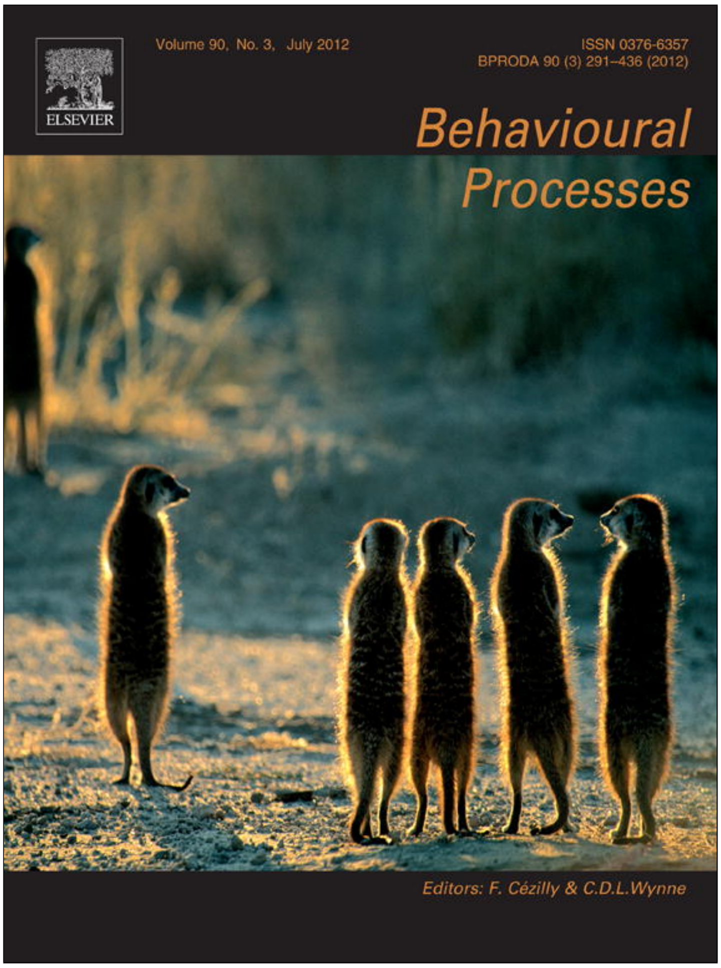
Volume 90, No. 3, July 2012
ISSN 0376-6357
BPRODA 90 (3) 291–436 (2012)
ELSEVIER
Behavioural Processes
Editors: F. Cézilly & C.D.L.Wynne

Behavioural Processes 90 (2012) 323–330

Contents lists available at SciVerse ScienceDirect

Behavioural Processes

journal homepage: www.elsevier.com/locate/behavproc

The ontogeny of acoustic individuality in the nasal calls of captive goitred gazelles, *Gazella subgutturosa*

Ekaterina N. Lapshina[a], Ilya A. Volodin[a,b,*], Elena V. Volodina[b], Roland Frey[c], Kseniya O. Efremova[a], Natalia V. Soldatova[d]

[a] Department of Vertebrate Zoology, Faculty of Biology, Lomonosov Moscow State University, Vorobievy Gory, 12/1, Moscow 119991, Russia
[b] Scientific Research Department, Moscow Zoo, B. Gruzinskaya, 1, Moscow 123242, Russia
[c] Leibniz Institute for Zoo and Wildlife Research (IZW), P.O. Box 60 11 03, D-10252 Berlin, Germany
[d] Ecocenter “Djeiran”, Bukhara, Uzbekistan

ARTICLE INFO

Article history:
Received 31 January 2012
Accepted 18 March 2012

Keywords:
Individual identity
Sexual identity
Vocal development
Vocal stability
Nasal calls
Ruminant

ABSTRACT

Individualistic voices are important for establishing personalized relationships among individuals. In young animals, individual vocal identity is affected by permanent changes of the acoustics due to the growth of their vocal apparatus. Different acoustic variables change uncoordinatedly, so vocal individuality should be repeatedly upgraded along development. We compared classifying accuracy of individuals and sexes by nasal calls in fast-growing goitred gazelles *Gazella subgutturosa* at two ontogenetic stages, juvenile (3–6 weeks of age) and adolescent (23–26 weeks of age). Juvenile “spring” nasal calls and adolescent “fall” nasal calls were examined in the same 35 calves (18 males, 17 females), wild-born in May and then hand-raised. Discriminate function analysis based on four formants, fundamental frequency, duration and three power quartiles, revealed an equally high potential of spring and fall calls to encode sex. The individuality was very high in both ages but significantly higher in fall calls. Classifying calls to individuals was based on the same three acoustic variables (fundamental frequency and third and fourth formants) in both ages, although their actual values changed uncoordinatedly from spring to fall in most subjects. Our results suggest updating acoustic individuality in nasal calls of adolescent goitred gazelles accordingly to the newly emerged acoustic variation.

1. Introduction

Individualistic voices are important for personalized communication in animal groups. Consistently, individualistic voices were found in species breeding in dense aggregations such as pinnipeds (Insley et al., 2003a), alcids (Jones et al., 1987; Lefevre et al., 1998; Insley et al., 2003b), cranids (Klenova et al., 2009) and penguins (Aubin and Jouventin, 2002), and in group- or herd-living species, such as primates (Rendall et al., 2009), canids (Yin and McCowan, 2004; Volodina et al., 2006) and bovids (Sebe et al., 2007, 2010; Briefer and McElligott, 2011a; Volodin et al., 2011).

In bovids, discriminating individuals by voice might be essential for offspring survival and for avoiding misdirected maternal care. Juveniles rely on their mothers for milk and social support, therefore supporting mother–offspring contact should be favored by natural selection. Consistently, juvenile domestic goats *Carpa hircus* (Terrazas et al., 2003; Briefer and McElligott, 2011a) and goitred gazelles *Gazella subgutturosa* (Volodin et al., 2011) produce individualized contact calls, providing potential for reliable recognition of dependent offspring by their mothers.

Individualistic voices might result from inter-individual differences in the vocal anatomy and vocal production (Torriani et al., 2006; Lingle et al., 2007; Vannoni and McElligott, 2007; Rendall et al., 2009; Taylor and Reby, 2010; Briefer and McElligott, 2011a; Volodin et al., 2011). The anatomical base for individual differences results mainly from differences in sizes of sound-producing structures. In accordance to the source-filter framework (Fant, 1960; Titze, 1994; Taylor and Reby, 2010), the voice fundamental frequency (f0), generated by “source” (in the larynx of mammals or in the syrinx of birds) is filtered subsequently by the vocal tract (“filter”), selectively accentuating certain resonance frequencies (formants) and attenuating anti-resonances. In the simplest model of human- and animal vocal production (uniform tube closed at the end where the sound source is located) the f0 is inversely related to mass and length of the oscillating membranes of the source, whereas the formant frequencies are inversely related to the length of the vocal tract (Fant, 1960; Titze, 1994; Fitch and Reby, 2001; Fitch and Hauser, 2002; Taylor and Reby, 2010). Being developed

---

* Corresponding author at: Department of Vertebrate Zoology, Faculty of Biology, Lomonosov Moscow State University, Vorobievy Gory, 12/1, Moscow 119991, Russia.
E-mail address: volodinsvoc@gmail.com (I.A. Volodin).

0376-6357/$ – see front matter © 2012 Elsevier B.V. All rights reserved.
doi:10.1016/j.beproc.2012.03.011

initially for human speech (Fant, 1960), this main principle is well-applicable to calls of ruminants. Other factors, affecting vocalization in ruminants, are the viscoelasticity of the vocal folds (Riede et al., 2010), the presence of pads on vocal folds (Frey and Hofmann, 2000; Frey et al., 2007, 2011), hormonal effects (Briefer et al., 2010), the non-uniformity of vocal tract (Frey et al., 2007; Efremova et al., 2011b; Volodin et al., 2011), dynamics of laryngeal cartilages during calling (Volodin et al., 2011), the prominent tongue protrusion (Frey et al., 2012) and the source-filter coupling (Titze and Riede, 2010).

Along development of fast-growing male and female goitred gazelles, the vocal apparatus constantly changes its size, what affects the acoustics (Efremova et al., 2011a,b). Developmental changes may vary among individuals and between sexes, because of the accelerated growth of some parts of vocal apparatus, differences in physiology and/or in calling behavior. As a result, actual values of some acoustic variables overlap among callers, so that acoustic individuality attributive to particular caller is potentially confounded. In addition, in goitred gazelles sexual dimorphism of larynx size and position increases along ontogenesis (Efremova et al., 2011b; Volodin et al., 2011), so that in adult males the larynx is more enlarged and more pronouncedly descended than in females (Frey et al., 2011). Therefore, more accurate classification of sexes by calls is expected in adolescents, as a result of the developing vocal sexual dimorphism.

Similarly to juvenile goats (Briefer and McElligott, 2011b), juvenile goitred gazelles produce two types of contact calls: the loud oral and the softer nasal calls, as well as alarm snorts (Efremova et al., 2011a; Volodin et al., 2011). Both nasal and oral calls of goitred gazelles reveal periods of glottis opening and closing, representing the f0, whereas snorts represent soft calls without any sign of f0, produced during abrupt expiration through the nose. Both nasal and oral calls occurred at anticipation of food or brief separations from peer group; but the oral calls occurred at higher arousal (Efremova et al., 2011a). In the previous cross-sectional study, we compared the ability of the nasal and oral calls to encode sex and identity in 20 juvenile (3–6 weeks old) goitred gazelles. Both the nasal and oral call types encoded reliably the caller's sex and identity, but the oral calls were more individualized (Volodin et al., 2011).

Along ontogenesis from juveniles to adolescents, the ratio of oral-to-nasal calls steadily decreases, so that the 6-months adolescents produce exclusively nasal calls (Efremova et al., 2011a). Therefore, the comparison of the acoustic individuality between juvenile and adolescent goitred gazelles is possible only with nasal calls. In this study we (1) examine 35 goitred gazelles calves at two ages, in the spring as juveniles and in the fall as adolescents, for potential of their nasal calls to classify individuals and sexes, (2) compare the classification accuracy between spring and fall calls, and (3) compare the acoustics of spring and fall calls within and between individuals.

2. Material and methods

2.1. Subjects, site, and dates of work

The study was conducted in the enclosures of Ecocenter "Djeiran" (Uzbekistan), for study site details see Volodin et al. (2011). Subjects were 35 (18 males, 17 females) wild-born goitred gazelles, captured shortly after birth and then hand-raised for conservation purposes. Among them, 16 (7 males, 9 females) were captured between April 29 and May 12, 2008 and 19 (11 males, 8 females) were captured between May 5 and May 13, 2009. By size, body mass and the state of the umbilical cord, the age of the captured individuals was estimated 1–8 days postpartum in 2008 and 6–14 days postpartum in 2009. We took May 2nd as a common conditional date of birth for all animals born in 2008 and May 1st as a common conditional date of birth for all animals born in 2009. The gazelles were individually marked with p-phenylenediamine (Rhodia, Paris, France) and ear-tagged. The animals were kept in groups of 5–7 individuals in a few small enclosures of 2 m × 4 m in a row with indoor shelters made of dried reeds. The enclosures had exits to a common passageway 1.5 m wide, leading to a large enclosure 25 m × 18 m, where the animals walked together during the day. The calves were fed three or two times a day, depending on the age (for keeping details, see Efremova et al., 2011a,b; Volodin et al., 2011).

2.2. Data collection

Each subject was recorded at two ages (as juvenile and as adolescent). The juvenile "spring" nasal calls were recorded in May–June, between 3 and 6 full weeks of age (from the 21st to 48th day inclusive). The adolescent "fall" nasal calls were recorded in October–November, between 23 and 26 full weeks of age (from the 161st to 188th day inclusive). Calls were recorded daily, 30–120 min before the morning or evening feeding, outdoor or indoor, as the reed walls had no echo effect. Recording sessions were scheduled with the aim of collecting a similar amount of acoustic data on each individual throughout the data collection period. Distance to the microphone was 1–5 m. The calls of the focal animal were labeled on the recorder by voice. For acoustic recordings (48 kHz, 16 bit), we used a Zoom-H4 (Zoom Corp., Tokyo, Japan) digital recorder with Sennheiser K6-ME66 cardioid electret condenser microphone (Sennheiser electronic, Wedemark, Germany).

Body mass measures (10 g precision, Kern DE 36K10NL scales, Kern & Sohn GmbH, Balingen-Frommern, Germany) were collected three times per individual, at ages of 4, 6 and 24 weeks, before the evening feeding. In addition to body mass, neck measures representing circumferences over the most prominent point of the larynx, were taking with a tape (1 cm precision) (see details in Efremova et al., 2011b). The mean value of the two first ("spring") body mass and neck measures was taken. All animals were measured in nontransparent cotton masks, covering the eyes, and were placed in a cotton bag, to decrease the anxiety. Neck measures were taken from animals, lying in the bag on earth with legs under the body. In this natural for goitred gazelles lying posture, the neck is vertical and the head is under the angle of 90° relative to the neck, allowing to standardize the neck measures.

2.3. Call samples

Only one type of calls was included into analyses, the nasal calls (hereafter "calls"), produced with closed mouth. The spring recordings contained both nasal and oral calls. Distinction between the nasal and oral calls followed Volodin et al. (2011) and only nasal spring calls were taken for analyses. The fall recordings contained only nasal calls.

For acoustic analyses, we selected calls not disrupted by wind and non-overlapped by noise or human voice. For each individual, we took measurements from 25 spring calls and from 25 fall calls. If less that 25 calls were available, we included into analyses all of them (from 20 to 24 calls). If more than 25 calls were available per animal per age, we selected calls for analysis randomly among calls of good quality. We took calls from different sessions per animal and from different parts within session. To reduce pseudoreplication, we took calls from different recording sessions per animal and from different parts within session (Reby et al., 1999; Briefer and McElligott, 2011b; Efremova et al., 2011a). The average number of sessions per animal per age was 9.4 ± 2.9 (5–20), and we took 1–5

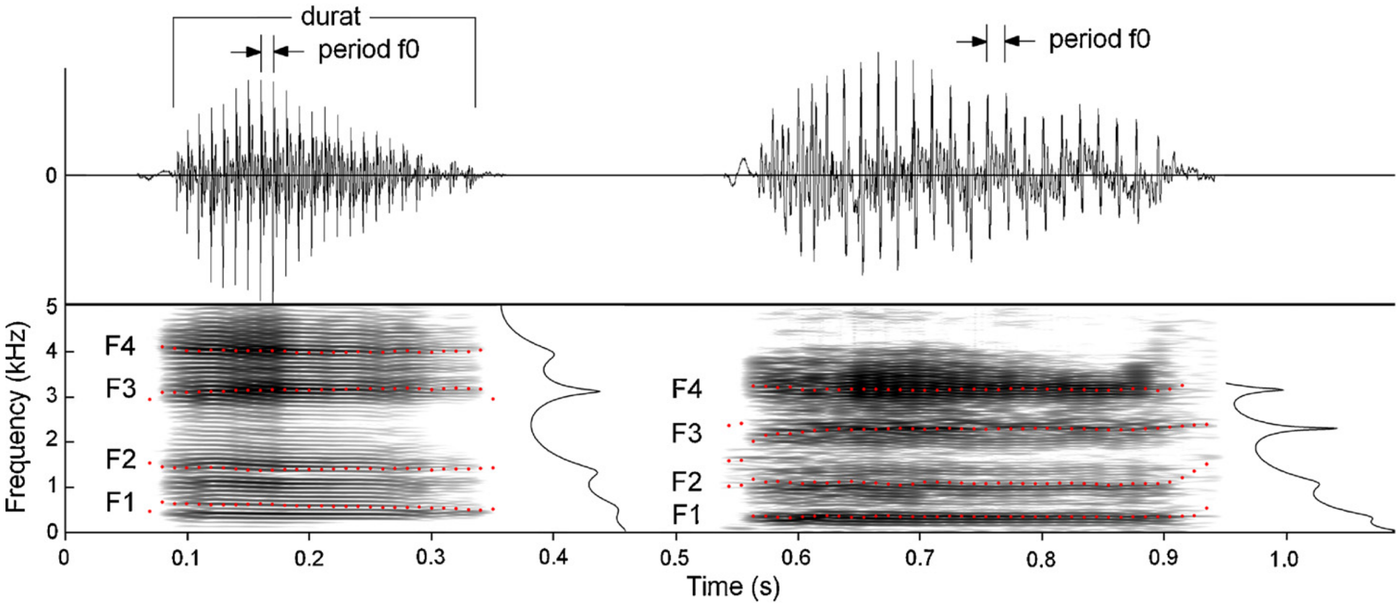

Fig. 1. Measured variables: duration (durat), fundamental frequency period (period f0) and tracks of the first 4 formants (F1–F4). Left: nasal call of 3–6 week female #45, right: nasal call of 23–26 week female #45. The LPC settings were: Burg analysis, window length 0.04 s, time step 0.01 s, maximum number of formants 4, maximum formant frequency 4500 Hz (at the age of 3–6 week) or 3400 Hz (at the age of 23–26 week). Measurements were taken from the call portions where the formant tracks are nearly horizontal (0.10–0.32 s and 0.57–0.89 in these calls). LPC spectra for the call portions where the formant tracks are nearly horizontal are given on the right of each call.

calls per session per animal. In total, we analyzed 1701 calls, 858 spring calls and 843 fall calls.

2.4. Call analysis

For each call, we measured 10 acoustic variables (Fig. 1). Using Avisoft SASLab Pro software (Avisoft Bioacoustics, Berlin, Germany) we measured the duration with the standard marker cursor in the spectrogram window (sampling frequency 48 kHz, Hamming window, FFT 1024 points, frame 50% and overlap 93.75%). From the mean power spectrum of Avisoft, we measured the maximum amplitude frequency (fpeak) and the upper, medium and lower quartile (q25, q50 and q75), covering respectively 25%, 50%, and 75% of call energy. With "Autocorrelation" option of Avisoft, we measured the mean fundamental frequency (f0). This option recognizes periodic components in the sound signal and measures their period with 0.25-ms precision, which allowed us to calculate the f0 with 1-Hz precision. All measurements were exported to Microsoft Excel (Microsoft Corp., Redmond, WA, USA).

The values of nasal vocal tract lengths (149 mm in two 3–4 week males, 150 mm in the 8 week female, 185 mm in the 7 month female and 220 mm in the 7 month male) were obtained earlier by anatomical dissections (Efremova et al., 2011a; Volodin et al., 2011) and were used in this study to establish settings for measuring formants. The four first formants (F1, F2, F3 and F4) were measured using linear prediction coding (LPC) with Praat DSP package v. 5.2.07 (P. Boersma, D. Weenink, University of Amsterdam, Netherlands, http://www.praat.org). Applying the model of a uniform tube closed at one end (Fitch and Reby, 2001), we approximated formant frequencies as:

$$Fn = \frac{(2n-1)*c}{4L},$$

where n are formant number (1, 2, 3, etc.), L is vocal tract length, and c is the speed of sound in air (350 m s^{-1}). The LPC-settings were Burg analysis, window length 0.04 s, time step 0.01 s, maximum number of formants 4–6. For spring calls, the range of maximum formant frequencies was 4000–5000 Hz, with limits from 2600 to 5500 Hz. For fall calls, the range of maximum formant frequencies was 2900–3500 Hz, with limits from 2600 to 4000 Hz (Fig. 1). 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 the given call was calculated as the average value from the point values.

2.5. Statistical analyses

All statistical analyses were conducted using STATISTICA v. 6.0 (StatSoft, Tulsa, OK, USA). Mean are given as mean ± SD, all tests were two-tailed, and differences were considered significant whenever $p < 0.05$. A Kolmogorov–Smirnov test showed that distributions of body mass, neck measurements and of acoustic parameter values did not depart from normality ($p > 0.05$), besides the fpeak. We used repeated measures ANOVA controlled for individuality and sex, to compare the parameter values between spring and fall calls. To estimate effects of individuality and sex on the acoustics, we used nested design ANOVA with individuality nested into sex; where individuality included as random factor and sex as fixed factor. We used a Student's t-test to compare body mass between sexes. We calculate Pearson's correlation between acoustic variables and neck measurements. Because body length (neck measurements) and body mass are tightly correlated in goitred gazelles in the spring ($R^2 = 0.51$, $n = 35$, $p < 0.001$) and in the fall ($R^2 = 0.64$, $n = 35$, $p < 0.001$), and because body mass should be proportional to the cube of a linear dimension like body size (Fitch, 1997; Charlton et al., 2009), we also used $\log_3$ body mass to calculate Pearson's correlation between body mass and acoustic variables.

We used discriminate function analysis (DFA) to calculate the probability of the assignment of calls to the correct individual or correct sex for each call sample (of spring and of fall calls). We used Wilks' Lambda values to estimate how strongly acoustic variables of calls contribute to discrimination of sex and individual. With a 2 × 2 χ^2 test we compared the values of correct assignment between spring and fall calls. We classified the calls recorded during the fall using the spring recordings, to estimate the ubiquity of

Table 1
Comparison between spring and fall nasal calls: mean ± SD values of 10 measured variables and repeated measures ANOVA results. Designations: F1, F2, F3, F4 – values of the first four formants; f0 – fundamental frequency; durat – call duration; q25, q50, q75 – lower, medium and upper quartiles; fpeak – maximum amplitude frequency.

Variable	Spring nasal calls	Fall nasal calls	ANOVA results
F1 (Hz)	502 ± 60	363 ± 30	$F_{1,34} = 209.94$, $p < 0.001$
F2 (Hz)	1352 ± 101	977 ± 68	$F_{1,34} = 387.42$, $p < 0.001$
F3 (Hz)	2739 ± 164	2077 ± 130	$F_{1,34} = 512.42$, $p < 0.001$
F4 (Hz)	3757 ± 198	2901 ± 127	$F_{1,34} = 615.37$, $p < 0.001$
f0 (Hz)	86 ± 11	64 ± 11	$F_{1,34} = 247.13$, $p < 0.001$
Durat (s)	0.253 ± 0.053	0.277 ± 0.070	$F_{1,34} = 5.03$, $p < 0.05$
q25 (Hz)	369 ± 35	276 ± 47	$F_{1,34} = 127.80$, $p < 0.001$
q50 (Hz)	836 ± 160	811 ± 303	$F_{1,34} = 0.26$, $p = 0.61$
q75 (Hz)	2525 ± 405	2303 ± 413	$F_{1,34} = 9.20$, $p < 0.01$
fpeak (Hz)	349 ± 46	277 ± 36	$F_{1,34} = 74.52$, $p < 0.001$

individual- and sex-related features between spring and fall calls. To validate DFA results for spring and fall call samples, we calculated the random values of correct assignment to individual or sex by applying randomization procedure with macros created in R software (R Development Core Team, 2009). The random values were averaged from DFAs performed on 1000 randomized permutations on the data sets. Using a distribution obtained by the permutations, we noted whether the observed value exceeded 95% or 99% of the values within the distribution (Solow, 1990).

3. Results

3.1. Comparison of spring and fall nasal calls acoustics

A repeated measures ANOVA controlling for individuality and sex revealed significantly lower f0 and the four first formants and slightly but significantly higher duration in fall calls (Table 1). Power quartiles (excluding q50) and fpeak were significantly lower in fall calls.

3.2. Effects of body mass, sex and individual identity on the acoustics of spring and fall calls

Body mass increased from spring to fall from 7.02 ± 0.73 to 14.98 ± 1.39 kg (from 7.24 ± 0.77 to 15.42 ± 1.47 kg in males, and from 6.79 ± 0.62 to 14.52 ± 1.16 kg in females) (Fig. 2). A repeated measures ANOVA showed that all differences were significant (pooled sample of two sexes: $F_{1,34} = 1407.57$, $p < 0.001$; males: $F_{1,17} = 633.78$, $p < 0.001$; females: $F_{1,16} = 831.41$, $p < 0.001$). However, between sexes, body mass differences were marginally significant both in the spring (Student's t-test: $t = 1.91$; $df = 33$, $p = 0.065$), and in the fall ($t = 2.0$; $df = 33$, $p = 0.054$) (Fig. 2).

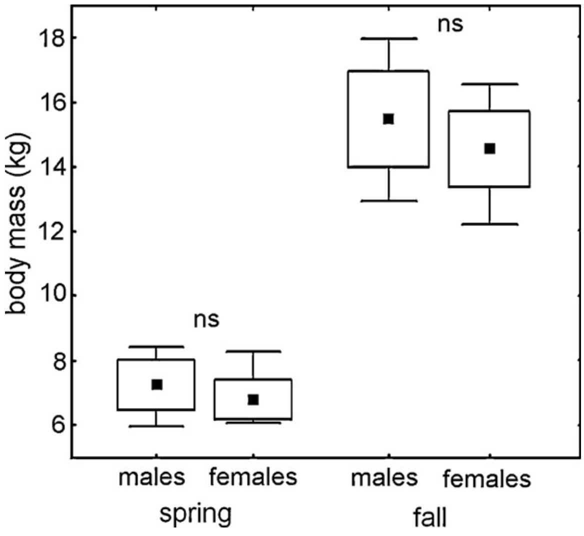

Fig. 2. Body mass of 3–6 week male and female juveniles (during the period of collecting spring nasal calls) and of 23–26 week male and female adolescents (during the period of collecting fall nasal calls). Points show means, boxes – SD; whiskers – minimum and maximum values; ns – non-significant.

For spring calls, significant negative correlations were found between F1, F3, F4, f0, fpeak and neck circumferences, and between F1, F4, f0 and body mass (Table 2). For fall calls, significant negative correlations were found between F3, F4, f0 and neck circumferences, and between F4, f0 and body mass. A significant positive correlation was found for the fpeak and body mass of fall calls (Table 2).

Although differences in body mass were marginally significant between sexes (Fig. 2), a nested ANOVA revealed significant effects of sex on the acoustics. Both in the spring and the fall, male f0 and upper formants (F3 and F4) were lower, and the acoustic energy was concentrated in lower parts of call spectra in males compared to females (Tables 3 and 4). Calls were longer in males, both in the spring and in the fall. No sex effects were found for the q25 in the spring, F1 and F2 in the fall, and for the fpeak both in the spring and in the fall (Tables 3 and 4). Therefore, effects of individual identity have been observed on all the 10 acoustic variables, but effects of sex only on 8 of them in the spring and on 7 of them in the fall (Tables 3 and 4).

As samples for caller's sex and identity were equal, we could compare F-ratios from the ANOVA. The effect of sex prevailed over the effect of identity for the upper formants (F3 and F4), f0, duration, and q75 of spring calls (Table 3) and for q75 of fall calls (Table 4). In spring calls, both effects were similar for the lower formants (F1 and F2) and for the q50, whereas the effect of identity prevailed over the effect of sex for q25 and fpeak (Table 3). In fall calls, the effect of identity prevailed over the effect of sex for the lower formants (F1 and F2), while for q25 and q50 both effects were similar (Table 4).

Table 2
Pearson's correlation coefficients (r) between acoustic variables, neck circumference and $\log_3$ body mass. Number of animals is 35 for all comparisons; other designations as in Table 1. Significant correlations are given in bold.

Variable	Spring nasal calls		Fall nasal calls	
	Neck circumference	$\log_3$ body mass	Neck circumference	$\log_3$ body mass
F1 (Hz)	**$r = -0.64$, $p < 0.001$**	**$r = -0.36$, $p < 0.05$**	$r = 0.26$, $p = 0.13$	$r = 0.20$, $p = 0.24$
F2 (Hz)	$r = -0.24$, $p = 0.17$	$r = -0.12$, $p = 0.48$	$r = -0.33$, $p = 0.052$	$r = -0.31$, $p = 0.07$
F3 (Hz)	**$r = -0.53$, $p < 0.01$**	$r = -0.26$, $p = 0.13$	**$r = -0.59$, $p < 0.001$**	$r = -0.32$, $p = 0.06$
F4 (Hz)	**$r = -0.61$, $p < 0.001$**	**$r = -0.49$, $p < 0.01$**	**$r = -0.48$, $p < 0.01$**	**$r = -0.42$, $p < 0.05$**
f0 (Hz)	**$r = -0.45$, $p < 0.01$**	**$r = -0.41$, $p < 0.05$**	**$r = -0.38$, $p < 0.05$**	**$r = -0.41$, $p < 0.05$**
Durat (s)	$r = 0.09$, $p = 0.61$	$r = 0.17$, $p = 0.32$	$r = -0.11$, $p = 0.53$	$r = -0.20$, $p = 0.24$
q25 (Hz)	$r = -0.01$, $p = 0.96$	$r = 0.13$, $p = 0.46$	$r = 0.05$, $p = 0.76$	$r = 0.16$, $p = 0.35$
q50 (Hz)	$r = 0.17$, $p = 0.34$	$r = 0.10$, $p = 0.57$	$r = -0.10$, $p = 0.56$	$r = 0.04$, $p = 0.83$
q75 (Hz)	$r = 0.19$, $p = 0.29$	$r = 0.21$, $p = 0.23$	$r = -0.27$, $p = 0.11$	$r = -0.08$, $p = 0.64$
fpeak (Hz)	**$r = -0.54$, $p < 0.001$**	$r = -0.16$, $p = 0.35$	$r = 0.29$, $p = 0.10$	**$r = 0.38$, $p < 0.05$**

Table 3
Comparison of spring nasal calls (mean ± SD) between sexes and nested ANOVA results for the effects of caller sex and identity on the spring calls variables. Identity nested into sex; identity included as a random factor and sex as a fixed factor. Designations as in Table 1.

Variable	Males	Females	Sex effect	Identity effect
F1 (Hz)	490 ± 85	515 ± 101	$F_{1,823} = 23.85$, $p < 0.001$	$F_{33,823} = 15.62$, $p < 0.001$
F2 (Hz)	1342 ± 169	1367 ± 148	$F_{1,823} = 7.73$, $p < 0.01$	$F_{33,823} = 15.65$, $p < 0.001$
F3 (Hz)	2669 ± 200	2818 ± 206	$F_{1,823} = 219.26$, $p < 0.001$	$F_{33,823} = 25.11$, $p < 0.001$
F4 (Hz)	3694 ± 240	3828 ± 251	$F_{1,823} = 142.91$, $p < 0.001$	$F_{33,823} = 31.84$, $p < 0.001$
f0 (Hz)	82 ± 9	92 ± 15	$F_{1,823} = 453.68$, $p < 0.001$	$F_{33,823} = 62.59$, $p < 0.001$
Durat (s)	0.265 ± 0.098	0.240 ± 0.103	$F_{1,823} = 18.04$, $p < 0.001$	$F_{33,823} = 8.41$, $p < 0.001$
q25 (Hz)	371 ± 80	367 ± 79	$F_{1,823} = 0.71$, $p = 0.40$	$F_{33,823} = 6.00$, $p < 0.001$
q50 (Hz)	813 ± 402	859 ± 374	$F_{1,823} = 4.14$, $p < 0.05$	$F_{33,823} = 4.81$, $p < 0.001$
q75 (Hz)	2421 ± 805	2634 ± 792	$F_{1,823} = 20.60$, $p < 0.001$	$F_{33,823} = 7.55$, $p < 0.001$
fpeak (Hz)	348 ± 79	351 ± 91	$F_{1,823} = 0.19$, $p = 0.66$	$F_{33,823} = 10.06$, $p < 0.001$

Table 4
Comparison of fall nasal calls (mean ± SD) between sexes and nested ANOVA results for the effects of caller sex and identity on the fall call variables. Identity nested into sex; identity included as a random factor and sex as a fixed factor. Designations as in Table 1.

Variable	Males	Females	Sex effect	Identity effect
F1 (Hz)	364 ± 53	360 ± 54	$F_{1,808} = 1.40$, $p = 0.24$	$F_{33,808} = 11.11$, $p < 0.001$
F2 (Hz)	973 ± 108	981 ± 115	$F_{1,808} = 2.46$, $p = 0.12$	$F_{33,808} = 13.76$, $p < 0.001$
F3 (Hz)	2031 ± 154	2128 ± 140	$F_{1,808} = 240.87$, $p < 0.001$	$F_{33,808} = 43.33$, $p < 0.001$
F4 (Hz)	2865 ± 177	2939 ± 122	$F_{1,808} = 127.47$, $p < 0.001$	$F_{33,808} = 39.29$, $p < 0.001$
f0 (Hz)	59 ± 9	69 ± 11	$F_{1,808} = 918.42$, $p < 0.001$	$F_{33,808} = 97.86$, $p < 0.001$
Durat (s)	0.296 ± 0.096	0.256 ± 0.104	$F_{1,808} = 52.77$, $p < 0.001$	$F_{33,808} = 20.22$, $p < 0.001$
q25 (Hz)	267 ± 82	284 ± 80	$F_{1,808} = 13.92$, $p < 0.001$	$F_{33,808} = 11.04$, $p < 0.001$
q50 (Hz)	738 ± 432	878 ± 511	$F_{1,808} = 29.97$, $p < 0.001$	$F_{33,808} = 14.81$, $p < 0.001$
q75 (Hz)	2170 ± 619	2434 ± 593	$F_{1,808} = 66.29$, $p < 0.001$	$F_{33,808} = 15.64$, $p < 0.001$
fpeak (Hz)	277 ± 73	274 ± 84	$F_{1,808} = 0.38$, $p = 0.54$	$F_{33,808} = 6.47$, $p < 0.001$

3.3. *Classifying calls to sexes with DFA*

Two DFAs were conducted, one for spring and one for fall calls. Both DFAs were based on the same 9 acoustic variables (fpeak was excluded for not meeting the criterion of normality). The DFAs revealed well-expressed sex-related differences both in spring and in fall calls (Fig. 3). Both values of correct assignment, of 74.4% for spring and of 75.9% for fall calls, exceeded significantly the random values (53.9 ± 1.4% and 54.2 ± 1.4%, respectively, $p < 0.01$ for both comparisons). In order of decreasing importance, the f0, F3 and q25 were mainly responsible for discriminating sexes by spring calls, and the f0, duration and F3 were mainly responsible for discriminating sexes by fall calls.

The values of correct assignment to sex did not differ significantly between spring and fall calls ($\chi_1{}^2 = 0.47$, $p = 0.49$). However, classifying fall calls using discriminant functions created for spring calls, showed only 51.0% correct assignment to sex, not differing from the random value (Fig. 3). This indicated that fall calls lost those features, on which classification of calls to sex was based in spring.

3.4. *Classifying calls to individuals with DFA*

Two DFAs were conducted, one for spring and one for fall calls. Both DFAs were based on the same 9 acoustic variables (fpeak was excluded for not meeting the criterion of normality). In both DFAs, the values of correct assignment to individual (Fig. 3), 52.1% for the spring calls and 64.4% for the fall calls, strongly and significantly exceeded the random values (8.8 ± 0.9% and 9.0 ± 0.9% respectively, $p < 0.01$ for both comparisons). In order of decreasing importance, f0, F3 and F4 were mainly responsible for classifying calls to correct individuals both by spring and by fall calls. Of these three variables, two (f0 and F3) were the same that were most important for classifying calls to the correct sex.

The values of correct assignment to individual were significantly higher for fall calls than for spring calls ($\chi_1{}^2 = 26.0$, $p < 0.001$). Since we measured the same set of variables for spring and fall calls of the same calves, we could compare the values of correct assignment of calls to particular individuals between ages. A repeated measures ANOVA showed, that individuality was expressed stronger in fall calls than in spring calls ($F_{1,34} = 11.36$, $p < 0.01$). However,

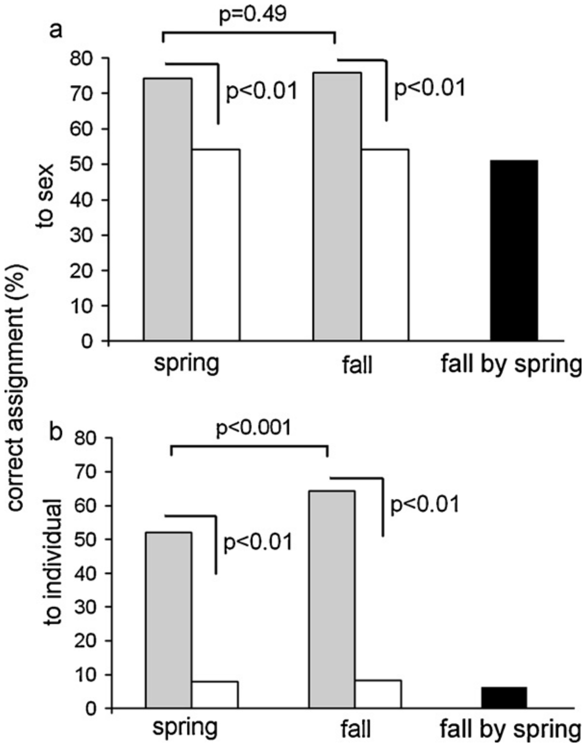

Fig. 3. Sex (a) and individual (b) discrimination on the basis of spring and fall nasal call features. Grey bars point values of discriminate function analysis (DFA) and white bars point random values, calculated with randomization procedure. Comparisons between observed and random values and between spring and fall nasal calls with chi-squared test are shown by brackets above. The black bar points the classifying value of fall calls with discriminant functions created for spring calls.

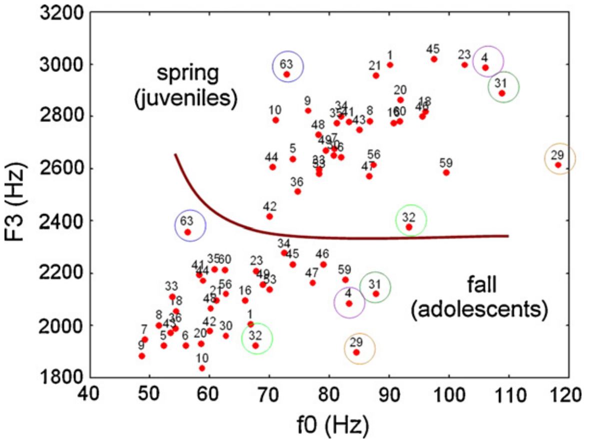

Fig. 4. Scatterplot, depicting spring and fall nasal calls of 35 calves in the space of two acoustic variables: fundamental frequency (f0) and frequency of the third formant (F3), mainly responsible for classifying individuals with DFA. Points depict average values of each juvenile and adolescent nasal calls. The curve line separates the spring (juvenile) and fall (adolescent) call samples. Each individual is represented by a unique number, from 1 to 63, and the same individual has the same number. Circles show five individuals, keeping their individualistic combinations of f0 and F3 across ages, from juvenile to adolescence.

classifying fall calls using discriminant functions created for spring calls, showed only 6.3% correct assignment to sex, thus not differing from classification by chance (Fig. 3).

Fig. 4 plots average values of spring and fall calls of each individual in the space of two acoustic variables (f0 and F3), identified as mainly responsible for classifying calls to correct individuals with DFA. The scatterplot shows that the f0 and F3 changed coordinately from spring to fall only in 5 of the 35 subject calves. For instance, calls of female 63 were lowest in f0 and highest in F3, whereas calls of female 29 were high in f0 and low in F3, both in the spring and in the fall. Females 4 and 31 and male 32 also retained their individual combinations of f0 and F3 (Fig. 4). In all other calves, their individual combinations of f0 and F3 changed uncoordinatedly from spring to fall. These uncoordinated changes in most individuals could be responsible for poor classification accuracy of the fall calls by discriminant functions created for the spring calls (Fig. 3).

4. Discussion

4.1. Effects of age and body mass on the acoustics

In this study of the nasal calls of goitred gazelles, the f0, formants, fpeak and quartiles were significantly higher in juveniles compared to adolescents, and the duration significantly more in adolescents. Body mass, used as a proxy of body growth from spring to fall, doubled from juveniles to adolescents. Therefore, the changes in the acoustics, revealed with controlled for sex and identity analyses, reflected the growth of the entire body and the respective growth of the sound-producing morphological structures.

The inverse relation between the sizes of the sound-producing structures and the acoustics is a common rule for mammals (Morton, 1977; Fitch and Hauser, 2002; Taylor and Reby, 2010). Accordingly, in this study the longer vocal tracts of adolescents produced respectively lower formants and quartiles than the shorter vocal tracts of juveniles, consistently to previous findings of the ontogeny of formants in goitred gazelles (Efremova et al., 2011a) and reported data for humans (Fitch and Giedd, 1999; Lee et al., 1999), chacma baboons *Papio cynocephalus* (Fischer et al., 2002), Southern elephant seal *Mirounga leonina* (Sanvito et al., 2008) and domestic goats (Briefer and McElligott, 2011a). Similarly, the longer vocal folds of adolescents produced a lower f0 compared to the shorter vocal folds of juveniles, in accordance with previous findings of decreasing f0 along the ontogeny of goitred gazelles (Efremova et al., 2011a,b) and reported data for humans (Lee et al., 1999), red deer *Cervus elaphus* (Kidjo et al., 2008), fallow deer *Dama dama* (Torriani et al., 2006), domestic goats (Briefer and McElligott, 2011b), African wild dogs *Lycaon pictus* (Wilden, 1997), pygmy marmosets *Cebuella pygmaea* (Elowson et al., 1992), Japanese macaques *Macaca fuscata* (Inoue, 1988), chacma baboons (Fischer et al., 2002), harbor seals *Phoca vitulina richardii* (Khan et al., 2006), black-tailed prairie dogs *Cynomys ludovicianus* (Owings and Loughry, 1985) and yellow-bellied marmots *Marmota flaviventris* (Matrosova et al., 2011). Distinctive data, of the lacking ontogenetic changes in f0 between juveniles and adults, were obtained for speckled *Spermophilus suslicus* and yellow *S. fulvus* ground squirrels (Volodina et al., 2010).

Theoretically, the age-related increase of call duration also could result from the ontogenetic increase in body size and the respective increase of the lung volume and capacity (Fitch and Hauser, 2002). Besides goitred gazelles, the ontogenetic increase of call duration was reported for fallow deer (Torriani et al., 2006), domestic goats (Briefer and McElligott, 2011b), chacma baboons (Fischer et al., 2002) and speckled ground squirrels (Volodina et al., 2010). However, nasal calls of goitred gazelle calves are relatively short (Table 1), so unlikely that the lung capacity actually limits call duration in juveniles.

Logarithm of body mass proved to be a good indicator of body size. Strong positive correlation has been found between body mass and skull length in rhesus macaques *Macaca mulatta* ($R^2 = 0.89$, Fitch, 1997), domestic dogs *Canis familiaris* ($R^2 = 0.92$, Riede and Fitch, 1999), between body mass and body length in giant panda *Ailuropoda melanoleuca* ($R^2 = 0.61$, Charlton et al., 2009) and between body mass and neck circumferences in goitred gazelles in this study. Consistently, correlations between the juvenile and adolescent goitred gazelle acoustics and two body size esteems (neck circumferences and logarithm body mass) were found very similar (Table 2). Within the two age classes, only f0, F3 and F4 negatively correlated with body mass, whereas no correlation was found with other acoustic variables. Consistently, in oral calls of domestic goat kids (Briefer and McElligott, 2011a) body size-related changes were only found for f0 and the two upper formants, but not for the two lower formants. Compared to the previous study with goitred gazelles (Volodin et al., 2011), where analysis of 483 nasal calls of 20 juveniles did not reveal correlations between body mass and acoustics, in this study we analyzed 858 juvenile and 843 adolescent nasal calls of 35 individuals. This might account for reaching significance level of correlations between f0 and F4 and body mass. Distinctively, for juvenile distress calls of 31 mule deer (*Odocoileus hemionus*) and 20 white-tailed deer (*O. virginianus*), no correlation was found between body mass and f0 (Lingle et al., 2007), although such a relationship was found earlier for distress calls of 10 white-tailed deer calves (Richardson et al., 1983).

4.2. Effects of sex on the acoustics

In both age classes, male body mass exceeded female body mass, although non-significantly. Nevertheless, strong and significant sex-related differences were found in the nasal calls in both ages. The f0, two formants (F3 and F4) and power quartiles were lower in males, than in females, and the duration was longer in males. Accordingly, the potential to classify sexes by nasal calls was similarly high in both juveniles (74.4%) and adolescents (75.9%).

Comparative data for other ruminants suggest less prominent sex-related differences in the acoustics. In 1–2 week white-tailed deer, no significant differences in the acoustics were found between sexes, whereas in 4–11 week fallow deer and 1–2 week mule deer, only f0 was lower in males than in females (Torriani et al., 2006; Lingle et al., 2007). In domestic goat kids, examined from shortly after birth, no sex-related differences were found in the duration or formants, and the f0 was found higher in females only to the end of the study period at 18 weeks of age (Briefer and McElligott, 2011b).

This study confirms previous findings (Efremova et al., 2011a) that only the upper formants are affected by the age- and sex-related lengthening of the vocal tract in goitred gazelles. In juveniles, the two lower formants were lower in males, whereas in adolescents they were undistinguishable between sexes. At the same time, the two upper formants were expectedly lower in the larger (male) sex in both ages. Similar data, suggesting that the first two formants are affected by configuration rather than length of the vocal tract, were reported for the rutting groans of fallow deer bucks (McElligott et al., 2006; Briefer et al., 2010).

In contradiction to previous data, that sex is encoded exclusively in formants of nasal and oral calls of juvenile goitred gazelles (Volodin et al., 2011), this study, with larger sample of individuals, revealed that sex was mainly encoded not only in the filter-related (F3) variable of nasal calls, but also in the source-related variable (f0). We do not know other studies on ruminants, classifying calls to sexes with DFA, so further comparative research is necessary for better understanding the role of the source and filter-related acoustics, encoding sex in calves.

The accuracy of classifying calls to sex was the same in both ages, consistently to the lack of abrupt changes in the ontogeny of f0 and formants in both sexes (Efremova et al., 2011a, 2011b), but inconsistently to findings of sexual dimorphism in neck circumferences over the larynx from 6 week onwards (Efremova et al., 2011b). Probable, effects of sex variation were partly masked by individual level variation, that was stronger in adolescents. This could occur because, in both ages, the key variables for classification to sex (f0 and F3) were the same as for encoding identity. Similar effects, suggesting that individual-level variation is involved in sex-related discrimination, were found in two species of ground-dwelling sciurids (Matrosova et al., 2011).

4.3. Effects of individual identity on the acoustics

In this study of 35 goitred gazelles, the individual discrimination by nasal calls was 52.1% for juveniles (6.5 times higher the random value) and 64.4% for adolescents (8 times higher the random value), significantly higher for adolescents compared to juveniles. Comparable values were obtained for 20 juvenile goitred gazelles (64.8%, Volodin et al., 2011) and calves of other ruminants (Richardson et al., 1983; Terrazas et al., 2003; Lingle et al., 2007; Briefer and McElligott, 2011a), excluding fallow deer calves, with as low as 32% correct assignment value for 12 calves (Torriani et al., 2006). Consistently to previous data for juvenile goitred gazelles (Volodin et al., 2011), encoding individual identity was based both on source- (f0) and filter-related acoustics (F3 and F4). Although two key variables discriminating individuals were the same in both ages, their actual values changed strongly and uncoordinatedly to each other in most subjects between the spring and the fall recordings. These results suggest that vocal individuality was upgraded from spring to fall accordingly to the newly emerged acoustic variation.

The observed result of more individualized calls of adolescent goitred gazelles could be a mechanistic consequence of more stable growth in the fall than in the spring. Previous studies revealed the faster increase in body mass and neck circumferences in the first four months of ontogenesis compared to the next two months (Efremova et al., 2011a,b). Consistently, increasing individuality was found at the early ontogenesis from 1 to 5 weeks of age in oral calls of domestic goat kids (Briefer and McElligott, 2011a) and in chicks of some non-passerine birds, developing individualized vocal signatures at some ontogenetic stages (Jones et al., 1987; Lefevre et al., 1998; Insley et al., 2003b; Klenova et al., 2009).

In juvenile bovids, individualized calls of dependent offspring serve for mother–offspring communication (Terrazas et al., 2003; Torriani et al., 2006; Sebe et al., 2007, 2010; Briefer and McElligott, 2011a). In juvenile goitred gazelles, the function of advertising identity is shared between nasal and oral contact calls, and even preferentially accounted for by the oral calls (Volodin et al., 2011). However, the proportion of nasal calls increases along ontogenesis, and in adolescents, the oral calls disappear from their repertoire (Efremova et al., 2011a). Thus, the function of advertising own identity is transferred to the only type of contact calls of adolescents, i.e. to the nasal calls. Such delegation of advertising identity to the nasal calls may partly compensate the loss of more individualized oral calls by adolescents.

Individualistic calls of adolescents may serve for supporting mother–offspring or other social relationships in goitred gazelles. Observations of free-ranging individually identified goitred gazelles in Ecocenter «Djeiran» documented some mother–calf bonds lasting for 1.5–2 years. The mother–daughter bond could be retained even after calving of both females, whereas the mother–son bond could be restored after the rut (N.V. Soldatova, unpublished observations). The full-grown offspring can benefit from social support of a mother in finding the best forage sites, in effective avoiding predators, or in socialization with conspecifics.

Otherwise, a greater individualization of nasal calls in adolescents may emerge in response to social constraints in captivity. In this study, animals were kept during the day in large common groups, where communicating identity involves communicating social position of the caller to group mates. Similar functions were demonstrated for chacma baboons and rhesus macaques (Owren and Rendall, 1997, 2001) and hypothesized for an obligatory social canid, the dhole *Cuon alpinus* (Volodin et al., 2006; Volodina et al., 2006). This suggests flexibility of vocal communication system in a ruminant species with much less elaborated social relations compared to primates or canids.

Acknowledgements

We thank the staff of the Ecocenter 'Djeiran' for their help and support, especially E.T. Juldashev and two anonymous reviewers, for their constructive comments. During our work, we adhered to the 'Guidelines for the treatment of animals in behavioural research and teaching' (Anim. Behav. 71, 245–253, 2006) and to the laws of the Russian Federation, the Republic of Uzbekistan and Germany, the countries where the research was conducted. Research protocol # 2008-03 was approved by the Committee of bio-ethics of Lomonosov Moscow State University. No animal has suffered somehow due to the data collection. This study was supported by the Russian Foundation for Basic Research grant 12-04-00260 (for EL, IV, EV and KE).

References

Aubin, T., Jouventin, P., 2002. How to vocally identify kin in a crowd: the penguin model. Adv. Study Behav. 31, 243–277.

Briefer, E., McElligott, A.G., 2011a. Mutual mother–offspring recognition in an ungulate hider species (*Capra hircus*). Anim. Cogn. 14, 585–598.

Briefer, E., McElligott, A.G., 2011b. Indicators of age, body size and sex in goat kid calls revealed using the source–filter theory. Appl. Anim. Behav. Sci. 133, 175–185.

Briefer, E., Vannoni, E., McElligott, A.G., 2010. Quality prevails over identity in the sexually selected vocalisations of an ageing mammal. BMC Biol. 8, 35, doi:10.1186/1741-7007-8-35.

Charlton, B.D., Zhihe, Z., Snyder, R.J., 2009. The information content of giant panda, *Ailuropoda melanoleuca*, bleats: acoustic cues to sex, age and size. Anim. Behav. 78, 893–898.

Efremova, K.O., Volodin, I.A., Volodina, E.V., Frey, R., Lapshina, E.N., Soldatova, N.V., 2011a. Developmental changes of nasal and oral calls in the goitred gazelle

Gazella subgutturosa, a nonhuman mammal with a sexually dimorphic and descended larynx. Naturwissenschaften 98, 919–931.

Efremova, K.O., Volodin, I.A., Volodina, E.V., Frey, R., Soldatova, N.V., Lapshina, E.N., Makarov, I.S., Gorbunov, K.S., 2011b. Sex and age effects on the structural features of nasal calls and body size in the goitred gazelle (*Gazella subgutturosa*, Artiodactyla, Bovidae) calves. Zool. Z. 90, 603–615 (in Russian).

Elowson, A.M., Snowdon, C.T., Sweet, C.J., 1992. Ontogeny of trill and j-call vocalizations in the pygmy marmoset *Cebuella pygmaea*. Anim. Behav. 43, 703–715.

Fant, G., 1960. Acoustic Theory of Speech Production. Mouton & Co, The Hague, Netherlands.

Fischer, J., Hammerschmidt, K., Cheney, D.L., Seyfarth, R.M., 2002. Acoustic features of male baboon loud calls: influences of context, age and individuality. J. Acoust. Soc. Am. 111, 1465–1474.

Fitch, W.T., 1997. Vocal tract length and formant frequency dispersion correlate with body size in rhesus macaques. J. Acoust. Soc. Am. 102, 1213–1222.

Fitch, W.T., Giedd, J., 1999. Morphology and development of the human vocal tract: a study using magnetic resonance imaging. J. Acoust. Soc. Am. 106, 1511–1522.

Fitch, W.T., Hauser, M.D., 2002. Unpacking "honesty": vertebrate vocal production and the evolution of acoustic signals. In: Simmons, A., Fay, R.R., Popper, A.N. (Eds.), Acoustic Communication, Springer Handbook of Auditory Research. Springer, New York, pp. 65–137.

Fitch, W.T., Reby, D., 2001. The descended larynx is not uniquely human. Proc. R. Soc. Lond. B 268, 1669–1675.

Frey, R., Hofmann, R.R., 2000. Larynx and vocalization of the takin (*Budorcas taxicolor* Hodgson, 1850 – Mammalia, Bovidae). Zool. Anz. 239, 197–214.

Frey, R., Volodin, I.A., Volodina, E.V., 2007. A nose that roars: anatomical specializations and behavioural features of rutting male saiga. J. Anat. 211, 717–736.

Frey, R., Volodin, I., Volodina, E., Carranza, J., Torres-Porras, J., 2012. Vocal anatomy, tongue protrusion behaviour and the acoustics of rutting roars in free-ranging Iberian red deer stags (*Cervus elaphus hispanicus*). J. Anat. 220, doi:10.1111/j.1469-7580.2011.01467.x.

Frey, R., Volodin, I.A., Volodina, E.V., Soldatova, N.V., Juldaschev, E.T., 2011. Descended and mobile larynx, vocal tract elongation and rutting roars in male goitred gazelles (*Gazella subgutturosa* Güldenstaedt, 1780). J. Anat. 218, 566–585.

Inoue, M., 1988. Age gradation in vocalization and body weight in Japanese monkeys (*Macaca fuscata*). Folia Primatol. 51, 76–86.

Insley, S.J., Phillips, A.V., Charrier, I., 2003a. A review of social recognition in pinnipeds. Aquat. Mamm. 29, 181–201.

Insley, S.J., Paredes, R., Jones, I.L., 2003b. Sex differences in razorbill *Alca torda* parent – offspring vocal recognition. J. Exp. Biol. 206, 25–31.

Jones, I.L., Falls, J.B., Gaston, A.J., 1987. Vocal recognition between parents and young of ancient murrelets, *Synthliboramphus antiquus* (Aves: Alcidae). Anim. Behav. 35, 1405–1415.

Khan, C.B., Markowitz, H., McCowan, B., 2006. Vocal development in captive harbor seal pups, *Phoca vitulina richardii*: age, sex, and individual differences. J. Acoust. Soc. Am. 120, 1684–1694.

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.

Klenova, A.V., Volodin, I.A., Volodina, E.V., 2009. The variation in reliability of individual vocal signature throughout ontogenesis in the red-crowned crane *Grus japonensis*. Acta Ethol. 12, 29–36.

Lee, S., Potamianos, A., Narayanan, S., 1999. Acoustics of children's speech: developmental changes of temporal and spectral parameters. J. Acoust. Soc. Am. 105, 1455–1468.

Lefevre, K., Montgomery, R., Gaston, A.J., 1998. Parent-offspring recognition in thick-billed murres (Aves: Alcidae). Anim. Behav. 55, 925–938.

Lingle, S., Rendall, D., Pellis, S.M., 2007. Altruism and recognition in the antipredator defence of deer: 1. Species and individual variation in fawn distress calls. Anim. Behav. 73, 897–905.

Matrosova, V.A., Blumstein, D.T., Volodin, I.A., Volodina, E.V., 2011. The potential to encode sex, age, and individual identity in the alarm calls of three species of Marmotinae. Naturwissenschaften 98, 181–192.

McElligott, A.G., Birrer, M., Vannoni, E., 2006. Retraction of the mobile descended larynx during groaning enables fallow bucks (*Dama dama*) to lower their formant frequencies. J. Zool. 270, 340–345.

Morton, E.S., 1977. On the occurrence and significance of motivation – structural rules in some bird and mammal sounds. Am. Nat. 111, 855–869.

Owings, D.H., Loughry, W.J., 1985. Variation in snake-elicited jump-yipping by black-tailed prairie dogs: ontogeny and snake specificity. Z. Tierpsychol. 70, 177–200.

Owren, M.J., Rendall, D., 1997. An affect-conditioning model of nonhuman primate vocal signals. In: Owings, D.H., Beecher, M.D., Thompson, N.S. (Eds.), Perspectives in Ethology, vol. 12. Plenum Press, New York, pp. 299–346.

Owren, M.J., Rendall, D., 2001. Sound on the rebound: bringing form and function back to the forefront in understanding nonhuman primate vocal signalling. Evol. Anthropol. 10, 58–71.

R Development Core Team, 2009. R Foundation for Statistical Computing., http://www.R-project.org.

Reby, D., Cargnelutti, B., Hewison, A.J.M., 1999. Contexts and possible functions of barking in roe deer. Anim. Behav. 57, 1121–1128.

Rendall, D., Notman, H., Owren, M.J., 2009. Asymmetries in the individual distinctiveness and maternal recognition of infant contact calls and distress screams in baboons. J. Acoust. Soc. Am. 125, 1792–1805.

Richardson, L.W., Jacobson, H.A., Muncy, R.J., Perkins, C.J., 1983. Acoustics of white-tailed deer (*Odocoileus virginianus*). J. Mammal. 64, 245–252.

Riede, T., Fitch, W.T., 1999. Vocal tract length and acoustics of vocalization in the domestic dog (*Canis familiaris*). J. Exp. Biol. 202, 2859–2867.

Riede, T., Lingle, S., Hunter, E., Titze, I.R., 2010. Cervids with different vocal behavior demonstrate different visco-elastic properties of their vocal folds. J. Morphol. 271, 1–11.

Sanvito, S., Galimberti, F., Miller, E.H., 2008. Development of aggressive vocalizations in male southern elephant seals (*Mirounga leonina*): maturation or learning? Behaviour 145, 137–170.

Sebe, F., Duboscq, J., Aubin, T., Ligout, S., Poindron, P., 2010. Early vocal recognition of mother by lambs: contribution of low- and high-frequency vocalizations. Anim. Behav. 79, 1055–1066.

Sebe, F., Nowak, R., Poindron, P., Aubin, T., 2007. Establishment of vocal communication and discrimination between ewes and their lamb in the first two days after parturition. Dev. Psychobiol. 49, 375–386.

Solow, A.R., 1990. A randomization test for misclassification probability in discriminant analysis. Ecology 71, 2379–2382.

Taylor, A.M., Reby, D., 2010. The contribution of source–filter theory to mammal vocal communication research. J. Zool. 280, 221–236.

Terrazas, A., Serafin, N., Hernandez, H., Nowak, R., Poindron, P., 2003. Early recognition of newborn goat kids by their mother: II. Auditory recognition and evidence of an individual acoustic signature in the neonate. Dev. Psychobiol. 43, 311–320.

Titze, I.R., 1994. Principles of Voice Production. Prentice-Hall, Englewood Cliffs, NJ.

Titze, I.R., Riede, T., 2010. A cervid vocal fold model suggests greater glottal efficiency in calling at high frequencies. PLoS Comput. Biol. 6 (8), e1000897, doi:10.1371/journal.pcbi.1000897.

Torriani, M.V.G., Vannoni, E., McElligott, A.G., 2006. Mother–young recognition in an ungulate hider species: a unidirectional process. Am. Nat. 168, 412–420.

Vannoni, E., McElligott, A.G., 2007. Individual acoustic variations in fallow deer (*Dama dama*) common and harsh groans: a source-filter theory perspective. Ethology 113, 223–234.

Volodin, I.A., Lapshina, E.N., Volodina, E.V., Frey, R., Soldatova, N.V., 2011. Nasal and oral calls in juvenile goitred gazelles (*Gazella subgutturosa*) and their potential to encode sex and identity. Ethology 117, 294–308.

Volodin, I.A., Nagaylik, M.M., Volodina, E.V., 2006. Cues to orientation of a caller to a listener in biphonic and non-biphonic close range contact calls in the dhole (*Cuon alpinus*). Advances in Bioacoustics 2, Dissertationes Classis IV: Historia Naturalis, vol. 47. Slovenian Academy of Sciences and Arts, Ljubljana, pp. 245–255.

Volodina, E.V., Matrosova, V.A., Volodin, I.A., 2010. An unusual effect of maturation on the alarm call fundamental frequency in two species of ground squirrels. Bioacoustics 20, 87–98.

Volodina, E.V., Volodin, I.A., Isaeva, I.V., Unck, C., 2006. Biphonation may function to enhance individual recognition in the dhole, *Cuon alpinus*. Ethology 112, 815–825.

Wilden, I., 1997. Phonetische Variabilität in der Lautgebung Afrikanischer Wildhunde (*Lycaon pictus*) und deren frühe Ontogenese. Shaker Verlag, Aachen.

Yin, S., McCowan, B., 2004. Barking in domestic dogs: context specificity and individual identification. Anim. Behav. 68, 343–355.