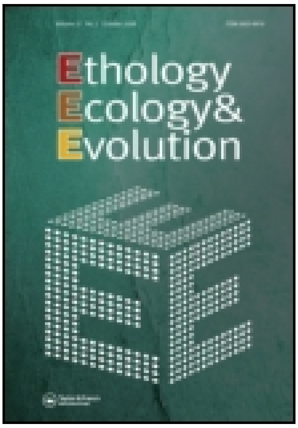

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Group specific vocal signature in free-ranging wolf packs

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Group specific vocal signature in free-ranging wolf packs

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Acoustic communication conveys a variety of information that is a helpful tool for animal conservation. The wolf is an elusive species, which can be detected through the howls that individuals emit. In this study we investigated the acoustic features of wild wolf pack howls from five locations in the province of Arezzo, Italy. We tested the hypothesis that each group had a distinctive vocal signature. Our results showed that these wolf packs emitted howls with significantly distinctive acoustic structures. We hypothesized that group-specific vocal signatures require temporal stability to be functional. Indeed, we did not find any statistical differences in howls collected from the same location during the same season or for 2 consecutive years. We suggest that the acoustic features of howls can be used to distinguish wolf packs in the wild.

KEY WORDS: wolf, howling, acoustic communication, group signature, vocalizations.

INTRODUCTION

Animal communication is not only just a subject for behavioural studies, but acoustic signals also convey diverse information that can be used to census individuals as well as groups of the same species (MCGREGOR 2005). Bioacoustic research is known to provide useful insights for the census and the monitoring of species, a central criterion for the conservation of animal diversity (BAPTISTA & GAUNT 1997).

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The wolf (*Canis lupus*) is one of the most widely distributed land mammals and a protected species under the Bern Convention and the European Council Directive 92/43/EEC ('Habitat Directive'). However, this species is endangered in several European countries, or was severely threatened until recently (Promberger & Schröder 1993; Apollonio et al. 2004). The pack is the social unit of a wolf population and generally consists of a breeding pair and their offspring (Mech 1970). Acoustic signals play a key role in wolf social behaviour (Harrington & Asa 2003). The howl is considered the main long-distance vocalization and its structure has been widely investigated in both wild and captive populations (Harrington 1989; Tooze et al. 1990; Palacios et al. 2007; Passilongo et al. 2010). The howl is a long sound, whose fundamental frequency (F0) generally ranges between 150 and 1300 Hz in adults. Its characteristics are stable over distance, as observed in a closely related species, the coyote (*Canis latrans*) (Mitchell et al. 2006). Howling is a relevant vocalization with several functions, regulating intra and inter-pack interactions, such as social spacing, defence of resources and mate attraction (Joslin 1967; Harrington & Mech 1979; Harrington & Asa 2003). Howling is also involved in the coordination of social activities such as the re-joining of separated members to the pack (Mech 1966; Theberge & Falls 1967). Wolf chorus howls are a series of vocalizations emitted by a pack, in which one wolf begins howling, with some or all other members forming the chorus (Joslin 1967). Importantly, howling can provide information on individual identity and position (Theberge & Falls 1967; Tooze et al. 1990).

Since wolves tend to respond to vocal stimuli, tracking wolf-howling is a technique that enables operators to locate packs even in areas with dense vegetation, where direct observation is difficult. Wolf-howling tracking was described by Pimlott (1960) and requires an observer either to playback recorded howls, or to produce human imitations of them. When the pack is within hearing distance, the wolves may reply by howling back (Joslin 1967). Packs are more likely to respond when pups and/or food resources are present (Harrington & Mech 1979; Harrington & Asa 2003). This method was used in several studies on wolf pack behaviour as well as to census wolf packs (Harrington & Mech 1979; Fuller & Sampson 1988). Elicited howls have been used to acquire information on wolf behaviour related to territorial maintenance, resources defence and activity rhythms (Harrington & Mech 1978a; Gazzola et al. 2002; Nowak et al. 2007).

In captivity, individual wolves can be recognized by the characteristics of their howling (Tooze et al. 1990; Palacios et al. 2007) and the fundamental frequency was found to be the most effective variable to distinguish individuals (Tooze et al. 1990). Individual vocal features have been recognized in a large variety of taxa, from birds (Peake et al. 1999) to several mammalian species, including canids (Durbin 1998; Darden et al. 2003; Frommolt et al. 2003; Hartwig 2005). It was recently shown that it was possible to distinguish individuals within a group of conspecifics by virtue of their vocalizations both in birds (Baker 2004; Radford 2005) and in mammals (Boughman 1997; Crockford et al. 2004; Townsend et al. 2010). No research has yet addressed the potential for group-specific differences, especially in the wild.

Individual recognition by vocal print has been proposed as a possible species conservation tool (Darden et al. 2003; Hartwig 2005), even if it was noted that there are cases in which a species may alter its vocalizations in relation to the territory in which it is located (Walcott et al. 2006). However, there are only a few reports of acoustic identification used as a monitoring tool for mammals in the wild (O'Farrell & Gannon 1999; Oswald et al. 2007).

In this study we tested the hypothesis that free-ranging wolf packs have a group-specific vocal signature by analysing howls extracted from the choral responses of five wolf packs in central Italy.

MATERIALS AND METHODS

Data were collected during the years 2007, 2008 and 2009 from June to October in the province of Arezzo (3230 km^2), eastern Tuscany, Italy. The topography of this area is mountainous ranging from 300 to 1654 m a.s.l. and more than 50% of the area is covered by forests. From 1998 to 2010 spatial distribution and reproductive success of wolf packs in the province of Arezzo were monitored using wolf howling tracking, snow tracking and molecular analyses (Scandura et al. 2001, 2006; Gazzola et al. 2002; Apollonio et al. 2004; Scandura 2005; Capitani et al. 2006; Iacolina et al. 2010). During the field study, the number of wolf packs in the province ranged from 7–13, while the pack size ranged from two to eight individuals, with a mean of 4.5 individuals.

Wolf howling tracking was performed in summer, when the pack activity was focused on a restricted area (home-site) due to the presence of pups, and the response rate to vocal stimuli was high (Harrington & Mech 1978b, 1979, 1983; Gazzola et al. 2002; Nowak et al. 2007). Sampling sites were chosen to maximize the audible range and minimize sound dispersion, while their location and number were planned to cover the whole study area. Two groups of operators conducted concurrent sessions to determine the presence of two adjacent packs. To elicit the vocalizations of wolves, we used a playback of recorded chorus howls by a captive wolf pair (duration: 1 min 29 sec). Trials were carried out at night and in good weather conditions, i.e. with low wind and no rain, using a tape player connected to an amplifier with an output of 40 w and an exponential horn with high emission directionality (120° horizontal coverage and 60° vertical), as described in detail in Passilongo et al. (2010).

In order to analyse vocalizations of free-ranging wolf packs, we selected the five locations out of those reported by census data to have the highest number of recorded vocalizations: Lignano (LI), Vallesanta (VS), Catenaia (CT), Camaldoli (CM), and Pratomagno (PM) (Fig. 1).

Vocalizations were recorded using a Sennheiser microphone with windshield (ME67 head with K6 power module) and a digital recorder (M-Audio Micro TRACK 24/96) with a sampling rate of 44.1 kHz and 16 bits accuracy. Analysis of recorded howling was performed using Raven Pro 1.3 (Cornell Lab of Ornithology). Spectrogram parameters selected for the analysis were: 2048-point discrete Fourier transform; frequency resolution: 21.5 Hz; filter bandwidth: 37.5 Hz; time overlap: 10 msec; Hanning window. For the purposes of this study, we analysed only howling (flat and breaking) and did not consider other types of vocalizations such as whimpers, barks and growls, that often occur in choral responses (Mech 1966; Joslin 1967; Harrington & Mech 1978b; McCarley 1978). Howls by pups, recognizable until 6/7 months of age for their high frequency and instability of the vocal structure due to physical growth (Harrington & Mech 1978b; Harrington & Asa 2003), were not taken into consideration. We measured the entire length of the fundamental frequency (F0) of the howl (Fig. 2) every 0.05 sec to obtain 12 variables for each howl, as in previous studies on wolf vocalization (Tooze et al. 1990; Palacios et al. 2007; Passilongo et al. 2010) (Table 1, Fig. 2). Harmonics, which were sometimes visible in the spectrogram, were not considered for the analysis.

Statistical analysis

Univariate and multivariate non-parametric methods were used to test vocal differences (i) between years in the same pack, and (ii) among packs. Each vocal variable difference between years were tested by Mann Whitney U test and among packs by Kruskal-Wallis test (Zar 1996; Hammer et al. 2001). A one-way PERMANOVA, based on a similarity matrix created on Gower similarity criteria, was used to test the null hypothesis (H_0) that there were no differences among

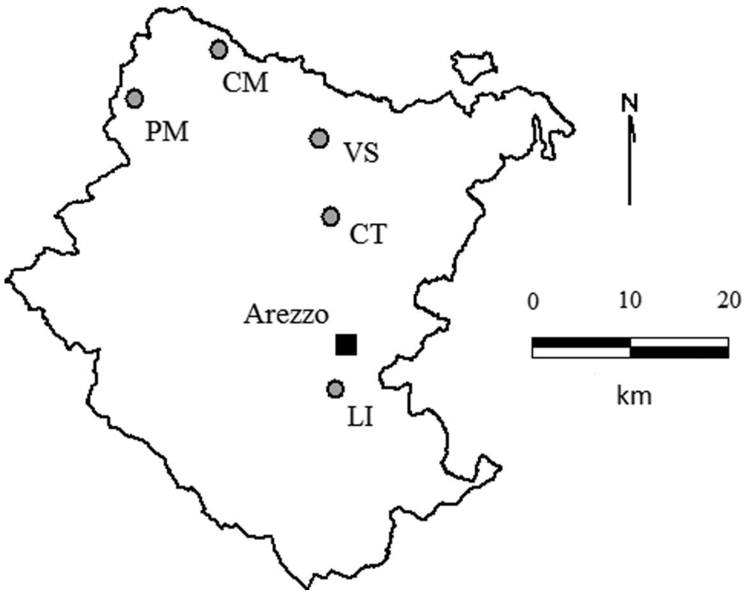

Fig. 1. — Geographical distribution of the analysed packs.

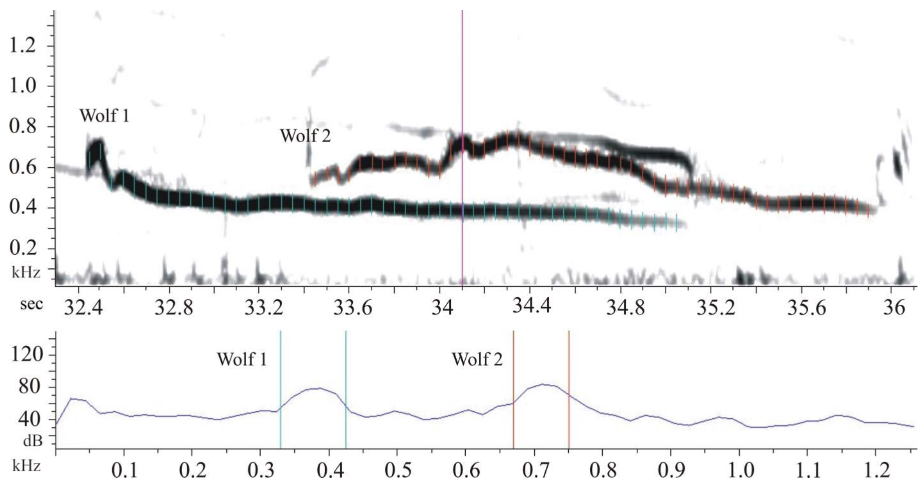

Fig. 2. — Spectrogram with spectrum of an example of howls analyzed. Purple line shows the position of the spectrum at 34.1 sec. Blue and brown bars in the spectrum show the peak frequency of each howl in that time span. Peak frequency was collected every 0.05 sec from the beginning to the end of each howl.

acoustic variables of packs; post hoc pair-wise tests were applied after PERMANOVA (ANDERSON 2001). Principal coordinates analysis was used to visualize their relationships (TORGERSON 1958), by using the Gower similarity matrix among samples. Spearman correlation indexes among the scores of the samples were computed for each PCO axis. The values related to each variable were then considered to facilitate interpretation of the meaning of the axes. Vectors of the variables

Table 1.

Description of variables used for the analysis of wolf howls.

Pitch variables	Meanf	Mean of the fundamental frequency calculated every 0.05 sec (Hz)
	Modef	Mode of the fundamental frequency calculated every 0.05 sec (Hz)
	Rangef	Difference between maximum and minimum frequencies (Hz)
	Minf	Minimum frequency (Hz)
	Maxf	Maximum frequency (Hz)
	Endf	Frequency at the end of the howl (Hz)
Shape variable	Duration	Duration of the howl (sec)
	Posmin	Position at which the minimum frequency occurs (time of Minf/Duration) in the howl
	Posmax	Position at which the maximum frequency occurs (time of Maxf/Duration) in the howl
	Cofv	Coefficient of frequency variation (SD/Meanf) × 100)
	Cofm	Coefficient of frequency modulation $\Sigma\lvert f(t)–f(t+1)\rvert (n–1)/\text{Meanf} \times 100$
	Abrupt	Number of sudden abrupt changes in frequency (> 25 Hz)

were superimposed on the PCO plot to improve graphical results. To avoid multicollinearity the variables Meanf and Cofv, were excluded from the multivariate analysis. All statistical analyses were performed using SPSS 18 (Chicago, Illinois, USA), PRIMER v. 6.1 (Clarke & Gorley 2006) and PERMANOVA+ for PRIMER routines (Anderson et al. 2008).

RESULTS

From 2007 to 2009, in the five locations considered, wolves replied to 59 of the 180 trials (33%). A total of 271 howls were found to be suitable for a quantitative analysis (Table 2). The presence of pups was recorded in all packs, which ranged from four to seven individuals (Table 2). Each trial was obtained from a minimum of three wolves with the exception of PM where we used a minimum of two wolves per trial.

No significant difference among most variables in the CM pack between 2008 and 2009 were observed, with the exception of duration (N = 48, 24; U = 269; $P < 0.001$) and posmin (N = 48, 24; U = 401; $P < 0.05$), demonstrating some persistence in the structure of CM howls in subsequent years.

Univariate comparisons among packs showed significant differences for 10 out of 12 variables analysed; the only variables that showed no difference among howls by different packs were the posmin and posmax (Table 3). Multivariate comparisons among howls by different packs showed significant difference in their structure as a whole (pseudo-F = 8.6956; df = 5; $P < 0.0001$, PERMANOVA test). The pair-wise test among groups was used as a post-hoc test and showed significant differences among all packs, with the exception of VS vs CT, and CM 2008 vs CM 2009 (Table 4). The two-dimensional scatter plot of principle coordinates (Fig. 3) shows that LI pack clusters apart and is characterized by stable and long duration howls. In fact these howls are distributed on the positive side of the PCO_1 (49.9% of total variance explained) which is inversely correlated with Rangef (R = − 0.86), Abrupt (R = − 0.54), Cofm (R = − 0.45),

Table 2.

Summary of data collected during the study period. Minimum number of wolves was estimated by means of visual inspection of the narrow band spectrograms.

Pack	Study period	Trials	No. of successful trials	Analyzable trials	No. of howls analyzed	Minimum no. of adult wolves (no. of puppies)
LI	07/10/2007	15	5 (33%)	4	39	4(3)
VS	05/6/2008–10/10/2008	64	10 (16%)	6	31	4(3)
CT	30/7/2008–09/9/2008	42	14 (33%)	11	91	3(2)
CM08	19/8/2008–13/10/2008	29	11(38%)	8	24	3(2)
CM09	13/8/2009–13/9/2009	11	9 (82%)	6	48	4(2)
PM	06/8/2009–23/8/2009	29	10 (34%)	5	38	2(2)
		180	59 (33%)	Tot 40	Tot 271	Mean 5.66

Table 3.

Results of univariate comparison among packs of the variables considered for the analysis (Kruskall Wallis with Monte Carlo exact test).

Variables	χ^2	df	*P*
Meanf	107.966	5	<0.0001
Modef	83.050	5	<0.0001
Rangef	61.605	5	<0.0001
Minf	85.010	5	<0.0001
Maxf	106.943	5	<0.0001
Endf	80.335	5	<0.0001
Duration	61.874	5	<0.0001
Posmin	4.511	5	0.478
Posmax	6.346	5	0.274
Cofv	25.746	5	<0.0001
Cofm	29.753	5	<0.0001
Abrupt	54.024	5	<0.0001

Maxf (R = − 0.56), and on the positive side of the PCO_2 (17.5% of total variance explained) which is directly correlated with Duration (R = 0.41) and inversely correlated with Endf (R = − 0.74).

DISCUSSION

In this study we tested, for the first time, the hypothesis that group-specific vocal signatures exist for wolves. Our results are from wild populations and a limitation is that it was not possible to exactly estimate the contribution of each wolf in the

Table 4.

Results of PERMANOVA paired test among packs. Packs are labeled as follows. Number of howls in brackets.

Packs	Paired test *P* values					
	LI(39)	VS(31)	CT(91)	CM 08(24)	CM 09(48)	PM(38)
LI	–					
VS	<0.001	–				
CT	<0.001	**0.467**	–			
CM 08	<0.001	0.007	0.002	–		
CM 09	<0.001	0.003	<0.001	**0.595**	–	
PM	<0.001	<0.001	<0.001	<0.001	<0.001	–

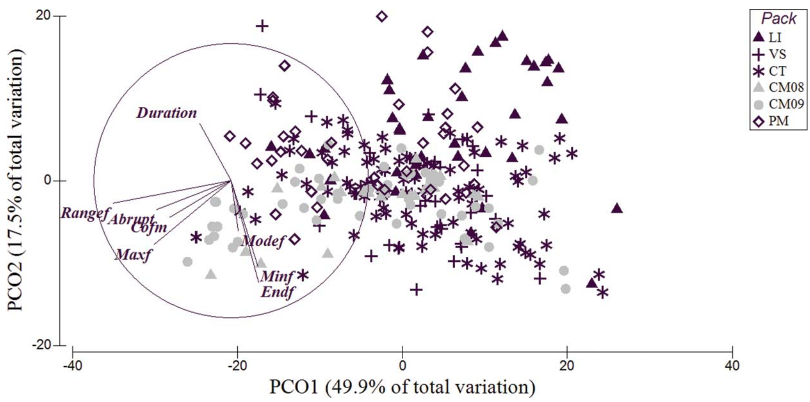

Fig. 3. — Two-dimensional scatter plot of first and second principal coordinates axis of 10 acoustic parameters of howls recorded for 6 wolf packs in the province of Arezzo.

pack. On the other hand, we collected vocalizations from choruses of howling composed by a minimum of two to three wolves per trial so that the possibility that the group vocal signature of a pack is due to the vocal characteristics of a single individual should be minimal. To investigate the presence of a group specific vocal signature, we decided to collect howls from wild populations living in an interconnected territory. Harrington & Mech (1979, 1983; Harrington 1987) suggested that howling serves: (1) to maintain or to increase the distance between packs, (2) to help establish and preserve exclusive territories, (3) to reduce the probability of contact with unfamiliar wolves or packs. Further, they suggested that howls might hold promise as a non-invasive conservation management tool to recognize packs in the wild. Our results revealed significant differences among howls emitted by different packs supporting the hypothesis that packs have a group-specific vocal signature suitable for census and monitoring. Several mammalian species show group-specific vocal signatures (primates: Crockford et al. 2004; Cheney & Seyfarth 2007; Herbinger et al. 2009; bats: Boughman 1997; cetaceans: Ford 1991; Tyack 2000); all these species, including wolves, have complex social structures, defend their territory from intruders, and live in habitats where long-range acoustic communication is employed to convey messages. To be functional, a group-specific vocal signature requires stability over time. Therefore, we tested the acoustic stability of the howls in different years. In Camaldoli, howls recorded in two different years (2008–2009), and very likely emitted by the same pack (CM), were compared and no significant differences were observed. Our data seems to support the hypothesis that group howling has a vocal stability because we found that a similar acoustic structure was maintained over 2 years, despite possible changes in pack composition due to high winter mortality, new births and dispersion of young individuals.

In the two packs living in CT and VS no statistical differences were recorded that could help distinguish the two groups' howls. This could be accounted for by the proximity of the two locations and by the migration of at least one female from the CT to the VS pack. The migration was tracked using genetic analysis of droppings and the individual was reported to belong to the CT pack in 2003 and to the VS pack in 2008 (M. SCANDURA pers. comm.).

Howls recorded in CM are characterized by higher frequencies of Maxf and Rangef compared to other packs, and in particular compared to LI, the most geographically distant, which has lower frequencies in maxf, rangef and a low number of abrupts. The acoustic structure of CT and VS have intermediate values compared to CM and LI and they are located between the two packs described above. However, it should be noted that pack PM, geographically closest to CM, has vocal characteristics that are not clearly explainable from a geographical point of view. This suggests that the distance among packs increases the differences in the vocalizations, but the reduced number of packs sampled does not allow us to go into further detail.

Identifying individuals using acoustic cues is a non-invasive method that has been the focus of much work in bioacoustics as well as in behavioural sciences (TERRY et al. 1995) and could be especially useful when species have nocturnal acoustic activity (DARDEN et al. 2003). The wolf is a gregarious and territorial species. Howls therefore should carry a group-specific vocal signature and our results support this hypothesis. We conclude that group-specific vocal signatures could be used as a non-invasive tool to recognize packs and for the management of this species. It is possible that group-specific vocal signatures represent a sort of cultural tradition, but further studies are necessary to determine whether group signatures are due to genetic features, are acquired, or are due to a mixture of both.

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