

Advertising individual identity by mother and adolescent contact calls in Siberian wapiti *Cervus elaphus sibiricus*

Olga V. Sibiryakova¹ | Ilya A. Volodin^{1,2}  | Elena V. Volodina²

¹Department of Vertebrate Zoology, Faculty of Biology, Lomonosov Moscow State University, Moscow, Russia

²Scientific Research Department, Moscow Zoo, Moscow, Russia

Correspondence

Ilya A. Volodin, Department of Vertebrate Zoology, Faculty of Biology, Lomonosov Moscow State University, Vorobiev Gory, 12/1, 119991 Moscow, Russia.
Email: volodinsvoc@gmail.com

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Abstract

Individualistic contact calls facilitate mother-offspring reunion after separation. However, in many mammals, both the acoustic structure and individuality of contact calls differ between mother and young. In contrast, in Siberian wapiti *Cervus elaphus sibiricus*, contact calls are similar in the acoustics between mother and young, whereas effects of this similarity on vocal individuality were not investigated. In this study, we analyzed acoustic differences between closed-mouth (nasal) and open-mouth (oral) contact calls and examined individuality of the most usual oral calls of 19 Siberian wapiti (9 hinds and 10 5–6-month adolescents) emitted in response to mother-offspring separation. In the oral calls, the values of frequency and power variables were higher than in the nasal calls. Calls of hinds and adolescents did not differ by the maximum fundamental frequency and duration, whereas the peak frequency was higher in the young. Discriminant function analysis (DFA) based on 11 acoustic variables of oral calls accurately classified to individual 92.5% of hind calls and 96.9% of adolescent calls (chi-square test for differences between hinds and adolescents, $p = 0.19$). Variables mainly contributing to vocal identity (duration, start, and maximum fundamental frequency) were the same in calls of mothers and adolescents. We conclude that similarities in the acoustics calls of mothers and adolescents mean that they do not differ in their potential for encoding individual identity, suggesting a mutual process of mother-offspring vocal recognition in Siberian wapiti.

KEYWORDS

acoustic behavior, emotional arousal, mother-offspring communication, nasal and oral contact calls, red deer, vocal individuality

1 | INTRODUCTION

Mother-offspring vocal recognition is critically important for survival of the offspring in ungulates (Lingle, Rendall, & Pellis, 2007; Lingle, Rendall, Wilson, Deyoung, & Pellis, 2007; Lingle, Wyman, Kotrba, Teichroeb, & Romanow, 2012; Nowak, Porter, Levy, Orgeur, & Schaal, 2000; Teichroeb, Riede, Kotrba, & Lingle, 2013; Torriani, Vannoni, & McElligott, 2006). Mother-offspring vocal recognition is based on individualistic contact calls (Sibiryakova et al., 2017, 2015; Torriani et al., 2006; Volodin, Lapshina, Volodina, Frey, & Soldatova, 2011).

Age-class (young vs. adult) strongly affects vocal individuality (Lapshina et al., 2012; Sibiryakova et al., 2015; Torriani et al., 2006). In many species of ruminants, individuality of contact calls increases with age: from neonates to adolescents in goitered gazelle *Gazella subgutturosa* (Lapshina et al., 2012) and from neonates to adults in fallow deer *Dama dama* (Torriani et al., 2006), Iberian red deer *Cervus elaphus hispanicus* (Sibiryakova et al., 2015), and saiga *Saiga tatarica* (Sibiryakova et al., 2017). The age-related increase in acoustic individuality might be related to remarkable differences in the acoustic structure of vocalizations at different ages: in many species of ruminants, calls are substantially higher frequency in the young than in

the adults, as in fallow deer (Torriani et al., 2006), Central European red deer *C.e. hippelaphus* (Vaňková & Málek, 1997), Corsican red deer *C.e. corsicanus* (Kidjo, Cargnelutti, Charlton, Wilson, & Reby, 2008), Iberian red deer (Sibiryakova et al., 2015), saiga (Sibiryakova et al., 2017; Volodin, Sibiryakova, Kokshunova, Frey, & Volodina, 2014), and goitred gazelle (Volodin, Efremova, Frey, Soldatova, & Volodina, 2017a).

Siberian wapiti (*Cervus elaphus sibiricus*) are peculiar among ruminants as the oral contact calls produced during mother-offspring communication do not differ by the maximum fundamental frequency (f_{0max}) and duration between calves and hinds (Volodin, Sibiryakova, & Volodina, 2016a). This provides an opportunity to estimate the effect of factor "age-class" (adolescents vs. hinds) on vocal individuality of contact calls without masking effects of acoustic differences in f_{0max} between adults and young.

Siberian wapiti produce two types of contact calls, nasal and oral (Volodin et al., 2016a). The oral calls are emitted through an opened mouth, whereas the nasal calls are emitted through the nose with a closed-mouth. These two different modes of vocal emission have been reported also for white-tailed deer *Odocoileus virginianus* (Richardson, Jacobson, Muncy, & Perkins, 1983), goitred gazelles (Efremova et al., 2011; Volodin et al., 2011), for mother domestic sheep *Ovis aries* (Sebe, Duboscq, Aubin, Ligout, & Poindron, 2010) and domestic cattle *Bos taurus* (Padilla de la Torre, Briefer, Reader, & McElligott, 2015), for mother and young saiga (Sibiryakova et al., 2017; Volodin et al., 2014), and for mother and young Iberian red deer (Sibiryakova et al., 2015; Volodin et al., 2015).

In ruminants, the oral calls are commonly more individualized compared to the nasal calls (Sibiryakova et al., 2017, 2015; Volodin et al., 2011). The oral and nasal calls are also different in the acoustic structure: the oral calls are commonly higher in fundamental frequency (f_0) than the nasal calls (Padilla de la Torre et al., 2015; Sebe et al., 2010; Sibiryakova et al., 2017, 2015; Volodin et al., 2011, 2014). The oral calls are produced at situations of higher arousal than the nasal calls (Padilla de la Torre et al., 2015; Sebe et al., 2010; Volodin et al., 2011). In red deer and Siberian wapiti, oral and nasal contact calls may be produced in the same sequences (Sibiryakova et al., 2015; Volodin et al., 2015, 2016a).

Neonate calves are more vulnerable to predation compared to hinds, and so if a calf produces calls that need to be recognized by its mother, it simultaneously advertises itself to predators (Torriani et al., 2006). At the same time, for a mother, advertising its presence to a calf by her strongly individualistic calls is less dangerous. In a hider species, the fallow deer, an unilateral process of mothers-offspring vocal recognition of a mother by the young, has been demonstrated for calves within 2 months after birth (Torriani et al., 2006). At the same time, in a follower species, the saiga, the highly individualistic calls of both mother and neonates suggest mutual vocal recognition (Sibiryakova et al., 2017).

Siberian wapiti are hidiers within about 2 weeks after births; from 2 weeks to 3 months of age, they are opportunistic followers and from 3 months onwards permanently follow their mothers (Fedosenko, 1980; own unpublished observations). Hinds and calves

produce contact calls in calm situations, probably for supporting mother-offspring contact; these calls can be heard by humans from a distance of up to 100 m (Fedosenko, 1980; Volodin et al., 2016a). Hinds drive away and bite yearlings and adults that approach their hider young, but they never seem to defend them against people in the wild (Fedosenko, 1980) or in enclosures (our unpublished observations) as do, for example, the white-tailed or mule deer *Odocoileus hemionis* (Lingle, Rendall, & Pellis, 2007; Lingle, Rendall, Wilson, et al., 2007). In enclosures, hinds produce high-arousal contact and bugle calls when researchers approach their hider young (Volodin et al., 2016a).

Mother-offspring separation provokes emission of contact calls in many species of ruminants (Lingle et al., 2012; Padilla de la Torre et al., 2015) including red deer (Sibiryakova et al., 2015) and Siberian wapiti (Volodin et al., 2016a). For farmed Siberian wapiti bred for velvet antlers in Russia, China, and Kazakhstan (Kim et al., 2015; Lunitsin & Borisov, 2012; Volodin, Volodina, & Golosova, 2016b), the separation of mother and offspring to different herds represents a regular management practice (Lunitsin & Borisov, 2012). The adolescent Siberian wapiti reach body mass approximately 50–83 kg (from about one-third to about half of hind body mass of 154–178 kg) and are independent of mothers' milk (Fedosenko, 1980).

In a preceding study (Volodin et al., 2016a), we analyzed frequency, temporal, and power variables of contact and bugle calls, collected from Siberian wapiti calves (ranged in age from birth to about 5 weeks) and adults (hinds and stags) to estimate the potential acoustic differences between age and sex-classes. The open-mouth (oral) and closed-mouth (nasal) contact calls were registered in all sex and age-classes, whereas the open-mouth bugles were found in both stags and hinds but not in the calves. The f_{0max} of contact calls was found similar between calves and hinds (Volodin et al., 2016a). Vocal individuality has not yet been investigated in any sex or age-class of Siberian wapiti.

The focus of this study was on individuality of mother and adolescent contact calls in Siberian wapiti. The research questions of this study of mother and adolescent Siberian wapiti were as follows: whether the oral and nasal calls differ by their acoustic features? What are acoustic differences in contact calls between hinds and adolescents? And whether the calls are more individualistic in hinds than in adolescents? To respond on these questions, we (a) compare the values of acoustic variables of nasal and oral contact calls separately for hinds and for adolescents and (b) compare the classifying accuracies of individual hinds and of individual adolescents by their oral contact calls.

2 | MATERIALS AND METHODS

2.1 | Study site, animals, and dates

Contact calls of hinds and adolescents were recorded from 30 November to 4 December 2015 at the Siberian wapiti farm located

at Kostroma region of Central Russia (58°24'N, 43°15'E). The population originated in 2010 from about one hundred pure Siberian wapiti, translocated from farms of Altai/Khakasian region (Central Siberia, Russia) where the Siberian wapiti are native animals. Before transfer to the smaller winter enclosures where the animals were recorded during this study, the entire herd of 140 animals, including 38 stags, 57 hinds, and 45 calves (23 males, 22 females), was kept in the summer 70-hectare enclosure. The summer enclosure was an enclosed property of former agricultural grounds with gardens and forest of *Populus* sp., *Pinus silvestris*, and *Salix* sp. Supplementary food (grain) was provided each day, and water was available ad libitum. The calves were born in period from end of May to the middle of July 2015, so the age of adolescents during data collection varied from 5 to 6 months. The age range of the hinds was unknown. All animals were habituated to the presence of people in close vicinity.

2.2 | Mother-offspring separation

Production of contact calls by hinds and adolescents was provoked by transfer of the herd from the 70-hectare summer enclosure to the smaller winter enclosures and separation of mother and adolescent for winter in two neighboring enclosures: the 1-hectare enclosure for adolescents and the 5-hectare enclosure for adults (stags and hinds). The adolescents were placed in their winter enclosure together with three hinds, for decreasing the anxiety. The separation was a routine procedure of subdividing a herd for winter keeping (Lunitsin & Borisov, 2012). During separation, all adolescents were sexed and tagged with individual Allflex (Palmerston North, New Zealand) plastic ear tags. All adults were already individually ear-tagged.

The wire-mesh walls of the winter enclosures slightly complicated the visual contacts of mother and offspring, but did not prevent the audio contacts of hinds and adolescents. The distance between the nearest walls of the adolescent and adult winter enclosures was 20 m, so, the animals could contact vocally.

After separation, the adolescents tended to eat hay for 1 hr and then some of them started vocalizing. Hinds (many of them) started vocalizing immediately after separation. Vocal activity of the adolescents and especially of the hinds was high on the day of separation and in the next day and then reduced. As the moment of separation onwards, there were periods lasting up to 1 hr when all animals were silent. During the data collection, hinds separated from the young vocalized substantially more active than adolescents. Three hinds placed in the same enclosure together with their adolescents only vocalized to a small extent. The adolescents mostly vocalized in response to calls of the hinds. However, the actual mother-offspring dyads could not be established based on their vocal communication, because many hinds (up to five) could simultaneously respond to calls of the adolescents. In addition, the actual mother-offspring dyads were unknown. So calls of mother and offspring could only be collected and analyzed as independent call samples.

2.3 | Acoustic recordings

For acoustic recordings (48 kHz, 16 bit), we used Marantz PMD-660 solid state recorders (D&M Professional, Kanagawa, Japan) with Sennheiser K6-ME66 cardioid electret condenser microphones (Sennheiser electronic, Wedemark, Germany). The distance from the hand-held microphone to the animals was 5–20 m; the level of recording was adjusted during the recordings accordingly to the intensity of the produced calls.

Two researchers (one near the adolescent enclosure and another near the adult enclosure) recorded calls during 5 days, in daytime, from 10:00 to 16:30. The recording started when a researcher determined the individual identity of a caller. Caller identity was established by the ear tag, by vapor from the mouth or nose and movements of muscles of stomach, and then adjusted by reading the tag and/or based on photograph of a caller. During recording, the individual identity of a caller and vocal emission of each call through the mouth or through the nose was labeled by voice. All recordings were conducted outdoors. In total, we collected 9.1 hr of recordings of hind and adolescent contact calls, stored in a total of 81 digital acoustic files. Each file had duration up to 10 min (mean \pm SD = 6.7 \pm 3.2 min) and comprised calls of 1–5 individually identified animals.

2.4 | Call samples

For acoustic analyses, we took only calls of good quality with high signal-to-noise ratios that were not disrupted by wind, overlapped by calls of other animals, or saturated with very high amplitude in the recording. We analyzed only individually identified calls of known call type (nasal or oral). Calls were classified to nasal and oral call types based on voice comments of researchers made during recording.

To compare the acoustic structure between the oral and nasal contact calls, we selected the animals that provided calls of both types. We included in analysis 72 oral and 50 nasal calls of nine hinds (from 1 to 10 calls of each type per individual, on average 8.0 \pm 3.0 oral and 5.6 \pm 3.4 nasal calls per individual), 122 hind calls in total. We also included in analysis 92 oral and 39 nasal calls of 10 adolescents (4 males and 6 females, from 1 to 10 calls of each type per individual, on average 9.2 \pm 2.5 oral and 3.9 \pm 2.4 nasal calls per individual), 131 adolescent calls in total. For further analyses, we calculated average values of acoustic variables for each individual, separately for the oral and for the nasal calls.

To estimate classifying accuracy of individual hinds and adolescents by their oral calls, we analyzed 134 oral calls of nine hinds (14–15 calls per individual) and 129 oral calls of 9 adolescents (3 males and 6 females, 14–15 calls per individual from eight adolescents and 10 calls from the 9th adolescent). To avoid pseudoreplication, we used calls from different recordings per animal and from different parts within audio files, because calls from the same sequence are commonly more similar in their acoustic structure than calls from different sequences (Durbin, 1998). Contact calls of Siberian wapiti were given either singly or in sequences with irregular intervals and

contained from two calls to about a few dozen calls. The animals started and stopped vocalizing spontaneously or in response to different external events, for example, vocalizing or movements of other animals in the enclosure. The mean \pm SD number of audio files that provided calls for analyses was 3.1 ± 1.7 per animal.

In total, we analyzed 366 contact calls; 146 oral and 50 nasal calls of 12 hinds and 131 oral and 39 nasal calls of 10 adolescents. Sixty oral calls of hinds (10 calls per animal from 6 hinds) and 90 oral calls of adolescents (10 calls per animal from 9 adolescents) were used in both call samples, for analysis of the acoustic differences between the oral and nasal calls and for analysis of individual identity.

2.5 | Call analyses

Acoustic analyses were conducted in the same way for hinds and adolescents and for both types of contact calls, nasal and oral. For each call, we measured the same set of 14 acoustic variables: 2 temporal variables, 6 variables of fundamental frequency (f_0), and 6 power variables. Before analysis, the calls were downsampled to 11.025 kHz for better frequency resolution and high-pass filtered

at 50 Hz to reduce the low-frequency background noise. We measured the duration of each call and the duration from call onset to the point of maximum f_0 (dur-to-max) manually on the screen with the reticule cursor in the spectrogram window (Hamming window, FFT = Fast Fourier Transform 1,024 points, frame 50% and overlap 96.87%) using Avisoft SASLab Pro software (Avisoft Bioacoustics, Berlin, Germany). Then, we performed manual measurements on the screen with the standard marker cursor of the initial ($f_{0\text{beg}}$), maximum ($f_{0\text{max}}$), and end ($f_{0\text{end}}$) fundamental frequencies of each call (Figure 1; Supporting Information Audio S1). Measurements were exported automatically to Microsoft Excel (Microsoft Corp., Redmond, WA, USA). In addition, for each call, we calculated the dur-to-max% as ratio dur-to-max to the call duration (in percents).

In a 0.05-s call fragment symmetrical about f_0 (comprising about 10% of average call duration), we created the power spectrum, from which we automatically measured f_{peak} , representing the value of the frequency of maximum amplitude and the q25, q50, and q75, representing the lower, medium, and upper quartiles, covering 25%, 50%, and 75% of the energy of the call spectrum, respectively (Figure 1). On the same spectrum, we estimated (in dB) the power- f_0 ,

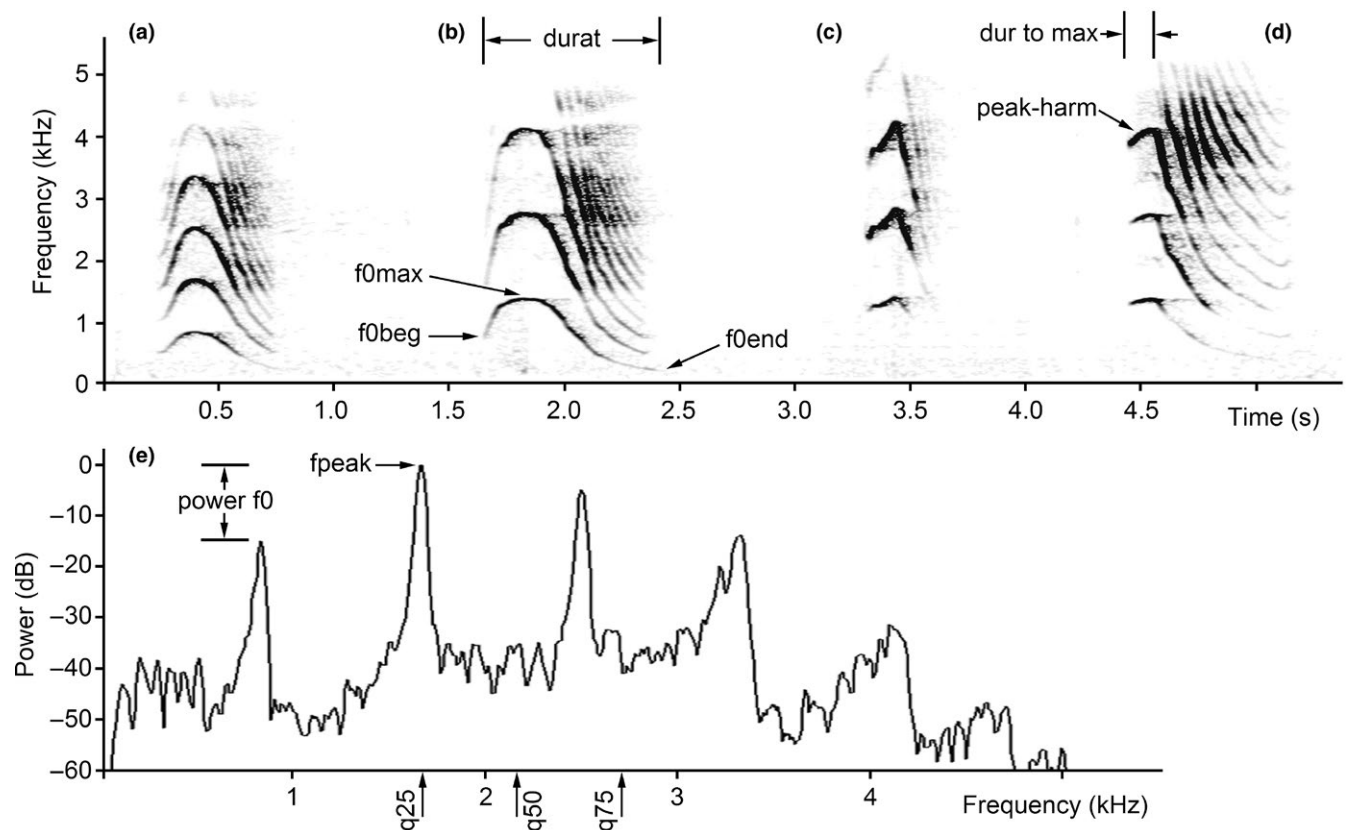


FIGURE 1 Measured acoustic variables. Spectrograms of (a) nasal and (b) oral hind contact calls and (c) nasal and (d) oral contact calls of a 5- to 6-month-old male adolescent, (e) mean power spectrum of 0.05-s fragment of a hind nasal call. Designations: durat: call duration; dur-to-max: duration from call onset to the point of the maximum fundamental frequency; $f_{0\text{max}}$: the maximum fundamental frequency; $f_{0\text{beg}}$: the fundamental frequency at the onset of a call; $f_{0\text{end}} = f_{0\text{min}}$: the fundamental frequency at the end of a call; peak-harm: the frequency band with the maximum energy; f_{peak} : the frequency of maximum amplitude within a call; power- f_0 : the relative power of the f_0 band compared to the peak harmonic; q25, q50, q75: the lower, the medium, and the upper quartiles, covering, respectively, 25%, 50% and 75% energy of a call spectrum. The spectrogram was created with Hamming window; 11,025 kHz sampling rate; FFT 1,024 points; frame 50%; and overlap 96.87%. The audio file of these calls is available as Supporting Information Audio S1

representing the relative power of the f0 band compared to the peak harmonic, on the screen using two harmonic cursors (Figure 1). The power-f0 was equal to 0 when the f0 band coincided with the fpeak band. In addition, we recorded the peak-harm, representing the order number of the harmonic with the maximum energy.

We measured the f0 variables following Reby and McComb (2003) using the Praat DSP package (Boersma & Weenink, 2013). The f0 contour was extracted using a cross-correlation algorithm (to Pitch (cc) command in Praat). The time steps in the analysis were 0.005 s for adolescents and 0.01 s for hinds; the lower and upper limits of the f0 range were 100–2000 Hz (following Volodin et al., 2016a). A preliminary visual analysis of the spectrograms in Avisoft showed that the lower limit was lower than the minimum f0 for calls of either hinds or adolescents. Spurious values and octave jumps in the f0 contour were corrected manually on the basis of the spectrograms. Values of f0min, f0max, the depth of frequency modulation $\Delta f_0 = f_{0\max} - f_{0\min}$, and average f0 of a call (f0mean) were taken automatically using the Pitch info command in the Pitch edit window.

Two different methods of measuring f0max (one using Avisoft and another using Praat) applied to the same calls, resulted in very similar values. Coefficients of correlation, calculated separately for the oral and for the nasal calls, ranged between 0.997 and 0.998 ($0.994 < R^2 < 0.996$). Thus, for subsequent acoustic analyses, we could select between these methods and we used the f0 values measured with Avisoft. We did not measure formants, as they cannot be measured in such high-frequency calls with widely spaced harmonics (Taylor & Reby, 2010; Volodin et al., 2016a).

2.6 | Statistics

Statistical analyses were made with STATISTICA, v. 8.0 (StatSoft, Tulsa, OK, USA) and R v.3.2.0; all means are given as mean \pm SD. Significance levels were set at 0.05, and two-tailed probability values are reported. Distributions of 240 measured parameter values of 280 distributions did not depart from normality (excepting fpeak and peak-harm), and distributions of all 56 mean parameter values did not depart from normality (Kolmogorov-Smirnov test, $p > 0.05$). As parametric ANOVA and discriminant function analysis (DFA) are relatively robust to departures from normality (Dillon & Goldstein, 1984), this was not an obstacle to the application of these tests.

We applied a repeated-measures ANOVA controlled for individuality, to compare the mean parameter values between contact oral and nasal calls separately for adolescents and for hinds. Then, we used one-way ANOVA to compare the mean parameter values between adolescents and hinds separately for oral and nasal calls. We provided effect size (ES) statistics to measure the strength of an effect in addition to statistical significance. We calculated the effect size for GLM using η^2 ($\eta^2 = 0.01$ for a small effect, 0.06 for a medium effect and 0.14 for a large effect; Cohen, 1992; Fritz, Morris, & Richler, 2012).

We used DFA to calculate the probability of the assignment of calls to the correct individual for oral call samples for either hinds or

adolescents. We included 11 of the 14 measured call variables in the DFA, excluding fpeak and peak-harm (for not meeting the criterion of normality), and f0min (because it was used for calculating another variable). The numbers of individually identified nasal calls were not sufficient for analysis of individual identity neither in hinds nor in adolescents.

We used Wilks' Lambda values to estimate how strongly acoustic variables of calls contribute to the discrimination of individuals. With a 2×2 Yates' chi-squared test, we compared the values of correct assignment of nasal and oral calls to individuals. To validate our DFA results, we calculated the random values of correct assignment of calls to individual by applying randomization procedure with macros, created in R. The random values were averaged from DFAs performed on 1,000 randomized permutations on the data sets as described by Solow (1990). For example, to calculate the random value of classifying oral calls to individual hinds, each permutation procedure included the random permutation of 134 calls among nine randomization groups, respectively, to nine individual hinds which were examined, and followed by DFA standard procedure built-in in STATISTICA. All other permutation procedures were made similarly. Using a distribution obtained by the permutations, we noted whether the observed value exceeded 95%, 99%, or 99.9% of the values within the distribution (Solow, 1990). If the observed value exceeded 95%, 99%, or 99.9% of values within this distribution, we established that the observed value did differ significantly from the random one with a probability $p < 0.05$, $p < 0.01$, or $p < 0.001$, respectively (Matrosova, Volodin, Volodina, & Vasilieva, 2010a; Matrosova, Volodin, Volodina, Vasilieva, & Kochetkova, 2010b; Sibiryakova et al., 2015; Solow, 1990).

3 | RESULTS

3.1 | Comparison of oral and nasal calls

Adolescents and hinds produced both oral and nasal contact calls. A contour of f0 was very similar between hinds and adolescents and between oral and nasal calls (Figure 1). The f0beg always exceeded the f0end, and the f0end was equal to the f0min. The point of maximum f0 was shifted toward the start of a call, being located at the distance of 18.8%–24.9% of the total call duration for both oral and nasal calls of all age-classes (Table 1).

In the oral contact calls, the band with the maximum energy was never higher than the 4th frequency band (considering f0 as the first frequency band) in both hinds and adolescents. The f0 was the band with the maximum energy in 21% of oral contact calls of adolescents and in 57% of oral contact calls of hinds. In the nasal contact calls, the highest band with the maximum energy was the 4th frequency band in adolescents and the 5th frequency band in hinds. The f0 was the band with the maximum energy in 31% of nasal contact calls of adolescents and in 34% of nasal contact calls of hinds.

We compared the average values of acoustic variables of oral and nasal calls separately for the 10 adolescents and for the nine hinds (Table 1). Repeated-measures ANOVA showed the lack of

TABLE 1 Values (mean \pm SD) of oral and nasal call variables of adolescents and hinds, repeated-measures ANOVA results for comparison the mean parameter values between contact oral and nasal calls separately for adolescents and for hinds and one-way ANOVA results for comparison the mean parameter values between adolescents and hinds separately for oral and nasal calls

Acoustic variable	Adolescents (n = 10)			Hinds (n = 9)			Adolescent-hind calls ANOVA comparison	
	Oral calls	Nasal calls	ANOVA	Oral calls	Nasal calls	ANOVA	Oral calls	Nasal calls
Duration (s)	0.47 \pm 0.12	0.47 \pm 0.10	$F_{1,9} = 0.01$ $p = 0.92$ $\eta^2 = 0.001$	0.54 \pm 0.17	0.51 \pm 0.10	$F_{1,8} = 0.95$ $p = 0.36$ $\eta^2 = 0.11$	$F_{1,17} = 1.00$ $p = 0.33$ $\eta^2 = 0.05$	$F_{1,17} = 0.54$ $p = 0.47$ $\eta^2 = 0.03$
Dur-to-max% (%)	19.4 \pm 10.3	18.8 \pm 10.6	$F_{1,9} = 0.16$ $p = 0.70$ $\eta^2 = 0.02$	24.9 \pm 8.9	22.1 \pm 8.0	$F_{1,8} = 0.60$ $p = 0.24$ $\eta^2 = 0.17$	$F_{1,17} = 1.55$ $p = 0.23$ $\eta^2 = 0.08$	$F_{1,17} = 0.58$ $p = 0.46$ $\eta^2 = 0.03$
f0mean (kHz)	1.07 \pm 0.17	0.98 \pm 0.17	$F_{1,9} = 9.87$ $p = 0.01$ $\eta^2 = 0.52$	0.98 \pm 0.21	0.75 \pm 0.15	$F_{1,8} = 27.14$ $p < 0.001$ $\eta^2 = 0.77$	$F_{1,17} = 1.14$ $p = 0.30$ $\eta^2 = 0.06$	$F_{1,17} = 9.64$ $p = 0.006$ $\eta^2 = 0.36$
f0max (kHz)	1.45 \pm 0.23	1.29 \pm 0.19	$F_{1,9} = 19.73$ $p = 0.002$ $\eta^2 = 0.67$	1.43 \pm 0.25	1.11 \pm 0.23	$F_{1,8} = 51.19$ $p < 0.001$ $\eta^2 = 0.87$	$F_{1,17} = 0.04$ $p = 0.84$ $\eta^2 = 0.002$	$F_{1,17} = 3.65$ $p = 0.07$ $\eta^2 = 0.18$
f0beg (kHz)	1.26 \pm 0.18	1.15 \pm 0.14	$F_{1,9} = 13.53$ $p = 0.005$ $\eta^2 = 0.60$	1.13 \pm 0.28	0.87 \pm 0.25	$F_{1,8} = 78.27$ $p < 0.001$ $\eta^2 = 0.91$	$F_{1,17} = 1.40$ $p = 0.25$ $\eta^2 = 0.08$	$F_{1,17} = 9.54$ $p = 0.007$ $\eta^2 = 0.36$
f0end (kHz)	0.66 \pm 0.17	0.62 \pm 0.16	$F_{1,9} = 2.31$ $p = 0.16$ $\eta^2 = 0.20$	0.35 \pm 0.08	0.32 \pm 0.03	$F_{1,8} = 1.74$ $p = 0.22$ $\eta^2 = 0.18$	$F_{1,17} = 25.82$ $p < 0.001$ $\eta^2 = 0.60$	$F_{1,17} = 29.28$ $p < 0.001$ $\eta^2 = 0.63$
$\Delta f0$ (kHz)	0.81 \pm 0.21	0.68 \pm 0.14	$F_{1,9} = 10.52$ $p = 0.01$ $\eta^2 = 0.54$	1.07 \pm 0.22	0.79 \pm 0.22	$F_{1,8} = 27.02$ $p < 0.001$ $\eta^2 = 0.77$	$F_{1,17} = 6.86$ $p = 0.02$ $\eta^2 = 0.29$	$F_{1,17} = 1.77$ $p = 0.20$ $\eta^2 = 0.09$
fpeak (kHz)	2.93 \pm 0.50	2.35 \pm 0.81	$F_{1,9} = 6.94$ $p = 0.03$ $\eta^2 = 0.43$	2.13 \pm 0.43	2.16 \pm 0.87	$F_{1,8} = 0.01$ $p = 0.93$ $\eta^2 = 0.001$	$F_{1,17} = 13.92$ $p = 0.002$ $\eta^2 = 0.45$	$F_{1,17} = 0.26$ $p = 0.62$ $\eta^2 = 0.01$
q25 (kHz)	1.86 \pm 0.38	1.24 \pm 0.54	$F_{1,9} = 42.22$ $p < 0.001$ $\eta^2 = 0.82$	1.50 \pm 0.49	1.00 \pm 0.49	$F_{1,8} = 14.04$ $p = 0.006$ $\eta^2 = 0.64$	$F_{1,17} = 3.21$ $p = 0.09$ $\eta^2 = 0.16$	$F_{1,17} = 1.04$ $p = 0.32$ $\eta^2 = 0.05$
q50 (kHz)	2.92 \pm 0.40	2.10 \pm 0.48	$F_{1,9} = 26.58$ $p < 0.001$ $\eta^2 = 0.75$	2.43 \pm 0.54	1.88 \pm 0.65	$F_{1,8} = 8.64$ $p = 0.02$ $\eta^2 = 0.52$	$F_{1,17} = 5.16$ $p = 0.04$ $\eta^2 = 0.23$	$F_{1,17} = 0.72$ $p = 0.41$ $\eta^2 = 0.04$
q75 (kHz)	3.71 \pm 0.35	3.35 \pm 0.40	$F_{1,9} = 16.18$ $p = 0.003$ $\eta^2 = 0.64$	3.27 \pm 0.32	2.87 \pm 0.62	$F_{1,8} = 7.27$ $p = 0.03$ $\eta^2 = 0.48$	$F_{1,17} = 8.12$ $p = 0.01$ $\eta^2 = 0.32$	$F_{1,17} = 4.13$ $p = 0.06$ $\eta^2 = 0.20$
Power-f0 (dB)	6.48 \pm 3.57	5.57 \pm 5.54	$F_{1,9} = 0.81$ $p = 0.39$ $\eta^2 = 0.08$	3.40 \pm 3.24	4.13 \pm 4.17	$F_{1,8} = 0.30$ $p = 0.61$ $\eta^2 = 0.03$	$F_{1,17} = 3.85$ $p = 0.07$ $\eta^2 = 0.18$	$F_{1,17} = 0.40$ $p = 0.54$ $\eta^2 = 0.02$
Peak-harm	2.09 \pm 0.45	1.95 \pm 0.91	$F_{1,9} = 0.52$ $p = 0.49$ $\eta^2 = 0.05$	1.56 \pm 0.44	2.13 \pm 0.94	$F_{1,8} = 3.36$ $p = 0.10$ $\eta^2 = 0.30$	$F_{1,17} = 6.65$ $p = 0.02$ $\eta^2 = 0.28$	$F_{1,17} = 0.17$ $p = 0.68$ $\eta^2 = 0.01$

Notes. Designations: duration: call duration; dur-to-max%: the duration from call onset to the point of the maximum fundamental frequency; f0mean: the average fundamental frequency of a call; f0max: the maximum fundamental frequency of a call; f0beg: the fundamental frequency at the onset of a call; f0end: the fundamental frequency at the end of a call; $\Delta f0$: the depth of frequency modulation, calculated as the difference between f0max and f0min; fpeak: the frequency of maximum amplitude within a call; q25, q50, q75: the lower, medium, and upper quartiles of a call; power-f0: the relative power of the f0 band compared to the peak frequency band; peak-harm: the order number of the harmonic with the maximum energy. Significant differences are highlighted in bold. η^2 : measure for estimating the effect size ($\eta^2 = 0.01$ for a small effect, 0.06 for a medium effect and 0.14 for a large effect)

differences between oral and nasal contact calls regarding the duration and dur-to-max% for either adolescents or hinds. All f0 variables for the exclusion of f0end were significantly higher in the oral than in the nasal contact calls of either adolescents or hinds. The values of

all quartiles (q25, q50, and q75) were also significantly higher in the oral than in the nasal calls of either adolescents or hinds, whereas fpeak was higher in the oral than in the nasal calls only in adolescents but not in hinds. The values of power-f0 and peak-harm did

not differ between oral and nasal contact calls in either adolescents or hinds (Table 1). Effect sizes also indicated that the sizes of these differences in fundamental frequency and quartiles were larger than in duration, peak frequency, power-f₀, and peak-harm (Table 1).

3.2 | Comparison of adolescent and hind calls

In the oral contact calls, the duration and dur-to-max% did not differ between adolescents and hinds (Table 1). Among f₀ variables, only f_{0end} = f_{0min} was significantly higher in adolescents than in hinds, whereas Δf₀ was significantly lower in adolescents than in hinds. The values of f_{peak}, q₅₀, q₇₅, and peak-harm were significantly higher in adolescents than in hinds, whereas other power variables did not differ between adolescents and hinds (Table 1). The least effect sizes were found for duration and maximum fundamental frequency (Table 1).

Similarly, in the nasal contact calls, the duration and dur-to-max% did not differ among adolescents and hinds (Table 1). Among f₀ variables, f_{0mean}, f_{0beg}, and f_{0end} were significantly higher in adolescents than in hinds. The values of all other f₀ as well as of all power variables did not differ between age-classes (Table 1). The least effect sizes were found for duration, dur-to-max%, peak frequency, power-f₀, and peak-harm (Table 1).

3.3 | Individual discrimination with DFA

For either adolescent or hind oral calls, the average value of correct classification to individual with DFA (96.9% for adolescent oral calls, 92.5% for hind oral calls) exceeded our random expectations (33.1% ± 3.5%, 33.0% ± 3.3%, respectively, all $p < 0.001$; Figures 2 and 3). In order of decreasing importance, dur-to-max%, f_{0beg}, f_{0mean}, and f_{0max} were mainly responsible for discriminating individuals for adolescent oral calls, and the duration, f_{0beg}, f_{0max}, and f_{0mean} were mainly responsible for discriminating individuals

for hind oral calls. Thus, in both DFAs, similar sets of key discriminating variables were found.

As both DFAs used the same number of individuals (9 hinds and 9 adolescents) and nearly equal numbers of calls (14–15 per animal), we could directly compare classifying accuracy for adolescents and hinds. The average value of correct classification of individuals based on their oral contact calls did not differ significantly between adolescents and hinds ($\chi^2_1 = 1.69$, $p = 0.19$; Figure 3).

4 | DISCUSSION

This study revealed that the acoustic individuality of oral contact calls was equally high in the adolescents and in the hinds of Siberian wapiti. In contrast, in Iberian red deer, more individualistic oral contact calls were found in the hinds than in the neonates (Sibiryakova et al., 2015). We suggest that in Siberian wapiti, the elevated individuality in the acoustic structure of adolescent calls has developed to compensate for the limited amount of age-related acoustic variation of their contact calls compared with those in Iberian red deer (Sibiryakova et al., 2015). Whereas in the Iberian red deer, the maximum fundamental frequency of hind oral calls (0.21 kHz) is much lower than in 4-month-old calves (0.57 kHz; Volodin et al., 2015); in the Siberian wapiti, the age-related differences in the maximum fundamental frequency and duration are lacking (Table 1). Moreover, whereas the oral calls of 5–6 months adolescents became nearly two times longer compared to the neonates recorded on the same farm during the calving season of the same year (from the mean 0.29–0.47 s), their maximum fundamental frequency remained similar (from 1.56 kHz to 1.45 kHz; Volodin et al., 2016a). The lack of variation in maximum fundamental frequency is important, as this variable is most resistant against degradation in the environment among other frequency variables, encoding

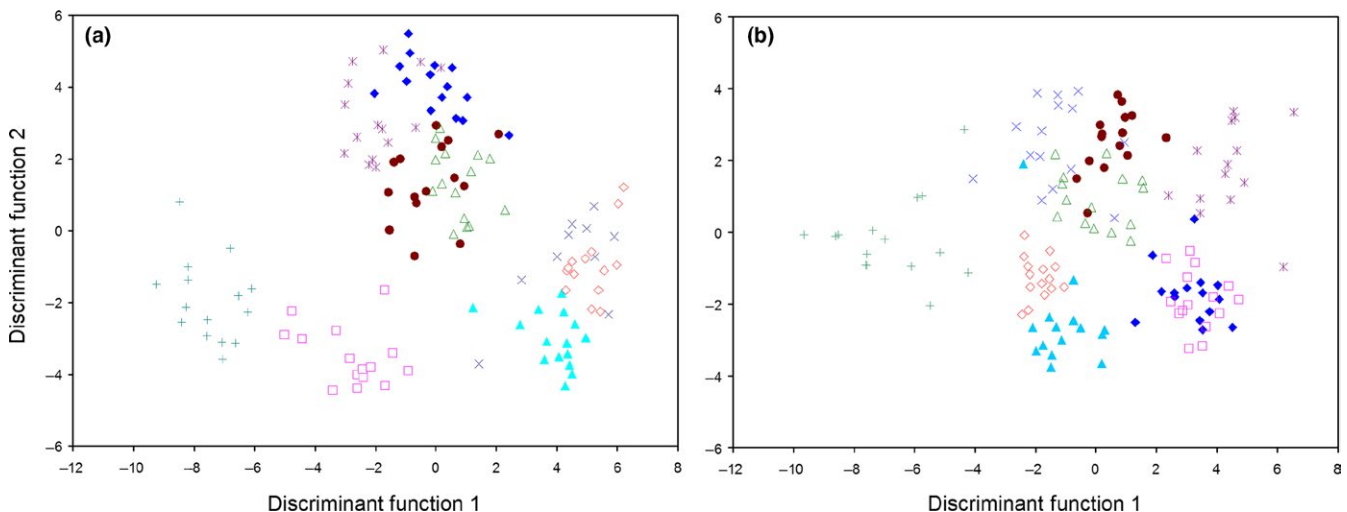


FIGURE 2 Scatterplots showing separation produced by the first two discriminant functions of the oral contact calls of (a) 9 adolescents and (b) 9 hinds [Colour figure can be viewed at wileyonlinelibrary.com]

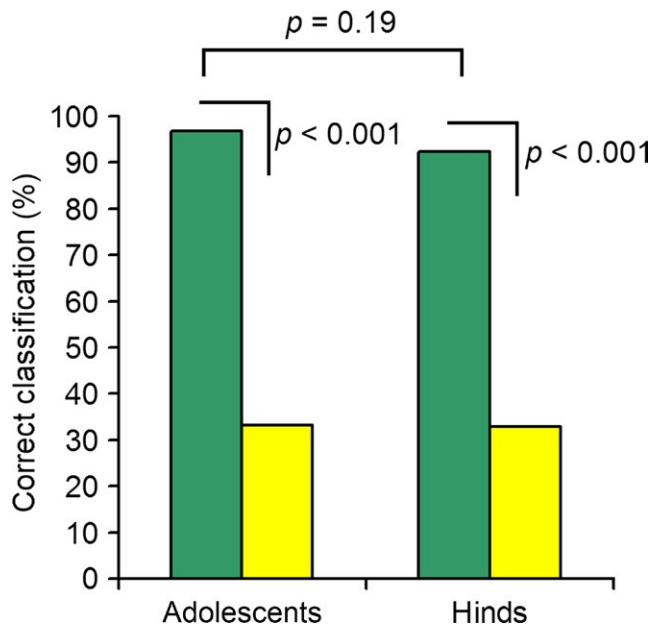


FIGURE 3 Individual discrimination of adolescents and hinds based on oral contact calls. Green bars indicate values of discriminant function analysis (DFA), and yellow bars indicate random values, calculated with randomization procedure. Comparisons between observed and random values with permutation tests are shown above the bars, and comparison between adolescent and hind calls with *chi-square* tests is shown by bracket [Colour figure can be viewed at wileyonlinelibrary.com]

individual identity (Maciej, Fischer, & Hammerschmidt, 2011; Matrosova et al., 2010a).

Vocal cues to young age may be shared across mammalian taxa (Lingle & Riede, 2014) similar to the shared across taxa vocal cues to discomfort (Briefer, 2012; Filippi et al., 2017; Klenova, 2015; Lingle & Riede, 2014; Volodin, Volodina, Gogoleva, & Doronina, 2009). The study by Lingle and Riede (2014) demonstrated that female mule deer and white-tailed deer respond to vocalizations of the young of many taxonomically distant species if the fundamental frequency falls or is manipulated to fall within the frequency range in which deer respond to young of their own species. In species that have strong acoustic differences in the acoustic variables of mother and offspring calls, the vocal cues to age (primarily the fundamental frequency) might represent an important trigger for mothers responding to calls of the young. Individual identification in these species might represent a two-step process, of discriminating conspecifics to “calves” and “hinds” at first step based on call frequency (Lingle & Riede, 2014; Lingle, Rendall, Wilson, et al., 2007) and recognizing individuals at the second step based on other acoustic variables (Lingle, Rendall, & Pellis, 2007). Two-step process of recognizing the individual signature of mother’s calls by pups based on different acoustic variables was previously reported for the Antarctic fur seal *Arctocephalus gazella* (Aubin, Jouventin, & Charrier, 2015).

However, in the Siberian wapiti and probably also in American wapiti *Cervus canadensis* that also display the similar fundamental frequency in hind and calf calls (Feighny, 2005), recognizing

age-classes is complicated. So, wapiti mother and young should base mother-offspring recognition only on the individualistic traits of their contact calls. At the same time, the lack of age-related changes in frequency due to the growing process might facilitate memorization the successive versions of the voice of the growing young. This use of memory was shown in the studies subantarctic fur seals *Arctocephalus tropicalis* (Charrier, Mathevon, & Jouventin, 2001, 2002) and of domestic goats (Briefer, Padilla de la Torre, & McElligott, 2012). Further research should focus on revealing potential factors that constrain the age-related variation of fundamental frequency in contact calls of wapiti.

Similar f_0 values between mother and young were also reported for cows and calves of domestic cattle (Padilla de la Torre et al., 2015). However, compared to contact calls of domestic cattle cows and calves, calls of Siberian wapiti are very high frequency. While to date, it is unclear how wapiti are able to produce such a high f_0 , as vocal fold elasticity alone cannot explain this extreme divergence from biomechanical predictions (Riede & Titze, 2008; Riede, Lingle, Hunter, & Titze, 2010), this example provides a clear illustration of the independence of f_0 from body size and even in this case from vocal fold length (Riede & Brown, 2013; Taylor & Reby, 2010). At the same time, this study of contact calls of mother and adolescent Siberian wapiti is in line with studies suggesting potentially distinctive mechanics for production of the high-frequency calls in Siberian wapiti (Volodin et al., 2016a), American wapiti (Reby et al., 2016), European red deer (Volodin, Volodina, Frey, Carranza, & Torres-Porras, 2013), and domestic cattle (Hall, Vince, Walser, & Garson, 1988; Volodin, Volodina, & Frey, 2017b) compared to those produced with normal vocal fold vibration.

In Siberian wapiti mother and offspring, contact calls display similar degrees of individuality. This suggests potential for a mutual (bilateral) process of vocal recognition of mother and young, as in domestic goats *Capra hircus* (Briefer & McElligott, 2011) but is distinctive to an unilateral process of recognition of a mother by the young in fallow deer (Torriani et al., 2006) and in Central European red deer (Vaňková, Bartoš, & Malek, 1997).

During nursing period, vocal recognition is primarily important for selective feeding one’s own offspring (Keller et al., 2003; Nowak et al., 2000; Sebe, Nowak, Poindron, & Aubin, 2007; Sibiryakova et al., 2017), whereas after weaning, it is important only for maintaining of spatial proximity between mother and young (Lapshina et al., 2012; Torriani et al., 2006). The adolescent animals in our study were not fully independent of their mothers socially, but were independent in food and ability to flee of predators. So, for them was not so dangerous to advertise their own presence to their mothers. Nevertheless, we observed that the mothers vocalized more actively than the calves, so their vocal contacts were not perfectly symmetrical, similar to reports for the Central European red deer (Vaňková et al., 1997) and saiga (Sibiryakova et al., 2017).

Siberian wapiti adolescents and hinds produced both oral and nasal contact calls. While the oral and the nasal contact calls did not differ regarding the temporal variables for either adolescents or

hinds, the values of most variables of fundamental frequency were significantly higher in the oral than in the nasal contact calls of both adolescents or hinds. The higher fundamental frequency in the oral than in the nasal calls might be related to different mechanics for the emission of the oral calls (Volodin et al., 2011, 2014). Compared to production of nasal calls, for production of oral calls, the larynx slightly lowers, which results in loss of contact between epiglottis and soft palate. This movement should create additional tension and thinning of the vocal folds and may result in a higher f_0 of oral calls than of nasal calls (for details, see discussion in Volodin et al., 2014). Our data of the higher fundamental frequency in the oral than in the nasal calls are consistent with results of other studies on ruminants: goitred gazelles (Volodin et al., 2011), domestic sheep (Sebe et al., 2010), saiga (Sibiryakova et al., 2017; Volodin et al., 2014), and on African elephants *Loxodonta africana* (Stoeger et al., 2012).

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ORCID

Ilya A. Volodin  <http://orcid.org/0000-0001-6278-0354>

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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