Journal of Mammalogy, 88(3):606–613, 2007

IBERIAN WOLF HOWLS: ACOUSTIC STRUCTURE, INDIVIDUAL VARIATION, AND A COMPARISON WITH NORTH AMERICAN POPULATIONS

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We present a detailed description of the acoustic structure of howls emitted by Iberian wolves and a comparison with published descriptions of North American wolf howls. We recorded and analyzed 176 howls emitted by 11 wolves held in captivity in social groups of 1–5 individuals. Our sample included solo howls as well as howls included in choruses. Iberian wolf howls are long (1.1- to 12.8-s) harmonic sounds, with a mean fundamental frequency between 270 and 720 Hz. Our results revealed striking similarities between Iberian and North American wolf howls in all variables analyzed except for the number of discontinuities in the frequency of the howl, which was lower for Iberian wolves. Using discriminant function analysis we could assign 84.7% of howls to the correct individual. Variables related to fundamental frequency (mean and maximum) and the coefficient of fundamental modulation best discriminate individuals. We suggest that Iberian wolves could use howls for individual recognition.

Key words: *Canis lupus*, geographic variation, howl, Iberian wolf, individual recognition, vocalizations, wolves

Behavior, like other phenotypic traits, often exhibits geographic variation within a species (Foster and Endler 1999). In fact, population comparisons provide some of the best insights into the causes and mechanisms of adaptive differentiation. Vocalizations are not an exception. Recent research has revealed that, far from being invariant, vocalizations often show geographic variation at macrogeographic or microgeographic scales (Mundinger 1982). Vocal geographic variation has been documented for American pikas (*Ochotona princeps*—Conner 1982), Gunnison's prairie dogs (*Cynomys gunnisoni*—Perla and Slobodchikoff 2002), leopard seals, (*Hydrurga leptonyx*—Thomas and Golladay 1995), bottlenose dolphins (*Tursiops truncatus*—Wang et al. 1995), sperm whales (*Physeter catodon*—Weilgart and Whitehead 1997), and Barbary macaques (*Macaca sylvanus*—Fischer et al. 1998). Geographic variation in vocalizations can be based on genetic differences, environmental differences, or vocal learning (Janik and Slater 1997).

The wolf (*Canis lupus*) is a wide-ranging social carnivore with a complex spatial organization for which acoustic communication plays an important role (Harrington and Asa 2003; Mech 1970). Wolves are found throughout the northern hemisphere, inhabiting a great variety of habitats. Eurasian and North American wolves have been isolated for 10,000 years, since the closing of the Bering land bridge, and wolf populations show evidence of genetic differentiation on regional and continental scales (Wayne and Vilá 2003). Thus, it is conceivable that the acoustic structure of wolf vocalizations shows geographic variation. However, to our knowledge, no attempt to look for variation in wolf vocalizations among different populations has been made. Most studies of wolf vocalizations have been carried out with North American wolves (Coscia 1995; Harrington 1989; Harrington and Mech 1983; Holt 1998; Theberge and Falls 1967; Tooze et al. 1990). Schassburger (1993) described the vocal repertoire of Eurasian and North American timber wolves kept in captivity, but the bulk of the data in his study belonged to North American wolves and he did not look for geographic differences.

The largest population of wolves in western Europe is found in the Iberian Peninsula (Boitani 2003). This population has been isolated from the rest of European wolves for more than a century (Boitani 2003; Vilá 1993). Based on morphological characteristics Iberian wolves may represent a subspecies (i.e., *Canis lupus signatus*) distinct from other European wolves (Vilá 1993). There have been only 2 surveys dealing with

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Table 1.—Characteristics of Iberian wolves and number of howls (*n*) analyzed at 3 wolf recovery centers.

Center	Enclosure area (m^2)	Social group	Wolf	Sex	Weight (kg)	Age (years)	Howls			
							n	Season (A/B)[a]	S/Ch[b]	S/I[c]
CRLI	310	Adult male and adult female	C-1	♀	28	7	15	3/12	0/15	1/14
			C-2	♂	42	7	19	1/18	0/19	0/19
	1,830	Adult male and adult female	C-3	♀	30	11	15	1/14	1/14	0/15
			C-4	♂	39	11	16	9/7	0/16	0/16
	1,753	Adult male and adult female	C-5	♀	28	11	26	6/20	16/10	14/12
	8,387	Four adult males and 1 adult female	C-6	♀	27	7	14	0/14	0/14	0/14
			C-7	♂	43	7	15	0/15	0/15	0/15
La Dehesa	500	Adult male, adult female, and subadult male	D-1	♂	42	4	25	9/16	19/6	1/24
	1,500	Two adult males	D-2	♂	36	2	14	4/10	14/0	0/14
	1,000	Adult male and 2 adult females	D-3	♀	?	3	11	11/0	0/11	0/11
Fauna Ibérica	600	Adult female	F-1	♀	23	2	6	0/6	6/0	0/6
Sample size (*n*)			11				176	44/132	56/120	16/160

[a] A/B: Autumn/breeding.

[b] S/Ch: Solo/chorus.

[c] S/I: Spontaneous/induced.

European wolf vocalizations. Kappe (1997) studied the threat vocalizations emitted by European wolves when competing over a food item and Feddersen-Petersen (2000) compared the ontogeny of acoustic communication in European wolves and in various dog breeds. However, the acoustic structure of Iberian wolf vocalizations is completely unknown.

Howls allow wolves to communicate over distances up to several kilometers (Harrington and Asa 2003). Howls have been described as long harmonic sounds with a fundamental frequency from 150 Hz to more than 1,000 Hz for adults (Harrington and Asa 2003). Two types of vocalizations involving howls have been reported: solo (lone) and chorus howls. Solo howls are emitted by a single individual (alone or with other pack members that do not howl). Chorus howls have been described as a vocalization in which one wolf begins howling, with other members joining in until several or all members of a pack are howling together (Joslin 1967). Usually, chorus howls include not only howls but also other vocalizations such as growls, barks, squeaks, and howl variations such as ''woa-woa howls'' (Holt 1998).

Recognizing individuals could be advantageous for social mammals and some long-distance vocalizations do contain information about individual identity (e.g., African lions [*Panthera leo*—McComb et al. 1993], spotted hyenas [*Crocuta crocuta*—Holekamp et al. 1999], African bush elephants [*Loxodonta africana*—McComb et al. 2000], yellow baboons [*Papio cynocephalus*—Fischer et al. 2002], and arctic foxes [*Vulpes lagopus*—Frommolt et al. 2003]). The role of howling in individual recognition in wolves has been explored in some detail (Theberge and Falls 1967; Tooze et al. 1990). Tooze et al. (1990) identified vocal signatures in the solo howls of 7 North American wolves. With respect to chorus howling, it has been suggested that the initial howls of choruses may provide signature information about individual or pack identity (Harrington 1989).

In this study, we analyzed 176 howls from 11 Iberian wolves held in captivity. Howls were emitted by a single wolf (solo howls) or by 2 or more wolves howling successively or simultaneously (chorus howls). We present a detailed description of the acoustic structure of howls emitted by wolves belonging to this population and investigate whether howls provide information regarding the individual identity of the emitter. Furthermore, we compare our results with those obtained by Tooze et al. (1990) for 7 timber wolves from North America to assess whether acoustic structure of howls shows differences between these 2 populations.

Materials and Methods

Howls were recorded from 2001 to 2003 from wolves held in captivity at 3 locations in the Iberian Peninsula: Centro de Recuperação do Lobo Ibérico (CRLI, Malveira, Portugal), La Dehesa (Riopar, Albacete, Spain), and Fauna Ibérica (El Rebollar, Valencia, Spain). Ninety-one percent of the howls included in the analysis were evoked by human imitations of wolf howling, whereas the remaining 9% were howls that were emitted spontaneously. Recordings were made during 2 seasons: from January to March (corresponding to the mating season of wolves in the Iberian Peninsula—M. Barrientos, pers. comm.) and from September to November. There were typically 2 recording sessions per day during times when the wolves howl regularly and are visually identifiable: 0600–1000 h and 1800–2100 h. The wolves were habituated to humans. Recordings were made 5–40 m from the wolves, with the researcher often in full sight of the animals. We analyzed howls of 11 wolves held in captivity in 8 different enclosures, each with 1–5 individuals (Table 1). We analyzed solo howls and howls included in choruses (Table 1). Two types of choruses were recorded: choruses that included only howls ($n = 20$); and choruses that included, in addition to howls, other vocalizations such as growls, barks, squeaks, and woa-woa howls ($n = 22$).

Audio recordings were made on TDK SA-60 cassette tapes (TDK Electronics Corp., New York, New York) using a Sennheiser MK 66 unidirectional microphone with K-6 power unit (Sennheiser Electric GmbH & Co. kG, Wedemark, Germany) connected to a Marantz PMD 222 cassette recorder (Marantz America, Inc., Mahwah, New Jersey). Recordings were digitized with 44.1-kHz sampling frequency and 16 bits

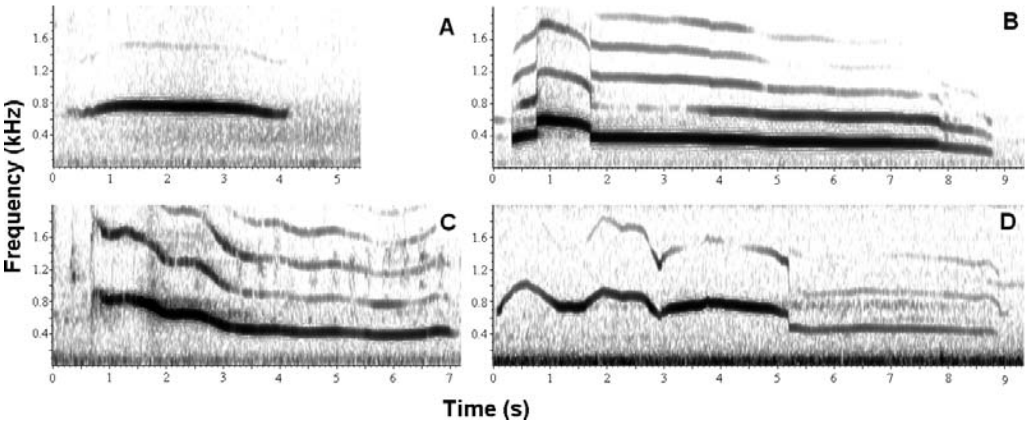

Fig. 1.—Types of howls recorded from wolves held in captivity at 3 locations in the Iberian Peninsula from 2001 to 2003: A) flat, B) breaking, C) continuous wavy, and D) breaking wavy.

in the Fonoteca Zoológica, Museo Nacional de Ciencias Naturales (CSIC, Madrid, Spain), using Delta 66 (Irwindale, California) or Digi 001 (Bucks, United Kingdom) digitizer cards connected to Apple Macintosh G4 computers (Cupertino, California). Recordings were saved in ''.wav'' format in CD-ROM. Recordings were subsequently deposited in the animal sounds collection of the Fonoteca Zoológica. Tape recordings, once digitized, were analyzed using commercially available software (Spectrogram 7.2, 2002; Visualization Software LLC, Stafford, Virginia). We generated audiospectrograms conducting a fast Fourier transform (2,048-point fast Fourier transform; Hanning window; time step: 10 ms; frequency range: 9,000 Hz; frequency resolution: 21.5 Hz). We used the cursor to measure the fundamental frequency and amplitude at intervals of 0.05 s along the entire length of the howl. For each howl we measured 16 variables (Appendix I), 13 of which have been used in previous works (Coscia 1995; Tooze et al. 1990). All procedures complied with guidelines of the American Society of Mammalogists (Animal Care and Use Committee 1998).

Statistical analyses.—For statistical analyses we used SPSS (12.0) for Windows (SPSS Inc., Chicago, Illinois) and the R statistical package (Dalgaard 2002). We used discriminant function analysis to classify 176 howls from 11 known individuals. Discriminant function analysis identifies a linear combination of independent variables that best discriminates groups from each other. The assumptions of multivariate normality and equal covariance matrices were not met even with transformed variables, but discriminant analysis is robust to violations of these 2 assumptions (Klecka 1980; Selvin 1995). When the assumptions of multivariate normality and equal covariance are not met, it is advisable to use the leave-one-out cross-validation results (Huberty 1994). In this method, each observation is systematically dropped, the discriminant function is reestimated, and then the excluded observation is classified (Huberty 1994). Our data set included cases of temporally close howls, thus violating the independence assumption. We grouped howls recorded in the same session and conducted a 1-way analysis of variance for each individual using session as the independent variable and the acoustic variables as dependent variables. We found differences in only 1 variable (frequency modulation) of howls from 1 individual recorded in different sessions. Therefore, we assume that such a small amount of temporal autocorrelation should not affect the overall results.

We compared our results with those reported by Tooze and colleagues (Tooze 1987; Tooze et al. 1990) for a sample of 308 howls recorded from 7 wolves. Because there are errors in the figures for duration reported in Tooze et al. (1990: table 2; F. Harrington, pers. comm.), we used the original values reported in Tooze (1987: table 1.8). Because of nonnormality, the presence of outliers, and the limited sample size, we used the Yuen–Welch test for equality of trimmed ($\alpha = 0.2$) means to compare 11 variables recorded in both studies (Yuen 1974). We used sequential correction to account for the number of pairwise comparisons made (Rice 1989).

RESULTS

Iberian wolf howls were long-duration (1.1- to 12.8-s), harmonic sounds (1–18 harmonics), with a mean fundamental frequency between 270 and 720 Hz (Appendix II). Fundamental frequencies in howls ranged from 92 to 1,116 Hz. The coefficient of frequency modulation ranged from 0.21 to 6.72, and the range of the coefficient of frequency variation was between 2.03 and 44.63. Iberian wolf howls usually had inflexion points (1–15) and discontinuities (1–8) in the fundamental frequency. The maximum fundamental frequency occurred in most cases (79% of the howls analyzed) during the 1st quarter of the howl, and the minimum during the last quarter (78%). The fundamental peak amplitude occurred in the 1st half of the howl (83%).

The 2 acoustic characteristics that best distinguish each howl are the presence of frequency discontinuities and frequency modulations. Thus, howls were arbitrarily assigned to 1 of 4 groups based on these 2 attributes (Fig. 1). The 1st group consisted of flat howls, which were relatively constant-frequency howls, without frequency discontinuities and with low values of both frequency modulation and variation (Table 2). The shape of the audiospectrogram was flat, not wavy. The 2nd group consisted of continuous wavy howls, which were

Table 2.—Shape variables (mean and range [maximum – minimum value]) for each type of howl. Variables are described in Appendix I.

		Howl type			
Variable	Statistic	Flat	Breaking	Continuous wavy	Breaking wavy
Cofv	$\bar{X} \pm SD$	5.7 ± 2.5	18.3 ± 6.9	19.5 ± 7.1	23.4 ± 8.1
	Range	8.0	32.7	32.5	26.5
Range	$\bar{X} \pm SD$	125 ± 57	279 ± 88	318 ± 137	437 ± 167
	Range	187	425	550	572
Cofm	$\bar{X} \pm SD$	0.7 ± 0.5	1.3 ± 0.6	1.4 ± 1.5	1.9 ± 0.8
	Range	1.8	3.7	6.2	3.3
Abrupt	$\bar{X} \pm SD$	0.0 ± 0.0	2.1 ± 1.1	0.0 ± 0.0	3.3 ± 1.9
	Range	0.0	7.0	0.0	7.0
Changf	$\bar{X} \pm SD$	1.1 ± 1.8	2.2 ± 2.0	1.6 ± 1.7	5.9 ± 3.0
	Range	6.0	9.0	5.0	14.0
Dur	$\bar{X} \pm SD$	5.5 ± 2.3	6.9 ± 2.3	5.3 ± 1.8	6.4 ± 2.6
	Range	8.4	9.7	6.5	10.0

howls without frequency discontinuities and with frequency modulations (i.e., wavy audiospectrograms). The 3rd group consisted of breaking howls, which were howls with large (21- to 250-Hz) frequency discontinuities, and low values of the coefficient of frequency modulation (Table 2). The audiospectrogram was not wavy. The 4th group consisted of breaking wavy howls, which were howls with large (21- to 250-Hz) frequency discontinuities and numerous frequency modulations (Table 2). The audiospectrogram was wavy.

Breaking wavy howls had the greatest coefficients of frequency modulation and variation, and flat howls had the lowest (Table 2). Howls with frequency discontinuities had the longest duration. In most cases, both solo howls and howls included in choruses had discontinuities, with breaking howls being the most frequent type of howl (Table 3). Solo howls of Iberian wolves were significantly shorter than howls included in a chorus ($t = -5.734$, $d.f. = 174$, $P < 0.001$).

The discriminant function analysis identified mean fundamental frequency, maximum frequency of the fundamental, number of harmonics, and frequency modulation as the most important discriminating variables. Using discriminant function analysis with independent variables entered simultaneously, we could assign 84.7% of howls to the correct individual. The cross-validation procedure resulted in 72.7% of howls correctly assigned, a percentage much higher than expected by chance (10.15%). Using only the howls included in chorus howling, 81.7% of howls were assigned to the correct individual, and the leave-one-out cross-validation resulted in 72.5% of howls correctly assigned.

Comparing our results with those reported by Tooze and colleagues (Tooze 1987; Tooze et al. 1990) we found statistically significant differences only for the variable Abrupt (Table 4). The Iberian wolf howls analyzed have fewer frequency discontinuities than the howls recorded from 7 North American timber wolves. Nevertheless, the 2 data sets are not homogeneous. All the wolves in our study were adults, whereas in the study of Tooze and colleagues (Tooze 1987; Tooze et al. 1990) 2 individuals were yearlings. However, an age effect seems unlikely because the results are similar when only data from adult wolves are compared (Table 4).

DISCUSSION

Iberian wolf howls can be classified into 4 types (flat, continuous wavy, breaking, and breaking wavy howls) based on the 2 criteria that best define howl shape in the audiospectrogram: the presence of discontinuities in the fundamental frequency and the pattern of frequency modulation. Before our study, 2 types of howls had been reported for North American wolves: flat howls and breaking howls. Although these 2 types were singled out as representing the extremes seen in frequency modulation, there is a fair degree of variation within each type (revised in Harrington and Asa 2003). It is unclear to what extent the 4 howl types identified in our study for descriptive purposes represent, to the wolves, natural or functionally distinct vocalizations. Using discriminant function analysis with howl type as the grouping variable (results not shown) we could assign 89% of howls to the correct type, showing that the 4 howl types have a different acoustic structure. It has been proposed that variation in howls may be related to general arousal or to the sequence of the howl

Table 3.—Frequency of the different types of howls identified in this study. See Table 1 for characteristics of individual wolves.

	Solo					Chorus				
Wolf	Flat	Breaking	Continuous wavy	Breaking wavy	Total	Flat	Breaking	Continuous wavy	Breaking wavy	Total
C-1	0	0	0	0	0	1	13	0	1	15
C-2	0	0	0	0	0	1	13	2	3	19
C-3	0	1	0	0	1	0	4	10	0	14
C-4	0	0	0	0	0	2	7	2	5	16
C-5	1	13	1	1	16	0	9	1	0	10
C-6	0	0	0	0	0	1	10	1	2	14
C-7	0	0	0	0	0	0	13	0	2	15
D-1	1	17	0	1	19	0	4	1	1	6
D-2	0	1	3	10	14	0	0	0	0	0
D-3	0	0	0	0	0	0	1	1	9	11
F-1	4	2	0	0	6	0	0	0	0	0
No. howls	6	34	4	12	56	5	74	18	23	120
%	10.71	60.71	7.14	21.43	100	4.17	61.67	15.00	19.17	100

TABLE 4.—Yuen–Welch test for equality of trimmed ($\alpha = 0.2$) means to compare acoustic features of North American timber wolves (Tooze 1987; Tooze et al. 1990) and Iberian wolf howls. Statistically significant differences are set in boldface. See Appendix I for descriptions of variables.

	Meanf	Maxf	Minf	Range	Cofv	Cofm	Dur	Changf	Abrupt	Posmax	Narm
All wolves											
Yuen's test statistic	0.84	0.25	1.68	0.93	2.90	0.49	1.25	0.07	7.93	1.91	2.40
d.f.	7.73	7.96	7.92	9.99	7.67	9.49	6.96	6.72	10.00	9.51	9.70
P	0.425	0.809	0.132	0.372	0.021	0.638	0.252	0.944	**<0.001**	0.087	0.038
Critical *P* value (Rice 1989)	0.013	0.025	0.007	0.01	0.005	0.017	0.008	0.05	0.005	0.006	0.006
Adult wolves only											
Yuen's test statistic	0.64	0.15	2.15	1.02	3.77	0.53	1.55	0.67	6.76	1.86	2.64
d.f.	2.65	2.73	3.49	5.29	4.36	7.96	6.69	2.89	6.21	3.74	5.24
P	0.571	0.894	0.107	0.351	0.017	0.609	0.167	0.554	**<0.001**	0.141	0.044
Critical *P* value (Rice 1989)	0.017	0.05	0.006	0.01	0.005	0.025	0.008	0.013	0.005	0.007	0.006

in a chorus, among other factors (Harrington 1989; Harrington and Asa 2003). The fact that we have identified solo howls of the 4 types suggests that, under certain circumstances, wolves can emit highly modulated howls not necessarily integrated in a chorus. It would be interesting to investigate whether the different howl types reported in this study are functionally distinct and if so, how they are produced, under what circumstances they arise, and what information might they transmit.

Tooze et al. (1990) found individual differences among the solo howls of 7 North American timber wolves. Our results show that solo and chorus howls of 11 Iberian wolves are individually distinct. The acoustic structure of wolf howls allowed us to identify individuals, and wolves could use this information for individual recognition. Our results agree with those obtained in Tooze et al. (1990) in emphasizing variables related to fundamental frequency (mean and maximum) and coefficient of fundamental modulation as the variables that best discriminate individuals. Frequency characteristics usually encode individuality because they are mostly determined by the characteristics of an animal's vocal apparatus (Fitch 1997). The fundamental frequency is one of the acoustic features that best discriminate among individuals in other mammal vocalizations, including isolation calls of Amazonian manatees (*Trichechus inunguis*—Sousa-Lima et al. 2002), calls of African bush elephants (*L. africana*—McComb et al. 2003), domestic dog barks (*Canis familiaris*—Yin and McCowan 2004), and the whistle call of dholes (*Cuon alpinus*—Durbin 1998). Frequency modulation also plays an important role in individual recognition as reported in chirps of Belding's ground squirrels (*Spermophilus beldingi*—McCowan and Hooper 2002), whistles of bottlenose dolphins (*T. truncatus*—Caldwell and Caldwell 1965), and calls of subantarctic fur seal pups (*Arctocephalus tropicalis*—Charrier et al. 2002). Transmission characteristics of the atmosphere impose constraints on acoustic communication, and frequency modulation represents one of the best ways to encode information in long-range vocal signals (Wiley and Richards 1978). Although fundamental frequency is highly determined by morphological characteristics, acoustic features related to the shape of the spectrum (e.g., frequency modulation) are determined by details of the opening and closing movement of the vocal folds (Rubin and Vatikiotis-Bateson 1998). Morphological characteristics of the vocal apparatus and the development of an individually specific howling technique could be the basis for individual recognition by means of howling in wolves, as it has been suggested for coyotes (*Canis latrans*—Mitchell 2004). Nevertheless, the fact that acoustic structure of howls is individually specific does not imply that wolves use this information for individual recognition. To confirm this hypothesis would require playback experiments (e.g., Frommolt et al. 2003; McComb et al. 2001; Mitchell 2004).

Animal vocalizations commonly vary over the geographic range of the species. However, our results reveal many similarities between the acoustic structure of howls of Iberian and North American wolves (Harrington 1989; Harrington and Mech 1978; Theberge and Falls 1967; Tooze et al. 1990). Furthermore, when comparing our results with those obtained by Tooze and colleagues (Tooze 1987; Tooze et al. 1990), we only found significant differences in the number of frequency discontinuities. This difference could be due to Iberian wolves emitting relatively fewer breaking howls than North American wolves. However, this explanation seems unlikely considering that most howls produced by Iberian wolves have frequency discontinuities (Table 3). Alternatively, Iberian and North American wolves could be producing a similar proportion of breaking howls but those of Iberian wolves would have fewer discontinuities per howl. Further data, including a larger sample of howls and individuals, will be required to assess the importance of these interpopulation differences.

Thus, in spite of possible genetic, morphological, or environmental differences, it seems that Iberian wolf howls and North American timber wolf howls show few detectable differences, at least with the variables used in this study. Lack of geographic differences in vocalizations has been reported for other large mammals, such as West Indian manatees (*Trichechus manatus*—Nowacek et al. 2003), and in the songs of gibbons (*Hylobates*—Marshall and Marshall 1976). Genetic differences are not always correlated with variation in vocal signals. For example, on a microgeographic scale, Wright et al. (2005) did not find concordance between vocal dialects and population genetic structure in the yellow-naped parrot

(*Amazona auropalliata*). Geographic variation in vocalizations can also arise because of environmental differences. Selection could shape the structure of long-distance acoustic signals to maximize transmission through different environments (Blumstein and Turner 2005; Morton 1975). Both North American timber wolves and Iberian wolves live in mountainous and forested areas. It is possible that the similarities found in their howls are due to selection for acoustic characteristics that maximize their transmission in similar habitats. Further research including samples of vocalizations from wolves living in different environments is needed to clarify this issue.

ACKNOWLEDGMENTS

We thank F. Petrucci-Fonseca and S. Pinho (CRLI), J. Escudero (La Dehesa), and R. Peris (Fauna Ibérica) for allowing us to obtain recordings from the captive wolves under their care. The Fonoteca Zoológica of the Museo Nacional de Ciencias Naturales (CSIC) in Madrid provided support for the sound analyses (projects CGL2005-0092/BOS, CGL2005-25130-E/BOS, and CGL2004-21489-E, Ministerio de Educación y Ciencia). We thank M. Kramer for help with the statistical analyses.

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Submitted 18 June 2006. Accepted 29 November 2006.

Associate Editor was Floyd W. Weckerly.

APPENDIX I

Description of structural variables used in analysis of wolf howls and units of measure (in parentheses).

Variable type	Abbreviation	Structural variables
Frequency	Meanf	Mean frequency of the fundamental at 0.05 intervals over the duration (Hz)
	Maxf	Maximum frequency of the fundamental (Hz)
	Minf	Minimum frequency of the fundamental (Hz)
	Range	Range of the fundamental: Range = Maxf − Minf (Hz)
	Cofm	Coefficient of frequency modulation: $\mathrm{Cofm} = \frac{\sum_1^{n-1} \lvert f(t) - f(t+1) \rvert / (\mathrm{n} - 1)}{\mathrm{Meanf}} \times 100$
	Cofv	Coefficient of frequency variation: $\mathrm{Cofv} = (\frac{SD}{\mathrm{Meanf}}) \times 100$
	Changf	Number of inflexions of the fundamental
	Abrupt	Number of discontinuities of the fundamental
	Posmax	Position in the howl at which the maximum frequency occurs: Posmax = time of Maxf/Dur
	Posmin	Position in the howl at which the minimum frequency occurs: Posmin = time of Minf/Dur
	Endf	Frequency at the end of the fundamental (Hz)
	Dur	Duration of the howl measured at the fundamental (s)
	Narm	Maximum number of harmonics to 2,000 Hz
Amplitude	Frecpaf	Fundamental at its amplitude peak (Hz)
	Pospaf	Position in the howl at which Frecpaf occurs: Pospaf = time of Frecpaf/Dur
	Coidv	Coefficient of amplitude variation at the fundamental frequency (%)

APPENDIX II

Parameters of Iberian wolf howls analyzed in this study. Range denotes minimum and maximum values for each variable. See Table 1 for characteristics of each wolf and Appendix I for descriptions of variables.

Wolf	Meanf	Maxf	Minf	Range	Cofm	Cofv	Narm	Changf	Abrupt	Dur	Posmax	Posmin	Pospaf
C-1													
$\bar{X} \pm SD$	373 ± 32	430 ± 41	234 ± 55	196 ± 57	1.1 ± 0.5	11.8 ± 5.3	4.5 ± 0.5	3.5 ± 2.9	2.5 ± 1.9	8.3 ± 2.5	0.48 ± 0.34	0.38 ± 0.48	0.31 ± 0.18
Range	320–431	367–504	108–335	103–274	0.5–2.0	5.2–20.3	4.0–5.0	0.0–10.0	0.0–6.0	3.8–11.0	0.00–0.99	0.00–1.00	0.06–0.63
C-2													
$\bar{X} \pm SD$	474 ± 48	596 ± 60	318 ± 75	278 ± 97	0.8 ± 0.3	15.7 ± 7.1	3.1 ± 0.6	2.3 ± 1.8	2.1 ± 1.9	8.0 ± 1.6	0.04 ± 0.06	0.90 ± 0.17	0.26 ± 0.12
Range	360–588	496–712	173–524	114–539	0.4–1.2	6.2–38.0	2.0–5.0	0.0–6.0	0.0–8.0	4.6–10.6	0.00–0.02	0.42–1.00	0.10–0.57
C-3													
$\bar{X} \pm SD$	466 ± 25	587 ± 23	346 ± 17	241 ± 29	0.8 ± 0.2	18.1 ± 3.1	2.9 ± 0.8	1.3 ± 1.6	0.6 ± 0.9	5.8 ± 1.3	0.05 ± 0.06	0.88 ± 0.15	0.25 ± 0.27
Range	417–517	547–647	302–376	205–302	0.5–1.0	12.9–22.4	2.0–5.0	0.0–5.0	0.0–2.0	3.0–7.6	0.00–0.17	0.51–1.00	0.07–0.80
C-4													
$\bar{X} \pm SD$	357 ± 39	472 ± 75	222 ± 53	250 ± 100	1.2 ± 0.3	15.4 ± 5.1	4.1 ± 0.9	3.6 ± 2.8	1.6 ± 1.1	8.3 ± 1.9	0.30 ± 0.28	0.64 ± 0.45	0.39 ± 0.22
Range	274–405	296–570	114–319	68–456	0.4–1.7	4.4–23.0	2.0–5.0	0.0–10.0	0.0–3.0	4.8–11.7	0.00–0.92	0.00–1.00	0.02–0.80
C-5													
$\bar{X} \pm SD$	395 ± 47	562 ± 74	240 ± 74	324 ± 70	1.3 ± 0.3	21.4 ± 5.1	4.9 ± 0.4	2.6 ± 2.6	1.6 ± 0.9	7.3 ± 1.8	0.08 ± 0.10	0.96 ± 0.07	0.21 ± 0.24
Range	345–533	389–672	92–349	114–456	0.8–2.1	10.0–32.8	4.0–5.0	0.0–9.0	0.0–3.0	2.7–9.5	0.02–0.52	0.70–1.00	0.01–0.86
C-6													
$\bar{X} \pm SD$	407 ± 34	524 ± 60	294 ± 38	229 ± 78	1.1 ± 0.5	15.1 ± 5.8	2.9 ± 0.4	1.9 ± 2.6	1.9 ± 1.2	6.6 ± 1.7	0.14 ± 0.14	0.75 ± 0.41	0.40 ± 0.28
Range	340–454	388–615	205–324	64–410	0.3–2.6	2.8–24.4	2.0–3.0	0.0–8.0	0.0–4.0	2.1–8.8	0.00–0.41	0.00–1.00	0.01–0.85
C-7													
$\bar{X} \pm SD$	332 ± 47	459 ± 70	201 ± 19	258 ± 65	1.3 ± 0.4	17.3 ± 5.6	5.1 ± 0.9	2.5 ± 2.6	3.2 ± 1.9	8.2 ± 2.4	0.08 ± 0.21	0.95 ± 0.10	0.21 ± 0.15
Range	273–424	342–583	173–227	137–367	0.6–2.0	8.3–27.5	3.0–6.0	0.0–8.0	1.0–8.0	4.2–12.8	0.00–0.77	0.63–1.00	0.02–0.51
D-1													
$\bar{X} \pm SD$	409 ± 39	568 ± 65	246 ± 50	322 ± 100	2.0 ± 0.9	21.5 ± 8.2	4.6 ± 0.6	2.2 ± 1.8	1.6 ± 0.7	4.4 ± 1.3	0.13 ± 0.09	0.95 ± 0.19	0.22 ± 0.15
Range	359–491	456–661	159–342	114–456	0.8–4.7	6.3–31.7	3.0–6.0	0.0–7.0	0.0–3.0	1.1–7.1	0.00–0.41	0.03–1.00	0.04–0.56
D-2													
$\bar{X} \pm SD$	598 ± 52	961 ± 111	340 ± 44	621 ± 138	3.0 ± 1.4	31.6 ± 7.7	3.6 ± 1.0	6.5 ± 3.6	3.1 ± 2.6	4.9 ± 1.6	0.22 ± 0.15	0.62 ± 0.48	0.32 ± 0.20
Range	524–711	691–1116	281–432	259–777	1.2–6.7	14.4–44.6	2.0–5.0	1.0–15.0	0.0–8.0	1.3–6.5	0.02–0.53	0.00–1.00	0.05–0.68
D-3													
$\bar{X} \pm SD$	570 ± 52	744 ± 79	326 ± 41	418 ± 70	1.6 ± 0.4	21.9 ± 5.7	3.0 ± 0.5	3.0 ± 1.8	2.5 ± 1.4	4.3 ± 1.3	0.18 ± 0.14	0.96 ± 0.10	0.25 ± 0.14
Range	463–641	615–842	251–388	319–540	1.1–2.2	16.1–30.1	2.0–4.0	1.0–7.0	0.0–5.0	2.8–6.6	0.06–0.53	0.67–1.00	0.04–0.46
F-1													
$\bar{X} \pm SD$	666 ± 60	731 ± 34	543 ± 95	188 ± 78	0.9 ± 0.5	7.0 ± 5.3	2.5 ± 0.6	1.7 ± 2.4	0.5 ± 0.8	4.3 ± 0.9	0.24 ± 0.24	0.51 ± 0.51	0.41 ± 0.10
Range	565–723	684–775	387–638	91–297	0.2–1.7	2.0–16.9	2.0–3.0	0.0–6.0	0.0–2.0	3.3–5.7	0.00–0.57	0.00–1.00	0.22–0.53