BRILL

Behaviour 160 (2023) 869–888

Behaviour
brill.com/beh

Meows of captive feral domestic cats (*Felis silvestris catus*) in the mating season: acoustic correlates of caller identity and sex

Liliya M. Sedova [a], **Ilya A. Volodin** [a,*], **Mariya N. Erofeeva** [b], **Galina S. Alekseeva** [b], **Sergey V. Naidenko** [b] and **Elena V. Volodina** [b]

[a] Department of Vertebrate Zoology, Lomonosov Moscow State University, Vorobievy Gory 1/12, Moscow 119234, Russia

[b] Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, Moscow 119071, Russia

*Corresponding author's e-mail address: volodinsvoc@gmail.com

ORCID iDs: Sedova: 0009-0005-5156-5209; Volodin: 0000-0001-6278-0354; Erofeeva: 0000-0002-4672-6160; Alekseeva: 0000-0002-1996-2387; Naidenko: 0000-0001-6400-5108; Volodina: 0000-0001-9755-4576

Received 25 May 2023; initial decision 28 June 2023; revised 22 August 2023; accepted 22 August 2023; published online 29 September 2023

Abstract

This study investigates the frequency, temporal and power parameters in 11 (5 males, 6 females) captive feral domestic cats *Felis silvestris catus*, vocalising in their individual outdoor enclosures during the mating season. Discriminant function analysis (DFA) classified the meows to correct callers with 79.2% accuracy, which exceeded the chance level of 22.9 ± 2.8%, calculated with permutation test. Male meows were lower-frequency, with the maximum fundamental frequency of 0.37 ± 0.05 kHz vs 0.61 ± 0.16 kHz in females. Sex differences in the maximum, beginning and end fundamental frequencies varied from 32 to 39%, depending on acoustic parameter. The DFA classified the meows to correct sex with accuracy of 88.0%, which exceeded the chance level of 58.2 ± 3.1%. We discuss that the meows encode information about individual identity and sex and that acoustic differences in frequency parameters of the meows exceed sexual dimorphism of body size in domestic cat.

Keywords

acoustic communication, *Felis silvestris catus*, individuality, mate meows, non-socialized cats, reproductive behaviour, sex differences, vocalisation.

Published with license by Koninklijke Brill NV | DOI: 10.1163/1568539X-bja10239
 | ISSN: 0005-7959 (print) 1568-539X (online)

1. Introduction

During the spring mating season, both sexes of domestic cat (*Felis silvestris catus*) produce many meows, containing acoustic correlates of caller sex (Shimizu, 2001). Probably, these intense calls can be used by animals for the distant identification of sex and individual identity of a potential mate. Acoustic parameters may also contain the attributes of mate quality, which, for females, includes the stages of receptivity (e.g., the levels of oestrogen) and, for males, the degree of aggression (modulated by the levels of testosterone) (Pfefferle et al., 2007; Tavernier et al., 2020).

The vocal repertoire of adult domestic cats contains several call types, differing in the acoustic structure: meow, purr, squeak, trill, chirp, howl, growl, gargle, hiss and copulatory cry (Schötz, 2015; Fermo et al., 2019; Tavernier et al., 2020). The most prominent call type of the vocal repertoire in domestic cat is meow, which varies substantially in the acoustic structure with the behavioural context (Brown et al., 1978; Yeon et al., 2011; Owens et al., 2017; Ntalampiras et al., 2019; Prato-Previde et al., 2020). Meows are calls with clearly visible fundamental frequency bands and harmonics, with duration of about 0.6 s, the maximum fundamental frequency ($f_{0,\max}$) of about 0.6–0.8 kHz, and the beginning and end fundamental frequencies ($f_{0,\text{beg}}$ and $f_{0,\text{end}}$) lower than the $f_{0,\max}$ of 0.1–0.15 kHz (Farley et al., 1992; Nicastro, 2004; Hubka et al., 2015; Urrutia et al., 2022).

During the mating season, both males and females produce meows, rutting cries and yowls (Shimizu, 2001). The rutting cry represents a sequence of prolonged, monotonous, weakly modulated in frequency calls, emitted with short inter-call intervals (2–3 times shorter than the durations of separate rutting cries) (Shimizu, 2001). The yowls are long meows, usually produced during counter-callings of two animals at confrontation, similar to dog howls (Shimizu, 2001).

The meows of domestic cats are generally similar in acoustic structure to the meows of the wild felid species, but are higher-frequency and shorter in duration than in their immediate ancestor, the African wild cat *Felis silvestris lybica* (Nicastro, 2004; Peters et al., 2009) or in the other wild species from the genus *Felis* (Peters et al., 2009). The degree of socialization with humans affects the ranges of variation in the acoustic parameters of meows within the species, as was revealed by a comparison of feral and human-socialized domestic cats (Yeon et al., 2011). In the agonistic test situation, meows of human-socialized house cats were shorter than in feral cats and higher in fundamental frequency, first formant frequency, peak frequency, 1-st power quartile frequency and 3rd power quartile frequency (Yeon et al., 2011).

Sex-related differences in vocalisations of domestic cats were only found previously in call rates of different call types, especially in the rutting cry (Shimizu, 2001). Individual-related differences in adult domestic cat meows were found in the call counts in a stressful context (Urrutia et al., 2019), in call duration and fundamental frequency of the calls produced in response to 2-min isolation along ontogeny of cats from 2 to 18 months (Urrutia et al., 2022), and in the fundamental and peak frequencies of the isolation meows of 10-days old kittens (Scheumann et al., 2012). A lower call rate was found in male than in female kittens across the first four postnatal weeks during separation with a mother (Hudson et al., 2015). No other studies investigating acoustic parameters potentially encoding the sexual and individual identity in calls of domestic cats are available.

Domestic house cats are sensitive to traits of individual identity encoded in the voices of their owners and can recognize them among the voices of other people (Saito & Shinozuka, 2013). Domestic house cats are capable of recognizing their names among other words (Saito et al., 2019). One months old kittens display stronger responses to chirps and meows of their own mothers compared with calls of other mother cats (Szenczi et al., 2016). Although for adult cats no experiments on recognizing the calls of the species' vocal repertoire have been conducted, it is reasonable to hypothesize that adult cats are also capable of recognizing the sexual and individual-related properties of meows and other call types.

We can also propose that cues encoding individual and sexual identity may be important for discriminating potential mating partners by vocalisation in feral domestic cats. Females in multi-male multi-female groups may mate with multiple males at any one oestrus, which results in litters with multiple paternities (Say et al., 1999; Natoli et al., 2007). Experiments including consecutive matings with two males showed that first males sired a higher percent of offspring in the litters (Erofeeva et al., 2018). The aim of this study was to describe the acoustic parameters of cat meows during the spring mating period and to evaluate the potential of these calls to provide information about individual and sexual identity of the callers.

2. Materials and methods

2.1. Site, animals and dates of work

Meows were recorded from eleven (5 males, 6 females) individually identified adult (2–13 years old) domestic cats (*Felis silvestris catus*), from 13 March to 5 May 2021 during the mating season. Data collecting was done at the Joint Usage Center 'Live collection of wild species of mammals' at A.N. Severtsov Institute of Ecology and Evolution (the biological station 'Tchernogolovka'), Moscow Region, Russia, located 50 km NE from Moscow city. At this station, a captive colony of domestic cats is kept for conducting behavioural and physiological research (Alekseeva et al., 2020; Soboleva et al., 2021; Erofeeva et al., 2022, 2023) along with captive colonies of wild felids, kept in a separate enclosure complex from the domestic cats (Jewgenow et al., 2006; Erofeeva et al., 2014; Pavlova et al., 2018). The founders of the colony of the domestic cats were 19 (10 females and 9 males) adult feral cats, captured in 2008 in different districts of Moscow city.

During data collection, subject cats were kept singly in outdoor enclosures (2 × 1.5 × 2 m size), wholly made of wire-mesh with 3-cm cells, with natural sandy/earth floor. There were 24 enclosures, 12 in a row, with a 1.5-m passage between them. Cats could communicate with their same or opposite sex neighbours through wire mesh acoustically or by touching each other by paws, either on the floor or climbing up the enclosure ceiling by the wire mesh. Each enclosure contained a wooden den of 55 × 40 × 50 cm, for protection against rain, snow and low temperatures and one or two tree stumps, for sitting on and claw sharpening. Six days a week, the animals were fed with minced chicken, fish or red meat with supplements of commercial cat food, vitamins and minerals; water was available ad libitum. Toys for domestic cats were available as enrichment; in addition, cats could play with natural objects (e.g., conifer cones), hunt flying and crawling insects, dig the earth.

Feeding time was irregular, so the cats did not vocalise specially for food in relation to feeding expectation and all calls included in the analysis were produced by animals in the context of self-advertising to potential mates or same-sex rivals. At time of recording, 10 of the 11 subject cats (one 2-year-old female, 'Alma', excluded) had mating experience either in previous years and/or in the current mating season of 2021. Cats were taken for pairing for mating (1–3 times in the mating season of 2021) and for blood and hair sampling each two weeks for control of reproductive health (Erofeeva et al., 2022; Naidenko et al., 2022). No additional handling or socialisation from people was applied to the cats. Pairings occurred in female home enclosures, so all animals could hear the calls related to advertisement, courting and mating behaviour through the wire mesh. Body mass was unknown for most individuals.

2.2. Audio recording and call samples

Cat meows were recorded by one researcher (IAV) using a Marantz PMD-660 (D&M Professional, Kanagawa, Japan) solid-state recorder with Sennheiser ME-64 (Sennheiser electronic, Wedemark, Germany) microphone, sampling rate 48 kHz, 16-bit resolution, range 40–20 000 Hz, in .wav format. Two sessions of audio recording were conducted, from 18:00 to 22:00, as the animals were more vocal at this time of day. The distance from the microphone to the focal caller varied from 0.5 to 4 m, which allowed recording calls with good signal-to-noise ratio. A researcher recording the calls was always outside the enclosure and recorded the calls through the wire mesh. During call collection, each caller was in its home enclosure alone. Cats produced all their vocalisations spontaneously; people did not provoke the animals to call. During call recording pairings for mating were not conducted. Between some calls, a researcher commented the calls of the focal cat, to identify the caller. Name and age of each subject cat were labelled at the enclosure door and researcher could check caller identity at each moment of conducting the recording.

For measuring the acoustic parameters, we only selected the meows with high signal-to noise ratio, non-overlapped with alien noise (wind, airplanes, calls of non-focal cats or forest birds and researcher voice). To decrease pseudoreplication from inclusion in analysis of similar calls from meow sequences of the same individual, we tried, where possible, to select for acoustic measurements the meows from different parts of audio files. In total, we included in the analysis 183 meows from 11 (5 males and 6 females) domestic cats, 20 meows per animal from 5 individuals and from 9 to 19 meows from the remaining 6 individuals which did not provide 20 high-quality meows per animal. On average, we took for analysis 16.6 $\pm$ 4.2 meows per individual.

2.3. Call analysis

For acoustic analysis, we used Avisoft SASLab Pro software (Avisoft Bioacoustics, Berlin, Germany). Before measurements, we decreased the sampling rate from 48 to 24 kHz, and used for the measurements the following settings: Hamming window, FFT (Fast Fourier Transform) length 1024 points, frame 50%, and overlap 96.87%. These settings provided 23 Hz frequency resolution and 1.3 ms time resolution. We also filtered out the background noise using a high pass filter 0.2 kHz. This filtering did not affect the values of the acoustic measurements, because the preliminary visual inspection of spectrograms showed that values of fundamental frequency (f_0) were always higher than 0.2 kHz.

For each meow call, one researcher (LMS), blind to the data collection procedure, measured manually, in the spectrogram window of Avisoft, call duration (duration) using the reticule cursor and the fundamental frequency parameters in three points of the call spectrum: start ($f_{0,beg}$), maximum ($f_{0,max}$) and end ($f_{0,end}$) (Figure 1). In addition, for each call, four power parameters were semi-automatically measured within a 50-ms time window (centred around the point of call maximum fundamental frequency): the peak frequency (f_{peak}) and the three power quartiles (q25, q50 and q75) covering 25, 50 and 75% of call energy from the mean power spectrum of each call, respectively (Figure 1). The window of 50 ms was selected for the measurements because it provided a better ratio of signal to noise compared with the

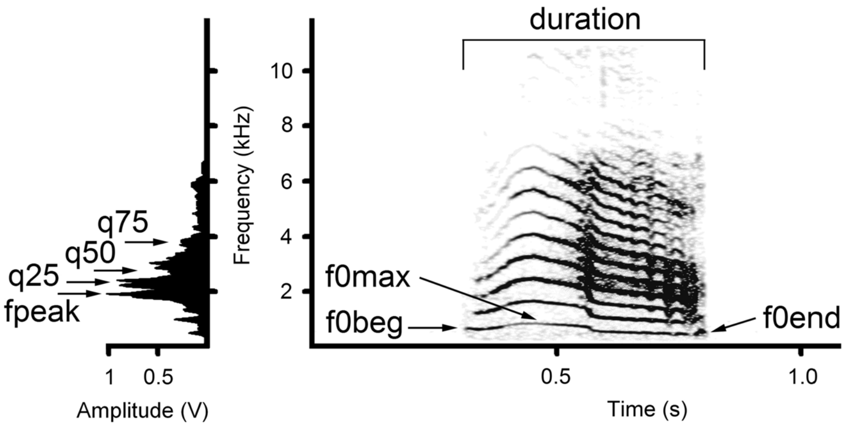

Figure 1. Measured acoustic parameters for cat meows. Spectrogram (right) and mean power spectrum of the meow (left). Designations: duration, call duration; $f_{0,max}$, the maximum fundamental frequency; $f_{0,beg}$, the fundamental frequency at the onset of a call; $f_{0,end}$, the fundamental frequency at the end of a call; f_{peak}, the frequency of maximum amplitude within a call; q25, q50, q75, the lower, medium and upper quartiles, covering 25, 50 and 75% energy of a call spectrum, respectively. The spectrogram was created at 24 kHz sampling frequency, FFT length 1024, Hamming window, frame 50%, overlap 96.87%.

measurements taken over the entire call spectrum (Volodin et al., 2022). All measurements were exported to Microsoft Excel (Microsoft, Redmond, WA, USA) table.

In each meow, we noted the presence of two nonlinear vocal phenomena: subharmonics and deterministic chaos (Scheumann et al., 2012; Hubka et al., 2015) and the articulation effect 'wave' (Gogoleva et al., 2008). We only noted a presence of subharmonics and chaos if duration of call parts with these nonlinear phenomena exceeded 10% of call duration.

2.4. Statistical analyses

Statistical analyses were carried out with STATISTICA v. 8 (StatSoft, Tulsa, OK, USA) and R 4.1.0 (R Development Core Team, 2021). All means are given as mean ± SD, significance levels were set at $p < 0.05$. Only 7 of 104 distributions of acoustical parameters differed significantly from the normal (Kolmogorov-Smirnov test, $p > 0.05$). As ANOVA is relatively robust to small departures from normality (Dillon & Goldstein, 1984), this was not an obstacle to applying parametrical tests. We used a nested design of ANOVA with Tukey HSD (Honest Significantly Different) test with an individual nested within sex to estimate the effects of factors 'individuality' and 'sex', on the acoustic parameters of meows, with sex as fixed factor and individual as random factor (to control for inclusion of more than one call from each individual).

We used the standard procedure of Discriminant Function Analysis (DFA) to calculate the probability of classifying the meows to the correct individual caller, and another DFA to calculate the probability of classifying the meows to the correct sex. In both DFAs, we included all the 8 measured acoustic parameters: duration, $f_{0,\text{max}}$, $f_{0,\text{beg}}$, $f_{0,\text{end}}$, f_{peak}, q25, q50 and q75.

We used Wilks' Lambda, to estimate the impact of each acoustic parameter in the DFA. For validating the DFA results, we calculated the values of probability of correctly classifying the meows to individuals and sexes, by applying the randomization test for probability of incorrect classifying in the DFA (Solow, 1990), with macros created in R. Random values were calculated from DFA on 1000 randomized permutations of datasets (Solow, 1990; Mundry & Sommer, 2007). For each distribution obtained with permutations, we noted whether the observed value exceeded 95% (950 values), 99% (990 values) or 99.9% (999 values) within distributions (Solow, 1990; Mundry & Sommer, 2007). If the observed value exceeded 95%, 99% or 99.9% values within the distribution, we established that the observed value differed significantly from the chance value with a probability $p < 0.05$, $p < 0.01$ or $p < 0.001$, respectively (Solow, 1990; Briefer et al., 2010; Chelysheva et al., 2023).

2.5. Ethical note

The study was conducted according to the ASAB/ABS 'Guidelines for the Treatment of Animals in Behavioural Research and Teaching' (Animal Behaviour, 2020, 159, I-XI) and approved by the Regulatory Commission of Experimental Research (Bioethics Commission) of the A.N. Severtsov Institute of Ecology and Evolution of the Russian Academy of Sciences (permission No. 21 of 24 April 2018).

3. Results

3.1. Acoustic variation of meows

Cat meows represented the calls with a clearly visible fundamental frequency (f_0) band and its harmonics (Figure 2). Call duration was on average 0.69 ± 0.22 s and ranged from 0.28 to 1.90 s; the average $f_{0,\max}$ was 0.50 ± 0.17 kHz and ranged from 0.30 to 1.11 kHz (Table 1). Cat meows could contain nonlinear vocal phenomena: subharmonics (9.3%, 17 calls from 6 individuals) and deterministic chaos (5.5%, 10 calls from 4 individuals). In addition, some meows contained the articulation effect 'wave' (21.9%, 40 calls from 8 individuals).

Cat meows displayed both individual and sex-related variation (Table 1). Two-way ANOVA showed that the factor individuality affected all the 8 acoustic parameters, whereas factor sex only affected the parameters of fundamental frequency: $f_{0,\max}$, $f_{0,\text{beg}}$ and $f_{0,\text{end}}$ (Figure 3). Male meows were lower in maximum fundamental frequency (0.37 ± 0.05 kHz) than female meows (0.61 ± 0.16 kHz) (Table 1). The means of each acoustic parameter for each individual are given in Table 2.

3.2. DFA for classifying meows to individuals

We conducted DFA for classifying the meows to correct individual callers. The DFA included all the 8 measured acoustic parameters (duration, $f_{0,\max}$, $f_{0,\text{beg}}$, $f_{0,\text{end}}$, f_{peak}, q25, q50, q75). The average value of correct classifying the meows to individual with DFA was 79.2%, which was significantly

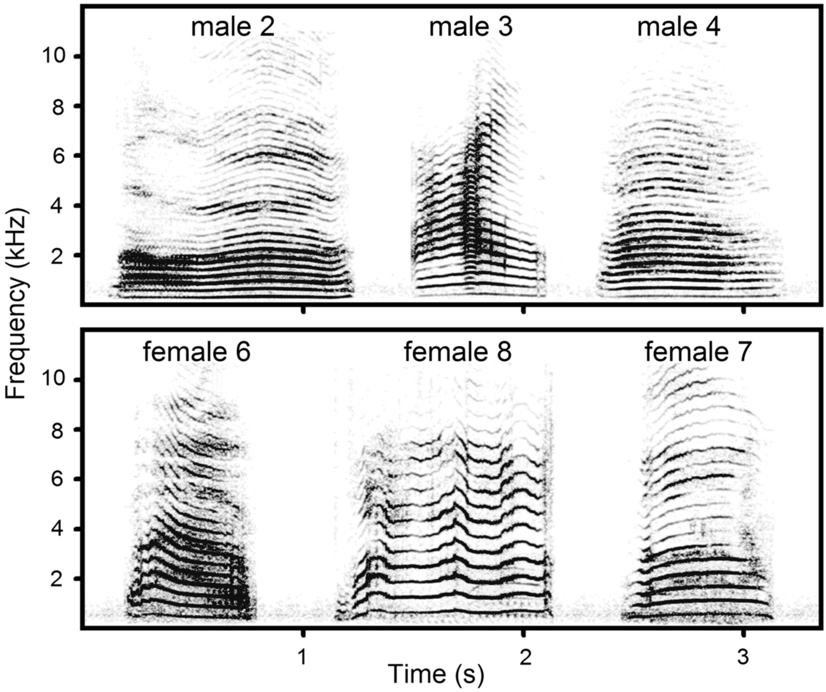

Figure 2. Spectrogram illustrating individual and sex-related differences of adult cat meows. Meows from three individual males and meows from three individual females, one meow per animal. The spectrogram was created at 24 kHz sampling frequency, FFT length 1024, Hamming window, frame 50%, overlap 93.75%. The .wav-file of these calls is available as Supplementary Audio 1 at 10.6084/m9.figshare.24025593.

higher than the level expected by chance of 22.9 ± 2.8%, min = 13.5%, max = 31.7% (permutation test, 1000 permutations, $p < 0.001$) (Table 3). In order of decreasing importance, $f_{0,\text{max}}$, duration and $f_{0,\text{end}}$ were mainly responsible for discrimination of individuals by the meows. Among individuals, the value of correct assignment of the meows varied from 65 to 100%; all the 11 individuals differed from the chance level (Table 3). Therefore, the meows had a high potential to encode caller individuality.

3.3. DFA for classifying meows to sex

We also conducted DFA for classifying the meows to correct sex. The DFA included all the 8 measured acoustic parameters (duration, $f_{0,\text{max}}$, $f_{0,\text{beg}}$, $f_{0,\text{end}}$, f_{peak}, q25, q50, q75). The DFA for sex showed the average value of correct assignment of the meows of 88.0%, which was significantly higher

Table 1.
Values (mean ± SD) of meow parameters and the results of nested two-way ANOVA for individual and sex-related differences.

Acoustic parameter	Mean ± SD			ANOVA	
	All animal meows ($N = 183$)	Male meows ($N = 87$)	Female meows ($N = 96$)	Individual differences	Sex differences
Duration (s)	0.69 ± 0.22	0.71 ± 0.24	0.67 ± 0.20	$F_{9,172} = 18.63$; $p < 0.001$	$F_{1,172} = 0.15$; $p = 0.708$
$f_{0,max}$ (kHz)	0.50 ± 0.17	0.37 ± 0.05	0.61 ± 0.16	$F_{9,172} = 70.68$; $p < 0.001$	$F_{1,172} = 10.64$; $p = 0.010$
$f_{0,beg}$ (kHz)	0.40 ± 0.12	0.32 ± 0.05	0.47 ± 0.11	$F_{9,172} = 23.67$; $p < 0.001$	$F_{1,172} = 13.11$; $p = 0.006$
$f_{0,end}$ (kHz)	0.42 ± 0.16	0.33 ± 0.06	0.51 ± 0.17	$F_{9,172} = 57.29$; $p < 0.001$	$F_{1,172} = 5.65$; $p = 0.041$
f_{peak} (kHz)	1.46 ± 0.70	1.39 ± 0.51	1.52 ± 0.84	$F_{9,172} = 19.03$; $p < 0.001$	$F_{1,172} = 0.05$; $p = 0.832$
q25 (kHz)	1.27 ± 0.55	1.22 ± 0.39	1.31 ± 0.66	$F_{9,172} = 21.40$; $p < 0.001$	$F_{1,172} = 0.06$; $p = 0.814$
q50 (kHz)	1.79 ± 0.71	1.64 ± 0.51	1.92 ± 0.83	$F_{9,172} = 20.16$; $p < 0.001$	$F_{1,172} = 0.29$; $p = 0.605$
q75 (kHz)	2.81 ± 1.05	2.68 ± 0.98	2.92 ± 1.10	$F_{9,172} = 15.79$; $p < 0.001$	$F_{1,172} = 0.08$; $p = 0.788$

An individual was nested within sex, with sex as fixed factor and individual as random factor. Designations: duration, call duration; $f_{0,max}$, the maximum fundamental frequency; $f_{0,max}$, the fundamental frequency at the onset of a call; $f_{0,max}$, the fundamental frequency at the end of a call; f_{peak}, the frequency of maximum amplitude within a call; q25, q50, q75, the lower, medium and upper quartiles. $N = 11$ adult cat callers (5 males and 6 females).

than the level expected by chance of 58.2 ± 3.1%, min = 50.1%, max = 70.5% (permutation test, 1000 permutations, $p < 0.001$) (Table 4). In order of decreasing importance, $f_{0,max}$ and $f_{0,beg}$ were mainly responsible for discrimination of sex by the meows. Therefore, the meows provided reliable cues to sex (the higher fundamental frequency in females than in males).

4. Discussion

4.1. Acoustic parameters of meows

This study is one of the first quantitative analyses of acoustic parameters of meows, emitted by male and female captive feral domestic cats during a mating season. Call duration was on average 0.69 ± 0.22 s and ranged

Table 2.
Values (mean ± SD) of meow frequency and temporal parameters for 11 adult cats, included in DFA for sex and individuality.

Animal ID	No. of meows	Meow acoustic parameters							
		Duration (s)	$f_{0,max}$ (kHz)	$f_{0,beg}$ (kHz)	$f_{0,end}$ (kHz)	f_{peak} (kHz)	q25 (kHz)	q50 (kHz)	q75 (kHz)
Male 1 Dekster	17	0.52 ± 0.09	0.38 ± 0.06	0.28 ± 0.04	0.31 ± 0.04	1.63 ± 0.32	1.47 ± 0.30	2.10 ± 0.52	4.00 ± 0.99
Male 2 Leo	20	1.02 ± 0.28	0.34 ± 0.03	0.32 ± 0.04	0.33 ± 0.06	1.29 ± 0.52	1.16 ± 0.28	1.50 ± 0.40	2.33 ± 0.69
Male 3 Serval	20	0.57 ± 0.07	0.43 ± 0.03	0.37 ± 0.04	0.39 ± 0.05	1.46 ± 0.47	1.26 ± 0.35	1.59 ± 0.34	2.27 ± 0.51
Male 4 Beorn	20	0.74 ± 0.11	0.35 ± 0.02	0.33 ± 0.03	0.33 ± 0.03	1.17 ± 0.52	1.07 ± 0.46	1.42 ± 0.56	2.40 ± 0.76
Male 5 Jivs	10	0.66 ± 0.17	0.35 ± 0.02	0.26 ± 0.03	0.28 ± 0.02	1.48 ± 0.68	1.11 ± 0.52	1.74 ± 0.46	2.50 ± 0.72
Female 6 Gameta	19	0.48 ± 0.06	0.67 ± 0.10	0.53 ± 0.07	0.45 ± 0.07	2.33 ± 0.47	2.05 ± 0.42	2.76 ± 0.38	3.66 ± 0.36
Female 7 Rioha	20	0.72 ± 0.09	0.54 ± 0.04	0.40 ± 0.04	0.43 ± 0.05	1.94 ± 0.68	1.48 ± 0.41	2.08 ± 0.64	2.70 ± 0.91
Female 8 Alma	20	0.76 ± 0.30	0.83 ± 0.12	0.49 ± 0.13	0.75 ± 0.12	1.39 ± 0.61	1.26 ± 0.45	2.12 ± 0.55	3.58 ± 0.99
Female 9 Lamia	9	0.59 ± 0.07	0.71 ± 0.03	0.67 ± 0.05	0.69 ± 0.06	2.00 ± 0.72	1.72 ± 0.70	2.10 ± 0.65	2.88 ± 0.78
Female 10 Elka	15	0.82 ± 0.13	0.41 ± 0.02	0.37 ± 0.03	0.38 ± 0.04	0.75 ± 0.23	0.70 ± 0.15	1.31 ± 0.61	2.80 ± 1.20
Female 11 Astrid	13	0.59 ± 0.10	0.48 ± 0.03	0.41 ± 0.07	0.35 ± 0.10	0.45 ± 0.02	0.47 ± 0.04	0.70 ± 0.21	1.35 ± 0.36

Designations: duration, call duration; $f_{0,max}$, the maximum fundamental frequency; $f_{0,max}$, the fundamental frequency at the onset of a call; $f_{0,max}$, the fundamental frequency at the end of a call; f_{peak}, the frequency of maximum amplitude within a call; q25, q50, q75, the lower, medium and upper quartiles.

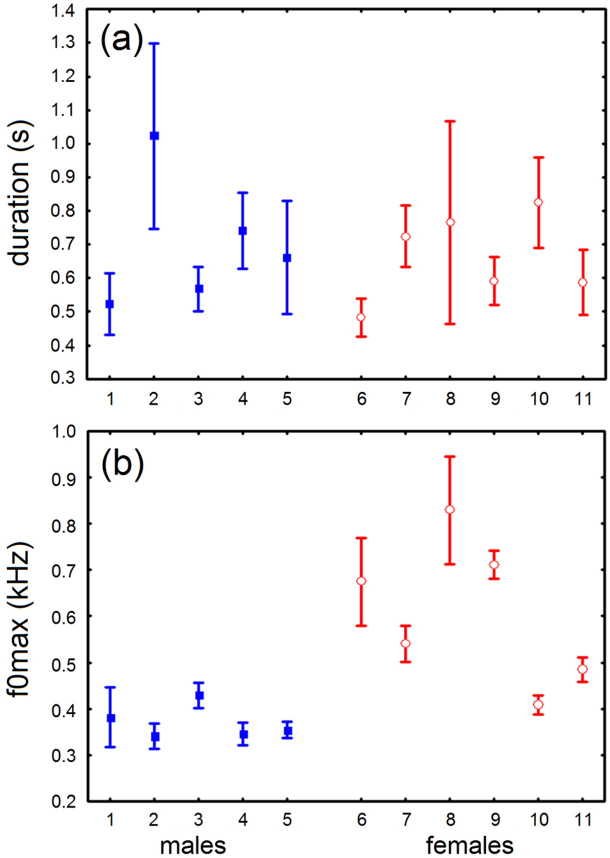

Figure 3. Individual and sex-related variation of acoustic parameters of meows in adult cats: (a) call duration (duration); (b) the maximum fundamental frequency ($f_{0,\max}$). Points with whiskers represent individuals. Central points indicate the means, whiskers indicate SD. The numbers of meows taken from each individual are given in Table 2.

from 0.28 to 1.90 s; the maximum fundamental frequency was on average 0.50 ± 0.17 kHz and ranged from 0.30 to 1.11 kHz. Previously, only a single study provided illustrative spectrograms of the meows produced by feral cats during the mating season, but without measuring the acoustic parameters of the calls (Shimizu, 2001).

The obtained values of the acoustic parameters are consistent with those reported by earlier studies of domestic cat meows, recorded out of the mating season. For comparison with our data, adult domestic house cats trained to meow for a reward produced meows of 0.61 ± 0.24 s, with average

Table 3.
Assignment of cat meows to a predicted caller with DFA.

Animal ID	No. of meows	No. of correctly assigned meows	Correctly assigned meows (%)
Male 1 Dekster	17	15	88.2
Male 2 Leo	20	13	65.0
Male 3 Serval	20	18	90.0
Male 4 Beorn	20	13	65.0
Male 5 Jivs	10	7	70.0
Female 6 Gameta	19	17	89.5
Female 7 Rioha	20	16	80.0
Female 8 Alma	20	16	90.0
Female 9 Lamia	9	9	100.0
Female 10 Elka	15	10	66.7
Female 11 Astrid	13	11	84.6
Total	183	145	79.2

maximum fundamental frequency of 0.60 ± 0.16 kHz (Farley et al., 1992). Meows of 12 adult house cats, averaged across 5 behavioural contexts, had duration of 0.78 ± 0.45 s and maximum fundamental frequency of 0.77 ± 0.19 kHz (Nicastro & Owren, 2003). Meows of 74 cats (29 males and 45 females) recorded in two situations: aversive (the cat in a transport box in a moving car) and pleasant (delicious food offered to the cat) had a duration from 0.62 to 1.02 s and $f_{0,\text{mean}}$ from 0.50 to 0.59 kHz (Schnaider et al., 2022). However, in the study of acoustic responses of mother domestic cats to removal of a kitten, the recorded meows had a duration of 0.4 ± 0.1 s and very high fundamental frequencies, $f_{0,\text{beg}}$ of 0.8 ± 0.4 kHz and $f_{0,\text{max}}$ of 1.3 ± 0.2 kHz (Brown et al., 1978). Young domestic house cats of 18 months old produced meows of 0.54 s in duration and with an average $f_{0,\text{max}}$ of

Table 4.
Assignment of cat meows to a predicted sex with DFA.

Actual group	Predicted group membership		Total	Correctly assigned (%)
	Males	Females		
Males	86	1	87	98.9
Females	21	75	96	78.1
Total	107	76	183	88.0

1.19 kHz (Schötz, 2012). However, during the tests involving isolation and restriction, the 18-months old house cats (36 males, 38 females) produced meows of about 0.60–0.70 s in duration and the $f_{0,\mathrm{mean}}$ of 0.30–0.35 kHz, that is, with a substantially lower frequency than in all other studies (Urrutia et al., 2022).

The study by Yeon et al. (2011) compared the meows of 35 adult feral cats and 13 adult house cats (all were females), tested across several contexts. The meows of the house cats were higher in fundamental frequency than in the feral cats (0.50–0.55 kHz and 0.40 kHz, respectively), with a substantially higher peak frequency (1.7–2.3 kHz and 0.5–0.7 kHz, respectively), and were substantially shorter in duration (0.6–1.0 s and 1.7–1.8 s, respectively). Our data on the acoustics of meows recorded from captive feral cats in the mating season were closer to the values reported for meows of house cats produced without relation to the cat mating season (Yeon et al., 2011).

4.2. Cues to caller individuality in meows

We found that the average value of correctly classifying of meows to 11 individuals with DFA was 79.2%, suggesting a high potential of the meows produced in the mating season to advertise individual identity of the callers. At the same time, cat meows produced in non-mating season in mother-offspring context seem to be not prominently individualistic: playback experiments indicated that kittens recognized their own mother by her chirp calls rather than by meow calls (Szenczi et al., 2016). For the three mother cats whose calls were analysed, the DFA accuracy rate of correct recognition was 93.4% for the chirps and only 77.8% for the meows (Szenczi et al., 2016). However, judging by the spectrograms of the chirps and meows used as playback stimuli to kittens in the study by Szenczi et al. (2016), the only difference of the chirp call type from the meow call type was the inclusion of the articulatory phenomenon ‘wave’, described previously in detail for the whine vocalisations of red fox *Vulpes vulpes* (Gogoleva et al., 2008). The individualistic traits in the meows were also investigated for 10-day old house kittens at isolation and handling (Scheumann et al., 2012). For the 18 individual kittens, the DFA accuracy rate of correct classification was 53.1% for the meows at isolation and 63.3% for the meows at handling, primarily on the basis of parameters of fundamental frequency, peak frequency and formants (Scheumann et al., 2012).

Strongly individualistic distant mating calls were also found in six captive male Eurasian lynxes *Lynx lynx* (Rutovskaya et al., 2009) and in the roars of five free-living male lions *Panthera leo* (Wijers et al., 2021). For the lynxes, DFA assigned 84.6% calls to correct individuals, primarily on the basis of call duration and mean entropy, reflecting the ratio of noisy and tonal energy in call spectra (Rutovskaya et al., 2009). For the five lions, a Hidden Markov Model (HMM) assigned 91.5% calls to correct individuals on the basis of call fundamental frequency contour (Wijers et al., 2021). For six captive tigers *Panthera tigris*, classification rate of individuals by their distant calls with DFA was 69.9% and the parameter most important for discrimination was call duration, whereas the $f_{0,\max}$ did not differ among individuals (Ji et al., 2013).

For 20 wild-living adult cheetahs *Acinonyx jubatus*, classification rate of individuals by their distant chirps with DFA was 79.5%, primarily on the basis of call duration and fundamental frequency (Chelysheva et al., 2023). For 12 captive adult cheetahs, classifying rate of individuals by their meows with DFA was 59.6%, primarily on the basis of $f_{0,\max}$ and two power quartiles (Smirnova et al., 2016). Thus, we can conclude that the distant calls of many felid species, and in particular the mating meows of domestic cats, likely contain well-expressed individualistic traits.

4.3. Cues to caller sex in meows

We found that male meows were noticeably lower in all parameters of fundamental frequency than female meows and differences in fundamental frequency were between 32 and 39% (Table 1). As the fundamental frequency of mammalian calls is inversely proportional to the length of the vocal folds in the larynx (Baotic et al., 2015; Titze et al., 2016; Garcia et al., 2017), acoustic differences between sexes may result from the size-related sexual dimorphism in domestic cat. For example, in free-ranging domestic cats, living around the steppe villages of Dauria (Far East of Russia), sex differences in body mass are 15–20%, with males heavier than females (Naidenko et al., 2020). However, the intersexual differences in the skull dimensions in domestic cat are as little as 4–7% (Petrov et al., 1992; Pitakarnnop et al., 2017).

Consistently, meows and chirps of adult male cheetahs were lower in fundamental frequency than those of adult females (Smirnova et al., 2016; Chelysheva et al., 2023), in agreement with sex dimorphism of body size in this species, up to 15% in captivity (Wildt et al., 1993) and from 15 to 22% in the wild (Caro, 1994; Marker & Dickman, 2003). As in domestic cats, the sex-related dimorphism in skull dimensions in the cheetah is also substantially lower than the differences in call fundamental frequency between sexes (Marker & Dickman, 2003). Probably the intersexual differences in the values of fundamental frequency develop during maturation, because they are still lacking in the meows of neonate domestic cats (Scheumann et al., 2012) or in the distant chirps of yearling cheetahs (Nagorzanski, 2018).

In contrast to domestic cats and cheetahs, in lions, only the minimum fundamental frequency differed between male and female roars, so that the $f_{0,\mathrm{max}}$ and $f_{0,\mathrm{mean}}$ did not display significant differences between sexes (Pfefferle et al., 2007). Furthermore, there were no differences in the fundamental frequency of the roars between captive male and female adult tigers (Ji et al., 2013). So, we can conclude that intersexual differences in the fundamental frequency of the distant calls in felid species can be not only due to morphological or body size differences. Hormonal profiles of males and females can also be important. The relationship between sex-related hormones and acoustical parameters has yet to be studied in felids.

This study showed that male and female domestic cat meows encode information about individual identity and sex of the callers. The findings raise questions about how conspecifics can decode this information.

Acknowledgements

We thank the staff of the Joint Usage Center 'Live collection of wild species of mammals' of A.N. Severtsov Institute of Ecology and Evolution (the biological station 'Tchernogolovka') for their help and support during data collection. We thank two anonymous reviewers for their valuable comments.

References

Alekseeva, G.S., Loshchagina, J.A., Erofeeva, M.N. & Naidenko, S.V. (2020). Stressed by maternity: changes of cortisol level in lactating domestic cats. — Animals 10: 903. DOI:10.3390/ani10050903.

Baotic, A., Sicks, F. & Stoeger, A.S. (2015). Nocturnal "humming" vocalizations: adding a piece to the puzzle of giraffe vocal communication. — BMC Res Notes 8: 425. DOI:10.1186/s13104-015-1394-3.

Briefer, E., Vannoni, E. & McElligott, A.G. (2010). Quality prevails over identity in the sexually selected vocalisations of an ageing mammal. — BMC Biol. 8: 35. DOI:10.1186/1741-7007-8-35.

Brown, K.A., Buchwald, J.S., Johnson, J.R. & Mikolich, D.J. (1978). Vocalization in the cat and kitten. — Dev. Psychobiol. 11: 559-570. DOI:10.1002/dev.420110605.

Caro, T.M. (1994). Cheetahs of the Serengeti: group living in an asocial species. — University of Chicago Press, Chicago, IL.

Chelysheva, E.V., Klenova, A.V., Volodin, I.A. & Volodina, E.V. (2023). Advertising sex and individual identity by long-distance chirps in wild-living mature cheetahs (*Acinonyx jubatus*). — Ethology 129: 288-300. DOI:10.1111/eth.13366.

Dillon, W.R. & Goldstein, M. (1984). Multivariate analysis: methods and applications. — Wiley, New York, NY.

Erofeeva, M.N., Pavlova, E.V., Antonevich, A.L. & Naidenko, S.V. (2014). Seasonal changes in activity of males' reproductive system in Eurasian lynx. — Russ. J. Theriol. 13: 9-16. DOI:10.15298/rusjtheriol.13.1.02.

Erofeeva, M.N., Alekseeva, G.S., Sorokin, P.A. & Naidenko, S.V. (2018). Effect of the number of mating partners and sperm quality on reproductive success in the domestic cat (*Felis catus*). — Biol. Bull. 45: 756-765. DOI:10.1134/S1062359018070063.

Erofeeva, M.N., Alekseeva, G.S., Kim, M.D., Sorokin, P.A. & Naidenko, S.V. (2022). Inbreeding coefficient and distance in MHC genes of parents as predictors of reproductive success in domestic cat. — Animals 12: 165. DOI:10.3390/ani12020165.

Erofeeva, M.N., Vasilieva, N.A., Ananyeva, M.S., Klyuchnikova, P.S. & Naidenko, S.V. (2023). Meeting with a male can lead to stress: female reaction to a pairing with a partner in Felidae. — Behav. Process. 208: 104876. DOI:10.1016/j.beproc.2023.104876.

Farley, G.R., Barlow, S.M., Netsell, R. & Chmelka, J.V. (1992). Vocalizations in the cat: behavioral methodology and spectrographic analysis. — Exp. Brain Res. 89: 333-340. DOI:10.1007/BF00228249.

Fermo, J.L., Schnaider, M.A., Pescatori Silva, A.H. & Maiolino Molento, C.F. (2019). Only when it feels good: specific cat vocalizations other than meowing. — Animals 9: 878. DOI:10.3390/ani9110878.

Garcia, M., Herbst, C.T., Bowling, D.L., Dunn, J.C. & Fitch, W.T. (2017). Acoustic allometry revisited: morphological determinants of fundamental frequency in primate vocal production. — Sci. Rep. 7: 10450. DOI:10.1038/s41598-017-11000-x.

Gogoleva, S.S., Volodin, I.A., Volodina, E.V. & Trut, L.N. (2008). To bark or not to bark: vocalization in red foxes selected for tameness or aggressiveness toward humans. — Bioacoustics 18: 99-132. DOI:10.1080/09524622.2008.9753595.

Hubka, P., Konerding, W. & Kral, A. (2015). Auditory feedback modulates development of kitten vocalizations. — Cell Tissue Res. 361: 279-294. DOI:10.1007/s00441-014-2059-6.

Hudson, R., Rangassamy, M., Saldaña, A., Bánszegi, O. & Rödel, H.G. (2015). Stable individual differences in separation calls during early development in cats and mice. — Front. Zool. 12: S12. DOI:10.1186/1742-9994-12-S1-S12.

Jewgenow, K., Goeritz, F., Neubauer, K., Fickel, J. & Naidenko, S.V. (2006). Characterization of reproductive activity in captive male Eurasian lynx (*Lynx lynx*). — Eur. J. Wildl. Res. 52: 34-38. DOI:10.1007/s10344-005-0002-6.

Ji, A., Johnson, M.T., Walsh, E.J., McGee, J. & Armstrong, D.L. (2013). Discrimination of individual tigers (*Panthera tigris*) from long distance roars. — J. Acoust. Soc. Am. 133: 1762-1769. DOI:10.1121/1.4789936.

Marker, L.L. & Dickman, A.J. (2003). Morphology, physical conditions, and growth of the cheetah (*Acinonyx jubatus jubatus*). — J. Mammal. 84: 840-850. DOI:10.1644/BRB-036.

Mundry, R. & Sommer, C. (2007). Discriminant function analysis with nonindependent data: consequences and an alternative. — Anim. Behav. 74: 965-976. DOI:10.1016/j.anbehav.2006.12.028.

Nagorzanski, T. (2018). Vocal communication in cheetahs: Investigating the cheetah's high-frequency contact chirps. — Master of Science Thesis, University of Vienna, Vienna. Available online at http://othes.univie.ac.at/52070/.

Naidenko, S.V., Klyuchnikova, P.S., Kirilyuk, V.E. & Alekseeva, G.S. (2020). Effect of population density on number of leukocytes in domestic cats. — Nature Conserv. Res. 5: 89-96. DOI:10.24189/ncr.2020.021.

Naidenko, S.V., Alekseeva, G.S., Klyuchnikova, P.S. & Erofeeva, M.N. (2022). Application of felid hair for non-invasive tracking of animal reproductive status and adrenal activity. — Animals 12: 2792. DOI:10.3390/ani12202792.

Natoli, E., Schmid, M., Say, L. & Pontier, D. (2007). Male reproductive success in a social group of urban feral cats (*Felis catus* L.). — Ethology 113: 283-289. DOI:10.1111/j.1439-0310.2006.01320.x.

Nicastro, N. (2004). Perceptual and acoustic evidence for species-level differences in meow vocalizations by domestic cats (*Felis catus*) and African wild cats (*Felis silvestris lybica*). — J. Comp. Psychol. 118: 287-296. DOI:10.1037/0735-7036.118.3.287.

Nicastro, N. & Owren, M.J. (2003). Classification of domestic cat (*Felis catus*) vocalizations by naive and experienced human listeners. — J. Comp. Psychol. 117: 44-52. DOI:10.1037/0735-7036.117.1.44.

Ntalampiras, S., Ludovico, L.A., Presti, G., Previde, E.P., Battini, M., Cannas, S., Palestrini, C. & Mattiello, S. (2019). Automatic classification of cat vocalizations emitted in different contexts. — Animals 9: 543. DOI:10.3390/ani9080543.

Owens, J.L., Olsen, M., Fontaine, A., Kloth, C., Kershenbaum, A. & Waller, S. (2017). Visual classification of feral cat vocalizations. — Curr. Zool. 63: 331-339. DOI:10.1093/cz/zox013.

Pavlova, E.V., Alekseeva, G.S., Erofeeva, M.N., Vasilieva, N.A., Tchabovsky, A.V. & Naidenko, S.V. (2018). The method matters: the effect of handling time on cortisol level and blood parameters in wild cats. — J. Exp. Zool. 329: 112-119. DOI:10.1002/jez.2191.

Peters, G., Baum, L., Peters, M.K. & Tonkin-Leyhausen, B. (2009). Spectral characteristics of intense mew calls in cat species of the genus *Felis* (Mammalia: Carnivora: Felidae). — J. Ethol. 27: 221-237. DOI:10.1007/s10164-008-0107-y.

Petrov, I., Nikolov, H. & Gerasimov, S. (1992). Craniometrical sex determination of wild cat *Felis silvestris* in Bulgaria. — Acta Theriol. 37: 381-396. DOI:10.4098/AT.arch.92-39.

Pfefferle, D., West, P.M., Grinnell, J., Packer, C. & Fischer, J. (2007). Do acoustic features of lion, *Panthera leo*, roars reflect sex and male condition? — J. Acoust. Soc. Am. 121: 3947-3953. DOI:10.1121/1.2722507.

Pitakarnnop, T., Buddhachat, K., Euppayo, T., Kriangwanich, W. & Nganvongpanit, K. (2017). Feline (*Felis catus*) skull and pelvic morphology and morphometry: gender-related difference? — Anat. Histol. Embryol. 46: 294-303. DOI:10.1111/ahe.12269.

Prato-Previde, E., Cannas, S., Palestrini, C., Ingraffia, S., Battini, M., Ludovico, L.A., Ntalampiras, S., Presti, G. & Mattiello, S. (2020). What's in a meow? A study on human classification and interpretation of domestic cat vocalizations. — Animals 10: 2390. DOI:10.3390/ani10122390.

R Development Core Team (2021). R: a language and environment for statistical computing. — R Foundation for Statistical Computing, Vienna. Available online at http://www.R-project.org.

Rutovskaya, M.V., Antonevich, A.L. & Naidenko, S.V. (2009). Distant cries emitted by males of the Eurasian lynx (*Lynx lynx*, Felidae). — Zool. Zh. 88: 1377-1386 (in Russian).

Saito, A. & Shinozuka, K. (2013). Vocal recognition of owners by domestic cats (*Felis catus*). — Anim. Cogn. 16: 685-690. DOI:10.1007/s10071-013-0620-4.

Saito, A., Shinozuka, K., Ito, Y. & Hasegawa, T. (2019). Domestic cats (*Felis catus*) discriminate their names from other words. — Sci. Rep. 9: 5394. DOI:10.1038/s41598-019-40616-4.

Say, L., Pontier, D. & Natoli, E. (1999). High variation in multiple paternity of domestic cats (*Felis catus* L.) in relation to environmental conditions. — Proc. Roy. Soc. Lond. B: Biol. Sci. 266: 2071-2074. DOI:10.1098/rspb.1999.0889.

Scheumann, M., Roser, A.-E., Konerding, W., Bleich, E., Hedrich, H.-J. & Zimmermann, E. (2012). Vocal correlates of sender-identity and arousal in the isolation calls of domestic kitten (*Felis silvestris catus*). — Front. Zool. 9: 36. DOI:10.1186/1742-9994-9-36.

Schnaider, M.A., Heidemann, M.S., Silva, A.H.P., Taconeli, C.A. & Molento, C.F.M. (2022). Cat vocalization in aversive and pleasant situations. — J. Vet. Behav. 55–56: 71-78. DOI:10.1016/j.jveb.2022.07.009.

Schötz, S. (2012). A phonetic pilot study of vocalisations in three cats. — In: Proceedings from Fonetik 2012, University of Gothenburg, Sweden, p. 45-48.

Schötz, S. (2015). Agonistic vocalisations in domestic cats: a case study. — In: Proceedings of Fonetik 2015, Lund University, Sweden, p. 85-90.

Shimizu, M. (2001). Vocalizations of feral cats: sexual differences in the breeding season. — Mammal Stud. 26: 85-92. DOI:10.3106/mammalstudy.26.85.

Smirnova, D.S., Volodin, I.A., Demina, T.S. & Volodina, E.V. (2016). Acoustic structure and contextual use of calls by captive male and female cheetahs (*Acinonyx jubatus*). — PLoS ONE 11: e0158546. DOI:10.1371/journal.pone.0158546.

Soboleva, A.S., Alekseeva, G.S., Erofeeva, M.N., Klyuchnikova, P.S., Sorokin, P.A. & Naidenko, S.V. (2021). Leukocytes count and profile during early postnatal ontogenesis in domestic cat: effect of litter size and multiple paternity. — J. Exp. Zool. A 335: 637-648. DOI:10.1002/jez.2508.

Solow, A.R. (1990). A randomization test for misclassification probability in discriminant analysis. — Ecology 71: 2379-2382. DOI:10.2307/1938650.

Szenczi, P., Banszegi, O., Urrutia, A., Farago, T. & Hudson, R. (2016). Mother-offspring recognition in the domestic cat: kittens recognize their own mother's call. — Dev. Psychobiol. 58: 568-577. DOI:10.1002/dev.21402.

Tavernier, C., Ahmed, S., Houpt, K.A. & Yeon, S.C. (2020). Feline vocal communication. — J. Vet. Sci. 21: e18. DOI:10.4142/jvs.2020.21.e18.

Titze, I., Riede, T. & Mau, T. (2016). Predicting achievable fundamental frequency ranges in vocalization across species. — PLoS Comput. Biol. 12: e1004907. DOI:10.1371/journal.pcbi.1004907.

Urrutia, A., Bánszegi, O., Szenczi, P. & Hudson, R. (2022). Scaredy-cat: assessment of individual differences in response to an acute everyday stressor across development in the domestic cat. — Appl. Anim. Behav. Sci. 256: 105771. DOI:10.1016/j.applanim.2022.105771.

Urrutia, A., Martinez-Byer, S., Szenczi, P., Hudson, R. & Banszegi, O. (2019). Stable individual differences in vocalisation and motor activity during acute stress in the domestic cat. — Behav. Process. 165: 58-65. DOI:10.1016/j.beproc.2019.05.022.

Volodin, I.A., Karaseva, K.D., Volodina, E.V., Tari, T. & Náhlik, A. (2022). European-native vocalizing: sex and age-class acoustic variation in the central European red deer (*Cervus elaphus*). — Behaviour 159: 1463-1482. DOI:10.1163/1568539X-bja10186.

Wijers, M., Trethowan, P., Du Preez, B., Chamaille-Jammes, S., Loveridge, A.J., Macdonald, D.W. & Markham, A. (2021). Vocal discrimination of African lions and its potential for collar-free tracking. — Bioacoustics 30: 575-593. DOI:10.1080/09524622.2020.1829050.

Wildt, D.E., Brown, J.L., Bush, M., Barone, M.A., Cooper, K.A., Grisham, J. & Howard, J.G. (1993). Reproductive status of cheetahs (*Acinonyx jubatus*) in North American zoos: the benefits of physiological surveys for strategic planning. — Zoo Biol. 12: 45-80. DOI:10.1002/zoo.1430120107.

Yeon, S.C., Kim, Y.K., Park, S.J., Lee, S.S., Lee, S.Y., Suh, E.H., Houpt, K.A., Chang, H.H., Lee, H.C., Yang, B.G. & Lee, H.J. (2011). Differences between vocalization evoked by social stimuli in feral cats and house cats. — Behav. Process. 87: 183-189. DOI:10.1016/j.beproc.2011.03.003.

Supplementary material

Supplementary Audio 1. Vocalisations of adult cat meows. Meows from three individual males and meows from three individual females, one meow per animal. This file can be accessed at 10.6084/m9.figshare.24025593.