Nasal and Oral Calls in Juvenile Goitred Gazelles (*Gazella subgutturosa*) and their Potential to Encode Sex and Identity

Ilya A. Volodin*†, Ekaterina N. Lapshina*, Elena V. Volodina†, Roland Frey‡ & Natalia V. Soldatova§

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

† Scientific Research Department, Moscow Zoo, Moscow, Russia

‡ Leibniz Institute for Zoo and Wildlife Research, Berlin, Germany

§ Ecocenter ''Djeiran'', Bukhara, Republic of Uzbekistan

Abstract

Like many other gazelles, goitred gazelles (*Gazella subgutturosa*) are capable of calling either through the nose or through the open mouth. In particular, juvenile goitred gazelles provide a convenient model for contrasting acoustic characteristics of nasal and oral calls, and for estimating their communicative functions. In this study, acoustic variables (formants, fundamental frequency, duration and power quartiles) of 480 oral and 483 nasal calls, recorded from 20 (9 male, 11 female) individually identified captive juvenile goitred gazelles, were examined for their potential to encode sex and identity of the caller. Discriminant function analysis revealed an equally high potential of oral and nasal calls to encode sex, whereas encoding the individual identity was significantly more accurate for oral calls. Sex was encoded exclusively in formants, whilst individual identity was encoded in a combination of all investigated variables. No correlation was found between body mass and values of any acoustic variable. Analyses controlling for age and sex revealed higher average values for all investigated variables of oral calls compared to nasal calls. We discuss the results in relation to the source-filter theory, mother–offspring communication and production mechanisms of nasal and oral calls in mammals.

Introduction

Bovids represent a convenient group for studying the acoustical variation, functions and evolution of vocal communication. Among bovids, a wide spectrum of vocal adaptations and examples of parallel evolution with cervids and humans can be found (Fitch & Reby 2001; McElligott et al. 2006; Frey et al. 2007, 2008a,b). For instance, in the goitred gazelle (*Gazella subgutturosa*), a strong sexual dimorphism resembles the situation in humans: the 'Adam's apple' of adult human males and the larynx of adult male goitred gazelles are similarly larger and rest lower in the neck than in females. This anatomical feature is very prominent (Kingswood & Blank 1996; Frey et al.

unpubl. data) and was noted already in the first scientific description of this species (Güldenstaedt 1780).

In addition to such interesting anatomical adaptations, bovids demonstrate variable modes of vocal production. While adult male and female saiga antelopes (*Saiga tatarica*) vocalize exclusively through the nose (Frey et al. 2007; Volodin et al. 2009), most African gazelles call mainly through the nose, but optionally also through the mouth (Walther et al. 1983). Adult rutting male Mongolian gazelles (*Procapra gutturosa*) and goitred gazelles vocalize through the widely opened mouth, whilst the non-rutting males and adult females of these species produce both oral and nasal calls (Blank 1998; Frey et al.

2008a,b; our personal observations). The ability to produce both oral and nasal calls is also found in adult female sheep (*Ovis aries*; Sebe et al. 2010), juvenile saigas and goitred gazelles (Volodin et al. 2009; Efremova et al. 2011) and juvenile white-tailed deer (*Odocoileus virginianus*; Richardson et al. 1983). Thus, juvenile bovids and cervids provide a good model for contrasting the acoustic features between the nasal and oral calls, and for comparing their potential to communicate information about specific attributes of a caller.

In goitred gazelles, vocalization represents an essential component of rutting behaviour of adult males (Jevnerov 1984; Marmasinskaya 1996a; Blank 1998; Frey et al. unpubl. data). As has been shown for other polygynous cervids and bovids, vocal features advertising quality of a rutting male to potential mates and rivals may play a decisive role in the reproductive success of the caller (Reby & McComb 2003; Reby et al. 2005; Charlton et al. 2007, 2008; Briefer et al. 2010). Unlike adult male goitred gazelles, which are prominently vocal only during the rut, adult female goitred gazelles often vocalize post-partum and during the nursing period (Jevnerov 1984; Pereladova & Pereladov 1986; Kingswood & Blank 1996; Marmasinskaya 2008). Juveniles regularly produce soft calls when grazing with their mothers at 1 mo of age, and when lost, call loudly (our personal observations). Mothers can produce soft calls, causing the young to approach (Jevnerov 1984; Blank 1985; Pereladova & Pereladov 1986; Marmasinskaya 2008). These observations suggest that, in the goitred gazelle, vocalization of females and juveniles serves mainly for communication between a mother and her offspring.

In nature, goitred gazelles are hiders for 2–3 wk post-partum, allowing their mothers to use spatial cues for their location and recognition. Before parturition, occurring from mid-April to beginning of June (Jevnerov 1984; Marmasinskaya 1996b, 2008; Blank 1998), females occupy individual parcels of land with low vegetation cover (Soldatova 1983; Jevnerov 1984). Juveniles older than 2 wk can outrun approaching humans or cars, but they will return to the same place after having made a 1.5–2 km arc (Soldatova 1983; Jevnerov 1984; Blank 1985). In captivity, juveniles only approach their mothers in response to her vocalization, staying on the place if the female is silent (Pereladova & Pereladov 1986). Individual recognition of young by their mothers through vocal communication may thus be less important in early ontogenesis. For mothers, the need of vocal recognition among their own and non-related same-age young should increase when offspring start grazing and visiting watering places together with their mothers at the age of 4 wk. When following their mothers, juveniles can run forward or remain behind up to 200 m apart, or run wide circuses around a mother, as a component of playful behaviour, as well as join other mother–offspring units (Soldatova 1983; our personal observations). If a mother is lost, individually recognizable juvenile calls may serve for re-uniting mother and offspring, as it has been reported for the white-tailed deer (Lingle et al. 2007a,b), a species in which mother and offspring are not constantly together, and for reindeer (*Rangifer tarandus*) (Espmark 1975); domestic sheep (Searby & Jouventin 2003) and domestic goats (*Capra hircus*) (Terrazas et al. 2003), representing species in which juveniles are constantly with their mothers but eventually in mixed groups with other offspring of the same age. In red deer (*Cervus elaphus*) and fallow deer (*Dama dama*), however, mainly the juveniles recognize their mothers by voice but not *vice versa* (Vankova & Malek 1997; Vannoni et al. 2005; Torriani et al. 2006).

The study of Sebe et al. (2010) showed that nasally and orally produced calls of adult mother sheep differed in their potentials to encode individual identity. We would therefore expect to find similar differences in calls of juvenile goitred gazelles, who also produce calls through both the nose and the mouth. According to the source-filter theory (Fant 1960), the nasally and orally produced calls should differ in their formant frequencies. The vocal output emitted either from the nose or from the mouth is the result of combined work of the larynx, which is the sound source, and of the vocal tract, which acts as a resonance filter. The source-filter theory suggests the independence of source and filter. Thus, vocal tract filtering should not affect the fundamental frequency ($f0$) of the sound created in the larynx (source-filter theory: Fant 1960; review: Taylor & Reby 2010). The signal of the sound source can be described by variables related to the fundamental frequency, reflecting the vibrating frequency of the vocal folds (Titze 1994), while the effects of the vocal tract on the signal can be described by variables related to formant frequencies, reflecting the length and dimensions of the vocal tract (Riede & Fitch 1999; Fitch 2000a; Owren & Rendall 2001; Fitch & Hauser 2002). As formant frequencies are inversely related to the length of the vocal tract, and as the length of the nasal vocal tract always exceeds that of the oral vocal tract, consistently lower and more closely spaced formant frequencies are expected to be found in nasal than in

oral calls (Titze 1994; Fitch & Reby 2001; Fitch & Hauser 2002).

Our focus here is on the relative contributions of the vocal source and vocal filter to encoding sex and identity in the nasal and oral calls of juvenile goitred gazelles aged 3–6 wk. Our particular purposes were (1) to describe the acoustic structures of nasal and oral calls of juvenile goitred gazelles in terms of duration, fundamental frequency and formant frequencies; (2) to reveal the variables mainly responsible for the encoding sex and identity of a caller; (3) to compare the abilities of nasal and oral calls to encode sex and identity in juvenile gazelles; and (4) to examine the effect of body mass on the acoustic features of nasal and oral calls.

Materials and Methods

Subjects, Site and Dates of Work

The study was conducted in the Ecocenter 'Djeiran' (Uzbekistan, Bukhara region, 39°41′N, 64°35′E). The state breeding centre, Ecocenter 'Djeiran', is located on a fenced 5145 hectare area of semidesert, inhabited by 600–1200 free-ranging goitred gazelles in different years (Pereladova et al. 1998), about 900 individuals in Oct. 2009. Adult females give birth to one or two young from end-April to mid-May. Each May, the staff of the Ecocenter captures 25–35 juveniles (preferentially one per twin), which are hand-raised and then transferred to other breeding centres or zoos. Study subjects were 20 (9 male, 11 female) juvenile goitred gazelles, captured between 5 and 13 May 2009 at the age estimated to be 3–10 d postpartum. We took May 1 as a common conditional date of birth for all of them. Animals were individually dye-marked with p-phenylenediamine (Rhodia, Paris, France).

Subject animals were kept in groups of 5–7 individuals in a few small enclosures 2 × 4 m in a row, with an indoor shelter made of dried reeds in each enclosure, providing protection from wind, rain and sun. The small enclosures had exits to a common passageway 1.5 m wide, leading to a large common enclosure 25 × 18 m, where all the 20 individuals walked together during the day, played with each other and communicated through a wire mesh with a few adult goitred gazelles kept in neighbouring enclosures (Soldatova et al. 2010). The subject animals were fed twice a day (with fresh goat and cow milk, pre-dried grass, mainly *Megicago* sp., mixed fodder, vitamins and minerals, and *Haloxylon* sp. naturally growing in the enclosure). Water was available *ad libitum*.

Data Collection

Acoustic recordings (48 kHz, 16 bit) were made between May 21 and June 17 2009 (thus covering a period when subject animals were 3–6 wk of age). Each individual was recorded a few times evenly distributed throughout the data collection period. Calls were recorded daily, 30–120 min before the morning and before the evening feeding, outdoor or indoor, as the reed walls had no echo effect. Distance to microphone varied of 1–7 m. The animals emitted calls through the nose or through the mouth, anticipating for food or being separated for a short time in the small enclosure. If a non-focal animal called concurrently with the focal one, the calls of the focal animal were labelled on the recorder by voice, to distinguish between the calls of focal and non-focal animals during subsequent analysis. We used a Zoom-H4 (Zoom Corp., Tokyo, Japan) digital recorder with Sennheiser K6-ME64 (Sennheiser electronic, Wedemark, Germany) cardioid electret condenser microphone. Of a total of 49 h of audio recordings, 9 h were made with synchronous video recordings, using a miniDV Panasonic NV-GS250 camcorder (Panasonic Corp., Kadoma, Japan). Body mass data, with 10-g precision using Kern De 15K5 scales (Kern & Sohn GmbH, Balingen-Frommern, Germany), were collected twice per individual (on May 25 and June 11) at 16.00–19.00 before the evening feeding. The eyes of the young gazelles were covered with a cotton mask to decrease their arousal (Soldatova et al. 2010). The mean value of the two measures was taken.

Oral and Nasal Call Samples

Calls of juveniles produced through the nose or through the mouth differed strongly by energy distribution (Fig. 1). This was stated from video clips where we could see whether mouth was opened or closed during the calling and visually by corresponding spectrograms of these calls. Also, nasal calls had a specific 'nasal' quality of sounding (Supplementary Audio S1). Two researchers (IV and EL) classified calls to the oral or nasal type by spectrograms and by hearing. We took for analysis only calls, where both researchers were concordant in their judgments concerning their type.

For each individual, we took measurements from 25 randomly selected oral and 25 nasal calls of good quality, not disrupted by wind and non-overlapped by noise or human voice (nine animals provided only 18–24 oral calls, and eight animals provided only 21–24 nasal calls). To reduce pseudoreplication,
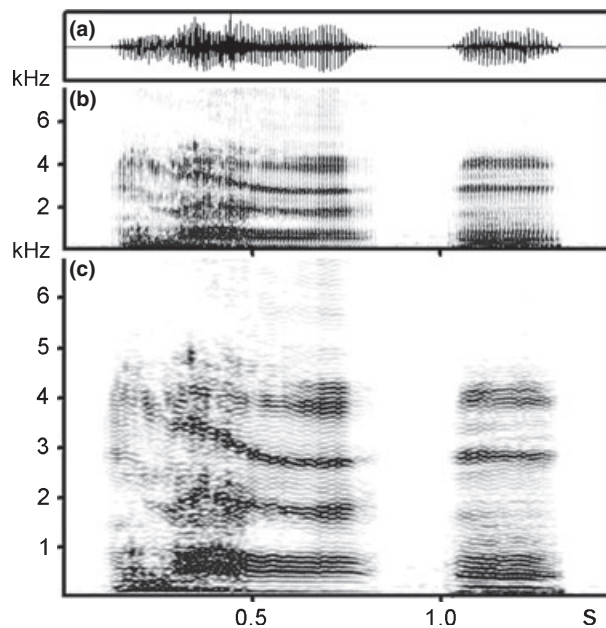
Fig. 1: The oral call (left) and the nasal call (right) of a 4-wk-old male goitred gazelle: (a) waveform, (b) wideband spectrogram and (c) narrowband spectrogram. The oral call starts nasally and passes to oral at ~0.3 s, when the animal opens its mouth. The wideband spectrogram is created with Hamming window, 24 kHz sampling rate, FFT 512 points, frame 50% and overlap 87.5%. The narrowband spectrogram is created with Hamming window, 16 kHz sampling rate, FFT 1024 points, frame 50% and overlap 96.87%.

we took calls from different recording sessions per animal and from different parts within session. The average number of sessions per animal was 10.9 ± 3.4 (6–18), and we took 1–5 calls per session per animal. We analysed 480 oral calls (218 male and 262 female) and 483 nasal calls (218 male and 265 female), 963 calls in total.

Measuring Vocal Tract and Vocal Folds

Three dissected specimens, two fresh males (~3–4 wk of age) and one deeply frozen-melted female (~8 wk of age), naturally predated or dead of diseases in 2008–2009 were used for the anatomical measurements. The vocal fold length was measured in all the three specimens, whilst the vocal tract length only in one male and in one female specimen. The dorsoventral length of the vocal folds was measured along their medial surface, facing the glottis, from their attachment to the thyroid cartilage dorsally up to the vocal process of the arytenoid cartilage. Measurements were made using the electronic calipers (Aerospace; Brüder Mannesmann Werkzeuge GmbH, Remscheid, Germany) with 0.5-mm precision.
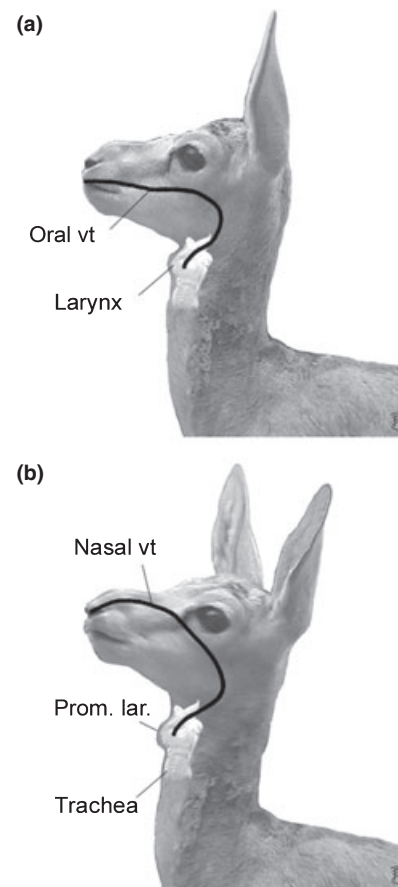

Fig. 2: Illustration of measurements: (a) of the oral vocal tract length and (b) of the nasal vocal tract length in juvenile goitred gazelles at the age of 3–6 wk. Abbreviations: vt, vocal tract; prom. lar, laryngeal prominence.

As the post-mortem position of the larynx approximately corresponds to its resting position in the live animal, the resting lengths of the oral and nasal vocal tract could be measured. The oral tract was measured from the vocal folds to the edges of the lips along the pharyngeal and oral cavities, and the nasal vocal tract was measured from the vocal folds to the nostrils along the pharyngeal and nasal cavities (Fig. 2). After removal of the left half of the mandible including the attaching musculature (masseter, pterygoid muscles), oral and nasal vocal tract lengths were ascertained with a tape measure (1-mm precision). Each measurement was repeated three times for each specimen, and the mean value was calculated.

Call Analysis

The mean values of vocal tract lengths served to establish linear prediction coding (LPC) settings for further analysis of formant frequencies of nasal

and oral calls with Praat DSP package v. 4.3.21 (P. Boersma & D. Weenink, University of Amsterdam, Netherlands, http://www.praat.org), as the age of our subject animals during the study period corresponded to that of the dissected specimens. The basic model for the analysis of formants is the model of a uniform tube closed at one end, considering sound source (larynx with vocal folds) was the closed end, whilst the mouth or nostrils represented the open end (Fitch & Reby 2001). According to this model, formant frequencies can be approximated as:

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

where n – are formant numbers (1, 2, 3 etc.), L – is vocal tract length, and C is the speed of sound in air, approximated as 350 m/s.

From each oral and nasal call (Fig. 1), we measured the same 10 acoustic variables: one temporal, one frequency, four power and four formants (Fig. 3). With Avisoft SASLab Pro software (Avisoft Bioacoustics, Berlin, Germany), we measured the duration from the screen with the standard marker cursor in the spectrogram window (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). With the 'Autocorrelation' option of Avisoft, we measured the mean fundamental frequency. 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 automatically to Microsoft Excel (Microsoft Corp., Redmond, WA, USA).

Four first formants (F1, F2, F3 and F4) were measured using LPC with Praat. The LPC settings for creation formant tracks were Burg analysis, window length 0.04 s, time step 0.01 s, maximum number of formants 4–5 and maximum formant frequency 4000–5000 Hz (range 3600–5500 Hz) (Fig. 4). 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. Formant dispersion (dF) was calculated as the mean difference between frequencies of neighbouring formants (Riede & Fitch 1999).

Statistical Analyses

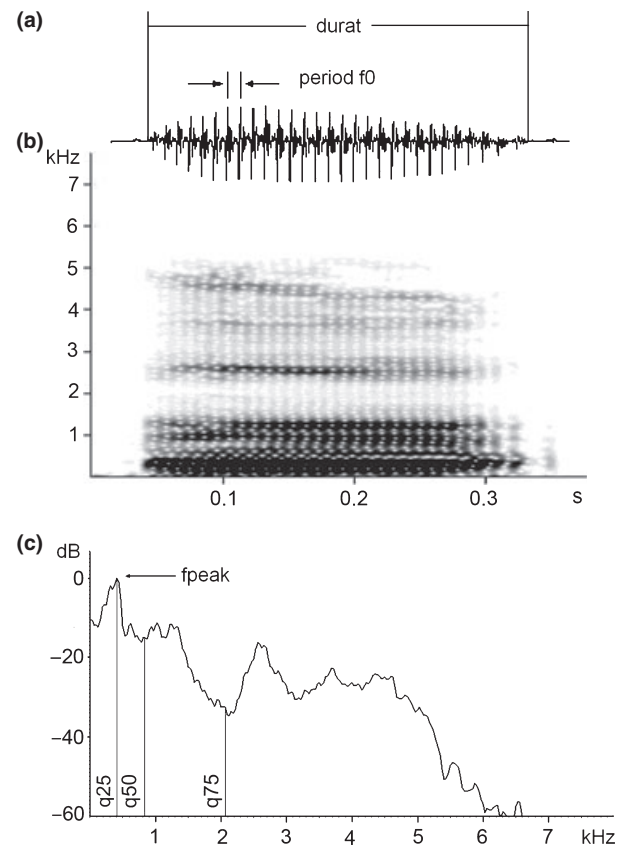All statistical analyses were made with STATISTICA, v. 6.0 (StatSoft, Tulsa, OK, USA). Means are given

Fig. 3: The nasal call of a 4-wk-old female goitred gazelle: (a) waveform, (b) spectrogram and (c) mean power spectrum. Measured acoustic variables: duration (durat); fundamental frequency period (period f0); maximum amplitude frequency (fpeak); lower (q25), medium (q50) and upper quartiles (q75). The spectrogram was created with Hamming window; 16 kHz sampling rate; FFT 512 points; frame 50%; and overlap 96.87%.

as mean ± SD, all tests were two-tailed, and differences were considered significant where p < 0.05. A Kolmogorov–Smirnov test showed that distributions of parameter values did not depart from normality (p > 0.05), besides the fpeak. To estimate effects of individuality and sex on call characteristics, we used nested-design ANOVA with individuality nested into sex, where individuality included as random factor and sex as fixed factor. We used repeated measures ANOVA controlled for individuality and sex to compare the parameter values between and within nasal and oral calls, with Newman–Keuls post hoc tests. We used discriminant function analysis (DFA) to calculate the probability of the assignment of calls to the correct individual or correct sex for each call sample (of nasal calls and of oral calls) with jackknife cross-validation of DFA results. We used Wilks' Lambda values to estimate how strongly acoustic
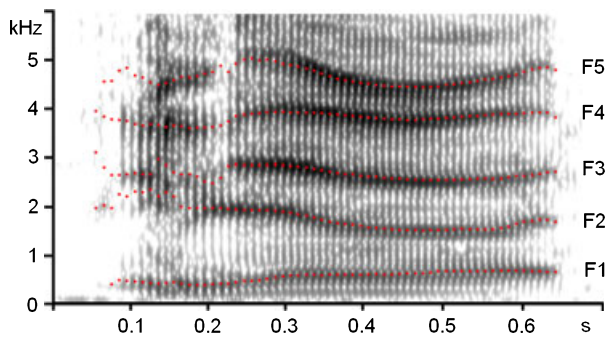
Fig. 4: Spectrogram illustrating tracks of the first five formants (F1 – F5), created with Praat software, of the oral call of a 4-wk-old male goitred gazelle. The animal opened its mouth at ~0.24 s. The linear prediction coding settings were: Burg analysis, window length 0.04 s, time step 0.01 s, maximum number of formants 5, and maximum formant frequency 5400 Hz. Measurements of the first four formants were taken from the call portion where the formant tracks are nearly horizontal (0.3–0.6 s in this call).

variables of calls contribute to discrimination of sex and individual. With a 2×2 chi-squared test, we compared the values of correct assignment of nasal and oral calls to correct individual or sex. Because body mass should theoretically be proportional to the cube of a linear dimension like body size, we used log body mass to calculate Pearson's correlation between body mass and acoustic characteristics. We used a Student's *t*-test to compare body mass between sexes, as a Kolmogorov–Smirnov test showed that distributions of body mass values of males and females did not depart from normality (p > 0.20).

We calculated the expected level of correct classification with DFA if the calls we analysed were randomly distributed among individuals or between sexes (Solow 1990). To perform each randomization analysis, 500 permutation procedures with macros, specially created for STATISTICA software, were used. Using a distribution obtained by the permutation, we noted whether the observed value exceeded 95% or 99% of the values within the distribution (Solow 1990; Klenova et al. 2008; Matrosova et al. 2010).

Results

Vocal Tract and Vocal Fold Length

The vocal fold length was 15 mm in both male specimens and 13.5 mm in the female specimen. The oral vocal tract length with the larynx in resting position was 132 mm in the male and 135 mm in

the female specimen. The nasal vocal tract length with the larynx in resting position was 149 mm in the male and 150 mm in the female specimen. As the age of the female specimen was twice older than those of the male specimens (8 wk vs. 3–4 wk), we infer the existence of sex dimorphism in the size of vocal folds and in the vt in juvenile goitred gazelles.

Comparison of Oral and Nasal Calls

Both nasal and oral calls occurred when the animals anticipated feeding or were separated for a short time, but animals producing the oral calls looked more aroused. The analysis of video clips showed that oral calls mostly started with a closed mouth but then were produced through the widely opened mouth, while all nasal calls were produced through the nose with the closed mouth. This could be the reason of the non-constancy of the distance between two subsequent formants for the duration of oral calls compared to the nasal calls (Figs 1 and 4). Both oral and nasal calls showed pulsation, representing the call fundamental frequency, well visible on the narrowband spectrogram (Fig. 1).

A repeated measures ANOVA controlling for individuality and sex revealed significantly higher values in all 10 measured variables and in the calculated formant dispersion for the oral calls compared to the nasal calls (Table 1). At the same time, the distance

Table 1: Comparison between oral and nasal calls: mean ± SD values of 10 measured variables and of the calculated formant dispersion, and repeated measures ANOVA results

Variable	Oral calls	Nasal calls	ANOVA
F1 (Hz)	707 ± 121	469 ± 94	$F_{1,19} = 137.61$, p < 0.001
F2 (Hz)	1941 ± 293	1334 ± 156	$F_{1,19} = 124.91$, p < 0.001
F3 (Hz)	2894 ± 299	2677 ± 204	$F_{1,19} = 16.61$, p < 0.001
F4 (Hz)	4043 ± 285	3667 ± 220	$F_{1,19} = 61.66$, p < 0.001
dF (Hz)	1112 ± 73	1066 ± 68	$F_{1,19} = 13.85$, p = 0.001
f0 (Hz)	101 ± 16	85 ± 11	$F_{1,19} = 62.81$, p < 0.001
durat (s)	0.506 ± 0.142	0.252 ± 0.118	$F_{1,19} = 240.47$, p < 0.001
fpeak (Hz)	800 ± 635	325 ± 142	$F_{1,19} = 43.06$, p < 0.001
q25 (Hz)	660 ± 227	373 ± 78	$F_{1,19} = 72.68$, p < 0.001
q50 (Hz)	1687 ± 631	885 ± 455	$F_{1,19} = 113.76$; p < 0.001
q75 (Hz)	3187 ± 802	2649 ± 783	$F_{1,19} = 25.27$, p < 0.001
F2-F1 (Hz)	1234 ± 224	865 ± 159	$F_{1,19} = 69.29$, p < 0.001
F3-F2 (Hz)	953 ± 142	1343 ± 244	$F_{1,19} = 69.34$; p < 0.001
F4-F3 (Hz)	1148 ± 205	990 ± 210	$F_{1,19} = 11.95$, p = 0.003

Designations: F1, F2, F3, F4 – values of the first four formants; dF – formant dispersion; f0 – fundamental frequency; durat – call duration; fpeak – maximum amplitude frequency; q25, q50, q75 – lower, medium and upper quartiles; F2–F1, F3–F2, F4–F3 – distances between neighbouring formants.

between neighbouring formants F3 and F2 (F3–F2) was significantly shorter in the oral than in the nasal calls, whereas the F2–F1 and F4–F3 distances were both significantly larger in the oral than in the nasal calls (Table 1).

Also, we found significant differences in distances between neighbouring formants both within the oral ($F_{2,38} = 16.28$, $p < 0.001$) and within the nasal calls ($F_{2,38} = 48.51$, $p < 0.001$). In the oral calls, the F2–F1 and F4–F3 distances were both significantly larger than the F3–F2 distance ($p < 0.001$ in both cases,

Newman–Keuls post hoc test). By contrast, in the nasal calls, the F3–F2 distance was significantly larger than either the F2–F1 or F4–F3 distance ($p < 0.001$ in both cases), and the F4–F3 distance was significantly larger than the F2–F1 distance ($p < 0.05$, Newman–Keuls post hoc test). If the filtering properties of vocal tract filter were well described by a simple uniform tube model, the differences in frequency between neighbouring formants should be equal. However, we observed that the differences between neighbouring formants were not equal, neither in the oral nor in the nasal calls, which indicates that the vocal tract in juvenile goitred gazelles is not uniform.

Effects of Body Mass, Sex and Individual Identity on the Acoustics

Body mass did not differ significantly between sexes (males: 7.48 ± 0.72 kg, n = 9; females: 7.27 ± 0.66 kg, n = 11; Student's t-test: $t = 0.66$; $p = 0.52$), and none of the 10 variables of nasal or oral calls showed significant correlation to log body mass (Table 2). Nevertheless, males showed significantly lower values for the 10 variables of the oral calls and for the seven variables of the nasal calls (Tables 3 and 4). On average, the male calls had lower values of f0, formants and power characteristics compared to the

Table 2: Pearson's correlation coefficients (*r*) for log body mass and variables of the oral and nasal calls

Variable	Oral calls (n = 20)	Nasal calls (n = 20)
F1 (Hz)	$r = -0.137$, $p = 0.564$	$r = 0.226$, $p = 0.339$
F2 (Hz)	$r = -0.064$, $p = 0.788$	$r = -0.043$, $p = 0.856$
F3 (Hz)	$r = -0.016$, $p = 0.946$	$r = -0.008$, $p = 0.975$
F4 (Hz)	$r = -0.163$, $p = 0.491$	$r = -0.136$, $p = 0.567$
dF (Hz)	$r = -0.161$, $p = 0.499$	$r = -0.236$, $p = 0.318$
f0 (Hz)	$r = -0.150$, $p = 0.528$	$r = -0.206$, $p = 0.383$
durat (s)	$r = 0.178$, $p = 0.453$	$r = 0.220$, $p = 0.351$
fpeak (Hz)	$r = -0.010$, $p = 0.966$	$r = 0.187$, $p = 0.430$
q25 (Hz)	$r = -0.225$, $p = 0,340$	$r = 0.182$, $p = 0.443$
q50 (Hz)	$r = -0.270$, $p = 0.250$	$r = -0.080$, $p = 0.738$
q75 (Hz)	$r = -0.161$, $p = 0.497$	$r = -0.129$, $p = 0.588$

n, number of animals; other designations as in Table 1.

Variable	Males	Females	Sex effect	Identity effect
F1 (Hz)	662 ± 98	745 ± 126	$F_{1,460} = 119.87$, $p < 0.001$	$F_{18,460} = 21.80$, $p < 0.001$
F2 (Hz)	1778 ± 233	2077 ± 267	$F_{1,460} = 352.41$, $p < 0.001$	$F_{18,460} = 30.82$, $p < 0.001$
F3 (Hz)	2745 ± 247	3019 ± 281	$F_{1,460} = 271.70$, $p < 0.001$	$F_{18,460} = 33.30$, $p < 0.001$
F4 (Hz)	3939 ± 225	4129 ± 300	$F_{1,460} = 155.40$, $p < 0.001$	$F_{18,460} = 43.70$, $p < 0.001$
dF (Hz)	1093 ± 68	1128 ± 74	$F_{1,460} = 55.60$, $p < 0.001$	$F_{18,460} = 26.70$, $p < 0.001$
f0 (Hz)	97 ± 13	104 ± 17	$F_{1,460} = 95.00$, $p < 0.001$	$F_{18,460} = 116.00$, $p < 0.001$
durat (s)	0.513 ± 0.140	0.501 ± 0.144	$F_{1,460} = 1.57$, $p = 0.211$	$F_{18,460} = 22.47$, $p < 0.001$
fpeak (Hz)	670 ± 575	908 ± 663	$F_{1,460} = 24.02$, $p < 0.001$	$F_{18,460} = 6.27$, $p < 0.001$
q25 (Hz)	592 ± 206	716 ± 228	$F_{1,460} = 61.95$, $p < 0.01$	$F_{18,460} = 16.28$, $p < 0.001$
q50 (Hz)	1501 ± 568	1842 ± 640	$F_{1,460} = 55.17$, $p < 0.001$	$F_{18,460} = 13.42$, $p < 0.001$
q75 (Hz)	3054 ± 877	3298 ± 718	$F_{1,460} = 14.67$, $p < 0.001$	$F_{18,460} = 12.89$, $p < 0.001$

Table 3: Comparison of oral calls (mean ± SD) between sexes and nested ANOVA results for the effects of caller sex and identity on the oral call variables

Identity nested into sex; identity included as random factor and sex as fixed factor. Designations as in Table 1.

Table 4: Comparison of nasal calls (mean ± SD) between sexes and nested ANOVA results for effects of a caller's sex and identity on the nasal call variables

Variable	Males	Females	Sex effect	Identity effect
F1 (Hz)	457 ± 80	478 ± 103	$F_{1,463} = 7.54$, p = 0.006	$F_{18,463} = 8.96$, p < 0.001
F2 (Hz)	1325 ± 173	1341 ± 140	$F_{1,463} = 2.10$, p = 0.148	$F_{18,463} = 12.57$, p < 0.001
F3 (Hz)	2580 ± 188	2757 ± 181	$F_{1,463} = 209.50$, p < 0.001	$F_{18,463} = 25.0$, p < 0.001
F4 (Hz)	3579 ± 194	3740 ± 214	$F_{1,463} = 157.90$, p < 0.001	$F_{18,463} = 31.10$, p < 0.001
dF (Hz)	1040 ± 66	1087 ± 63	$F_{1,463} = 108.70$, p < 0.001	$F_{18,463} = 19.70$, p < 0.001
f0 (Hz)	83 ± 10	87 ± 12	$F_{1,463} = 51.13$, p < 0.001	$F_{18,463} = 58.76$, p < 0.001
durat (s)	0.253 ± 0.113	0.251 ± 0.121	$F_{1,463} = 0.25$, p = 0.619	$F_{18,463} = 12.90$, p < 0.001
fpeak (Hz)	325 ± 81	326 ± 177	$F_{1,463} = 0.001$, p = 0.987	$F_{18,463} = 2.27$, p = 0.002
q25 (Hz)	369 ± 82	377 ± 74	$F_{1,463} = 1.69$, p = 0.194	$F_{18,463} = 6.88$, p < 0.001
q50 (Hz)	836 ± 474	925 ± 435	$F_{1,463} = 6.52$, p = 0.011	$F_{18,463} = 5.06$, p < 0.001
q75 (Hz)	2520 ± 796	2755 ± 758	$F_{1,463} = 16.97$, p < 0.001	$F_{18,463} = 9.06$, p < 0.001

Identity nested into sex; identity included as random factor and sex as fixed factor. Designations as in Table 1.

female calls. The effect of individual identity was significant for all variables, both in nasal and in oral calls (Tables 3 and 4). As the samples for the 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 all formant and power variables of the oral calls (Table 3) and for two formant and one power variable of the nasal calls, while one formant and one power variables of the nasal calls were stronger influenced by identity (Table 4). Both in oral and in nasal calls, the effect of the caller's identity on the duration prevailed over the effect of sex, whilst on the f0, both effects were similar (Tables 3 and 4).

Sex Discrimination with DFA

We conducted three DFAs for assignment to sex, with different sets of variables introduced into each analysis. The 1st DFA was based on nine variables (the 10th measured variable, fpeak, was excluded for not meeting the criterion of normality). The 2nd DFA was based only on four formant variables (F1–F4). The 3rd DFA was based on five remaining variables (f0, durat, q25, q50, q75). The 1st DFA showed the average values of correct assignment to sex of 74.0% for the oral calls and of 74.3% for the nasal calls. Jackknife cross-validation did not show a

decrease in correct assignment to sex, neither for the oral (73.5%) nor for the nasal calls (74.1%); the values of correct assignment were significantly higher (p < 0.01) than the random values (57.1% and 56.6%, respectively) and did not differ significantly between the nasal and oral calls ($\chi^2_1 = 0$, p = 0.96) (Fig. 5). In order of decreasing importance, the F2 and f0 were mainly responsible for discrimination of sex for the oral calls, and the F3, F4, q25 and q50 were mainly responsible for discrimination of sex for the nasal calls.

The 2nd DFA, with only four formant variables included, did not show any decrease in correct assignment to sex: of 74.0% for oral calls ($\chi^2_1 = 0$, p = 1), and of 72.3% for nasal calls ($\chi^2_1 = 0.43$, p = 0.51) (Fig. 5). In contrast, the 3rd DFA with only five (non-formant) variables included into it has resulted in significantly decreased value of correct assignment to sex both for oral (65.6% correct assignment; $\chi^2_1 = 7.51$, p = 0.006) and for nasal calls (61.3% correct assignment; $\chi^2_1 = 18.23$, p < 0.001) (Fig. 5).

Individual Discrimination with DFA

We conducted three DFAs for assignment to individual, with different sets of variables introduced into analyses. The 1st DFA, conducted on the base
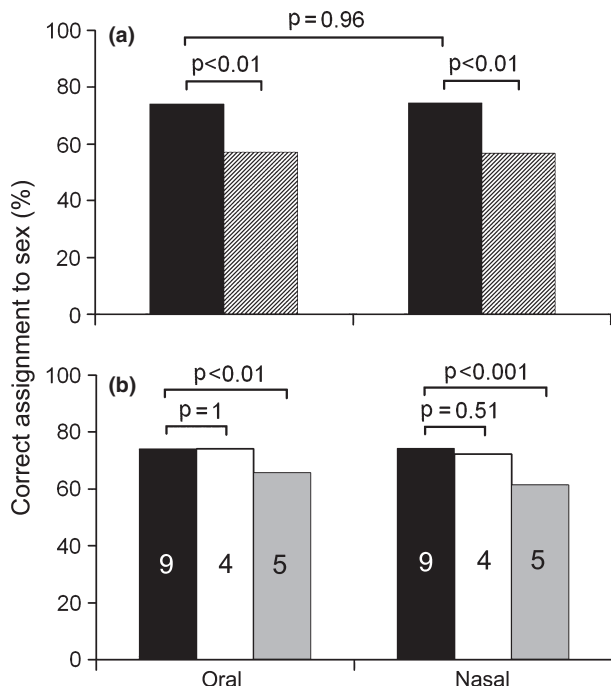
Fig. 5: Sex discrimination on the basis of oral and nasal call features. (a) Values of discriminant function analysis (DFA), based on nine acoustic variables (black bars) and random values, calculated with randomization procedure (grey bars). Comparisons between observed and random values and between oral and nasal calls with chi-squared test are shown by brackets above. (b) Values of three DFAs, based on 9, 4 and 5 acoustic variables, respectively. Comparisons between DFAs with chi-squared test are shown by brackets above.

Fig. 6: Individual discrimination on the basis of oral and nasal call features. (a) Values of discriminant function analysis (DFA), based on nine acoustic variables (black bars) and random values, calculated with randomization procedure (grey bars). Comparisons between observed and random values and between oral and nasal calls with chi-squared test are shown by brackets above. (b) Values of three DFAs, based on 9, 4 and 5 acoustic variables, respectively. Comparisons between DFAs with chi-squared test are shown by brackets above.

of 9 variables, showed 75.2% average value of correct assignment for the oral calls and 64.8% for the nasal calls. Jackknife cross-validation showed a slight decrease in correct assignment to individual both for the oral calls (68.1%) and for the nasal calls (57.1%). Both the values exceeded strongly and significantly the random values (13.0% and 13.2%, respectively, for the oral and nasal calls, $p < 0.01$ in both cases), but the value for the oral calls was significantly higher than the value for the nasal calls ($\chi^2_1 = 11.92$, $p < 0.001$, Fig. 6). Comparison of individual values of correct assignment to individual with repeated measures ANOVA revealed a significantly higher individuality encoded in the oral calls when compared to the nasal calls ($F_{1,19} = 6.82$, $p = 0.017$). In order of decreasing importance, the f0, F4, F2 and F3 were mainly responsible for discrimination of individual for the oral calls, and the f0, F3, F4 and F2 were mainly responsible for discrimination of individual for the nasal calls.

The 2nd DFA, with only 4 formant variables included, showed the strong and significant decrease
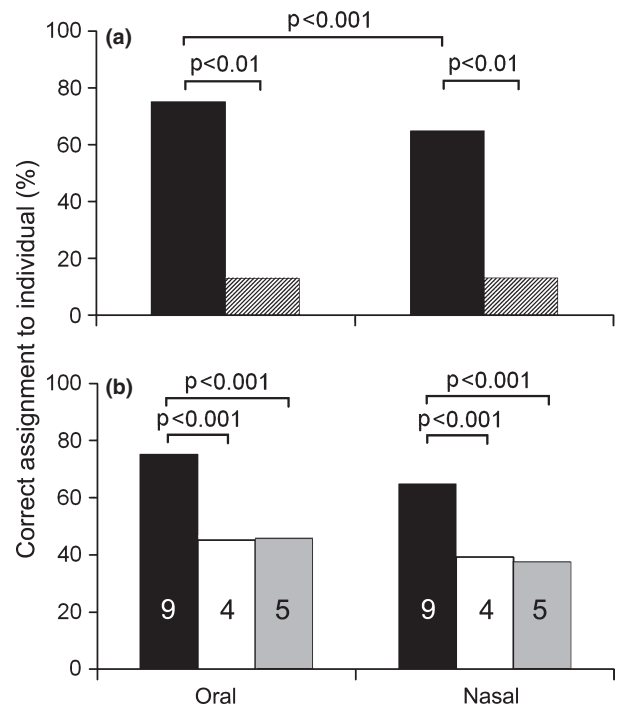
in the value of correct assignment to individual both for the oral ($\chi^2_1 = 88.91$, $p < 0.001$) and for the nasal calls ($\chi^2_1 = 61.74$, $p < 0.001$) (Fig. 6). The 3rd DFA with only 5 (non-formant) variables included has also showed the strong and significant decrease in the value of correct assignment to individual both for the oral ($\chi^2_1 = 85.45$, $p < 0.001$) and for the nasal calls ($\chi^2_1 = 71.10$, $p < 0.001$) (Fig. 6). Both 2nd and 3rd DFAs showed very similar values of correct assignment to individual for the oral calls (45.2 and 45.8%, $\chi^2_1 = 0.02$, $p = 0.897$) and for the nasal calls (39.3 and 37.5%, $\chi^2_1 = 0.28$, $p = 0.597$).

Discussion

In juvenile goitred gazelles, we found that the mean values of all acoustic variables were higher in oral calls than in nasal calls. No correlation was found between body mass and acoustic features. Discriminant function analysis revealed an equally high potential of oral and nasal calls to encode sex, whereas individuals were discriminated significantly

more reliable with oral calls. Sex identity was encoded exclusively in formant frequencies, whilst individual identity was encoded in a combination of all investigated acoustic variables.

Controlling for caller's sex and identity, analyses revealed higher values in all variables of the oral calls compared to the nasal calls. Nasal calls, produced through the relatively longer vocal tract, showed lower and more closely spaced formants than oral calls did. This is in accordance with the source-filter theory, which predicts an inverse relation between formants and vocal tract length (Fant 1960; Titze 1994; Fitch & Reby 2001; Fitch & Hauser 2002). At the same time, the findings of non-equal distances between two subsequent call formants indicate a non-uniform vocal tract.

In juvenile goitred gazelles, we found a strongly and significantly higher fundamental frequency in the oral calls when compared to nasal calls. These data are consistent with findings of higher f0 values in oral than in nasal calls in a single juvenile female saiga (Volodin et al. 2009) and in adult ewes (Sebe et al. 2010). As the source-filter theory predicts independent effects of the larynx and of the vocal tract on vocal output, a shortening of the vocal tract by opening of the mouth affects only formants, but not the fundamental frequency (Fant 1960; review in Taylor & Reby 2010). The current finding of a higher fundamental frequency in oral calls than in nasal calls can be explained by slight laryngeal lowering for production of oral calls resulting in loss of contact between epiglottis and soft palate (Fitch 2000b). During nasal calls of juvenile goitred gazelles, the larynx appears not to be pronouncedly lowered, so that the epiglottis and laryngeal entrance still protrude into the nasopharynx, thereby retaining the typical breathing position of the larynx in non-human mammals and in human newborns (Laitman et al. 1977; Laitman & Reidenberg 1993; Crompton et al. 1997; Davidson 2003). For the production of oral calls, the juvenile goitred gazelle lowers the larynx and is assumed to simultaneously raise the soft palate and bulge the dorsal pharyngeal wall rostrally, thereby closing off the nasal airway, to guarantee a complete emission of the phonatory air stream through the mouth. The lowering or slight momentary descent of the larynx for phonation has been demonstrated for a carnivore (the domestic dog, *Canis familiaris*), a New World primate (the cotton-top tamarin, *Saguinus oedipus*), a non-ruminating herbivore (the domestic pig, *Sus scrofa*), a ruminant herbivore (the domestic goat) and newborn humans (Fitch 2000b; Davidson 2003).

Laryngeal lowering, mostly effected by the sternothyroid and sternohyoid muscles, produces ventro-caudal tilting of the larynx, bending and dilation of the trachea and an increase in subglottic pressure (Sonninen 1968; Hong et al. 1997). In addition, tilting of the entire larynx involves rotation of the thyroid cartilage relative to the cricoid cartilage (pivoting around the cricothyroid joint) and entails a shortening of the cricothyroid distance (Hong et al. 1997). As the vocal fold is attached on one end to the dorsal surface of the thyroid cartilage prominence and on the other end to the vocal process of the arytenoid cartilage, which articulates with the cricoid cartilage (Titze 1994; Harrison 1995), such rotation movement should create additional tension and thinning of the vocal folds and may result in a higher f0 of oral calls than of nasal calls. Besides, shortening of the cricothyroid distance as a result of sternothyroid and sternohyoid muscle contraction may be accompanied by adjusting contraction of the cricothyroid muscle, thereby contributing to the raising of f0 (cf. Sonninen 1956; Vilkman et al. 1996). The rotational movement of the thyroid cartilage, lengthening of the vocal fold and raising of f0 after stimulation of the sternothyroid and sternohyoid muscles have been experimentally demonstrated to occur in domestic dogs (Hong et al. 1997). A rise of f0 after experimental stimulation of the sternothyroid muscle has also been reported for rhesus macaques (*Macaca mulatta*) (Sapir et al. 1981).

Although in our study of juvenile goitred gazelles body mass was higher in males, the differences between sexes were non-significant, and no correlation was found between body mass and any acoustic variable. Similar findings are reported for juvenile white-tailed deer and for mule deer (*Odocoileus virginianus*), in which no relation was found between body mass and the fundamental frequency (Lingle et al. 2007a), although an earlier study on juvenile white-tailed deer had revealed such a relationship (Richardson et al. 1983). Nevertheless, we found that juvenile male goitred gazelles had lower fundamental and formant frequencies than females. These sex-related differences can be explained partly by a noticeable sex dimorphism in the size of vocal folds, and by anatomical differences of the vocal tract in juvenile goitred gazelles. We suggest therefore that the sexual dimorphism in larynx size and vocal tract length that is well expressed in adult polygynous ruminants may arise already early in ontogenesis (Fitch & Reby 2001; McElligott et al. 2006; Frey et al. 2008a).

As a mammalian larynx grows independently from the rest of body (Fitch & Hauser 2002), correlation between body mass and fundamental frequency is commonly not found for mammals (e.g. Lass & Brown 1978; McComb 1991; Collins 2000; Rendall et al. 2005; Tanaka et al. 2006; Matrosova et al. 2007). At the same time, the size of the vocal tract is predetermined by bone structures of the skull, what results in a relationship between body mass and formants (Fitch & Hauser 2002). Between the formant dispersion and body mass, an inverse relationship has been reported for rhesus macaques (Fitch 1997), domestic dogs (Riede & Fitch 1999), red deer (Reby & McComb 2003), black and white colobus monkey (*Colobus guereza*) (Harris et al. 2006) and giant panda (*Ailuropoda melanoleuca*) (Charlton et al. 2009). Furthermore, an inverse relationship between formant dispersion and body length has been reported for southern elephant seals (*Mirounga leonina*) (Sanvito et al. 2007), fallow deer (Vannoni & McElligott 2008) and humans (Fitch & Giedd 1999; Rendall et al. 2005). Except for humans, all these studies had been made with adult subjects. In contrast, the current study was carried out with juvenile subjects. In addition to the non-uniform vocal tract geometry, it could be responsible for a lack of correlation between formants and body mass.

We found that both oral and nasal calls were individually and sexually distinctive in juvenile goitred gazelles. However, classification to individual and to sex was based on different sets of variables. Both ANOVA and DFA showed that the cues to sex were exclusively based on formants. The DFA, based only on four formant variables, classified calls to sex as accurate as the DFA based on all nine variables. On the one hand, this result was expected, because in males, all formant frequencies were significantly lower than those of females. On the other hand, this was unexpected, because a significant difference between sexes was also found in the fundamental frequency. However, the exclusion of the fundamental frequency from the variables introduced into DFA did not result in poorer discrimination. To our knowledge, there are no other studies on ruminants, providing data of classifying calls to sex with DFA. However, for juvenile fallow and mule deer (but not for white-tailed deer), the lower values of fundamental frequency in males than in females have been reported (Torriani et al. 2006; Lingle et al. 2007a). Comparative data on other species are necessary to investigate the relationship between source- and filter-related acoustics (cf. fundamental frequency vs. formant frequencies) and sex in other juvenile ruminants.

In contrast to the findings with respect to the sex of the caller, the individual identity of juvenile goitred gazelles was encoded both in the source- and in the filter-related acoustic features, i.e. in a combination of formants, fundamental frequency, temporal and power variables. Similar outcomes, based on analyses of fundamental frequency and formants, have been reported for juveniles, for adult males and for adult females in fallow deer (Torriani et al. 2006; Vannoni & McElligott 2007; Briefer et al. 2010) and for juvenile reindeer (Espmark 1975). However, in juvenile fallow deer, the reported value of correct classification to individual (32.1% for 12 juveniles, Torriani et al. 2006) was nearly two times lower than those obtained in our study for the 20 juvenile goitred gazelles. Nevertheless, studies in which only the fundamental frequency variables and the duration were used for individual discrimination with DFA report values of correct classification that are comparable with our data for juvenile goitred gazelles: 73% for 10 juvenile white-tailed deer (Richardson et al. 1983); 70% for 10 juvenile white-tailed deer (Lingle et al. 2007a), 66% for 16 juvenile mule deer (Lingle et al. 2007a) and 68% for 13 juvenile domestic goats (Terrazas et al. 2003).

The oral calls of juvenile goitred gazelles encoded caller identity better than the nasal calls. The oral calls were louder, as their vocal energy is not absorbed by the nasal epithelium (Fitch 2000b). Oral calls represent over 50% of the vocal emissions in goitred gazelles younger than 4 wk, when they are dependent on their mothers, but disappear at 6 mo, when adolescents become independent (Efremova et al. 2011). Louder and more individualistic oral calls should be more effective in rejoining mothers and young, but their production enhances the risk of predation, making the caller more noticeable. We assume that juvenile goitred gazelles appear to benefit from varying the ratio of production of the oral and nasal calls according to a trade-off between the risk of predation and the need of parental care. In non-passerine birds, similar adjustments of the caller's vocal identity in accordance with the chicks' needs of parental care were found in red-crowned cranes (*Grus japonensis*) (Klenova et al. 2009).

Both oral and nasal calls of juvenile goitred gazelles may serve for individual identification of callers by their mothers. Our study covered the period when juveniles leave their natal territories and start following their mothers, sometimes in temporal groups of a few mother–offspring units (Soldatova

1983). Therefore, females lose the spatial landmarks, which may increase the risk of confusing their own young and for unrelated ones. High vocal distinctiveness may promote individual recognition of young by their mothers (Torriani et al. 2006), although this does not automatically mean that mother goitred gazelles will respond selectively to vocalizations of their offspring. Such selectiveness occurs in domestic sheep (Shillito-Walser et al. 1981; Sebe et al. 2008), reindeer (Espmark 1971), domestic goats (Terrazas et al. 2003), domestic sows (Weary et al. 1996) and white-tailed deer (Lingle et al. 2007b). In contrast, mule deer hinds respond equally strongly to calls of any juvenile, as costs of the loss of their own calf from predation exceed the time and energy costs for defending non-relatives (Lingle et al. 2007b). Consistently, a few days post-partum, red deer and goitred gazelles approach in response to even imperfect imitations of juvenile calls by humans (Vankova et al. 1997; own personal observations), probably because the females have not learned the individual characteristics of their young yet (Soldatova 1983; Jevnerov 1984). As they keep territories, where their offspring are hidden, they can use spatial cues for their identification, similarly to fallow deer (Vannoni et al. 2005; Torriani et al. 2006), some pinnipeds (review Insley et al. 2003) and birds (e.g. Jouventin & Aubin 2002) and use a strategy of active defence of predators, similarly to mule deer (Lingle et al. 2007b). Newborn goitred gazelles may be predated by red foxes (*Vulpes vulpes*), steppe cats (*Felis libyca*) or jackals (*Canis aureus*), which are not dangerous to adults. Potential time delays in an anti-predatory response based on individual recognition may be fatal for the young and more costly, in terms of reproductive success, when compared to the loss of time for responding to calls of unrelated offspring (Lingle et al. 2007a,b). Further research of mother–offspring interactions in the goitred gazelle is necessary to clear these questions.

Acknowledgements

Literature Cited

Blank, D. A. 1985: Peculiarities of social and reproductive behaviour of *Gazella subgutturosa* in the Iliisky valley. Zool. Zhurnal **64**, 1059—1070. [in Russian].

Blank, D. A. 1998: Mating behavior of the Persian Gazelle *Gazella subgutturosa* Güldenstaedt 1780. Mammalia **62**, 499—519.

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

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

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

Charlton, B. D., Zhihe, Z. & Snyder, R. J. 2009: Giant panda perceive and attend to formant frequency variation in male bleats. Anim. Behav. **78**, 893—898.

Collins, S. A. 2000: Men's voices and women's choices. Anim. Behav. **60**, 773—780.

Crompton, A. W., German, R. Z. & Thexton, A. J. 1997: Mechanisms of swallowing and airway protection in infant mammals (*Sus domesticus* and *Macaca fascicularis*). J. Zool. **241**, 89—102.

Davidson, T. M. 2003: The great leap forward: the anatomic basis for the acquisition of speech and obstructive sleep apnea. Sleep Med. **4**, 185—194.

Efremova, K. O., Volodin, I. A., Volodina, E. V., Frey, R., Soldatova, N. V., Lapshina, E. N., Makarov, I. S. & Gorbunov, K. S. 2011: Sex and age effects on the structural features of nasal calls and body size in the goitred gazelle (*Gazella subgutturosa*, Artiodactyla, Bovidae) calves. Zool. Zhurnal **90**, 551—563. [in Russian].

Espmark, Y. 1971: Individual recognition by voice in reindeer mother-young relationship. Behaviour **40**, 295—301.

Espmark, Y. 1975: Individual characteristics in the calls of reindeer calves. Behaviour **54**, 50—59.

Fant, G. 1960: Acoustic Theory of Speech Production. The Hague, Mouton.

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. 2000a: The evolution of speech: a comparative review. Trends Cog. Sci. **4**, 258—267.

Fitch, W. T. 2000b: The phonetic potential of nonhuman vocal tracts: comparative cineradiographic observations of vocalizing animals. Phonetica **57**, 205—218.

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: Acoustic Communication. Springer Handbook of Auditory Research (Simmons, A., Fay, R. R. & Popper, A. N., eds). Springer, Berlin, 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., Volodin, I. & Volodina, E. 2007: A nose that roars: anatomical specializations and behavioural features of rutting male saiga. J. Anat. **211**, 717—736.

Frey, R., Gebler, A., Olson, K. A., Odonkhuu, D., Fritsch, G., Batsaikhan, N. & Stuermer, I. W. 2008a: Mobile larynx in Mongolian gazelle: retraction of the larynx during rutting barks in male Mongolian gazelle (*Procapra gutturosa* Pallas, 1777). J. Morph. **269**, 1223—1237.

Frey, R., Gebler, A., Olson, K. A., Odonkhuu, D., Fritsch, G., Batsaikhan, N. & Stuermer, I. W. 2008b: Head anatomy of male and female Mongolian gazelle – a striking example of sexual dimorphism. In: Anatomical Imaging – Towards a New Morphology (Endo, H. & Frey, R., eds). Springer, Tokyo, pp. 1—13.

Güldenstaedt, A. I. 1780: *Antilope subgutturosa* descripta. Acta Academiae Scientiarum Imperialis Petropolitanae. Petropoli, **11**, 251—274. Part 1 (1778) Plts. IX–XII.

Harris, T. R., Fitch, W. T., Goldstein, L. M. & Fashing, P. J. 2006: Black and white colobus monkey (*Colobus guereza*) roars as a source of both honest and exaggerated information about body mass. Ethology **112**, 911—920.

Harrison, D. F. N. 1995: The Anatomy and Physiology of the Mammalian Larynx. Cambridge Univ. Press, Cambridge.

Hong, K. H., Ye, M., Kim, T. M., Kevorkian, K. F. & Berke, G. S. 1997: The role of strap muscles in phonation – in vivo canine laryngeal model. J. Voice **11**, 23—32.

Insley, S. J., Phillips, A. V. & Charrier, I. 2003: A review of social recognition in pinnipeds. Aquatic Mamm. **29**, 181—201.

Jevnerov, V. V. 1984: Goitred gazelles of Barsakelmes Island. Alma-Ata. Nauka. p. 145 [in Russian].

Jouventin, P. & Aubin, T. 2002: Acoustic systems are adapted to breeding ecologies: individual recognition in nesting penguins. Anim. Behav. **64**, 747—757.

Kingswood, S. C. & Blank, D. A. 1996: *Gazella subgutturosa*. Mammalian Species **518**, 1—10.

Klenova, A. V., Volodin, I. A. & Volodina, E. V. 2008: Duet structure provides information about pair identity in the red-crowned crane (*Grus japonensis*). J. Ethol. **26**, 317—325.

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.

Laitman, J. T. & Reidenberg, J. S. 1993: Specializations of the human upper respiratory and upper digestive systems as seen through comparative and developmental anatomy. Dysphagia **8**, 318—325.

Laitman, J. T., Crelin, E. S. & Conlogue, G. J. 1977: The function of the epiglottis in monkey and man. Yale J. Biol. Med. **50**, 43—48.

Lass, N. J. & Brown, W. S. 1978: Correlational study of speakers heights, weights, body surface areas and speaking fundamental frequencies. J. Acoust. Soc. Am. **63**, 1218—1220.

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

Lingle, S., Rendall, D., Wilson, W. F., Deyoung, R. W. & Pellis, S. M. 2007b: Altruism and recognition in the antipredator defence of deer: 2. Why mule deer help non-offspring fawns. Anim. Behav. **73**, 907—916.

Marmasinskaya, N. V. 1996a: Territorial and marking behaviour of the goitred gazelle *Gazella subgutturosa* (Artiodactyla, Bovidae) in Bukhara breeding centre. Zool. Zhurnal **75**, 1737—1751 [in Russian].

Marmasinskaya, N. V. 1996b: Reproduction of goitred gazelles *Gazella subgutturosa* (Artiodactyla, Bovidae) in Bukhara breeding centre. In: Proc. Natural Reserves of Uzbekistan (Azimov, D. A., ed). Fan, Tashkent, pp. 53—62. [in Russian].

Marmasinskaya, N. V. 2008: Mother-offspring interactions in the goitred gazelle *Gazella subgutturosa* Guldenstaedt, 1780. In: Proc. Natural Reserves of Uzbekistan (Azimov, D. A., & Vashetko, E. V., eds). State Committee of Nature of Uzbekistan, Tashkent, pp. 84—102 [in Russian].

Matrosova, V. A., Volodin, I. A. Volodina, E. V. & Babitsky, A. F. 2007: Pups crying bass: vocal adaptation for avoidance of age-dependent predation risk in ground squirrels? Behav. Ecol. Sociobiol. **62**, 181—191.

Matrosova, V. A., Volodin, I. A., Volodina, E. V., Vasilieva, N. A. & Kochetkova, A. A. 2010: Between-year stability of individual alarm calls in the yellow ground squirrel *Spermophilus fulvus*. J. Mammal. **91**, 620—627.

McComb, K. E. 1991: Female choice for high roaring rates in red deer, *Cervus elaphus*. Anim. Behav. **41**, 79—88.

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.

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.

Pereladova, O. B. & Pereladov, S. V. 1986: Reproduction of goitred gazelles in enclosures of Sunt-Hasargag Natural Reserve. In: Protection and Perspectives of Restoring Population of Goitred Gazelles in USSR (Flint, V. E., Ed.). VNIIPriroda, Moscow, pp. 49—59 [in Russian].

Pereladova, O. B., Bahloul, K., Sempere, A. J., Soldatova, N. V., Schadilov, U. M. & Prisiadznuk, V. E. 1998: Influence of environmental factors on a population of goitred gazelles (*Gazella subgutturosa subgutturosa* Guldenstaedt, 1780) in semi-wild conditions in an arid environment: a preliminary study. J. Arid Environ. **39**, 577—591.

Reby, D. & McComb, K. 2003: Anatomical constraints generate honesty: acoustic cues to age and weight in the roars of red deer stags. Anim. Behav. **65**, 519—530.

Reby, D., McComb, K., Cargnelutti, B., Darwin, C. J., Fitch, W. T. & Clutton-Brock, T. H. 2005: Red deer stags use formants as assessment cues during intrasexual agonistic interactions. Proc. Roy. Soc. Lond. B **272**, 941—947.

Rendall, D., Kollias, S., Ney, C. & Lloyd, P. 2005: Pitch (F0) and formant profiles of human vowels and vowel-like baboon grants: the role of vocalizer body size and voice-acoustic allometry. J. Acoust. Soc. Am. **117**, 944—955.

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.

Sanvito, S., Galimberti, P. & Miller, E. H. 2007: Vocal signalling of male southern elephant seals is honest but imprecise. Anim. Behav. **73**, 287—299.

Sapir, S., Larson, C. & Campbell, C. 1981: Effect of geniohyoid, cricothyroid and sternothyroid muscle stimulation on voice fundamental frequency of electrically elicited phonation in rhesus macaque. Laryngoscope **91**, 457—468.

Searby, A. & Jouventin, P. 2003: Mother-lamb acoustic recognition in sheep: a frequency coding. Proc. Roy. Soc. Lond. B **270**, 1765—1771.

Sebe, F., Aubin, T., Boué, A. & Poindron, P. 2008: Mother-young vocal communication and acoustic recognition promote preferential nursing in sheeps. J. Exp. Biol. **211**, 3554—3562.

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.

Shillito-Walser, E. E., Hague, P. & Walters, E. 1981: Vocal recognition of recorded lambs' voices by ewes of three breeds. Behaviour **78**, 260—272.

Soldatova, N. V. 1983: To behaviour of goitred gazelles Bukhara breeding centre. In: Ecology of Plants and Animals of Natural Reserves of Uzbekistan (Flint, V. E., ed). Fan, Tashkent, pp. 86—90 [in Russian].

Soldatova, N., Juldashev, E., Volodin, I., Volodina, E., Efremova, K. & Lapshina, E. 2010: Keeping, raising and body mass dynamics of the goitred gazelle calves (*Gazella subgutturosa*) in captivity. Sci. Res. Zoo. Parks **26**, 64—71 [in Russian].

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

Sonninen, A. A. 1956: The role of the external laryngeal muscles in length-adjustment of the vocal cords in singing. Acta Otolaryngol. Suppl. **130**, 1—102.

Sonninen, A. A. 1968: The external frame function in the control of pitch in the human voice. Ann. N Y Acad. Sci. **155**, 68—90.

Tanaka, T., Sugiura, H. & Masataka, N. 2006: Cross-sectional and longitudinal studies of the development of group differences in acoustic features of coo calls in two groups of Japanese macaques. Ethology **112**, 7—21.

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.

Torriani, M. V. G., Vannoni, E. & McElligott, A. G. 2006: Mother-young recognition in an ungulate hider species: a unidirectional process. Amer. Nat. **168**, 412—420.

Vankova, D. & Malek, J. 1997: Characteristics of the vocalizations of red deer *Cervus elaphus* hinds and calves. Bioacoustics **7**, 281—289.

Vankova, D., Bartos, L. & Malek, J. 1997: The role of vocalisations in the communication between red deer hinds and calves. Ethology **103**, 795—808.

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.

Vannoni, E. & McElligott, A. G. 2008: Low frequency groans indicate larger and more dominant fallow deer (*Dama dama*) males. PLoS ONE **3**(9), e3113. DOI: 10.1371/journal.pone.0003113.

Vannoni, E., Torriani, M. V. G. & McElligott, A. G. 2005: Acoustic signaling in Cervids: a methodological approach for measuring vocal communication in fallow deer. Cogn. Brain Behav. **9**, 551—566.

Vilkman, E., Sonninen, A., Hurme, P. & Körkkö, P. 1996: External laryngeal frame function in voice production revisited: a review. J. Voice **10**, 78—92.

Volodin, I. A., Volodina, E. V. & Efremova, K. O. 2009: Antelope, calling through the nose: structure of sounds and effect of sexual selection on the vocal behavior of the saiga (*Saiga tatarica*). Zool. Zhurnal **88**, 113—124 [in Russian].

Walther, F. R., Mungall, E. C. & Grau, G. A. 1983: Gazelles and their Relatives. A Study in Territorial Behaviour. Noyes Publ., Park Ride, NJ, USA.

Weary, D. M., Lawson, G. L. & Thompson, B. K. 1996: Sows show stronger responses to isolation calls of piglets associated with greater levels of piglet need. Anim. Behav. **52**, 1247—1253.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Audio S1. Four nasal calls and four oral calls (one per individual) produced by juvenile goitred gazelles of 3–4 wk of age.

Please note: Wiley-Blackwell are not responsible for the content or functionality of any supporting materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.