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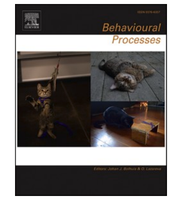

Relationship between acoustic traits of protesting cries of domestic kittens (*Felis catus*) and their individual chances for survival

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A R T I C L E I N F O

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A B S T R A C T

Domestic cat (*Felis catus*) mothers may rely on offspring cries to allocate resources in use of individuals with greater chances for survival and sacrifice the weak ones in case of impossibility to raise the entire large litter. Potential victims of this maternal strategy can enhance their chances of survival, by producing vocalizations with traits mimicking those of higher-quality offspring. We compared acoustic traits of 4990 cries produced during blood sampling by 57 two-week-old captive feral kittens (28 males, 29 females); 47 of them survived to 90 days of age and 10 died by reasons not related to traumas or aggression. No relationship was found between acoustic parameters and kitten survival, however, positive relationship was found between survival and body weight. The cries had moderate cues to individuality and lacked cues to sex. Body weight correlated positively with fundamental frequency and negatively with call rate, duration, peak frequency and power quartiles. We discuss that dishonesty of acoustic traits of kitten quality could develop as adaptation for misleading a mother from allocation resources between the weaker and stronger individuals, thus enhancing individual chances for survival for the weaker littermates. Physical constraint, as body weight, may prevent extensive developing the deceptive vocal traits.

1. Introduction

Mammalian infants produce cries in response to discomfort evoked by isolation, hunger, cold, unpleasant handling and pain (Romand and Ehret, 1984; 2019; Pisanski et al., 2022). These cries act for attracting attention of adult individuals both within and across taxa of mammals (Lingle et al., 2012; Kelly et al., 2017; Massenet et al., 2022) and even between taxa so distant as reptiles and mammals (e.g., Thevenet et al., 2023). The cries express a high level of emotional arousal (Volodin et al., 2009; Briefer, 2012; Silberstein et al., 2023) and might attract attention of parents or other adult individuals which can potentially resolve the problematic situation (Teichroeb et al., 2013; Lingle and Riede, 2014). As these cries need urgent responses from adults, they are commonly very intense and contain different nonlinear vocal phenomena (Wilden et al., 1998) and have dissonant or harsh sounding (Riede et al., 1997; Riede and Stolle-Malorny, 1999; Stoeger et al., 2011, 2012), complicating their ignorance from the side of individuals hearing these calls (Fitch et al., 2002).

Kittens of domestic cat (*Felis catus*) produce protesting cries during isolation (Scheumann et al., 2012; Urrutia et al., 2022; Szenczi et al., 2023), unpleasant handling (Scheumann et al., 2012), restraint and exposure to cold (Haskins, 1979), and at pain (Riede and Stolle-Malorny, 1999). Kittens younger than one month of age produce isolation calls at loss of contact with a mother and littermates (Brown et al., 1978; Scheumann et al., 2012; Hudson et al., 2015, 2017). These calls contain individualistic traits based on parameters of fundamental and peak frequencies (Scheumann et al., 2012) and call rate (Hudson et al., 2015, 2017; Szenczi et al., 2023) but lack sex-related traits in the acoustics (Scheumann et al., 2012). With increase of discomfort, call duration and peak frequency increase, whereas call fundamental frequency (f0) decreases (Scheumann et al., 2012; Szenczi et al., 2023).

In this study, we test whether acoustic traits of kitten's cries and call

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rate may serve as indicators of individual's physical health and chances for survival. The physical status ("kitten quality") and body weight depend on litter size (Sikes and Ylönen, 1998). We propose that in case of impossibility to rear the entire large litter, a mother cat potentially allocate the resources towards those her kittens which have higher chances of surviving and sacrifice the kittens weakened by diseases or physiological disorders. We suppose that clear relationship between the acoustical traits of kitten cries and their survival might indicate that the cries provide honest cues to kitten quality to a mother.

Alternately, the lack of relationship between the acoustical traits of kitten cries and their survival would indirectly indicate dishonesty of these acoustic traits. Potentially, kittens with lower chances for survival can enhance them, by producing the calls with more prominent characteristics attracting attention of a mother, expressing an exaggerated emotional arousal (McComb et al., 2009; Gogoleva et al., 2011; Pisanski et al., 2022). These traits are a higher call rate, the higher fundamental and peak frequencies, the higher power quartiles and large amounts of nonlinear vocal phenomena (Volodin et al., 2009; Stoeger et al., 2011, 2012; Briefer, 2012; Massenet et al., 2022; Mártinez-Byer et al., 2023).

Female domestic cats can mate with more than one male during one estrus, so kittens within a litter can be sired by different males (Say et al., 1999; Natoli et al., 2007; Erofeeva et al., 2018). Multiple paternity is a common phenomenon across mammals (Boellstorff et al., 1994; Baker et al., 1999; Dean et al., 2006; Dugdale et al., 2007; Yamamoto et al., 2013; Shimozuru et al., 2019), provoking allogenic stimulation of embryos in such litters and thus affecting their physical parameters and perspectives of survival (Firman and Simmons, 2008; Thonhauser et al., 2014; Gerlinskaya et al., 2018; Soboleva et al., 2021). So, we expected to find that kittens from litters with multiple paternity will have a better health/quality, reflected in their cries.

Litters of domestic cats can contain from 1 to 7 kittens (Alekseeva et al., 2020; Soboleva et al., 2021), on average 3 kittens at female pairing with one male and on average 4.3 kittens at female pairing with two males (Erofeeva et al., 2018). The number of kittens per litter affects physiological parameters at early ontogeny of kittens (Soboleva et al., 2021). The greater is litter size the lower might be their weight at birth and the higher competition for milk and maternal care (Sikes and Ylönen, 1998). Thus, we expect that kittens from the smaller litters would have better health/quality, reflected in their cries. In particular, we expect that kittens which survived to 90 days of age will be heavier in body weight and that kittens which survived to 90 days of age will more often origin from the litters with multiple paternity.

The aim of this study was to estimate whether call rate, nonlinear phenomena and acoustic parameters of discomfort cries of domestic cat kittens may serve reliable indicators of their individual quality and chances of survival. In addition, we estimate whether kitten cries provide information about individual and sexual identity of the callers and whether the acoustical parameters depend on kitten body weight, litter size and origin from litters sired by one or more males.

2. Material and methods

2.1. Study site, subjects and dates

Cries of kittens were recorded in July-August 2021 and in May-July 2022 during procedures of blood and fur sampling and weighting for physiological studies 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. The 57 kittens (28 males and 29 females) were aged from 12 to 17 days (on average, 13.9 ± 1.7 days of age). All these individually identified kittens belonged to a captive colony of domestic cats started at 2008 from 19 adult mongrel feral cats (10 females and 9 males) captured from basements of multi-apartment houses in different districts of Moscow city (Alekseeva et al., 2020; Soboleva et al., 2021; Erofeeva et al., 2022, 2023; Sedova et al., 2023). Previous experience of the founder cats with people was unknown, but people in Moscow city are commonly indifferent or tolerant to feral cats; sometimes the feral cats are fed by cat lowers but practically never touched or caressed.

Subject kittens belonged to 12 litters delivered by 10 females (3 litters in July 2021 and 9 litters in May-June 2022); two females had litters in both 2021 and 2022. At birth, 4 litters contained 4 kittens, 5 litters contained 5 kittens, one litter contained 6 kittens, one litter contained 7 kittens and one litter contained 8 kittens. Of the total of 62 kittens delivered in the 12 litters, 5 did not survive to the start of data collection (one kitten from the litter of 4, one kitten from the litter of 5, another kitten from the litter of 5 and 2 kittens from the litter of 8 individuals).

Each female with kittens was kept in an individual outdoor enclosure (2 × 1.5 × 2 m) 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. Each enclosure contained a wooden den 55 x 40 x 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, the animals played with natural objects, conifer cones, hunt flying and crawling insects, dig the earth (Sedova et al., 2023).

2.2. Kitten attributes

For each kitten, we considered four attributes, potentially affecting vocalization: litter size at birth; single or multiple paternity, sex and survival to 90 days of age. *Litter size at birth*. For analysis, we separated the litters by number of kittens at birth to three groups: litters of 4 kittens (4 litters, 15 kittens), litters of 5 kittens (5 litters, 23 kittens) and litters of 6 and more kittens (3 litters, 19 kittens). *Multiple paternity*. Four litters (two litters with 4 kittens, one litter with 5 kittens and one litter with 7 kittens, 19 kittens in total) were obtained at mating of a mother cat with three males, and multiple paternity of the kittens in these litters was confirmed genetically (Erofeeva et al., 2022). In each of remaining 8 litters, all 38 kittens were sired by one male. *Sex*. Of 57 kittens, there were 28 males and 29 females. *Survival to 90 days of age*. Of the 57 kittens, 47 were alive at 90 days of age; remaining 10 individuals died before this age in their home enclosures by unknown reasons, not related with traumas or aggression during animal captures or experimental procedures.

2.3. Call-eliciting procedure

Calls of each kitten were recorded at individual basis during the blood and fur sampling procedure, which was conducted at approximately two weeks of age (average age 13.9 ± 1.7 days old). Before recording, all littermates were taken off the nest box, placed to a commercial cat carrier box and then transferred to an experimental room. Littermates participated in the procedure one by one; all kittens for the exclusion of the focal one were taken off the experimental room by experimenter helper (to avoid the overlapping vocalization with non-focal kittens in the audio recording). The focal kitten was initially inspected visually being kept in hands, sexed and individually identified and then fixed on the table surface by human hands for taking a blood sample up to 1 ml from the femoral vein for subsequent analyses of hormones for another longitudinal research (Alekseeva et al., 2020; Soboleva et al., 2021; Erofeeva et al., 2023). After the end of blood sampling, the experimenter (MNE or MDK) cut of 3–4 cm^2 of fur from croup for subsequent determining the titres of hormone metabolites (Naidenko et al., 2022). Then, a kitten was weighted on electronic scale with 5 g precision. After the end of the blood and fur sampling procedure, a kitten was placed to the carrier box together with other littermates and the next focal kitten took out. After the end of all procedures with all littermates they were simultaneously returned to the nest box to their mother. No negative consequences on animals in the result of the blood and fur sampling procedure were detected.

2.4. Audio recording

Calls of kittens were recorded using 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, at sampling rate 48 kHz, 16-bit resolution, range 40–20000 Hz, in wav format. The distance from microphone to the focal kitten was 0.2–0.5 m. Calls were solely recorded during blood sampling. Start of blood sampling (manual fixation of a kitten by hands in gloves on a table surface and penetrating the femoral vein by a needle) and end of blood sampling (raising the kitten up fixed in hands up for cutting fur on croup) were labeled by sound signals. Duration of recording during blood sampling varied between individuals from 1.5 to 10 min and lasted 4.5 ± 2.2 min on average. Each audio recording was stored as one wave-file per individual, 57 audio files in total.

2.5. Call samples and analysis

Spectrograms of all audio files were inspected using Avisoft SASLab Pro software (Avisoft Bioacoustics, Berlin, Germany). Based on sound labels present in the audio files, we calculated the duration of the blood sampling period for each kitten. Four individual kittens did not vocalize; for other 53 kittens we calculated the number of calls during the blood sampling procedure and measured the duration of each call using a semi-automatic option of Avisoft. Then we calculated call rate (the number of calls per minute) for each kitten. For the four kittens which were silent during the blood sampling call rate was 0 calls/min.

In total, for 53 kittens which vocalized during the blood sampling procedure, we analyzed acoustic parameters of 4990 calls, from 2 to 274 calls per kitten. For each call, we noted a presence of nonlinear vocal phenomena: subharmonics, deterministic chaos, frequency jumps and biphonations (Wilden et al., 1998; Scheumann et al., 2012; Hubka et al., 2015). We only noted a presence of subharmonics and chaos if duration of call parts with these nonlinear phenomena exceeded 10% of call duration (Sedova et al., 2023). Frequency jump was noted when the change of frequency reached 100 Hz or more; a few frequency jumps per call were noted as one frequency jump. Biphonation was noted when in the call (as a rule, at a small part of the call) two independent fundamental frequencies were found, which displayed a different run of frequency modulation (Wilden et al., 1998; Rutovskaya et al., 2009). For each kitten, we counted the percentage of calls which contained nonlinear phenomena.

Of 53 kittens, which vocalized during the blood sampling procedure, 9 individuals produced less than 20 calls; remaining 44 kittens produced 25 or more calls. For each of these 44 kittens (21 males, 23 females) with number of calls over 20, we selected for further spectrographic analysis 20 calls per individual (880 calls in total, Dataset 1). As duration of blood sampling procedure depended on how quickly blood samples could be taken and as kitten produced their meows irregularly during the procedures, we could not select comparable natural sequences of meows uniformly in the middle or another part of the procedure. For spectrographic analysis, we selected the calls with high signal-to-noise ratio, non-overlapped with alien noise. To decrease pseudoreplication from inclusion in analysis of similar calls, we tried, where possible, to select for acoustic measurements the calls from different parts of audio file. We tried to select the calls based on a preceding analysis (involving calculation of call rate and presence of nonlinear vocal phenomena), to have a representative sample of calls of different acoustic structures corresponding to their occurrence in total call sample of each individual.

For spectrographic analysis of acoustic parameters, we used Avisoft SASLab Pro. Before measurements, we decreased 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 values of f0 of calls in domestic cat adults or kittens always exceed 0.2 kHz (Scheumann et al., 2012; Sedova et al., 2023).

For each call, one researcher (MVR), blindly to data collection procedure, measured manually, in the spectrogram window of Avisoft, call duration (duration) and f0 parameters in three points of call spectrum: start (f0beg), maximum (f0max) and end (f0end) (Fig. 1). In addition, for each call, four power parameters were semi-automatically measured in 50-ms time window (centered around the point of call f0max): the peak frequency (fpeak) and the three power quartiles (q25, q50 and q75) covering respectively 25%, 50% and 75% of call energy from the power spectrum of each call (Fig. 1). The window of 50 ms was selected for the measurements because it provided a better ratio of signal to noise compared with the measurements taken over the entire call spectrum (Volodin et al., 2022; Sedova et al., 2023). All measurements were exported to Microsoft Excel (Microsoft Corp., Redmond, WA, USA) table.

For estimating the effects of kitten attributes (number of individuals per litter, single/multiple paternity, kitten sex and survival to 90 days of age) we created Dataset 2 which included body weight (for 57 kittens), call rate (for 57 kittens), the percentage of calls which contained nonlinear phenomena (for 53 kittens which vocalized during blood sampling), and average values of the measured acoustic parameters of the calls (for 44 kittens which provided sufficient number of calls for acoustic analysis). Average values of the acoustic parameters were calculated over 20 calls per individual taken from Dataset 1.

2.6. Statistical analyses

All statistical analyses were carried out with STATISTICA v. 8 (StatSoft, Tulsa, OK, USA). We also used R 4.1.0 (R Development Core Team, 2022) for conducting the randomization test for probability of incorrect classifying. All means were given as mean ± *SD*, significance levels were set at $p < 0.05$. Only 35 distributions of acoustical parameters of 360 did differ significantly from the normal (Kolmogorov-Smirnov test, $p > 0.05$). As ANOVA is relatively robust to small departs of normality (Dillon and Goldstein, 1984), this was not an obstacle for applying the parametrical tests.

We used two different Datasets: Dataset 1 based on the number of

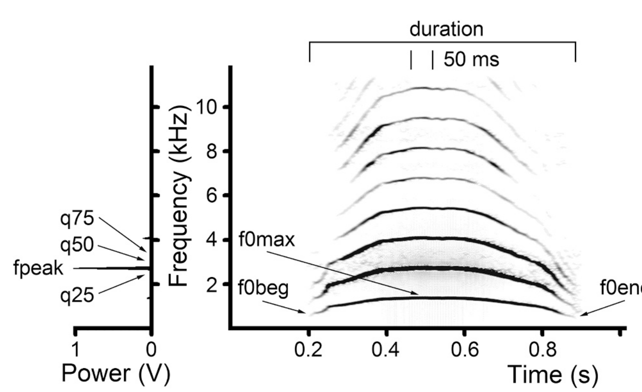

Fig. 1. Measured acoustic parameters for kitten cries, spectrogram (right) and mean power spectrum of 50 ms time window of a call (left). Designations: duration – call duration; f0max – the maximum fundamental frequency; f0beg – the fundamental frequency at the onset of a call; f0end – the fundamental frequency at the end of a call; fpeak – the frequency of maximum amplitude within a call; q25, q50 q75 – the lower, medium and upper quartiles, covering respectively 25%, 50% and 75% energy of a call spectrum. The spectrogram was created at 24 kHz sampling frequency, FFT length 1024, Hamming window, frame 50%, overlap 96.87%.

calls (880 calls, 20 per individual from 44 kittens) and Dataset 2 based on the individuals (57 kittens, for calls, the average parameter values per individual were used). We used a nested design of ANOVA with Tukey HSD (Honest Significantly Different) post hoc with an individual nested within sex to estimate the effects of factors "individuality" and "sex" on the acoustic parameters of calls (Dataset 1), with sex as fixed factor and individual as random factor (to control for inclusion of more than one call from each individual). We used GLM with Tukey HSD post hoc for estimating the effects of predictor factors (number of individuals per litter, single/multiple paternity, kitten sex and survival to 90 days of age) on kitten body weight and the acoustic parameters of the calls (Dataset 2), with all predictors included as fixed factors. We used Pearson correlation coefficient for estimating the effect of kitten body weight on the acoustic parameters of the calls (Dataset 2).

We used the standard procedure of Discriminant Function Analysis (DFA, also called Linear Discriminant Analysis) to calculate the probability of classifying the calls to correct individual caller (Dataset 1), and other DFAs to calculate the probability of classifying the calls to correct sex based on acoustic parameters of all calls (Dataset 1) and based on the average parameter values of the calls per individual (Dataset 2), to exclude the effect of taking more than one call per individual. In all DFAs, we included all the 8 measured acoustic parameters: duration, f0max, f0beg, f0end, fpeak, q25, q50 and q75.

We used Wilks' Lambda, to estimate the impact of each acoustic parameter in DFA. For validating the DFA results, we calculated the values of probability of correct classifying the calls to individuals and sexes, by applying the randomization test for probability of incorrect classifying in DFA with a custom-made script created in R based on Solow (1990). Random values were calculated from DFA on 1000 randomized permutations of datasets (Solow, 1990; Mundry and Sommer, 2007). For each distribution obtained with permutations, we noted whether the observed value exceeds 95% (950 values), 99% (990 values) or 99.9% (999 values) within distribution (Solow, 1990; Mundry and Sommer, 2007). If the observed value exceeded 95%, 99% or 99.9% of values within this distribution, we established that the observed value did differ significantly from the random 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; Sedova et al., 2023).

2.7. Ethical note

The authors adhered to the "Guidelines for the treatment of animals in behavioural research and teaching" (Anim. Behav. 2020, 159, I-XI) and the legal requirements of Russia pertaining to the protection of animal welfare. The study was approved by the Regulatory Commission of Experimental Research (Bioethics Commission) of A.N. Severtsov Institute of Ecology and Evolution of the Russian Academy of Sciences (permission no. 21 of 24.04.2018).

3. Results

3.1. Acoustic variation of kitten cries

Kitten cries represented the calls with clearly visible fundamental frequency (f0) and its harmonics (Fig. 2). Call duration was on average 0.62 ± 0.24 s and ranged from 0.37 to 0.97 s between individuals; the f0max was on average 1.55 ± 0.33 kHz and ranged from 1.12 to 2.01 kHz between individuals (Table 1). Kitten cries displayed individual variation but did not display sex-related variation (Table 1). Two-way ANOVA showed that factor individuality affected all the 8 measured acoustic parameters. Factor sex did not affect any single acoustic parameter (Table 1).

Kitten cries could contain nonlinear vocal phenomena (Fig. 2): subharmonics (30.3% calls), deterministic chaos (20.6% calls), frequency jump (20.1% calls) and biphonations (0.9% calls). In total, 50.8% of calls contained nonlinear phenomena, because some calls could contain

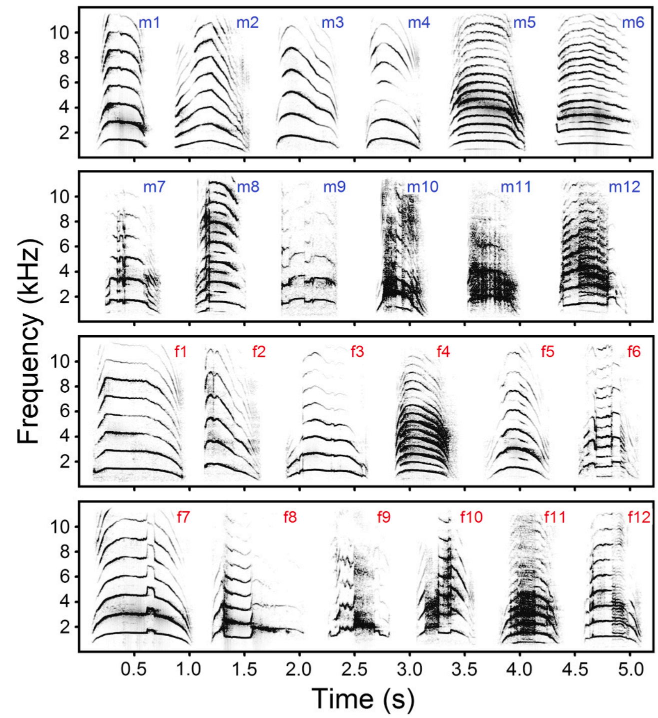

Fig. 2. Spectrogram illustrating inter-individual variation of cries in two-weeks-old kittens. One call per individual from 12 males (m1-m12) and 12 females (f1-f12) are given. Designations: (m1-m4) – tonal calls without nonlinear phenomena; (m5-m6) – calls with subharmonics; (m7-m8) – calls with subharmonics and frequency jumps; (m9) – call with frequency jumps; (m10) – call with subharmonics and deterministic chaos; (m11) – call with deterministic chaos; (m12) – call with subharmonics, frequency jumps and biphonation; (f1-f2) – tonal calls without nonlinear phenomena; (f3) – call with frequency jump; (f4-f5) – calls with subharmonics; (f6) – call with subharmonics and frequency jumps; (f7-f8) – calls with frequency jumps; (f9-f10) – calls with frequency jumps and deterministic chaos; (f11) – call with subharmonics and deterministic chaos; (f12) – call with biphonation. The spectrogram was created at 24 kHz sampling frequency, FFT length 1024, Hamming window, frame 50%, overlap 93.75%. The audio file of these calls is available as Supplementary Audio A1.

more than one kind of nonlinear phenomena (up to all the four kinds of nonlinear phenomena within a call). Percent of calls with nonlinear phenomena varied from 0% to 100% between individuals. Call rate during the experimental procedure was 22.17 ± 16.77 calls/min and varied from 0 to 54.87 calls/min between individuals.

3.2. DFAs for classifying calls to individuals and sexes

We conducted DFA for classifying the cries to correct individual callers. The DFA included all the 8 measured acoustic parameters (duration, f0max, f0beg, f0end, fpeak, q25, q50, q75). The average value of correct classifying of the calls to individual with DFA was 37.4%, which was significantly higher than the random level of 7.5 ± 0.8%, min = 5.3%, max = 10.8% (permutation test, 1000 permutations, $p < 0.001$) (Fig. 3). In order of decreasing importance, f0end and f0max were mainly responsible for discrimination of individuals by their calls. However, among individuals, the value of correct assignment of the calls varied from 0% to 75% and did not exceed 10% for 7 individuals. Thus, only for 37 kittens the value of correct assignment of calls to individual exceeded the maximum meaning of the DFA random value. Although the average value of correct classifying exceeded the random value, only a part of individuals could be reliably recognized by their calls (Fig. 3).

We also conducted two DFAs for classifying the calls to correct sex. The DFAs included all the 8 measured acoustic parameters (duration,

Table 1
Values (mean± *SD*) of measured acoustic parameters and results of nested two-way ANOVA for individual and sex-related differences. Individual was nested within sex, with sex as fixed factor and individual as random factor. Designations: duration – call duration; f0max – the maximum fundamental frequency; f0beg – the fundamental frequency at the onset of a call; f0end – the fundamental frequency at the end of a call; fpeak – the frequency of maximum amplitude within a call; q25, q50 q75 – the lower, medium and upper quartiles; *N* – number of kittens; *n* – number of calls. Significant differences are given in bold.

Acoustic parameter	Mean ± *SD* values			ANOVA	
	All calls, *N*=44, *n*=880	Male calls, *N*=21, *n*=420	Female calls, *N*=23, *n*=460	Individual differences	Sex differences
duration (s)	0.62 ±0.25	0.61 ±0.26	0.63 ±0.23	$F_{42,836}$=7.56; ***p*<0.001**	$F_{1,836}$=0.38; *p*=0.54
f0max (kHz)	1.55 ±0.33	1.57 ±0.33	1.54 ±0.33	$F_{42,836}$=30.18; ***p*<0.001**	$F_{1,836}$=0.17; *p*=0.68
f0beg (kHz)	0.89 ±0.32	0.94 ±0.31	0.84 ±0.32	$F_{42,836}$=29.18; ***p*<0.001**	$F_{1,836}$=1.82; *p*=0.18
f0end (kHz)	0.82 ±0.36	0.82 ±0.30	0.83 ±0.40	$F_{42,836}$=44.68; ***p*<0.001**	$F_{1,836}$=0.01; *p*=0.98
fpeak (kHz)	2.40 ±1.20	2.44 ±1.20	2.36 ±1.20	$F_{42,836}$=5.86; ***p*<0.001**	$F_{1,836}$=0.25; *p*=0.62
q25 (kHz)	2.13 ±0.81	2.19 ±0.85	2.07 ±0.76	$F_{42,836}$=9.20; ***p*<0.001**	$F_{1,836}$=0.78; *p*=0.38
q50 (kHz)	2.88 ±1.20	2.97 ±1.20	2.80 ±1.19	$F_{42,836}$=8.01; ***p*<0.001**	$F_{1,836}$=0.73; *p*=0.40
q75 (kHz)	4.17 ±1.74	4.37 ±1.74	3.99 ±1.72	$F_{42,836}$=8.75; ***p*<0.001**	$F_{1,836}$=1.72; *p*=0.20

f0max, f0beg, f0end, fpeak, q25, q50, q75). The first DFA for sex based on acoustic parameters of all calls, showed the average value of correct assignment of the calls of 58.6%, which was significantly higher the random level of 53.5 ± 1.4%, min = 48.9%, max = 58.8% (permutation test, 1000 permutations, $p < 0.01$) (Fig. 3). The value of correct assignment of the calls to female sex was 66.5%, whereas the value of correct assignment to male sex was only 50.0%, thus not differing from the random level of correct assignment to sex (Fig. 3). The second DFA for sex based on the average parameter values of the calls per individual, showed 63.6% correct assignment of the calls of (69.6% for females and 57.1% for males), which did not differ from the random level of 68.8 ± 6.3%, min = 45.1%, max = 86.5% (permutation test, 1000 permutations, $p = 0.753$). Thus, DFA results suggest that kitten sex could not be recognized by their calls.

3.3. Effects of kitten attributes on body weight and acoustics parameters

Litter size affected body weight, body weight was found the highest in litters of 4 kittens, intermediate in litters of 5 kittens and the lowest in litters of 6 and more kittens (Table 2). Multiple paternity and sex did not affect body weight. Survival to 90 days of age depended on body weight, being lower in kittens which did not survive (Table 2).

Litter size affected most parameters of kitten cries (Table 2). Call rate and percent of calls with nonlinear phenomena were higher in individuals from litters of 6 and more kittens. The values of f0 parameters were higher (for f0max only marginally) in individuals from litters of 4 kittens. In contrast, the values of q50 and q75 were higher in individuals from litters of 6 and more kittens (Table 2).

In individuals from litters with multiple paternity the values of f0max and f0end were higher than in individuals from litters sired by one male; remaining acoustic parameters did not depend on single/multiple paternity. Sex and survival to 90 days of age did not affect any one parameter of kitten cries (Table 2).

3.4. Body weight and acoustic parameters

Body weight correlated positively with f0max, f0beg and f0end, and correlated negatively with call rate, duration, fpeak, q25 and g50 (Table 3). Percent of calls with nonlinear phenomena correlated marginally negatively with body weight (Table 3).

4. Discussion

4.1. Survival perspective vs arousal traits in kitten cries

In this study, no one single acoustic parameter of kitten cries differed between individuals which survived to 90 days of age and which did not survive (Table 2). Thus, these results do not support a hypothesis that the acoustic parameters of kitten cries honestly reflect their chances for survival. Instead, these results support a hypothesis that dishonest acoustic signals of kitten quality could develop as vocal adaptation for misleading a mother from allocation resources between the weaker and stronger individuals, thus enhancing individual chances for survival for the weaker littermates. Playback experiments are necessary to estimate maternal reactions to voices of kittens which then survived or not survived up to weaning.

A single attribute differing between the survived and non-survived kittens was body weight; kittens which survived to 90 days of age

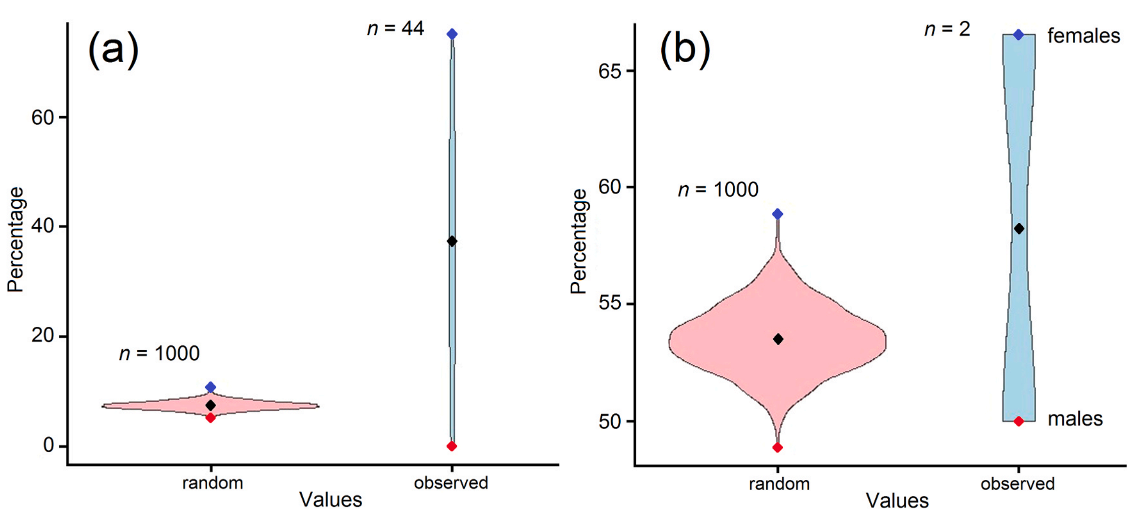

Fig. 3. Violin plots for comparison of percentages of correct classification between random and observed values of DFAs for (a) individuality and (b) sex. Blue rhomb – maximum value of distribution, black rhomb – average value of distribution, red rhomb – minimum value of distribution. *n* indicate 1000 random values; 44 observed values of assignment of calls to 44 individuals; and 2 observed values of assignment of calls to 2 sexes (males and females).

Table 2
Values (mean ± *SD*) of body weight and parameters of kitten cries and the results of GLM for the effects of litter size (4 kittens, 5 kittens, 6 and more kittens), single/multiple paternity, kitten sex and survival to 90 days of age. Designations: duration – call duration; f0max – the maximum fundamental frequency; f0beg – the fundamental frequency at the onset of a call; f0end – the fundamental frequency at the end of a call; fpeak – the frequency of maximum amplitude within a call; q25, q50 q75 – the lower, medium and upper quartiles; *N* – number of kittens. Significant differences are given in bold. Different superscripts ([a], [b], [c]) indicate statistically different values (Tukey post hoc, $p < 0.05$).

Parameter	Litter size, kittens			Single/multiple paternity		Kitten sex		Survival to 90 days of age	
	4 *N* =15	5 *N* =23	6 and more *N* =19	single *N* =38	multiple *N* =19	males *N* =28	females *N* =29	yes *N* =47	no *N* =10
body weight, g	276±23[a]	208±45[b]	175±39[c]	217±47	211±67	227±54	203±54	228±47	154±48
	$F_{2,51}$=23.27, ***p*<0.001**			$F_{1,51}$=0.51, *p*=0.48		$F_{1,51}$=0.15, *p*=0.70		$F_{1,51}$=10.33, ***p*=0.002**	
call rate, calls/min	15.3±13.3[a]	16.0±13.8[a]	35.0±15.6[b]	21.1±16.0	24.3±18.5	23.5±17.3	20.9±16.5	21.1±16.8	27.2±16.4
	$F_{2,51}$=9.89, ***p*<0.001**			$F_{1,51}$=0.52, *p*=0.47		$F_{1,51}$=0.40, *p*=0.53		$F_{1,51}$=0.01, *p*=0.97	
% calls with nonlinear phenomena	51.4±19.9[a,b]	38.0±24.4[a]	63.1±26.4[b]	47.5±27.1	56.4±23.3	50.8±26.0	50.2±26.5	48.8±23.5	58.0±35.4
	$F_{2,47}$=4.32, ***p*=0.019**			$F_{1,47}$=0.59, *p*=0.45		$F_{1,47}$=0.02, *p*=0.90		$F_{1,47}$=0.35, *p*=0.56	
duration, s	0.57±0.10	0.68±0.15	0.60±0.11	0.63±0.13	0.60±0.13	0.61±0.13	0.63±0.13	0.61±0.13	0.67±0.12
	$F_{2,38}$=2.39, *p*=0.10			$F_{1,38}$=0.58, *p*=0.45		$F_{1,38}$=0.02, *p*=0.90		$F_{1,38}$=1.10, *p*=0.30	
f0beg, kHz	1.14±0.19[a]	0.81±0.27[b]	0.80±0.13[b]	0.85±0.25	0.95±0.25	0.94±0.24	0.84±0.26	0.92±0.25	0.76±0.22
	$F_{2,38}$=7.35, ***p*=0.002**			$F_{1,38}$=2.19, *p*=0.15		$F_{1,38}$=0.68, *p*=0.41		$F_{1,38}$=0.55, *p*=0.46	
f0max, kHz	1.73±0.25	1.50±0.27	1.49±0.21	1.49±0.23	1.69±0.25	1.57±0.26	1.54±0.27	1.56±0.26	1.52±0.28
	$F_{2,38}$=2.89, *p*=0.068			$F_{1,38}$=8.79, ***p*=0.005**		$F_{1,38}$=0.27, *p*=0.60		$F_{1,38}$=−0.05, *p*=0.83	
f0end, kHz	1.09±0.36[a]	0.81±0.27[a]	0.65±0.09[b]	0.76±0.23	0.92±0.37	0.82±0.25	0.83±0.34	0.86±0.31	0.67±0.16
	$F_{2,38}$=7.83, ***p*=0.001**			$F_{1,38}$=4.56, ***p*=0.039**		$F_{1,38}$=0.42, *p*=0.52		$F_{1,38}$=1.54, *p*=0.22	
fpeak, kHz	2.31±0.48	2.27±0.72	2.60±0.43	2.48±0.61	2.26±0.52	2.44±0.60	2.36±0.57	2.36±0.56	2.57±0.66
	$F_{2,38}$=1.41, *p*=0.26			$F_{1,38}$=2.21, *p*=0.15		$F_{1,38}$=0.30, *p*=0.59		$F_{1,38}$=1.04, *p*=0.31	
q25, kHz	2.07±0.34	2.01±0.57	2.28±0.39	2.16±0.48	2.07±0.44	2.19±0.47	2.07±0.46	2.12±0.46	2.15±0.53
	$F_{2,38}$=1.50, *p*=0.24			$F_{1,38}$=0.45, *p*=0.51		$F_{1,38}$=0.65, *p*=0.43		$F_{1,38}$=0.05, *p*=0.83	
q50, kHz	2.88±0.66[a,b]	2.59±0.72[a]	3.20±0.42[b]	2.98±0.62	2.74±0.70	2.97±0.58	2.80±0.77	2.87±0.65	2.94±0.72
	$F_{2,38}$=4.29, ***p*=0.021**			$F_{1,38}$=2.43, *p*=0.13		$F_{1,38}$=0.37, *p*=0.55		$F_{1,38}$=0.17, *p*=0.68	
q75, kHz	4.25±0.98[a,b]	3.76±0.92[a]	4.56±0.93[b]	4.33±1.00	3.92±0.93	4.37±0.98	3.99±0.97	4.21±1.00	3.99±0.93
	$F_{2,38}$=3.51, ***p*=0.040**			$F_{1,38}$=2.13, *p*=0.15		$F_{1,38}$=0.64, *p*=0.43		$F_{1,38}$=0.09, *p*=0.76	

Table 3
Pearson's correlation coefficients between body weight of kittens and acoustic parameters. Designations: duration – call duration; f0max – the maximum fundamental frequency; f0beg – the fundamental frequency at the onset of a call; f0end – the fundamental frequency at the end of a call; fpeak – the frequency of maximum amplitude within a call; q25, q50 q75 – the lower, medium and upper quartiles; *N* – number of kittens. Significant differences are given in bold.

Acoustic parameter	Body weight
call rate	*r*= −0.38; ***p*=0.003**; *N*=57
% calls with nonlinear phenomena	*r*= −0.25; *p*=0.069; *N*=53
duration	*r*= −0.33; ***p*=0.033**; *N*=44
f0beg	*r*= 0.58; ***p*<0.001**; *N*=44
f0max	*r*= 0.33; ***p*=0.031**; *N*=44
f0end	*r*= 0.65; ***p*<0.001**; *N*=44
fpeak	*r*= −0.43; ***p*=0.003**; *N*=44
q25	*r*= −0.38; ***p*=0.011**; *N*=44
q50	*r*= −0.35; ***p*=0.020**; *N*=44
q75	*r*= −0.15; *p*=0.35; *N*=44

were heavier. Body weight correlated with nearly all acoustic parameters of kitten cries (Table 3).

At the same time, earlier studies showed that in mammals, including domestic cats, acoustic parameters reflect a degree of negative emotional arousal (Scheumann et al., 2012; Silberstein et al., 2023; Szenczi et al., 2023). For kitten cries, recorded during discomfort-evoking procedure of blood sampling in our study, would be impossible to separate between effects of discomfort and kitten quality on vocal parameters. We did not measure discomfort of subject kittens directly, but we can propose that kittens with lower body weight experienced a higher degree of discomfort because their higher degree of competition for maternal resources (milk, heating, licking care), especially actual in litters of large size. Because in our study (as in the related study on vocalizations of 10-days-old kittens, Scheumann et al., 2012), kitten sex did not affect its body weight and acoustic parameters of kitten cries, we could not take into account kitten sex in the analysis of correlations between body weight and parameters of kitten cries. In our study, the lower was kitten body weight, the higher was call rate, the longer were the calls, the lower were all parameters of fundamental frequency, the higher were peak frequency and quartiles, and the more numbers of calls contained nonlinear phenomena.

In case if kittens with lower body weight experienced a higher degree of discomfort, so these relationships fitted well to the changes of parameters characteristic of mammalian calls at high discomfort. The increasing call rate with increase of arousal is characteristic for many mammals (e.g., Gogoleva et al., 2010; Stoeger et al., 2012; Linhart et al., 2015; Martin et al., 2022), including 1.5-months-old kittens (Szenczi et al., 2023). The high percentage of calls with nonlinear vocal phenomena was also observed at increasing arousal in the young of African elephants *Loxodonta africana* (Stoeger et al., 2011) and giant pandas *Ailuropoda melanoleuca* (Stoeger et al., 2012), although the study of 10-days-old kittens did not find the differences in percentages of kitten cries with nonlinear vocal phenomena at low (50% of calls) and high (45% of calls) degrees of arousal (Scheumann et al., 2012). The increase of call duration, decrease of fundamental frequency and increase of peak frequency at higher arousal agrees entirely with results, obtained earlier at direct comparison of effects of arousal on the acoustic structure of cries in 10-days-old kittens (Scheumann et al., 2012) and in 1.5-months-old kittens (Szenczi et al., 2023). Thus, kitten cries may provide information about a degree of kitten's discomfort, mediated by kitten's body weight.

4.2. Acoustic parameters of kitten cries

While in most mammals a higher arousal corresponds to the higher fundamental frequency of calls (review Briefer, 2012), in domestic kittens three independent studies (Scheumann et al., 2012; Szenczi et al., 2023 and this study) found that a higher level of arousal corresponds to the lower fundamental frequency of the cries. We conclude that some mammalian species (at least domestic cat kittens) do not follow to the common rule of increasing fundamental frequency with increasing arousal (see also Silberstein et al., 2023).

In our study of 2-weeks-old kittens, their cries emitted in the discomfort situation of blood sampling had the average f0max of 1.55 ± 0.33 kHz, peak frequency of 2.40 ± 1.20 kHz and duration 0.62 ±

0.24 s. Other data on the acoustic parameters of kitten cries obtained in this study are also well-comparable with those reported by other studies for kittens younger one month of age under discomfort. Overall, at different discomfort-related situations, kittens aged from neonates to one month of age produced the calls with f0max of 1.3–1.55 kHz and duration of 0.44–1.0 s (Brown et al., 1978; Haskins, 1979; Romand and Ehret, 1984; Scheumann et al., 2012; Hubka et al., 2015; Banszegi et al., 2017).

At isolation, the 2-weeks-old kittens produced the cries with f0max of 1.39 ± 0.39 kHz and duration of 0.44 ± 0.13 s (Haskins, 1979) or the cries with f0max from 1.5 to 1.7 kHz and duration from 0.4 до 0.7 s (Romand and Ehret, 1984) and the cries with average f0 of 1.54 kHz (Banszegi et al., 2017). At isolation only, the 10-days-old kittens produced the cries with f0max of 1.52 ± 0.25 kHz and duration of 0.57 ± 0.17 s (Scheumann et al., 2012). At isolation and handling, the same 10-days-old kittens produced the cries with f0max of 1.32 ± 0.22 kHz and duration of 0.71 ± 0.19 s (Scheumann et al., 2012). At restraint, the 2-weeks-old kittens produced the cries with f0max of 1.49 ± 0.26 kHz and duration of 0.67 ± 0.07 s (Haskins, 1979). At cooling, the 2-weeks-old kittens produced the cries with f0max of 1.79 ± 0.37 kHz and duration of 0.57 ± 0.14 s (Haskins, 1979).

In our study, call rate during the experimental procedure was on average 22.17 ± 16.77 calls/min. For comparison, in another study the 2-weeks-old kittens produced at isolation the cries with call rate of 12–16 calls/min, at restraint the cries with call rate of 42–44 calls/min and at cooling the cries with call rate of 30–34 calls/min (Haskins, 1979).

In our study, 50.8% of kitten cries contained nonlinear phenomena. Consistently to our data, in the study by Scheumann et al. (2012), 47.46% of discomfort-related kitten cries contained nonlinear vocal phenomena: chaos (33.61% calls), frequency jumps (15.43% calls) and subharmonics (9.26% calls).

Kitten cries analyzed in this study and in other studies were substantially lower-frequency than cub calls of other studied Felidae species. This contradicts to the common rule for carnivores, in which vocalizations are commonly lower-frequency in larger species (Bowling et al., 2017). For instance, distant calls of wild-living cheetah cubs *Acinonyx jubatus* younger one month of age have f0max of 7.92 ± 0.82 kHz (Klenova et al., 2024), the calls of captive 1.5–3-months cheetah cubs have f0max of 3.89 ± 0.23 kHz (Volodina, 1998) and the calls of captive puma cubs *Puma concolor* younger one month of age have the f0max of about 5 kHz (Peters, 2011; Allen et al., 2016). Consistently, distant calls of cubs younger one month of age in the Eurasian lynx *Lynx lynx* and in bobcat *L. rufus* have the f0max as high as about 3 kHz (Peters, 1987). We conclude that kittens produce substantially lower-frequency calls than other felid cubs, in spite of their smaller body size, excluding data for tiger cubs *Panthera tigris* (for a pooled sample of cubs from birth to 10 months of age), producing the calls with f0max of about 0.59 kHz (Kong et al., 2022). Tiger seems a single studied felid species, in which the f0 of cub calls is lower than in domestic cat kittens, however, tiger cubs are much larger than kittens and the cubs of cheetahs, pumas and lynxes.

4.3. Individual and sex-related variation of kitten cries

We found a moderate individuality in kitten cries, with average 37.7% of cries correctly assigned to individuals for 44 kittens. Moderate individuality of kitten cries was also reported in another study (53.13% correctly assigned to individual low-arousal cries for 16 kittens and 63.3% correctly assigned to individual high-arousal cries for 18 kittens) (Scheumann et al., 2012). In our study, 7 of 44 kittens were not distinctive by their calls among other individuals; in the study by Scheumann et al. (2012) one of 16 kittens (low-arousal cries) and two of 18 kittens (high-arousal cries) were also classified by their calls at chance level.

Compared to discomfort cries of kittens, meows of adult domestic cats produced in reproductive season have well-expressed individual acoustic differences (79.2% classification success with DFA for 11 individuals) (Sedova et al., 2023). Calls of adult cats produced in the nest box when with kittens, also had prominent individual differences (93.4% classification success with DFA for 3 individuals, Szenczi et al., 2016). Individuality of calls produced by adult domestic cats at discomfort situations (e.g., blood sampling) has yet to be investigated.

We did not find sex-related differences in the acoustic parameters or call rates of kitten cries. Consistently, Scheumann et al. (2012) did not find sex-related differences in the acoustic parameters of kitten cries related to isolation or isolation and handling. However, the study by Hudson et al. (2015) reported sex-related differences in call rates at separation at 1–4 weeks of age (33 kittens, 19 males and 14 females). Call rate was higher in females than in males, and at the age of 2 weeks was, on average, about 39 calls/min in males and 50 calls/min in females. The differences with results of study by Hudson et al. (2015) could be related to different call-eliciting situations (isolation *vs* blood sampling) or subject life-histories (free-ranging domestic *vs* captive feral) or both.

In contrast to kitten cries, acoustic parameters of meows produced by adult domestic cats in reproductive season have well-expressed sex differences; male calls (f0max = 0.37 ± 0.05 kHz) were significantly lower-frequency than female calls (f0max = 0.61 ± 0.16 kHz) (Sedova et al., 2023). Sex differences were also found in adult domestic cats in the aversive situation for call duration (1.02 s in males and 0.81 s in females) and mean f0 (0.50 kHz in males and 0.59 kHz in females) (Schnaider et al., 2022). Sex-related differences of calls produced by adult domestic cats at discomfort situations (e.g., blood sampling) have yet to be investigated.

CRediT authorship contribution statement

Mariya D. Kim: Writing – original draft, Visualization, Validation, Software, Investigation, Formal analysis. **Kseniya A. Volobueva:** Writing – original draft, Visualization, Validation, Software, Investigation, Formal analysis. **Polina S. Zhuravleva:** Visualization, Validation, Software, Formal analysis. **Galina S. Alekseeva:** Writing – review & editing, Writing – original draft, Supervision, Resources, Methodology, Investigation, Data curation, Conceptualization. **Mariya N. Erofeeva:** Writing – review & editing, Writing – original draft, Supervision, Resources, Methodology, Investigation, Data curation, Conceptualization. **Sergey V. Naidenko:** Writing – review & editing, Writing – original draft, Supervision, Resources, Investigation, Data curation, Conceptualization. **Ilya A Volodin:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Resources, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Marina V. Rutovskaya:** Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Resources, Methodology, Investigation, Formal analysis, Data curation. **Elena V. Volodina:** Writing – review & editing, Writing – original draft, Supervision, Resources, Investigation, Data curation, Conceptualization.

Declaration of Competing Interest

The authors declare no competing or financial interests.

Data availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.beproc.2024.105009.

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