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European-native vocalizing: sex and age-class acoustic variation in the Central European red deer (*Cervus elaphus*)

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Abstract

Within-population acoustic variation of European red deer *Cervus elaphus* follows two empirically established common rules: Rule 1: suggesting similar-pitched stag and hind calls because of potential prevalence of natural over sexual selection on call pitch; and Rule 2: predicting lower-pitched calls in adults, because larger vocal folds normally produce lower-pitched calls in mammals. We found that both rules were supported for native Pannonian red deer from Central Europe. All fundamental frequency (f_0) parameter values of hind contact calls (for the exclusion of the beginning f_0) were indistinguishable from those of stag rutting roars. These results agree with published data on vocalization of male and female American and Asian wapiti *Cervus canadensis*. Calls of adults of either sex were lower in frequency than calf calls. These results disagree with data collected from adult and young American wapiti producing same-frequency calls, probably because of a distinctive mechanism of sound production (whistling).

Keywords

acoustic traits, population characteristics, mother and offspring, Pannonian red deer, stags, hinds.

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1. Introduction

Taxon red deer *Cervus elaphus* sensu lato includes three species: the Central Asian hanglu *Cervus hanglu*, the European red deer *Cervus elaphus* and the East-Asian and American wapiti *Cervus canadensis* (Lorenzini & Garofalo, 2015; Mukesh et al., 2015; Kumar et al., 2017; Niedziałkowska et al., 2021). These three species have a common origin in Central Asia and hybridize with providing fertile hybrids both in captivity or being translocated to other wild habitats (Perez-Espona et al., 2011; Frantz et al., 2017).

Vocal repertoire of the European red deer *Cervus elaphus* includes the contact calls, produced by hinds and calves (Vaňková & Málek, 1997; Sibiryakova et al., 2015; Volodin et al., 2015a) and rutting roars, produced by stags (Reby & McComb, 2003; Frey et al., 2012; Golosova et al., 2021). Stags are vocal primarily during the autumnal rutting periods (Frey et al., 2012; Della Libera et al., 2015; Rusin et al., 2021), whereas hinds and calves are vocal primarily during the spring-summer calf-raising periods (Vaňková & Málek, 1997; Kidjo et al., 2008; Sibiryakova et al., 2015; Volodin et al., 2015a). Stag rutting roars attract hinds and deter rival stags (Clutton-Brock & Albon, 1979; Reby et al., 2005; Charlton et al., 2007). Hinds produce contact calls for re-storing spatial proximity with their young (Vaňková & Málek, 1997; Sibiryakova et al., 2015). Acoustic variables of stag and hind calls represent important behavioural characteristics of populations of red deer *Cervus elaphus* sensu lato (Volodin et al., 2016, 2019; Golosova et al., 2017, 2021).

The main acoustic variables of red deer calls (the fundamental frequency (f_0) representing the rate of vibration of the vocal folds in the larynx, and formants representing resonances of the vocal tract) may be differently affected by natural and sexual selection (Clutton-Brock & Albon, 1979; Reby & McComb, 2003). Call fundamental frequency (f_0) seems to be more strongly affected by natural selection. The rationale for this is that within populations, the f_0s of stag and hind calls are similar (Feighny et al., 2006; Volodin et al., 2015a, 2016), whereas between populations, f_0s vary up to two dozen times (e.g., Kidjo et al., 2008; Della Libera et al., 2015; Volodin et al., 2015a, 2016; Reby et al., 2016).

In contrast to f_0, call formants are under strong pressure of sexual selection (Taylor & Reby, 2010). Formants are inversely related to vocal tract length, so rutting roars of European red deer, with lower-frequency formants, serve to apparent body size exaggeration, effective for attracting potential mates and deterring rival stags (Fitch & Reby, 2001; Reby & McComb, 2003). Based on formants, hinds choose the apparently larger-sized mates (Reby & McComb, 2003; Reby et al., 2005; Charlton et al., 2007, but see Charlton et al., 2008 for exclusion, indicating preference by females of formants characteristic for voices of young males). Under strong force of sexual selection, European red deer stags developed an ability to additionally elongate the vocal tract, by retracting the larynx deeply down for producing their rutting roars with lower-frequency formants (Reby & McComb, 2003; Frey et al., 2012; Volodin et al., 2019). In contrast to stags, hinds only weakly retract the larynx during their contact calls and their calls are usually relatively short (Sibiryakova et al., 2015).

Whereas within populations of European red deer sex-related differences in f_0 are negligible or small, the respective age-related differences in f_0 are prominent. In all studied European-origin populations of red deer, calls of calves are substantially higher in frequency than in adults (Vaňková & Málek, 1997; Kidjo et al., 2008; Sibiryakova et al., 2015; Volodin et al., 2015a). This ontogenetic pathway, with decreasing f_0, is typical for mammals and might be related with physical growth of body and vocal folds rather than any pressures of natural or sexual selection (Charlton & Reby, 2016; Garcia et al., 2017; Garcia & Ravignani, 2020; De Gregorio et al., 2022).

So far, all studies of sex and age-class acoustic variation across European red deer populations have suggested the use of two hypothesized rules. Rule 1: stags and hinds use calls of similar-frequencies, and Rule 2: the fundamental frequency of calls in adults is lower than that of calves. At the same time, sex and age-class acoustic variation in all studied populations of American and Asian wapiti *Cervus canadensis* only follow Rule 1, producing calls with similar f_0s between sexes (Feighny et al., 2006; Volodin et al., 2016). However, they do not follow Rule 2, producing adult and young contact calls with similar or equal f_0s (Feighny, 2005; Feighny et al., 2006; Volodin et al., 2016; Sibiryakova et al., 2018).

In this study, we investigate whether acoustic variation of Central European Pannonian red deer (Banwell, 1998, 2002; Bana et al., 2018; Volodin et al., 2019; Golosova et al., 2021; Frank et al., 2022) follows the trend typical for other studied populations of European red deer or represents an exception following those trends which are typical for wapiti. This comparison is legitimate as rutting calls of stags, and contact calls of hinds and calves partly share the same function: all of them are designed to attract (Lingle et al., 2012).

Pannonian red deer population from South Hungary includes both wild-living and farmed animals (OVA, 2018; Volodin et al., 2019). Native Pannonian red deer from South Hungary display many shared traits with other populations of European red deer in morphology (Banwell, 1998, 2002) and genetics (Bana et al., 2018; Golosova et al., 2021; Frank et al., 2022). Based on mitochondrial and nuclear genetic markers, Pannonian red deer represent the native Central European population of red deer (Golosova et al., 2021; Frank et al., 2022).

Stag rutting roars of Pannonian red deer are reminiscent of the roars of other European populations of *C. e. hippelaphus* (Volodin et al., 2019; Golosova et al., 2021). Pannonian stags produce their rutting roars in bouts of 3.18 ± 2.17 roars per bout on average. Duration of longest roars within bouts ranges from 0.47 s to 4.60 s (1.13 ± 0.50 s on average) and the maximum fundamental frequency ($f_{0\,\mathrm{max}}$) ranges from 63 Hz to 584 Hz (168.3 ± 60.5 Hz on average) (Volodin et al., 2019). For comparison, $f_{0\,\mathrm{max}}$ of the rutting roars of other European subspecies ranges of 52–274 Hz on average depending on subspecies/population (Golosova et al., 2021). Hind and calf vocalizations of Pannonian red deer have yet to be investigated.

The aim of this study was to compare the acoustic variables of contact calls between farmed hinds and calves and to compare them with the acoustic variables of rutting calls of wild-living stags. This comparison was intended to test, for Pannonian red deer, Rule 1, predicting similar fundamental frequencies of stags and hinds within population, because of potential prevalence of natural over sexual selection on call pitch, and Rule 2, predicting an ontogenetic decrease of fundamental frequency, because larger vocal folds of larger adults commonly produce lower-pitched calls than smaller vocal folds of the young in mammals.

2. Materials and methods

2.1. Sites, animals and dates of work

Vocalizations were recorded in South Hungary, where Pannonian red deer are native. Stag rutting calls were recorded during the rutting period, on the 12 800 ha at the hunting area nearby the city of Nagyatád, Hungary (46.067 N, 17.492 E) from 9 September to 6 October 2015 (Volodin et al., 2019). The estimated total population number in Hungary in 2018 was 111 450 individuals (OVA, 2018). Hind and calf contact calls were recorded during the calving period, at the Deer Farm of the Game Management and Landscape Center of Kaposvár University (Bőszénfa, Hungary) (46.236 N; 17.832 E) (Nagy et al., 2019), from 11 May to 15 June 2016, from a herd of 66 mothers and their young in an enclosure of about 25 ha, separated visually and acoustically from stag enclosures of this farm. Individuals could not be identified from automated recordings, so the precise numbers of recorded animals were unknown.

All stags and hinds were mature breeding adults, participating in the rut (stags) or giving birth to the young (hinds). For calves, we used as a proxy of age the date of first appearance of calf calls (14 May) on the spectrograms of audio recordings. As recording was started on 11 May (i.e., three days before the appearance of first calls of the calves in the recordings), we considered 14 May as zero day of calf life. Therefore, we inferred from the recordings that during call collection, the age of calves during the recording period varied from 1 day of age (on 15 May) to 32 days of age (on 15 June, end of audio recording). Stag vocal features only slightly vary depending on management conditions: captive, semi-captive, free-ranging, wild-living or translocated (Hurtado et al., 2012; Volodin et al., 2015a, 2019; Golosova et al., 2017). In addition, we used passive audio recording without human presence for all sex and age classes, so comparison of acoustic data obtained from free-ranging stags and from farmed hinds and calves was appropriate in this study.

2.2. *Call recording*

All audio recordings (sampling rate of 22.05 kHz, 16 bit resolution, stereo) were made by using two automated recording devices SongMeter SM2+ (Wildlife-Acoustics, Maynard, MA, USA), one for stags and one for hinds and calves. The devices, equipped with two microphones directed oppositely and set to the highest possible sensitivity of recording, were established at pillars or trees on 5 meters above the ground and recorded most stag roars in the radius of 0.5 km around device (Volodin et al., 2019) and large amounts of hind and calf contact calls within the study enclosure.

Stag rutting calls were recorded daily from 05:00 to 08:00 and from 18:00 to 21:00 in the mode 9 min of recording with 1-min pause and from 21:00 to 05:00 in the mode 9 min of recording with 21-min pause. Each 9-min recording was stored as a separate wav-file. This recording schedule enabled to cover the daily periods of the highest vocal activity. We collected fifty-two 9-min audio files per 24-h period, 210.6 h of recordings in 1404 audio files in total.

Hind and calf contact calls were recorded daily from 04:20 to 05:50 and from 19:50 to 21:20, in the mode 9 min of recording with 1-min pause. We collected eighteen 9-min audio files per 24-h period, 94.2 h of recordings in 628 audio files in total.

2.3. Call samples

For acoustic analyses, we selected 264 stag rutting roars. We included in analysis only main common roars (tonal roars, the longest within bouts, thereafter 'main roars') (Reby & McComb, 2003; Volodin et al., 2019) (Figure 1). As the number of roars per bout influences f_0 of main roar (Frey et al., 2012; Volodin et al., 2019), we selected for analysis a balanced set of main roars occupying different positions within their bouts. Of the 264 main roars selected for analysis, 40 were extracted from single-roar bouts, 127

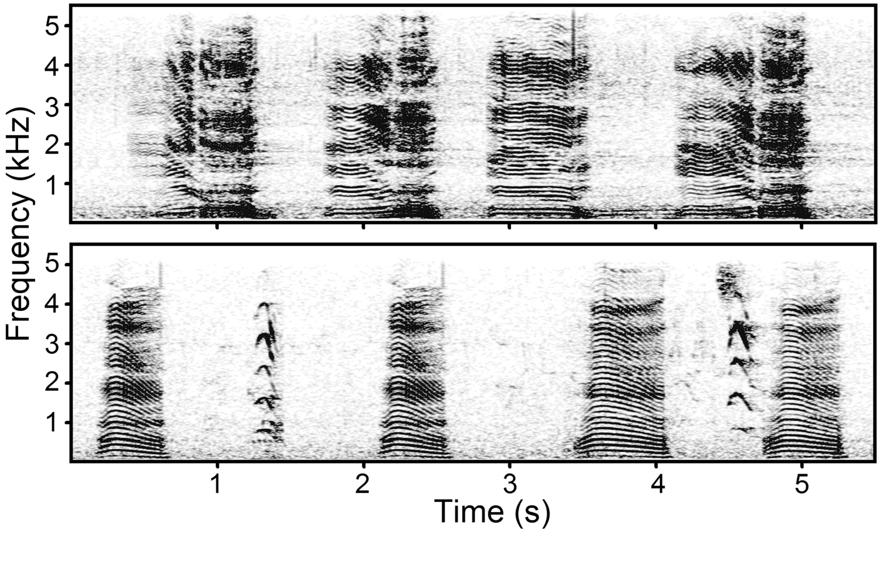

Figure 1. Spectrogram illustrating vocalizations of Pannonian red deer. Upper panel: A four-roar bout of stag rutting roars, the last roar represents the main (longest) roar of the bout. Lower panel: Alternating hind contact calls (1st, 3rd, 4th, and 6th) and calf contact calls (2nd and 5th). The spectrogram was created with Hamming window, 11 025 Hz sampling rate, FFT 1024 points, frame 50% and overlap 96.87%. Wav-file of these calls is available in Supplementary Audio 1.

were the highest-frequency roars within bouts (40 first calls within bouts, 41 last calls within bouts, 46 calls from the middle of the bouts), and 97 were not highest-frequency calls within bouts (14 first calls within bouts, 40 last calls within bouts, 43 calls from the middle of the bouts).

For acoustic analyses, we selected 228 oral contact calls of hinds and 309 oral contact calls of 1–32-day-old calves. We considered calls with a low f_0 as belonging to hinds and calls with a high f_0 as belonging to calves, because before calving, only low-frequency calls were present in the recordings (Figure 1). We included in the acoustic analysis only the oral calls (thereafter 'contact calls') of hinds and calves. Calls were classified to nasal or oral (produced through the nose or through the mouth) by an experienced researcher (IAV) on the basis a specific 'nasal' sounding of calls produced through the nose and differences in energy distribution characteristic of nasal and oral contact calls of red deer (Sibiryakova et al., 2015). If a call had a short nasal part at the beginning (not exceeding 20% of call duration), such calls were also considered as oral calls.

2.4. Call measurements

Measurements of acoustic variables of the total sample of 801 calls were conducted uniformly for all calls of stags, hinds and calves. Before measurements, calls were down-sampled from 22.05 kHz to 11.025 kHz using Avisoft SASLab Pro (Avisoft Bioacoustics, Berlin, Germany) for better frequency resolution and high-pass filtered at 50 Hz to delete low-frequency background noise. A preliminary visual on-screen inspection of spectrograms showed that f_0 always exceeded 50 Hz, so this filtering did not affect the measured acoustic variables. Spectrograms for acoustic analyses were created with the following settings: a Hamming window, Fast Fourier Transform (FFT) 1024, frame 50%, overlap 96.87%.

For each call, we measured a total of 10 acoustic variables by using two spectrographic software, Avisoft SASLab Pro and Praat (www.praat.org). All measurements were automatically exported to Microsoft Excel (Microsoft, Redmond, WA, USA). With Avisoft, we measured 8 variables, and with Praat, we measured 3 variables; the maximum fundamental frequency ($f_{0\max}$), which was primarily important for the acoustic comparison of sex and age-classes, was measured with both Avisoft and Praat. As formants could not be measured in the relatively high-frequency calls of calves, we restricted a comparison between sex and age-classes with parameters of f_0, duration, and power parameters.

In the spectrogram window of Avisoft, we manually measured call duration with the standard marker cursor and the maximum, beginning and end fundamental frequencies ($f_{0\max}$, $f_{0\mathrm{beg}}$ and $f_{0\mathrm{end}}$) with the reticule cursor (Figure 2). In the power spectrum window, within 0.05 s time frame taken around the point of the $f_{0\max}$, we semi-automatically measured the peak frequency (f_{peak}) and three power quartiles, the lower (q25), the medium (q50)

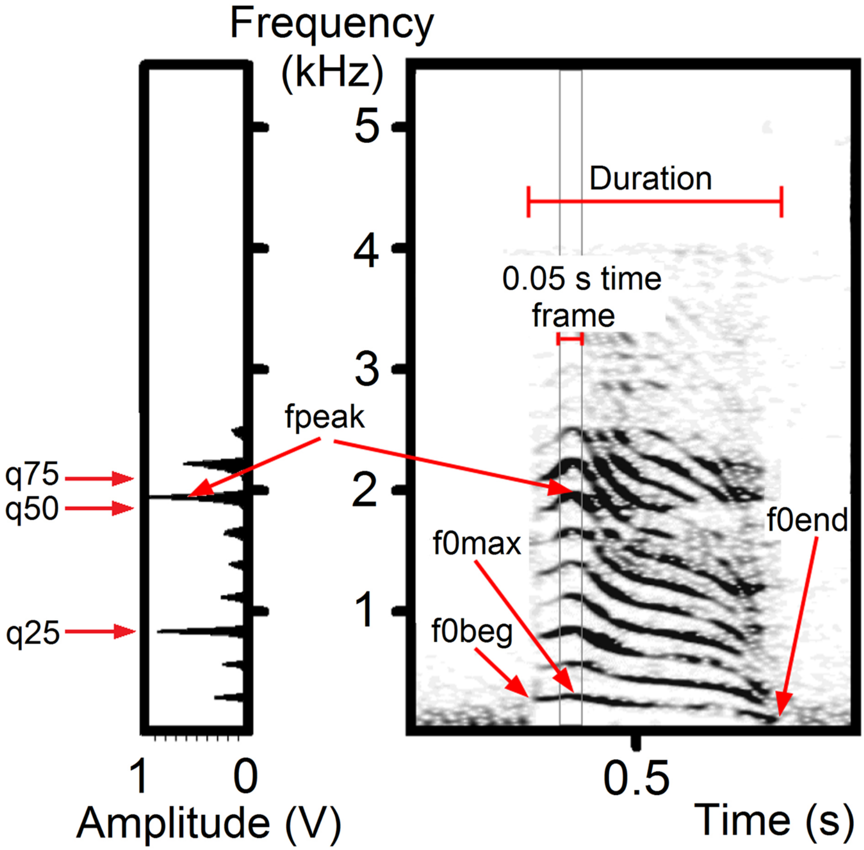

Figure 2. Measured acoustic variables: spectrogram of hind oral call (right) and mean power spectrum of 0.05 s time frame of a call. Designations: duration, call duration; $f_{0\max}$, the maximum fundamental frequency; $f_{0\min}$, the minimum fundamental frequency; $f_{0\mathrm{beg}}$, the beginning fundamental frequency; $f_{0\mathrm{end}}$, the end fundamental frequency; f_{peak}, the maximum amplitude frequency; q25, the lower quartile of power spectrum; q50, the medium quartile of power spectrum; q75, the upper quartile of power spectrum. The spectrogram was created with Hamming window, 11 025 Hz sampling rate, FFT 1024 points, frame 50% and overlap 96.87%.

and the upper (q75), covering respectively 25%, 50% and 75% of call energy (Figure 2).

With Praat, the fundamental frequency band was tracked with cross-correlation algorithm, with time step 0.01 s for calls of adults and 0.005 s for calves and the limits of the spectrographic window from 0 to 5000 Hz. Then, the minimum, maximum and mean fundamental frequencies ($f_{0\,\mathrm{min}}$, $f_{0\,\mathrm{max}}$ and $f_{0\mathrm{mean}}$) were calculated automatically based on tracked f_0. As $f_{0\,\mathrm{max}}$ values obtained by Avisoft and Praat provided very close values (coefficient of determination R^2 of Pearson correlation ranged from 0.972 to 0.979), we only used the $f_{0\,\mathrm{max}}$ values measured with Praat for further analyses.

2.5. Statistical analyses

Statistical analyses were performed with STATISTICA, v. 8.0 (StatSoft, Tulsa, OK, USA). Means are given as mean ± SD, all tests were two-tailed, and differences were considered significant whenever $p < 0.05$. Distributions of 22 measured parameter values of 30 distributions did not depart from normality (Kolmogorov-Smirnov test, $p > 0.05$). As ANOVA is relatively robust to departures from normality (Dillon & Goldstein, 1984), this was not an obstacle to the application of the parametric tests.

We applied a one-way ANOVA with Tukey HSD (Honest Significantly Different) test to compare the acoustic variables between sex and age-classes. We used Pearson's correlation coefficient for estimating the relationship between calf age and the acoustic variables of hinds and calves.

3. Results

3.1. Sex and age-class acoustic differences

Duration of stag rutting roars was longer than those of either hind contact calls or calf contact calls, and hind contact calls were longer than calf contact calls (Table 1). All f_0 variables, for the exclusion of $f_{0\mathrm{beg}}$, did not differ between stag rutting roars and hind contact calls (Table 1). All f_0 variables of stag rutting roars and hind contact calls were significantly lower than those of calf contact calls (Table 1). The $f_{0\mathrm{beg}}$, f_{peak} and all the three quartiles of power spectrum were the lowest in stag rutting roars, intermediate in hind contact calls and the highest in calf contact calls (Table 1).

Table 1.
Values (mean ± SD) of the acoustic variables of Pannonian red deer stag rutting roars, hind contact calls and calf contact calls and one-way ANOVA results for their comparison.

Acoustic variable	Stags ($N = 264$)	Hinds ($N = 228$)	Calves ($N = 309$)	ANOVA	p
Duration (s)	1.39 ± 0.55^{a}	1.26 ± 0.66^{b}	0.29 ± 0.11^{c}	$F_{1,798} = 451.4$	<0.001
$f0_{\max}$ (Hz)	177.4 ± 52.9^{a}	167.1 ± 31.3^{a}	735.2 ± 134.3^{b}	$F_{1,798} = 3680.2$	<0.001
$f0_{\min}$ (Hz)	80.1 ± 16.2^{a}	89.8 ± 17.6^{a}	472.8 ± 105.0^{b}	$F_{1,798} = 3231.8$	<0.001
$f0_{\mathrm{beg}}$ (Hz)	81.2 ± 19.1^{a}	121.2 ± 33.8^{b}	677.6 ± 141.9^{c}	$F_{1,798} = 3870.6$	<0.001
$f0_{\mathrm{end}}$ (Hz)	78.0 ± 23.8^{a}	83.9 ± 19.6^{a}	443.1 ± 100.0^{b}	$F_{1,798} = 3004.4$	<0.001
$f0_{\mathrm{mean}}$ (Hz)	139.5 ± 28.3^{a}	139.6 ± 23.0^{a}	639.6 ± 109.1^{b}	$F_{1,798} = 4741.8$	<0.001
f_{peak} (Hz)	705 ± 714^{a}	1044.0 ± 814^{b}	1865.0 ± 1011^{c}	$F_{1,798} = 136.6$	<0.001
q25 (Hz)	528 ± 324^{a}	931 ± 430^{b}	1413 ± 554^{c}	$F_{1,798} = 273.5$	<0.001
q50 (Hz)	1276 ± 620^{a}	1860 ± 635^{b}	2626 ± 707^{c}	$F_{1,798} = 302.7$	<0.001
q75 (Hz)	2213 ± 556^{a}	2975 ± 722^{b}	3714 ± 615^{c}	$F_{1,798} = 404.7$	<0.001

N, number of calls; duration, call duration; $f0_{\max}$, the maximum fundamental frequency; $f0_{\min}$, the minimum fundamental frequency; $f0_{\mathrm{beg}}$, the beginning fundamental frequency; $f0_{\mathrm{end}}$, the end fundamental frequency; $f0_{\mathrm{mean}}$, the mean fundamental frequency; f_{peak}, the maximum amplitude frequency; q25, the lower quartile of power spectrum; q50, the medium quartile of power spectrum; q75, the upper quartile of power spectrum. The same uppercase symbols indicate that call variables are not significantly different ($p > 0.05$, Tukey HSD test).

3.2. Changes of mother and young contact calls during calf-raising season

With calf growth during calf-raising season (from 1 to 32 days old), call duration, $f_{0\,\max}$, $f_{0\,\min}$, $f_{0\text{beg}}$, $f_{0\text{end}}$ and $f_{0\text{mean}}$ of hind contact calls significantly decreased, whereas f_{peak} and all the three power quartiles (q25, q50, q75) significantly increased (Figure 3, Table 2). For calves, the duration of calf contact calls did not show correlation with age (Figure 3, Table 2). At the same time, the $f_{0\,\max}$, $f_{0\,\min}$, $f_{0\text{beg}}$, $f_{0\text{end}}$ and $f_{0\text{mean}}$ of calf contact calls decreased with age, whereas the f_{peak}, q25 and q50 increased with age (Table 2).

4. Discussion

In this study, acoustic variables of Pannonian red deer stag rutting roars and hind and calf contact calls were studied in detail and compared among sex and age-classes. As predicted by Rule 1 for calls of adults, most variables of fundamental frequency (f_0) were indistinguishable between the sexes. At the same time, f_0 characteristics were distinctive for the Pannonian red deer population compared to other studied populations/subspecies (Volodin et al., 2019; Golosova et al., 2021). Even the closest f_0 values of Alpine population stags of presumably the same subspecies *C. e. hippelaphus* ($f_{0\,\max} = 274$ Hz, Bocci et al., 2013) are substantially higher than in Pannonian red deer stags in our study (177 Hz). Earlier, similar or indistinguishable values of stag and hind fundamental frequencies were reported for Iberian red deer (Volodin et al., 2015a), Corsican red deer (Kidjo et al., 2008), American wapiti (Feighny, 2005; Feighny et al., 2006) and Siberian wapiti (Volodin et al., 2016).

Therefore, we can conclude that the similarity in frequency variables of stags and hinds within populations/subspecies (at strong differences in values of fundamental frequency between subspecies) represents a common rule (Rule 1) for all studied subspecies of red deer and wapiti. These data do not agree with the hypothesis that acoustic structure of stag rutting calls evolved under strong influence of sexual selection, directed to attraction of mates and deterring rival stags (Clutton-Brock & Albon, 1979). Of course, fundamental frequency may not be the only parameter under sexual or natural selection. We can hypothesize that fundamental frequency of different subspecies of red deer and wapiti emerged under the influence of natural selection, which similarly acted on stags and hinds as adaptation to social communication in certain environmental and climate conditions. A broad variation of the

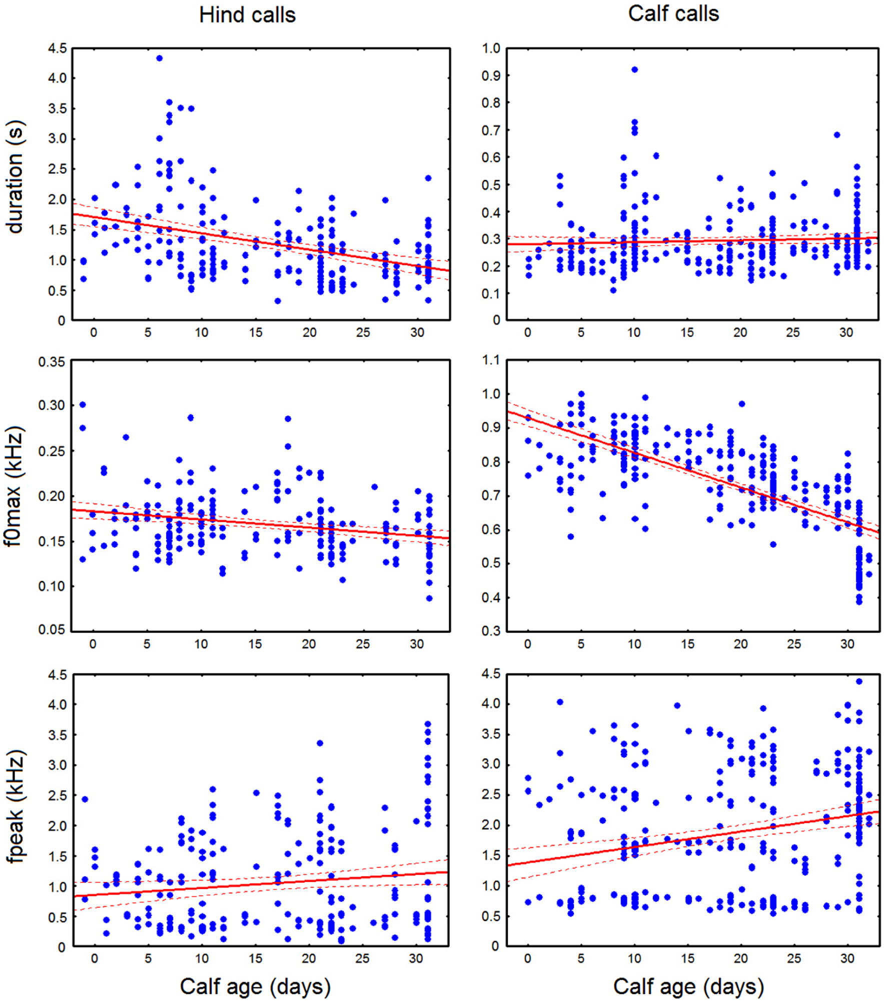

Figure 3. Scatterplots illustrating the relationships between calf age during 32-day-long period from first detection of newborn calf calls in the recordings after parturitions and acoustic variables of hind and calf contact calls: duration, call duration; $f_{0\,\mathrm{max}}$, the maximum fundamental frequency; f_{peak}, the maximum amplitude frequency. Linear regression lines with 95% confidence intervals are shown.

acoustic structure of stag rutting calls at the lack of data on the acoustic structure of hind calls in the Central-Asian red deer (*Cervus* (*elaphus*) *hanglu*) (Nikolskii, 1975; Volodin et al., 2013) from the center of origin of species *Cervus elaphus* do not allow to conclude about whether fundamental fre-

Table 2.
Pearson correlation coefficients between acoustic variables of Pannonian red deer hind and calf contact calls and calf age (estimated in time period from the day of first appearance of newborn calf calls to 32nd day of the recordings).

Acoustic variable	Hind contact calls ($N = 228$)		Calf contact calls ($N = 309$)	
	r	p	r	p
Duration (s)	−0.40	<0.001	0.06	0.290
$f0_{\mathrm{max}}$ (Hz)	−0.24	<0.001	−0.69	<0.001
$f0_{\mathrm{min}}$ (Hz)	−0.34	<0.001	−0.61	<0.001
$f0_{\mathrm{beg}}$ (Hz)	−0.27	<0.001	−0.68	<0.001
$f0_{\mathrm{end}}$ (Hz)	−0.43	<0.001	−0.57	<0.001
$f0_{\mathrm{mean}}$ (Hz)	−0.35	<0.001	−0.70	<0.001
f_{peak} (Hz)	0.14	0.040	0.24	<0.001
q25 (Hz)	0.24	<0.001	0.29	<0.001
q50 (Hz)	0.28	<0.001	0.16	0.006
q75 (Hz)	0.19	0.005	0.08	0.170

N, number of calls; duration, call duration; $f0_{\mathrm{max}}$, the maximum fundamental frequency; $f0_{\mathrm{min}}$, the minimum fundamental frequency; $f0_{\mathrm{beg}}$, the beginning fundamental frequency; $f0_{\mathrm{end}}$, the end fundamental frequency; $f0_{\mathrm{mean}}$, the mean fundamental frequency; f_{peak}, the maximum amplitude frequency; q25, the lower quartile of power spectrum; q50, the medium quartile of power spectrum; q75, the upper quartile of power spectrum.

quency decreased or increased during the circumpolar radiation of red deer to Europe and to Asia and America (Mahmut et al., 2002; Ludt et al., 2004).

In this study, we also found that, along ontogeny up to the age of 32 days, the contact calls of Pannonian red deer calves become lower in frequency, whereas duration of their calls remains unchanged. Decrease of f_0 with age from calves to adults was previously reported for other populations/subspecies of European red deer, e.g., Corsican red deer (Kidjo et al., 2008), and Iberian red deer (Sibiryakova et al., 2015). We can therefore conclude that f_0 of Pannonian red deer vocalizations decreases along ontogeny, thus following the common rule for most ruminants and other mammals, that small offspring with their short vocal folds produce audible calls higher in frequency than adults with their longer vocal folds (Matrosova et al., 2007; Volodin et al., 2017a). Exceptions can be potentially related to different mechanics of the vocal folds, e.g., in very small-sized mammals as shrews (Volodin et al., 2015b).

Alternatively, similarity of f_0 in calls of calves and adults can result from using a distinctive (whistling) mechanism of sound production than those based on phonation with vibration of vocal folds in wapiti compared to red deer (Reby et al., 2016). Probably due to the whistling mechanism of sound production in Asian and American wapiti, in contrast to European red deer, the f_0 does not decrease along ontogeny and remains unchangeably high in adult stags and hinds, as in calves (Feighny, 2005; Volodin et al., 2016; Sibiryakova et al., 2018). In ruminants, the whistling mechanism was also proposed for the very high-frequency calls in domestic cattle (Hall et al., 1988; Volodin et al., 2017b) and camels (Volodin et al., 2022).

The acoustics of contact calls of red deer hinds and calves are poorly studied compared to the acoustics of stag rutting calls, so, comparison of the obtained data from hind and calf calls is especially interesting. The oral contact calls of Pannonian red deer hinds in our study were the longest (1.26 s) compared to any studied European red deer subspecies/population: Corsican red deer (0.60 s, Kidjo et al., 2008), Iberian red deer (0.76 s, Sibiryakova et al., 2015) and Central European red deer (0.27 s, Vankova & Malek, 1997), as well as compared to Siberian wapiti *C. e. sibiricus* (0.38 s, Volodin et al., 2016) or American wapiti (0.28 s, Feighny, 2005). The maximum fundamental frequency of Pannonian red deer hind contact calls in this study (167 Hz) was intermediate among European subspecies, higher than in Corsican red deer (103 Hz, Kidjo et al., 2008) and Central European red deer (108 Hz, Vankova & Malek, 1997), but lower than in Iberian red deer (180 Hz Sibiryakova et al., 2015). The maximum fundamental frequency of Pannonian red deer hinds was also substantially lower than in Siberian wapiti hinds (1570 Hz, Volodin et al., 2016) and American wapiti hinds (1410–1590 Hz, Feighny, 2005).

We can therefore conclude that Pannonian red deer hinds produce the longest known contact calls among studied red deer populations. Duration of hind contact calls decreases with calf growth, but remains very long even after a month after the start of parturitions. The reason of such long duration of the contact calls in Pannonian red deer hinds remains unclear. At the same time, the f_0 range of Pannonian red deer hind contact calls is within the frequency range of European red deer in general.

Duration of calf contact calls was close between Pannonian red deer in our study (0.29 s in 1–32-day-old calves) to those reported for calves of other subspecies of European red deer and wapiti: 0.26 s in 1–2-day-old calves of Central European red deer (Vankova & Malek, 1997), 0.26 s in 1–40-day old calves of Iberian red deer (Sibiryakova et al., 2015), 0.42 s in 1–120-day old calves of Corsican red deer (Kidjo et al., 2008), 0.29 s in 1–30-day old Siberian wapiti (Volodin et al., 2016) and 0.28 s in 1-day-old American wapiti (Feighny, 2005). Similar to duration, the maximum fundamental frequency of calf contact calls was also close between Pannonian red deer in our study (735 Hz) and other subspecies of European red deer: 737 Hz in Central European red deer (Vankova & Malek, 1997), 875 Hz in Iberian red deer (Sibiryakova et al., 2015) and 710 Hz in Corsican red deer (Kidjo et al., 2008). In contrast to European subspecies of red deer, the maximum fundamental frequency is substantially higher in wapiti calves: 1560 Hz in Siberian wapiti (Volodin et al., 2016) and 1480–1520 Hz in American wapiti (Feighny, 2005). The reason for the substantially higher-frequency calls in wapiti than in European red deer calves can be the difference in sound production mechanisms, vocal fold vibration in red deer *vs* whistle mechanism in wapiti (Reby et al., 2016).

We found that Pannonian red deer mother contact calls become shorter and lower in frequency during the 32-day-long period after the start of calf-raising season, probably as the result of decrease of anxiety of the hinds, which might be very high during parturitions following by steady decrease of anxiety with calf growth. Previously, a decrease of f_0 with decrease of emotional arousal and discomfort was reported for many mammalian species as an important vocal indicator of internal state in mammals (Briefer, 2012).

Comparative data displaying the relationship between the acoustics of hind contact calls with calf age are scarce. In Siberian wapiti, the maximum fundamental frequency of hind contact calls decreases from 1570 Hz in June, when the age of offspring is about one month, to 1430 Hz in November, when the age of offspring is about six months (Volodin et al., 2016; Sibiryakova et al., 2018). However, the maximum fundamental frequency of Iberian red deer hind contact calls increased from 180 Hz in May-June, when the age of offspring is below 40 days, to 209 Hz in September, when the age of offspring is about four months (Sibiryakova et al., 2015; Volodin et al., 2015a). Aside the effect of calf age, these different trends of changes could be related to differences in recording procedures, passive acoustic recording (this study), manual recording outside enclosure (Sibiryakova et al., 2018) and manual recording inside enclosure, with separation of mother and young (Sibiryakova et al., 2015; Volodin et al., 2015a).

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References

Bana, N.A., Nyiri, A., Nagy, J., Frank, K., Nagy, T., Stéger, V., Schiller, M., Lakatos, P., Sugár, L., Horn, P., Barta, E. & Orosz, L. (2018). The red deer *Cervus elaphus* genome CerEla1.0: sequencing, annotating, genes, and chromosomes. — Mol. Genet. Genomics 293: 665-684. DOI:10.1007/s00438-017-1412-3.

Banwell, D.B. (1998). Identification of the Pannonian, or Danubian, red deer. A maraloid — *Cervus elaphus pannoniensis*. — Deer 10: 495-497.

Banwell, D.B. (2002). In defense of the Pannonian *Cervus elaphus pannoniensis*. — Deer 12: 198-203.

Bocci, A., Telford, M. & Laiolo, P. (2013). Determinants of the acoustic behaviour of red deer during breeding in a wild Alpine population, and implications for species survey. — Ethol. Ecol. Evol. 25: 52-69. DOI:10.1080/03949370.2012.705331.

Briefer, E.F. (2012). Vocal expression of emotions in mammals: mechanisms of production and evidence. — J. Zool. 288: 1-20. DOI:10.1111/j.1469-7998.2012.00920.x.

Charlton, B., Reby, D. & McComb, K. (2008). Effect of combined source (F0) and filter (formant) variation on red deer hind responses to male roars. — J. Acoust. Soc. Am. 123: 2936-2943.

Charlton, B.D. & Reby, D. (2016). The evolution of acoustic size exaggeration in terrestrial mammals. — Nature Commun. 7: 12739. DOI:10.1038/ncomms12739.

Charlton, B.D., Reby, D. & McComb, K. (2007). Female red deer prefer the roars of larger males. — Biol. Lett. 3: 382-385.

Clutton-Brock, T.H. & Albon, S.D. (1979). The roaring of red deer and the evolution of honest advertising. — Behaviour 69: 145-170. DOI:10.1163/156853979X00449.

De Gregorio, C., Carugati, F., Estienne, V., Valente, D., Raimondi, T., Torti, V., Miaretsoa, L., Ratsimbazafy, J., Gamba, M. & Giacoma, C. (2021). Born to sing! Song development in a singing primate. — Curr. Zool. 67: 597-608. DOI:10.1093/cz/zoab018.

Della Libera, M., Passilongo, D. & Reby, D. (2015). The acoustics of male rutting roars in the endangered population of Mesola red deer *Cervus elaphus italicus*. — Mammal. Biol. 80: 395-400. DOI:10.1016/j.mambio.2015.05.001.

Dillon, W.R. & Goldstein, M. (1984). Multivariate analysis: methods and applications. — Wiley, New York, NY.

Feighny, J.A.J. (2005). Ontogeny of wapiti vocalizations: development, environmental and anatomical constraints. — Ph.D. thesis, University of Northern Colorado, Greeley, CO.

Feighny, J.J., Williamson, K.E. & Clarke, J.A. (2006). North American elk bugle vocalizations: male and female bugle call structure and context. — J. Mammal. 87: 1072-1077.

Fitch, W.T. & Reby, D. (2001). The descended larynx is not uniquely human. — Proc. Roy. Soc. Lond. B: Biol. Sci. 268: 1669-1675. DOI:10.1098/rspb.2001.1704.

Frank, K., Szepesi, K., Bleier, N., Sugár, L., Kusza, S., Barta, E., Horn, P., Orosz, L. & Stéger, V. (2022). Genetic traces of dispersal and admixture in red deer (*Cervus elaphus*) populations from the Carpathian Basin. — Eur. J. Wildl. Res. 68: 55. DOI:10.1007/s10344-022-01602-w.

Frantz, A.C., Zachos, F.E., Bertouille, S., Eloy, M.-C., Colyn, M. & Flamand, M.-C. (2017). Using genetic tools to estimate the prevalence of non-native red deer (*Cervus elaphus*) in a Western European population. — Ecol. Evol. 7: 7650-7660. DOI:10.1002/ece3.3282.

Frey, R., Volodin, I.A., Volodina, E.V., 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. DOI:10.1111/j.1469-7580.2011.01467.x.

Garcia, M., Herbst, C.T., Bowling, D.L., Dunn, J.C. & Fitch, W.T. (2017). Acoustic allometry revisited: morphological determinants of fundamental frequency in primate vocal production. — Sci. Rep. 7: 10450. DOI:10.1038/s41598-017-11000-x.

Garcia, M. & Ravignani, A. (2020). Acoustic allometry and vocal learning in mammals. — Biol. Lett. 16: 20200081. DOI:10.1098/rsbl.2020.0081.

Golosova, O.S., Kholodova, M.V., Volodin, I.A., Volodina, E.V., Likhatsky, E.Y., Náhlik, A. & Tari, T. (2021). Vocal phenotype of male rutting roars and genetic markers delineate East European red deer (*Cervus elaphus*) from Central and West European populations. — Sci. Nat. 108: 30. DOI:10.1007/s00114-021-01742-0.

Golosova, O.S., Volodin, I.A., Isaeva, I.L. & Volodina, E.V. (2017). Effects of free-ranging, semi-captive and captive management on the acoustics of male rutting calls in Siberian wapiti *Cervus elaphus sibiricus*. — Mammal. Res. 62: 387-396. DOI:10.1007/s13364-017-0322-4.

Hall, S.J.G., Vince, M.A., Walser, E.S. & Garson, P.J. (1988). Vocalisations of the Chillingham cattle. — Behaviour 104: 78-104.

Hurtado, A.M., Smith-Flueck, J.M. & Black-Decima, P. (2012). Comparison of vocalisations of introduced European red deer stags (*Cervus elaphus*) in north-western Patagonia (Argentina) with native European populations. — Anim. Prod. Sci. 52: 714-719. DOI:10.1071/AN11361.

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. DOI:10.1080/09524622.2008.9753598.

Kumar, V.P., Thakur, M., Rajpoot, A., Joshi, B.D., Nigam, P., Ahmad, K., Kumar, D. & Goyal, S.P. (2017). Resolving the phylogenetic status and taxonomic relationships of the Hangul (*Cervus elaphus hanglu*) in the family Cervidae. — Mitochondrial DNA A 28: 835-842. DOI:10.1080/24701394.2016.1197217.

Lingle, S., Wyman, M.T., Kotrba, R., Teichroeb, L.J. & Romanow, C.A. (2012). What makes a cry a cry? A review of infant distress vocalizations. — Curr. Zool. 58: 698-726. DOI:10.1093/czoolo/58.5.698.

Lorenzini, R. & Garofalo, L. (2015). Insights into the evolutionary history of *Cervus* (Cervidae, tribe Cervini) based on Bayesian analysis of mitochondrial marker sequences, with first indications for a new species. — J. Zool. Syst. Evol. Res. 53: 340-349. DOI:10.1111/jzs.12104.

Ludt, C.J., Schroeder, W., Rottmann, O. & Kuehn, R. (2004). Mitochondrial DNA phylogeography of red deer (*Cervus elaphus*). — Mol. Phylogenet. Evol. 31: 1064-1083. DOI:10.1016/j.ympev.2003.10.003.

Mahmut, H., Masuda, R., Onuma, M., Takahashi, M., Nagata, J., Suzuki, M. & Ohtaishi, N. (2002). Molecular phylogeography of the red deer (*Cervus elaphus*) populations in Xinjiang of China: comparison with other Asian, European, and North American populations. — Zool. Sci. 19: 485-495. DOI:10.2108/zsj.19.485.

Matrosova, V.A., Volodin, I.A., Volodina, E.V. & Babitsky, A.F. (2007). Pups crying bass: vocal adaptation for avoidance of age-dependent predation risk in ground squirrels? — Behav. Ecol. Sociobiol. 62: 181-191. DOI:10.1007/s00265-007-0452-9.

Mukesh, M., Sharma, L.K., Charoo, S.A. & Sathyakumar, S. (2015). Species identification and molecular sexing from feces of Kashmir stag (*Cervus elaphus hanglu*). — Conservation Genet. Resour. 7: 677-680. DOI:10.1007/s12686-015-0475-x.

Nagy, J., Szabó, A., Donkó, T., Bokor, J., Romvári, R., Repa, I., Horn, P. & Fébel, H. (2019). Body composition and venison quality of farmed red deer (*Cervus elaphus*) Hinds reared on grass, *papilionaceous* or mixed pasture paddocks. — Arch. Anim. Breed. 62: 227-239. DOI:10.5194/aab-62-227-2019.

Niedziałkowska, M., Doan, K., Górny, M., Sykut, M., Stefaniak, K., Piotrowska, N., Jędrzejewska, B., Ridush, B., Pawełczyk, S., Mackiewicz, P., Schmölcke, U., Kosintsev, P., Makowiecki, D., Charniauski, M., Krasnodębski, D., Rannamäe, E., Saarma, U., Arakelyan, M., Manaseryan, N., Titov, V.V., Hulva, P., Bălăşescu, A., Fyfe, R., Woodbridge, J., Trantalidou, K., Dimitrijević, V., Kovalchuk, O., Wilczyński, J., Obadă, T., Lipecki, G., Arabey, A. & Stanković, A. (2021). Winter temperature and forest cover have shaped red deer distribution in Europe and the Ural Mountains since the Late Pleistocene. — J. Biogeograph. 41: 147-159. DOI:10.1111/jbi.13989.

Nikolskii, A.A. (1975). Main modifications of mating call in *Cervus elaphus bactrianus*. — Zool. Zh. 54: 1897-1900. (In Russian).

OVA (2018). The National Game Management Database. OVA, Budapest. Available online at http://www.vvt.gau.hu/adattar/index-en.html.

Pérez-Espona, S., Pérez-Barbería, F.J. & Pemberton, J.M. (2011). Assessing the impact of past wapiti introductions into Scottish Highland red deer populations using a Y chromosome marker. — Mammal. Biol. 76: 640-643. DOI:10.1016/j.mambio.2010.10.001.

Reby, D. & McComb, K. (2003). Anatomical constraints generate honesty: acoustic cues to age and weight in the roars of red deer stags. — Anim. Behav. 65: 519-530. DOI:10.1006/anbe.2003.2078.

Reby, D., McComb, K., Cargnelutti, B., Darwin, C.J., Fitch, W.T. & Clutton-Brock, T.H. (2005). Red deer stags use formants as assessment cues during intra-sexual agonistic interactions. — Proc. Roy. Soc. Lond. B: Biol. Sci. 272: 941-947. DOI:10.1098/rspb.2004.2954.

Reby, D., Wyman, M.T., Frey, R., Passilongo, D., Gilbert, J., Locatelli, Y. & Charlton, B.D. (2016). Evidence of biphonation and source-filter interactions in the bugles of male North American wapiti (*Cervus canadensis*). — J. Exp. Biol. 219: 1224-1236. DOI:10.1242/jeb.131219.

Rusin, I.Y., Volodin, I.A., Sitnikova, E.F., Litvinov, M.N., Andronova, R.S. & Volodina, E.V. (2021). Roaring dynamics in rutting male red deer *Cervus elaphus* from five Russian populations. — Russ. J. Theriol. 20: 44-58. DOI:10.15298/rusjtheriol.20.1.06.

Sibiryakova, O.V., Volodin, I.A., Matrosova, V.A., Volodina, E.V., Garcia, A.J., Gallego, L. & Landete-Castillejos, T. (2015). The power of oral and nasal calls to discriminate individual mothers and offspring in red deer, *Cervus elaphus*. — Front. Zool. 12: 2. DOI:10.1186/s12983-014-0094-5.

Sibiryakova, O.V., Volodin, I.A. & Volodina, E.V. (2018). Advertising individual identity by mother and adolescent contact calls in Siberian wapiti *Cervus elaphus sibiricus*. — Ethology 124: 733-742. DOI:10.1111/eth.12804.

Taylor, A.M. & Reby, D. (2010). The contribution of source-filter theory to mammal vocal communication research. — J. Zool. 280: 221-236. DOI:10.1111/j.1469-7998.2009.00661.x.

Vaňková, D. & Málek, J. (1997). Characteristics of the vocalizations of red deer *Cervus elaphus* Hinds and calves. — Bioacoustics 7: 281-289.

Volodin, I., Volodina, E., Frey, R., Carranza, J. & Torres-Porras, J. (2013). Spectrographic analysis points to source-filter coupling in rutting roars of Iberian red deer. — Acta Ethol. 16: 57-63. DOI:10.1007/s10211-012-0133-1.

Volodin, I., Matrosova, V., Volodina, E., Garcia, A.J., Gallego, L., Márquez, R., Llusia, D., Beltrán, J.F. & Landete-Castillejos, T. (2015a). 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. 18: 19-29. DOI:10.1007/s10211-013-0179-8.

Volodin, I., Sibiryakova, O.V. & Volodina, E. (2016). Sex and age-class differences in calls of Siberian wapiti *Cervus elaphus sibiricus*. — Mammal. Biol. 81: 10-20. DOI:10.1016/j.mambio.2015.09.002.

Volodin, I.A., Zaytseva, A.S., Ilchenko, O.G. & Volodina, E.V. (2015b). Small mammals ignore common rules: a comparison of vocal repertoires and the acoustics between pup and adult piebald shrews *Diplomesodon pulchellum*. — Ethology 121: 103-115. DOI:10.1111/eth.12321.

Volodin, I.A., Efremova, K.O., Frey, R., Soldatova, N.V. & Volodina, E.V. (2017a). Vocal changes accompanying the descent of the larynx during ontogeny from neonates to adults in male and female goitred gazelles (*Gazella subgutturosa*). — Zoology 120: 31-41. DOI:10.1016/j.zool.2016.09.001.

Volodin, I.A., Volodina, E.V. & Frey, R. (2017b). Bull bellows and bugles: a remarkable convergence of low and high-frequency vocalizations between male domestic cattle *Bos taurus* and the rutting calls of Siberian and North American wapiti. — Bioacoustics 26: 271-284. DOI:10.1080/09524622.2016.1275805.

Volodin, I.A., Nahlik, A., Tari, T., Frey, R. & Volodina, E.V. (2019). Rutting roars in native Pannonian red deer of Southern Hungary and the evidence of acoustic divergence of male sexual vocalization between Eastern and Western European red deer (*Cervus elaphus*). — Mammal. Biol. 94: 54-65. DOI:10.1016/j.mambio.2018.10.009.

Volodin, I.A., Volodina, E.V. & Rutovskaya, M.V. (2022). Camel whistling vocalisations: male and female call structure and context in *Camelus bactrianus* and *Camelus dromedarius*. — Bioacoustics 31: 132-147. DOI:10.1080/09524622.2021.1889403.

Supplementary Materials

Supplementary Audio file. Vocalizations of Pannonian red deer. A four-roar bout of stag rutting roars, the last roar represents the main (longest) roar of the bout, and alternating hind contact calls (1st, 3rd, 4th, and 6th) and calf contact calls (2nd and 5th). This file can be accessed at 10.6084/m9.figshare.20746165.