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Individuality of distress and discomfort calls in neonates with bass voices: Wild-living goitred gazelles (*Gazella subgutturosa*) and saiga antelopes (*Saiga tatarica*)

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Abstract

Neonate ruminants produce distress calls when captured by a predator and discomfort milk begging calls when hungry. In many neonate ruminants, the distress and discomfort calls are high-frequency vocalizations, in which the fundamental frequency is the key variable for recognition of their emotional arousal by caregivers. In contrast, in this study, we examine the low-frequency open-mouth distress and discomfort calls in the neonates of two species of wild-living ungulates, which clearly highlight vocal tract resonances (formants). In the goitred gazelle (*Gazella subgutturosa*), the distress calls were higher in fundamental frequency (f0) and in the first and third formants than the discomfort calls. The accuracy of classifying individuals by variables of distress calls with discriminant function analysis (67%) was significantly lower than that of discomfort calls (85%). In the saiga (*Saiga tatarica*), only the third formant was higher in the distress calls than in the discomfort calls. The accuracy of classifying individuals by variables of distress calls (89%) did not differ significantly from that of discomfort calls (94%). Thus, the use of acoustic cues to vocal identity and to the degree of arousal differs between the two species. Calls were significantly more individualistic in the saiga, probably because this species lives in large herds and neonates use a 'following' antipredatory strategy, in which vocal individuality is crucial for mother–offspring communication. In contrast, goitred gazelles live in smaller groups and neonates use a 'hiding' antipredatory strategy. Accordingly, mothers can rely on additional environmental cues for spotting their young and this may decrease the necessity for individualization of the calls of neonates.

KEYWORDS
acoustic behaviour, antipredatory strategy, emotional arousal, mother–offspring communication, ruminants, vocal identity

1 | INTRODUCTION

In neonate ruminants, the acoustic structure of distress calls produced in the context of capture by a predator differs from that of discomfort calls produced in the context of hunger (Lingle, Wyman, Kotrba, Teichroeb, & Romanow, 2012). Acoustic variables reflect the degree of emotional arousal of the callers (Briefer, 2012; Gogoleva, Volodin, Volodina, Kharlamova, & Trut, 2010; Lingle et al., 2012; Volodin, Volodina, Gogoleva, & Doronina, 2009; Zaytseva, Volodin, Ilchenko, & Volodina, 2016) and in some cases may disclose their individual

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identity (Briefer & McElligott, 2011a; Charrier, Mathevon, & Jouventin, 2002; Espmark, 1975; Sebe, Duboscq, Aubin, Ligout, & Poindron, 2010; Shillito-Walser, Hague, & Walters, 1981; Sibiryakova et al., 2015, 2017; Terrazas, Serafin, Hernandez, Nowak, & Poindron, 2003).

The acoustic cues to the degree of arousal are largely similar across species (Briefer, 2012; Lingle & Riede, 2014). Distress calls of animals attacked by a predator force the predator to release its prey or attract additional predators that might frighten the first one (e.g., Branch & Freeberg, 2012; Brodie, 1978). In species that defend their offspring against predators (Jacques & Jenks, 2010; Lingle, Rendall, & Pellis, 2007; Lingle, Rendall, Wilson, Deyoung, & Pellis, 2007; Scornavacca & Brunetti, 2016; Smith, 1987), the distress calls of the young may stress the urgent need for their caregiver's response (Lingle, Rendall, & Pellis, 2007; Lingle, Rendall, Wilson, et al., 2007; Teichroeb, Riede, Kotrba, & Lingle, 2013).

Discomfort calls of hungry animals advertise the nutritional needs of the callers (Illmann, Hammerschmidt, Špinka, & Tallet, 2013; Manteuffel, Puppe, & Schön, 2004; Tallet et al., 2013; Weary, Lawson, & Thompson, 1996; Weary, Ross, & Fraser, 1997), their body size (Briefer & McElligott, 2011b; Efremova, Volodin, Volodina, Frey, Lapshina, et al., 2011; Efremova, Volodin, Volodina, Frey, Soldatova, et al., 2011) and their individual identity (Briefer & McElligott, 2011a; Searby & Jouventin, 2003; Shillito-Walser et al., 1981; Terrazas et al., 2003). The individuality of the calls is important for the caregivers in order to recognize their own offspring and to reject alien young (Marmasinskaya, 2008; Torriani, Vannoni, & McElligott, 2006) to avoid potential allosuckling (for review, see Brandlová, Bartoš, & Haberová, 2013).

Topographic cues (landmarks) facilitate vocal recognition of the offspring by their parents by providing additional spatial information and act as regulators of the amount of individuality encoded in the calls of the young (Torriani et al., 2006). When topographic cues are lacking, the calls of bird chicks are substantially more individualistic than when these cues are available (Beecher, Beecher, & Hahn, 1981; Beecher, Beecher, & Lumpkin, 1981; Insley, Phillips, & Charrier, 2003; Jones, Falls, & Gaston, 1987; Klenova, Volodin, & Volodina, 2009; Lefevre, Montgomery, & Gaston, 1998; McArthur, 1982; Seddon & Heezik, 1993). The presence of landmarks may also facilitate spotting of the young by their mothers in ruminants and may therefore reduce the need for highly individualistic calls (Torriani et al., 2006). Therefore, neonate discomfort calls produced in the context of hunger are expected to be less individualistic in those species for which topographic cues are available as an additional cue for offspring recognition than in other species that cannot rely on such landmarks.

Neonate goitred gazelles (*Gazella subgutturosa*) and saiga antelopes (*Saiga tatarica*) use different strategies against predation. Goitred gazelle neonates are hiders for 2–3 weeks post-partum on individual parcels of land occupied by their mothers within the breeding grounds of this species in the semideserts of Central Asia (Blank, 1998; Blank, Ruckstuhl, & Yang, 2015; Jevnerov, 1984; Marmasinskaya, 1996, 2008). For the remaining year, they forage together with their mothers and other young in small groups or herds (Blank, Ruckstuhl, & Yang, 2012). In contrast, saiga neonates are followers after birth. Within

30 min after birth, they are already capable of standing, suckling and walking, and they even try to run (Danilkin, 2005; Kokshunova, 2012). A few hours after birth, they transfer to another place together with their mothers; after 2–3 days, they follow their mothers permanently, and after 10 days, they are capable of following the herd and running as quickly as adults in the case of danger (Danilkin, 2005; Sokolov & Zhirnov, 1998). For the remaining year, they forage in herds of many thousand individuals in the steppes of Russia and Kazakhstan (Bannikov, Jirnov, Lebedeva, & Fandeev, 1961; Danilkin, 2005; Sokolov & Zhirnov, 1998). As a consequence of these behavioural differences, goitred gazelle mothers have a much greater opportunity to rely on landmarks in addition to acoustic cues for the spotting of their offspring than saiga mothers.

All sex and age classes of goitred gazelle and saiga vocalize (goitred gazelle: Volodin, Lapshina, Volodina, Frey, & Soldatova, 2011; Efremova, Volodin, Volodina, Frey, Lapshina, et al., 2011; Efremova, Volodin, Volodina, Frey, Soldatova, et al., 2011; Lapshina et al., 2012; saiga: Frey, Volodin, & Volodina, 2007; Volodin, Volodina, & Efremova, 2009; Volodin, Sibiryakova, Kokshunova, Frey, & Volodina, 2014). Both goitred gazelles and saigas produce calls through the nose (nasal calls) and through the mouth (oral calls). Vocal output is the joint product of both vocal fold vibrations in the larynx, determining the call fundamental frequency (f0), and filtering by the supra-laryngeal vocal tract, determining the values of the vocal tract resonances, representing the formant frequencies (Fant, 1960; Taylor & Reby, 2010; Titze, 1994). The formant frequencies are inversely related to the length of the vocal tract (Fant, 1960; Fitch & Hauser, 2002; Taylor & Reby, 2010; Titze, 1994). In most mammals, the nasal vocal tract is longer than the oral vocal tract. This refers not only to saigas with their trunk-like nose (Volodin, Sibiryakova, et al., 2014) but also to goitred gazelles with their typical mammalian nose (Efremova et al., 2016; Volodin et al., 2011). Correspondingly, the formants of oral calls are always higher than those of nasal calls in goitred gazelles (Efremova, Volodin, Volodina, Frey, Lapshina, et al., 2011) and saigas (Volodin, Sibiryakova, et al., 2014). According to the source-filter theory of voice production, source and filter variables are independent of each other (Fant, 1960; Titze, 1994; Volodin, Sibiryakova, et al., 2014). However, in goitred gazelle and in saiga neonates, the f0 is higher in the oral than in the nasal calls (Volodin et al., 2011; Volodin, Sibiryakova, et al., 2014).

As the acoustics of the oral and nasal calls differ, analyses of the effects of individuality and arousal on the acoustics should be conducted separately for the nasal and oral calls. In captive 3- to 6-week-old goitred gazelles, acoustic individuality is more strongly expressed in the oral than in the nasal contact calls (Volodin et al., 2011) and individuality of the nasal contact calls increases between 3–6 weeks and 6 months of age (Lapshina et al., 2012). In goitred gazelles, neonate vocalizations have not yet been studied to date. Some aspects of the acoustic structure of saiga neonate vocalizations have been investigated (Volodin, Sibiryakova, et al., 2014), but information on acoustic individuality is lacking for all call types and ages.

It is unclear why the calls of young goitred gazelles and saiga are very low-frequency (Efremova, Volodin, Volodina, Frey, Lapshina, et al., 2011; Efremova, Volodin, Volodina, Frey, Soldatova, et al., 2011;

Lapshina et al., 2012; Volodin et al., 2011; Volodin, Sibiryakova, et al., 2014) compared to the calls of many other neonate ruminants (Briefer & McElligott, 2011b; Lingle, Rendall, & Pellis, 2007; Lingle et al., 2012; Sibiryakova et al., 2015; Teichroeb et al., 2013). These 'bass voices' of the young clearly highlight formants, similar to the low-frequency distress calls of 10- to 32-day-old reindeer *Rangifer tarandus* (Espmark, 1975). The close acoustic similarity between neonate goitred gazelles and saiga antelopes makes their calls a convenient model for a comparative study, as the same acoustic variables can be measured in both species (Volodin et al., 2011; Volodin, Sibiryakova, et al., 2014). In this study, we investigate acoustic cues to individuality and to the degree of emotional arousal in the orally produced distress and discomfort calls of neonates in these ruminant species. We compare the acoustic individuality of the distress calls produced as a reaction of neonates (1–10-day neonate goitred gazelles and 1- to 3-day neonate saigas) to being 'captured' by a 'surrogate predator' (human) with the discomfort calls produced when neonates are hungry. We expected to find: (i) less individualistic calls in the 'hider' (goitred gazelle) than in the 'follower' species (saiga antelope); (ii) intraspecific differences in the acoustics of the distress and discomfort calls; (iii) less individualistic distress calls than discomfort calls within both species.

2 | MATERIALS AND METHODS

2.1 | Study sites and dates

Goitred gazelle distress and discomfort calls were recorded between April 29 and May 12 2008 and between May 5 and May 13 2009 from neonate (1–10 days post-partum) goitred gazelles in the Ecocenter 'Djeiran' (Uzbekistan, Bukhara region, 39°41′N, 64°35′E). The Ecocenter 'Djeiran' is located on a fenced 5,145 hectare area of semidesert, inhabited by 600 – 1,200 free-ranging goitred gazelles in different years (Pereladova et al., 1998; Volodin et al., 2011). Adult females give birth to one or two young from the end of April to mid-May (Blank & Yang, 2015). Distress calls were recorded during capturing of neonate goitred gazelles on their breeding grounds by the staff of the Ecocenter 'Djeiran', whereas the discomfort calls were recorded within 1–3 days after capture in enclosures of the Ecocenter where the animals were human-raised for subsequent transfer to other breeding centres or zoos.

Saiga distress and discomfort calls were recorded between 12 May and 18 May 2014 from wild neonate (1–3 days post-partum) saigas on their natural breeding grounds in the Turgai steppe of northern Kazakhstan (49°53′N, 65°48′E). Adult females give birth to one or two young in May (Bannikov et al., 1961). In May 2014, the entire saiga population of Kazakhstan comprised approximately 200 thousand animals. The study subpopulation of the Turgai steppe at the start of the study comprised approximately 30–40 thousand pregnant females. Distress calls were recorded during capturing saiga neonates by human counters conducting the yearly population census on the breeding grounds. Discomfort calls were recorded on the same breeding grounds within 1–3 days after the censuses using automated recording systems in the absence of people.

2.2 | Data collection

Goitred gazelle distress calls were collected from 36 wild neonates vocalizing for a few minutes after having been captured by humans. Captures were made after the onset of darkness. The animals were identified as distinctive individuals by order of capture but not sexed. Calls of each individual were stored as a separate WAV file. After capture, the animals were housed in enclosures of the Ecocenter where they were individually marked and sexed during the next morning. For acoustic recordings (48 kHz, 16 bit), we used a Marantz PMD-660 solid state recorder (D&M Professional, Kanagawa, Japan) with an AKG-C1000S (AKG-Acoustics Gmbh, Vienna, Austria) cardioid electret condenser microphone. Distance to the microphone varied between 1 and 3 m.

Goitred gazelle discomfort calls were collected from 24 captured animals in the small enclosures (2 × 4 m) of the Ecocenter in the context of hunger. There were 5–7 individuals per enclosure, and the animals were individually dye-marked and sexed (for keeping, marking and sexing details, see Volodin et al., 2011). The animals were most vocally active during food anticipation before the time of feeding, so these calls could be interpreted as discomfort calls at hunger. The calls of the focal animal were labelled by human voice during the recordings. From 1 to 4 recordings were made per animal (mean ± *SD* = 1.83 ± 0.87 recordings) within 1–3 days after capture; each recording lasted a few minutes. For the acoustic recordings (48 kHz, 16 bit), we used a Zoom-H4 (Zoom Corp., Tokyo, Japan) with an AKG-C1000S (AKG-Acoustics Gmbh, Vienna, Austria) cardioid electret condenser microphone. Distance to the microphone varied between 1 and 5 m. Not all individuals (90%) produced distress calls during captures and not all individuals provided discomfort calls later in the enclosures; in 13 callers, distress and discomfort calls were sampled from the same individuals.

Saiga distress calls were collected from 25 wild neonates vocalizing for a few minutes after capture when being handled by humans. Captures were made during daylight hours. The animals were identified as distinctive individuals by order of capture and sexed. Calls of each individual were stored as a separate WAV file. The entire handling procedure lasted 3–5 min per animal. Approximately 15% of the captured animals vocalized during this procedure. Then, the animal was returned to the place of capture, with its legs bent carefully under the body and the eyes tightly covered by human hands to decrease arousal evoked by the preceding capture. Usually, the young remained at this place when human counters left. Each day, the census started at a distance at least 1 km apart from the place of the previous census, to exclude repeated capturing of the same individuals. For recordings, we used a Marantz PMD-660 solid state recorder (D&M Professional, Kanagawa, Japan) with an AKG-C1000S (AKG-Acoustics Gmbh, Vienna, Austria) cardioid electret condenser microphone. Distance to the microphone varied between 1 and 3 m.

Saiga neonate discomfort calls were collected on the same sites as the neonate distress calls from 22 wild neonate saigas begging to be nursed by their mothers. For the recordings (22.05 kHz, 16 bit, stereo), we used three devices of the automated recording system Song

Meter SM2+ (Wildlife Acoustics Inc., Maynard, MA, USA). Each Song Meter device was positioned horizontally 20 cm above the ground. All the Song Meters were positioned while conducting the censuses and collecting the distress calls, but automatic recording of the discomfort calls started 1 hr later after the human counters had left. The Song Meters were collected 2–3 days later, when the saiga females together with their young had already left their breeding grounds for joining the large onward moving herd. As the recordings were made in the absence of humans, they were made without identification of individuals and sex. Notwithstanding this, individual callers could be identified as distinctive individuals by separating different call series. Potential overlapping between samples of distress callers and discomfort callers was negligible, as hundreds of saiga females and neonates aggregated around each Song Meter.

Although calls of twin-siblings could potentially be included in data sets (especially of saiga discomfort calls), a potential effect of this on the acoustic results was weak. In bovids, the effect of kinship on the acoustics is unnoticeable at 7 days of life (Briefer & McElligott, 2012) and later in ontogeny is indistinguishable from social effects on vocalization (Briefer & McElligott, 2012; Volodin, Volodina, Lapshina, Efremova, & Soldatova, 2014).

2.3 | Call samples

We analysed only oral distress and discomfort calls, which both goitred gazelle and saiga neonates produce with widely opened mouth, as in the studied contexts of capture or hunger, the oral distress and discomfort calls were emitted much more often than the nasal calls (Figure 1; Audio S1). For each goitred gazelle and saiga neonate caller, we took measurements from distress and discomfort calls of good quality, with clearly visible formant structure, not disrupted by wind and not overlapped by noise or human voice. All equipment used for the acoustic recordings of both species accurately reflected all measured acoustic variables in both contexts.

For goitred gazelles, we selected up to 15 (7.5 ± 4.4) distress calls per caller (in total 270 calls from 36 callers of unidentified sex) and up to 15 (11.7 ± 3.7) discomfort calls per caller (280 calls from 24 callers, 12 males and 12 females). For saigas, we selected up to 15 (11.0 ± 2.6) distress calls per caller (275 calls from 25 callers, 14 males and 11 females) and up to 15 (9.0 ± 0.8) discomfort calls per caller (197 calls

FIGURE 1 Neonate calls in contexts of capture by a predator (distress calls) and when being hungry (discomfort calls): (a) goitred gazelle distress call, (b) goitred gazelle discomfort call, (c) saiga distress call, (d) saiga discomfort call; waveforms (above) and spectrograms (below). The spectrogram was created with Hamming window, 24 kHz sampling rate, FFT 1,024 points, frame 50% and overlap 87.5%. The audio file of these calls is available as Audio S1
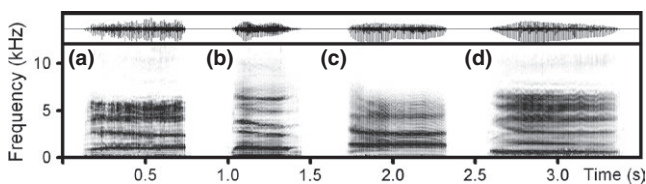
from 22 callers of unidentified sex). For each of these 107 callers, we calculated average values of the acoustic variables and used them to compare the parameter values of distress and discomfort calls within the two species.

For the analysis of individuality in distress and discomfort calls, we selected 144 distress calls from 15 callers (8–10 calls per caller) and 150 discomfort calls from 15 callers (10 calls per caller) of goitred gazelles, and 150 distress calls from 15 callers (10 calls per caller) and 141 discomfort calls from 15 callers (8–10 calls per caller) of saiga. We took these calls from animals that provided 8 - 10 distress or discomfort calls and, additionally, randomly selected 10 calls per type from animals for which more than 10 measured calls of either type were available.
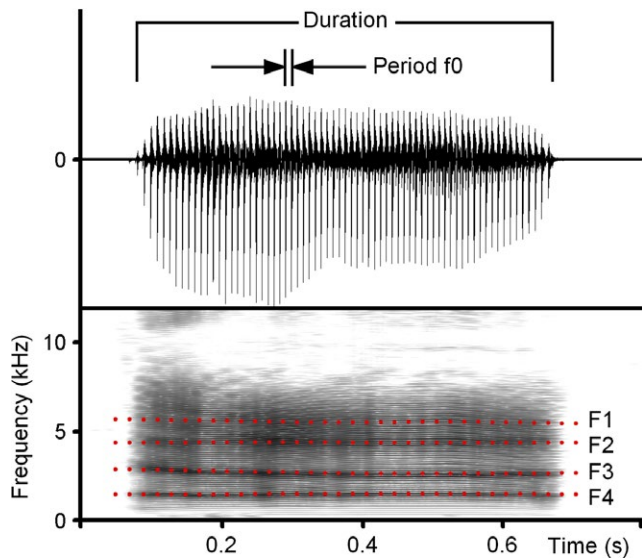
2.4 | Call analysis

For each call, we measured the same six acoustic variables: duration, fundamental frequency period and four formant frequencies (Figure 1). These variables that do not depend on the distance between animal and microphone proved their use as the best variables encoding vocal individual identity in goitred gazelles and were selected here also for comparability with previous studies (Lapshina et al., 2012; Volodin et al., 2011; Volodin, Volodina, et al., 2014). Prior to analysis, calls were downsampled to 22.05 kHz. We measured call duration with Avisoft SASLab Pro software (Avisoft Bioacoustics, Berlin, Germany) from the screen with the standard marker cursor in the main window of Avisoft. The mean f0 period (i.e., the mean distance from the previous pulse to the following pulse) was measured from the screen with the standard marker cursor in the main window of Avisoft, displaying the spectrogram and the waveform, with the following settings: Hamming window, FFT length 512, frame 50%. Frequency resolution of the spectrographic analysis was 43 Hz, time resolution varied between 0.3 and 0.5 ms, depending on call duration. All measurements were exported automatically to Microsoft Excel (Microsoft Corp., Redmond, WA, USA). Then, we calculated the mean f0 of each call as the inversed value of the mean f0 period of the call (Figure 2).

The four first formants (F1, F2, F3 and F4) were measured using LPC with Praat DSP package (P. Boersma & D. Weenink, University of Amsterdam, Netherlands, www.praat.org). The LPC settings were based on measurements of the oral vocal tract lengths obtained during previous studies: 117 mm for neonate goitred gazelles (Efremova et al., 2016) and 116 mm for neonate saiga antelopes (Volodin, Sibiryakova, et al., 2014). The LPC settings for creating the formant tracks were Burg analysis, window length 0.04 s, time step 0.01 s; maximum number of formants 4–5, the maximum formant frequency (the upper limit of frequency range) 5,200-6,700 Hz (Figure 2). Point values of formant tracks were extracted and exported to Excel, and the value of each formant for the given call or call part was calculated as the average value from the point values. In addition, for each call, we calculated the formant dispersion dF as average value of the differences between neighbouring formants (F2–F1, F3–F2 and F4–F3) following Riede and Fitch (1999).

FIGURE 2 Measuring acoustic variables: duration, fundamental frequency period (period f0) and tracks of the first four formants (F1, F2, F3 and F4); example of waveform (above) and spectrogram (below) of a saiga neonate distress call. The LPC settings were Burg analysis, window length 0.04 s, time step 0.01 s, maximum number of formants 4, maximum formant frequency 6,400 Hz [Colour figure can be viewed at wileyonlinelibrary.com]

2.5 | Statistical analyses

Statistical analyses were conducted using STATISTICA v. 6.0 (StatSoft, Tulsa, OK, USA) and R v.3.0.1 (R Development Core Team 2012). Means are given as mean ± *SD*, all tests were two-tailed, and differences were considered significant whenever $p < .05$. Twenty-one of 24 distributions of measured parameter values did not depart from normality, and all distributions of mean parameter values did not depart from normality (Kolmogorov–Smirnov test, $p > .05$). As parametric ANOVA and discriminant function analysis (DFA) are relatively robust to departures from normality (Dillon & Goldstein, 1984), this was not an obstacle to the application of these tests.

We used Student's *t* test and a two-way factorial ANOVA with Tukey HSD test to compare the average parameter values between distress and discomfort calls within and between species. We used DFA to calculate the probability of the assignment of calls to the correct individual for the two call samples, of distress calls and discomfort calls, in both goitred gazelles and saigas. We included all six measured call variables (f0, duration, F1, F2, F3 and F4) in all the DFAs. For interspecies comparison of individuality, we used unified samples of 8–10 calls per caller from 15 callers for each species (goitred gazelle and saiga) and for each context (distress and discomfort calls).

We used Wilks' lambda values to estimate how strongly the acoustic variables of the calls contribute to the discrimination among individuals. With a 2 × 2 Yates' chi-squared test, we compared the values of correct assignment of distress and discomfort calls to individuals between and within species. To validate our DFA results, we calculated the random values of correct assignment of calls to individual by applying a randomization procedure with macros, created in R. The random values were averaged from DFAs performed on 1,000 randomized permutations on the data sets (Mundry & Sommer, 2007; Solow, 1990). For example, to calculate the random value of classifying distress calls to individual goitred gazelles, each permutation procedure included the random permutation of 144 calls among 15 randomization groups, respectively, to 15 individual gazelles which were examined, and followed by DFA standard procedure built-in in STATISTICA. All other permutation procedures were made similarly. Using a distribution obtained by the permutations, we noted whether the observed value exceeded 95%, 99% or 99.9% of the values within the distribution (Solow, 1990). If the observed value exceeded 95%, 99% or 99.9% of values within this distribution, we established that the observed value did differ significantly from the random one with a probability $p < .05$, $p < .01$ or $p < .001$, respectively (Mundry & Sommer, 2007; Sibiryakova et al., 2015; Solow, 1990).

2.6 | Ethical note

All captures of animals and audio recordings were conducted in tight cooperation with authorized bodies of Uzbekistan (Ecocenter 'Djeiran') and of Kazakhstan (Association for the Conservation of the Biodiversity of Kazakhstan) in the framework of species censuses and conservation. During our work, we strictly adhered to the special welfare instructions developed by the authorized bodies for work with goitred gazelles and saigas and to the 'Guidelines for the treatment of animals in behavioural research and teaching' (Anim. Behav., 2006, 71, 245–253). The study protocol was approved by the Committee of Bioethics of Lomonosov Moscow State University (protocol # 2011-36).
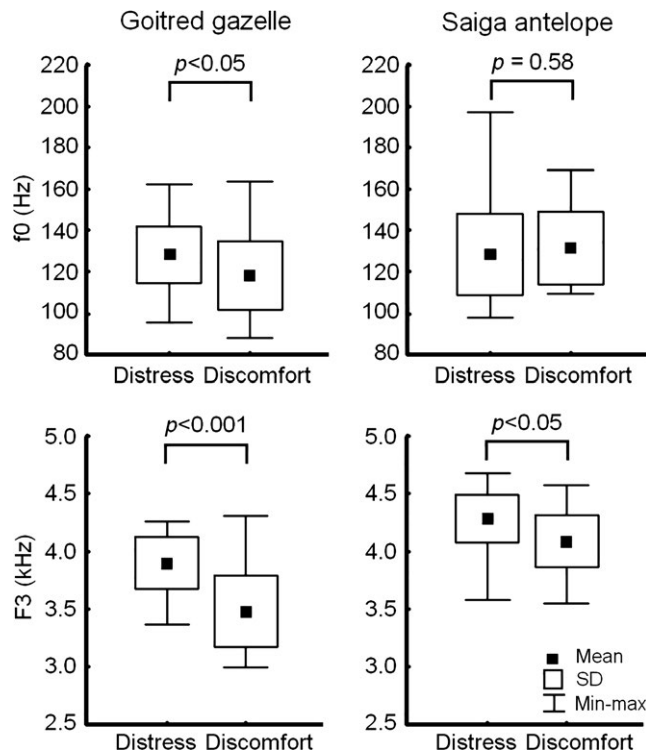
3 | RESULTS

3.1 | Acoustics of distress and discomfort calls

In neonate goitred gazelles, distress calls were higher in f0, F1 and F3 compared to discomfort calls (Table 1, Figure 3). The duration, F2, F4

TABLE 1 Comparison between distress and discomfort calls of neonate goitred gazelles: mean ± *SD* values of the measured acoustic variables and Student's *t* test results. Designations: f0, mean fundamental frequency; durat, call duration; F1, F2, F3, F4, values of the first four formants; dF, formant dispersion; *n*, number of calls with averaged characteristics (one per individual). Significant differences are presented in bold

Call variable	Distress calls, *n* = 36	Discomfort calls, *n* = 24	*t* test results
f0 (Hz)	129 ± 14	118 ± 17	$t = 2.59$; ***p* = .01**
Durat (s)	0.52 ± 0.17	0.47 ± 0.16	$t = 1.16$; $p = .25$
F1 (kHz)	1.02 ± 0.15	0.95 ± 0.09	$t = 2.11$; ***p* = .04**
F2 (kHz)	2.43 ± 0.25	2.40 ± 0.24	$t = 0.35$; $p = .73$
F3 (kHz)	3.90 ± 0.22	3.48 ± 0.31	$t = 6.12$; ***p* < .001**
F4 (kHz)	4.95 ± 0.24	4.94 ± 0.23	$t = 1.16$; $p = .35$
dF (kHz)	1.31 ± 0.07	1.33 ± 0.07	$t = 1.08$; $p = .29$

FIGURE 3 Differences in fundamental frequency (f0) and in the third formant (F3) between neonate goitred gazelle and saiga antelope distress and discomfort calls. Student's t test results for comparison are presented

and dF did not differ between distress and discomfort calls. In neonate saigas, the values of the acoustic variables were very similar between distress and discomfort calls and did not differ significantly, except F3, which was higher in distress than in discomfort calls (Table 2, Figure 3).

Comparison of the acoustics between distress and discomfort calls and between the two species revealed that both distress and discomfort calls were shorter in duration and lower in F1, F3 and F4 in goitred gazelle than in saiga (two-way ANOVA with Tukey HSD test, $p < .001$ for all comparisons) (Tables 1, 2). At the same time, the values of f0, F2 as well as formant dispersion did not differ between the two species neither in distress nor in discomfort calls (Tables 1, 2).

3.2 | Classifying distress and discomfort calls to individuals with DFA

For both neonate goitred gazelles and saigas, we estimated the values of correct classification to individual for distress calls and for discomfort calls (Figure 4). In neonate goitred gazelles in both DFAs, the average value of correct assignment to individual (67.4% for distress calls, 84.7% for discomfort calls) significantly exceeded our random expectation (21.7% ± 2.9% and 21.1% ± 2.8%, respectively, all $p < .001$). The average value of correct assignment to individual was higher for discomfort than for distress calls ($\chi^2_1 = 11.19$, $p < .001$) (Figure 4). For neonate goitred gazelle distress calls, the F1, F4 and F2 (in the order of decreasing importance) were mainly responsible for discrimination

TABLE 2 Comparison between distress and discomfort calls of neonate saiga antelopes: mean ± SD values of the measured acoustic variables and Student's t test results. Designations: f0, mean fundamental frequency; durat, call duration; F1, F2, F3, F4, values of the first four formants; dF, formant dispersion; n, number of calls with averaged characteristics (one per individual). Significant differences are presented in bold

Call variable	Distress calls, n = 25	Discomfort calls, n = 22	t test results
f0 (Hz)	128 ± 25	131 ± 17	$t = 0.56$; $p = .58$
Durat (s)	0.79 ± 0.21	0.75 ± 0.20	$t = 0.70$; $p = .48$
F1 (kHz)	1.33 ± 0.08	1.32 ± 0.15	$t = 0.43$; $p = .67$
F2 (kHz)	2.53 ± 0.21	2.52 ± 0.18	$t = 0.18$; $p = .86$
F3 (kHz)	4.22 ± 0.25	4.09 ± 0.22	$t = 2.05$; **$p = .04$**
F4 (kHz)	5.26 ± 0.26	5.24 ± 0.17	$t = 0.30$; $p = .76$
dF (kHz)	1.31 ± 0.08	1.31 ± 0.06	$t = 0.08$; $p = .94$

of individuals (Table 3). For discomfort calls, the f0mean, F3 and F4 (in the order of decreasing importance) were mainly responsible for discrimination of individuals (Table 3).

In neonate saigas in both DFAs, the average value of correct assignment to individual (87.7% for distress calls, 93.6% for discomfort calls) significantly exceeded our random expectation (21.1% ± 2.8% and 21.3% ± 2.8%, respectively, all $p < .001$). The average values of correct assignment to individual did not differ significantly between discomfort and distress calls ($\chi^2_1 = 1.62$, $p = .20$) (Figure 4). For neonate saigas, the f0mean, F2 and F3 (in the order of decreasing importance) were mainly responsible for discrimination of individuals in either distress or discomfort calls (Table 3).

The samples of animals and calls (15 callers, 8–10 calls per caller) were similar for each of the four DFAs, and we included the same call variables (f0, duration, F1, F2, F3 and F4) in all four DFAs. Therefore, we could directly compare the values of correct assignment to individual between goitred gazelle and saiga (Figure 4). The average value of correct assignment to individual was higher in saiga distress calls than in goitred gazelle distress calls ($\chi^2_1 = 18.35$, $p < 0.001$) and also higher in saiga discomfort calls than in goitred gazelle discomfort calls ($\chi^2_1 = 5.07$, $p = .02$) (Figure 4).

4 | DISCUSSION

Our results confirmed that the acoustic structure of vocalizations of goitred gazelle and saiga neonates is very similar. In accordance with one of our predictions, the acoustic individuality in neonate goitred gazelles, which use a 'hiding' strategy as antipredatory defence, was less expressed than in neonate saigas, which use a 'following' strategy as antipredatory defence. The other two of our predictions, that is, intraspecific differences between the acoustics of distress and discomfort calls and less individualistic distress calls than discomfort calls within the two species, were confirmed only for the goitred gazelle. Against our predictions, neither the acoustics (except the third

TABLE 3 DFA results for individuality of goitred gazelle and saiga antelope neonate calls. The Wilks' lambda values and call variable effects are presented for each acoustic variable included in the four independent DFAs for call assignment to individual on the basis of distress calls and discomfort calls for both species. The smaller the Wilks' lambda value, the greater the contribution of the given call variable to the overall discrimination. For each DFA, the three variables that mainly contributed to discrimination are highlighted in bold. Designations: f0, mean fundamental frequency; durat, call duration; F1, F2, F3, F4, values of the first four formants
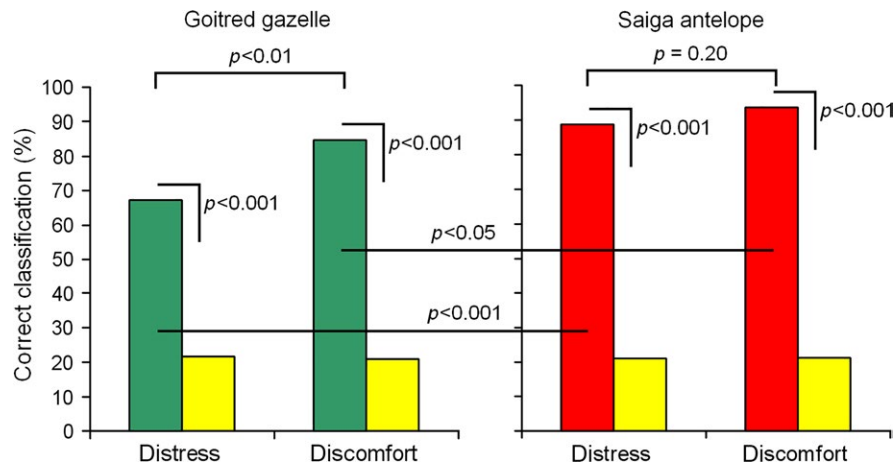
| | Goitred gazelle | | | | Saiga antelope | | | |
| | Distress calls | | Discomfort calls | | Distress calls | | Discomfort calls | |
Call variable	Wilks' lambda	Variable effect	Wilks' lambda	Variable effect	Wilks' lambda	Variable effect	Wilks' lambda	Variable effect
f0	0.66497	F = 4.46	**0.13672**	F = 58.63	**0.15057**	F = 52.39	**0.04719**	F = 174.5
Durat	0.66816	F = 4.40	0.46221	F = 10.80	0.55516	F = 7.44	0.40542	F = 12.68
F1	**0.36740**	F = 15.25	0.69570	F = 4.06	0.32599	F = 19.20	0.22294	F = 30.12
F2	**0.47567**	F = 9.76	0.49094	F = 9.63	**0.24723**	F = 28.27	**0.10716**	F = 72.01
F3	0.63885	F = 5.01	**0.29223**	F = 22.49	0.29658	F = 22.02	0.15288	F = 47.89
F4	**0.41537**	F = 12.47	**0.38017**	F = 15.14	0.47126	F = 10.42	0.45539	F = 10.34

formant) nor individuality differed between distress and discomfort calls in the saiga neonates.

The acoustic differences between vocalizations of goitred gazelle and saiga neonates mainly concerned the duration, which was longer in saiga, and the values of the first, third and fourth formants, which were higher in saiga. At the same time, the formant dispersion did not differ between the two species, in accordance with the practically identical values of oral vocal tract length in goitred gazelle and saiga neonates. The acoustic similarity between neonate calls of these two bovid species is also observed in the overall acoustic pattern and in the very low fundamental frequency compared to the very high-frequency (over 500 Hz) neonate calls reported for other ruminant species (Antilocapridae (Teichroeb et al., 2013), Cervidae (Bogomolova, Kurochkin, & Nikol'skii, 1984; Kidjo, Cargnelutti, Charlton, Wilson, & Reby, 2008; Lingle, Rendall, & Pellis, 2007; Lingle et al., 2012; Sibiryakova et al., 2015; Teichroeb et al., 2013; Torriani et al., 2006; Vaňková & Málek, 1997; Volodin, Sibiryakova, & Volodina, 2016) and another species of Bovidae (Briefer & McElligott, 2011b; Lenhardt, 1977; Terrazas et al., 2003).

Our study shows that such low-frequency calls clearly highlight vocal tract resonances (formants) as important cues to acoustic individuality in both goitred gazelle and saiga neonates. Low-frequency vocalizations were also reported for neonate and juvenile reindeer (Espmark, 1975; Teichroeb et al., 2013), domestic pigs *Sus scrofa* (Illmann et al., 2013), eland *Taurotragus oryx* (Teichroeb et al., 2013), domestic cattle *Bos taurus* (Weary & Chua, 2000) and in earlier studies of goitred gazelle (Efremova, Volodin, Volodina, Frey, Lapshina, et al., 2011; Efremova, Volodin, Volodina, Frey, Soldatova, et al., 2011) and saiga (Volodin, Volodina, & Efremova, 2009; Volodin, Sibiryakova, et al., 2014). The important role of formants in encoding individual identity of the young was previously reported for the low-frequency calls of both the juvenile reindeer (Espmark, 1975) and goitred gazelles (Lapshina et al., 2012; Volodin et al., 2011).

Against our predictions, a prominent effect of the context on the acoustics (capture vs. hunger) occurred only in neonate goitred gazelles, but not in saiga neonates. We had expected that the life-threatening context 'capture by a predator' would be more urgent and stressful and, therefore, evoke higher levels of negative arousal than the 'context of hunger prior to nursing' in both species. A shift of the fundamental frequency and call energy to higher frequencies represents a common/general reaction of mammals during increased levels of emotional arousal (Briefer, 2012; Volodin, Volodina, Gogoleva, et al., 2009). However, the distress calls were higher in fundamental frequency and in the first and third formants only in neonate goitred gazelles but not in saigas. In neonate saigas, only the third formant was higher in distress than in discomfort calls, whereas the fundamental frequency was the same in both contexts. This suggests that contrary to goitred gazelle neonates, the two recording contexts (capture and hunger) did not differ in the level of negative arousal for saiga neonates. Indirect support for this perceptual difference can be inferred from the fact that in the context of capture by a predator 90% of goitred gazelle neonates vocalized but only 15% of saiga neonates.

FIGURE 4 Individual discrimination on the basis of goitred gazelle and saiga antelope distress and discomfort call features. Green and red bars represent values of the discriminate function analysis (DFA), and yellow bars represent random values calculated with randomization procedures. Comparisons between distress and discomfort calls and between species with chi-squared tests are shown by brackets above and by horizontal lines between bars. Comparisons between observed and random values are shown by the right angle lines [Colour figure can be viewed at wileyonlinelibrary.com]

The distress calls of neonate goitred gazelles at capture were less individualized than discomfort calls when hungry whereas the individuality did not differ between both contexts in neonate saigas. Yet, individuality was more strongly expressed in both call types for saiga neonates than for goitred gazelle neonates. These differences might result from the different neonate strategies against predation ('hiding' vs. 'following'). Goitred gazelle mothers occupy individual parcels of land for giving birth to their young. Within the first 2–3 weeks of life, neonate goitred gazelles are 'hiders', so that their mothers may use spatial landmarks in addition to acoustic cues for recognition of their own young (Blank et al., 2015; Jevnerov, 1984; Marmasinskaya, 1996, 2008). When hiding close to their place of birth, newborn goitred gazelles may be predated by red foxes (*Vulpes vulpes*), steppe cats (*Felis libyca*) or jackals (*Canis aureus*), which normally are not dangerous to their mothers and can be deterred by them. Therefore, when being attacked by a predator, eliciting immediate maternal physical reaction to their distress calls is more important for neonate goitred gazelles than advertising own individual identity by these calls. Goitred gazelle mothers rapidly approach to defend their young in response to even imperfect imitations of neonate distress calls by humans (Blank & Yang, 2015; Blank et al., 2015; Volodin et al., 2011). Potential time delays in deterring an attacking predator due to individual recognition may be fatal for the young and more costly, in terms of reproductive success, than the time and energy lost for erroneously responding to distress calls of unrelated offspring (Lingle, Rendall, & Pellis, 2007; Lingle, Rendall, Wilson, et al., 2007). Consequently, distress calls emitted during a predator attack are higher in fundamental and formant frequencies in neonate goitred gazelles, thus reflecting higher levels of arousal (Briefer, 2012; Volodin, Volodina, Gogoleva, et al., 2009), whereas the advertisement of individual identity is less important in this context. In contrast, the acoustic individuality was highlighted much stronger in the discomfort calls of neonate goitred gazelles, emitted in the less urgent context of hunger, in which moderate time

delays are tolerable. The acoustic cues to individual identity were shared with those found in juvenile goitred gazelles at the age of 3–6 weeks (f0, F4, F2, F3), that is, at an age when hiding behaviour was already abandoned and young goitred gazelles in their natural habitat are following their mothers in small groups (Volodin et al., 2011). In bovids, the individuality of food begging calls of the young might be favoured by natural selection to increase offspring survival (Marmasinskaya, 2008; Torriani et al., 2006) and to avoid misdirected maternal care (Brandlová et al., 2013).

Saiga antelopes breed in dense aggregations of many thousands of individuals on restricted areas, without any individually occupied parcels of land. Within these large aggregations, the females breed in groups of 15–20 individuals where distances between individuals are around 20 m and up to 200–300 m between groups (Bannikov et al., 1961; Sokolov & Zhirnov, 1998; Danilkin, 2005; our own observations). Newborn saigas may be predated by wolves (*Canis lupus*), which are also threatening for saiga mothers (Bannikov et al., 1961). Consequently, we did not observe saiga mothers approaching in response to neonate distress calls. In the lack of maternal defence against predators, the vast aggregations of breeding saiga females are considered as an adaptation for decreasing neonate mortality by predation (Bannikov et al., 1961; Danilkin, 2005; Sokolov & Zhirnov, 1998). Wolves are strictly territorial in the spring season; thus, only few wolf packs will hunt in the saiga breeding area and thus can consume only a limited number of neonate saiga prey. Saiga young are precocial followers, and within 30 min after birth are already capable of standing, suckling, walking and even trying to run (Danilkin, 2005; Kokshunova, 2012; Volodin, Sibiryakova, et al., 2014). A few hours after birth, they transfer to another place together with their mothers; after 2–3 days, they follow their mothers permanently and are capable of running as quickly as adults in the case of danger (Sokolov & Zhirnov, 1998; Danilkin, 2005; our own observations). For neonate saigas, fast development of highly individualistic calls is considered to

be much more important than in goitred gazelles, as vocalization represents the most important channel for maintaining mother–offspring contact in the large herds of conspecifics (similar to domestic sheep *Ovis aries*, Sebe, Nowak, Poindron, & Aubin, 2007). Therefore, in neonate saigas, a strong vocal individuality arises immediately after birth and is equally highly expressed irrespective of the context, as saigas use calls of the same acoustic structure in both contexts.

The high vocal individuality of discomfort calls in the context of hunger is more critically important for the survival of neonate saigas than for neonate goitred gazelles. In the saiga, the time period from mass parturitions to departure of the herd from the breeding grounds is very short (2–3 days) (Bannikov et al., 1961; our own observations). As a consequence, in a landscape providing few spatial landmarks available only for a few hours after birth, when the young are still relatively immobile, saiga mothers have to rely mainly on the highly individualistic discomfort calls and smell for spotting their own young among hundreds of others. Saiga mothers that cannot find their young before departure of the herd, never continue searching and leave the breeding grounds together with the herd (our own observations). Hungry neonate saigas that were not found by their mothers are prone to die. Thus, there is a strong selection pressure for evolving highly individualistic discomfort calls.

In contrast, the time period during which the hungry, hiding neonate can be spotted by its mother is much longer in goitred gazelle. Even after having been frightened, goitred gazelle neonates return to their place of birth (Jevnerov, 1984) and goitred gazelle mothers need not discriminate their own young among hundreds of alien neonates. Therefore, the selection pressure for evolving individualistic discomfort calls can be expected to be much weaker in neonate goitred gazalles than in neonate saigas.

High rates of classification success with DFA may not always be confirmed by the, respectively, high individual discrimination of playback stimuli (Lingle, Rendall, & Pellis, 2007; Lingle, Rendall, Wilson, et al., 2007). So, the high classification success with DFA is not equivalent to demonstrating discrimination or recognition of individual neonates by their mothers. However, for wild goitred gazelles and saigas in their open semidesert or steppe habitats, the necessary playback-based validation of DFA was methodological impossible with the current technique available.

REFERENCES

Bannikov, A. G., Jirnov, L. V., Lebedeva, L. S., & Fandeev, A. A. (1961). *Saiga biology*. Moscow: Agricultural Literature Press [in Russian].

Beecher, M. D., Beecher, I. M., & Hahn, S. (1981). Parent-offspring recognition in bank swallows (*Riparia riparia*): II. Development and acoustic basis. *Animal Behaviour*, *29*, 95–101.

Beecher, M. D., Beecher, I. M., & Lumpkin, S. (1981). Parent-offspring recognition in bank swallows (*Riparia riparia*): I. Natural history. *Animal Behaviour*, *29*, 86–94.

Blank, D. A. (1998). Mating behavior of the Persian gazelle *Gazella subgutturosa* Güldenstaedt, 1780. *Mammalia*, *62*, 499–519.

Blank, D. A., Ruckstuhl, K., & Yang, W. (2012). Influence of population density on group sizes in goitered gazelle (*Gazella subgutturosa* Guld., 1780). *European Journal of Wildlife Research*, *58*, 981–989.

Blank, D. A., Ruckstuhl, K., & Yang, W. (2015). Antipredator strategy of female goitered gazelles (*Gazella subgutturosa* Guld., 1780) with hiding fawn. *Behavioural Processes*, *119*, 44–49.

Blank, D. A., & Yang, W. (2015). Suckling behavior in goitered gazelle: Do females invest more in twins or singletons? *Zoology*, *118*, 348–356.

Bogomolova, E. M., Kurochkin, Y. A., & Nikol'skii, A. A. (1984). Sound signals in communicative behaviour of the moose (*Alces alces*). *Zoologicheskii Zhurnal*, *63*, 1872–1882. [in Russian].

Branch, C. L., & Freeberg, T. M. (2012). Distress calls in tufted titmice (*Baeolophus bicolor*): Are conspecifics or predators the target? *Behavioral Ecology*, *23*, 854–862.

Brandlová, K., Bartoš, L., & Haberová, T. (2013). Camel calves as opportunistic milk thefts? The first description of allosuckling in domestic bactrian camel (*Camelus bactrianus*). *PLoS One*, *8*(1), e53052. doi:10.1371/journal.pone.0053052

Briefer, E. F. (2012). Vocal expression of emotions in mammals: Mechanisms of production and evidence. *Journal of Zoology*, *288*, 1–20.

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

Briefer, E. F., & McElligott, A. G. (2011b). Indicators of age, body size and sex in goat kid calls revealed using the source–filter theory. *Applied Animal Behaviour Science*, *133*, 175–185.

Briefer, E. F., & McElligott, A. G. (2012). Social effects on vocal ontogeny in an ungulate, the goat, *Capra hircus*. *Animal Behaviour*, *83*, 991–1000.

Brodie, E. D. (1978). Biting and vocalization as antipredator mechanisms in terrestrial salamanders. *Copeia*, *1*, 127–129.

Charrier, I., Mathevon, N., & Jouventin, P. (2002). How does a fur seal mother recognize the voice of her pup? An experimental study of *Arctocephalus tropicalis*. *Journal of Experimental Biology*, *205*, 603–612.

Danilkin, A. A. (2005). *Hollow-horned Ruminants (Bovidae)*. Moscow: KMK Scientific Press [in Russian].

Dillon, W. R., & Goldstein, M. (1984). *Multivariate analysis: Methods and applications*. New York: Wiley.

Efremova, K. O., Frey, R., Volodin, I. A., Fritsch, G., Soldatova, N. V., & Volodina, E. V. (2016). The postnatal ontogeny of the sexually dimorphic vocal apparatus in goitred gazelles (*Gazella subgutturosa*). *Journal of Morphology*, *277*, 826–844.

Efremova, K. O., Volodin, I. A., Volodina, E. V., Frey, R., Lapshina, E. N., & Soldatova, N. V. (2011). Developmental changes of nasal and oral calls in the goitred gazelle *Gazella subgutturosa*, a nonhuman mammal with a sexually dimorphic and descended larynx. *Naturwissenschaften*, *98*, 919–931.

Efremova, K. O., Volodin, I. A., Volodina, E. V., Frey, R., Soldatova, N. V., Lapshina, E. N., … 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. *Zoologicheskii Zhurnal*, *90*, 603–615. [in Russian].

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., & Hauser, M. D. (2002). Unpacking "honesty": Vertebrate vocal production and the evolution of acoustic signals. In A. Simmons, R. R. Fay, & A. N. Popper (Eds.), *Acoustic communication. Springer handbook of auditory research* (pp. 65–137). Berlin: Springer.

Frey, R., Volodin, I., & Volodina, E. (2007). A nose that roars: Anatomical specializations and behavioural features of rutting male saiga. *Journal of Anatomy*, *211*, 717–736.

Gogoleva, S. S., Volodin, I. A., Volodina, E. V., Kharlamova, A. V., & Trut, L. N. (2010). Sign and strength of emotional arousal: Vocal correlates of positive and negative attitudes to humans in silver foxes (*Vulpes vulpes*). *Behaviour*, *147*, 1713–1736.

Illmann, G., Hammerschmidt, K., Špinka, M., & Tallet, C. (2013). Calling by domestic piglets during simulated crushing and isolation: A signal of need? *PLoS One*, *8*(12), e83529. doi:10.1371/journal.pone.0083529

Insley, S. J., Phillips, A. V., & Charrier, I. (2003). A review of social recognition in pinnipeds. *Aquatic Mammals*, *29*, 181–201.

Jacques, C. N., & Jenks, J. A. (2010). Antipredatory defense of neonatal pronghorn (*Antilocapra americana*) by yearling male pronghorn in Southwestern South Dakota. *Western North American Naturalist*, *70*, 570–572.

Jevnerov, V. V. (1984). *Goitred Gazelles of Barsakelmes Island*. Alma-Ata: Nauka.

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

Kidjo, N., Cargnelutti, B., Charlton, B. D., Wilson, C., & Reby, D. (2008). Vocal behaviour in the endangered Corsican deer: Description and phylogenetic implications. *Bioacoustics*, *18*, 159–181.

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

Kokshunova, L. (2012). *Ecology and behaviour of the Saiga Antelope (Saiga tatarica tatarica L., 1766) in conditions of extreme anthropogenic press*. Saarbrücken: Lambert Academic Publishing [in Russian].

Lapshina, E. N., Volodin, I. A., Volodina, E. V., Frey, R., Efremova, K. O., & Soldatova, N. V. (2012). The ontogeny of acoustic individuality in the nasal calls of captive goitred gazelles, *Gazella subgutturosa*. *Behavioural Processes*, *90*, 323–330.

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

Lenhardt, M. L. (1977). Vocal contour cues in maternal recognition of goat kids. *Applied Animal Ethology*, *3*, 211–219.

Lingle, S., Rendall, D., & Pellis, S. M. (2007). Altruism and recognition in the antipredator defence of deer: 1. Species and individual variation in fawn distress calls. *Animal Behaviour*, *73*, 897–905.

Lingle, S., Rendall, D., Wilson, W. F., Deyoung, R. W., & Pellis, S. M. (2007). Altruism and recognition in the antipredator defence of deer: 2. Why mule deer help nonoffspring fawns. *Animal Behaviour*, *73*, 907–916.

Lingle, S., & Riede, T. (2014). Deer mothers are sensitive to infant distress vocalizations of diverse mammalian species. *American Naturalist*, *184*, 510–522.

Lingle, S., Wyman, M. T., Kotrba, R., Teichroeb, L. J., & Romanow, C. A. (2012). What makes a cry a cry? A review of infant distress vocalizations. *Current Zoology*, *58*, 698–726.

Manteuffel, G., Puppe, B., & Schön, P. C. (2004). Vocalization of farm animals as a measure of welfare. *Applied Animal Behaviour Science*, *88*, 163–182.

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

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

McArthur, P. D. (1982). Mechanisms and development of parent-young recognition in the pinon jays (*Gimnorhinus cyanocephalus*). *Animal Behaviour*, *30*, 62–72.

Mundry, R., & Sommer, C. (2007). Discriminant function analysis with nonindependent data: Consequences and an alternative. *Animal Behaviour*, *74*, 965–976.

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. *Journal of Arid Environments*, *39*, 577–591.

R Development Core Team (2012). *R: a language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing, http://www.R-project.org/

Riede, T., & Fitch, T. (1999). Vocal tract length and acoustics of vocalization in the domestic dog (*Canis familiaris*). *Journal of Experimental Biology*, *202*, 2859–2867.

Scornavacca, D., & Brunetti, C. (2016). Cooperative defence of female chamois successfully deters an eagle attack. *Mammalia*, *80*, 453–456.

Searby, A., & Jouventin, P. (2003). Mother-lamb acoustic recognition in sheep: A frequency coding. *Proceedings of the Royal Society of London B: Biological Sciences*, *270*, 1765–1771.

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. *Animal Behaviour*, *79*, 1055–1066.

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

Seddon, P. J., & Heezik, Y. (1993). Parent-offspring recognition in the jackass penguin. *Journal of Field Ornithology*, *64*, 27–31.

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

Sibiryakova, O. V., Volodin, I. A., Frey, R., Zuther, S., Kisebaev, T. B., Salemgareev, A. R., & Volodina, E. V. (2017). Remarkable vocal identity in wild-living mother and neonate saiga antelopes: A specialization for breeding in huge aggregations? *The Science of Nature*, *104*(11), doi:10.1007/s00114-017-1433-0

Sibiryakova, O. V., Volodin, I. A., Matrosova, V. A., Volodina, E. V., Garcia, A. J., Gallego, L., & Landete-Castillejos, T. (2015). The power of oral and nasal calls to discriminate individual mothers and offspring in red deer, *Cervus elaphus*. *Frontiers in Zoology*, *12*, 2. doi:10.1186/s12983-014-0094-5

Smith, W. P. (1987). Maternal defense in Columbian white-tailed deer: When is it worth it? *American Naturalist*, *130*, 310–316.

Sokolov, V. E., & Zhirnov, L. V. (1998). *The Saiga Antelope. Phylogeny, systematic, ecology, conservation and use*. Moscow: Russian Academy of Sciences [in Russian].

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

Tallet, C., Linhart, P., Policht, R., Hammerschmidt, K., Šimeček, P., Kratinova, P., & Špinka, M. (2013). Encoding of situations in the vocal repertoire of piglets (*Sus scrofa*): A comparison of discrete and graded classifications. *PLoS One*, *8*(8), e71841. doi:10.1371/journal.pone.0071841

Taylor, A. M., & Reby, D. (2010). The contribution of source–filter theory to mammal vocal communication research. *Journal of Zoology*, *280*, 221–236.

Teichroeb, L. J., Riede, T., Kotrba, R., & Lingle, S. (2013). Fundamental frequency is key to response of female deer to juvenile distress calls. *Behavioural Processes*, *92*, 15–23.

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. *Developmental Psychobiology*, *43*, 311–320.

Titze, I. R. (1994). *Principles of voice production*. Engelwood Cliffs, New Jersey: Prentice Hall.

Torriani, M. V. G., Vannoni, E., & McElligott, A. G. (2006). Mother-young recognition in an ungulate hider species: A unidirectional process. *The American Naturalist*, *168*, 412–420.

Vaňková, D., & Málek, J. (1997). Characteristics of the vocalizations of red deer *Cervus elaphus* hinds and calves. *Bioacoustics*, *7*, 281–289.

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

Volodin, I. A., Sibiryakova, O. V., Kokshunova, L. E., Frey, R., & Volodina, E. V. (2014). Nasal and oral calls in mother and young trunk-nosed saiga antelopes, *Saiga tatarica. Bioacoustics*, *23*, 79–98.

Volodin, I. A., Sibiryakova, O. V., & Volodina, E. V. (2016). Sex and age-class differences in calls of Siberian wapiti *Cervus elaphus sibiricus*. *Mammalian Biology*, *81*, 10–20.

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*). *Zoologicheskii Zhurnal*, *88*, 113–124. [in Russian].

Volodin, I. A., Volodina, E. V., Gogoleva, S. S., & Doronina, L. O. (2009). Indicators of emotional arousal in vocal emissions of the humans and nonhuman mammals. *Journal of General Biology*, *70*, 210–224. [in Russian].

Volodin, I. A., Volodina, E. V., Lapshina, E. N., Efremova, K. O., & Soldatova, N. V. (2014). Vocal group signatures in the goitred gazelle *Gazella subgutturosa. Animal Cognition*, *17*, 349–357.

Weary, D. M., & Chua, B. (2000). Effects of early separation on the dairy cow and calf: 1. Separation at 6 h, 1 day and 4 days after birth. *Applied Animal Behaviour Science*, *69*, 177–188.

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. *Animal Behaviour*, *52*, 1247–1253.

Weary, D. M., Ross, S., & Fraser, D. (1997). Vocalizations by isolated piglets: A reliable indicator of piglet need directed towards the sow. *Applied Animal Behaviour Science*, *53*, 249–257.

Zaytseva, A. S., Volodin, I. A., Ilchenko, O. G., & Volodina, E. V. (2016). Discomfort-related changes in pup ultrasonic calls of fat-tailed gerbils *Pachyuromys duprasi. Bioacoustics*, doi:10.1080/09524622.2016.1164076

SUPPORTING INFORMATION

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