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Acoustic analysis of wolf howls recorded in Apennine areas with different vegetation covers

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In animal communication, acoustic signals can be used to census individuals as well as groups of individuals of the same species. The wolf (*Canis lupus*) is a protected species in Europe, and the study of its vocalizations may furnish information about its spatial distribution, reproductive success, and social behaviour. This study was conducted in seven locations of the Tuscan Apennines over 2 years. Seven different free-ranging wolf-packs, from different environmental habitats, were recorded. The minimum wolf number of each pack was ascertained along with the presence of pups. Different acoustic characteristics were found among packs, confirming that the group-specific vocal signature is a useful method to recognize packs in the wild. Howls were also analysed in relation to different environmental characteristics, and different frequencies were found to correlate open/closed habitats, so environmental variables should be included in sound analysis models to recognise individual packs.

KEY WORDS: acoustics characteristics, non-invasive monitoring, wolf, *Canis lupus*, mammal communication.

INTRODUCTION

Animal communication by means of acoustic signals is used for several functions such as aggressive behaviour, defending territories, attracting mates, or maintaining contact with members of the same social group (Blumstein et al. 2011). Increasingly advanced bioacoustic technologies are providing new techniques to study the ecology and behaviour of animals. For example, bioacoustics is used in

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wildlife management and conservation projects to recognise species, as well as to count the number of animals or study the relations among individuals (Marques et al. 2013; Teixeira et al. 2019).

Identifying a vocal signature of single or group of animals is useful in management and conservation programs (McGregor 2005). The wolf (*Canis lupus*) is an elusive protected species, and bioacoustics can be particularly adapted for the study of this species (Terry et al. 2005). Their main system of communication over long distances is howling, which can be detected by other wolves up to 11 km away in wooded areas (Harrington & Mech 1978) and up to 16 km in tundra areas (Henshaw & Stephenson 1974). Within the vocal repertoire of a pack, there are individual howls and chorus howls.

Packs of wolves are stimulated to respond to howling to defend their territories, and this characteristic is used to obtain a response from wolves present in a monitored area (Harrington & Mech 1982). In fact, it can be used to ascertain the response rate, the success of reproduction, and to investigate the maintenance of the territory (Gazzola et al. 2002; Nowak et al. 2007; Hall & Sharp 2014; Suter et al. 2016). Studies of wolf vocalizations have also been conducted in captivity (Tooze et al. 1990; Palacios et al. 2007) highlighting some structural aspects and features of howling. Furthermore, bioacoustics analysis of wolf howls can be used to recognize subspecies in the *C. lupus* clade (Hennelly et al. 2017), and the fundamental frequency is the most effective variable to distinguish individuals (Root-Gutteridge et al. 2014).

In Italy, wolf populations are distributed through the Apennine mountain and the Alps with the highest population densities in the Tuscany region. Although the acoustic structure and the group vocal signature of free-ranging packs have been described (Passilongo et al. 2010, 2015; Zaccaroni et al. 2012; Root-Gutteridge et al. 2014), wolves could also modulate sounds in relation to the characteristics of the environment. Similarly, acoustic adaptation is well known in birds (Hansen 1979; Morton 1986; Boncoraglio & Saino 2007), as well as the long-range songs of some primate species that are structurally adapted to the acoustics of local habitats (Brown 1989; Brown & Gomez 1992). Richards and Wiley (1980) demonstrated the influence of foliage on acoustic impedance between air and vegetation.

In this study, we analysed the howls extracted from the choral responses of wolf packs from seven different areas of the Tuscan Apennines. We have correlated the responses obtained with the vegetation characteristics of the sites, to test whether the wolves adapt their vocal signature to the occupied area.

MATERIALS AND METHODS

Data collection

Data were collected in 2011 and 2012 from June to October in seven different locations in Tuscany, central Italy: two in province of Arezzo (Lat. 43.5°N, Long. 11.9°E) (Camaldoli and Bocca Pecorina); one in province of Lucca (Lat. 43.8°N, Long 10.5°E) (Orecchiella Natural Reserve) and four in the province of Massa-Carrara (Lat. 44.0°N, Long. 10.1°E) (Casola, Cerreto, Logarghena, and Passo della Cisa) (Fig. 1).

To elicit the vocalization of wolves, we used playback of recorded chorus howls by a captive wolf pack (duration 1 min 20 sec), using a digital player connected to an amplifier with an output of 40 W and an exponential horn with directional emission (120° horizontal coverage and 60° vertical). Two groups of operators conducted a concurrent session to determine

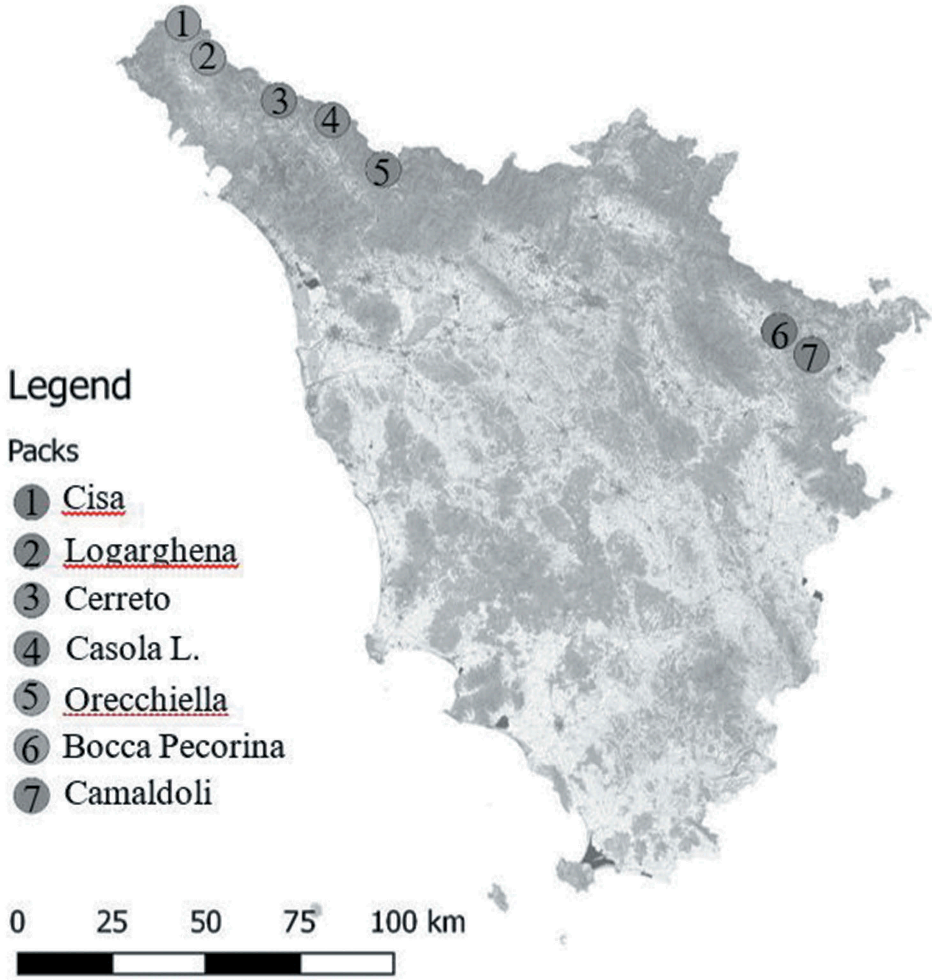

Fig. 1. — Study areas.

the presence of two adjacent packs. In addition, for a better response we followed the standard procedure by Harrington and Mech (1982): (1) no sessions were conducted during rain or strong winds; (2) wolf howling was performed overnight to minimize the noise; (3) two trials, the first one lower in volume, were conducted per site.

Wolf-howling technique was applied in summer, when the packs were concentrated at rendezvous sites due to the presence of pups, and the response rate to vocal stimuli was high (Harrington & Mech 1978; Gazzola et al. 2002). We used the "saturation census" described by Harrington and Mech (1982) adapted to local requirements, considering mountainous topography. Consequently, sampling sites were chosen to cover the whole study area (from a minimum of five to a maximum of 10). If after the first playback stimulus no answer followed, a second trial was attempted 2 min later and subsequently the operators left the site. Otherwise, when a response was elicited, we repeated one or more trials from a place closer to the presumed site of response, in order to obtain higher quality recordings. To increase the sample of choral howls, we collected vocalizations until the end of summer because in this season, the rendez-vous sites were known; thus, the response rate was higher (Gazzola et al. 2002).

Wolf vocalizations were recorded using a Sennheiser microphone with the windshield (ME67 head with k6 power module) and a digital recorder (M-Audio microtrack 24/96) with a sampling rate of 44.1 kHz and 16 bit accuracy. The analysis of recorded howling was performed using Raven Pro 1.3 (Cornell Lab of Ornithology). Spectrogram parameters selected for the analysis were: frequency resolution: 10.9 Hz; filter bandwidth: 21.5 Hz; time overlap: 10 msec; Hanning window.

Data analysis

In this study, we analysed only howling (flat and breaking) of adult individuals. Indeed, we recognize pups howling because they reach a higher frequency than adult howls: 1.554 Hz vs 1.116 Hz, respectively (Harrington 1989; Palacios et al. 2007). We did not consider other types of vocalization such as whimpers, barks, and growls (Joslin 1967; Harrington & Mech 1978), and we measured the entire length of the fundamental frequency of the howl every 0.05 sec to obtain 10 variables, as in previous studies on wolf vocalization (Tooze et al. 1990; Palacios et al. 2007).

In particular, we used the following variables to typify howls: the maximum frequency (Maxf), mean of the fundamental frequency calculated every 0.05 sec (Meanf); difference between maximum and minimum frequencies (Rangef); duration of the howl (Duration); position at which the minimum frequency occurs (time of Minf/Duration) in the howl (Posmin); Position at which the maximum frequency occurs (time of Maxf/Duration) in the howl (Posmax); Coefficient of frequency variation (CofV) as (SD/Meanf) × 100; Coefficient of frequency modulation (CofM) as $\sum|f(t) - f(t+1)|(n-1)/\text{Meanf} \times 100$.

Vocalization parameters were analysed using the Kolmogorov–Smirnov test for normality, and if some parameters were not normally distributed, they were log-transformed to use them in parametric statistical analysis. Thus, differences among acoustic variables of the packs were analysed using a one-way ANOVA, while a DFA (Discriminant Function Analysis) was used in order to assign each howl to a unique pack, with validation through Jack-knife analysis (Durbin 1998).

Acoustic variables were correlated with the environmental variables and following acoustic adaptation hypothesis we considered Rangef, Maxf, Meanf, Minf, and Duration (Boncoraglio & Saino 2007).

The environmental variables were calculated at the response site, which was estimated by triangulation from three reference points, creating a buffer area with a radius of 50 m (the radius measure was chosen to avoid errors in estimating the response site). We considered environmental variables as follows: vegetation cover as a percentage of close habitat; exposure as a degree compared to the north; distance from the river, road, and village, expressed in meters. We determined the distances between different response sites to verify the possibility that vocalizations, recorded by different positions, could belong to a single pack or not. We used the distance between response sites to attribute the vocalizations to different packs following Bassi et al. (2015).

Statistical analysis was performed using SPSS version 14.0 for Windows.

RESULTS

From 2011 to 2012, we recorded 37 chorus howls out of a total of 260 trials. The spectrographic analysis was adopted to display the minimum number of individuals in a pack, which ranged from four to seven individuals; moreover, the presence of pups was recorded in three response cases (Table 1).

The analysis of variance showed a significant difference in the structure of vocalizations (Table 2).

After testing the differences in wolf packs' vocalization, we performed a predictive model to generate discriminant functions based on linear combinations of the predictor variables to check if the analysis of the vocalizations had a spatial correspondence with the packs monitored. The main discriminant functions explained 51.4% and 17.7% of the variance, respectively (Table 3).

In addition, the chi-square test showed significant differences in the first group of functions, at the same time all other groups showed no significant changes (Table 3). The model correctly discriminated 35.1% of the cases analysed, in particular, it does not associate vocalizations of Cerreto pack with itself (Table 4).

Distances between consecutive response sites were as follows: Cisa–Logarghena 7 km; Logarghena–Cerreto 23 km; Cerreto–Casola 6 km; Casola–Orecchiella 5 km; Camaldoli–Bocca Pecorina 9 km; we have not considered the distances between individual response sites and associated wolf packs in the Arezzo province, as they are 100 km away. Consequently, we analysed the vocalizations obtained from two adjacent packs, as if they belonged to the same pack. The best model was the one that considered the pack of Orecchiella as a single pack and paired the packs of Cisa and Logarghena and those of Cerreto and Casola, respectively (Table 5). Furthermore, the packs considered coupled have shown an identical minimum number of individuals (Cisa–Logarghena, n = 4) or very similar (Casola–Cerreto, n = 4 and n = 3, respectively). Then, we considered the vocal structure in relation to environmental variables, and we found a significative correlation, except for exposure, for Maxf (Pearson's correlation — vegetation cover: $\rho = 0.375$, $P = 0.022$; exposition: $\rho = -0.94$, $P = 0.579$; river distance: $\rho = -0.439$, $P = 0.007$; village distance: $\rho = -0.396$, $P = 0.015$; road distance: $\rho = -0.334$, $P = 0.048$) and the highest value of Maxf was recorded in the closest environment. The same result was found when we considered Meanf, whose highest value was recorded in the closest environment considered (Pearson's correlation — vegetation cover: $\rho = 0.356$, $P = 0.031$), while with other environmental variables, no correlations were found.

When we considered both Minf and Duration as vocalization parameters, we did not observe a significant interaction with environmental parameters. Rangef showed a different correlation in regards to the environmental variable considered (Pearson's correlation — vegetation cover: $\rho = 0.243$, $P = 0.147$; exposition: $\rho = -0.91$, $P = 0.591$; river distance: $\rho = -0.459$, $P = 0.004$; village distance: $\rho = -0.515$, $P = 0.515$; road distance: $\rho = -0.234$, $P = 0.163$), and the highest value of Rangef was recorded on the site closest to river.

DISCUSSION

In this study, we described the spatial distribution of five wolf packs through the spectrographic analysis of choral vocalizations emitted in different habitat types.

The analysis of sonograms and wolf-howling technique is an excellent tool to support wildlife management, as it allows to ascertain the presence of packs, while avoiding errors of overestimation of the population. For example, using this approach, we were able to recognise vocalisations recorded in the two areas of Cerreto and Casola, as belonging to the same pack. The site of Cerreto is included in Tosco-Emilian Apennine National Park, and a wolf monitoring protocol has been in place

Table 1.
Minimum number of wolves in the pack (visual inspection of the narrowband spectrograms).

Pack	Province	Sessions (n)	Howls (n)	Min. no. adults	Min. no. pups	Min. no. of wolves/pack
Logarghena	Massa-Carrara	8	3	4	0	4
Cerreto	Massa-Carrara	6	8	2	0	2
Casola	Massa-Carrara	6	5	3	1	4
Cisa	Massa-Carrara	5	9	2	0	2
Orecchiella	Lucca	5	2	3	0	3
Camaldoli	Arezzo	5	5	5	2	7
Bocca Pecorina	Arezzo	4	5	4	0	4

Table 2.

Comparison among packs of the variables considered for the statistical analysis (Kruskal–Wallis with Monte Carlo exact test).

Parameters	df	χ^2	*P*
Meanf	6	4.307	0.003
Rangef	6	6.172	< 0.001
Maxf	6	8.699	< 0.001
Ln (Minf)	6	2.859	0.025
Ln (Endf)	6	2.177	0.073
Duration	6	1.478	0.219
Posmin	6	1.992	0.098
Posmax	6	1.703	0.155
CofV	6	0.605	0.724
CofM	6	2.929	0.023

for several years, confirming the presence of a stable pack in that area. In addition, during the monitoring sessions in Cerreto area, a wolf pack with pups was recorded, while in the adjacent Casola area a choral response was recorded without the presence of pups. It would have been reasonable to assume that the recorded vocalizations belonged to distinct groups, as the two locations are divided by an area with high anthropogenic disturbance, and geomorphological features, with bibliographic data estimating the home range of Apennine packs around 80 km^2 (Ciucci et al. 1997). However, the analysis of acoustic variables is in contrast with the initial hypothesis because the vocal signatures of howling recorded in the two sites are very similar. Furthermore, a discriminant analysis returned a grouping with a higher percentage match when recordings of Casola and Cerreto were considered to belong to a single pack, confirming the importance of this technique for monitoring this species. The presence of pups is strongly linked to the permanence in the rendezvous site (Harrington & Mech 1978; Capitani et al. 2006; Zaccaroni et al. 2012; Iliopoulos et al. 2014; Bassi et al. 2015) and probably the choral response recorded in Cerreto was given by a rendez-vous site. Instead, the choral response in Casola area could have been carried out during a displacement of some individuals of the pack, without the presence of the pups; this is confirmed by the analysis of the sonograms which highlighted the high similarity of the vocal structure.

The behavioural adaptability of mammals is not only a function of sex and age but depends on environmental factors that combine to determine the home-range (Albon et al. 1992). The home-range variations in mammals occur in environments with strong seasonal changes (Georgii & Schröder 1983; Jeppesen 1990; Tufto et al. 1996) or in function of the trophic availability (Boyce 1991; Carranza et al. 1991; Bertrand et al. 1996). Similarly, for the wolf, territory size is not static but may change seasonally, including areas best suited to the biological needs of that particular time of year (Mech 1994). In the presence of pups, a pack must find safe and secure sites, where they stabilize until the pups grow up.

Table 3.
Eigen values and canonical correlation of the discriminant function.

Functions	Eigen values	Variance %	Cumulative %	Canonical correlation	Function test	Wilks' lambda	χ^2	df	*P*
1	2.373	51.4	51.4	0.839	From 1 to 6	0.050	82.55	60	0.028
2	0.818	17.7	69.1	0.671	From 2 to 6	0.168	49.11	45	0.312
3	0.611	13.2	82.3	0.616	From 3 to 6	0.305	32.68	32	0.433
4	0.412	8.9	91.2	0.540	From 4 to 6	0.491	19.56	21	0.549
5	0.260	5.6	96.9	0.454	From 5 to 6	0.693	10.08	12	0.609
6	0.145	3.1	100	0.356	6	0.874	3.72	5	0.591

Table 4.

Pack classification without considering the environmental variables and considering each response site as belonging to different packs.

Correct percentage (%)	Logarghena	Camaldoli	Orecchiella	Bocca Pecorina	Cerreto	Casola	Cisa
Logarghena	66.7	0	33.3	0	0	0	0
Camaldoli	0	60	0	20	20	0	0
Orecchiella	0	0	100	0	0	0	0
Bocca Pecorina	40	0	20	20	20	0	0
Cerreto	12.5	25	0	37.5	0	25	0
Casola	20	0	0	0	0	60	20
Cisa	22	0	55.6	0	0	0	22.2

Table 5.

Pack classification considering the environmental variables and grouping the answers in relation to the distances of the response sites.

Correct percentage (%)	Cisa–Logarghena	Camaldoli	Orecchiella	Bocca Pecorina	Cerreto–Casola
Cisa–Logarghena	75	0	16.7	8.3	0
Camaldoli	0	70	0	0	30
Orecchiella	0	0	91.2	0	8.8
Bocca Pecorina	0	20	0	60	20
Cerreto–Casola	25	4.4	25	0	45.6

If we consider these aspects, it is possible that the pack is stimulated in different locations, with different environmental characteristics and that it modulates its vocalizations slightly, depending on the type of vegetation present, creating an error in the attribution of vocalizations. The acoustic properties of an environment can influence the evolution of vocalization and its propagation in the air (Brown et al. 1995), and how forests, grassland, and wetlands support a diverse array of sounds produced by animals (Marler & Slabbekoorn 2004). Thusly wolves could produce vocalisations of different frequencies in relation to the environment, to optimise vocalisation efforts. For this reason, at first time the packs of Casola and Cerreto, as well as that of Cisa and Logarghena, were considered as separate nuclei because they showed a significant difference in statistical analysis. However, we considered the possibility that this difference is due to a modulation of frequencies because the sounds were emitted in different environments, and not by distinct packs, with the statistical analysis providing a more precise model.

Our results showed that the selection of safer areas means denser vegetation and that this selection could impact on the type of communication. To improve the range a howl reaches, packs could adopt higher frequencies that are better propagated in closed habitats while maintaining the fundamental sound structures. This concept has been recorded in other studies, i.e. Japanese macaques (*Macaca fuscata*), which use lower frequencies to communicate in open habitats, but each individual maintains a well-defined speech module (Tanaka et al. 2006). The use of howls in the monitoring of wolf populations is increasingly widespread, even with the use of autonomous recorders that do not provide for the direct stimulation of the packs howling, taking weather conditions into account as an influence of sound propagation and signal detection (Papin et al. 2018).

Given the results presented here, we argue that environmental characteristics could have an influence on the frequencies used by wolves during vocalizations and should therefore be included in sound analysis models to recognise individual packs.

The spectrographic analysis of the vocal parameters incorporating the analysis of environmental characteristics can be considered a valid analytical technique to support long-standing 'classical' methods.

DISCLOSURE STATEMENT

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