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To cite this article: Ilya A. Volodin, Elena V. Volodina & Marina V. Rutovskaya (2021): Camel whistling vocalisations: male and female call structure and context in *Camelus bactrianus* and *Camelus dromedarius*, *Bioacoustics*, DOI: [10.1080/09524622.2021.1889403](https://doi.org/10.1080/09524622.2021.1889403)

To link to this article: <https://doi.org/10.1080/09524622.2021.1889403>



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Published online: 26 Mar 2021.



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Camel whistling vocalisations: male and female call structure and context in *Camelus bactrianus* and *Camelus dromedarius*

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ABSTRACT

Among ruminants, some species of cervids, bovids and camelids are capable of producing very high-frequency (HF) calls potentially produced by the aerodynamic whistle mechanism. We analysed the HF calls of six individual adult captive camels: three male and one female two-humped *Camelus bactrianus* and one male and one female one-humped *C. dromedarius*. Context of emission differed between sexes and individuals. Males of both species vocalised when guarding females during the rut. Females of both species vocalised towards their mates, postpartum (female *C. bactrianus*) or when protesting against preventing locomotion over enclosure (female *C. dromedarius*). In either species or sex, the HF calls were faint tonal vocalisations slightly modulated in fundamental frequency (f_0). Between species, the calls were significantly lower-frequency (1.7 ± 0.16 kHz) and longer (0.23 ± 0.08 s) in *C. bactrianus* than in *C. dromedarius* (3.12 ± 0.11 kHz; 0.16 ± 0.05 s). Nonlinear vocal phenomena (subharmonics and sidebands) occurred in both species but not in all individuals. We discuss the relationship of the f_0 of the HF calls with body size and vocal fold length in ruminants. We conclude that the 'whistling' HF calls of *C. dromedarius* are the highest-frequency vocalisations in Artiodactyla.

ARTICLE HISTORY

Received 3 December 2020
Accepted 8 February 2021

KEYWORDS

Artiodactyla; *Camelus bactrianus*; *Camelus dromedarius*; sex differences; high-frequency calls; ruminant; rutting vocalisation; whistle mechanism

Introduction

Aside phonation based on air flow-induced vibrations of the vocal folds (e.g. Berke and Long 2010; Herbst et al. 2012; Herbst 2014), mammals can vocalise by using another mechanism, the aerodynamic whistle. With the aerodynamic whistle mechanism, the sound wave is created at blowing the air through the narrowings of the vocal tract (Roberts 1975; Brudzynski and Fletcher 2010) or as an edge tone at facing/bypassing obstacles (Riede et al. 2017). The whistling mechanism has been confirmed in rodents by experiments displaying the predicted increase of call f_0 in light gas (heliox), which would be impossible for calls produced by a phonation mechanism in the larynx (Riede 2011, 2013; Pasch et al. 2017).

For terrestrial mammals aside the rodents, experiments confirming sound production with the whistle mechanism have yet to be done. Nevertheless, in many mammalian taxa,

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high-frequency (HF) calls, potentially representing aerodynamic whistles, are reported along with low-frequency calls produced with phonation mechanism: canids (Volodin and Volodina 2002; Schneider and Anderson 2011; Frey et al. 2016; Sibiryakova et al. 2020); elephants (de Silva 2010; Herler and Stoeger 2012); lagomorphs (Volodin et al. 2021); primates (Zimmermann et al. 2000; Ramsier et al. 2012; Gursky 2015; Hasiniaina et al. 2018; Grow 2019); colugos (Miard et al. 2019); cervids (Long et al. 1998; Frey and Riede 2013; Yen et al. 2013; Reby et al. 2016; Volodin et al. 2016; Golosova et al. 2017); bovids (Hall et al. 1988; Volodin et al. 2017).

Anatomical studies have discovered some potential sources for producing the ‘whistling’ HF calls in the vocal apparatus of rodents (Riede et al. 2017; Riede and Pasch 2020), canids (Frey et al. 2016) and cervids (Frey and Riede 2013; Reby et al. 2016). For bovids (cattle bulls), the anatomical sources for producing their HF calls over 1 kHz (Volodin et al. 2017) have yet to be studied. However, accordingly to the physical laws describing the string mechanics and accordingly to the experiments with excised 30-mm vocal folds of cervids (Riede and Titze 2008; Titze and Riede 2010; Frey and Riede 2013) it can be reasonable proposed that the HF calls of cattle bulls could not be produced with vibrations of their vocal folds over 40 mm in length (Metwally et al. 2018).

When produced simultaneously, the high fundamental frequency g_0 and the low fundamental frequency f_0 create a biphonic signal (Wilden et al. 1998), what proves the existence of two independent sound sources for these two frequencies. In the biphonic calls, the low f_0 is created by the vocal folds with the phonation mechanism, whereas the high g_0 is hypothetically created by the whistling mechanism (Volodin et al. 2013, 2016; Frey et al. 2016; Reby et al. 2016; Sibiryakova et al. 2020; Volodin et al. 2021).

For rutting male camels, ‘whistling’ HF calls were reported along to low-frequency ‘grunting’ and ‘gurgling’ vocalisations, but were only described verbally, without presenting spectrograms or measuring the acoustic parameters (*Camelus bactrianus*: Magash and Indra 2002; Nath et al. 2016; *C. dromedarius*: Yagil and Etzion 1980; Bhakat et al. 2005; Fatnassi et al. 2014a, 2014b; Padalino et al. 2015; Nath et al. 2016). For rutting male *C. dromedarius*, an extrusion of an extended soft palate (dulaa) is also reported as a part of male self-advertising and courting ritual (Padalino et al. 2015), but the relationship of this behaviour to vocalisation is not documented. In rutting male *C. bactrianus*, the dulaa is lacking. For female camels, vocalisations have not yet been reported. The aim of this study was to describe the potentially ‘whistling’ HF calls of male and female two-humped *C. bactrianus* and one-humped camels *C. dromedarius* and to compare the acoustics of these calls between species and sexes.

Materials and methods

Locations and animals

Audio recordings of camel ‘whistling’ HF calls were collected from 2001 to 2019 from six adult individuals (four *C. bactrianus*, two *C. dromedarius*) at three locations: the Volokolamsk Zoo Brooder of Moscow Zoo, Moscow Region, Russia (two male *C. bactrianus*), the Joint Usage Center’s ‘Collection of live mammals’ at the A.N. Severtsov Institute of Ecology and Evolution Chernogolovka biological station, RAS, Moscow Region, Russia (one male and one female *C. bactrianus*) and in Haifa Zoo, Haifa,

Israel (one male and one female *C. dromedarius*) (Table 1). Audio recordings were made from unrestrained camels in enclosures familiar to the animals. All study camels were habituated to people and were not afraid of them.

Call recording

The HF calls of study camels were collected during a few daily recording sessions per individual, separated with time spaces ranging from one to four days. In total, we collected 102 min of audio recordings from the four individual *C. bactrianus* and 131 min of recordings from the two individual *C. dromedarius*. During the audio recordings, the distance from the hand-held microphone to a caller varied between 1–3 m.

In 2001 and 2004, for audio recordings (frequency range 0.04–12.5 kHz, post-recording digitising at 48 kHz, 16 bit) we used an analogue SONY WM-D6C cassette tape recorder (Sony Corp., Tokyo, Japan) with Type II chrome audiocassettes EMTEC-CS II (EMTEC Consumer Media, Ludwigshafen, Germany) and with cardioid electret condenser microphones Sennheiser K6-ME64 (Sennheiser electronic, Wedemark, Germany). In 2015 and 2019, for audio recordings (frequency range 0.04–24 kHz, sampling rate 48 kHz), we used Zoom-H1 digital recorders (Zoom Corp., Tokyo, Japan) with built-in microphones.

Call analysis

Digitising, visual inspection of spectrograms and acoustic analyses of audio files were conducted using Avisoft SASLab Pro software (Avisoft Bioacoustics, Berlin, Germany). Before the start of the acoustic analyses, the analogue audio recordings (of *C. bactrianus* males Bm1 and Bm2) were digitised at a sampling rate of 48 kHz. The stereo digital audio files, recorded with Zoom-H1, were converted from stereo to mono mode by screening both channels and selecting the channel with best signal-to-noise ratios.

For the males of either species, we included in analysis only whistle calls of good quality (free of wind noise, non-overlapped with environmental noise or calls of other animals, with a high signal-to noise ratio). For the females of either species (*C. bactrianus* female Bf4 and *C. dromedarius* female Df6), we included in spectrographic analysis all measurable HF calls. In total, we analysed spectrographically 295 HF calls of *C. bactrianus* and 165 HF calls of *C. dromedarius* camels (Table 1).

Before the spectrographic analysis, we applied a high-pass filter at 0.2 kHz to remove background noise (of the wind, of the animal steps over the snow, human voices etc.), as the preliminary visual inspection of spectrograms of all audio files showed that fragments of camel HF calls were outside this frequency range. Spectrograms were created with a sampling rate of 48 kHz, Hamming window, Fast Fourier Transform (FFT) 1024 kHz, Frame 50%, Overlap 93.75%.

For each HF call, we measured 7 (1 temporal, 4 frequency and 2 power) acoustic variables. In the spectrogram window, we measured call duration with the standard marker cursor and the beginning ($f_{0\text{beg}}$), the end ($f_{0\text{end}}$), the maximum ($f_{0\text{max}}$) and the minimum ($f_{0\text{min}}$) fundamental frequencies with the reticule cursor (Figure 1). On the power spectrum of the entire call, we measured the peak frequency (f_{peak}) and the

Table 1. Animals, recording locations, and data collection summary. Caller species, sex, age, identity, date and duration of audio recording, total number of daily sessions of recording, study site, animal housing details, the context of vocalising, recording equipment and the number of the ‘whistling’ HF calls included in analysis are provided.

Caller species, sex, age	Caller ID	Recording date, <i>n</i> sessions, total duration	Location/context	Equipment	<i>n</i> HF calls
<i>Camelus bactrianus</i> , male, adult (precise age unknown)	Bm1	04–10 January 2001, 3 sessions, 29 min in total	Volokolamsk Zoo Brooder. Harem-holder, kept with 20 females during the rut in a 1-hectare outdoor enclosure.	Sony-D6C, Sennheiser-K6-ME64, analogue recording, post-recording digitising at 48 kHz	82
<i>Camelus bactrianus</i> , male, adult (precise age unknown)	Bm2	17–19 January 2004, 2 sessions, 17 min in total	Volokolamsk Zoo Brooder. Harem-holder, kept with 5 females during the rut in a 1-hectare outdoor enclosure.	Sony-D6C, Sennheiser-K6-ME64, analogue recording, post-recording digitising at 48 kHz	47
<i>Camelus bactrianus</i> , male, born in 2004	Bm3	24–26 November 2019, 3 sessions, 48 min in total	Chernogolovka Usage Center’s ‘Collection of live mammals’. Harem-holder, kept with 1 female (Bf4) and a 6-month old calf during the rut in a 0.4-hectare outdoor enclosure, without releasing for grazing in non-vegetation periods.	Zoom-H1, built-in microphones, stereo mode, 48 kHz sampling rate	147
<i>Camelus bactrianus</i> , female, born in 2002	Bf4	6 March 2015, 1 session, 8 min in total	Chernogolovka Usage Center’s ‘Collection of live mammals’. Postpartum dam, kept with her newborn calf and 1 male (Bm3) in a 0.4-hectare outdoor enclosure, with everyday releasing for grazing.	Zoom-H1, built-in microphones, stereo mode, 48 kHz sampling rate	19
<i>Camelus dromedarius</i> , male, adult (precise age unknown)	Dm5	04–5 February 2015, 2 sessions, 131 min in total	Haifa Zoo. Harem-holder, kept with 1 female (Df6) during the rut in a 0.2-hectare outdoor enclosure.	Zoom-H1, built-in microphones, stereo mode, 48 kHz sampling rate	160
<i>Camelus dromedarius</i> , female, adult (precise age unknown)	Df6	04–5 February 2015, 2 sessions, 131 min in total	Haifa Zoo. Harem female, kept with 1 male (Dm5) during the rut in a 0.2-hectare outdoor enclosure.	Zoom-H1, built-in microphones, stereo mode, 48 kHz sampling rate	5

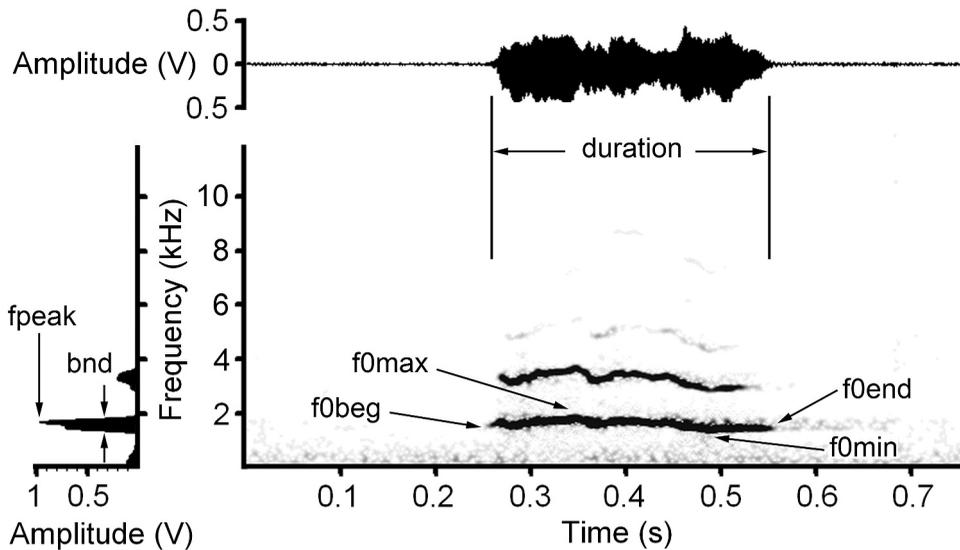


Figure 1. Waveform (above), mean power spectrum of the entire call (left) and spectrogram (right) indicate the measured acoustic variables of the ‘whistling’ HF calls of camels, exemplified by male *C. bactrianus* # Bm3. Designations: duration – call duration; $f0_{max}$ – the maximum fundamental frequency; $f0_{min}$ – the minimum fundamental frequency; $f0_{beg}$ – the fundamental frequency at the onset of a call; $f0_{end}$ – the fundamental frequency at the end of a call; f_{peak} – the frequency of maximum amplitude within a call; bnd – bandwidth of peak frequency. The spectrogram was created with a Hamming window, 48 kHz sampling rate, FFT 1024 points, frame 50% and overlap 93.75%. A file of the call is available in supplementary audio 1.

bandwidth of peak frequency (bnd) of each call at the distance of 10 dB from the maximum (Figure 1). We did not measure the power quartiles of the calls, because the high level of environmental noise and different recording equipment could affect these acoustic variables. All measurements were exported automatically to Microsoft Excel (Microsoft Corp., Redmond, WA, USA). Then we calculated in Excel the depth of $f0$ modulation as $df0 = f0_{max} - f0_{min}$.

Some HF calls displayed a broken contour of $f0$; in these calls we measured the duration of the silent space within the contour and calculated a percent of the silent space to the entire call duration. In addition, we scored each whistle call for presence of nonlinear vocal phenomena: subharmonics (appearance of frequency bands above and below the $f0$ band equal 1/2 of the $f0$ value), frequency jumps (breaks of calls contour due to the sudden changes of $f0$ value) and sidebands (modulation of $f0$ with another, much lower, fundamental frequency, resulting in amplitude modulation of call wave-form and in appearance of combinatory frequency bands above and below $f0$ and its harmonics on the spectrogram) (Wilden et al. 1998). For sidebands, the modulating frequency period (estimated as the distance from a previous pulse to the following pulse) was measured from the screen with the standard marker cursor in the main window of Avisoft, displaying both the wave-form and spectrogram (following Volodin et al. 2011, 2014). Then, for each HF call, we calculated the mean modulating frequency as an inverse value of the mean period of the modulating frequency of the call.

Video recording and analysis

We recorded and visually inspected a few video clips of camels producing the HF calls. For making videos, we used a full HD digital camera Panasonic HC-V720M (Panasonic Corporation, Osaka, Japan) and a PowerShot SX50HS digital camera (Canon USA, Melville, New York). The selected two video clips (one clip for male *C. bactrianus* and one for male *C. dromedarius*) with animals calling in the frontal position to the camera, were inspected visually frame-by-frame on a PC using Light Alloy 4.10.3 software (Europages, Paris, France) to document the asymmetrical face grimace during the ‘whistling’.

Statistics

Statistical analyses were carried out with STATISTICA, v. 8.0 (StatSoft, Inc., Tulsa, OK, USA). Means are given as mean \pm SD. Significance levels were set at 0.05, and two-tailed probability values are reported. We used a nested design of ANOVA with an individual nested within species (with species – fixed factor and individual – random factor) to compare the values of the acoustic parameter of HF calls between camel species (*C. bactrianus* and *C. dromedarius*). We used a one-way ANOVA with a Tukey Honestly Significant Difference (HSD) post hoc test to compare the acoustic parameter values of HF calls between the four individual *C. bactrianus* and between the two individual *C. dromedarius* camels.

Results

Context of emission

Overall, the HF calls were emitted when the animals were slightly or moderately aroused because of disturbance by people or conspecifics in close vicinity (Table 1). The HF calls of all males of both species (*C. bactrianus* Bm1-Bm3) and of the *C. dromedarius* female Df6 were produced during the autumnal-winter rutting periods. The HF calls of the *C. bactrianus* female Bf4 were produced during the spring calving period (Table 1).

All males of both species produced their HF calls in a sexual context. A rutting male that had been herding the female(s), standing or moving between the females and a researcher and occasionally would weakly threat against a researcher. Camel males vocalised standing in the lateral position towards a researcher, thus separating the harem female(s) from a human, probably accepted as a surrogate rival. The *C. dromedarius* male Dm5 protruded the dulaa during the rutting behaviour, but never produced the whistle calls with the protruded dulaa. In all male *C. bactrianus*, any behaviour reminiscent of protrusion of the dulaa was absent.

The *C. dromedarius* Df6 female produced her HF calls in the disturbance context during the rut. She vocalised towards her conspecific pair-mate Dm5, in response to his attempts to prevent here entering a broader part of the enclosure from a small paddock through a narrow pass.

The *C. bactrianus* Bf4 female produced her HF calls in the context of maternal care. She vocalised immediately after giving birth to a calf, in response to examination of the newborn calf by a researcher/owner (MVR) followed by sniffing the newborn by her pair



Figure 2. The asymmetrical calling grimace of male Dm5 *C. dromedarius* at the start of emission of a ‘whistling’ high-frequency call. The right nostril is tightly closed whereas the left one is widely opened.

mate (male Bm3). The *C. bactrianus* Bf4 female started producing her HF calls towards the human when lying nearby her newborn and then stood up, trying to keep a position between the calf and researcher. No signs of aggression towards the human or the pair mate was noticed.

Calling grimace

Visual inspection frame-by frame of two frontal-view video clips of HF calling (one for male Bm3 *C. bactrianus*, one for male Dm5 *C. dromedarius*) indicated that animals can produce their HF calls with a strongly asymmetrical face grimace, while one nostril was tightly closed whereas another one was fully opened (Figure 2). The degree of the shifting the low jaw for the creating this calling grimace, as well as the movements of the nostrils, could vary between calls within individual, and the same individual (Dm5 *C. dromedarius*) could produce the HF calls with either right or left nostril closed. Some calls were produced without a well-expressed face grimace.

Only the superficial phenomenological description of the calling grimace was possible, because of the lack of sufficient number of high-qualitative video clips. Only the close-up, perfectly frontal-view videos of calling animals were appropriate for observing the details of the asymmetrical face posture during the whistling, whereas the lateral-view video clips were completely uninformative for describing the face grimace of camel callers.



Table 2. Values (mean \pm SD) of the acoustic variables of the ‘whistling’ HF calls of *C. bactrianus* and *C. dromedarius* camels and ANOVA results for their comparison between species and individuals. The same letters next to values indicate the lack of significant differences between them ($p > 0.05$, Tukey HSD test). Designations: duration – call duration; f0beg – the fundamental frequency at the onset of a call; f0end – the fundamental frequency at the end of a call; f0max – the maximum fundamental frequency; f0min – the minimum fundamental frequency; df0 – the depth of frequency modulation; fpeak – the frequency of maximum amplitude, bnd – bandwidth of the peak frequency.

Species/caller ID	Acoustic variable									
	Duration (s)	f0beg (kHz)	f0end (kHz)	f0max (kHz)	f0min (kHz)	df0 (kHz)	fpeak (kHz)	bnd (kHz)		
<i>C. bactrianus</i>	0.23 \pm 0.08	1.45 \pm 0.17	1.47 \pm 0.10	1.70 \pm 0.16	1.34 \pm 0.16	0.36 \pm 0.12	1.55 \pm 0.16	0.37 \pm 0.10		
<i>C. dromedarius</i>	0.16 \pm 0.05	2.72 \pm 0.23	2.98 \pm 0.09	3.12 \pm 0.11	2.66 \pm 0.23	0.45 \pm 0.25	2.90 \pm 0.09	0.37 \pm 0.09		
ANOVA	$F_{1,454} = 30.9$, $p < 0.001$	$F_{1,454} = 1209$, $p < 0.001$	$F_{1,454} = 5675$, $p < 0.001$	$F_{1,454} = 5655$, $p < 0.001$	$F_{1,454} = 1547$, $p < 0.001$	$F_{1,454} = 2.93$, $p = 0.09$	$F_{1,454} = 4240$, $p < 0.001$	$F_{1,454} = 1.13$, $p = 0.29$		
Bm1	0.24 \pm 0.03 ^a	1.30 \pm 0.10 ^a	1.44 \pm 0.09 ^a	1.61 \pm 0.07 ^a	1.15 \pm 0.07 ^a	0.46 \pm 0.08 ^a	1.45 \pm 0.10 ^a	0.37 \pm 0.06 ^a		
Bm2	0.14 \pm 0.04 ^b	1.35 \pm 0.10 ^a	1.37 \pm 0.05 ^b	1.48 \pm 0.04 ^b	1.28 \pm 0.05 ^b	0.20 \pm 0.06 ^b	1.37 \pm 0.03 ^b	0.24 \pm 0.02 ^b		
Bm3	0.26 \pm 0.06 ^a	1.57 \pm 0.13 ^b	1.52 \pm 0.10 ^c	1.84 \pm 0.06 ^c	1.47 \pm 0.09 ^c	0.37 \pm 0.07 ^c	1.68 \pm 0.12 ^c	0.42 \pm 0.09 ^c		
Bf4	0.20 \pm 0.10 ^c	1.44 \pm 0.08 ^c	1.42 \pm 0.09 ^{ab}	1.61 \pm 0.12 ^a	1.36 \pm 0.06 ^d	0.25 \pm 0.11 ^b	1.46 \pm 0.06 ^a	0.27 \pm 0.05 ^b		
ANOVA	$F_{3,291} = 58.1$, $p < 0.001$	$F_{3,291} = 119.6$, $p < 0.001$	$F_{3,291} = 39.2$, $p < 0.001$	$F_{3,291} = 437.7$, $p < 0.001$	$F_{3,291} = 285.6$, $p < 0.001$	$F_{3,291} = 126.5$, $p < 0.001$	$F_{3,291} = 172.6$, $p < 0.001$	$F_{3,291} = 74.4$, $p < 0.001$		
Dm5	0.16 \pm 0.05	2.72 \pm 0.23	2.98 \pm 0.09	3.11 \pm 0.11	2.66 \pm 0.23	0.46 \pm 0.26	2.90 \pm 0.08	0.37 \pm 0.09		
Df6	0.12 \pm 0.02	2.86 \pm 0.05	3.01 \pm 0.08	3.16 \pm 0.07	2.84 \pm 0.07	0.32 \pm 0.04	2.97 \pm 0.09	0.33 \pm 0.07		
ANOVA	$F_{1,163} = 4.82$, $p = 0.03$	$F_{1,163} = 1.83$, $p = 0.18$	$F_{1,163} = 0.36$, $p = 0.55$	$F_{1,163} = 0.95$, $p = 0.33$	$F_{1,163} = 3.21$, $p = 0.07$	$F_{1,163} = 1.50$, $p = 0.22$	$F_{1,163} = 3.92$, $p = 0.049$	$F_{1,163} = 1.10$, $p = 0.30$		

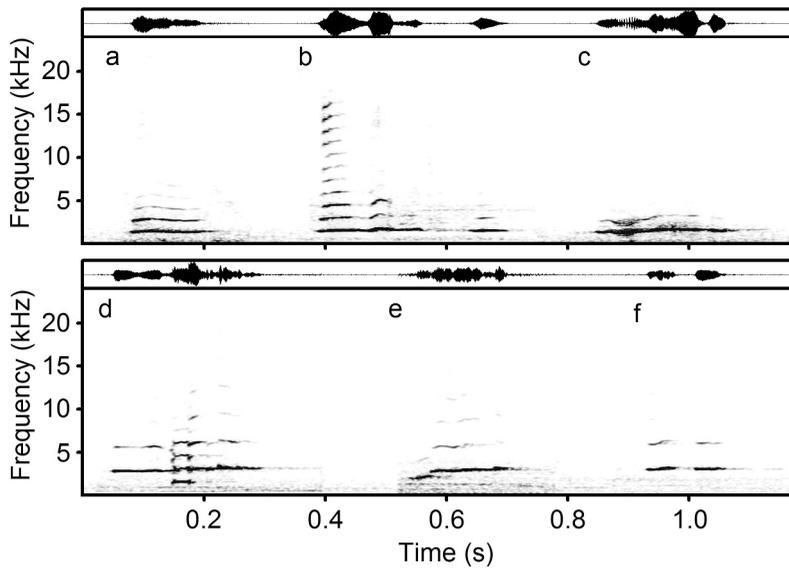


Figure 3. Spectrograms and waveforms illustrating the ‘whistling’ HF calls of *C. bactrianus* (upper panel) and of *C. dromedarius* (lower panel). (a) male # Bm2 call; (b) female # Bf4 call with broken contour; (c) male # Bm1 call with sidebands, see amplitude modulation on waveform; (d) male # Dm5 call with subharmonics; (e) male # Dm5 call with frequency jump; (f) female # Df6 call with broken contour. The spectrograms were created with a Hamming window, 48 kHz sampling rate, FFT 1024 points, frame 50% and overlap 96.87%. A file of the calls is available in supplementary audio 1.

The acoustics

Between species, the acoustic pattern of HF calls was very similar; although the calls of *C. bactrianus* and *C. dromedarius* were strongly different in f_0 values (Table 2, Figure 3). In both species, the HF calls were short and only slightly modulated in frequency. The f_0 band slightly increased or decreased from the start to the end of a call, or it had a slight wave-like modulation with small local maxima and minima (Figure 3). The peak frequency always coincided with the f_0 band of a call (Table 2).

Between species, the duration of HF calls was longer in *C. bactrianus* than in *C. dromedarius* (Table 2). All f_0 parameters and the peak frequency were twice as low in the *C. bactrianus* than in *C. dromedarius* (Table 2). Moreover, the maximal values of frequency parameters in *C. bactrianus* were lower than the minimal values of these parameters in *C. dromedarius*, so that the ranges of values did not overlap between species (Figure 4). In contrast, the values of the depth of f_0 modulation and of the bandwidth of peak frequency did not differ between species (Table 2, Figure 4).

In HF calls, the values of duration and of the peak frequency varied between individuals in either species. However, a substantial interindividual variation in values of all parameters of f_0 , of the depth of frequency modulation and of the bandwidth of peak frequency was only found in *C. bactrianus* but not in *C. dromedarius* (Table 2).

Nonlinear vocal phenomena were present in HF calls of both species, but not in all individuals. The nonlinear phenomena were only present in *C. bactrianus* male Bm1 and in *C. dromedarius* male Dm5 but absent in other study animals (Figure 3). In

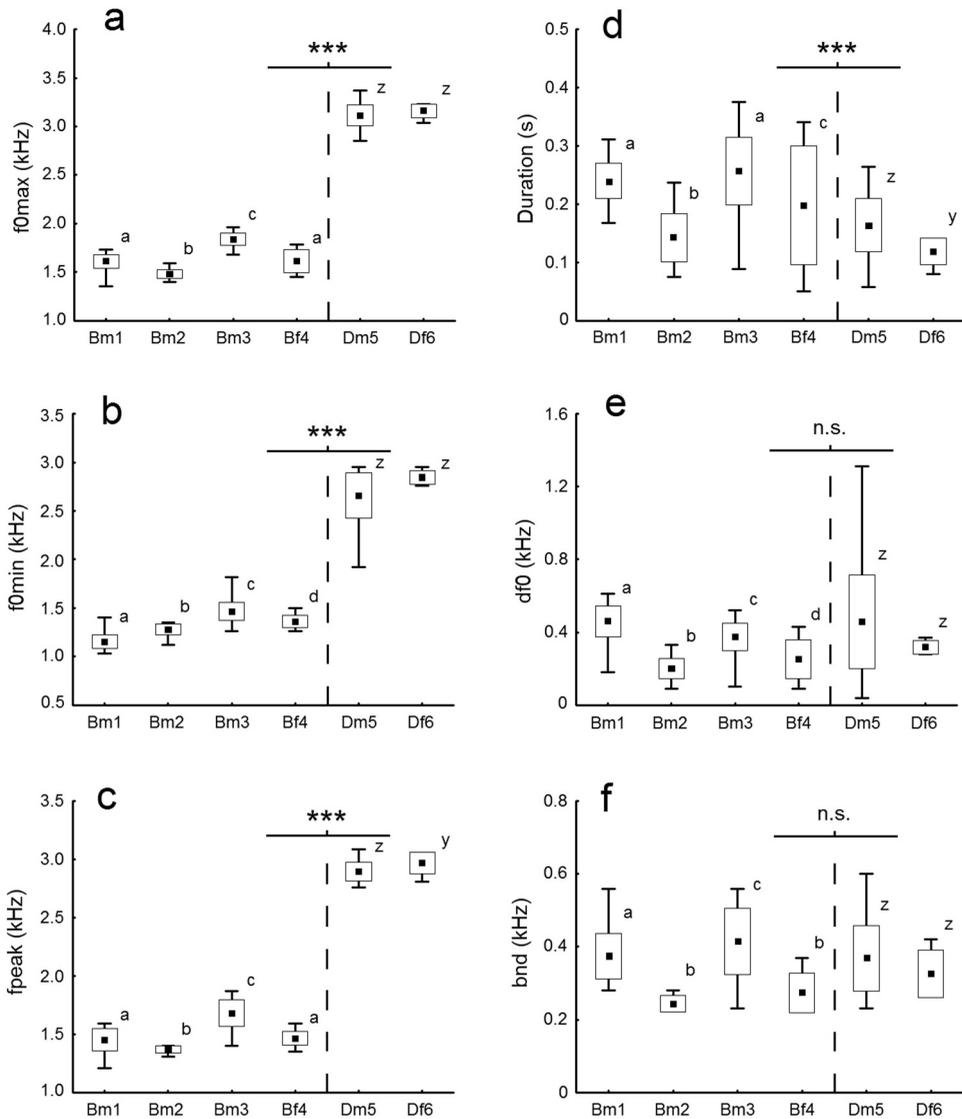


Figure 4. Values (mean \pm SD) of acoustic variables for the ‘whistling’ HF calls of *C. bactrianus* (Bm1, Bm2, Bm3, Bf4) and *C. dromedarius* (Dm5, Df6) camels. Points indicate means, boxes indicate SD, whiskers indicate min-max values. (a) the maximum fundamental frequency; (b) the minimum fundamental frequency; (c) the peak frequency; (d) call duration; (e) depth of fundamental frequency modulation; (f) bandwidth of peak frequency. Results for comparison of acoustics between animals within species are given with letters; means sharing the same letter are not significantly different. Results for comparison of acoustics between species are given with brackets, where *** – $p < 0.001$ and n.s. – non significant.

C. bactrianus male Bm1, 50% of whistle calls contained nonlinear phenomena: sidebands were present in 39 (47.6%) and subharmonics in 2 (2.4%) of HF calls. In *C. dromedarius* male Dm5, 23.8% of HF calls contained nonlinear phenomena: sidebands were present in

3 (1.9%), subharmonics in 28 (17.5%) and frequency jumps in 9 (5.6%) of the HF calls; 2 HF calls contained both subharmonics and frequency jumps.

The modulating frequency in HF calls with sidebands was always lower in *C. bactrianus* than in *C. dromedarius* camels. Samples of values did not overlap between species: in *C. bactrianus*, the modulating frequency ranged from 215 to 300 Hz (254 ± 20 Hz), whereas in *C. dromedarius*, it ranged from 373 to 385 Hz (378 ± 6 Hz).

The breaks of f_0 contour were also present in HF calls of both species, but not in all individuals. They were only present in *C. bactrianus* female Bf4 and in both individual *C. dromedarius* (male Dm5 and female Df6) but absent in other animals (Figure 3). The breaks of f_0 contour were present in 10 (52.6%) HF calls of *C. bactrianus* female Bf4, in 57 (35.6%) HF calls of *C. dromedarius* male Dm5, and in 2 (40.0%) HF calls of *C. dromedarius* female Df6. The percent of the break-related silence space to the entire call duration was $29.9 \pm 11.3\%$ in the broken HF calls of *C. bactrianus* female Bf4, $13.9 \pm 6.7\%$ in the broken HF calls of *C. dromedarius* male Dm5, and $24.6 \pm 6.9\%$ in the broken HF calls of *C. dromedarius* female Df6. Only in *C. dromedarius* male Dm5, the broken HF calls contained nonlinear phenomena: 8 of these calls contained subharmonics and 6 of these calls contained frequency jumps.

Discussion

In this study, we analysed for the first time the ‘whistling’ high-frequency calls of two camel species. We documented different contexts for production these calls by males and females. In addition, we identified an asymmetrical calling grimace for call emission.

The acoustics

The very high-frequency calls found in this study (over 1.5 kHz in *C. bactrianus* and over 3 kHz in *C. dromedarius*) do not correlate with the very long vocal folds of camels (e.g. 55–60 mm in *C. dromedarius*, Metwally et al. 2018). For comparison, in other species of Artiodactyla, the maximum fundamental frequencies produced with the phonation mechanism by the vocal folds of similar length are substantially lower, e.g. 129–338 Hz for the 30-mm vocal folds of male Iberian red deer *Cervus elaphus hispanicus* (Frey et al. 2012) or 112–170 Hz for the 40-mm vocal folds of male cattle (Hall et al. 1988; Watts and Stookey 1999; Volodin et al. 2017).

The very high fundamental frequency of the camel ‘whistling’ HF calls seems to be also disproportionally high for the large body size of the camels: about 600 kg in male *C. bactrianus* (Nurseitova et al. 2015), over 500 kg in male *C. dromedarius* (Fatnassi et al. 2014a; Aubè et al. 2017) and over 400 kg in nonpregnant female *C. dromedarius* (420 kg; Fatnassi et al. 2014a). Following a common rule for relationship between body size and call fundamental frequency in mammals (Fletcher 2004; Charlton and Reby 2016; Martin et al. 2017), the predicted f_0 produced by vibration of the vocal folds in the larynx should be substantially lower-frequency for such large-sized animals as camels. So, we can reasonably propose that camels probably produce their high-frequency calls by using another production mode than phonation, most probably the aerodynamic whistle mechanism, recently confirmed for rodents (Riede 2011, 2013; Pasch et al. 2017) and previously proposed also for some ruminants producing high-frequency calls (Frey and Riede 2013; Reby et al. 2016).

Among other camelids, very high-frequency calls are also reported in vicuna *Vicugna vicugna*. A spectrogram of about 2-kHz tonal call of vicuna is present in the study by Kiley (1972). In addition, an audio file of the high-frequency vocalisation of vicuna can be found at http://www.bioacoustica.org/gallery/mammals_eng.html#Artiodactyla.

Our data suggest that, among large-sized ruminants producing high-frequency calls, the *C. dromedarius* camels are champions in the achieved upper limits of maximum f_0 of their ‘whistling’ calls. The discovered upper limit of the maximum f_0 of camel HF calls (up to 3.37 kHz) is higher than in cattle bulls (up to 1.125 kHz, Volodin et al. 2017) and is comparable with upper limits of f_0 in wapiti *Cervus canadensis* (up to 3.4 kHz, Reby et al. 2016) and sika deer *C. nippon* (up to 2.18 kHz, Long et al. 1998).

By duration, the HF calls of camels were much shorter (0.16–0.23 s) than high-frequency rutting calls of cervids from the genus *Cervus* (from 2 to 5 s, Long et al. 1998) or bovids of the genus *Bos* (from 0.73 to 3.19 s, Volodin et al. 2017), but were comparable in duration with the high-frequency alarm and contact calls of the genus *Cervus* (*C. nippon*: from 0.17 to 0.23 s, Minami and Kawamichi 1992; Long et al. 1998; *C. elaphus sibiricus*: from 0.38 to 0.45 s, Volodin et al. 2016).

Context

Our data highlighted an interesting parallel between camels and the bugling cervids in the context of emission of the ‘whistling’ HF calls by males and females. Male camels produced their HF calls in the sexual rutting context, whereas the female *C. bactrianus* camel produced her HF calls at elevated arousal in the calf guarding context. Similarly, male cervids produce their bugling calls in the rutting context, whereas the females at elevated arousal in the calf guarding context (Feighny et al. 2006; Volodin et al. 2016). Therefore, we can note the surprising similarity with other ‘whistling’ Artiodactyla: the same call type used in the rutting context by males and calf guarding context by females.

At the same time, we noted a surprising dissimilarity in the intensity between the bugles of male and female cervids (Feighny et al. 2006; Volodin et al. 2016) and camel ‘whistling’ HF calls. In this study, we did not measure the intensity of the HF calls of camels. However, we can reasonable note that camel ‘whistling’ calls of either sex were faint compared to the ‘whistling’ bugles, because the camel HF calls could be heard and recorded only within vicinity of a few metres from a caller, whereas the bugles of cervids propagate to a distance of 1.5 km (Volodin et al. 2013). Factors limiting the production of the intense whistling calls in camels have yet to be studied. Probably these factors are related to camel adaptations to their arid windy environment (Schmidt-Nielsen et al. 1981).

Calling grimace

Data from our study suggest a potential role of calling grimace in the production of HF calls by male and female camels. Probably, the calling grimace enables the creation of an unilateral gap for whistling through. Otherwise, the asymmetrical call production is potentially advantageous as a mechanism for protecting the nostrils of camels against sand, in addition to the anatomy of the closable slit-like nostrils (Schmidt-Nielsen et al. 1981; Alsafty et al. 2014). A caller probably can turn out the closed nostril to the wind side,

whereas the open nostril on the collateral side can still be further used for breathing and vocalising.

The calling grimace is created by using articulation, moving the lower jaw on the left and right side, with closed mouth (*C. dromedarius*: Padalino et al. 2015; both camel species: this study). Although vocal anatomy of both camel species is studied in much detail (Saber 1983; Smuts and Bezuidenhout 1987; Alsafy et al. 2014; Metwally et al. 2018) further experimental research is necessary to highlight, what special traits of vocal anatomy of camels are responsible for production of their HF calls. In our study, whereas the grimace was clearly asymmetrical during production of some HF calls, some other HF calls of some individual males and females were emitted without a notable movement of the lower jaw and without the asymmetrical calling grimace. Therefore, the role of the calling grimace can probably be a visual demonstration enhancing the impressiveness or increasing the intensity of HF calls. However, our video analyses were restricted with small amount of close-up video clips in the frontal position to animals, whereas the videos made in the lateral position are inappropriate for the reliable documenting the facial asymmetry of camel callers. Further study is necessary, including analyses of high-quality close-up videos in the frontal view to elucidate the potential role of the asymmetrical calling grimace in camel vocal behaviour.

Acknowledgements

We greatly thank Andrey V. Popov for his valuable help with recordings of male and female *C. bactrianus* at the Chernogolovka biological station.

Data accessibility

Audio and video files supporting this article have been uploaded as supplementary material.

Disclosure statement

No potential conflict of interest was reported by the authors.

Ethics

All recordings were conducted non-invasively. During our work, we adhered to the ‘Guidelines for the treatment of animals in behavioural research and teaching’ (Anim. Behav., 2020, 159, I-XI). Protocol of recordings for this study was approved by the Committee of Bio-ethics of Lomonosov Moscow State University (research protocol # 2011-36).

Funding

This study was supported by the Russian Science Foundation (grant number 19-14-00037).

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