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ORIGINAL PAPER

Developmental changes of nasal and oral calls in the goitred gazelle *Gazella subgutturosa*, a nonhuman mammal with a sexually dimorphic and descended larynx

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Abstract In goitred gazelles (*Gazella subgutturosa*), sexual dimorphism of larynx size and position is reminiscent of the case in humans, suggesting shared features of vocal ontogenesis in both species. This study investigates the ontogeny of nasal and oral calls in 23 (10 male and 13 female) individually identified goitred gazelles from shortly after birth up to adolescence. The fundamental frequency (f0) and formants were measured as the acoustic correlates of the developing sexual dimorphism. Settings for LPC analysis of formants were based on anatomical dissections of 5 specimens. Along ontogenesis, compared to females, male f0 was consistently lower both in oral and nasal calls and male formants were lower in oral calls, whereas the first two formants of nasal calls did not differ between sexes. In goitred gazelles, significant sex differences in f0 and formants appeared as early as the second week of life, while in humans they emerge only before puberty. This result suggests different pathways of vocal ontogenesis in the goitred gazelles and in humans.

Keywords Vocalization · Ontogenesis · Sexual dimorphism · Formants · Fundamental frequency · *Gazella subgutturosa*

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Introduction

In two polygynous gazelles, the Mongolian (*Procapra gutturosa*) and the goitred gazelle (*Gazella subgutturosa*), the male larynx is much larger and more pronouncedly descended than in females (Frey and Gebler 2003; Frey and Riede 2003; Frey et al. 2008, 2011). The descended larynx was also reported for red deer (*Cervus elaphus*) and fallow deer (*Dama dama*) (Fitch and Reby 2001). Combined occurrence of an enlarged and descended larynx has been reported for adult humans (Negus 1949; Fitch 2000a;

Rendall et al. 2005) but was not found in newborns, neither in humans (Negus 1949; Fitch and Giedd 1999; Fitch 2000a) nor in the gazelles (Efremova et al. 2011).

In humans, sexual dimorphism in larynx size and position results in a lower fundamental frequency (f0) and lower formant frequencies in male voices compared to female voices (Fitch and Giedd 1999; Lee et al. 1999; Rendall et al. 2005). According to the source-filter theory of voice production, the f0 of mammalian vocalizations is generated by vibrations of the vocal folds ("source") and is subsequently filtered by the vocal tract ("filter"), selectively accentuating and attenuating certain frequencies, formants and anti-resonances respectively (Fant 1960; Titze 1994; Taylor and Reby 2010). In humans, the f0 is inversely related to mass and length of the oscillating portions of the vocal folds (Titze 1994). In cervids, the f0 is also related to the species-specific viscoelasticity of the vocal folds (Riede et al. 2010). In bovids, such as takins (*Budorcas taxicolor*), saigas (*Saiga tatarica*) and goitred gazelles, the very low f0 values are probably related to the presence of connective tissue pads on their vocal folds (Frey and Hofmann 2000; Frey et al. 2007, 2011).

Formant frequencies are inversely related to the vocal tract length (VTL) (Titze 1994; Fitch and Reby 2001; Fitch and Hauser 2002). The nasal VTL is always longer than the oral VTL (Frey et al. 2007; Volodin et al. 2011). In goitred gazelles at 3–6 weeks of age, consistently lower and more closely spaced formants were found in nasal compared to oral calls (Volodin et al. 2011). At the same time, in a previous cross-sectional study we found that sex of 3–6-week goitred gazelles was encoded in formants of their oral and nasal calls (Volodin et al. 2011). So, we expected to find sex-specific differences in formants along ontogenesis of goitred gazelles.

Among nonhuman primates, a slight descent of the larynx in early ontogenesis of chimpanzees (*Pan troglodytes*) and Japanese macaques (*Macaca fuscata*) did not result in sexual dimorphism in position of the larynx (Nishimura et al. 2006, 2008). In humans, the larynx descends from 3 months to approximately 3 years of age (Negus 1949; Lieberman 1984; Fitch and Giedd 1999; Fitch 2000a). This early ontogenetic descent of the larynx is not sex-specific and is sufficient for providing the speaking ability to both sexes (Lieberman 1973, 1984; Fitch and Giedd 1999; Fitch 2000a). The late ontogenetic descent of the larynx of humans is male-specific. Only in boys at puberty the larynx additionally enlarges and further descends by 10–15 mm, creating the "Adam's apple" (Fitch and Giedd 1999). After this ontogenetic stage, the male voice acquires its masculine features, the low f0 and formants (Lee et al. 1999). The concomitant to this stage abrupt decrease of voice, so-called "voice breaking", was not reported to date for any mammal besides humans, although it is found in some non-passerine birds (Radford 2004; Klenova et al. 2010). The goitred gazelle, a nonhuman mammal with a sexually dimorphic and descended larynx, may be a good candidate species for such pathway of vocal ontogenesis.

In adult male goitred gazelles, rutting vocalizations—roars, growls and grunts—represent an essential component of the rutting display (Frey et al. 2011), while adult females vocalize postpartum and during the nursing period (Jevnerov 1984; Kingswood and Blank 1996; Blank 1998). In nature, young males become interested in females by the age of 6 months. At this time they do not display any distinct posture; however, they do begin to follow females, often their own mothers, and sniff their hindquarters. Females respond to them just as they do to mature males, by raising their tails and walking away. Displaying characteristic mating postures begins when males are 1 year, and in 2-year-old males sexual behavior is similar to that of 3–6-year-old mature males. However, these young males are not involved in the rut, do not have territories of their own and are driven away from the females by the territorial males. Only during the third or even fourth year of life a male can succeed in getting control over his own territory and starting to mate. More than one-fourth of the yearling females participate in the rut by the age of 7 months, under favorable conditions, while in the following year all females become involved in breeding. Young females respond to courting males similarly as mature females and as a rule, give birth to one infant (Blank 1998).

Juvenile goitred gazelles (both males and females) regularly produce oral and nasal calls (Volodin et al. 2011), whereas adolescents of both sexes produce only nasal calls (Efremova et al. 2011). All sex and age classes of goitred gazelles produce also snorts (Fig. 1, Online Resource 1). However, the acoustic characteristics of snorts and proportions of different call types among age classes have not yet been studied to date. In a preceding study (Efremova et al. 2011), we compared age-related changes in duration, f0, maximum amplitude frequency and three

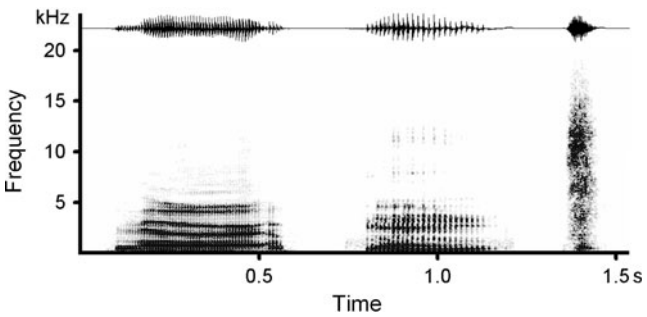

Fig. 1 Waveform (*above*) and spectrogram (*below*) of an oral call, nasal call and snort of juvenile goitred gazelles (Online Resource 1). The spectrogram settings: sampling frequency 48 kHz, Hamming window, FFT 1024, frame 50%, overlap 93.75%

power quartiles in nasal calls with the ontogenetic increase of neck circumferences over the larynx. In this study, we (1) investigate anatomically the vocal folds and the vocal tract (VT) of five specimens, (2) compare the acoustics of nasal and oral calls and snorts and analyze the occurrence of these three call types in nine age classes across the 6-month ontogenetic period and (3) investigate the changing f0, formants and duration of nasal and oral calls of goitred gazelles from shortly after birth until the animals are 6 months old.

Materials and methods

Subjects, site and dates of work

The study was conducted in the Ecocenter "Djeiran" (Uzbekistan, Bukhara region; for study site details see Volodin et al. (2011)). Subjects were 23 (10 male, 13 female) goitred gazelles, captured on a fenced 5145 ha area of semidesert between April 29 and May 12, 2008 at an age estimated to be 1 to 8 days postpartum (by size, body mass and the state of the umbilical cord) and then hand-raised for conservation purposes. Differences in age among subjects did not exceed 7 days. An earlier date of capture indicated a younger age. Precision of expert estimation of age was about 2 days. We took the date May 2 as a common conditional date of birth for all of the calves.

The calves were individually marked with *p*-phenylenediamine (Rhodia, Paris, France) and with ear-tag. The animals were kept in groups of 5–7 individuals in a few enclosures of 2×4 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 25×18 m, where all the 23 individuals walked together during the day. The animals were fed three or two times a day, depending on the age (for keeping details, see Volodin et al. (2011)). Calls were recorded between May 8 and Aug 28, 2008 from all the 23 subjects and between Oct 17 and Oct 28, 2008 from 18 of the 23 (7 male, 11 female) subjects (5 were transferred to another place).

Data collection

On a typical day, one or two researchers recorded calls and video 30–120 min before the morning or evening feeding. 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 varied from 1 to 5 m. The calls of the focal animal were labeled on the recorder by voice. For acoustic recordings (48 kHz, 16 bit resolution), we used Marantz PMD660 (D&M Professional, Kanagawa, Japan) and Zoom-H4 (Zoom Corp., Tokyo, Japan) digital recorders with Sennheiser K6-ME64 and Sennheiser K6-ME66 cardioid electret condenser microphones (Sennheiser electronic, Wedemark, Germany). Of a total of 100 h of audio recordings, 19 h were made with synchronous video, using a miniDV Panasonic NV-GS250 camcorder (Panasonic Corp., Kadoma, Japan). Weight measures (10-g precision, Kern De 36K10N scales, Kern & Sohn GmbH, Balingen-Frommern, Germany), were taken every 2 weeks between May 15 and Aug 20 and on Oct 19, 2008, for all subjects on the same days.

Call samples

We chronologically subdivided acoustic recordings into 9 age classes of 1–2, 3–4, 5–6, 7–8, 9–10, 11–12, 13–14, 15–16 and 23–24 weeks. Age classes included calls recorded during a week before and during a week after the weightings, taken at 2, 4, 6, 8, 10, 12, 14, 16 and 24 weeks of age. This provided matched data on the acoustics and body mass along development of each individual. For acoustic analyses, we selected calls of good quality, not broken by wind and non-overlapped by noise or human voice. To reduce pseudoreplications, we took calls from different recording sessions per animal and from different parts within session. Nasal and oral calls differ strongly from snorts by sound. Also calls produced through the nose or through the mouth differed strongly by energy distribution (Volodin et al. 2011), and nasal calls had a specific "nasal" quality of sounding (Fig. 1, Online Resource 1).

A total of 29884 calls (21375 nasal calls, 7758 oral calls, 851 snorts) were identified as produced by particular individual callers. Then three analyses were conducted. First, to describe the acoustics of nasal, oral and snort call types, we used a sample of 2 age classes, of 3–4 weeks and of 5–6 weeks of age, taking 1–5 calls (mean±SE=4.53±0.25) per animal per call type, 290 calls in total. Second, to analyze percentages of nasal calls, oral calls and snorts in each age class, we used a sample of 9 age classes. We took up to 100 calls per animal per age class (irrespective of the call type), ordered chronologically and then selected randomly (all calls when ≤100 calls were available, each third when 300 calls were available, each fifth when 500 calls were available, etc.), 1447–2291 calls per age class (8031 male, 8912 female), 16943 calls in total. Third, to analyze the ontogeny of f0, formants and durations, we used a sample of 9 age classes, 1–10 nasal (mean±SE=6.69±0.13) and 1–10 oral calls (mean±SE=5.31±0.23) per animal per age class, 849 oral (412 male, 437 female) and 1318 nasal calls (583 male, 735 female), 2167 calls in total. Only calls with clearly traceable formants were included into this analysis.

Measuring vocal tract and vocal folds and histological investigation

Five dissected specimens, two fresh males (~3–4 weeks of age), two deeply frozen and then thawed females (~8 weeks and ~7 months) and one deeply frozen and then thawed male (~7 months) preyed on or died of diseases in 2008–2009 were used for the anatomical measurements. Three of them were used in the previous study (Volodin et al. 2011) only to measure the lengths of vocal tract (VT) and vocal folds. A comparison of photo and video images of lateral profiles, taken from live and dead animals of the same age, suggests that the post-mortem position of the larynx approximately corresponds to its resting position in the live animal. In this study, for all the five specimens, 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. The dorsoventral height of the larynx was measured from the laryngeal prominence to the most dorsal part of the larynx by using electronic calipers with 0.5-mm precision (Aerospace, Brüder Mannesmann Werkzeuge GmbH, Remscheid, Germany).

The oral VT was measured from the vocal folds along the pharyngeal and oral cavities up to the edges of the lips, and the nasal VT from the vocal folds along the pharyngeal and nasal cavities up to the nostrils (Fig. 2). After removal of the left half of the mandible and temporalis, masseter and pterygoid muscles, oral and nasal VTLs were ascertained with a tape measure (1-mm precision). Each measurement was repeated three times for each specimen by the same researcher (RF), and then the mean value was calculated.

The formalin-preserved left and right laryngeal vocal pads of a ~3–4–week male goitred gazelle were histologically processed in the Leibniz Institute for Zoo and Wildlife Research (IZW), Berlin. Sections (thickness 3–5 μm) were stained with Hematoxylin–Eosin, Azan and van Gieson.

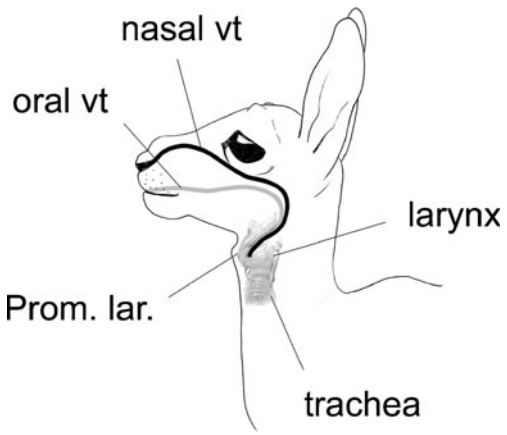

Fig. 2 Measuring nasal and oral vocal tract lengths in a 3–4 week goitred gazelle. *Prom. lar.* laryngeal prominence

Call analysis

For each oral and nasal call (Figs. 1 and 3), we measured the same 10 variables (duration, f0, 4 power variables and the first 4 formants) and for each snort 5 variables (duration and 4 power variables). 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%) using Avisoft SASLab Pro software (Avisoft Bioacoustics, Berlin, Germany) (Fig. 3). From the mean power spectrum of the entire call, we measured the maximum amplitude frequency (fpeak) and the upper, medium and lower quartiles (q25, q50 and q75), covering respectively 25%, 50%, and 75% of call energy. With "Autocorrelation" option of Avisoft, we measured the mean f0 of the entire call. 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 first four formants were measured using linear predictive coding (LPC) with the Praat DSP package, version 4.3.21 (P. Boersma & D. Weenink, University of Amsterdam, Netherlands, http://www.praat.org). The mean VTL values of dissected specimens served to establish LPC

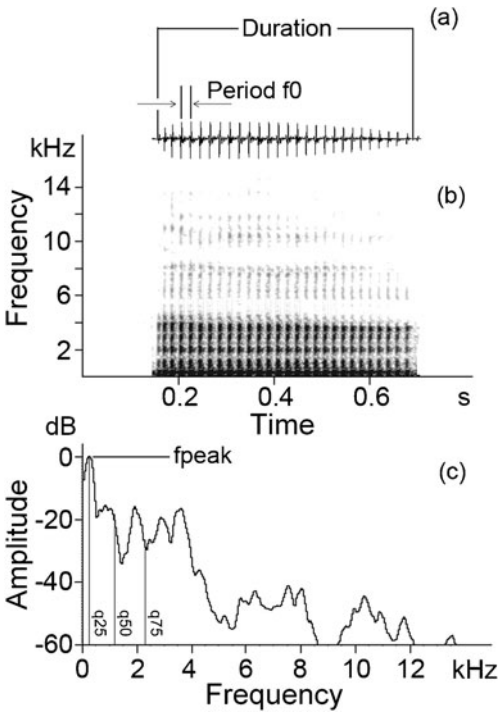

Fig. 3 The nasal call of a 15–16-week male goitred gazelle: **a** waveform, **b** spectrogram and **c** mean power spectrum. Measured variables: duration, fundamental frequency period (period f0), maximum amplitude frequency (fpeak), lower (q25), medium (q50) and upper (q75) quartiles. The spectrogram settings: sampling frequency 48 kHz, Hamming window, FFT 1024, frame 50%, overlap 93.75%

parameters for creation of formant tracks. 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 numbers, L is VTL and c is the speed of sound in air (350 ms^{-1}). LPC settings were Burg analysis, window length 0.04 s, time step 0.01 s and maximum number of formants 4–5. Ranges of maximum formant frequencies varied according to call type and age class from 4500–6500 Hz (for 1–2 weeks) to 2600–4000 Hz (for 23–24 weeks). Formant measurements were taken from the call portion where the formant tracks are nearly horizontal (Fig. 4). Positions of formants were verified by superposition on the spectrogram. Point values of formant tracks were extracted and exported to Excel, and the value of each formant for the given call was calculated as the average value from the point values.

Statistical analyses

Statistical analyses were made with STATISTICA, v. 6.0 (StatSoft, Tulsa, OK, USA). Means are given as mean±SE. All tests were two-tailed, and significance levels were set at 0.05. Distributions of all measured parameter values did not depart from normality (Kolmogorov–Smirnov test, $p > 0.05$). We used a one-way ANOVA with Newman–Keuls post hoc to compare the values of variables between call types. We used Spearman rank correlation to calculate the correlation between percentages of different call types and ages. We used GLM with Newman–Keuls post hoc to compare the effects of age and sex on body mass. We used Pearson correlation to calculate the correlation between body mass, age and the acoustics (using mean values of nasal and oral call variables per animal per age). Because some animals did not produce any nasal or oral calls during any session at some ages, not every subject was represented at every age class. Therefore, we applied a GLMM (with age and sex as fixed factors and animal as random factor), with Newman–Keuls post hoc, appropriate for analysis of data with missing values, to compare the effects of age and sex on the acoustics. For the analysis with GLMM, we used the mean values of each variable of nasal and oral calls for each animal in each age class. This decreased the number of degrees of freedom and allowed to reveal more strictly the effects of age and sex.

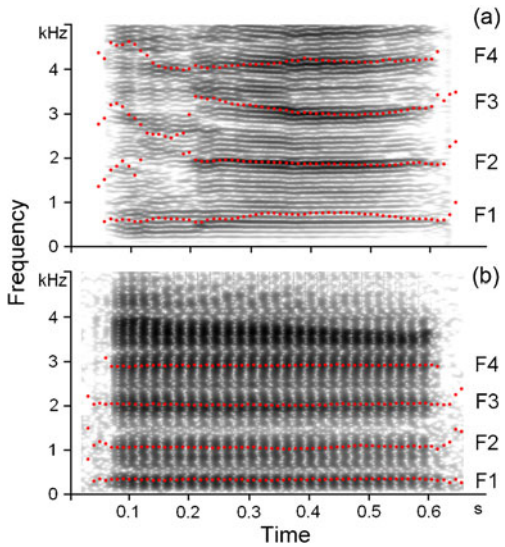

Fig. 4 Tracks of the first 4 formants (F1–F4), created with Praat software: **a** oral call of 1–2-week male, **b** nasal call of 15–16-week male (the same call as in Fig. 3). The LPC settings were Burg analysis, window length 0.04 s, time step 0.01 s, maximum number of formants 4, maximum formant frequency 4800 Hz (oral call) or 3200 Hz (nasal call). In the oral call, the animal opened its mouth at ~0.22 s; measurements were taken from the call portion where the formant tracks are nearly horizontal (0.24–0.58 s). In the nasal call, measurements were taken from the entire call

Results

Measures of vocal tract and larynx

The dorsoventral height of the larynx, from the thyroid prominence to its most dorsal part, was 26 mm in both 3–4-week males, 25 mm in the 8-week female, 31 mm in the 7-month female and 33 mm in the 7-month male. The vocal fold length was 15 mm in both 3–4-week males and 13.5 mm in the 8-week female. Ventrally, the vocal folds attached to the dorsal aspect of the most prominent part of the thyroid cartilage. The vocal folds were oriented perpendicularly to the longitudinal axis of the larynx. Connective tissue vocal pads were attached to the latero-caudal edges of vocal folds. The dorsoventral length of the left vocal pad of both 3–4-week males was 15 mm, 9 mm rostrocaudally and 4 mm in transverse width (Fig. 5). Dorsally, the vocal folds attached to the vocal process of the arytenoid cartilage. The vocal folds of the 7-month male and females were not measured, as they were poorly preserved.

The oral VTL, from the vocal folds along the pharynx and the oral cavity to the edges of the lips, was 132 mm in both 3–4-week males, 135 mm in the 8-week female, 165 mm in the 7-month female and 200 mm in the 7-month male. The nasal VTL, from the vocal folds along the pharynx and the nasal cavity to the nostrils, was 149 mm in both 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. These values suggest the development of sexual dimorphism of vocal folds and VTL in goitred gazelles.

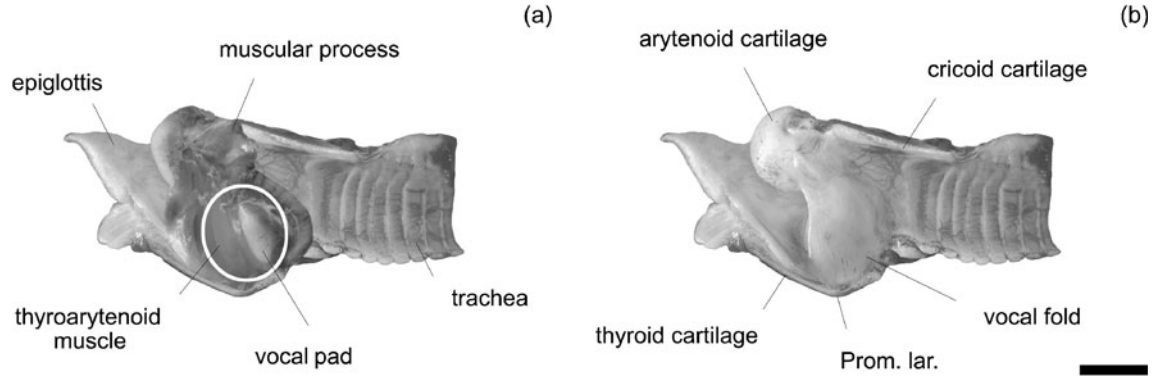

Fig. 5 Larynx and vocal folds: **a** right half of larynx with left arytenoid cartilage and left vocal fold still in situ, illustrating the lateral aspect of the left vocal fold; middle and caudal portions of thyroarytenoid muscles pulled apart to expose the laterally bulging left vocal pad; its contours are approximated by the white ellipse; **b** right half of the same larynx after removal of the left arytenoid cartilage and the left vocal fold to expose the medial aspect of the right vocal fold, medial view. Scale bar=10 mm

Microscopic structure of vocal pads

Towards the laryngeal cavity the vocal pads were covered by a stratified squamous epithelium. The bulk of vocal pad tissue consisted of collagen fibers and elastic fibers, embedded in extracellular matrix, with few interspersed fat cells and small blood vessels. Both fiber types were partly arranged in larger bundles and partly occurred as single fibers. Close to the epithelium the elastic fibers were more frequent than in the opposite, lateral direction towards the thyroarytenoid muscle. In the medial third of the vocal pad elastic fibers appeared cross-sectioned as well as longitudinally. Roughly estimated, relative overall fiber abundance was 60% collagen and 40% elastic. Laterally, close to the thyroarytenoid muscle and medially, close to the epithelium, glandular packets were identified. They were larger laterally and smaller close to the epithelium. Small invaginations of the epithelium seemed to be the opening sites of the excretory ducts of the medially located glands. Excretory ducts of the lateral glands were not identified. Microscopic structure of the vocal pad suggests its evolutionary derivation from a vocal ligament.

Call types, produced by gazelles

Three call types were identified: nasal calls, oral calls and snorts (Fig. 1, Table 1). Both nasal and oral calls revealed periods of glottis opening and closing, representing the f0. Nasal calls were produced through the nose with closed mouth. Oral calls mostly started with a closed mouth but then were produced through the widely opened mouth. A one-way ANOVA revealed significantly higher mean values in all the 10 variables for oral calls compared to nasal calls (Table 1). Snorts were soft calls without any sign of f0, produced during abrupt expiration through the nose. Snorts were shortest in duration and highest in fpeak and in all three quartiles compared to either nasal or oral calls (Table 1).

Both nasal and oral calls were produced when animals anticipated feeding or at brief separations, but oral calls were louder and apparently attended a state of higher arousal. In addition, nasal calls attended suckling milk from a bottle and playful or weakly aggressive butting, displayed by both sexes since 2 weeks. Preceding analyses revealed very close characteristics between nasal calls recorded in different contexts (Efremova et al. 2010). Snorts attended sudden appearance of humans.

Percentages of oral calls, nasal calls and snorts through age classes

Percentages of oral calls, nasal calls and snorts were calculated for each age class (Fig. 6). Snorts occurred in all age classes at percentages not higher than 9%, decreasing with age ($r=-0.75$, $p<0.05$). Percentages of nasal calls increased steadily with age ($r=0.88$, $p<0.01$) to over 50% at 3–4 weeks, up to 98% at 23–24 weeks. Conversely, initially high percentages of oral calls decreased steadily with age ($r=-0.88$. $p<0.01$) and disappeared at 23–24 weeks. Thus, only nasal calls could be analyzed over the entire study period.

Effects of age and sex on body mass

GLM revealed separate strong and significant effects of age ($F_{8,184}=420.5$; $p<0.001$) and sex ($F_{1,184}=60.5$; $p<0.001$) on body mass but no conjoint effects ($F_{8,184}=1.7$; $p=0.10$). Body mass increased with age ($r=0.936$, $p<0.001$). Although mean body mass was always higher in males than in females, significant differences between sexes were not found before 10 weeks (Fig. 7).

Table 1 Mean±SE values for the acoustic variables of oral calls, nasal calls and snorts (n=23 animals) at 3–6 weeks of age, and one-way ANOVA results for comparison (*p<0.001) between call types

Variable	Oral calls (n=94)	Nasal calls (n=115)	Snorts (n=81)	ANOVA results
f0 (Hz)	106.9±1.8	90.6±1.4	–	$F_{1,207}$=54.7*
Dur (s)	0.51±0.02[a]	0.23±0.01[b]	0.18±0.01[c]	$F_{2,287}$=205.1*
F1 (Hz)	736±13	546±15	–	$F_{1,207}$=178.6*
F2 (Hz)	2022±31	1402±15	–	$F_{1,207}$=372.9*
F3 (Hz)	3003±35	2827±20	–	$F_{1,207}$=20.3*
F4 (Hz)	4232±30	3928±28	–	$F_{1,207}$=54.7*
fpeak (Hz)	717±38[a]	434±38[a]	3057±423[b]	$F_{2,287}$=44.3*
q25 (Hz)	560±28[a]	371±10[a]	1847±179[b]	$F_{2,287}$=76.5*
q50 (Hz)	1328±57[a]	785±36[b]	5023±285[c]	$F_{2,287}$=237.5*
q75 (Hz)	2832±77[a]	2216±87[b]	9008±272[c]	$F_{2,287}$=567.8*

Different superscripts indicate which acoustic variables differed significantly between call types (p<0.05, Newman–Keuls post hoc test). n indicates number of calls, – indicates no measure

f0 fundamental frequency, *Dur* duration, *F1*, *F2*, *F3*, *F4* first four formants, *fpeak* maximum amplitude frequency, *q25* lower quartile, *q50* medium quartile, *q75* upper quartile

Effects of sex and age on the acoustics of nasal and oral calls

GLMM showed significant effects for both age and sex on formants (excluding F2 of nasal calls, the values of which did not depend on sex) and also on f0 and on the duration of oral and nasal calls (Table 2). A conjoint effect of age and sex was found only on f0 of oral calls and was not found on formants and duration of oral and nasal calls or on f0 of nasal calls (Table 2).

Pearson's correlation showed a significant decrease of all four formants of nasal and oral calls with age and increase of body mass (Table 2). In all age classes, frequencies of all four formants of oral calls were significantly lower in males than in females. In nasal calls, only F3 and F4 were significantly lower in males than in females in all age classes (Fig. 8), while F2 were undistinguishable and F1 were very close between sexes, showing significant differences only at 5–6 weeks and 13–14 weeks (Fig. 8).

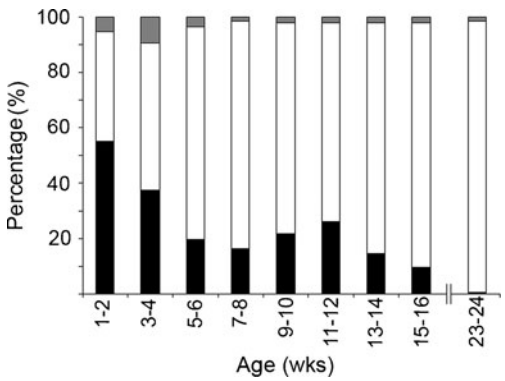

Fig. 6 Percentages of oral calls (*black*), nasal calls (*white*) and snorts (*gray*) in 9 age classes from newborn to adolescence

In the oral calls, the F3–F2 distance was minimal compared to other distances between neighboring formants in both sexes. By contrast, in nasal calls, the F3–F2 distance was maximal compared to the F2–F1 or F4–F3 distance. This formant pattern of nasal and oral calls was constant along ontogenesis in all age classes and in both sexes.

Similar to formants, the f0 of oral and nasal calls decreased significantly with age and increase of body mass, and sex differences appeared as early as at 1–2 weeks, with male f0 significantly lower than female f0 in all age classes (Fig. 8, Table 2). In oral calls of both sexes, the steady decrease of f0 reached a plateau at older ages (Fig. 8). Pairwise comparisons revealed no differences in f0 of male oral calls between age classes 8–10 weeks, 11–12 weeks, 13–

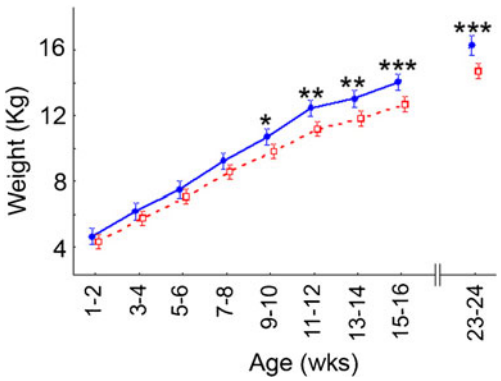

Fig. 7 Age-related changes in body mass (one weighting per animal per age class) in males (*solid line*) and females (*dashed line*). n=23 animals (10 males, 13 females) from 1–2 to 15–16 weeks of age and n=18 animals (7 males, 11 females) at 23–24 weeks of age. *Central points* show means, *whiskers* show 0.95 confidence intervals. Significant differences between sexes: *p<0.05, **p<0.01, ***p<0.001; Newman–Keuls post hoc test

Table 2 Results of GLMM for separate and conjoint effects of age and sex, and results of Pearson's correlation between age or body mass and mean values of variables for the first four formants (F1, F2, F3 and F4), fundamental frequency (f0) and duration (Dur) of oral and nasal calls

Variable	GLMM results			Pearson's correlation results	
	Age	Sex	Age and sex	Age	Body mass
	Oral calls (n=159)				
F1	$F_{7,119}$=66.2; p<0.001	$F_{1,119}$=8.6; p<0.01	$F_{7,119}$=1.1; p=0.37	r=−0.756; p<0.001	r=−0.778; p<0.001
F2	$F_{7,119}$=66.6; p<0.001	$F_{1,119}$=14.0; p=0.001	$F_{7,119}$=1.0; p=0.45	r=−0.755; p<0.001	r=−0.773; p<0.001
F3	$F_{7,119}$=56.0; p<0.001	$F_{1,119}$=14.6; p<0.001	$F_{7,119}$=0.3; p=0.94	r=−0.748; p<0.001	r=−0.778; p<0.001
F4	$F_{7,119}$=118.5; p<0.001	$F_{1,119}$=20.8; p<0.001	$F_{7,119}$=0.3; p=0.94	r=−0.838; p<0.001	r=−0.881; p<0.001
f0	$F_{7,122}$=94.6; p<0.001	$F_{1,122}$=13.2; p<0.01	$F_{7,122}$=2.1; p<0.05	r=−0.650; p<0.001	r=−0.705; p<0.001
Dur	$F_{7,122}$=6.2; p<0.001	$F_{1,122}$=0.5; p=0.48	$F_{7,122}$=1.8; p=0.10	r=0.313; p<0.001	r=0.282; p<0.001
	Nasal calls (n=197)				
F1	$F_{8,158}$=96.7; p<0.001	$F_{1,158}$=7.0; p<0.05	$F_{8,158}$=1.4; p=0.20	r=−0.846; p<0.001	r=−0.855; p<0.001
F2	$F_{8,158}$=164.3; p<0.001	$F_{1,158}$=0.3; p=0.60	$F_{8,158}$=1.0; p=0.41	r=−0.857; p<0.001	r=−0.888; p<0.001
F3	$F_{8,158}$=372.1; p<0.001	$F_{1,158}$=6.5; p<0.05	$F_{8,158}$=0.9; p=0.52	r=−0.885; p<0.001	r=−0.933; p<0.001
F4	$F_{8,158}$=285.2; p<0.001	$F_{1,158}$=16.5; p<0.001	$F_{8,158}$=1.6; p=0.13	r=−0.854; p<0.001	r=−0.924; p<0.001
f0	$F_{8,158}$=120.9; p<0.001	$F_{1,158}$=18.0; p<0.001	$F_{8,158}$=1.1; p=0.36	r=−0.653; p<0.001	r=−0.744; p<0.001
Dur	$F_{8,158}$=17.1; p<0.001	$F_{1,158}$=5.7; p<0.05	$F_{8,158}$=0.3; p=0.93	r=0.331; p<0.001	r=0.424; p<0.001

n—number of mean values

14 weeks and 15–16 weeks and in f0 of female oral calls between age classes 13–15 and 15–17 weeks (p>0.05 for all comparisons, Newman–Keuls post hoc test).

Unlike f0, the duration of oral and nasal calls increased slightly but significantly with age and increase of body mass (Fig. 8, Table 2). In oral calls, sex-related differences were found only at 15–16 weeks. In nasal calls, sex-related differences were not found (Fig. 8).

Discussion

Comparison of the anatomical dimensions and the acoustics with other ruminants and humans

Despite the considerable difference of body mass, the sizes of the anatomical structures and the related acoustics were very close between juvenile goitred gazelles and adult humans. Sizes of vocal folds of 13.5–15 mm of juvenile gazelles were comparable to the reported values of 17–25 mm for male and 12.5–19 mm for female humans (Titze 1994; Roers et al. 2009). Consistently, low f0 values were found in gazelles: 93 and 112 Hz in male and female nasal calls and 105 and 125 Hz in male and female oral calls, which approached the ranges of f0 reported for adult humans: 107–129 Hz for men and 189–210 Hz for women (Monsen and Engebretson 1977; Lass and Brown 1978; Rendall et al. 2005; Evans et al. 2006; Apicella et al. 2007). The VT lengths of 132–150 mm at 3–8 weeks and of 165–220 mm at 7 months found in gazelles were comparable to 135 and 195 mm reported respectively for adult male and female humans (Fant 1960; Fitch and Giedd 1999).

The f0 of juvenile goitred gazelles was much lower compared to that reported for other juvenile ruminants, e.g. 400–800 Hz in moans and 800–1000 Hz in squeaks of moose (*Alces alces*) (Bogomolova et al. 1984), 611–653 Hz in fallow deer (Torriani et al. 2006), 737 Hz in red deer *Cervus elaphus hippelaphus* (Vankova and Malek 1997) and 623 Hz in *C. elaphus corsicanus* (Kidjo et al. 2008), 509 Hz in white-tailed deer (*Odocoileus virginianus*) and 1016 Hz in mule deer (*O. hemionus*) (Lingle et al. 2007), 153–161 Hz in saiga (Volodin et al. 2009), 345 Hz in lambs (Searby and Jouventin 2003), and from 627–742 Hz in juvenile to 440–477 Hz in adolescent domestic goats (Lenhardt 1977; Terrazas et al. 2003; Briefer and McElligott 2011). The f0 of juvenile reindeer (*Rangifer tarandus*) of 110–240 Hz (Espmark 1975) and domestic cows of 103–124 Hz (Weary and Chua 2000) are comparable to those of the gazelles; however, body mass of newborn reindeer is twice higher (5.8–6.1 kg) and body mass of newborn cattle ten times higher (average 41.9 kg) (Weary and Chua 2000; Couturier et al. 2009) than in newborn gazelles.

The low f0 of young goitred gazelles may result from a weight increase of the vocal folds and changes of their viscoelasticity due to evolution of a vocal pad (Fig. 5) that may execute stronger resistance to tensile forces. Tensile forces can be expected to occur predominantly along the dorsoventral axis of the vocal folds by muscular-induced movements of the arytenoid cartilage. The collagen fibers

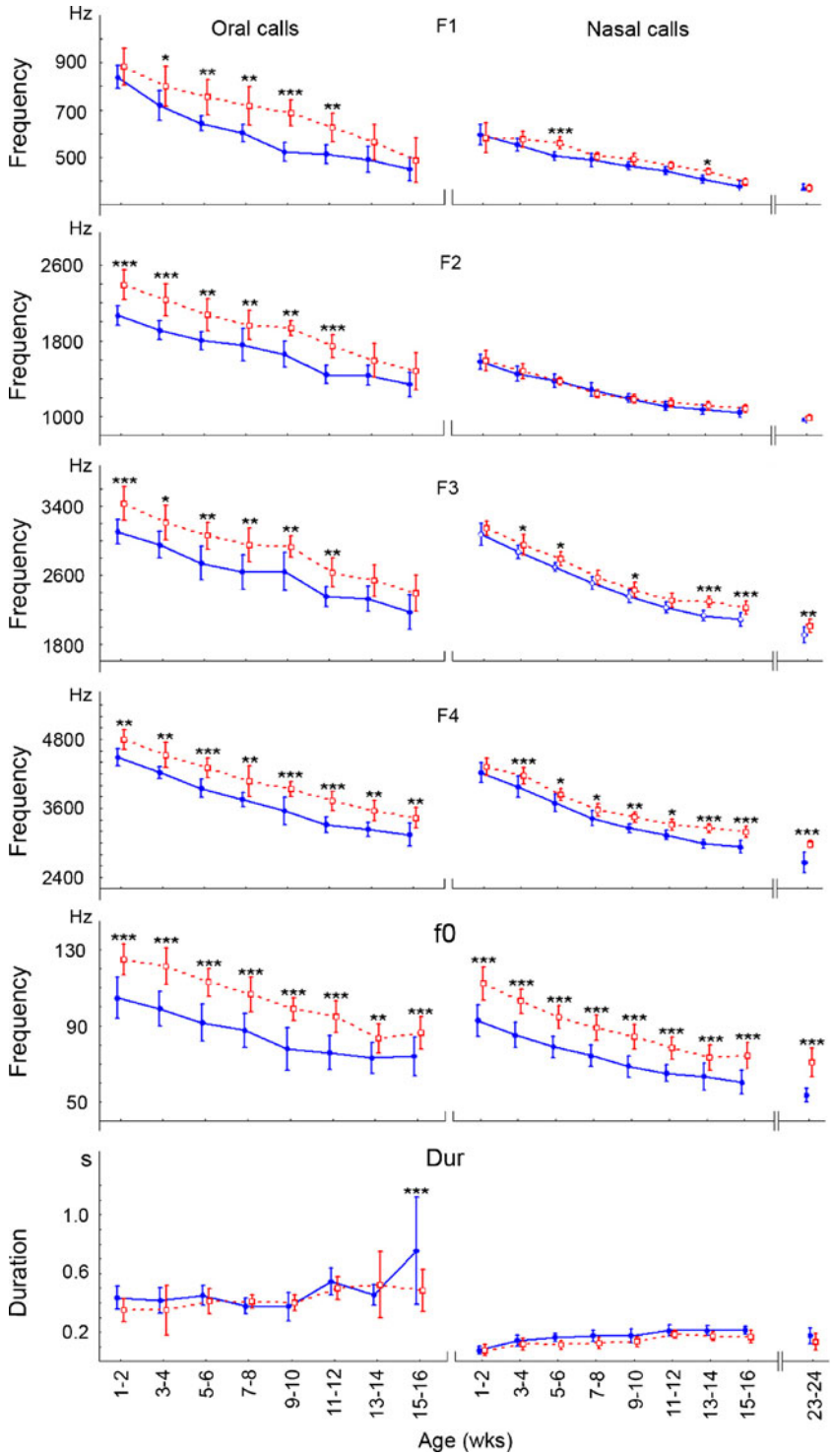

Fig. 8 Age-related changes in the first four formants (*F1*, *F2*, *F3* and *F4*), fundamental frequency (*f0*) and duration (*Dur*) of oral and nasal calls in males (*solid line*) and females (*dashed line*). $n=23$ animals (10 males, 13 females) from 1–2 to 15–16 weeks of age and $n=18$ animals (7 males, 11 females) at 23–24 weeks of age. *Central points* show means of means, *whiskers* show 0.95 confidence intervals. Significant differences between sexes: $*p<0.05$, $**p<0.01$, $***p<0.001$; Newman–Keuls post hoc test

themselves are almost inextensible, but restricted extension may occur by a change in arrangement of the fibers under tension. The elastic fibers are easily extensible, but resistance to tensile forces increases with increasing tension (Bucher and Wartenberg 1997). Thus, the elastic fibers can be expected to restore the initial relaxed vocal pad shape subsequent to restricted extension. The higher amount of elastic fibers in the medial portion suggests an increasing elasticity towards the glottis. Excretions of the medially located glands of the vocal pad may serve to lubricate its glottic surface. Vocal pads were found also in adult males in goitred gazelles (Frey et al. 2011), takin (Frey and Hofmann 2000), Mongolian gazelles (Frey and Gebler 2003; Frey et al. 2008) and saigas (Frey et al. 2007).

During dissections of deep frozen specimens we noticed the lack of vocal pads while they were invariably present in freshly dissected specimens. From this we hypothesize that the vocal pad structure in goitred gazelles decisively depends on the water contents of the ground substance (hydration) in its constructive connective tissue. The observed lack of vocal pads might have resulted from postmortem water escape during the freeze–thawing procedure. In the living goitred gazelle the tight, gel-like consistency of the vocal pads is probably guaranteed to a large degree by their turgor that is generated by the internal protein/water ratio and a surrounding diffusion barrier. Generally, ground substance contents and tissue turgor decrease with age while fiber proportion increases, entailing a decrease of overall tissue permeability (Bucher and Wartenberg 1997). Therefore, in the second half of the lifespan of goitred gazelles, we expect a gradual transition from a turgor-dominated structure towards a fiber-dominated structure of the vocal pads.

Along development, the oral f0 was always higher than the nasal f0 (Fig. 8), in agreement with previous data on juvenile goitred gazelles (Volodin et al. 2011), one juvenile saiga (Volodin et al. 2009) and adult domestic sheep (Sebe et al. 2010). The difference between oral and nasal f0 may result from a rotational movement of the thyroid cartilage relative to the cricoid cartilage at retraction of the larynx from the nasopharynx prior to oral calls. This rotation is expected to create higher vocal fold tension during oral calls (Volodin et al. 2011).

Unequal distances between neighboring formants suggest a non-uniform vocal tract in goitred gazelles. Consistency of this formant pattern along ontogenesis and in both sexes suggests that deviation of the VT from a uniform tube shape depended on nasal vs oral production but not to sex or age of study animals. These data are in agreement with previous findings of non-uniformity of VT in a cross-sectional study with a separate sample of animals and calls of juvenile goitred gazelles (Volodin et al. 2011).

Proportions of nasal calls, oral calls and snorts along development

All study animals produced nasal calls, oral calls and snorts from their first week of life, but the ratio of nasal to oral calls increased with age. Oral calls were louder, probably because they were produced at higher arousal and their vocal energy was not absorbed by the nasal epithelium (Fitch 2000b). In the wild, oral calls are produced in situations when juveniles lose their mothers (our unpublished data). In enclosures, decreased ratio of oral calls with age could indicate that the animals became calmer and more tolerant to people. A decreasing ratio of snorts with age also indicates lower alertness, as snorts function as alarm signals in bovids (Walther et al. 1983; Bro-Jørgensen and Pangle 2010). However, for domestic lambs, opposite ratios of nasal and oral calls along development are reported (Sebe et al. 2007). Sebe et al. (2007) relate this to enhancing mobility and increasing demands on far-range communication with age. Alternative explanation is that oral calls of lambs are more audible in noisy environment of large herds, while juvenile goitred gazelles communicate with their mothers in small groups at low background noise (Jevnerov 1984).

Also, this difference between sheep and gazelles could be related to anti-predator strategies occurring after birth. Nasal calls are usually produced at close distance whereas oral calls are produced when mother and young are farther away. Sheep lambs follow their mother quickly after birth and are thus most of the time close to their mothers (Shillito Walser et al. 1984). In this case, they would probably produce mainly nasal calls until they spend an increasing amount of time farther away from their mother when older. At contrary, gazelles are hiders in first weeks of life (Soldatova 1983; Fitzgibbon 1990). Thus, just after birth, young gazelles spend more time away from their mother and would mainly produce oral calls when they have to communicate. Then, when they join the social group, they would be closer to their mother and switch to nasal calls.

Age-related and body mass-related changes in the acoustics

The f0 and formants decreased steadily with age and increase in body mass (Fig. 8, Table 2), in accordance with the growth of VT and vocal folds (Fitch and Hauser 2002). The acoustic properties changed accordingly (Online Resources 2 and 3). Decreasing f0 with age is usual for mammals (review: Matrosova et al. (2007)) and in particular for ruminants (Vankova and Malek 1997; Searby and Jouventin 2003; Torriani et al. 2006; Kidjo et al. 2008; Volodin et al. 2009; Briefer and McElligott 2011). Decreasing f0 and formants along ontogenesis were reported for both sexes of humans (Fitch and Giedd 1999; Lee et al. 1999). The increasing duration of nasal and oral calls with age in goitred gazelles (Fig. 8, Table 2) was probably related to increasing body size and lung capacity, responsible for the capability to expire a larger volume of air at one time (Fitch and Hauser 2002; Hewitt et al. 2002; Briefer and McElligott 2011).

In this study, we did not analyze the ontogeny of the fpeak and quartiles, as the previous study of nasal calls (Efremova et al. 2011) revealed very unsteady, although significant, decrease in values of these parameters with age. Similarly weak and strongly fluctuating changes of quartiles were reported for early vocal ontogenesis of domestic goats (Briefer and McElligott 2011).

Sex-related changes in the acoustics

In goitred gazelles, significant sex-related differences in body mass appeared at 10 weeks of age (Fig. 7). However, significant sex-related differences of f0 and formants emerged as early as the second week of life. Males consistently had a lower f0 than females (Fig. 8). The lower f0 in males can be explained by a larger size of their vocal folds, which were found larger in the 3–4-week males than in the 8-week female. Inconsistently, in the study of early vocal ontogenesis of oral calls in domestic goats, the f0 values and the mean values of all four formants did not differ between sexes, although the age-related decrease of f0, F1, F3 and F4 was faster in males than in females (Briefer and McElligott 2011).

In oral calls of goitred gazelles, the steady age-related decrease of f0 achieved a plateau of 73 Hz at 10 weeks in males and of 83 Hz at 14 weeks in females (Fig. 8). These values were close to the f0 of adult male rutting growls (68 Hz, Frey et al. 2011). Probably, some anatomical constraints prevent further f0 lowering in goitred gazelles, because Corsican red deer and fallow deer stags are capable of producing mean f0 as low as 40 and 35 Hz (Reby et al. 1998; Vannoni and McElligott 2007; Kidjo et al. 2008).

In nasal calls, F1 and F2 values did not differ between sexes. This result suggests that the configuration rather than the length of the resting VT affects the low formants in goitred gazelles. Similar effects on the low formants were reported for fallow deer bucks: the retraction of the larynx during rutting groans and concomitant VT elongation resulted in the lowering of high formants (F3–F6) but did not affect the low formants (F1 and F2) (McElligott et al. 2006; Briefer et al. 2010). Pronounced intersexual differences in all four formants were found only in oral calls (Fig. 8). Adult male goitred gazelles produce their rutting roars orally, with simultaneous pronounced dynamic retraction of the larynx down to the sternum (Frey et al. 2011). In oral calls of adult females, retraction of the larynx is less prominent (our unpublished data). Sex-specific differences in retraction of the larynx may emerge early in ontogenesis and result in sex-specific elongation of VT, affecting formants, especially in oral calls.

General conclusion

In goitred gazelles, sex-related differences in f0 and formants emerged much earlier in ontogenesis than in humans, already at second week of life. In humans, these differences appear before puberty, coinciding with the onset of testosterone-induced enlargement and descent of the larynx in boys (Fitch and Giedd 1999; Lee et al. 1999). This result suggests different pathways of vocal ontogenesis in two mammals with enlarged and descended larynx: goitred gazelles and humans. In male and female goitred gazelles, the ontogeny of f0 and formants was steady, resembling those of female humans. In male humans, fundamental and formant frequencies decrease abruptly at puberty. Therefore, male goitred gazelles do not show human-like vocal ontogenesis via voice breaking.

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