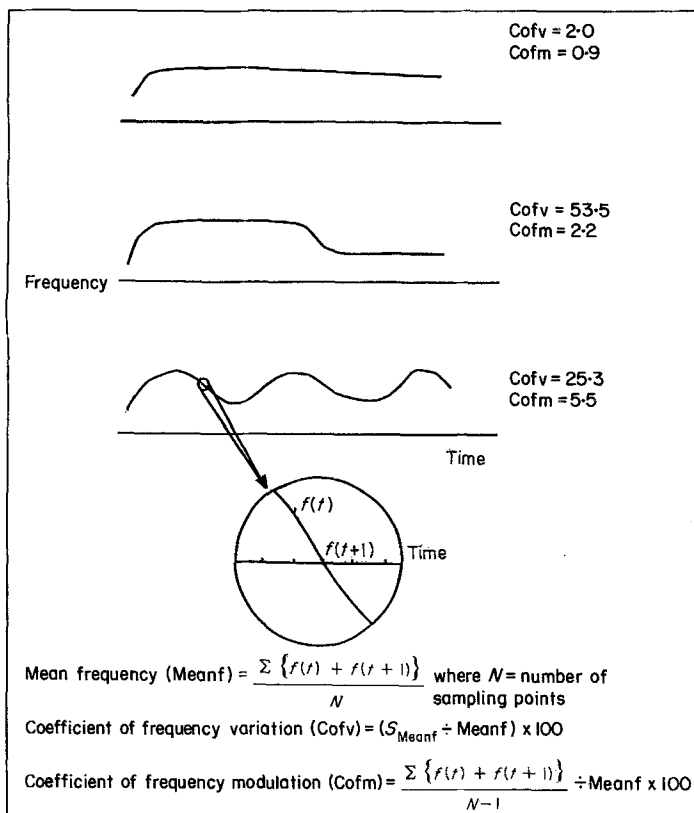


Figure 1. Illustration of measurements made on each howl, demonstrating differences and similarities in howls with high and low values for Cofv (coefficient of frequency variation around the mean) and Cofm (coefficient of frequency modulation: variation in frequency between samplings every 0.05 s). Although these howls all have the same mean frequency their shapes are very different, and this difference in shape is reflected in values of Cofv and CoFm.

RESULTS

Analysis of variability within and between individual wolves was performed on a sample of 308 howls from the seven individuals (C, D, G, J, R, T, 35). Discriminant functions were derived from a sample of 30 howls from each of six individuals ($N = 180$; wolf G was dropped from further analysis owing to small sample size); the rest of the howls ($N = 120$) were held back from the initial analysis and later used as an independent test of the success of the classification of the derived functions. Means and standard errors of the most important discriminating variables are shown for each individual, and for the combined sample, in Table II. Principal components analysis on the sample of 300 howls identified eight major components. The first component (fundamental frequency) explained 24.6% of the variability, and mean, maximum and

minimum frequency all explained a large proportion of the variance (eigenvalue > 0.9). The second component (range/modulation) explained 23.1% of the variability and range, coefficient of frequency variation, coefficient of frequency modulation and abrupt changes in frequency were all important. Subsequent components emphasized one variable only, and these were labelled accordingly.

Results of the discriminant function analysis using these eight component scores as the raw data identified the first component (fundamental frequency) as the most important discriminating variable (Table III). Shape (range/modulation) and the number of harmonics also contributed significantly to discrimination. The number of inflection points (change in frequency), duration of howls and the duration of sidebands were marginally significant, while the position of the minimum and

Table II. Mean \pm SE for selected howl parameters for each isolated wolf and the pooled sample ($N=308$)

Wolf*	Mean frequency	Maximum frequency	Minimum frequency	Range	Coefficient frequency variation	Coefficient frequency modulation	Duration	Harmonics
C $N=50$	366 \pm 4	388 \pm 5	326 \pm 5	62 \pm 4	6.1 \pm 0.3	0.9 \pm 0.0	4.3 \pm 0.1	2.8 \pm 0.2
D $N=56$	452 \pm 9	549 \pm 10	310 \pm 11	239 \pm 11	15.1 \pm 0.7	1.6 \pm 0.3	3.3 \pm 0.4	4.4 \pm 0.2
G† $N=8$	567 \pm 8	677 \pm 23	415 \pm 26	262 \pm 43	10.8 \pm 2.0	1.0 \pm 0.5	3.1 \pm 1.2	4.5 \pm 0.3
J $N=30$	670 \pm 8	749 \pm 16	542 \pm 21	207 \pm 26	9.2 \pm 0.8	1.1 \pm 0.1	1.1 \pm 0.2	4.3 \pm 0.6
R $N=59$	514 \pm 9	654 \pm 10	296 \pm 11	358 \pm 12	21.6 \pm 0.9	1.6 \pm 0.1	3.4 \pm 0.3	6.0 \pm 0.4
T $N=60$	604 \pm 6	693 \pm 6	416 \pm 13	277 \pm 13	11.5 \pm 0.9	1.2 \pm 0.1	2.7 \pm 0.2	3.8 \pm 0.5
35 $N=45$	328 \pm 8	418 \pm 13	165 \pm 8	251 \pm 12	5.9 \pm 0.8	2.1 \pm 0.2	2.4 \pm 0.3	3.9 \pm 0.6
All $N=308$	486 \pm 7	575 \pm 8	335 \pm 7	240 \pm 7	14.3 \pm 0.4	1.4 \pm 0.1	2.1 \pm 0.1	3.9 \pm 0.2

*C, G, J, 35: adult females; T: adult male; D, R: yearling males.

†This wolf was excluded from further analysis owing to small sample size.

Table III. Canonical loadings from discriminant function analysis; those 'variables' that loaded highest in each function are printed in bold type

	Functions				
	1	2	3	4	5
Canonical correlation	0.927	0.778	0.507	0.288	0.146
χ^2	558.5	229.1	71.1	20.4	3.7
df	40	28	18	10	4
P	0.0001	0.0001	0.0001	0.025	NS
Loadings					
Component label					
1 Fundamental frequency	0.739	-0.237	0.270	0.177	0.307
2 Range/modulation	0.126	0.629	-0.022	-0.238	-0.317
3 Position minimum frequency	-0.030	-0.059	0.142	-0.366	0.158
4 Duration	0.007	0.150	-0.292	0.662	-0.314
5 Duration of sidebands	-0.024	0.204	0.105	0.559	-0.486
6 Changes in direction	0.007	0.064	-0.464	0.134	0.410
7 Harmonics	-0.057	0.278	0.609	-0.026	0.527
8 Position maximum frequency	-0.015	0.220	-0.377	0.294	0.421

Fundamental frequency: includes mean frequency, maximum frequency, minimum frequency and end frequency. Range/modulation: includes range, coefficient of frequency variation, coefficient of frequency modulation and abrupt. The remaining labels correspond to abbreviations used in Table I.

maximum frequencies were unimportant (Table III). A plot of the first two discriminant functions (fundamental frequency and range/modulation) indicates little overlap among individuals (Fig. 2).

Separate evaluation of the relative amplitude of harmonics of howls, rather than simply the number of harmonics, added little information to individual identity, with the exception of wolf 35. The

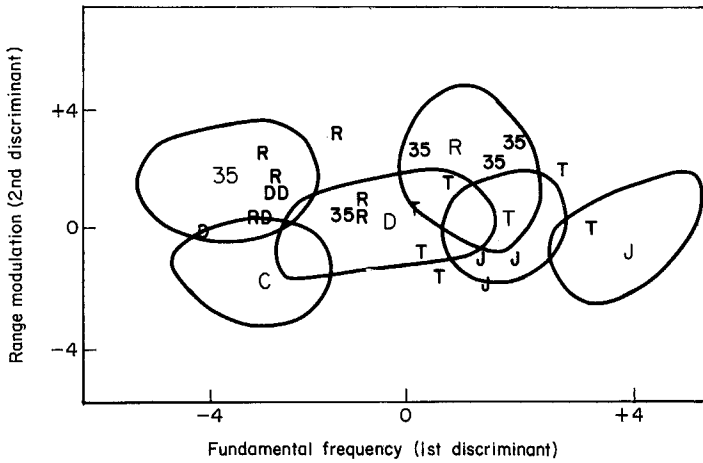


Figure 2. Plot of individuals' mean discriminant scores (group centroids) for the first two components. Discriminant 1 represents characteristics of the fundamental frequency of howls, and discriminant 2 represents range and modulation of howls. The trace outlines 90% of howl scores for each individual; howls that fell outside this trace are designated by respective wolf labels; C, J, 35: adult females; T: adult male; D, R: yearling males.

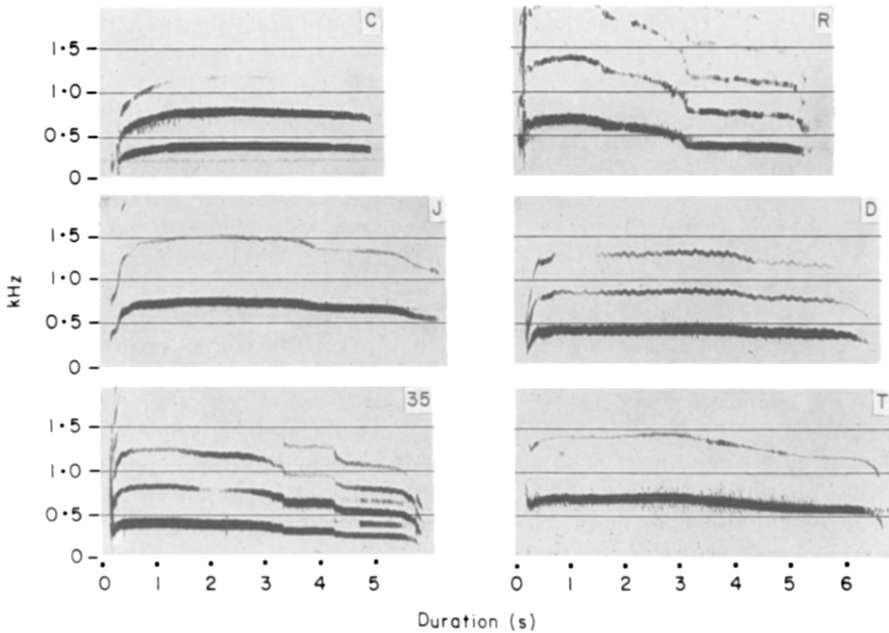


Figure 3. Sonographs of representative howls from the six individual wolves (C, J, 35: adult females; T: adult male; D, R: yearling males).

harmonic structure of her howls was very distinct from the howls of the other six wolves. Sixty-four per cent of wolf 35's howls with a fundamental frequency of 500 Hz or less contained more than two component harmonics, with the amplitude of the first and third harmonics greater than the second.

Successive harmonics of howls from the other wolves either gradually decreased in amplitude or were approximately equal (Fig. 3). The harmonic structure of howls from wolves D, C and T were all very similar, with relatively few harmonics (percentage of howls with two or fewer harmonics: D:

Table IV. Classification results from discriminant scores for combined analysis samples ($N=180$) and the unweighted hold-out sample ($N=120$)

Actual membership	Predicted group membership						Total	% Correctly classified
	C	D	J	R	T	35		
C	49	0	0	0	0	0	49	100
D	2	41	0	6	6	2	57	72
J	0	0	26	0	4	0	30	87
R	0	0	2	46	7	4	59	78
T	0	2	9	2	46	1	60	77
35	3	2	0	3	0	37	45	82
Total	54	45	37	57	63	44	300	82

C, J, 35: adult females; T: adult male; D, R: yearling males.

76%; C: 80%; T: 100%). Wolf R's howls, although richer in harmonic structure when below 500 Hz, were also characterized by decreasing amplitude in each successive harmonic.

How reliable is the discriminating ability of these howl characteristics? The classification success of the four significant functions was 86.5% for the sample of analysis howls ($N=180$) and 75.4% for an independent unweighted sample from four of the six individuals ($N=120$). Correct classification of individuals varied from 71.9% (D) to 100% (C; Table IV).

DISCUSSION

There were significant differences among the howls of individual wolves, which allowed individuals to be reliably discriminated using the structural features described in this analysis. Features of the fundamental frequency were most important to discrimination (maximum frequency, mean frequency). The variation around the mean frequency (coefficient of frequency variation) and the related variables, range of the fundamental and frequency modulation, were also important features.

Frequency components are important in a wide variety of mammalian species in which vocal signatures have been demonstrated (Gelfand & McCracken 1986; Macedonia 1986; Sieber 1986). The fundamental frequency (and richness of harmonic overtones) of vocalizations is largely determined by characteristics of individuals' vocal apparatus (such as glottal width, vocal chord length), and length and dimensions of the resonating 'tube' (from the chords to the lips; Keleman 1963;

Michelson 1983). These characteristics are probably relatively constant in adults, and therefore contribute to reliable discrimination between individuals over time. For example, the pitch profile of squirrel monkeys, *Saimiri sciureus*, is constant over a period of at least 2 years (Symmes et al. 1979). In addition, variability in the pitch of loud howls may be further restricted by the range of frequencies at which maximum amplitude is achieved, as maximum intensity is only achieved at the resonance frequencies of the sound radiator. The resonance frequencies can be controlled and varied by varying the tension of the radiator or the cross section of the vocal tract (Michelson 1983), and this range is likely to be very different for different individuals.

Immediate recognition of distant individuals could be important for wolves in several ways. Wolf packs are dynamic in the short term; individuals and small groups separate temporarily throughout the year (Mech 1970; Fritts & Mech 1981), and individuals in the process of dispersing from their natal pack make pre-dispersal forays from their natal area that lead them into alien territories (Van Ballenberghe 1983). The consequences of approaching alien wolves can be severe (Mech 1970; Fritts & Mech 1981); it would therefore be adaptive for lone individuals to differentiate between unfamiliar and familiar howls, and thus avoid potentially dangerous interactions. Theories of the dynamics of pack formation and splitting suggest that a wolf population is a mosaic of related and unrelated individuals (Mech 1970). Recognition of relatives as well as pack members may be important to dispersing individuals who are looking for a mate and territory while also avoiding aggression from alien packs and individuals. It may

therefore be fortuitous to recognize individuals with whom they have previously formed strong social bonds (e.g. older siblings who dispersed earlier; Mech 1970), and with whom temporary associations may be possible (Petersen 1977; Van Ballenberghe 1983). In addition, wolves could also identify and respond to changes in pack structure by identifying changes in the initial howls of choruses from neighbouring packs. Gibbons, *Hylobates lar*, avoid overlapping choruses of neighbouring gibbons, and may listen to introductory notes to identify the singer (Raemaekers & Raemaekers 1985), and wolves also will begin replying to choruses after the first single howls (Harrington & Mech 1979; Harrington 1986).

One might argue that discrimination of particular individuals is not essential. For example, Morton (1977) predicts that an animal's motivational state will be highly correlated with structural features of vocalizations such that affiliative sounds are higher pitched and more tonal, whereas aggressive sounds are relatively lower pitched and coarser. There is evidence that motivational-structural rules proposed by Morton apply to wolf howls (Harrington 1987). Thus, wolves could simply use information regarding the motivational state of the howler, and avoid 'aggressive sounding animals' and approach 'friendly sounding' ones. Information on motivational state could be assessed by evaluating the changing quality of howls within bouts (Harrington 1987). Initial howls in an exchange may represent an intermediate point on the aggressive-affiliative continuum, with the structure of subsequent howls changing to reflect more closely the animal's current motivational state. However, approaching or avoiding a conspecific based on information on that animal's identity provided by vocal signatures (i.e. familiar = approach, strange = avoid) would be less risky and also more efficient. Approaching an unfamiliar, though 'friendly sounding', wolf would still entail substantial risk. The system described above may, however, be one which would allow strange wolves to approach one another, as might occur for unmated wolves during breeding season, and for lone wolves throughout the year.

Do wolves respond differently to howls from different individuals, or to howls of different types? There are several accounts of separated wild wolves reuniting after howling (Joslin 1967; Clark 1971). Approach to unfamiliar howls is rare (Harrington & Mech 1979; Tooze 1988) and most often

aggressive, as would be predicted (Harrington 1987). Preliminary playback experiments with captive wolves (Tooze, unpublished data) indicate that wolves may respond differently to unfamiliar and familiar howls. Although responses were highly variable among individuals, wolves tended to howl or orient in the direction of the playback more often when the howl was from a familiar animal. The responses of free-roaming wolves to familiar howls (versus unfamiliar) is unknown. The significance of vocal signatures to wolves can only be delineated through further playback experiments.

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