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Vocal group signatures in the goitred gazelle *Gazella subgutturosa*

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Abstract The potential for vocal modification in mammals has recently been of great interest. This study focuses on the potential for vocal matching in juvenile and adolescent goitred gazelles *Gazella subgutturosa* that were group housed as part of an animal management programme. Two groups of animals (16 and 19 unrelated individuals, respectively) were recorded at two different ages, juvenile and adolescent, regarding 20–25 calls per individual per age; each group was evaluated in a separate year. Vocal similarity of group members compared to nonmembers was prominent in both ages, but higher in juveniles. Individual identity was prominent in both ages and higher in adolescents. The more prominent vocal indicators of group membership in juveniles could be related to their higher social dependence compared to adolescents. The more individualized calls of adolescents could be a mechanistic consequence of more stable growth at older age. Our results suggest vocal plasticity of goitred gazelles under social influences. These data add to recent evidence about domestic goat kids *Capra hircus*, suggesting that vocalizations of species that are not capable of imitation are more flexible than previously thought.

Introduction

Acoustic similarity of social group members is usual in non-human mammals which experience vocal learning from conspecific tutors, such as bats (e.g. Jones and Ransome 1993; Boughman 1997, 1998; Knörnschild et al. 2010, 2012), cetaceans (Janik and Slater 1997; Tyack 1997, 2008; Weiß et al. 2006) and pinnipeds (Sanvito et al. 2007; Schusterman 2008). At the same time, recent research focuses on potential vocal plasticity due to social effects in those mammals, whose vocal repertoires are assumed to be fixed at birth, e.g. non-human primates (Snowdon and Elowson 1999; Lemasson et al. 2003, 2011; Rukstalis et al. 2003; Crockford et al. 2004; Tanaka et al. 2006), carnivores (Townsend et al. 2010), rodents (Arriaga et al. 2012; Arriaga and Jarvis 2013) and ungulates (Briefer and McElligott 2012). Modifying call structures according to membership in social groups can indicate vocal production learning (Janik and Slater 1997, 2000; Seyfarth and Cheney 2010).

For ungulates, a recent study of juvenile domestic goats *Capra hircus* revealed more close vocal similarity in goat kids of the same social groups compared to members of alien groups. This study also suggests that the vocal similarity of same-group members increased along ontogeny from 1 to 5 weeks of age, pointing to the development of group-specific vocal signatures (Briefer and McElligott 2012). Another study with the same sample of goat kids and calls revealed that the calls became more individualized at 5 weeks compared to 1 week of age (Briefer and

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McElligott 2011b). Thus, two parallel processes could be observed in early vocal ontogeny of domestic goats: an increase in acoustic similarity of group mates along with an increase in vocal individuality.

Similarly to early vocal ontogeny of domestic goats, contact calls of goitred gazelles *Gazella subgutturosa* became more individualized during development from juveniles to adolescents (Volodin et al. 2011; Lapshina et al. 2012). However, these results were obtained with a pooled sample of animals from two different social groups (Lapshina et al. 2012), so the effect of social group on vocal individuality of this species remained unclear. Also, it remains unknown whether goitred gazelles are capable of developing some kind of the group-specific vocal signature, similarly to domestic goats (Briefer and McElligott 2012).

The goitred gazelle is an average-size ungulate, widely distributed over the steppes and semideserts of Central Asia (Kingswood and Blank 1996). Goitred gazelles have a wide span of group sizes from singletons to herds of several tens (Blank et al. 2012). The vocal ontogeny and vocal anatomy of this species have been investigated in some detail, because sexual dimorphism of the enlarged and descended larynx of adult goitred gazelles is strongly reminiscent of the case in humans (Efremova et al. 2011; Frey et al. 2011). In addition to brain development, the descended larynx and vocal learning represent the main precursors of human speech (Fitch 2000, 2010). So far, the combination of a descended larynx and vocal learning has been found only in humans. Thus, the goitred gazelle is an especially interesting species for studying the precursors of vocal production learning.

In this study of juvenile and adolescent goitred gazelles, we tested two predictions. First, we tested whether social group membership is responsible for vocal plasticity. If so, calls of members of the same group should be more similar in structure than calls from members of different groups. Second, we tested whether group vocal signature strengthens with age, as a joint function of maturation and of time that animals spent together. If so, calls of adolescents should be more similar in their acoustic structure than calls of juveniles of the same group.

Similarly to goat kids, young goitred gazelles produce nasal and oral contact calls when in contact with their mothers (Volodin et al. 2011). Closed-mouth nasal calls are produced at lower arousal levels compared to the oral calls (Efremova et al. 2011; Volodin et al. 2011). Both call types, oral and nasal, show the same ontogenetic trends, of decrease in fundamental frequency (f0) and the first four formants (F1–F4) (Efremova et al. 2011), similarly to oral calls of domestic goat kids (Briefer and McElligott 2011a). Adolescent goitred gazelles produce only nasal calls (Efremova et al. 2011), so for the comparative analysis between calls of juvenile and adolescent in this study, we selected only nasal calls, as a single call type shared by both age classes. In the wild, gazelles are hiders for the first 2–3 weeks of life, but from 3 to 6 weeks actively follow their mothers (Soldatova 1983). At 23–26 weeks, adolescent goitred gazelles are pre-mature and already demonstrate sexual behaviour (Blank 1998).

The purpose of this study was to compare the development of vocal group signature and individual vocal signature in two different social groups of unrelated goitred gazelles. In particular, we examined nasal calls for the presence of individual- and group-specific indicators, and for their prominence, at two ontogenetic stages, of 3–6 weeks juveniles and of 23–26 weeks adolescents.

Materials and methods

Study site and animal housing

The study was conducted in the "Djeiran" Ecocenter (Uzbekistan, Bukhara region, 39°41′N, 64°35′E) during two consecutive years (May–June and October–November in 2008 and 2009). The Djeiran Ecocenter state breeding centre is located on a fenced 5,145 hectare area of semidesert, inhabited by 600–1,200 free-ranging goitred gazelles, with number varying from year to year (Pereladova et al. 1998; Frey et al. 2011). Adult females give birth to one or two young from end-April to mid-May. Each May, the staff of the Ecocenter randomly captures 25–35 newborn calves out of the 200–300 born by unmarked free-ranging females on the fenced territory. These calves are then hand-reared and transferred to zoos or other breeding centres for conservation or management purposes.

The calves spend the day walking together in a large enclosure 25 × 18 m and spend the night in non-permanent subgroups (changing each night) of 5–7 individuals in small enclosures of 2 × 4 m with indoor shelters made of dried reeds. Thus, contact between all group members is unlimited throughout the rearing period. The subject animals are fed three or two times a day, depending on age (with fresh goat and cow milk, predried grass, mainly *Megicago* sp., mixed fodder, vitamins and minerals, and *Haloxylon* sp. growing naturally in the enclosure). Water is available ad libitum (Soldatova et al. 2010). This housing and rearing regime is kept the same from year to year, for each generation of gazelles.

Social groups

Two social groups of unrelated calves were bioacoustically monitored, Group 1 and Group 2. Group 1 comprised 30 (12 male and 18 female) calves captured between 29 April

and 12 May 2008 and Group 2 comprised 32 (16 male and 16 female) calves captured between 5 May and 13 May 2009. Animals were aged by size, body mass and the state of the umbilical cord (see Efremova et al. 2011 for details). All calves were unrelated to each other, as twins are never captured together. For the purposes of our study, all gazelles were individually marked with p-phenylenediamine (Rhodia, Paris, France) and ear-tagged. In August and September, some calves were transferred to other places (as this is an optimal age for transporting this species). As a result, in mid-October, Group 1 consisted of only 19 (7 male and 12 female) calves, and Group 2 consisted of 21 (12 male and 9 female) calves.

Animal and call samples

For acoustic analyses, we used the nasal calls of 35 subjects, of 16 (7 male and 9 female) calves from Group 1 and of 19 (11 male and 8 female) calves from Group 2. The remaining animals did not provide sufficient number of calls for analysis. Calls were recorded at two ages, as juvenile and then as adolescents. The juvenile calls were recorded in May–June, between 3 and 6 full weeks of age (from the 21st to 48th day inclusive). The adolescent calls were recorded in October–November, between 23 and 26 full weeks of age (from the 161st to 188th day inclusive). Calls were recorded daily, 30–120 min before the morning or evening feeding time. In the study site, the climate is extremely hot, so all animals were inactive from before 10:00 to about 18:00. Before the morning and evening feeding time, the calves started actively move and interact with one another, attended by an increase in vocal activity. Thus, these calls were not immediately begging for food. Recording sessions were scheduled with the aim of collecting a similar amount of acoustic data on each individual throughout the data collection period. Distance to the microphone was 1–5 m. The calls of the focal animal were labelled on the recorder orally. For acoustic recordings (48 kHz, 16 bit), we used a Zoom-H4 (Zoom Corp., Tokyo, Japan) digital recorder with Sennheiser K6-ME66 cardioid electret condenser microphone (Sennheiser electronic, Wedemark, Germany).

For acoustic analyses, we selected calls not disrupted by wind or overlapped by noise or human voice. For each individual, we took measurements from 20 to 25 juvenile calls and from 20 to 25 adolescent calls. If fewer than 25 calls were available, we included into analyses all of them. If more than 25 calls were available per animal per age, we selected calls for analysis randomly among calls of good quality. To reduce pseudoreplication, we took calls from different recording sessions for each animal and from different pieces within sessions (Reby et al. 1999; Briefer and McElligott 2011a; Efremova et al. 2011). The average

number of sessions per animal per age was 9.4 ± 2.9 (5–20), and we took 1–5 calls per session per animal. In total, we analysed 1,701 calls, 397 juvenile calls and 379 adolescent calls in Group 1 (2008), and 461 juvenile calls and 464 adolescent calls in Group 2 (2009).

Call analysis

For each call, we measured 9 acoustic variables (Fig. 1). Using Avisoft SASLab Pro software (Avisoft Bioacoustics, Berlin, Germany), we measured the duration with the standard marker cursor in the spectrogram window (sampling frequency 48 kHz, Hamming window, FFT 1,024 points, frame 50 % and overlap 93.75 %). From the mean power spectrum of Avisoft, we measured the upper, medium and lower quartile (q25, q50 and q75), covering
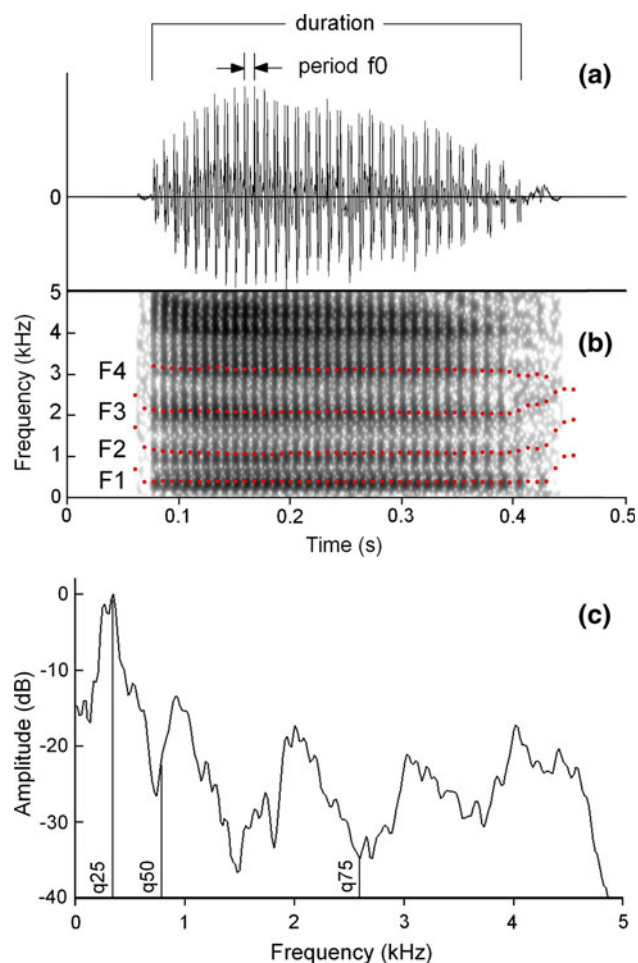

Fig. 1 The nasal call of adolescent female #31: **a** waveform, **b** spectrogram and **c** mean power spectrum. Measured acoustic variables: duration, fundamental frequency period (period f0), tracks of the first 4 formants (F1–F4), lower (q25), medium (q50) and upper quartiles (q75). The LPC settings were as follows: Burg analysis, window length 0.04 s, time step 0.01 s, maximum number of formants 4 and maximum formant frequency 3,400 Hz

respectively 25, 50, and 75 % of call energy. With the "Autocorrelation" option of Avisoft, we measured the mean fundamental frequency (f0). This option recognizes periodic components in the sound signal and measures their period with 0.25-ms precision, which allowed us to calculate the f0 with 1-Hz precision. All measurements were exported to Microsoft® Excel.

The values of nasal vocal tract lengths (149 mm in two 3–4 weeks males, 150 mm in the 8 weeks female, 185 mm in the 7 months female and 220 mm in the 7 months male) were obtained earlier by anatomical dissections (Efremova et al. 2011; Volodin et al. 2011) and were used in this study to establish settings for measuring formants. The four first formants (F1, F2, F3 and F4) were measured using linear prediction coding (LPC) with Praat DSP package v. 5.2.07 (Boersma and Weenink 2009). Applying the model of a uniform tube closed at one end (Fitch and Reby 2001), we approximated formant frequencies as:

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

where n is formant number (1, 2, 3, etc.), L is vocal tract length and c is the speed of sound in air (350 m s^{-1}). The LPC settings were Burg analysis, window length 0.04 s, time step 0.01 s and maximum number of formants 4–6. For juvenile calls, the range of maximum formant frequencies was 4,000–5,000 Hz, with limits from 2,600 to 5,500 Hz. For adolescent calls, the range of maximum formant frequencies was 2,900–3,500 Hz, with limits from 2,600 to 4,000 Hz (Fig. 1). Formant measurements were taken from the call portion where the formant tracks are nearly horizontal. Positions of formants were verified by superposition on the narrowband spectrogram. Point values of formant tracks were extracted 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 conducted using STATISTICA (StatSoft, Tulsa, OK, USA) and R v.3.0.1 (R Development Core Team 2009). A Kolmogorov–Smirnov test showed that distributions of acoustic parameter values did not depart from normality ($P > 0.05$). For each juvenile and adolescent subject of Group 1 and Group 2, we calculated mean values of the acoustic variables. Then, we used one-way ANOVA to estimate the effect of group on the acoustics.

We used discriminate function analysis (DFA) standard procedure with all the 9 acoustic variables (f0, duration, the first four formants and the q25, q50 and q75 quartiles) to calculate the probability of the assignment of calls to the correct individual for each of four call samples (Group 1 juveniles, Group 1 adolescents, Group 2 juveniles and Group 2 adolescents). We used Wilks' Lambda values to estimate how strongly the acoustic variables of calls contribute to discrimination of individual. Wilks' Lambda is the standard statistic that is used to denote the statistical significance of the discriminatory power. Its value will range from 1.0 (no discriminatory power) to 0.0 (perfect discriminatory power). So, the smallest Wilks' Lambda corresponds to the greatest contribution to the overall discrimination.

To estimate the effects of group and of age on individual vocal identity, we used two-tailed exact permutation tests (10,000 permutations) to compare the values of correct assignment for each individual between the following categories: Group 1 juveniles, Group 1 adolescents, Group 2 juveniles and Group 2 adolescents. We used Bonferroni adjustments to correct for multiple testing, and results of the permutation tests retained significance when $P < 0.025$ (i.e. 0.05/2, as each category was included in two comparisons). Also, we used the nonparametric Wilcoxon matched-pairs signed-ranks test to compare the values of correct assignment between juvenile and adolescent calls within Group 1 and within Group 2.

To assess the effect of group membership, we calculated Euclidean distances between individuals according to the characteristics of their calls (see Briefer and McElligott 2012; Knörnschild et al. 2012). Calls of juveniles and adolescents were treated separately in the various analyses. First, we calculated the position of each call of each subject in the space of canonical axes of DFA, drawn separately for all juveniles and all adolescents. Then, for each individual, we obtained individual centroids and calculated Euclidean distances between these centroids for each pair of animals. Euclidean distances were used as a measure of similarity in the structure of calls for each pair of animals. Shorter Euclidean distances between individuals indicated more similar call structure. Separately for juveniles and adolescents, we created two pairs of samples of Euclidean distances, one consisting of distances between individuals belonging to the same group ($N = 291$ between pair distances), and another consisting of distances between individuals belonging to different groups ($N = 304$ between pair distances). Kolmogorov–Smirnov test showed that none of the four distributions of Euclidean distances departed from normality ($P > 0.05$). To estimate the effects of group membership and age on similarity of call characteristics, we used two-tailed exact permutation tests (10,000 permutations) to compare overall distances between the following categories: Group 1 juveniles, Group 1 adolescents, Group 2 juveniles and Group 2 adolescents. We used Bonferroni adjustments to correct for multiple testing, and results of the permutation tests retained significance when $P < 0.025$ (i.e. 0.05/2, as each category was included in two comparisons).

Ethical note

Goitred gazelles are open country animals and extremely shy. So, transportation of wild-caught animals is impossible, as they immediately injure or even kill themselves in fenced conditions. Collecting wild-born animals (preferentially one per twin) shortly after birth and then hand rearing them is the only way to distribute these animals to other facilities or zoos. This does not result in imprinting on humans, and from adolescence, these animals are becoming wild again. As adults, they are capable of breeding, either in large enclosures or in the wild. The rearing conditions were in accordance with more than 30-year practice of animal care developed by the Djeiran Ecocenter (Soldatova et al. 2010). This rearing technique closely addresses very specific biological demands of this species. No animal suffered in any way due to the data collection. During our work, we adhered to the 2006 Guidelines for the treatment of animals in behavioural research and teaching of the Association for the Study of Animal Behaviour and to the laws of the Russian Federation and the Republic of Uzbekistan, the countries where the research was conducted. Research protocol #2008-03 was approved by the Committee of bio-ethics of Lomonosov Moscow State University.

Results

We estimated the group effect on mean values of acoustic variables in juveniles and adolescents (Table 1). The f0 did not differ significantly between Group 1 and Group 2 either for juveniles, or for adolescents. Call duration did not differ between the groups for juveniles, but was significantly higher in Group 2 compared to Group 1 for adolescents. The values of all first four formants were significantly higher in Group 1 for juveniles, however, in adolescents, the values of F3 and F4 were higher in Group 2, whereas the values of F1 and F2 did not differ between groups. Only q75 was marginally higher in Group 2 in juveniles, and only the q25 was significantly higher in Group 1 in adolescents.

We conducted 4 independent DFAs for assignment to individual with the same 9 variables: for Group 1 juveniles, Group 1 adolescents, Group 2 juveniles and Group 2 adolescents. Between Group 1 and Group 2, DFA scores of correct classification to individual did not differ either for juveniles (exact permutation test, $N = 35$, $P = 0.25$) or for adolescents ($N = 35$, $P = 0.22$) (Fig. 2). DFA scores of correct classification to individual were significantly lower in juveniles than in adolescents, in Group 1 (with DFA scores of 58.7 and 75.2 %, respectively, exact permutation test, $N = 32$, $P = 0.0046$), but not in Group 2 (with DFA scores of 63.6 and 71.1 %, respectively, $N = 38$, $P = 0.0915$) (Fig. 2). Also, the Wilcoxon matched-pairs test showed that DFA scores of correct classification to individual increased significantly from juveniles to adolescents in Group 1 ($N = 16$, $T = 24$, $P = 0.023$), but not in Group 2 ($N = 19$, $T = 44$, $P = 0.124$). For a pooled call sample of Group 1 and Group 2, DFA scores of correct classification to individual in juveniles were significantly lower than in adolescents (Wilcoxon test, $N = 35$, $T = 130$, $P = 0.007$).

For juveniles of both Group 1 and Group 2, the f0, F4, F3 and F2 (in order of decreasing importance) were mainly responsible for discrimination of individuals (Table 2). For adolescents of both Group 1 and Group 2, the f0, F4, F3 and duration (in order of decreasing importance) were

Table 1 Values (mean ± SD) of acoustic variables of nasal calls, recorded from juveniles and adolescents of Group 1 and Group 2, and ANOVA results for comparison between Groups, separately for juveniles and adolescents

Call variable	Juveniles			Adolescents		
	Group 1 $N = 16$	Group 2 $N = 19$	Group effect	Group 1 $N = 16$	Group 2 $N = 19$	Group effect
f0 (Hz)	90.2 ± 13.3	83.4 ± 8.9	$F_{1,34} = 3.24, P = 0.08$	63.0 ± 12.5	64.8 ± 9.0	$F_{1,34} = 0.24, P = 0.63$
Duration (s)	0.25 ± 0.03	0.26 ± 0.07	$F_{1,34} = 0.42, P = 0.52$	0.25 ± 0.07	0.30 ± 0.06	$F_{1,34} = 7.13, \boldsymbol{P = 0.012}$
F1 (Hz)	553 ± 30	458 ± 40	$F_{1,34} = 62.16, \boldsymbol{P < 0.001}$	372 ± 18	355 ± 36	$F_{1,34} = 3.11, P = 0.09$
F2 (Hz)	1,391 ± 89	1,320 ± 102	$F_{1,34} = 4.72, \boldsymbol{P = 0.037}$	957 ± 60	994 ± 71	$F_{1,34} = 2.69, P = 0.11$
F3 (Hz)	2,807 ± 135	2,681 ± 167	$F_{1,34} = 5.91, \boldsymbol{P = 0.021}$	1,999 ± 103	2,143 ± 114	$F_{1,34} = 15.08, \boldsymbol{P < 0.001}$
F4 (Hz)	3,864 ± 171	3,668 ± 175	$F_{1,34} = 11.06, \boldsymbol{P = 0.002}$	2,848 ± 136	2,946 ± 103	$F_{1,34} = 5.86, \boldsymbol{P = 0.021}$
q25 (Hz)	371 ± 32	367 ± 39	$F_{1,34} = 0.10, P = 0.75$	296 ± 41	259 ± 45	$F_{1,34} = 6.56, \boldsymbol{P = 0.015}$
q50 (Hz)	799 ± 95	867 ± 197	$F_{1,34} = 1.56, P = 0.22$	862 ± 330	768 ± 279	$F_{1,34} = 0.83, P = 0.37$
q75 (Hz)	2,381 ± 336	2,647 ± 426	$F_{1,34} = 4.09, P = 0.051$	2,340 ± 510	2,272 ± 322	$F_{1,34} = 0.23, P = 0.64$

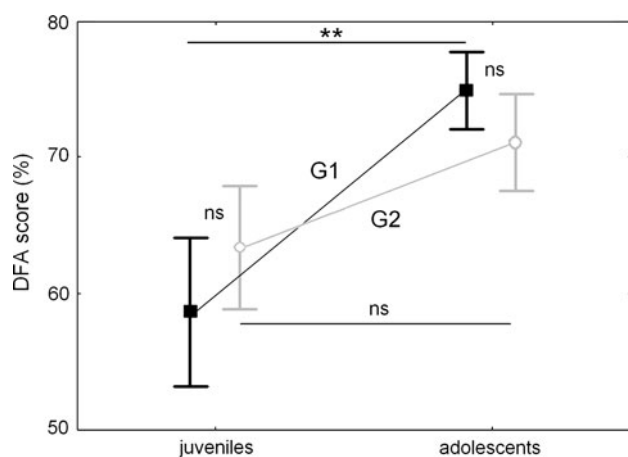Significant differences are given in bold

Fig. 2 DFA score of correct classification (mean ± SE) of nasal calls to individual within juveniles and adolescents of Group 1 (G1) and Group 2 (G2). The exact permutation test: **P < 0.01; ns differences are non-significant

Fig. 3 Euclidean distances (mean ± SE) between DFA centroids of individuals from the same group (SG) versus individuals from different groups (DG) in juvenile and adolescent goitred gazelles. Shorter distances between individuals indicate more similar call structure. The exact permutation test: ***P < 0.001

mainly responsible for discrimination of individuals (Table 2). Therefore, in both groups and in both ages, the variables mainly responsible for discriminating individuals were the same: f0 and frequencies of two upper formants.

The exact permutation tests revealed effects of group membership and of age on the Euclidean distances between DFA centroids of individuals (Fig. 3). Calls of individuals from the same group were more similar (i.e. Euclidean distances between DFA centroids of individuals were shorter) than calls of individuals from different groups, as for juveniles ($N = 595$, $P < 0.0001$) and for adolescents ($N = 595$, $P = 0.0001$). The similarity between calls decreased along ontogeny from juvenile to adolescent for members of the same group ($N = 582$, $P < 0.0001$) and for individuals from the different groups ($N = 608$, $P < 0.0001$).
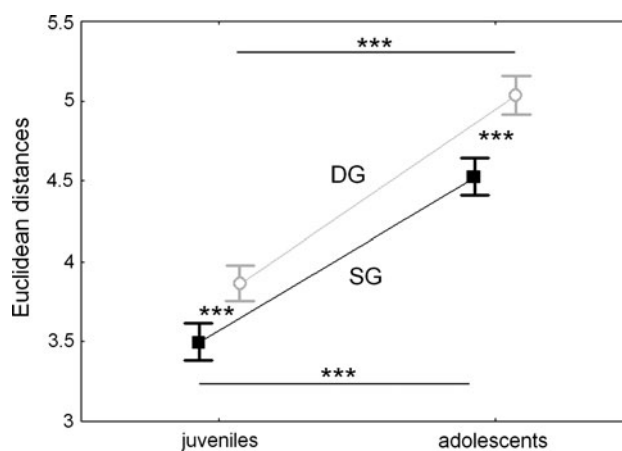
Discussion

This study of nasal contact calls of goitred gazelles revealed more similar calls within than between social groups in both juveniles and adolescents. This supports our first prediction that social group membership is responsible for the vocal signature in peer groups of goitred gazelles. These data suggest that goitred gazelle calves modify their calls based on vocal influences from group members, similarly to domestic goat kids (Briefer and McElligott 2012) and non-human primates (Lemasson et al. 2003, 2011; Crockford et al. 2004; Tanaka et al. 2006). Accordingly to the definition by Janik and Slater (2000), such call modification represents a kind of vocal production learning.

Table 2 Wilks' Lambda value and variable effect for each acoustic variable included into the four independent DFAs for assignment to individual (Group 1 juveniles, Group 1 adolescents, Group 2 juveniles and Group 2 adolescents)

Call variable	Group 1 juveniles		Group 2 juveniles		Group 1 adolescents		Group 2 adolescents	
	Wilks' Lambda	Variable effect	Wilks' Lambda	Variable effect	Wilks' Lambda	Variable effect	Wilks' Lambda	Variable effect
f0	**0.232100**	$F = 82.27$	**0.344294**	$F = 45.92$	**0.180519**	$F = 107.44$	**0.251872**	$F = 72.11$
Duration	0.843759	$F = 4.60$	0.768329	$F = 7.27$	**0.607437**	$F = 15.29$	**0.627640**	$F = 14.40$
F1	0.896057	$F = 2.88$	0.860656	$F = 3.90$	0.790121	$F = 6.29$	0.742564	$F = 8.42$
F2	**0.672119**	$F = 12.13$	**0.621855**	$F = 14.66$	0.743639	$F = 8.16$	0.705846	$F = 10.12$
F3	**0.669416**	$F = 12.28$	**0.499346**	$F = 24.17$	**0.552659**	$F = 19.16$	**0.459166**	$F = 28.60$
F4	**0.615843**	$F = 15.51$	**0.495383**	$F = 24.56$	**0.568746**	$F = 17.95$	**0.448121**	$F = 29.90$
q25	0.869309	$F = 3.74$	0.820540	$F = 5.27$	0.781049	$F = 6.63$	0.863711	$F = 3.83$
q50	0.887612	$F = 3.15$	0.895680	$F = 2.81$	0.747862	$F = 7.98$	0.782715	$F = 6.74$
q75	0.902491	$F = 2.69$	0.898156	$F = 2.73$	0.735424	$F = 8.51$	0.873807	$F = 3.51$

The smaller is the Wilks' Lambda value, the greater is the contribution of the call variable to the overall discrimination. For each DFA, the four variables, mostly contributed into discrimination, are given in bold

Within-group call similarity was significantly lower in adolescent than in juvenile goitred gazelles. This is contrary to our second prediction and data on domestic goat kids (Briefer and McElligott 2012), suggesting that group vocal identity increases with age, as a joint function of maturation and of time that animals spent together. On the other hand, the youngest (3–6-weeks) gazelles in our study matched the oldest (5-weeks) goat kids in the study by Briefer and McElligott (2012). Thus, both studies were consistent in that the juvenile age class showed group membership more prominently compared to other age classes (infants or adolescents).

An ontogenetic increase in within-group similarity has been reported also for Japanese macaques (Tanaka et al. 2006) and the greater sac-winged bats, *Saccopteryx bilineata* (Knörnschild et al. 2012). Only in the study by Knörnschild et al. (2012) the research design allowed to separate effects of maturation and of time that animals spent together in the same social groups. In our study with goitred gazelles, this was impossible, because acoustic variables changed drastically along ontogeny from juveniles to adolescents (Table 1, see also Fig. 4 in Lapshina et al. 2012). Although vocal individuality was based on the same acoustic variables in juveniles and adolescents (Table 2), in most subjects their actual values changed uncoordinatedly between ages (Lapshina et al. 2012).

While individual vocal identity increased along ontogeny from juveniles to adolescents, the group vocal identity decreased in both social groups of goitred gazelles. In contrast, in domestic goat kids, both individual and group identity increased with age (Briefer and McElligott 2011b, 2012), and in the greater sac-winged bats, only group identity increased, whereas the individual signature remained unchanged (Knörnschild and von Helversen 2008; Knörnschild et al. 2012). These different developmental trends of individual and group identity could be related to different needs of advertising individual or group identity between species and ages.

In the two species of ungulates, domestic goats and goitred gazelles, the prominence of vocal group indicators in juveniles compared to neonates or adolescents might be related to their adaptive function. Both species are hiders at early ontogeny and followers as juveniles (goitred gazelles: Soldatova 1983; Pereladova and Pereladov 1986; domestic goats: Terrazas et al. 2003). Free-ranging mother and young units of goitred gazelles join in small groups for travelling and foraging. The 3–6 weeks juvenile goitred gazelles in such groups are highly familiar with one another, keep together and often play with one another (Soldatova 1983). This pattern of spatial proximity may promote the development of vocal group signature in juvenile goitred gazelles in the wild. Juveniles already eat grass but still rely on the mother for milk up to weaning at

3–4 months of age. Although female goitred gazelles preferentially nurse their own offspring, in the case of the death of a mother, another female from the same group may start nursing an orphan. This is more probable if the calf is familiar to the female and vocalizes similarly to her own calf. Apart from nursing, social support from a group for searching for better places for foraging, watering and for detection of predators, will enhance calves' chances of survival. Therefore, vocal-based group cohesion would be adaptive even for non-kin group members. Allosuckling has been documented for goitred gazelles kept together in the same enclosures for prolonged time (Kruchenkova 2009). Mother and offspring feral domestic goats also travel in small groups and occasionally feed unrelated, but familiar kids from such groups (Packer et al. 1992).

Unlike the juvenile stage, the ontogenetic stage of premature adolescent goitred gazelles corresponds to a transition to social independence in fission–fusion groups of older animals (Blank et al. 2012). Adolescents do not depend on milk are more capable of running from predators and more familiar with foraging and watering places. Accordingly, the vocal group indicators became less prominent in adolescents than in juveniles in the same social groups of goitred gazelles. Taking into account data by Briefer and McElligott (2012) for domestic goats, we can hypothesize that group-specific vocal traits appear in these ungulate species only for a short period, when offspring travel with their mothers in small groups. Such traits are typical of the situation of animals living in permanent groups, where learned group signature encodes social group affiliation in the manner of a "badge" or password (Tyack 2008). For example, the learned vocal group signature of the polygynous greater sac-winged bats reliably associates group members with their natal colony (Knörnschild et al. 2012). Alternatively, a group-specific vocal signature can develop as a by-product of animal relatedness, as in meerkats, even though it is not used if other cues for kin recognition are available (Townsend et al. 2010).

In addition to social effects, other factors can be responsible for closer similarity of calls within groups. In Japanese macaques, differences in coo calls between groups were affected by propagation ability and the degree of ambient noise (Tanaka et al. 2006). An influence of environmental conditions on differences in alarm calls between colonies has been also proposed for Gunnison's prairie dog *Cynomys gunnisoni* (Perla and Slobodchikoff 2002). However, in our study of goitred gazelle calves, keeping conditions did not differ between years, and both Group 1 and Group 2 were housed in the same enclosures in two sequential years. Recording situations and distance to the animals were the same for both groups. In both groups, recordings were made from animals of matched

ages and body mass, which is similar between sexes among juvenile and among adolescent goitred gazelles (Lapshina et al. 2012). We examined only the nasal contact calls, produced by animals at low arousal (Efremova et al. 2011), which excluded the potential effects of the degree of arousal on the acoustic variables, primarily the fundamental frequency (Briefer 2012; Lingle et al. 2012).

In addition, call similarity may be influenced by genetic differences between individuals, which can be responsible for differences in the morphology of vocal apparatus or the means of producing sounds (e.g. Lieblich et al. 1980; Lemasson et al. 2003; Townsend et al. 2010). In domestic goat kids, effects of kinship on call structures were found, since siblings had more similar calls than half-siblings (Briefer and McElligott 2012). In our study of goitred gazelles, the social groups were matched in the degree of relatedness, as their members were born in two successive years on the same large fenced territory, inhabited by approximately 900 free-ranging individuals (Pereladova et al. 1998; Frey et al. 2011), comprising a genetically variable population (Sorokin et al. 2011). As twin siblings were never collected together, all calves within each group originated from different mothers, and, taking into account the size of the population, most of them would also have been sired by different fathers.

Therefore, social effects, mediating some kind of vocal production learning, represented the most plausible explanation for the observed vocal similarity of juveniles and adolescents within the social groups of goitred gazelles we studied (e.g. Janik and Slater 1997, 2000). Playback experiments are necessary, however, to confirm that group-specific vocal indicators indeed can be used by goitred gazelles for recognition of group members (Townsend et al. 2010).

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