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Acoustically different contact calls of mother and young goitred gazelle are equally individualized: is this a common relationship in ruminants?

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Abstract

Relationships between individualization and the acoustics of contact calls in ungulate mother and young are different between taxa. We compared the acoustic variables and individuality of adult female and neonate goitred gazelles *Gazella subgutturosa*. Discriminant function analysis based on six acoustic variables of nasal (closed-mouth) contact calls similarly accurately classified calls to neonate and adult individuals in spite of the prominent differences in the acoustic resonances (formants) and the mean fundamental frequency of their calls. In addition, we found prominent differences in duration, mean fundamental frequency and frequencies of the first four formants between nasal and oral (open-mouth) contact calls within and between adult and neonate age-classes. We discuss the effects on the acoustics of call production mode (oral versus nasal) and the relationship of acoustic differences and individuality in mother and young contact calls across species of ruminants (Bovidae and Cervidae).

Keywords

mother-offspring communication, ungulate vocal identity, nasal calls, oral calls, *Gazella subgutturosa*.

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1. Introduction

Mutual individual recognition in mother and offspring ungulates is based on their individualistic contact calls (Shillito-Walser et al., 1981; Searby & Jouventin, 2003; Terrazas et al., 2003; Sèbe et al., 2008, 2010; Briefer & McElligott, 2011; Padilla de la Torre et al., 2016). Neonates rely on individualistic contact calls of their mothers for rejoining after separation (Sèbe et al., 2010). Mothers use individualistic contact calls of their young to recognize own offspring among the alien ones for supporting spatial proximity (Torriani et al., 2006; Lingle et al., 2007a; Sèbe et al., 2007; Briefer & McElligott, 2011) and for avoiding potential allosuckling (Nowak et al., 2000; Brandlová et al., 2013).

In a Bovidae species, the saiga *Saiga tatarica*, contact calls of mother and young are similarly highly individualized in spite of the differences in the acoustic resonances (formants) and the mean fundamental frequency of their calls (Sibiryakova et al., 2017). This suggests a mutual process of mother-offspring vocal recognition (Briefer & McElligott, 2011). In contrast, in Cervidae species with acoustically different contact calls of mother and young (as in fallow deer *Dama dama* and Iberian red deer *Cervus elaphus hispanicus*), the substantially more individualized calls of the mothers suggest an unilateral mother-offspring vocal recognition (Torriani et al., 2006: Sibiryakova et al., 2015). At the same time, in Siberian wapiti *C. e. sibiricus*, the acoustically similar contact calls of mother and young are similarly individualized (Sibiryakova et al., 2018). Studying cross-taxa variation in the relationship between the acoustic differences and individuality of mother and young contact calls might highlight common rules of encoding individual identity by acoustic variables in mammals. Otherwise, the found differences raise the questions, what factors can explain the differences between species.

In both Bovidae and Cervidae species, both mother and young produce two types of contact calls, the closed-mouth nasal and the open-mouth oral calls (Sèbe et al., 2010; Volodin et al., 2011; Padilla de la Torre et al., 2016; Sibiryakova et al., 2017, 2018). Both oral and nasal contact calls can occur within one call series (Volodin et al., 2015; Sibiryakova et al., 2018). However, the oral calls are commonly produced at contexts of higher arousal than nasal calls (Volodin et al., 2011; Padilla de la Torre et al., 2015). Comparative study of nasal and oral contact calls in mother and young might reveal the effects on the acoustics of both call production mode (oral vs nasal) and age-class/body size (adults vs young) (Volodin et al., 2014, 2016; Sibiryakova et al., 2015, 2017).

Nasal and oral calls differ by the acoustic variables, with the oral calls commonly higher in fundamental frequency and with lower formants (Richardson et al., 1983; Sèbe et al., 2010; Efremova et al., 2011; Volodin et al., 2011; Padilla de la Torre et al., 2015). The primary source variable, the fundamental frequency (f0) is stated by rate of vocal fold vibration in the larynx, whereas the filter variables (the formants) are stated by filtering the source signal by the supra-laryngeal vocal tract (Fant, 1960; Titze, 1994; Taylor & Reby, 2010). The formant frequencies are inversely related to the vocal tract length (Fant, 1960; Titze, 1994; Fitch & Hauser, 2002; Taylor & Reby, 2010). The nasal vocal tract is longer than the oral vocal tract (Volodin et al., 2014; Efremova et al., 2016), so the formants are lower in the nasal than in the oral calls (Volodin et al., 2011, 2014). In both young and adult ungulates, the acoustic differences between the oral and nasal contact calls were reported for red deer *Cervus elaphus* (Sibiryakova et al., 2015; 2017), saiga (Sibiryakova et al., 2017) and domestic cattle *Bos taurus* (Padilla de la Torre et al., 2015). For goitred gazelles *Gazella subgutturosa*, the acoustic differences between the oral and nasal contact calls were only studied in 3–6 wk young (Volodin et al., 2011).

In the goitred gazelle, individual vocal identity is encoded by both source and filter acoustic variables (Volodin et al., 2011; Lapshina et al., 2012). The occurrence of the nasal and oral calls is different along ontogeny of either goitred gazelles (Volodin et al., 2011, 2017b; Lapshina et al., 2012) or other ungulates (Sibiryakova et al., 2015, 2017, 2018), with the oral calls prevailing at early ontogeny and the nasal calls prevailing in adolescents and adults. In the goitred gazelle, the potential to encode vocal identity varies with age: in 3–6-week-old goitred gazelles, both nasal and oral contact calls are highly individualistic; however, the oral calls have a higher potential for encoding vocal identity (Volodin et al., 2011). In adolescent goitred gazelles, the oral calls disappear, whereas the nasal calls are becoming increasingly individualistic (Lapshina et al., 2012).

Adult female goitred gazelles give birth to their young from mid-April to beginning of June at individual parcels of land (Soldatova, 1983; Jevnerov, 1984; Marmasinskaya, 1996, 2008; Blank, 1998; Blank et al., 2015). During the nursing period, mothers communicate with their young with contact calls

(Jevnerov, 1984; Blank, 1985; Pereladova & Pereladov, 1986; Marmasinskaya, 2008; Volodin et al., 2017a). Neonate goitred gazelles are hiders on territories of their mothers for 2–3 weeks postpartum, and only at 4 weeks leave the territories for foraging together with their mothers and other young in small groups or herds (Blank et al., 2012).

For the neonate goitred gazelles, both the acoustic structure and vocal identity were only investigated in the oral calls (Volodin et al., 2017b), whereas the acoustics and individual identity of the nasal calls were not yet investigated. For adult goitred gazelles, the acoustics of the oral calls were previously described only in males, in the context of courting females and deterring rival males during the rut (Frey et al., 2011). For adult female goitred gazelles, the acoustic structure was only investigated in the nasal calls (Volodin et al., 2017a). To our knowledge, calls of adult goitred gazelles have not been analysed for their individualistic traits before. Individual vocal identity was not yet ever compared between goitred gazelle mother and young. In this study, we estimate the differences in the acoustic structure of nasal and oral contact calls and compare the degrees of individualization on balanced samples of the nasal contact calls between adult female and neonate goitred gazelles.

2. Methods

2.1. Study site, animals and dates of work

Data were collected in May–June 2008–2013 from individually identified captive adult female and neonate goitred gazelles at the Ecocenter ‘Djeiran’ (Uzbekistan, Bukhara region, Kagan district, 39°41′N, 64°35′E). Adult females were individually identified by ear tags, neonates by their natural marks. Nasal and oral contact calls of 21 (11 male, 10 female) neonate (1–10 days old, based on the state of the umbilical cord) goitred gazelles were collected between 2–7 May 2008. Nasal and oral contact calls of eight adult females (i.e., older 2 years; Efremova et al., 2016; Volodin et al., 2017a) were collected in May–June 2009, 2010 and 2013.

Subject neonates were captured (preferentially one per twin) on 1–2 May 2008 on the 5145-ha fenced territory of the Ecocenter and then raised by humans for further transportation to other conservation areas or institutions (Soldatova et al., 2010; Efremova et al., 2011, 2016; Volodin et al., 2011, 2017a). The neonates were housed in groups of 5–7 individuals in a few enclosures of 2 × 4 m; one-half of the enclosure represented a house made of cane, another half was outdoor enclosure fenced with cane and wire mesh. The neonates were fed with goat and cow milk from 0.33-l bottles 3 times per day (for keeping and feeding details, see Soldatova et al., 2010; Efremova et al., 2011; Volodin et al., 2011).

Subject adult females were kept in groups of 6–8 individuals in two outdoor enclosures with trees sunscreens, together with their captive-born neonates and yearlings. The adult females were fed twice a day with fresh and semidried grass and mixed fodder; fresh water was available ad libitum.

2.2. *Call recording*

Calls were recorded (48 kHz, 16 bit) using digital recorders Zoom-H4 and Marantz-PMD-660 with condenser microphones AKG-C1000S and Sennheiser K6-ME64. The distance from microphone to animals was 1–5 m. Individual identity and oral/nasal vocal emission was labelled by a researcher's voice; in addition, a part of the audio recordings was done with a parallel video using Panasonic NV-GS250 or Panasonic NV-GS320 camcorders.

Contact calls were recorded daily (30–120 min, 2 times a day), commonly before and during the morning and evening feeding and during everyday activity. Calls of neonates were recorded from inside or outside the enclosures. Calls of adult females were recorded from outside the enclosures. In total, we collected about 14 h of recordings from neonates and about 24 h of recordings from adult females.

2.3. *Call samples*

For acoustic analyses, we selected calls of high quality, not superimposed of other calls or noises, evenly during the period of recordings, because calls in series could be more similar to each other (Durbin, 1998). We classified calls to nasal and oral (Figure 1) based on video clips where we could see whether the mouth was opened or closed during a call, and based on comments of researchers made during recordings. For the 21 neonates, we analysed a total of 388 contact calls (135 nasal and 253 oral calls, 3–14 nasal and 1–15 oral calls per individual). For the eight adult females, we analysed a total of 184 contact calls (151 nasal and 33 oral calls; 4–35 nasal and 1–18 oral calls per individual). One neonate and one adult female provided only one oral call for analyses.

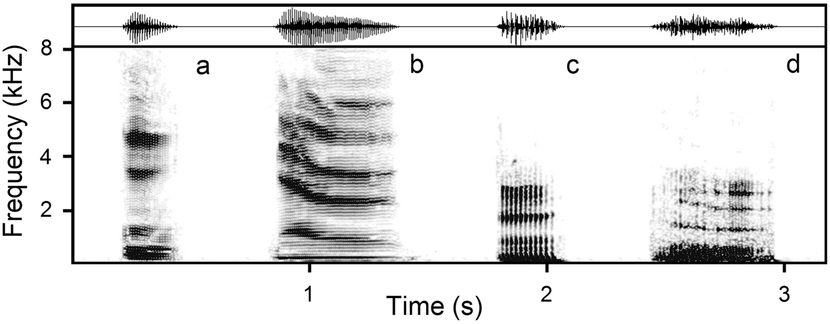

Figure 1. Waveform (top) and spectrogram (bottom) of contact calls of neonate and adult female goitred gazelles: the nasal call of a neonate (a); the oral call of a neonate (b); the nasal call of an adult female (c); and the oral call of an adult female (d). Settings for creating spectrograms were: sampling frequency 24 kHz, Hamming window, Fast Fourier Transform (FFT) 1024, frame 50%, overlap 93.75%. Whereas contact calls are tonal in both adult females and neonates, the spectrogram at the same spectrogram settings displays a pulsed spectrum in the adult female and a harmonic spectrum in the neonate calls, because fundamental frequency in calls of adult females is very low. An audio file with the nasal call of a neonate, the oral call of a neonate, the nasal call of an adult female, and the oral call of an adult female goitred gazelle can be accessed at 10.6084/m9.figshare.8052422.

Samples of nasal contact calls for discriminant function analysis for comparison vocal identity between adult females and neonates, comprised 131 nasal calls: 66 nasal calls from seven (5 male, 2 female) neonates, 8–10 calls per individual, and 65 nasal calls from seven adult females, 7–10 calls per individual. We used a balanced sample size for the discriminant function analysis, because an equal number of individuals and an equal number of calls are necessary for a comparative DFA. Available samples of the oral calls were not sufficient for comparative analyses of vocal individuality, as only four adult females provided the oral calls.

2.4. Call analysis

For each nasal and oral call, we measured the same six acoustic variables (Figure 2). We measured call duration and the mean fundamental frequency (f0mean) using Avisoft SASLab Pro software (Avisoft Bioacoustics, Berlin, Germany). We measured call duration using standard marker cursor in the spectrogram window of Avisoft, displaying waveform and spectrogram, with the following settings for creating spectrogram: sampling frequency 48 kHz; Hamming window; Fast Fourier Transform (FFT) 1024; frame 50%; overlap 93.75%. These settings enable a frequency resolution of 46 Hz and time res-

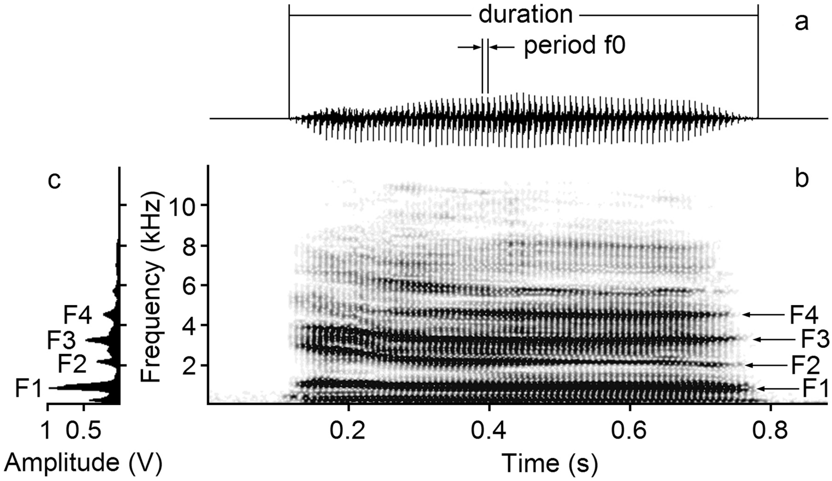

Figure 2. Measured acoustic variables shown on waveform (a), spectrogram (b) and the mean power spectrum (c) of the oral contact call of a 7-day-old neonate goitred gazelle. Duration, call duration; period f0, fundamental frequency period; F1, F2, F3, F4, frequencies of the four first formants.

olution of 0.0013 s. The f0mean was calculated as inverse value of the mean call fundamental frequency period (period f0, Figure 2). All measurements were automatically exported to Microsoft Excel (Microsoft, Redmond, WA, USA).

The four first formants (F1–F4) were measured using the Linear Predictive Coding (LPC) with Praat DSP software (P. Boersma and D. Weenink, University of Amsterdam, Netherlands, www.praat.org). For analysis of formants, we used a model of an uniform tube closed at one end, considering the sound source (larynx and vocal folds) as the closed end, whilst the mouth or nostrils represent the open end (Fitch & Reby, 2001). According to this model, the expected formant frequencies were calculated as:

$$\mathrm{F}n = \frac{(2n-1) * c}{4L}; \qquad (1)$$

where n are formant numbers (1, 2, 3, etc.), L is the vocal tract length and c is the speed of sound in air, approximated as 350 m/s. The age-classes of our subject animals, i.e., adult females older two years and 1–10-day-old neonates, corresponded to that of the dissected specimens in the study by Efremova et al. (2016). Therefore, we used the values reported by Efremova et al. (2016) for neonate nasal and oral vocal tract lengths (134 and 117 mm, respectively) and adult female nasal and oral vocal tract lengths (258 mm and 241 mm respectively), to establish the settings for LPC in Praat.

For tracking the formants, we used the following settings in Praat: Burg analysis, window length 0.04 s, time step 0.01 s, maximum number of formants 4–5. For neonates, the upper limit of frequency range was 5000–6500 Hz for the oral calls and 4900–5600 Hz for the nasal calls. For adult females, the upper limit of frequency range was 3400–3600 Hz for the oral calls and 2500–3000 Hz for the nasal calls. Formant measurements were taken from the call portion where the formant tracks are nearly horizontal. Positions of formants were verified by superposition on the narrowband spectrogram. Point values of formant tracks were extracted, exported to Excel and the value of each formant for a given call was calculated as the average value from the point values. Applying the model of a uniform tube closed at one end, we calculated the formant dispersion (dF) for the nasal and oral calls using linear regression according to Reby & McComb (2003).

2.5. Statistical analyses

Statistical analyses were conducted with STATISTICA package, v. 8.0 (StatSoft, Tulsa, OK, USA) and R (https://www.r-project.org). Means are given as mean ± SD, all tests were two-tailed, and differences were considered significant at $p < 0.05$.

We used averaged per individual values of each acoustic variable of the oral and nasal contact calls. We used a repeated measures ANOVA for comparison of the acoustics between the oral and nasal calls of neonates. We used a GLM with call type as fixed factor and individual as random factor to compare oral and nasal calls of adult females. We used a one-way ANOVA to compare oral calls and nasal calls between neonates and adult females. We used a repeated measures ANOVA with Tukey post hoc to compare the distances between neighbouring formants within calls for neonate nasal calls, for neonate oral calls, for adult female nasal calls and for adult female oral calls.

We used discriminant function analysis standard procedure to compare potentials for encoding individuality by nasal calls between neonates and adult females. The relative contribution of each acoustic variable in the correct assignment of calls to individual was estimated based on Wilks' Lambda values, the smaller is the value, the greater is the contribution of the given acoustic variable to the overall discrimination (Sibiryakova et al., 2015). We used a one-way ANOVA to compare the values of correct assignment of nasal calls to individuals between neonates and adult females.

Values of correct assignment by chance (random values) were calculated using randomization procedure (Solow, 1990) in R. The random values were averaged from DFAs performed on 1000 randomized permutations on the data sets. For example, to calculate the random value of classifying nasal calls to individual neonates, each permutation procedure included the random permutation of 66 calls among 7 randomization groups, respectively to 7 individual neonates which were examined, and followed by DFA standard procedure. The permutation procedure for the nasal calls of adult females was 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 (Sibiryakova et al., 2015).

3. Results

3.1. Oral and nasal calls

In both adult females and neonates, the oral calls were longer than the nasal calls. In neonates, all the four formants were lower in the nasal than in the oral calls (Table 1). In adult females, the F1, F2 and F4 formats were lower in the nasal than in the oral calls, whereas the values of the F3 formant did not differ between the nasal and oral call types (Table 1). The f0mean was lower in the nasal than in the oral calls only in neonates; in adult females this variable did not differ between nasal and oral calls (Table 1). In both adult females and neonates, the distance between neighbouring formants F2–F1 was shorter in the nasal than in the oral calls; and the distance F4–F3 did not differ between the nasal and oral call types (Table 1). In neonates, the distance F3–F2 was shorter in the oral than in the nasal calls, whereas in adult females, the distance F3–F2 did not differ between the nasal and oral call types (Table 1).

In neonates, the dF for the nasal calls (1303 Hz) fitted to the nasal vocal tract length of 134 mm, and the dF for the oral calls (1430 Hz) fitted to the oral vocal tract length of 122 mm (Figure 3). In adult females, the dF for the nasal calls (690 Hz) fitted to the nasal vocal tract length of 254 mm, and the

Table 1.
Values (mean ± SD) of acoustic variables for nasal and oral contact calls of adult female and neonate goitred gazelles and ANOVA results for their comparison.

Acoustic variable	Neonates			Adult females		
	Nasal calls, $N = 21$	Oral calls, $N = 21$	ANOVA	Nasal calls, $N = 8$	Oral calls, $N = 4$	ANOVA
Duration (s)	0.19 ± 0.05	0.45 ± 0.15	$F_{1,20} = 75.53$, $p < 0.001$	0.25 ± 0.06	0.49 ± 0.10	$F_{1,3} = 19.21$, $p = 0.022$
f0mean (Hz)	106.8 ± 16.3	118.3 ± 17.5	$F_{1,20} = 51.9$, $p < 0.001$	49.3 ± 2.5	57.3 ± 13.2	$F_{1,3} = 2.65$, $p = 0.20$
F1 (Hz)	581 ± 70	948 ± 80	$F_{1,20} = 261.9$, $p < 0.001$	273 ± 19	434 ± 81	$F_{1,3} = 10.27$, $p = 0.049$
F2 (Hz)	1740 ± 164	2405 ± 247	$F_{1,20} = 82.42$, $p < 0.001$	914 ± 102	1345 ± 142	$F_{1,3} = 42.48$, $p = 0.007$
F3 (Hz)	3273 ± 180	3470 ± 328	$F_{1,20} = 11.24$, $p < 0.001$	1802 ± 42	2064 ± 230	$F_{1,3} = 6.99$, $p = 0.08$
F4 (Hz)	4652 ± 207	4936 ± 246	$F_{1,20} = 34.92$, $p < 0.001$	2424 ± 77	2779 ± 234	$F_{1,11} = 13.78$, $p = 0.034$
F2–F1 (Hz)	1159 ± 146	1457 ± 204	$F_{1,20} = 22.24$, $p < 0.001$	641 ± 101	911 ± 90	$F_{1,3} = 150.07$, $p = 0.001$
F3–F2 (Hz)	1534 ± 246	1065 ± 170	$F_{1,20} = 67.57$, $p < 0.001$	887 ± 83	719 ± 111	$F_{1,3} = 3.73$, $p = 0.15$
F4–F3 (Hz)	1379 ± 189	1467 ± 187	$F_{1,20} = 3.96$, $p = 0.06$	623 ± 71	716 ± 161	$F_{1,3} = 3.36$, $p = 0.16$

Duration, call duration; f0mean, mean fundamental frequency; F1, F2, F3, F4, the frequencies of the first four formants; F2–F1, F3–F2, F4–F3, the distances between the neighbouring formants; N, number of individuals from which the average values of the acoustic variables were analysed (one average value per individual per acoustic variable).

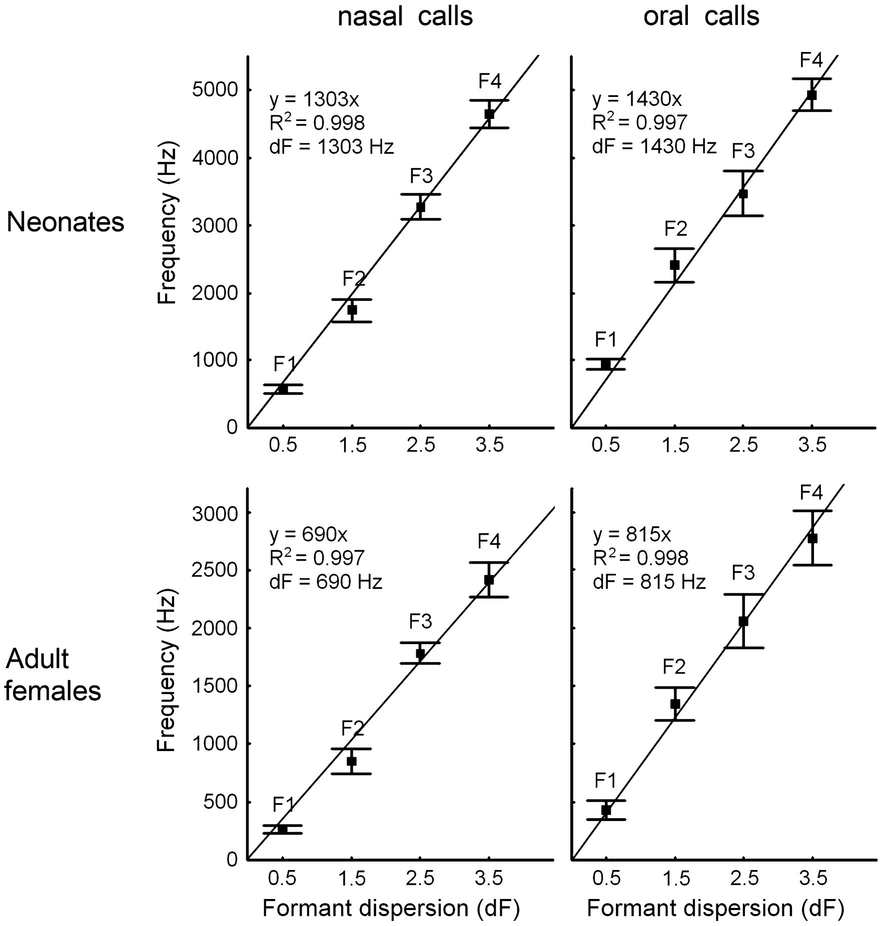

Figure 3. Estimating formant dispersion (dF) for the nasal and oral contact calls of neonate and adult female goitred gazelles using linear regression following Reby and McComb (2003). Central points indicate mean values for the first four formants (F1–F4), whiskers indicate SD.

dF for formants of the oral calls (815 Hz) fitted to the oral vocal tract length of 215 mm (Figure 3).

Formant positions differed strongly between nasal and oral calls and between adult females and neonates (Figure 4). For the nasal calls, the distance between the neighbouring formants differed in both adult females and neonates (adult females: $F_{2,14} = 17.63$, $p < 0.001$; neonates: $F_{2,40} = 15.05$, $p < 0.001$). For the oral calls, the distance between the neighbouring for-

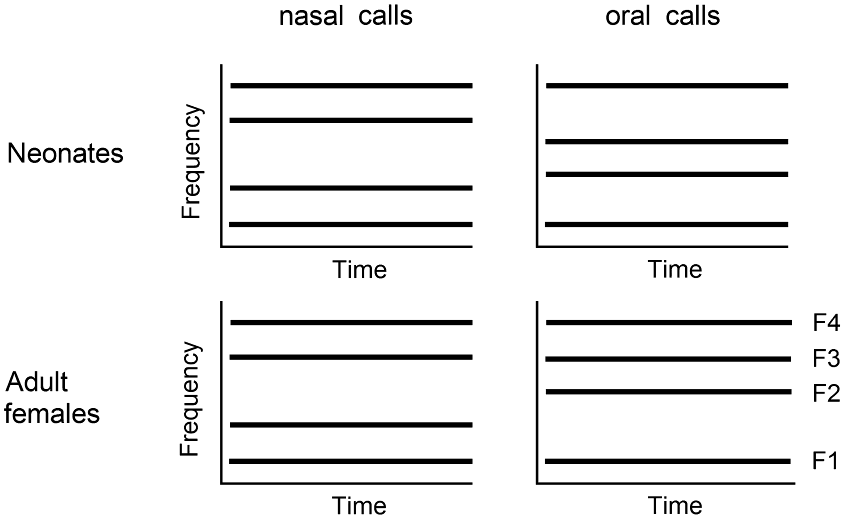

Figure 4. Scheme illustrating formant patterns for the nasal and oral contact calls of neonate and adult female of goitred gazelles. The bands indicate the relative positions for the first four formants (F1, F2, F3, F4).

mants differed in neonates ($F_{2,40} = 24.43$, $p < 0.001$) but not in adult females ($F_{2,6} = 2.76$, $p = 0.14$).

In the oral calls of neonates, the distances F2–F1 and F4–F3 were not significantly different and both exceeded the F3–F2 distance ($p < 0.001$ in both comparisons, Tukey post hoc). In the nasal calls of neonates, the distance F2–F1 was shorter than distance F3–F2 ($p < 0.001$) and shorter than distance F4–F3 ($p < 0.01$, Tukey post hoc), whereas the F3–F2 and F4–F3 distances did not differ significantly (Table 1; Figure 4).

In the adult female oral calls, the distances between formants were not significantly different, although F2–F1 exceeded both F3–F2 and F4–F3 distances. Probably, the sample of four animals (providing respectively only four averaged calls), was too small to reveal the differences in positions of formants. In the adult female nasal calls, the F3–F2 distance exceeded F2–F1 and F4–F3 distances ($p < 0.001$ in both cases, Tukey post hoc), whereas the F2–F1 and F4–F3 distances were not significantly different (Table 1, Figure 4).

3.2. *Adult female and neonate calls*

In both oral and nasal contact calls, all the four formants and the f0mean were lower in adult females than in neonates and the distances between neighbour-

Table 2.
One-way ANOVA results for comparison of acoustic variables of the oral and nasal calls between adult female and neonate goitred gazelles.

Acoustic variable	Oral calls	Nasal calls
Duration	$F_{1,23} = 0.31$, $p = 0.58$	$F_{1,27} = 8.32$, $p < 0.001$
f0mean	$F_{1,23} = 43.16$, $p < 0.001$	$F_{1,27} = 96.48$, $p < 0.001$
F1	$F_{1,23} = 138.73$, $p < 0.001$	$F_{1,27} = 149.10$, $p < 0.001$
F2	$F_{1,23} = 67.81$, $p < 0.001$	$F_{1,27} = 173.93$, $p < 0.001$
F3	$F_{1,23} = 66.16$, $p < 0.001$	$F_{1,27} = 515.51$, $p < 0.001$
F4	$F_{1,23} = 261.37$, $p < 0.001$	$F_{1,27} = 865.31$, $p < 0.001$
F2–F1	$F_{1,23} = 27.04$, $p < 0.001$	$F_{1,27} = 84.49$, $p < 0.001$
F3–F2	$F_{1,23} = 15.06$, $p < 0.001$	$F_{1,27} = 52.14$, $p < 0.001$
F4–F3	$F_{1,23} = 56.14$, $p < 0.001$	$F_{1,27} = 118.84$, $p < 0.001$

Duration, call duration; f0mean, mean fundamental frequency; F1, F2, F3, F4, the frequencies of the first four formants; F2–F1, F3–F2, F4–F3, the distances between the neighbouring formants.

ing formants were shorter in adult females than in neonates (Table 2). In the oral calls, the duration did not differ between adult females and neonates. In the nasal calls, the duration was longer in adult females than in neonates (Table 2).

3.3. Individuality of adult female and neonate nasal calls

Discriminant function analysis, with all the six acoustic variables included in the analysis, correctly classified to individuals on average 69.23% nasal calls of adult females and on average 78.79% nasal calls of neonates. These values exceeded the values of correct classifying by chance (37.4 ± 5.2% for adult females and 36.9 ± 5.2% for neonates, $p < 0.001$ for both cases) (Figure 5). These values of correct classifying to individual did not differ between adult females and neonates ($F_{1,12} = 0.62$, $p = 0.45$) (Figure 5). The three acoustic variables that mainly contributed to discrimination (in order of decreasing importance) were the duration, F2 and F4 in adult females and the f0mean, F2 and F4 in neonates.

4. Discussion

4.1. Relationship of individualization and the acoustics

This study revealed that acoustically different contact calls of adult female and neonate goitred gazelles were similarly individualized. This relationship

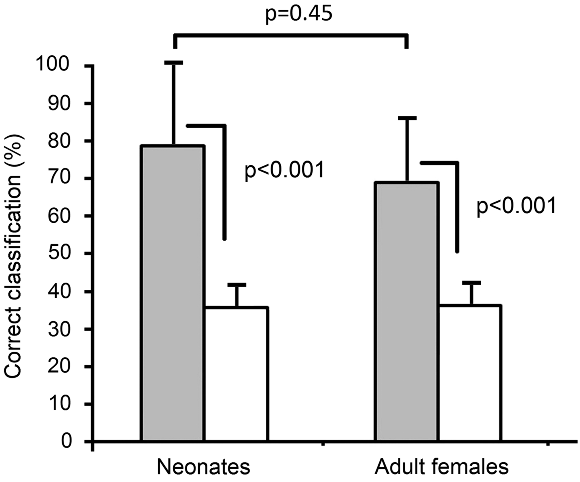

Figure 5. Comparison of values of correct classifying to individual with discriminant function analysis for the nasal contact calls of neonate and adult female goitred gazelles (grey bars) with by chance (random) values. Comparisons between the values of correct classifying to individual were done using one-way ANOVA (brackets above the bars); comparisons between the calculated and random values were done using the permutation test (angle brackets). Bars indicate averages, whiskers indicate SD.

between acoustics and individualization of mother and young contact calls is not common across ruminants. Among Cervidae species, mother and young contact calls differ in both acoustics and individualization in fallow deer and Iberian red deer (Torriani et al., 2006; Sibiryakova et al., 2015), but are similar in either acoustics or individualization in Siberian wapiti (Sibiryakova et al., 2018). Among Bovidae species, mother and young contact calls differ in the acoustics but similar in individualization in saiga and goitred gazelle (Sibiryakova et al., 2017; this study). To complete this puzzle for bovids, we suggest further research, comparing individuality of similar acoustically calls in mother and young domestic cattle (Padilla de la Torre et al., 2015).

4.2. Different acoustics of adult females and neonates

In the goitred gazelles, the mean fundamental frequency was lower in adult female than in neonate contact calls. This could be due to respectively longer vocal folds in adult female than in neonate goitred gazelles (16.6 mm versus 7.4 mm on average; Efremova et al., 2016). The length of the vocal folds represents an important predictor of the vocal fold vibration rate in mammals (Titze, 1994; Fitch & Hauser, 2002; Riede & Brown, 2013). The lower-frequency calls in adult females than in the young were also reported for red deer (Vaňková & Málek, 1997; Kidjo et al., 2008; Sibiryakova et al., 2015), fallow deer (Torriani et al., 2006), reindeer *Rangifer tarandus* (Espmark, 1975; Frey et al., 2007; Teichroeb et al., 2013), domestic goats *Capra hircus* (Briefer & McElligott, 2011), domestic sheep *Ovis aries* (Searby & Jouventin, 2003; Sèbe et al., 2010, 2018) and saiga (Volodin et al., 2014; Sibiryakova et al., 2017).

At the same time, in the American wapiti, *Cervus* (*elaphus*) *canadensis*, Siberian wapiti, *C. e. sibiricus*, and in domestic cattle, the maximum fundamental frequency of the contact calls is similar between mother and young (Feighny, 2005; Padilla de la Torre et al., 2015; Volodin et al., 2016; Sibiryakova et al., 2018). The reason for this acoustic similarity between mother and young calls can be using a distinctive, “whistle” vocal production mechanism, that does not involve vocal fold vibration (wapiti: Frey & Riede, 2013; Reby et al., 2016; Golosova et al., 2017; domestic cattle: Volodin et al., 2017c).

The results of comparison between formant frequencies of adult female and neonate goitred gazelles were in agreement with predictions of source-filter theory that the longer vocal tracts should produce the lower formants (Fant, 1960; Titze, 1994; Taylor & Reby, 2010). The lower formants in contact calls of mothers compared to the offspring were also reported for other Bovidae species, domestic goats (Briefer & McElligott, 2011) and saiga (Volodin et al., 2009a, 2014; Sibiryakova et al., 2017).

4.3. Ontogeny of vocal individuality in goitred gazelle

Across all age-classes of goitred gazelles, contact calls are individualistic: neonate nasal contact calls (this study), neonate oral distress calls (Volodin et al., 2017b), 3–6-week juvenile nasal and oral contact calls (Volodin et al., 2011; Lapshina et al., 2012), 6-month adolescent nasal contact calls (Lapshina et al., 2012) and adult female nasal contact calls (this study). Along ontogeny, the same variables (fundamental frequency and formants) encode individuality in the goitred gazelle contact calls up to adulthood (Volodin et al., 2011; Lapshina et al., 2012).

However, this study revealed that at adulthood, the main variable for encoding individuality turns to be the duration, because adult females have substantially longer nasal calls than neonates. The nasal calls are already longer in 6-month adolescent goitred gazelles compared to 3–6-week goitred gazelles, however in adolescent goitred gazelles, the duration is not yet the main cue to vocal identity (Lapshina et al., 2012).

4.4. Individual vocal recognition

The high classification success with DFA is not equivalent to demonstrating vocal recognition of individual neonates by their mothers and vice versa. Territorial mother goitred gazelles seem do not distinguish the voices of their neonates from those of the alien young and urgently approach to the calls of any young and even on their rough imitation by humans (Jevnerov, 1984; Marmasinskaya, 1996, 2008; Blank & Yang, 2015; Blank et al., 2015; Volodin et al., 2017b). During first two weeks after birth, neonates are hiders on territories of their mothers (Jevnerov, 1984; Marmasinskaya, 1996, 2008; Blank et al., 2015). Even after having been frightened, goitred gazelle neonates return to their place of birth (Jevnerov, 1984). Both mothers and young may rely on spatial landmarks and olfactory cues for mutual recognition, rather than on individualistic voices (Volodin et al., 2017b). Probably, vocal identity is becoming important at later stage, when hiding behaviour was already abandoned and the young start following their mothers at 4–6 weeks of age, so the spatial cues to individual identity are lacking (Volodin et al., 2011; Lapshina et al., 2012).

Neonate goitred gazelles may be predated by red foxes, *Vulpes vulpes*, steppe cats, *Felis libyca*, or jackals, *Canis aureus*, which normally are not dangerous to their mothers and can be deterred by them (Volodin et al., 2017b). Mother goitred gazelles urgently approach to defend neonates (Volodin et al., 2011; Blank & Yang, 2015; Blank et al., 2015). Potential time delays in deterring a predator for individual recognition may be fatal for the neonates and therefore more costly in terms of reproductive success than time loss for responding to distress calls of unrelated offspring (Lingle et al., 2007a,b; Volodin et al., 2017b).

4.5. Oral and nasal calls

In this study, the mean fundamental frequency was higher in the oral than in the nasal calls in both adult female and neonate goitred gazelles despite the predictions of source-filter theory that fundamental frequency is independent on the length of the vocal tract (Fant, 1960; Taylor & Reby, 2010; Volodin et al., 2011). This apparent "contradiction" to the source-filter theory was previously found in 3–6-wk goitred gazelles (Volodin et al., 2011). It was also found in other ruminants: domestic sheep (Sèbe et al., 2010), saiga (Volodin et al., 2014; Sibiryakova et al., 2017), Iberian red deer (Sibiryakova et al., 2015), Siberian wapiti (Sibiryakova et al., 2018) and African elephants *Loxodonta africana* (Stoeger et al., 2012).

This increase of fundamental frequency in the oral calls might be provoked by slight lowering the larynx during emission of the oral calls, which results in loss of contact between epiglottis and soft palate and in additional tension and thinning of the vocal folds (see detailed discussion in Volodin et al., 2011, 2014). In addition, the higher fundamental frequency in the oral than in the nasal calls could result from a higher emotional arousal during the emission of the oral calls. Increase of fundamental frequency in relation with increase of emotional arousal is common in both ruminants (Charlton & Reby, 2011; Lingle et al., 2012) and other mammals (for reviews: Volodin et al., 2009b; Briefer, 2012). Fundamental frequency increases when emotional arousal triggers the tensioning of the vocal fold because of increasing tissue hardness and shortening its vibrating portion (Titze, 1994; Riede, 2010).

Emotional arousal evokes more powerful air stream from the lungs, what could also be responsible for the longer duration of the oral than nasal calls in both adult females and neonates in goitred gazelles. For ruminants, the longer duration of oral than nasal calls was found in ewes (Sèbe et al., 2010), in 3–6-wk goitred gazelles (Volodin et al., 2011), in adult female and neonate saigas (Volodin et al., 2009a, 2014; Sibiryakova et al., 2017) and in neonate and juvenile red deer (Sibiryakova et al., 2015).

The lower formants in the nasal than in the oral calls were expectable because of the inverse relationship existing between formant frequencies and vocal tract length (Fant, 1960; Fitch & Reby, 2001; Taylor & Reby, 2010). As in most mammals, in goitred gazelles the nasal vocal tracts are longer than the oral vocal tracts at any age-class (Efremova et al., 2016). Therefore, formants are always lower in the nasal than in the oral calls (Volodin et al., 2017a). Consistently, the lower formants in the nasal than in the oral calls were found in contact calls of adult female and neonate saigas (Volodin et al., 2014; Sibiryakova et al., 2017), in 3–6-wk goitred gazelles (Volodin et al., 2011) and in rumbles of adolescent African elephants (Stoeger et al., 2012). The found in our study unequal distances between formants of both oral and nasal calls indicate the non-uniformity of vocal tract in the goitred gazelle, similarly to the findings in other ruminants (McElligott et al., 2006; Briefer & McElligott, 2011; Volodin et al., 2014; Reby et al., 2018).

4.6. Formant-based estimation of vocal tract length

In both adult female and neonate goitred gazelles, the formant-based calculations of the vocal tract length using formula (1) in the Methods (Figure 3), matched the values directly measured on the same-age anatomical specimens of goitred gazelles, reported by (Efremova et al., 2016). For the neonate nasal vocal tract, the coincidence was perfect, whereas for the neonate oral vocal tract, the difference was only 4%. For the adult female nasal vocal tract, the difference was only 2%, whereas for the adult female oral vocal tract, it was 11%. We conclude therefore that the model of uniform tube closed at one end (and the respective to this model formula (1) for formant measurements) (Fitch & Reby, 2001; Reby & McComb, 2003), correctly predicted positions of formants in the oral and nasal calls of adult female and neonate goitred gazelles.

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