



## Original Investigation

Acoustics of male rutting roars in the endangered population of Mesola red deer *Cervus elaphus italicus*Matteo Della Libera<sup>a,1</sup>, Daniela Passilongo<sup>b,\*,1</sup>, David Reby<sup>a</sup><sup>a</sup> Mammal Vocal Communication and Cognition Research, School of Psychology, University of Sussex, Falmer, United Kingdom<sup>b</sup> Department of Natural and Environmental Sciences, University of Sassari, via Muroni 25, I-07100 Sassari, Italy

## ARTICLE INFO

## Article history:

Received 11 September 2014

Accepted 4 May 2015

Handled by Juan Carranza

Available online 11 May 2015

## Keywords:

Acoustic behaviour

*Cervus elaphus*

Mesola red deer

Vocal signature

Roar

## ABSTRACT

Mesola red deer are the only native red deer population remaining in peninsular Italy (Mattioli and Ferretti 2014; Zachos et al. 2014). Their peculiar morphological aspects and genetic makeup have earned them the qualification of Evolutionary Significant Unit (ESU), and the status of subspecies has recently been proposed. Despite this, their behaviour remains poorly documented. Because vocal behaviour, including rutting vocalisations, can provide useful phylogenetic signals (Cap et al. 2008), we present the first description of the main sexually selected male call. We find that roars of Mesola red deer are characterised by a relatively low average fundamental frequency (79 Hz) compared to that of most continental red deer populations, confirming the phenotypic originality of Mesola red deer and strengthening the case for its conservation. We also report that roars contain cues to identity, which could support individual recognition tools for monitoring this endangered population.

© 2015 Deutsche Gesellschaft für Säugetierkunde. Published by Elsevier GmbH. All rights reserved.

## Introduction

Italy has two distinct native red deer populations: Corsican deer (*Cervus elaphus corsicanus*) in Sardinia and Corsica, and Mesola red deer (*Cervus elaphus*) in peninsular Italy (Lovari and Nobili 2010). The other populations (Alps and Apennine) are originated either from reintroductions of deer of Central European or from natural expansion of deer population of the northern side of the Alps (Apollonio et al. 2010). While Corsican deer are now considered as a subspecies and protected by European and national laws (Lovari and Nobili 2010) Mesola red deer have only recently been proposed as a distinct subspecies (*Cervus elaphus italicus* nova ssp. Zachos et al. 2014). Centuries of geographic isolation in flat coastal Sub-Mediterranean woodland have led to phenotypic peculiarities that differentiate this Mediterranean red deer from Central European red deer (Mattioli et al. 2003; Lovari and Nobili 2010): adult of both sexes have a relatively low weight (110 kg and 74 kg vs. 160 kg and 110 kg, males and females respectively; Mattioli et al. 2003), mean linear dimensions are 8–15% less than in Swiss, German and Norwegian populations (von Raesfeld and Reulecke 1988; Drechsler, 1988; Mattioli et al. 2003) and adult height at withers is

approximately 58% of head-trunk length compared to approximately 63% in Alpine red deer (Langvatn and Albon 1986; Mattioli et al. 2003). Other peculiar characteristics are white spotting on the summer coat in both sexes, a lower sexual dimorphism (males are only 40–50% heavier than females against 70% in Alpine populations) and a lower growing rate (males reach full body dimensions after 9 years of age, instead of 7–8 years in the Central European population) (Mattioli et al. 2003). Finally, antlers are simplified with only 3 tines per antler compared to 6 in European red deer, and the absence, or a reduction, of the crown (Mattioli 1993; Mattioli et al. 2003; Lovari and Nobili 2010; Mattioli and Ferretti 2014).

Moreover, Mesola deer's mitochondrial DNA (Lorenzini et al. 2005; Zachos et al. 2009; Zachos et al. 2014) is related to that of Corsican deer and Iberian deer, but strongly divergent from that of Central Europe populations (Lorenzini et al. 2005; Zachos et al. 2009; Lovari and Nobili 2010; Zachos et al. 2014). Thus the uniqueness of this population and its biogeographical importance make Mesola red deer a national conservation priority (Mattioli et al. 2003; Mattioli and Ferretti 2014; Zachos et al. 2014), as recognised by its Evolutionary Significant Unit (ESU) status (Zachos et al. 2009).

Communicative behaviour is a very important component of a species' behavioural repertoire (Laiolo 2010). Acoustic behaviour (Cap et al. 2002) and more specifically sexually selected calls (Cap et al. 2008) can constitute useful phylogenetic signals and therefore inform the status of specific populations, as well as provide indirect management tools (Terry et al. 2005).

\* Corresponding author. Tel.: +39 3338762597.

E-mail address: [dpassilongo@uniss.it](mailto:dpassilongo@uniss.it) (D. Passilongo).<sup>1</sup> These authors have contributed equally to this work.

Research on mammal vocal communication has benefited from the application of the ‘source–filter theory’ (Fant 1960; Titze 1994; Taylor and Reby 2010) to vertebrate vocal signals. According to this theory, voiced signals are composed of two main components produced by different parts of the vocal apparatus: the source-related fundamental frequency (F0) and the filter-related formant frequencies (Fant 1960; Titze 1994; Taylor and Reby 2010). The fundamental frequency is determined by the rate of the vibration of the vocal folds caused by the passage of air through the glottis into the larynx (the source) and the formants are resonance frequencies produced as the glottal wave travels through the supralaryngeal vocal tract (filter). While F0 determines the perceived pitch of the sound; formants contribute to the timbre of the vocalisation (Reby and McComb 2003a). Because of its dependence on the length of the supra laryngeal vocal tract (Titze 1994), formant frequency spacing provides a reliable indication of body size (red deer, *Cervus elaphus*: McComb 1988; Reby and McComb 2003a,b; rhesus monkeys, *Macaca mulatta*: Fitch 1997; dogs, *Canis lupus familiaris*: Riede and Fitch 1999). Moreover, the relative distribution of formant frequencies also encodes information on individual identity in many mammals species (rhesus monkey: Fitch 1997; Rendall et al. 1998; fallow deer, *Dama dama*: Vannoni and McElligott, 2007; red deer: Kidjo et al. 2008; goitred gazelle, *Gazella subgutturosa*: Volodin et al. 2011; Lapshina et al. 2012).

Red deer males have a descended and highly mobile larynx (Fitch and Reby 2001), which they are able to retract further towards the sternum while they vocalise. This allows them to increase their supralaryngeal vocal tract length (Fitch and Reby 2001), thereby retracting the formant frequencies in their roars. Minimum formant dispersion (the minimum spacing of formants during roaring), achieved when the vocal tract is fully extended, provides honest indication of body size to receivers (Reby and McComb 2003b). A similar anatomical adaptation, leading to honest communication of body size has been reported in the groans of fallow deer (McElligott et al. 2006; Vannoni and McElligott 2008).

Like other polygynous deer, Mesola red deer males display a very intense vocal activity during the mating season (Chinellato et al. 2010), which can be assumed to function as a means of attracting females and/or threatening opponents (Clutton-Brock and Albon 1979). While previous comparative investigations of sexually selected calls in red deer have revealed a high diversity of the composition of roaring sequences and the detailed acoustic structure of the roars between subspecies (*C. e. scoticus*: Reby and McComb 2003a, 2003b; *C. e. corsicanus*: Kidjo et al. 2008; *C. e. hispanicus*: Frey et al. 2012; Passilongo et al. 2013; Volodin et al. 2014; *C. e. hippelaphus*: Favaretto et al. 2006; Bocci et al. 2012) the rutting calls of Mesola red deer stags have not yet been described.

Thus, the aim of the current study was to provide a detailed description of the most common call type given by Mesola red deer stag – the roar – in order to contrast it with that of other subspecies. We also estimate the potential of this vocalisation for supporting the discrimination of individual stags.

## Material and methods

### Study area and population

The National Reserve of Mesola wood is a small forest (1058 ha) located along the coast of the Adriatic Sea in northern Italy. Woodlands are dominated by deciduous trees (mostly the Holm oak – *Quercus ilex*) and cover about 93% of the area. Two different forest communities are present: the Mediterranean xerophilic wood covering the oldest sand dunes (with *Fraxinus ornus*) and the mesophilic wood (with *Carpinus sp.*). Grasslands and wetland

occupy 3% and 4% respectively of the area (Mattioli et al. 2003). The fact that the woods are surrounded by the sea and malarial swamps has protected the deer population from manmade extinction (Lovari and Nobili 2010). However, the combination of human interference (including hunting, poaching and logging) with natural constraints (disease, flooding and isolation) have led Mesola red deer to experience a number of demographic crashes followed by slow recoveries (Lovari and Nobili 2010). During the 20th century, the population dropped from 250 to 300 individuals in the ‘30s to 10 animals after the Second World War. It then increased back to 40 in the 1970 and 120 in 1980, to decrease again to 59 in 1992 (Mattioli 1990; Mattioli et al. 2003). In 1999 population comprised 67 individuals, increasing to 120 individuals in 2006 (Lovari and Nobili 2010).

### Data collection

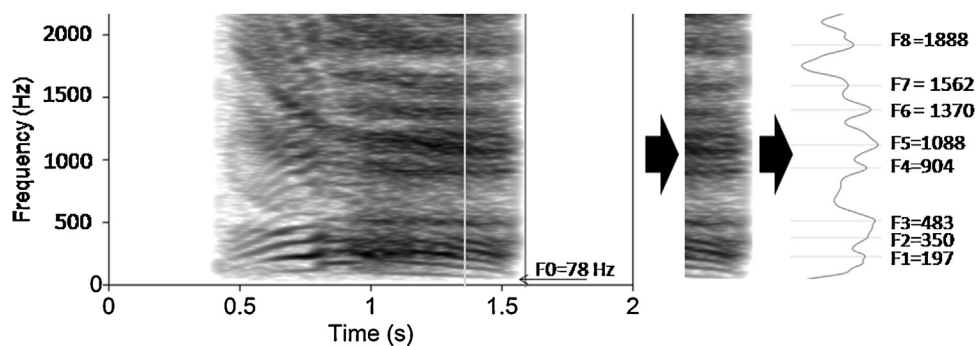
Data collection took place during the 2006 rutting season. Recordings were carried out from fixed hidden positions in areas where deer were known to be most active. Adult males were individually identified from the dimensions, shape and branching pattern of their antlers. Over 30 h of vocal displays from 6 of the 10 roaring adult males were recorded during 4 days (at distances ranging from 30 to 100 m). As a result a total of 113 vocalizations (between 6 and 35 per individual) were extracted and analysed.

Audio tracks were recorded with a microphone Sennheiser MKH 70 (Wedemark, Germany) and a hand-held M-Audio Microtrack 24/96 digital recorder (Cumberland, United States), and transferred onto Mac Book by means of an Edirol FA-66 Firewire audio card (Dee Why, Australia). Vocalizations were recorded in monophonic mode with 24 bit accuracy and 48 KHz sampling rate and saved in “.wav” format.

### Sound Analysis

All acoustic analyses were conducted using PRAAT speech analysis freeware package (Boersma and Weenick, 2008). The overall spectral structure of each vocalisation was initially investigated using narrow band spectrograms. The fundamental frequency contour for each call were extracted using a forward cross-correlation [to pitch (cc) command] algorithm in Praat. A purpose-written script calculated the start (StartF0), minimum (MinF0), mean (MeanF0), maximum (MaxF0) and end (EndF0) of the fundamental frequency as well as the call duration (Dur) and number of Inflexion points (Inflex) per unit time (seconds) of the frequency contour (an inflexion corresponding to a change in the sign of the derivative of the fundamental frequency contour). The analysis’ parameters (minimum and maximum F0) were set according to the F0 contour observed on the narrow band spectrogram (generally between 20 and 200 Hz). The time step in the analysis was 0.02 s.

A cepstral smoothing filter was applied to the spectrum in order to remove the contribution of the source periodicity (F0) from the frequency spectrum ([cepstral smoothing] command in Praat), thereby highlighting the effect of the filter (Fig. 1). The minimum values of the first 8 formant frequencies (F<sub>1</sub>–F<sub>8</sub>) were extracted from the resulting smoothed spectrum using the command [to formants] in Praat. Parameters were set as follow: time step: 0.01 s; maximum number of formants: 8–10; maximum formants: 2000–2300 Hz; window analysis: 0.01 s. For each call, we calculated the minimum formant dispersion ( $\Delta F$ ) and the corresponding maximum estimated VTL (eVTL), using the linear regression method outlined in Reby and McComb (2003a). All formant frequency values were verified by visual inspection of narrow band spectrograms. Calls with high levels of background noise



**Fig. 1.** Extraction of the minimum frequency of individual formants in a Mesola deer roar. A spectrum was computed on the section of the spectrogram where individual formants reach their lowest frequencies. Cepstral smoothing was applied to the spectrum in order to remove the periodicity of the source (F0), thereby highlighting the effect of the filter.

were excluded from the analysis. A total of 15 variables were extracted.

### Statistical analysis

All analyses were computed with R 2.14.0 (R Development Core Team 2008). Descriptive statistics (mean  $\pm$  standard deviation) were computed for all extracted variables. We quantified the individual distinctiveness of the roars by the means of a principal component analysis (PCA) followed by a discriminant function analysis (DFA). The PCA (“princomp”, in the default library “STATS”) was used to replace the original number of variables by a smaller set of uncorrelated variables which are linear composites of the original ones. Variables calculated from other variables such as formant dispersion and estimated vocal tract length were excluded from the PCA analysis as they were inherently correlated with the original variables. We retained principal components with eigenvalues greater than 1 (Kaiser’s criterion) for subsequent analyses. The scores of the retained components were tested for normality (Kolmogorov–Smirnov test). A linear DFA (using the “lda” function in the “MASS” library) was then applied in order to estimate the potential of the acoustic structure to support the discrimination of individual stags from their roars. Stag identities were used as the group identifier (with equal a priori probabilities) and the scores of the components were used as discriminant variables. A *Leave-one-out* procedure (where a model is built for each call and all the calls but the one being tested are used for building each model) was applied, and the percentage of calls attributed to the correct individual was compared to the chance percentage obtained by performing the discriminant function analysis on 1000 random permutations of the data set (“bootest” function in the “ipred” library). All values are reported as mean  $\pm$  standard deviation.

Tests were two-tailed and the significance level was set at  $\alpha = 0.05$ .

## Results

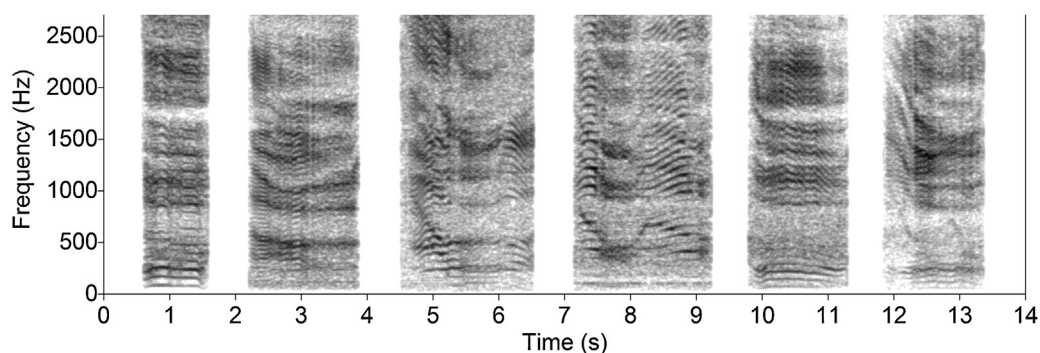
### Acoustic parameters of roars

The MeanF0 of the analysed roars ranged between 45 and 119 Hz ( $79 \pm 9$  Hz). The MinF0 of the roars ranged between 21 Hz and 113 Hz ( $60 \pm 10$  Hz), while the MaxF0 ranged between 49 to 180 Hz ( $91 \pm 8$  Hz). The duration (Dur) of the roars ranged between 0.43 and 3.05 s ( $1.5 \pm 0.3$  s). Finally, the number of abrupt change in frequency contour (Inflex) ranged between 0.7 and 10.5 per second ( $5.2 \pm 1.4$ ) (Table 1). Values are reported as (mean  $\pm$  SD) and were calculated as the averages of the means of the six individuals.

Formant frequencies descend at the beginning of the roar (Fig. 1 and Fig. 2) with the first three formants clustered in the lower portion of the spectrum (Fig. 1). The centre frequencies of the measured formants were F1:  $217 \pm 44$  Hz, F2:  $344 \pm 63$  Hz; F3:  $502 \pm 84$  Hz, F4:  $888 \pm 61$  Hz, F5:  $1086 \pm 44$  Hz, F6:  $1336 \pm 57$  Hz, F7:  $1560 \pm 65$  Hz and F8:  $1828 \pm 68$  Hz. The  $\Delta F$  was 241.7 Hz corresponding to an average eVTL of 72.4 cm. The average values of Fundamental and formant frequencies variables for each individual stag are reported in Table 1.

### Individual discrimination

The PCA produced 4 components (PC1–PC4) that exceeded Kaiser’s criterion (eigenvalues greater than 1). Together these components explained 62% of the variance. PC1, which explained about 25% of the variance, was mostly related to the MeanF0, EndF0 and MinF0. PC2 explained about 18% of the variance and was



**Fig. 2.** Roars of Mesola red deer. Each call corresponds to a distinct individual. Note formants descending at the beginning of the calls, indicating vocal tract elongation as the larynx is retracted towards the sternum.

**Table 1**  
Mean and standard deviations of acoustic variables and estimated vocal tract lengths measured from the roars of 6 Mesola red deer stags.

	Mesola red deer stag roars						All Stags (n=6)
	ID 1 (n=30)	ID 2 (n=19)	ID 3 (n=12)	ID 4 (n=11)	ID 5 (n=35)	ID 6 (n=6)	
Dur(s)	1.1 ± 0.3	1.6 ± 0.5	1.5 ± 0.5	2.0 ± 0.7	1.2 ± 0.3	1.3 ± 0.4	1.5 ± 0.3
StartF0(Hz)	68 ± 20	56 ± 17	86 ± 15	54 ± 21	62 ± 19	63 ± 13	65 ± 12
EndF0(Hz)	72 ± 22	53 ± 14	85 ± 18	47 ± 16	64 ± 20	77 ± 24	67 ± 14
MeanF0(Hz)	77 ± 15	70 ± 12	96 ± 5	76 ± 15	77 ± 15	75 ± 22	79 ± 9
MaxF0(Hz)	91 ± 23	81 ± 12	104 ± 6	93 ± 16	89 ± 18	89 ± 25	91 ± 8
MinF0(Hz)	62 ± 15	56 ± 13	77 ± 19	46 ± 22	62 ± 16	56 ± 22	60 ± 10
Inflex	4.8 ± 1.9	3.7 ± 1.9	6.9 ± 2.0	4.0 ± 1.0	4.3 ± 2.1	7.0 ± 1.5	5.2 ± 1.4
F1(Hz)	232 ± 38	220 ± 42	162 ± 49	248 ± 33	209 ± 33	231 ± 43	217 ± 30
F2(Hz)	350 ± 57	364 ± 71	325 ± 62	413 ± 57	314 ± 47	334 ± 48	350 ± 35
F3(Hz)	497 ± 59	526 ± 79	473 ± 62	596 ± 118	477 ± 86	497 ± 13	511 ± 46
F4(Hz)	903 ± 68	855 ± 69	851 ± 60	902 ± 53	899 ± 46	896 ± 35	884 ± 24
F5(Hz)	1101 ± 59	1053 ± 33	1070 ± 39	1066 ± 30	1102 ± 28	1095 ± 26	1081 ± 21
F6(Hz)	1354 ± 55	1299 ± 66	1320 ± 55	1321 ± 70	1355 ± 41	1322 ± 26	1329 ± 22
F7(Hz)	1568 ± 65	1513 ± 83	1534 ± 60	1571 ± 68	1581 ± 38	1589 ± 56	1559 ± 30
F8(Hz)	1862 ± 82	1776 ± 63	1806 ± 50	1814 ± 64	1837 ± 51	1844 ± 11	1823 ± 31
ΔF(Hz)	244 ± 9	236 ± 6	237 ± 6	243 ± 5	244 ± 5	243 ± 2	241 ± 4
eVTL(cm)	71.6 ± 2.8	74.2 ± 2.0	73.7 ± 1.9	72.1 ± 1.3	71.8 ± 1.3	71.9 ± 0.6	72.6 ± 1.1

associated with the F6, F5, F4, and F7. PC3 explained almost 13% of the variance and was related to the F2. Finally PC4 explained 7% of the variance and was highly related to Dur. The DFA based on the first four principal components attributed about 61% of the roars to the correct individual (Fig. 3). The percentage of correct classification was 51% when a more conservative *leave-one-out* cross validation was applied and was significantly better than expected in a random classification (30%,  $p < 0.0001$ , binomial test; Table 2).

The first discriminant function accounted for about 60% of the variance and highly correlated with PC1 and thus with the MeanF0, EndF0 and MinF0 (Table 3). The second discriminant function accounted for 26% of the variance and was associated with PC2 and thus to F6 and F5; the third discriminant was mostly related to the PC3, and thus to F2 and explained 13% of the inter-individual variance (Table 3). Finally the fourth discriminant function only accounted for 1% of the inter-individual variance and was mostly related to PC4, and thus duration (Dur) (Table 3).

## Discussion

We found that the roars of Mesola red deer stags are characterised by distinctive acoustic features: the mean fundamental

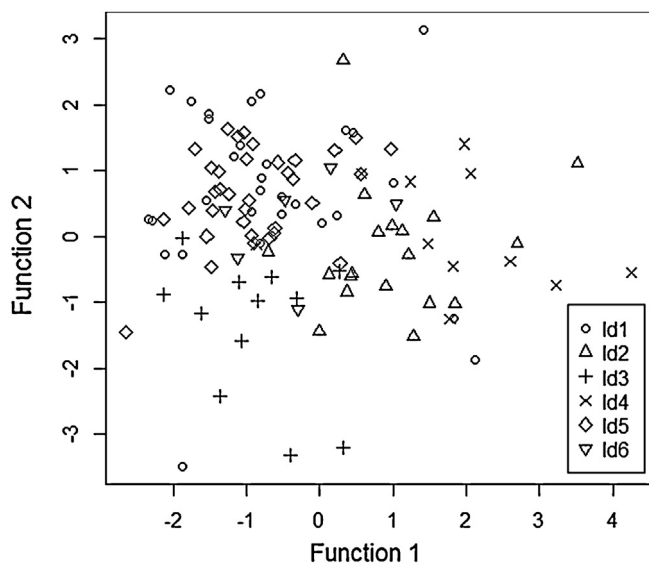
**Table 2**  
Factor loadings of the measured acoustic variables on the four principal components with eigenvalues >1. Factor loadings >0.4 are presented in bold.

Acoustic variables	PC1	PC2	PC3	PC4
Dur(s)	0.13	-0.24	-0.09	<b>0.74</b>
StartF0(Hz)	-0.39	0.04	-0.04	0.16
EndF0(Hz)	<b>-0.41</b>	0.08	-0.02	0.14
MeanF0(Hz)	<b>-0.45</b>	-0.03	-0.18	-0.06
MaxF0(Hz)	-0.37	0.00	-0.20	0.03
MinF0(Hz)	<b>-0.41</b>	-0.07	-0.10	-0.25
Inflex	-0.27	-0.02	-0.09	0.31
F1(Hz)	0.10	0.27	-0.36	-0.04
F2(Hz)	0.12	0.15	<b>-0.61</b>	-0.10
F3(Hz)	0.18	0.18	-0.47	0.09
F4(Hz)	0.06	<b>0.40</b>	-0.13	0.18
F5(Hz)	-0.07	<b>0.42</b>	0.15	-0.28
F6(Hz)	0.03	<b>0.43</b>	0.18	0.05
F7(Hz)	-0.10	<b>0.40</b>	0.13	0.26
F8(Hz)	-0.05	0.34	0.28	0.23
Eigenvalues	3.72	2.70	1.91	1.04
Variance %	25	18	13	7

frequency (79 Hz) is almost twice that of Corsican deer (40 Hz, Kidjo et al. 2008) but lower than that of Scottish red deer (112 Hz, Reby and McComb 2003b) or Iberian red deer (186 Hz, Frey et al. 2012;) and also considerably lower than that of Alpine red deer (MinF0=150 Hz and MaxF0=274 Hz, Bocci et al. 2012). As a consequence roars of Mesola red deer stags sound substantially lower-pitched than that of other continental red deer population. This characteristically low fundamental frequency may reflect disproportionately larger vocal folds, which would contrast with the typically reduced phenotypical features

**Table 3**  
Correlation matrix from the DFA based on the extracted principal components. The coefficients of the linear discriminant functions represent the contribution of each variable to discrimination. Coefficients with the largest unsigned values are presented in bold. The acoustic variables that correlate most with for each principal component are presented in bracket to facilitate interpretation.

	Linear discriminant functions			
	1	2	3	4
PC1 (MeanF0)	<b>0.67</b>	0.49	-0.36	0.37
PC2 (F6)	-0.24	<b>0.79</b>	0.19	-0.58
PC3 (F2)	-0.65	0.22	<b>-0.69</b>	0.26
PC4 (Dur)	0.27	-0.31	-0.60	<b>-0.68</b>
% of variance	59.9	25.8	13.2	1.1



**Fig. 3.** Scatterplot illustrating the distribution of the rutting calls of six Mesola red deer stags against the first two functions of the DFA.



characteristic of this population (relatively small body size, low sexual dimorphism and simple antlers (Mattioli 1993; Mattioli et al. 2003; Mattioli and Ferretti 2014)). Anatomical investigations are now needed to determine the contribution of the vocal anatomy to the observed acoustic features. Combined with the previously reported morphological and genetic peculiarity of the Mesola red deer population (Lorenzini et al. 2005; Mattioli and Ferretti 2014; Zachos et al. 2014) these vocal idiosyncrasies support its uniqueness and suggest that it deserves special protection (Lovari and Nobili 2010; Zachos and Hartl, 2011; Ferretti and Mattioli 2012; Mattioli and Ferretti 2014; Zachos et al. 2014)

Due to the high spectral density resulting from the relatively low fundamental frequency, roars are also characterised by well-defined formant frequencies. As in other red deer subspecies and ecotypes, (*C. e. scoticus*: Reby and McComb 2003a,b; *C. e. corsicanus*: Kidjo et al. 2008; *C. e. hispanicus*: Passilongo et al. 2013), formants descend at the beginning of the roar, suggesting an elongation of the vocal tract caused by retraction of the larynx during the roar (Frey and Riede 2013). Formants are also unevenly distributed, indicating that the shape of the vocal tract departs from that of a linear tube (Frey et al. 2012). The average estimated vocal tract length during roaring (eVTL) was 72.4 cm, thus longer than in Corsican deer (68.6 cm Kidjo et al. 2008). Interestingly, although Mesola stags have a lower body weight than Iberian stags (110 and 125 kg respectively), the vocal tract estimated from their roars is very similar to that estimated from the roars of Iberian stags (72.4 vs. 71.2 cm). However it remains lower than that estimated in Iberian deer using only roars containing chaotic segments (76.7 cm, Frey et al. 2012).

Roars of Mesola red deer are also individually distinctive, with 51% correct assignment of calls to individuals. This classification was largely supported by the fundamental frequency, confirming the contribution of source-related variables to individual variation, as previously reported in Alpine red deer (Bocci et al. 2012) and in fallow deer (Vannoni and McElligott, 2007). It was also supported by the highest filter-related formant frequencies, as previously identified in other subspecies of polygynous deer (Scottish red deer: Reby and McComb 2003b; Iberian deer: Passilongo et al. 2013), and probably reflecting inter-individual differences vocal tract dimensions. Although 6 individuals is a relatively small sample, it remains representative of Mesola red deer population, which only contained 10 rutting males in 2006.

In conclusion, this preliminary investigation of the vocal behaviour of Mesola red deer shows that male rutting roars are characterised by relatively low fundamental frequency, which gives them a relatively low pitch that distinguishes them from other continental red deer populations, but which is higher than that reported in Corsican red deer.

This observation reinforces the population's ESU status and supports its upgrade as a different subspecies. While further investigations of the vocal anatomy and full vocal repertoire of Mesola red deer are clearly needed, our study confirms the uniqueness of this small and threatened native Italian deer population.

## Acknowledgements

We are grateful to Marco Apollonio for advice during preparation of the manuscript.

## References

- Apollonio, M., Andersen, R., Putman, R. (Eds.), 2010. *European Ungulates and Their Management in the 21st Century*. Cambridge University Press, Cambridge.
- Bocci, A., Telford, M., Laiolo, P., 2012. Determinants of the acoustic behaviour of red deer during breeding in a wild alpine population, and implications for species survey. *Ethol. Ecol. Evol.* 1–18 (2012.), <http://dx.doi.org/10.1080/03949370.2012.705331>
- Boersma, P., Weenick, D., 2008. Praat: doing phonetics by computer (Computer program), Retrieved from: <http://www.praat.org> (August, 2008).
- Cap, H., Aulagnier, S., Deleporte, P., 2002. The phylogeny and behaviour of Cervidae (Ruminantia Pecora). *Ethol. Ecol. Evol.* 14, 199–216.
- Cap, H., Deleporte, P., Joachim, J., Reby, D., 2008. Cladistics Male vocal behavior and phylogeny in deer. *Cladistic* 24, 917–931.
- Chinellato, F., Carradore, F., Carradore, A., Bergamasco, P., Favaretto, A., Nobili, G., De Battisti, R., 2010. Indagini sull'attività di bramito della popolazione di cervo (*Cervus elaphus* Linnaeus, 1758) del Bosco della Mesola (Fe). *Risultati dell'approccio bioacustico del 2009*. *Hystrix Ital. J. Mammal (n.s.) Sup.*, 2010.
- Clutton-Brock, T.H., Albon, S.D., 1979. The roaring of red deer and the evolution of honest advertising. *Behaviour* 69, 145–170.
- Drechsler, H., 1988. *Altersentwicklung und Altersansprache beim Rotwild*. P. Parey, Hamburg and Berlin, Germany.
- Fant, G., 1960. *Acoustic Theory of Speech Production*. Mouton, The Hague.
- Favaretto, A., de Battisti, R., Pavan, G., Piccinin, A., 2006. Acoustic features of red deer (*Cervus elaphus*) stags vocalization in the Cansiglio forest (NE Italy, 2001–2002). In: *Razprave IV. Razpreda sazu*, Ljubljana, pp. 125–138.
- Ferretti, F., Mattioli, S., 2012. The Mesola red deer: present numbers and conservation perspectives. *Hystrix Ital. J. Mammal* 23, 35–43.
- Fitch, W.T., 1997. Vocal tract length and formant frequency dispersion correlate with body size in rhesus macaques. *J. Acoust. Soc. Am.* 102, 1213–1222.
- Fitch, W.T., Reby, D., 2001. The descended larynx is not uniquely human. *Proc. Biol. Sci.* 268, 1669–1675.
- Frey, R., Volodin, I., Volodina, E., Carranza, J., Torres-Porras, J., 2012. Vocal anatomy, tongue protrusion behaviour and the acoustics of rutting roars in free-ranging Iberian red deer stags (*Cervus elaphus hispanicus*). *J. Anat.* 220, 271–292, <http://dx.doi.org/10.1111/j.1469-7580.2011.01467.x>
- Frey, R., Riede, T., 2013. The anatomy of vocal divergence in North American elk and European red deer. *J. Morphol.* 274, 307–319.
- Kidjo, N., Cargnelutti, B., Charlton, B.D., Wilson, C., Reby, D., 2008. Vocal behaviour in the endangered Corsican deer: description and phylogenetic implications. *Bioacoustics* 18, 159–181.
- Laiolo, P., 2010. The emerging significance of bioacoustics in animal species conservation. *Biol. Conserv.* 143, 1635–1645.
- Langvatn, R., Albon, S.D., 1986. Geographic clines in body weight of Norwegian red deer: a novel explanation of Bergmann's rule? *Ecography* 9, 285–293, <http://dx.doi.org/10.1111/j.1600-0587.1986.tb01221.x>
- Lapshina, E.N., Volodina, I.A., Volodina, E.V., Frey, R., Efremova, K.O., Soldatova, N.V., 2012. The ontogeny of acoustic individuality in the nasal calls of captive goitred gazelles, *Gazella subgutturosa*. *Behav. Process.* 90, 323–330.
- Lorenzini, R., Fico, R., Mattioli, S., 2005. Mitochondrial DNA evidence for a genetic distinction of the native red deer of Mesola, northern Italy, from the Alpine populations and the Sardinian subspecies. *Mamm. Biol. Z. Säugetierkd.* 70, 187–198.
- Lovari, S., Nobili, G., 2010. Programma nazionale di conservazione del cervo della Mesola. *Quad. Cons. Natura*, n. 36. Ministero dell'Ambiente e della Tutela del Territorio e del Mare, Ministero delle Politiche Agricole Alimentari e Forestali – Corpo Forestale dello Stato, I.S.P.R.A., Roma (in Italian with an English summary).
- Mattioli, S., 1990. Red deer in the Italian peninsula with particular reference to the Po delta population. *Deer* 8, 95–98.
- Mattioli, S., 1993. Antler conformation in red deer of the Mesola Wood, northern Italy. *Acta Theriol.* 38, 443–450.
- Mattioli, S., Fico, R., Lorenzini, R., Nobili, G., 2003. Mesola red deer: physical characteristics, population dynamics and conservation perspectives. *Hystrix Ital. J. Mammal* 14, 87–94.
- Mattioli, S., Ferretti, F., 2014. Morphometric characterization of Mesola red deer *Cervus elaphus italicus* (Mammalia, Cervidae). *Ital. J. Zool.* 81, 144–154.
- McComb, K.E., (Ph.D. thesis) 1988. *Roaring and Reproduction in Red Deer Cervus elaphus*. University of Cambridge.
- McElligott, A.G., Birrer, M., Vannoni, E., 2006. Retraction of the mobile descended larynx during groaning enables fallow bucks (*Dama dama*) to lower their formant frequencies. *J. Zool.* 270, 340–345, <http://dx.doi.org/10.1111/j.1469-7998.2006.00144.x>
- Passilongo, D., Reby, D., Carranza, J., Apollonio, M., 2013. Roaring high and low: composition and possible functions of the Iberian Stag's vocal repertoire. *PLoS ONE* 8, e63841.
- R Development Core Team, 2008. *R: A Language and Environment for Statistical Computing*.
- von Raesfeld, F., Reulecke, K., 1988. *Das Rotwild*. P. Parey, Hamburg and Berlin, Germany.
- Reby, D., McComb, K., 2003a. Vocal communication and reproduction in deer. *Adv. Study Behav.* 33, 231–264.
- Reby, D., McComb, K., 2003b. Anatomical constraints generate honesty: acoustic cues to age and weight in the roars of red deer stags. *Anim. Behav.* 65, 519–530.
- Rendall, D., Owren, M.J., Rodman, P.S., 1998. The role of vocal tract filtering in identity cueing in rhesus monkey (*Macaca mulatta*) vocalizations. *J. Acoust. Soc. Am.* 103, 602L 614.
- Riede, T., Fitch, T., 1999. Vocal tract length and acoustic of vocalization in domestic dog (*Canis familiaris*). *J. Exp. Biol.* 202, 2859–2867.
- Taylor, A.M., Reby, D., 2010. The contribution of source-filter theory to mammal vocal communication research. *J. Zool.* 280, 221–236.
- Terry, A.M.R., Peake, T.M., McGregor, P.K., 2005. The role of vocal individuality in conservation. *Front. Zool.* 2, 10.
- Titze, I.R., 1994. *Principles of Voice Production*. Prentice Hall, Englewood Cliffs, NJ.

- Vannoni, E., McElligott, A.G., 2007. Individual acoustic variation in fallow deer (*Dama dama*) common and harsh groans: a source-filter theory perspective. *Ethology* 113, 223–234.
- Vannoni, E., McElligott, A.G., 2008. Low frequency groans indicate larger and more dominant Fallow Deer (*Dama dama*) males. *PLoS ONE* 3, e3113.
- Volodin, I.A., Lapshina, E.N., Volodina, E.V., Frey, R., Soldatova, N.V., 2011. Nasal and oral calls in juvenile goitred gazelles (*Gazella subgutturosa*) and their potential to encode sex and identity. *Ethology* 117, 294L 308.
- Volodin, I., Matrosova, V., Volodina, E., García, A.J., Gallego, L., Márquez, R., Llusia, D., Beltrán, J.F., Landete-Castillejos, T., 2014. Sex and age-class differences in calls of Iberian red deer during rut: reversed sex dimorphism of pitch and contrasting roars from farmed and wild stags. *Acta Ethol.*, <http://dx.doi.org/10.1007/s10211-013-0179-8>
- Zachos, F.E., Hajji, G.M., Hmwe, S.S., Hartl, G.B., Lorenzini, R., Mattioli, S., 2009. Population viability analysis and genetic diversity of the endangered red deer *Cervus elaphus* population from Mesola, Italy. *Wildl. Biol.* 15, 175–186.
- Zachos, F.E., Hartl, G.B., 2011. Phylogeography, population genetics and conservation of the European red deer *Cervus elaphus*. *Mamm. Rev.* 41, 138–150.
- Zachos, F.E., Mattioli, S., Ferretti, F., Lorenzini, R., 2014. The unique Mesola red deer of Italy: taxonomic recognition (*Cervus elaphus italicus nova ssp.*, Cervidae) would endorse conservation. *Ital. J. Zool.* 81, 136–143.