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ORIGINAL PAPER

Unusually high-pitched neonate distress calls of the open-habitat Mongolian gazelle (*Procapra gutturosa*) and their anatomical and hormonal predictors

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Abstract In neonate ruminants, the acoustic structure of vocalizations may depend on sex, vocal anatomy, hormonal profiles and body mass and on environmental factors. In neonate wild-living Mongolian gazelles *Procapra gutturosa*, hand-captured during biomedical monitoring in the Daurian steppes at the Russian-Mongolian border, we spectrographically analysed distress calls and measured body mass of 22 individuals (6 males, 16 females). For 20 (5 male, 15 female) of these individuals, serum testosterone levels were also analysed. In addition, we measured relevant dimensions of the vocal apparatus (larynx, vocal folds, vocal tract) in one stillborn male Mongolian gazelle specimen. Neonate distress calls of either sex were high in maximum fundamental frequency (800–900 Hz), but the beginning and minimum fundamental frequencies were significantly lower in males than in females. Body mass was larger in males than in females. The levels of serum testosterone were marginally higher in males. No correlations were found between either body mass or serum testosterone values and any acoustic variable for males and females analysed together or separately. We discuss that the high-frequency calls of neonate Mongolian gazelles are more typical for closed-habitat neonate ruminants, whereas other open-habitat neonate ruminants (goitred gazelle *Gazella subgutturosa*, saiga antelope *Saiga tatarica* and reindeer *Rangifer tarandus*) produce low-frequency (<200 Hz) distress calls. Proximate cause for the high fundamental frequency of distress calls of neonate Mongolian gazelles is their very short, atypical vocal folds (4 mm) compared to the 7-mm vocal folds of neonate goitred gazelles, producing distress calls as low as 120 Hz.

Keywords Newborn vocalization · Vocal anatomy · Testosterone · Body mass · Sex differences · Ruminants

Introduction

In neonate ruminants, distress calls represent an important part of antipredator behaviour (Lingle et al. 2007a, b, 2012; Teichroeb et al. 2013). Although neonate distress calls in the context of hand capture are species-specific (Lingle et al. 2007a, b, 2012; Sibiryakova et al. 2017; Volodin et al. 2017b), shared acoustic traits can be observed among species living in closed habitats (e.g. forest) versus species living in open habitats (grassland, steppe or semidesert). Neonate ruminants living in closed habitats commonly have high-frequency voices with a fundamental frequency f0 > 500 Hz, as for example in mule deer *Odocoileus hemionus* (Lingle et al. 2007a), white-tailed deer *Odocoileus virginianus* (Lingle et al. 2007a), red deer *Cervus elaphus* (Vaňková and Málek

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1997; Volodin et al. 2016) and fallow deer *Dama dama* (Lingle et al. 2012). In open habitats, neonate ruminants commonly have low-frequency voices (f0 < 200 Hz), as, for instance, goitred gazelles *Gazella subgutturosa* (Volodin et al. 2011, 2017a, b), saiga antelopes *Saiga tatarica* (Volodin et al. 2014, 2017b; Sibiryakova et al. 2017) and reindeer *Rangifer tarandus* (Espmark 1975; Teichroeb et al. 2013). As Mongolian gazelles *Procapra gutturosa* live in open habitats (Sokolov and Lushchekina 1997; Milner-Gulland and Lhagvasuren 1998; Olson et al. 2005a, b, 2009, 2014; Odonkhuu et al. 2009; Martinez-Garcia et al. 2013), one would expect a low-frequency voice in the neonates of this species.

In ruminants, as in mammals in general, fundamental frequency (f0) depends on the length of the vocal folds (Fant 1960; Volodin et al. 2014, 2017a). Commonly, shorter vocal folds produce higher f0s (Riede and Brown 2013; Sibiryakova et al. 2015; Volodin et al. 2017a), although other factors may affect f0 values, such as vocal fold elasticity (Riede and Titze 2008; Riede et al. 2010), vocal production mode (Frey and Riede 2013; Volodin et al. 2013, 2017c) and the presence of vocal pads attached to the vocal folds (Frey and Hofmann 2000; Frey et al. 2007, 2008a, b; Efremova et al. 2011, 2016). Therefore, in addition to habitat openness, we expected that the acoustic structure of the calls produced by neonate Mongolian gazelles would depend on the morphology of their vocal apparatus, specifically on the length and shape of the vocal folds inside the larynx.

Small but significant differences in body mass between sexes have been reported for neonate Mongolian gazelles (Olson et al. 2005a). In neonate goitred gazelles, small sex differences in body mass (Efremova et al. 2016) correlate with corresponding small differences in the acoustic parameters (Efremova et al. 2011; Volodin et al. 2017a). In adult goitred gazelles, the differences in body mass between males and females are small, but the acoustic differences are large due to a stronger sexual dimorphism of the vocal apparatus among adults than among neonates (Efremova et al. 2011, 2016; Volodin et al. 2017a).

In goitred gazelles, the ontogenetically developing sexual dimorphism of the vocal apparatus (Frey et al. 2011; Efremova et al. 2016) affects call f0 in males and females (Efremova et al. 2011; Volodin et al. 2017a). Potentially, similar ontogenetic relationships of the neonate and adult larynges and their acoustical correlates occur in Mongolian gazelles. So far, a strong sexual dimorphism of the vocal apparatus has been reported for adult Mongolian gazelles (Frey and Riede 2003; Frey et al. 2008a, b); however, only few acoustic data are available for adult male calls (Frey et al. 2008a). Neonate vocalizations of Mongolian gazelles have not yet been investigated.

In mammals, laryngeal tissues are highly receptive to steroid hormones, especially to androgens in males (Tuohimaa et al. 1981; Aufdemorte et al. 1983; Newman et al. 2000). Therefore, a sexual dimorphism of vocal morphology and lower-frequency vocalization in male bovids (Volodin et al. 2009, 2017a; Frey et al. 2007, 2011) might develop prematurely under the effects of elevated levels of testosterone around birth (review: Clarkson and Herbison 2016). In addition, the development of hormonal mechanisms regulating adult sexual behaviour (Asher and Peterson 1991) depends strongly on the perinatal levels of serum testosterone (Corbier et al. 1983, 1990; Roffi et al. 1987) both in humans (Corbier et al. 1990; Clarkson and Herbison 2016) and in nonhuman mammals (Corbier et al. 1978; Erskine et al. 1988; Motelica-Heino et al. 1988; Clarkson and Herbison 2016). Among ruminants, perinatal and/or neonatal serum testosterone levels were investigated in domestic bovids, e.g. in sheep *Ovis aries* (Lee et al. 1976; Yu et al. 1983) and in male buffalo *Bubalus bubalus* (Hemeida et al. 1985). In Mongolian gazelles, neonatal serum testosterone levels have not yet been investigated.

Ruminant species, in general, fall into one of two categories with regard to post-partum mother-infant relationship: “follower” young accompany their mothers from the time that they first get onto their feet, while “hider” young go through a resting stage and are separated from their mothers except during two or three nursing and care sessions per day (Lent 1974; Fisher et al. 2002; Torriani et al. 2006). The “hiders” remain hidden for about the first 10 days of life, and then, they also follow their mothers (Torriani et al. 2006; Blank et al. 2015). Both strategies are widely interpreted as providing antipredator-related benefits (e.g. Fitzgibbon 1990; Odonkhuu et al. 2009).

Similar to other migrating ruminants, as Tibetan antelopes *Pantholops hodgsonii* (Schaller et al. 2006) and saiga antelopes (Bannikov et al. 1961), Mongolian gazelles have synchronized calving periods, lasting about 10 days, from 20–25 June to 5–6 July, during which the gazelles are more sedentary than during other periods (Olson et al. 2005a; Kirilyuk and Zvichainaya 2011). Mongolian gazelle neonates mostly remain hidden for 7–8 days (Odonkhuu 2004; Odonkhuu et al. 2009; Olson et al. 2005a, b, 2009; Kirilyuk and Zvichainaya 2011), similar to neonate goitred gazelles (Blank et al. 2015), but different from the followers saiga (Bannikov et al. 1961) and Tibetan antelope (Schaller et al. 2006). Activity of the young increases from the second day after birth, and at 5–8 days of life, they move alone or together with their mother 6.6 km per day on average. At 24–26 days of life, they are located 41 km away from their birth place on average and join aggregations exceeding 1000 animals (Odonkhuu et al. 2009; Kirilyuk and Zvichainaya 2011).

The general research questions of this study were (1) do the acoustic properties of the distress calls of Mongolian gazelle neonates differ from those of other ruminant neonates and (2) do body mass, testosterone levels and anatomical dimensions predict the acoustic properties of Mongolian gazelle neonate distress calls. The particular aims were (1) to investigate the acoustic characteristics of the distress calls produced by neonate (1–4 days-old) male and female Mongolian gazelles in immediate response to hand-capture, (2) to investigate the dimensions and anatomical structure of the larynx and the vocal folds of a stillborn male Mongolian gazelle as a morphological basis for the acoustical investigation, and (3) to estimate body mass and levels of serum testosterone in those neonate Mongolian gazelles that provided calls for the bioacoustic analysis.

Materials and methods

Study area

The study was conducted in the buffer zone of Daursky State Natural Biosphere Reserve located south of Zabaikalskii Krai near the Russian–Mongolian border (50.06° N, 115.44° E). The study area is a grassland ecosystem undulating over elevations of 600–1100 m and dominated by species such as *Stipa* spp., *Cleistogenes* spp. and *Leymus* spp.; several species of forbs, particularly *Artemisia* spp., *Allium* spp. and *Astragulus* spp.; and sedges, e.g. *Carex* spp. (Olson et al. 2005b; Kirilyuk 2007). As trees and bushes are lacking and the height of the grass does not exceed 15 cm, this habitat of neonate Mongolian gazelles can be classified as open-type habitat. Water is available from earth depressions and shallow lakes. Potential predators of gazelle calves are wolves *Canis lupus*, red foxes *Vulpes vulpes* and raptors such as steppe *Aquila rapax* and golden eagles *Aquila chrysaetos*, upland buzzards *Buteo hemilasius* and cinereous vultures *Aegypius monachus* (Sokolov and Lushchekina 1997; Olson et al. 2005a, b; Kirilyuk and Zvichainaya 2011). Besides the wild Mongolian gazelles, there occur free-ranging herds of domestic livestock: sheep, horses *Equus caballus*, cattle and domestic Bactrian camels *Camelus bactrianus* (Kirilyuk 2007).

Data collection

Oral distress calls (produced with an open mouth), body mass and blood samples were collected in 22 neonate (1–4 days old) Mongolian gazelles (6 males, 16 females) that were hand-captured on June 28–30, 2016, at night-time using headlights. The higher proportion of female sex, contrasting with the 50:50 sex ratio averaged over 5 years (Olson et al. 2005a), could be due to our smaller sample size or reflects a true sex ratio of the neonate population in 2016. Capture teams located calving grounds (herds of females with the young hidden in the grass on mother parcels) then searched for calves from a slowly driving car or by walking through an area. When a calf was spotted, one person would approach from behind with a 0.8-m-diameter hand-held hoop net while another stood in front to distract the calf. The net was quickly placed over the resting calf, which was then immediately removed and calmed down by placing a cloth hood over its head. Surgical gloves were used when possible to minimize potential fawn abandonment by a mother owing to human scent. Cutting a small tuft of hairs in the neck region before releasing neonates avoided double sampling.

Oral distress calls of the 22 captured calves were recorded when they vocalized during 1–3 min after capture. For acoustic recordings (48 kHz, 16 bit), we used a solid-state recorder Marantz PMD-660 (D&M Professional, Kanagawa, Japan) with an AKG-C1000S (AKG-Acoustics GmbH, Vienna, Austria) cardioid electret condenser microphone. The distance from the hand-held microphone to the animals was 1–10 m. The recording level was adjusted during the recordings depending on the intensity of the produced calls. We did not specially stimulate the animals to vocalize; all calls were produced spontaneously in response to capture and handling. The hand capture and call collection were always conducted by different persons.

Neonates were weighed in a bag with 10-g precision using electronic scales Voltcraft HS-10L (Voltcraft, Hirschau, Germany) and sexed by external sexual traits. Neonate age in days was estimated from the condition of the umbilical cord (dry at the tip or completely dry). Blood samples (1–3 ml) were collected from the external jugular vein within 3–5 min after capture, mainly following Deem et al. (2001). After sampling, the blood was placed into Eppendorf tubes (Scientific Specialties, Inc. (SSI), Lodi, CA, USA) and kept at −5 °C for 1–4 h prior to centrifugation. After centrifugation (20 min at 2000 rev/min), serum samples were frozen and stored at −18 °C until testosterone analysis (for about 1 week). The entire handling per captured individual lasted 5–7 min. Once data collection was completed, neonates were returned to their original hiding spots and observers moved slowly away.

Testosterone measurements

Testosterone measurements were conducted at the A.N. Severtsov Institute of Ecology and Evolution, Moscow, Russia, using commercial testosterone EIA kits (Immunotek, Moscow, Russia). The sensitivity of the kit was 0.116 ng/ml, and accuracy of the kit was 90–110%. In total, we analysed samples of 20 (5 male, 15 female) neonates. For two animals (1 male, 1 female), the samples were too small for analyses. All measurements were conducted in duplicates on one plate. Intra-assay coefficient of variation (CV) was 2.46 ± 0.43% ($n = 20$).

Call analysis

We selected all recorded calls for analyses except those distorted by strong noise or wind. All calls were produced via the open mouth (oral calls); nasal calls (produced through the nose) were lacking. We measured all the acoustic variables with Avisoft-SASLab Pro software (Avisoft Bioacoustics, Berlin, Germany) 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 1024, frame 50% and overlap 96.87%. Prior to analysis, calls were downsampled to 22.05 kHz and high-pass filtered at 100 Hz (Gauss filter) to remove low-frequency noise. For each call, we measured the same five acoustic variables: duration, the start fundamental frequency (f0beg), the end fundamental frequency (f0end), the maximum fundamental frequency (f0max) and the minimum fundamental frequency (f0min) (Fig. 1). In addition, for each call, we calculated the df0 as the difference between f0max and f0min. All measurements were exported automatically to Microsoft Excel (Microsoft Corp., Redmond, WA, USA) for the statistic analyses. In total, for 22 individuals, we measured the acoustic variables in 330 neonate distress calls, from 2 to 32 calls per individual, on average 15.0 ± 9.2 calls per individual. Then, for each individual, we calculated the average values of each acoustic variable.

Vocal anatomy

The vocal anatomy of one fully developed, stillborn male cadaver collected on the breeding grounds of the Mongolian gazelles during data acquisition was investigated as an anatomical background for the acoustic analysis of neonate distress calls. This cadaver served for measuring the resting lengths of the nasal and oral vocal tracts, from the approximate position of the vocal folds (caudal end of thyroid cartilage) up to the nostrils or lips using a tape measure with 1-mm precision. In addition, nasal and oral vocal tract lengths were measured in digital on-site photographs of the cadaver with scale (Fig. 2). The position of the larynx was first established by palpation and later confirmed by direct inspection after mid-ventral opening of the skin in the throat region.

The length of the oral vocal tract was determined to provide a basis for measuring formants (resonances of the vocal tract) in the orally produced distress calls of neonate Mongolian gazelles. Formants can be measured either in low-frequency calls with closely spaced harmonics or in noisy calls where the sound energy is dispersed over the call spectrum (Riede and Fitch 1999; Taylor and Reby 2010). Formants provide important cues to sex in other open-habitat neonate ruminants with low-frequency voices (Volodin et al. 2011; Lapshina et al. 2012), and so we expected that formants can also be measured in voices of neonate Mongolian gazelles.

One larynx of an adult male Mongolian gazelle was collected by a joint German-Mongolian research expedition to the steppes of Eastern Mongolia (Chentie and Dornod Aimaks), May 1–June 15, 1995. The expedition was based on a cooperation of the Leibniz Institute for Zoo and Wildlife Research (IZW), Berlin, with the Mongolian Parasitological Society, Ulaanbaatar. The larynx had been excised by E. Lux and H. Mix during routine parasitological sampling, fixed in formalin and then transferred to the IZW, Berlin, where it was stored thereafter. The vocal anatomy of this adult male was investigated for comparison with the neonate male larynx and as an anatomical background for discussing the acoustic differences between neonate and adult male calls.

Dimensions of the larynx and of the vocal folds of the neonate male were taken with a ruler both during on-site field dissection and during dissection of the excised larynx later on (following Efremova et al. 2016). Dimensions of the excised larynx and vocal folds of the adult male were taken with a ruler during dissection. After cutting the entire larynx mediosagittally into two halves, the maximal dorsoventral length and the maximal rostrocaudal length of the right and left vocal folds in the neonate male were measured with electronic calipers (Aerospace, Brüder Mannesmann Werkzeuge

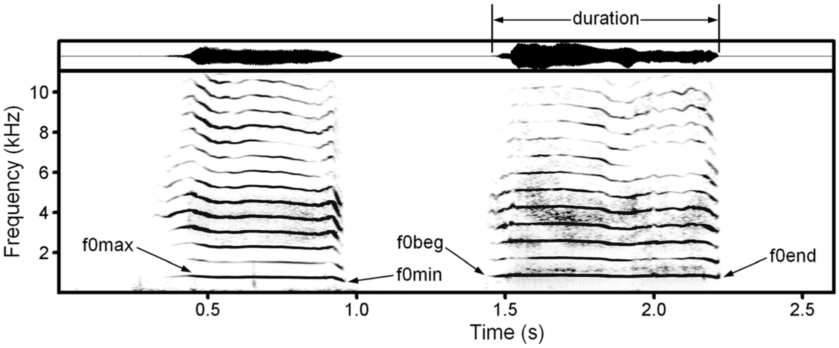

Fig. 1 Representative spectrogram (*below*) and waveform (*above*) of Mongolian gazelle neonate male (*left*) and neonate female (*right*) distress calls emitted in the context of hand capture. Measured acoustic variables: duration, start fundamental frequency (f0beg), end fundamental frequency (f0end), maximum fundamental frequency (f0max) and minimum fundamental frequency (f0min). The spectrogram was created with Hamming window, 22.05-kHz sampling rate, FFT 1024 points, frame 50% and overlap 96.87%. The audio file of these calls is available as Electronic Supplementary Material 1

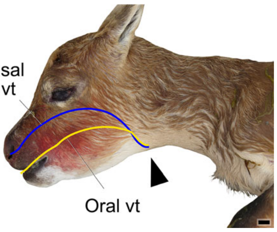

Fig. 2 Nasal (*blue*) and oral (*yellow*) vocal tract length estimation in a stillborn male Mongolian gazelle. The approximate position of the vocal folds, corresponding with the caudal edge of the thyroid cartilage, is indicated by the *arrowhead*. The position of the larynx was first established by palpation and later confirmed by direct inspection after mid-ventral opening of the skin in the throat region. *Nasal vt* nasal vocal tract, *Oral vt* oral vocal tract. *Scale bar* 10 mm

GmbH, Remscheid, Germany) with 0.5-mm precision (following Efremova et al. 2016). The dorsoventral length was measured along the medial surface of the vocal folds facing the glottis, from their ventral attachment to the thyroid cartilage dorsally up to their attachment to the vocal process of the arytenoid cartilage. The maximal rostrocaudal length was measured at the maximal rostrocaudal diameter in the dorsal third of the vocal fold, from its assumed rostral edge to its assumed caudal edge. These measurements served for estimating the size of the sound-producing structures in neonate Mongolian gazelles. The vocal folds of the adult male larynx were dissected and measured correspondingly.

Statistical analyses

Statistical analyses were conducted using STATISTICA v. 8.0 (StatSoft, Tulsa, OK, USA). Means are given as mean ± *SD*, all tests were two-tailed, and differences were considered significant whenever $P < 0.05$. All distributions of measured acoustic parameter values, body mass measurements and serum testosterone measurements did not depart from normality (Kolmogorov-Smirnov test, $P > 0.05$), so we could apply parametric tests for their analyses.

We used one-way ANOVA for estimating the effects of sex on body mass, serum testosterone and average values of acoustic variables of the distress calls. We used Pearson's correlation for analysis of correlation between body mass, serum testosterone values and acoustic variables. Because body mass should theoretically be proportional to the cube of a linear dimension like body length, we used lg body mass to calculate Pearson's correlation.

Results

Call fundamental frequency and formants

The fundamental frequency of the oral distress calls of neonate Mongolian gazelles ranged between 600 and 900 Hz (Table 1). Among acoustic variables, only the f0beg and f0min were significantly lower in males than in females. Duration, f0max, f0end and df0 did not differ between sexes.

In the dissected stillborn male Mongolian gazelle, the averaged oral vocal tract length was 132 mm and the averaged nasal vocal tract length 154 mm (Fig. 2). All distress calls of neonate Mongolian gazelles were oral, so the average distance between neighbouring formants was 1326 Hz, according to the formula $dF = \frac{c}{2L}$, where L is the vocal tract length and c is the speed of sound in moist air, approximated as 350 m s^{-1} (Riede and Fitch 1999; Reby and McComb 2003). This value is close to the distance between neighbouring harmonics of f0 (Fig. 1, Table 1). When approximating the vocal tract of a neonate Mongolian gazelle as a tube open at one end (mouth) and closed at the other (glottis closure during call-synchronous adduction of the vocal folds), the first formant value would be half of *df* and should comprise 663 Hz (Titze 1994; Reby and McComb 2003). Thus, the first formant can be expected at the same frequency level as the fundamental frequency (Table 1). Therefore, formant frequencies in the

Table 1 Mean ± *SD* values of body mass, serum testosterone and acoustic variables for neonate male and female Mongolian gazelles and ANOVA results for comparison between sexes

Variable	Male and female	Male	Female	Male/female ANOVA results
Body mass (kg)	5.06 ± 0.46	5.44 ± 0.26	4.91 ± 0.44	*$F_{1,21} = 7.50, P = 0.013$*
Testosterone (ng/ml)	0.17 ± 0.09	0.23 ± 0.12	0.15 ± 0.07	$F_{1,19} = 4.04, P = 0.060$
Duration (s)	0.38 ± 0.11	0.38 ± 0.13	0.38 ± 0.10	$F_{1,21} = 0.01, P = 0.99$
f0beg (Hz)	752 ± 114	663 ± 94	785 ± 105	*$F_{1,21} = 6.17, P = 0.022$*
f0end (Hz)	718 ± 136	632 ± 101	750 ± 135	$F_{1,21} = 3.75, P = 0.067$
f0max (Hz)	867 ± 126	796 ± 114	893 ± 123	$F_{1,21} = 2.85, P = 0.107$
f0min (Hz)	675 ± 106	602 ± 92	702 ± 100	*$F_{1,21} = 4.53, P = 0.046$*
df0 (Hz)	192 ± 59	194 ± 33	191 ± 67	$F_{1,21} = 0.01, P = 0.932$

Significant differences are given in italics

duration call duration, *f0beg* the start fundamental frequency, *f0end* the end fundamental frequency, *f0max* the maximum fundamental frequency, *f0min* the minimum fundamental frequency, *df0* the difference between f0max and f0min distress calls of neonate Mongolian gazelles either fell between the widely spaced harmonics and thus were invisible (as formants are only noticeable where sound energy is present), or formants were undistinguishable from harmonics because the frequencies of both closely matched. Therefore, formant frequencies could not be measured in the neonate Mongolian gazelles.

Body mass, serum testosterone and acoustics

Body mass was higher in males than in females (Table 1). Serum testosterone levels were marginally higher in males than in females (Table 1). No correlation was observed between body mass and serum testosterone values, for either the total sample of males and females ($r = 0.053$, $P = 0.82$) or separately for males ($r = -0.031$, $P = 0.96$) and females ($r = -0.292$, $P = 0.29$). No correlation was found between either body mass or serum testosterone values and any acoustic variable, both for the total sample of males and females ($0.023 < r < 0.253$, $P > 0.28$) and separately for males ($0.010 < r < 0.739$, $P > 0.15$) and females ($0.035 < r < 0.440$, $P > 0.10$).

Neonate male vocal anatomy

The very short vocal folds of the neonate male lack a rostrally directed flexible edge. Instead, they consist of an evenly smooth mucosal elevation between the laryngeal vestibule rostrally and the infraglottic cavity caudally. Dorsally, this inconspicuous, poorly delimited elevation involves the vocal process of the arytenoid cartilage and, ventrally, it fuses to the caudoventral end of the thyroid cartilage lateral to the cricothyroid ligament. The region between the tip of the vocal process of the arytenoid cartilage dorsally and the thyroid cartilage ventrally was considered as the vocal fold and measured. The dorsoventral vocal fold length was 4–5 mm; the maximal rostrocaudal vocal fold length was 2–3 mm, and the transverse width of the vocal folds (i.e. the height of the elevation) was also 2–3 mm (Fig. 3). It should be stated though that measurements were not easy to make as a result of the unusual vocal fold shape that hampered demarcation of the vocal fold contour.

The angle between the longitudinal axis of the larynx and the longitudinal axis of the vocal process was about 10°. The angle between the longitudinal axis of the larynx and the dorsoventral axis of the vocal fold was about 110°; i.e. the vocal fold was obliquely oriented from rostrodorsally to caudoventrally. The longitudinal axis of the larynx was established by connecting a dorsoventral half diameter at the rostral end of the thyroid cartilage with a dorsoventral half diameter of the trachea (Fig. 3).

The contours, shapes and relative sizes of the laryngeal cartilages in the neonate male are depicted in Fig. 4. Maximal rostrocaudal length and dorsoventral height of the laryngeal cartilages are given in Table 2. The length of the vocal process of the arytenoid cartilage (8 mm) is about 30% of the overall rostrocaudal length of this cartilage.

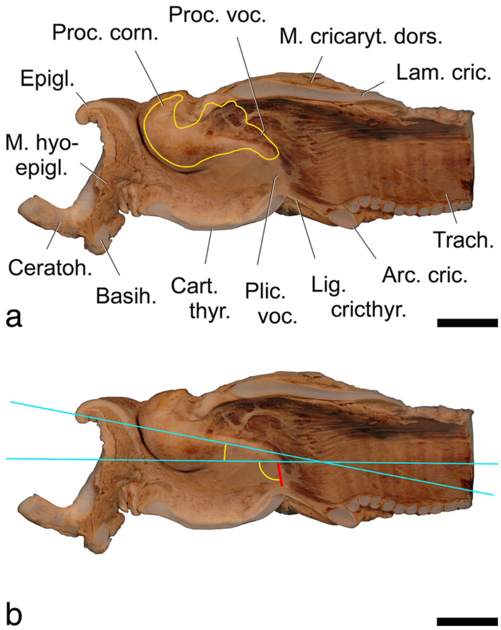

Fig. 3 Mediosagittal section of the alcohol-preserved larynx of a neonate male Mongolian gazelle, medial view. **a** The vocal fold region lacks a rostrally directed flexible mucosal fold. Instead, there is a smooth mucosal elevation between the laryngeal vestibule rostrally and the infraglottic cavity caudally. Contour of arytenoid cartilage inserted in *yellow*. **b** The vocal fold was taken as the region between the tip of the vocal process of the arytenoid cartilage and the ventrocaudal edge of the thyroid cartilage. Measured dorsoventral vocal fold length indicated by the *red bar*. The acute angle between the longitudinal axis of the vocal process and the longitudinal axis of the larynx is approximately 10°. The obtuse angle between the longitudinal axis of the larynx and the dorsoventral axis of the vocal fold is approximately 110°. Both angles indicated by *yellow arc lines*. *Arc. cric.* cricoid arc, *Basih.* basihyoid, *Cart. thyr.* thyroid cartilage, *Ceratoh.* ceratohyoid, *Epigl.* epiglottis, *Lam. cric.* cricoid lamina, *Lig. cricthyr.* cricothyroid ligament, *M. cricaryt. dors.* dorsal cricoarytenoid muscle, *M. hyoepigl.* hyoepiglottic muscle, *Plic. voc.* vocal fold, *Proc. corn.* corniculate process, *Proc. voc.* vocal process, *Trach.* trachea. *Scale bar* 10 mm

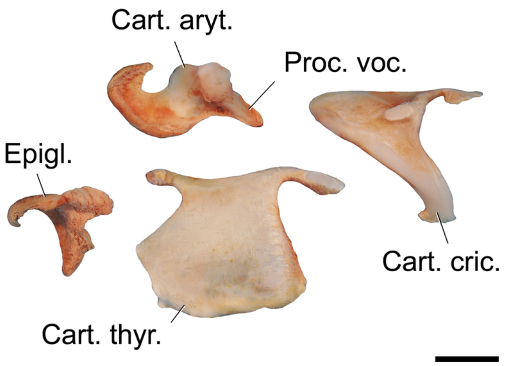

Fig. 4 Contours, shapes and relative sizes of the laryngeal cartilages in the stillborn neonate male Mongolian gazelle. *Cart. aryt.* arytenoid cartilage, *Cart. cric.* cricoid cartilage, *Cart. thyr.* thyroid cartilage, *Epigl.* epiglottis, *Proc. voc.* vocal process. Left lateral view. *Scale bar* 10 mm

Table 2 Overall dimensions of the laryngeal cartilages of a neonate male Mongolian gazelle

Cartilage	Maximal rostrocaudal length (mm)	Maximal dorsoventral height (mm)
Epiglottis	17	15
Thyroid cartilage	33	25
Arytenoid cartilage	26	14
Cricoid cartilage	28	23

Neonate and adult male vocal anatomy

In addition to size, the overall shape and relative proportions of the neonate male larynx differ markedly from those of the adult male Mongolian gazelle (Fig. 5). In the neonate larynx, the parts are mostly serially arranged along a straight rostrocaudal axis whereas in the adult larynx, a pronounced dorsal bending of the laryngeal vestibule and a dorsal shift of the epiglottis and the laryngeal entrance have occurred. In the neonate larynx, the base of the epiglottis is close to the ventrorostral edge of the thyroid cartilage, but in the adult larynx, the base of the epiglottis has sort of dorsally detached from that position. As a consequence, this middle part of the vestibulum is proportionally longer in the adult than in the neonate male and the relative positions of the epiglottis and the laryngeal entrance have changed accordingly (Fig. 5). The anlagen of the atypical adult male vocal folds are already recognizable in the neonate Mongolian gazelle (Figs. 3a and 5). However, the large vocal pad of the adult male vocal fold is lacking in the neonate and the pronounced caudal bulging of the adult male vocal fold from the inner laryngeal wall is absent in the neonate vocal fold. There is no trace of a rostrally directed flexible edge of the vocal folds, neither in the adult male nor in the neonate male.

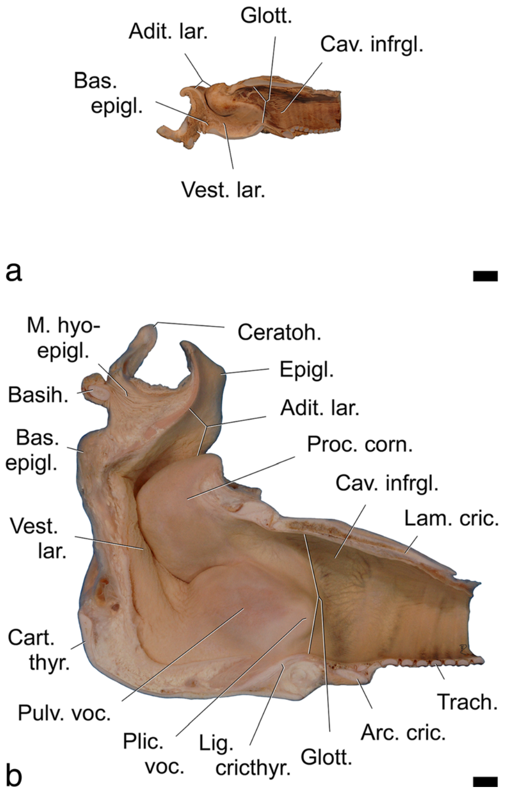

Fig. 5 Laryngeal mucosa relief of **a** a neonate male and **b** an adult male Mongolian gazelle. Right half, medial view. Straight longitudinal axis of the neonate larynx but strongly angled longitudinal axis in the adult male larynx. The neonate male vocal fold lacks a vocal pad whereas a large, voluminous vocal pad occurs in the adult male vocal fold. Caudal bulging from the inner laryngeal wall is pronounced in the adult male but absent in the neonate male vocal fold. Neither adult nor neonate male vocal fold shows any trace of a rostrally directed flexible edge. *Adit. lar.* laryngeal entrance, *Arc. cric.* cricoid arc, *Bas. epigl.* base of epiglottis, *Basih.* basihyoid, *Cart. thyr.* thyroid cartilage, *Cav. infrgl.* infraglottic cavity, *Ceratoh.* ceratohyoid, *Epigl.* epiglottis, *Glott.* glottis, *Lam. cric.* cricoid lamina, *Lig. cricthyr.* cricothyroid ligament, *M. hyoepigl.* hyoepiglottic muscle, *Plic. voc.* vocal fold, *Proc. corn.* corniculate process, *Pulv. voc.* vocal pad, *Trach.* trachea, *Vest. lar.* laryngeal vestibule. For additional labels of the neonate larynx, see Fig. 3. *Scale bar* 10 mm, respectively

Discussion

Neonate distress calls of Mongolian gazelles were high frequency in both sexes. This is very unusual for ruminants living in open habitats (grassland, steppe or semidesert). In striking contrast to our expectations, neonate Mongolian gazelles do not possess low-frequency "bass" voices as other wild open-habitat neonate ruminants (Sibiryakova et al. 2017; Volodin et al. 2017a, b). Instead, they produce high-frequency distress calls similar to ruminants living in closed habitats (Fig. 6, Table 3).

Apparently, the hider and follower strategies do not relate with the acoustics, as neonate hider Mongolian gazelles produce very high-frequency distress calls, as several other hider species do (red deer, fallow deer, mule deer, white-tailed deer and domestic goats), whereas neonate hider goitred gazelles produce very low-frequency distress calls (Fig. 6). Previously, a relationship between habitat openness/closeness and neonate antipredator strategies has been hypothesized (Torriani et al. 2006). However, based on Fig. 6, this relationship seems to hold only for the closed but not for the open habitats. All bioacoustically studied neonate ruminants living in closed habitats are hiders, whereas the neonates living in open habitats are either hiders or followers (Fig. 6, Table 3). Further study is necessary to reveal the reasons for this discrepancy, possibly resulting from different kinds of predators, their abundance and predation pressure.

In neonate ruminants, there is no prominent relationship between body mass and the fundamental frequency of distress calls (Fig. 6, Table 3). Neonates that are similar in body mass (for instance, saiga and fallow deer) produce calls that differ approximately tenfold in fundamental

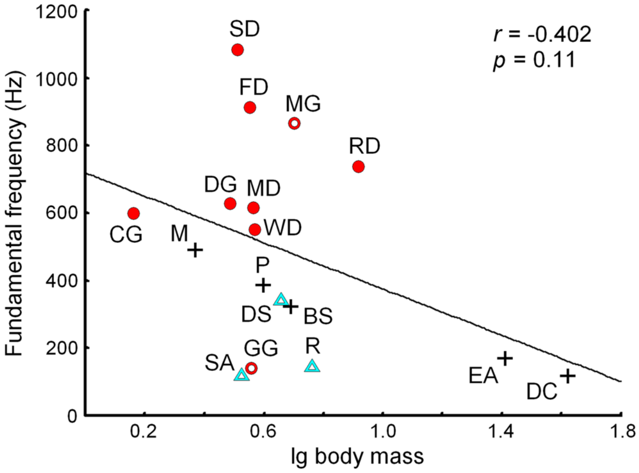

Fig. 6 Relationship between fundamental frequency of distress calls and lg body mass across species of neonate ruminants. *Empty symbols* open habitats; *solid symbols* closed habitats; *circles* hider species; *triangles* follower species; *crosses* species with unknown or undetermined hider/follower and habitat-type status. *BS* bighorn sheep, *CG* Cameroon domestic goat, *DC* domestic cattle, *DG* domestic goat, *DS* domestic sheep, *EA* eland, *FD* fallow deer, *GG* goitred gazelle, *M* markhor, *MD* mule deer, *MG* Mongolian gazelle, *P* pronghorn, *R* reindeer, *RD* red deer, *SA* saiga antelope, *SD* sika deer, *WD* white-tailed deer. Studies used for creating the figure are given in Table 3

frequency. In contrast, similar fundamental frequencies are produced by neonates that differ approximately tenfold in body mass (for instance, saiga and domestic cattle). Intra-specifically, no correlation was observed between body mass and the investigated acoustic parameters in the neonate Mongolian gazelles of this study. Likewise, a correlation between acoustic parameters and body mass was either weak or lacking in juvenile goitred gazelles (Volodin et al. 2011; Lapshina et al. 2012). However, a relationship between body mass and vocal tract length seems to exist between species of neonate ruminants as between the adults of some other species of mammals (Charlton and Reby 2016). In the larger-sized neonate Mongolian gazelles (Table 3), the lengths of the oral (132 mm) and of the nasal (154 mm) vocal tracts were longer compared to smaller-sized neonate goitred gazelles (oral 111–124 mm, nasal 127–141 mm; Efremova et al. 2016) and saigas (oral 111–116 mm, nasal 130–142 mm; Volodin et al. 2014; Sibiryakova et al. 2017).

We did not find a prominent correlation between the investigated acoustic parameters and sex in neonate Mongolian gazelles. Although body mass was larger in males, only the beginning and minimum fundamental frequencies were significantly lower in males than in females. Consistently, the effects of sex on the acoustics of oral calls were nonsignificant in juvenile domestic goats (Briefer and McElligott 2011) and red deer (Sibiryakova et al. 2015); a weak sex effect on call

Table 3 Compilation of studies on body mass, fundamental frequency (f0) of distress calls (mean or maximum), habitat type and antipredator strategy in neonate ruminants

Species	Latin name	Body mass (kg)	f0 (Hz)	Habitat type	Antipredator strategy	Reference body mass	Reference f0
Bighorn sheep	*Ovis canadensis*	4.93	329	No data	No data	Foreyt (1988)	Lingle et al. (2012)
Cameroon domestic goat	*Capra hircus*	1.46	599	Closed	Hider	Dhindsa et al. (1978)	Briefer and McElligott (2011)
Domestic cattle	*Bos taurus*	41.9	116	No data	No data	Weary and Chua (2000)	Weary and Chua (2000)
Domestic goat	*Capra hircus*	3.07	627	Closed	Hider	Mellado et al. (2011)	Terrazas et al. (2003)
Domestic sheep	*Ovis aries*	4.58	345	Open	Follower	Moreira et al. (2016)	Searby and Jouventin (2003)
Eland antelope	*Taurotragus oryx*	25.8	169	No data	No data	Jeffery and Hanks (1981)	Teichroeb et al. (2013)
Fallow deer	*Dama dama*	3.59	910	Closed	Hider	Pelabon (1997)	Lingle et al. (2012)
Goitred gazelle	*Gazella subgutturosa*	3.5	129	Open	Hider	Volodin et al. (2017a)	Volodin et al. (2017b)
Markhor	*Capra falconeri*	2.34	487	No data	No data	Alvarez (2015)	Lingle et al. (2012)
Mongolian gazelle	*Procapra gutturosa*	5.06	867	Open	Hider	This study	This study
Mule deer	*Odocoileus hemionus*	3.67	615	Closed	Hider	Teichroeb et al. (2013)	Lingle et al. (2007a, 2012)
Pronghorn	*Antilocapra americana*	3.96	385	No data	No data	Van Vuren et al. (2013)	Teichroeb et al. (2013)
Red deer	*Cervus elaphus*	8.3	737	Closed	Hider	Gallego et al. (2009)	Vaňková and Málek (1997)
Reindeer	*Rangifer tarandus*	5.79	148	Open	Follower	Couturier et al. (2009)	Teichroeb et al. (2013)
Saiga antelope	*Saiga tatarica*	3.37	126	Open	Follower	Sibiryakova et al. (2017)	Volodin et al. (2014)
Sika deer	*Cervus nippon*	3.24	1083	Closed	Hider	Kojo et al. (2012)	Lingle et al. (2012)
White-tailed deer	*Odocoileus virginianus*	3.68	546	Closed	Hider	Teichroeb et al. (2013)	Lingle et al. (2012); Teichroeb et al. (2013)

All data were obtained from animals younger than 10 days, except those for domestic sheep (3–13 days) fundamental frequency has been reported for juvenile fallow deer (Torriani et al. 2006).

The levels of serum testosterone were very low in both male and female neonate Mongolian gazelles of this study and were only marginally higher in males. The testosterone levels did not correlate with body mass. Very low serum testosterone concentrations (0.018 ± 0.003 ng/ml) were also found in male water buffalo from birth to 8 months of age (Hemeida et al. 1985) or less than 0.10 ng/ml from birth to 15 months of age (Sharma et al. 1984) followed by an increase (0.422 ± 0.079 ng/ml at 24 to 30 months and 0.793 ± 0.193 ng/ml at 42 to 48 months), corresponding to puberty and maturity, respectively (Sharma et al. 1984). Probably, the delayed rise of testosterone is a mechanism preventing nematode infestation of male bovids during their early development, as testosterone is an immunodepressive factor and positively related to the output of nematode eggs in the faeces of male bovids (Decristophoris et al. 2007). Consistently, in female domestic cattle *Bos taurus*, the comparable low serum testosterone levels at birth of 0.075 ± 0.005 ng/ml additionally decreased during the first week of life and remained low up to 9 months of age (Nakada et al. 2000). This is distinctive from humans (Andersson et al. 1998) and carnivores (Frank et al. 1991; Naidenko 2005; Naidenko et al. 2017), where neonates have quite high testosterone levels (almost like adults), in which there is an initial fall of testosterone after birth followed by a rise in testosterone levels during early postnatal ontogenesis. In a cervid species, neonate red deer, average neonate serum testosterone levels (0.387 ng/ml) were reported for both sexes, with highest levels in animals tested during the first 24 h of life (0.520 ng/ml) compared to those tested at following days (0.224 ng/ml) (Pavitt et al. 2014). Further research is necessary to estimate the ontogenetic development of testosterone levels in Mongolian gazelle and other bovids.

For the first time, we compared neonate testosterone levels and acoustic parameters in a mammalian species and did not find any correlation. At the same time, in adult mammals, including humans, some acoustic parameters correlate with testosterone levels (Evans et al. 2008; Rutovskaya et al. 2009; Fedurek et al. 2016); probably, these correlations develop during sexual maturation.

Generally, it is assumed that the length of the vocal folds correlates with their fundamental frequency: the longer the vocal folds, the lower the produced fundamental frequency and vice versa (Titze 1994; Riede and Brown 2013). Indeed, this appears to hold for several species of neonate ruminants. The very short 4–5-mm vocal folds of neonate Mongolian gazelles produce a high fundamental frequency of 600–900 Hz. Correspondingly, the longer 7-mm vocal folds of neonate saigas produce much lower distress fundamental frequencies of 126 Hz (Sibiryakova et al. 2017), and the 7–8-mm vocal folds of neonate goitred gazelles produce comparably low distress fundamental frequencies of 129 Hz (Efremova et al. 2016; Volodin et al. 2017a). However, the relatively long 9-mm vocal folds of neonate red deer, a cervid species (Volodin et al. 2016), produce high-frequency distress fundamental frequencies of 737 Hz (Vaňková and Málek 1997). Thus, the relationship between neonate vocal fold length and the call fundamental frequency appears to be variable across the taxa of ruminants. This might indicate a less tight connection between anatomical structures and their acoustic output than stated so far and, instead, suggest a higher flexibility of this connection as a result of the complex and highly dynamic system of the larynx and the entire vocal apparatus. Yet, potential mechanisms of a more flexible relationship between vocal structures and their acoustic output remain to be established. In any case, the current data on neonate vocal anatomy are still scarce for both bovids and cervids and more data are required for drawing more substantiated conclusions.

Neonate and adult male larynges of Mongolian gazelle differ markedly in their anatomical structure (Fig. 5, Frey et al. 2008a, b). And this results in the strongly different acoustic patterns of neonate male distress calls and adult male rutting calls (Fig. 7). All the major specialized features of the adult male larynx (enlarged and keeled thyroid cartilage, very short vocal process of the arytenoid cartilage, novel lateral laryngeal ventricles, rostrocaudally divided thyroarytenoid muscle) (Fig. 5, Frey and Gebler 2003; Frey and Riede 2003; Frey et al. 2008a, b) are not yet developed in the neonate male Mongolian gazelle. The general shape and proportions of the larynx in the neonate Mongolian gazelle resemble those of the widely unspecialized larynx of the adult female of this

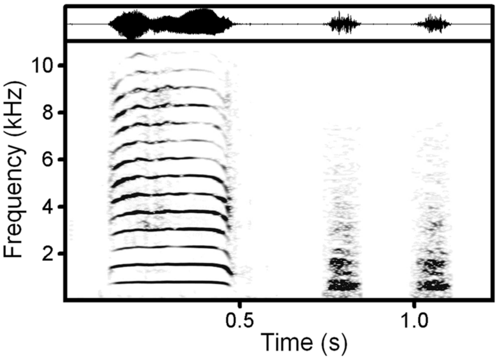

Fig. 7 Spectrogram illustrating the differences between the acoustics of a neonate male (first call) and an adult male (second and third calls) Mongolian gazelle. In the neonate call, the fundamental frequency is clearly visible, whereas the adult calls are noisy, so that the fundamental frequency cannot be traced. The neonate call was emitted by one of the hand-captured neonates of this study. The two adult calls, representing two sequential calls within a series of rutting calls of one male (the intercall interval was shortened), were kindly provided by Gennady Shalikov. The spectrogram was created with Hamming window, 22.05-kHz sampling rate, FFT 1024 points, frame 50% and overlap 96.87%. The audio file of these calls is available as Electronic Supplementary Material 2

species (Frey and Riede 2003). Possibly, development of the adult stage is similar to the situation in male goitred gazelles, in which the most pronounced changes of the vocal organs occur late in ontogeny and coincide with the age at which males achieve social maturity and become capable of defending a territory against rival males (Efremova et al. 2016; Volodin et al. 2017a).

When comparing the larynges of neonate male goitred gazelles and Mongolian gazelles, certain differences are noticeable. In lateral view, the thyroid cartilage in neonate male Mongolian gazelle is roughly rectangular hardly showing any laryngeal prominence. In contrast, the thyroid cartilage in neonate male goitred gazelle is bulging out ventrally, thus forming a very prominent laryngeal prominence (Efremova et al. 2016). To this prominence attaches the voluminous vocal fold of neonate male goitred gazelles, which is supported by a large vocal pad. Dorsally the vocal fold attaches to the relatively short vocal process of the arytenoid cartilage (Efremova et al. 2016). In contrast, the very short vocal fold of neonate Mongolian gazelle does not attach to a laryngeal prominence but to the caudoventral edge of the thyroid cartilage. A vocal pad is lacking, and dorsally the small vocal fold attaches to the relatively long vocal process of the arytenoid cartilage. This difference in structure causes a different resting position of the arytenoid cartilages: in neonate Mongolian gazelles, it is at a more obtuse angle relative to the longitudinal axis of the larynx whereas in neonate goitred gazelles, it is at a less obtuse angle. Correspondingly, the dorsoventral axis of the vocal fold in neonate goitred gazelles is steeper relative to the longitudinal axis of the larynx than in neonate male Mongolian gazelles. In neonate male goitred gazelles, the longitudinal axis of the ellipsoid vocal pad is in line with the dorsoventral axis of the vocal fold (Efremova et al. 2016). In neonate male Mongolian gazelles, however, the site where the vocal pad develops during ontogeny is rostral to the vocal fold. Taken together, the proximate causes for the high-frequency distress calls in neonate male Mongolian gazelles versus the low-frequency distress calls in neonate male goitred gazelles are the very short vocal folds, devoid of a vocal pad in the former, and the substantially longer vocal folds, equipped with a voluminous vocal pad in the latter.

Our study suggests that the acoustics (primarily the fundamental frequency) of neonate distress calls do not show relationships with either habitat openness/closeness or with neonate hiding/following antipredator strategies at birth. No relationship exists between fundamental frequency of distress calls and body mass across species of neonate ruminants. Phylogenetic distance may partly be responsible for the differences in the fundamental frequency between species, as Mongolian gazelle is not closely related to other open-habitat bovids, as saiga antelope and goitred gazelle (Lei et al. 2003; Bärmann et al. 2013). More data on the neonate distress calls of other ruminant species are necessary for a more conclusive comparison.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All applicable international, national and institutional guidelines for the care and use of animals were followed. All audio recordings and weighing of animals were conducted in tight cooperation with authorized bodies of Daursky State Natural Biosphere Reserve during biomedical monitoring. During our work, we strictly adhered to the special welfare instructions developed by the authorized bodies for work with Mongolian gazelles and to the "Guidelines for the treatment of animals in behavioural research and teaching" (Anim. Behav., 2006, 71, 245–253). No animal has suffered from our data collection. The data collection protocol no. 2011-36 was approved by the Committee of Bioethics of Lomonosov Moscow State University.

Informed consent Informed consent was not required.

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