



RESEARCH ARTICLE

Advertising sex and individual identity by long-distance chirps in wild-living mature cheetahs (*Acinonyx jubatus*)

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Abstract

Adult cheetahs (*Acinonyx jubatus*) use long-distance chirps for calling toward coalition partners (males), mates (both sexes), and cubs (females). Previously, these vocalizations were only investigated in captivity. This study estimates individual and sex-related acoustic variation of the long-distance chirps of 20 mature cheetahs (eight males and 12 females older than 4 years) in their natural habitats in Kenya. Male chirps were longer in duration and lower in the peak frequency and all fundamental frequency variables than female chirps. The average value for assignment of the chirps to correct sex with Discriminant Function Analysis (DFA) of 93.8% was significantly higher than by-chance level of 52.9%. The average value of correct assignment of the chirps to individual with DFA was 79.5%, which was significantly higher than the level by chance of 14.8%. For 10 cheetahs recorded twice with time space of one or 2 years, DFA showed high values of correct assignment of the chirps to individual for both years (91.4% in the first year and 83.9% in the second year of recording), but cross-validation of the chirps recorded in the second year by discriminant functions created for the chirps of the first year showed a dramatic decrease of correct assignment to the level expected by chance (27.2%). We discuss that long-distance chirps of wild mature cheetahs provide reliable cues to sex and may also encode caller individuality, although this is not stable over time.

KEYWORDS

Acinonyx jubatus, acoustic communication, Felidae, free-ranging cheetahs, high-frequency calls, vocalization

1 | INTRODUCTION

In many carnivorous species: Canids, hyaenas, and felids, long-distance tonal calls serve for mate attraction and territorial spacing (Durbin, 1998; East & Hofer, 1991a, 1991b; Ferreira et al., 2022; Gersick et al., 2015; Peters et al., 2004, 2009; Peters & Peters, 2010; Shimizu, 2001). Intense distant calls of felids are produced via open mouth with prominent articulation (Shipley et al., 1991). In captive cheetahs *Acinonyx jubatus*, the intense repetitive chirps produced in successions with quasi-regular intervals at loss of

visual contact to each other also serve as long-distant vocalizations (Nagorzanski, 2018; Ruiz-Miranda et al., 1998; Smirnova et al., 2016; Volodina, 1994a, 1997, 1998, 2000; Wachter et al., 2018). However, the communicative function of these calls in wild-living cheetahs in their natural habitats has yet to be investigated.

Distant vocal communication is important for wild cheetahs because of their special social structure, with broadly dispersed small social units (Marker et al., 2009; Wachter et al., 2018). In the wild, cheetah social structure is represented by temporary units of adolescent littermates separated from the mother, females with

their dependent cubs, and male coalitions consisting of related and unrelated individuals; singletons of either sex are also usual (Caro, 1994; Caro & Collins, 1987; Cornhill & Kerley, 2021; Frame & Frame, 1980; Laurenson, 1994; Mills & Mills, 2017; Wachter et al., 2011, 2018). Pairs of two heterosexual animals occur rarely (Frame & Frame, 1980): Wild male and female cheetahs commonly join for periods of up to 3 days, including courtship and mating (Wachter et al., 2018); however, there are cases of male stay with a female up to 18 days (Caro, 1994). Females try avoiding male coalitions when not in estrus, because males may be aggressive to females (Caro, 1994), although male cheetahs do not commit infanticide (Hunter & Skinner, 2003). Male coalitions compete for hunting territories and for mating partners (Caro, 1994; Wachter et al., 2018). Among other felids, some similarities in social/spatial structure were also reported for jaguars *Panthera onca*: Males of this species also form coalitions, mating with a few females, patrolling and marking territory together, invading territories, chasing and killing other jaguars, and sharing kills (Jędrzejewski et al., 2022). Distinctively, in the large solitary felid, the leopard *Panthera pardus*, males are lone (Rouse et al., 2021).

Wild cheetahs from different social units may benefit from communication by their intense chirps from a distance. Potentially, recognition of caller sex and individuality by voice may help avoiding undesirable conflicts between competing social units of cheetahs, or, otherwise, to help searching mating partners (Wachter et al., 2018). Previously, social regulation based on individual and sex recognition by distance calls was reported for free-ranging lions *Panthera leo* (McComb et al., 1993; Wijers et al., 2021). In captive non-domesticated felids aside cheetahs, vocal correlates of caller identity were found in the long-distance calls of tigers *Panthera tigris* (Ji et al., 2013) and male Eurasian lynxes *Lynx lynx* (Rutovskaya et al., 2009). In addition, individualistic isolation calls were also reported in domestic kittens *Felis silvestris catus* (Scheumann et al., 2012) and in meows of adult female domestic cats (Szenczi et al., 2016). Weak correlates of caller sex were found in calls of wild-living lions (Pfefferle et al., 2007) and in cats of genus *Felis* (Peters et al., 2009).

Previously, all vocalizations of cheetahs including the chirps were only investigated in captivity. The acoustics of the repetitive intense chirps were studied in captivity in the contexts of short-term separation of familiar males in different enclosures (Ruiz-Miranda et al., 1998; Volodina, 1994a). In captivity, intense chirps are also produced by mother cheetahs when cubs are out of sight (Volodina, 1994a, 2000) and by males during courtship behavior (Volodina, 2000). In the wild, the only context documented for producing intense chirps by adult cheetahs is male calling towards coalition partners (Wachter et al., 2018).

In captivity, characteristics of male cheetah distant chirps produced towards their coalition partners are individual-specific (Ruiz-Miranda et al., 1998). The acoustic traits of meows, used by adult cheetahs toward keepers, are also individual-specific at least at short terms (Smirnova et al., 2016). However, the prominently individualistic chirp and meow calls of the cheetahs in captivity (Ruiz-Miranda et al., 1998; Smirnova et al., 2016) may be, at least partly, an artifact

of highly conservative zoo routine, where situations of animal calling are typical and are repeatable from day to day. In these zoo conditions, the series of chirps may represent some kind or "vocal stereotypes" (Nagorzanski, 2018; Volodina, 1994b), analogous to animal pacing over the cage (Quirke et al., 2012). So, not surprisingly, a previous study using playback experiments in captive cheetahs to test whether they are attracted to different call types showed that such call series are least effective as playback stimuli for attracting adult cheetahs to a loudspeaker compared with other call types of cheetah vocal repertoire (Volodina, 1994b). Thus, whereas a common context for production of chirps can be defined as loss of visual contact between familiar/related animals and advertising own location (Ruiz-Miranda et al., 1998; Smirnova et al., 2016; Volodina, 2000), this definition has not yet been verified for wild cheetahs.

Meow calls of captive adult cheetahs also provide information about sex of a caller, as all variables of fundamental frequency (f_0) of these calls are lower in males than in females, for example, the maximum fundamental frequency is about 0.85 kHz in males and about 1.07 kHz in females (Smirnova et al., 2016). At the same time, sexual differences in f_0 of chirps lacked in 1-year cheetahs (Nagorzanski, 2018). Furthermore, hand-raised male and female cheetahs differ in their call type usage in the same contexts (Bouchet et al., 2022). Sex-related acoustic variation of the chirps may also be different in wild-living cheetahs. Thus, the acoustic correlates of sex and individual identity in the distant chirps have yet to be studied in cheetahs in the wild.

The aim of this study was to verify the context for producing the intense chirps in wild mature cheetahs and to investigate the potential of these long-distance calls to provide reliable information regarding caller vocal identity and sex. In addition, we analyze which acoustic parameters contribute the most to advertising sex and identity and estimate the stability of caller vocal identity over time.

2 | MATERIALS AND METHODS

2.1 | Study site, subjects, and dates

Long-distance chirps of 20 (eight males and 12 females) mature cheetahs *Acinonyx jubatus*, aged between 4 and 10 years, were recorded from 2014 to 2022 during regular observations of free-ranging cheetahs from the vehicle, in the daytime in a territory of about 2300 km². The study area belongs to the Maasai Mara Ecosystem (centered at 1°S, 35°E, elevation ca. 1700 m) in southwestern Kenya, comprising the Maasai Mara National Reserve (1510 km²), which borders the Serengeti National Park in Tanzania to the south, and the adjoining conservancies and pastoralist communities to the north, east, and west (Jacobson et al., 2015; Ogotu et al., 2009). There are no fences between the Maasai Mara National Reserve, the Serengeti National Park, Mara conservancies, and community areas, and wildlife moves freely within the Maasai Mara Ecosystem. The habitat types of the study are represented by dwarf shrubs/short grassland, tall grassland, shrubland, forest, and woody/

shrubby grassland (Oindo et al., 2003). During data collection period (2014–2022), population density of cheetahs in the Maasai-Mara National Reserve ranged from 0.61 (0.34–1.10) cheetahs/100 km² to 1.67 (1.00–2.80) cheetahs/100 km² (Linden et al., 2020). According to Prost et al. (2022), cheetahs in this area belong to subspecies *A. j. raineyi*. Aside the cheetahs, predators within the study area include lions *Panthera leo*, spotted hyenas *Crocuta crocuta*, leopards, African wild dogs *Lycaon pictus*, and black-backed jackals *Canis mesomela*.

Age of subject animals was established based on their known life histories; sexes were recognized by external sexual traits; individuals were identified using the distinct spot patterns on the front and back limbs and rings on the tail (Chelysheva, 2004). The age of 4 years was selected, because at this age, cheetahs in the wild have reached their full size and weight (Marker & Dickman, 2003). Exact age (year and month of birth) was known for 11 recorded individuals (one male and 10 females) out of 20 subject cheetahs. Other nine cheetahs (seven males and two females) have been first seen as adolescents without their mothers. Their exact year of birth was known, and the month of birth was estimated approximately based on the fact that cheetah cubs reach independence at the age of 18 months (Durant et al., 2004; Kelly et al., 1998).

2.2 | Audio recording

Cheetah monitoring team was searching for cheetahs between 6:00 and 18:30, driving in a vehicle, periodically stopping at the elevated points and scanning the surrounding landscape with binoculars (following Caro, 1994). When a cheetah/group of cheetahs was spotted, the researcher (EVC) slowly approached at a distance of about 25 m, photographed each animal, documented geographic coordinates of the sighting, and recorded cheetah vocalizations whenever they were produced by individually identified callers. Distance from a caller to microphone varied from about 10 to about 70 m.

All calls were produced spontaneously by the cheetahs; the researcher did not provoke the animals to vocalize. In between cheetah vocalizations, the researcher also commented on the distance changes and briefly described the ongoing events that caused the vocalizations. For audio recordings (48 kHz, 16-bit resolution, frequency range 40–20,000 Hz), a Marantz PMD-661MKII solid state recorder (D&M Professional) with a Sennheiser K6-ME67 microphone (Sennheiser electronic) was used. Recordings were stored as wav-files. In parallel with audio recording, video recording was done using a Sony FDR-AX33 4 K Ultra HD Handycam camcorder (Sony Corp.), for documenting the context of vocalization and behavior of the callers.

2.3 | Call contexts

Three contexts of producing long-distance chirps by mature cheetahs were identified. Common between these contexts is that a caller announces its location with loud calls at distance. Male–male

context was identified when a male lost visual contact with coalition members and produced repetitive chirps towards them. Male–female context was identified when male caller produced chirps when searching a potential sexual mate (the animal that found an olfactory mark started the chirping when looking for a mate of opposite sex). Occasionally, a male or female continued the chirping in the context of courtship, when the partner was in spatial proximity. Mother–cub context was identified when a mother produced the chirps towards cubs, who delayed following her, or who were out of sight (e.g., lost in the bush or left far behind from the spot of successful hunt), thus provoking them to approach for restoring spatial proximity. Contexts for producing the chirps were therefore not the same for both sexes: Female chirps lack in male–male context and male chirps lack in mother–cub context, so the effect of context on the acoustics of the chirps could not be considered in this study.

2.4 | Call samples

From 2790 hours of recordings of a total of 40 individually identified mature cheetahs (20 males and 20 females), we selected for acoustic analysis audio files from 20 (eight males and 12 females) individuals, which provided sufficient call samples for analysis. For estimating the effects of sex and individuality on the acoustic variables of chirps, we selected 15–20 calls per individual from all the 20 individuals, 390 chirps in total (Appendix Table A1). For estimating the stability of vocal individuality in chirps with time (over 1 or over 2 years), we additionally selected 6–20 calls per individual from 10 of the 20 individuals (five males and five females) recorded in different years, 160 chirps in total. We therefore included in analysis 550 chirps: 160 chirps of seven males produced in the male–male context, 126 chirps (89 from four males and 37 from three females) produced in the male–female context, and 264 chirps of 11 females produced in the mother–cub context. For each of 20 adult cheetahs (eight males and 12 females), we selected the chirps from one recording for estimating the individual and sex-related variation. For 10 of the 20 cheetahs (five males and five females), we additionally selected the chirps from the second recording separated with time space of one or 2 years from the first recording, for estimating call acoustic stability over time.

We selected high-quality chirps with high signal-to-noise ratios, not disrupted by wind and overlapped with extraneous noises (e.g., from water stream, airplane, car engine, birds, crickets, other animals, or human voices). We took the best quality calls regardless of distance, in which all necessary acoustic parameters could be measured. To decrease potential pseudoreplication by taking consecutive chirps, the chirps were primarily selected from different parts of audio files.

2.5 | Call analyses

For acoustic analyses, we used Avisoft SASLab Pro software (Avisoft Bioacoustics). Before the analyses, the acoustic files were

downsampled to 22,050Hz, and high-pass filtered at 200Hz for removing the background noise. The filtering did not affect the calculated values of f_0 , because the values of f_0 variables were higher than 200Hz (see below). For call analysis, we used Avisoft, with 22,050Hz sampling frequency, the Hamming window, FFT (Fast Fourier Transform) length 1024 points, frame 50%, and overlap 96.87%. These settings allowed frequency resolution 22Hz and time resolution 1.45ms. All measurements were made manually and exported to Microsoft Excel (Microsoft Corp).

For each chirp, we manually measured two temporal parameters: call duration and the duration from call onset to the point of maximum f_0 (dur-to-max) from the screen with the standard marker cursor in the spectrogram window (Figure 1). We calculated dur-to-max% as ratio dur-to-max to the total duration of each chirp. We measured, with the reticule cursor, four frequency parameters: the initial ($f_{0\text{beg}}$), end ($f_{0\text{end}}$), maximum ($f_{0\text{max}}$), and minimum ($f_{0\text{min}}$) fundamental frequencies of each chirp (Figure 1). In addition, we measured four power parameters: the maximum amplitude (= peak) frequency (f_{peak}) and three quartiles (q_{25} , q_{50} and q_{75}), covering, respectively, 25, 50, and 75% of call energy (hereafter the lower, medium, and upper quartiles) from the mean power spectrum of each chirp.

2.6 | Statistics

Statistical analyses were carried out with STATISTICA, v. 8.0 (StatSoft) and R 4.1.0 (R Development Core Team, 2021); all means are given as mean \pm SD. Significance levels were set at .05, and two-tailed probability values are reported. Only 34 of 230 distributions of measured parameter values did depart from normality (Kolmogorov–Smirnov test, $p > .05$). As ANOVA is relatively robust to departures from normality (Dillon & Goldstein, 1984), this was not an obstacle to the application of the parametric tests. We used

a nested design of ANOVA with Tukey HSD (Honest Significantly Different) test with an individual nested within sex to estimate effects of factors “individuality” and “sex,” on the acoustic variables of chirps, with sex as fixed factor and individual as random factor (to control for inclusion of more than one call from each individual).

We used standard procedure of Discriminant Function Analysis (DFA) to calculate the probability of the assignment of chirps, one DFA for assignment to correct individual, and another DFA for assignment to correct sex. Variables, used for the DFA, showed very low Pearson correlation values to each other. Among the total of 45 pairwise correlations, the R^2 values were lower 0.2 for 33 comparisons, between 0.2 and 0.4 for five comparisons, between 0.4 and 0.6 for three comparisons, and between 0.6 and 0.8 for three comparisons, and only for 1 comparison (between $f_{0\text{end}}$ and $f_{0\text{min}}$) the R^2 value was 0.92. So, we excluded $f_{0\text{min}}$ from analysis and included in the DFA only nine acoustic variables. We also carried out DFA for assigning calls to sex using average values of each acoustic parameter for each of the 20 cheetahs, to exclude the effect of taking more than one call per individual.

In addition, we estimated the stability of acoustic individuality of the chirps over time for those cheetahs (five males and five females of the 20 subject cheetahs) that provided calls repeatedly in two different years. We classified the chirps from the second recording with DFA functions derived from the first recording, considering the value of correct cross-validation as a measure of the retention of individuality over time (Briefer et al., 2010; Matrosova, Volodin, Volodina, Vasilieva, & Kochetkova, 2010; Smirnova et al., 2016). We used a repeated-measures ANOVA controlled for individuality, to compare the values of correct assignment of chirps to correct callers between recordings of different years (Volodin et al., 2018).

We used Wilks' Lambda to estimate how strongly acoustic variables contribute to discrimination of individuals. To validate our DFA results, we calculated the chance values of correct assignment of chirps to individual and sex by applying a randomization test for

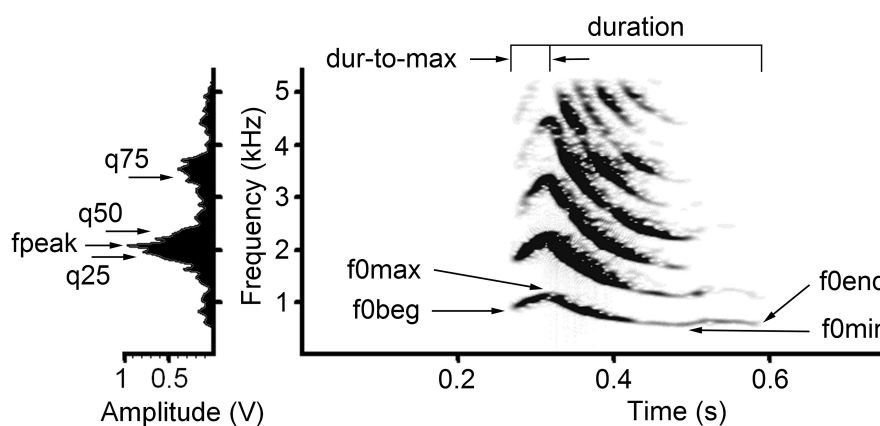


FIGURE 1 Measured variables for cheetah chirps. Spectrogram (right) and mean power spectrum of the chirp call (left). Designations: duration – call duration; dur-to-max – duration from call onset to the point of maximum f_0 ; $f_{0\text{beg}}$ – the fundamental frequency at the onset of a call; $f_{0\text{end}}$ – the fundamental frequency at the end of a call; $f_{0\text{max}}$ – the maximum fundamental frequency; $f_{0\text{min}}$ – the minimum fundamental frequency; f_{peak} – the frequency of maximum amplitude within a call; q_{25} , q_{50} q_{75} – the lower, medium and upper quartiles, covering respectively 25%, 50% and 75% energy of a call spectrum. The spectrogram was created at 11025Hz sampling frequency, FFT length 512, Hamming window, frame 50%, overlap 96.87%.

misclassification probability in discriminant analysis (Solow, 1990) with macros, created in R. The values by chance were calculated from DFAs performed on 1000 randomized permutations on the data sets (Mundry & Sommer, 2007; Solow, 1990). For example, to calculate the random value of classifying chirps to individuals, each permutation procedure included the random permutation of 390 calls among 20 randomization groups (18 groups, each including 20 calls, and two groups, each including 15 calls), respectively, to 20 individuals which were examined (Appendix Table), followed by DFA standard procedure built-in in R. Using a distribution obtained by the permutations, we noted whether the observed value exceeded 95% (950 values), 99% (990 values) or 99.9% (999 values) within the distribution (Mundry & Sommer, 2007; Solow, 1990). If the observed value exceeded 95%, 99%, or 99.9% of values within this distribution, we established that the observed value did differ significantly from the chance value with a probability $p < .05$, $p < .01$ or $p < .001$, respectively (Briefer et al., 2010; Smirnova et al., 2016; Solow, 1990).

2.7 | Ethical note

This study was a part of the long-term monitoring program of the Mara-Meru Cheetah Project. Permissions for data collection in the field were granted to EVC by the Kenya Wildlife Service (Permit No: KWS/BRM/5001), National Commission for Science, Technology and Innovations (Permit No: NACOSTI/P/19/0995/27656), Narok County Government (Permit No: NCG/MMNR/R/R/VOL.VII/53), and the management of the conservancies. We adhered to the "Guidelines for the treatment of animals in behavioral research and teaching" (Animal Behaviour, 2020, 159, I-XI) and to the Wildlife Conservation and Management Act 2013 – Protecting the welfare of wild animals (Kenya), where the study was conducted.

During observations, researchers prioritized welfare of animals, maintaining a distance recommended by the local rules to minimize disturbance.

3 | RESULTS

3.1 | Effects of individuality and sex on chirp acoustics

Cheetah chirps displayed both individual and sex-based variability (Figure 2). Two-way ANOVA revealed the effects of individuality on all acoustic variables, whereas factor sex only affected call duration, peak frequency, and variables of f_0 (Table 1, Figure 3, Appendix). Male chirps were longer in duration than female chirps (Table 1). The peak frequency and all fundamental frequency variables of the chirps were substantially lower in males than in females, for instance, the $f_0\text{max}$ was 0.76 ± 0.12 kHz in males and 0.98 ± 0.15 kHz in females (Table 1). The means of each acoustic variable for each individual are provided in Appendix Table.

We conducted two DFAs, for sex and individuality, each DFA based on nine measured variables of the chirps (duration, dur-to-max%, $f_0\text{max}$, $f_0\text{beg}$, $f_0\text{end}$, f_{peak} , q_{25} , q_{50} , q_{75}). The DFA for sex showed the average value of correct assignment of the chirps of 93.8%, which was significantly higher than the level expected by chance of $52.9 \pm 2.1\%$, $\text{min} = 48.2\%$, $\text{max} = 60.5\%$ (permutation test, 1000 permutations, $p < .001$) (Table 2). In order of decreasing importance, the f_{peak} , $f_0\text{beg}$, and dur-to-max% were mainly responsible for discrimination of sex by the chirps. The DFA carried out on the average parameter values of the chirps per individual showed 100% correct assignment to sex.

The average value of correct assignment of the chirps to individual with DFA was 79.5%, which was significantly higher than the

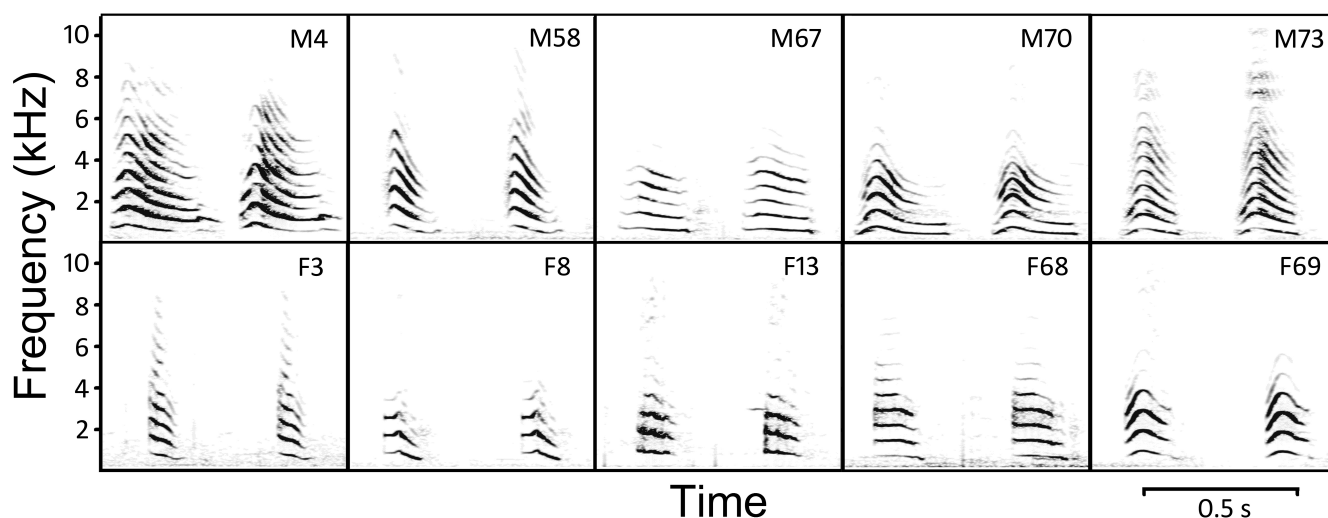


FIGURE 2 Spectrogram illustrating individual and sex-related differences of mature cheetah chirps. Upper panel: chirps from five individual males, two chirps per male. Lower panel: chirps from five individual females, two chirps per female. The spectrogram was created at 22050 Hz sampling frequency, FFT length 1024, Hamming window, frame 50%, overlap 96.87%. The audio file of these calls is available as Supporting Information [Audio S1](#).

TABLE 1 Values (mean \pm SD) of chirp variables and the results of nested two-way ANOVA for individual and sex-related differences.

Acoustic variable	Mean \pm SD values			ANOVA	
	All animal chirps (<i>n</i> = 390)	Male chirps (<i>n</i> = 155)	Female chirps (<i>n</i> = 235)	Individual differences	Sex differences
Duration (s)	0.19 \pm 0.07	0.24 \pm 0.06	0.16 \pm 0.05	$F_{18,370} = 54.98; p < .001$	$F_{1,370} = 11.92; p = .003$
dur-to-max%	0.27 \pm 0.12	0.24 \pm 0.09	0.30 \pm 0.13	$F_{18,370} = 25.91; p < .001$	$F_{1,370} = 2.33; p = .14$
f0beg (kHz)	0.70 \pm 0.21	0.52 \pm 0.13	0.82 \pm 0.16	$F_{18,370} = 57.03; p < .001$	$F_{1,370} = 21.27; p < .001$
f0end (kHz)	0.62 \pm 0.15	0.50 \pm 0.11	0.69 \pm 0.13	$F_{18,370} = 78.98; p < .001$	$F_{1,370} = 12.89; p = .002$
f0max (kHz)	0.89 \pm 0.17	0.76 \pm 0.12	0.98 \pm 0.15	$F_{18,370} = 36.29; p < .001$	$F_{1,370} = 17.09; p < .001$
f0min (kHz)	0.60 \pm 0.15	0.48 \pm 0.10	0.68 \pm 0.11	$F_{18,370} = 75.30; p < .001$	$F_{1,370} = 16.80; p < .001$
fpeak (kHz)	1.67 \pm 0.78	1.25 \pm 0.69	1.95 \pm 0.70	$F_{18,370} = 7.05; p < .001$	$F_{1,370} = 17.13; p < .001$
q25 (kHz)	1.50 \pm 0.40	1.39 \pm 0.34	1.57 \pm 0.43	$F_{18,370} = 10.27; p < .001$	$F_{1,370} = 2.30; p = .15$
q50 (kHz)	2.32 \pm 0.64	2.35 \pm 0.82	2.29 \pm 0.49	$F_{18,370} = 20.39; p < .001$	$F_{1,370} = 0.23; p = .64$
q75 (kHz)	3.39 \pm 1.11	3.62 \pm 1.32	3.24 \pm 0.93	$F_{18,370} = 44.86; p < .001$	$F_{1,370} = 1.06; p = .32$

Note: Individual was nested within sex, with sex as fixed factor and individual as random factor. *N* = 20 mature cheetah callers (eight males and 12 females).

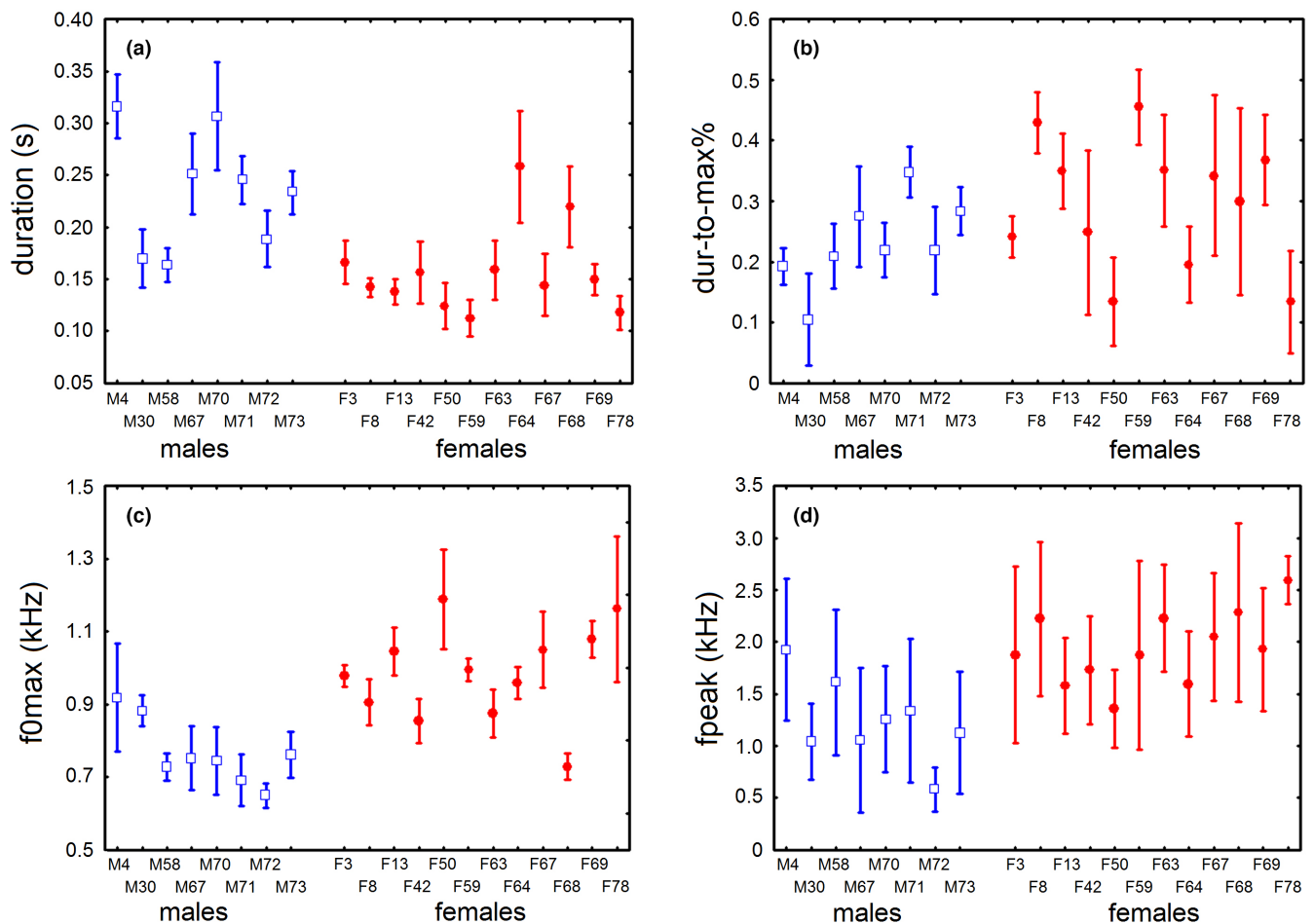


FIGURE 3 Individual and sex-related variation of acoustic variables of chirps in mature cheetahs: (a) call duration (duration); (b) ratio of the duration from call onset to the point of maximum *f*₀ to call duration (dur-to-max%); (c) the maximum fundamental frequency (*f*₀max); (d) the peak frequency (*f*_{peak}). Points with whiskers display individuals. Central points indicate the means, whiskers indicate SD.

level expected by chance of $14.8 \pm 1.6\%$, min = 10.3%, max = 20.2% (permutation test, 1000 permutations, $p < .001$) (Table 3). In order of decreasing importance, duration, the *f*₀beg, and *f*₀end were mainly

responsible for discrimination of individuals by the chirps. Among individuals, the value of correct assignment of the chirps varied from 45% to 100%; all the 20 individuals differed from the chance level.

TABLE 2 Assignment of chirps to a predicted sex with DFA.

Actual group	Predicted group membership		Total	Correctly assigned
	Males	Females		
Males	147	8	155	94.8%
Females	16	219	235	93.2%
Total	163	227	390	93.8%

TABLE 3 Assignment of chirps to a predicted caller with DFA.
n = number of chirps.

Animal ID	<i>n</i> chirps	<i>n</i> correctly assigned chirps	% correctly assigned chirps
Male M4	20	18	90.0
Male M30	15	14	93.3
Male M58	20	18	90.0
Male M67	20	14	70.0
Male M70	20	9	45.0
Male M71	20	19	95.0
Male M72	20	19	95.0
Male M73	20	18	90.0
Female F3	20	18	90.0
Female F8	20	19	95.0
Female F13	20	20	100.0
Female F42	20	11	55.0
Female F50	15	9	60.0
Female F59	20	17	85.0
Female F63	20	16	80.0
Female F64	20	18	90.0
Female F67	20	14	70.0
Female F68	20	11	55.0
Female F69	20	10	50.0
Female F78	20	18	90.0
Total	390	310	79.5

Therefore, the chirps provided reliable cues to sex (the higher fundamental and peak frequencies in females than in males) and also had a high potential to encode caller individuality.

3.2 | Stability of chirps over time

For 10 cheetahs (five males and five females) that provided sufficient numbers of chirps recorded twice with time space of one or 2 years, we compared the stability of vocal individuality over time (Figure 4). Within years, DFA displayed high values of correct assignment of the chirps to individual (91.4% in the first year and 83.9% in the second year of recording) significantly exceeding chance level ($25.3 \pm 2.8\%$, min = 17.2%, max = 34.6% in the first year, and $25.2 \pm 2.9\%$, min = 15.4%, max = 33.6% in the second year,

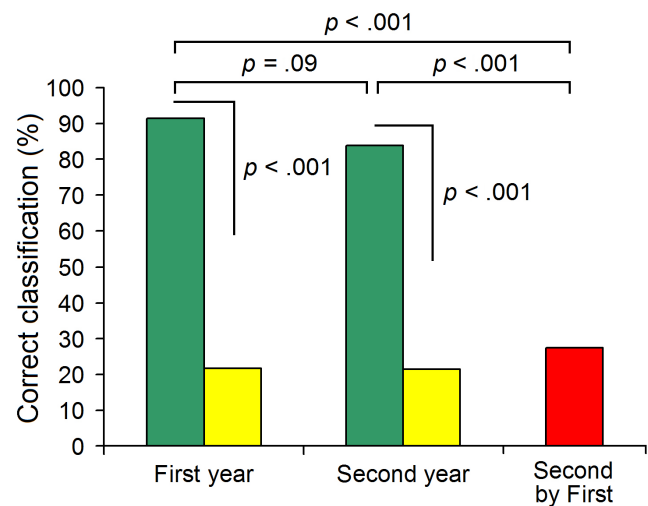


FIGURE 4 Discrimination of individual cheetahs by chirps over years. Green bars indicate DFA values and yellow bars indicate by chance values, calculated with a randomization procedure. Comparisons between observed and chance values with permutation tests and comparisons between chirps from recordings of the first and second years with a repeated measures ANOVA are shown by brackets above the bars. The red bar indicates the assignment value of the second-year chirps with discriminant functions created for chirps recorded in the first year of recording.

permutation test, $p < .001$ in both cases) and did not differ between years (r-m ANOVA, $F_{1,9} = 3.65$, $p = .09$). The value of correct assignment varied among individuals from 85% to 100% in the first year and from 65% to 100% in the second year of recording.

Cross-validation of chirps recorded in the second year using discriminant functions created for chirps recorded in the first year revealed a strong decrease in assignment of the chirps to correct callers (Figure 4). The average value of correct assignment decreased to the level expected by chance (27.2%) and became significantly lower compared with chirp samples from the first year ($F_{1,9} = 56.58$, $p < .001$) and from the second year of recording ($F_{1,9} = 37.90$, $p < .001$). The value of correct assignment varied among individuals from 0% to 85% and was below the chance level in six of the 10 individuals. Therefore, in subject cheetahs, individuality of the chirps was unstable over time.

4 | DISCUSSION

4.1 | Context of chirps

This is the first study investigating acoustic variation in wild cheetahs. Previously, all studies of the acoustic structure of cheetah vocalizations were only made in captivity (Bouchet et al., 2022; Eklund et al., 2010, 2012a, 2012b; Eklund & Peters, 2013; Imon, 2019; Nagorzanski, 2018; Ruiz-Miranda et al., 1998; Smirnova et al., 2016; Stoeger-Horwath & Schwammer, 2003; Volodina, 1994a, 1997, 1998, 2000). This study expands the knowledge about acoustic variation of long-distance vocalizations (chirps) of mature

cheetahs. Previous acoustic analyses of this prominent vocalization (Nagorzanski, 2018; Ruiz-Miranda et al., 1998; Smirnova et al., 2016; Stoeger-Horwath & Schwammer, 2003; Volodina, 1994a, 1997, 1998) could be potentially affected by limitations of captivity, as for example crowded enclosures preventing natural territorial spacing used by cheetahs when counter-calling in the wild. In captivity, chirping might be less frequent and occurred when cheetahs were out of sight in spacious enclosures (Smirnova et al., 2016) or during separations (Ruiz-Miranda et al., 1998). Additional factors affecting the acoustics of the chirps in some captive cheetahs probably were the non-naturalistic social structure of captive groups, as for example lack of male coalitions (Augustus et al., 2006; Caro, 1993) or keeping females together with other females (Wielebnowski & Brown, 1998), but see Ruiz-Miranda et al. (1998) and Chadwick et al. (2013), for the studies where males were kept in coalitions. Another reason might be the non-naturalistic contexts of calling, for example, vocalizing toward zoo keepers at food anticipation (Nagorzanski, 2018; Smirnova et al., 2016; Stoeger-Horwath & Schwammer, 2003; Volodina, 1994a).

In this study, we revealed three main contexts for producing the chirps by wild mature cheetahs: male calling toward coalition members, male or female calling toward a potential mate, and mother calling toward cubs. We therefore verified the previous findings made in captivity (Ruiz-Miranda et al., 1998; Smirnova et al., 2016; Volodina, 2000) that a common context for production of long-distance chirps might be defined as lack of visual contact with conspecifics and advertising own location by a caller to resume spatial proximity or to establish a novel contact. The context of male/female calling when a caller could be in spatial proximity toward a potential mate is consistent with the findings that producing chirps and meows by captive females is positively correlated with concentration of estradiol and may also serve as one of the behavioral markers of estrus enhancing attractiveness of females for males (Wielebnowski & Brown, 1998).

Acoustic recording of long-distance chirps of wild cheetahs in this study was complicated by several reasons. It was not easy to locate cheetahs, as some of them were shy and kept far distance from the vehicles. All listed contexts of chirping occurred very rarely. So, from 2014 to 2022, we recorded calls of 40 mature cheetahs (20 males and 20 females); however, for acoustic analysis of the chirps in this study, we could only select the calls from 20 individuals. Female chirps lacked in male-male context and male chirps lacked in mother-cub context, and only some individuals were recorded in more than one context. So, the effect of context on the acoustic variables could not be estimated in this study.

4.2 | Acoustic variables of chirps

The values of acoustic variables of the chirps in wild cheetahs are well comparable with the acoustics of chirps investigated in captive cheetahs. The chirp of mature cheetahs is a very short call (0.19 s in our study), displaying irregular variation of duration across ages: of

0.32 s in cubs (Volodina, 1998), of 0.12–0.20 s in 1-year-old adolescents (Nagorzanski, 2018; Stoeger-Horwath & Schwammer, 2003), of 0.08–0.11 s in 3-year-old males (Ruiz-Miranda et al., 1998), and of 0.09–0.30 s in mature adults over 4 years (Ruiz-Miranda et al., 1998; Smirnova et al., 2016; Volodina, 2000). A most characteristic trait of the chirp call type (a location of the fundamental frequency maximum close to the start of a call) is uniformly the same for the chirps recorded in the wild (this study) and in captivity (Ruiz-Miranda et al., 1998; Smirnova et al., 2016; Stoeger-Horwath & Schwammer, 2003; Volodina, 2000). The peak frequency of the chirps (1.67 kHz in this study) was also similar with those (1.64–1.76 kHz) in captive adult cheetahs (Ruiz-Miranda et al., 1998; Smirnova et al., 2016).

However, the fundamental frequency of the chirps in adult cheetahs in this study ($f_{0max} = 0.89$ kHz) was lower than in adult cheetahs in captivity, with f_{0max} of 1.19–1.81 kHz (Smirnova et al., 2016; Volodina, 2000). The reasons for these differences could be the factors of natural environment, including the level of emotional arousal of the callers and the differences in the contexts of vocalizing. A previous study reported that chirps of 1-year-old captive cheetahs, produced in the context of higher arousal (food anticipation), are longer and have higher f_{0max} and f_{0beg} compared with chirps not related to food anticipation (Nagorzanski, 2018).

Another factor strongly affecting the fundamental frequency of cheetah chirps is the caller's age. The average maximum fundamental frequency of the chirps is 5.85 kHz in 1.5–3.0-month-old cheetah cubs (Volodina, 1998) and 2.29–3.00 kHz in 1-year-old adolescent cheetahs (Nagorzanski, 2018; Stoeger-Horwath & Schwammer, 2003), which is substantially higher frequency than in 2-year-old and older cheetahs (1.19–1.81 kHz) (Smirnova et al., 2016; Volodina, 2000). Furthermore, chirps of 3-year-old males have fundamental frequency 1.5 times higher than chirps of 6-year-old males tested using identical experimental procedure in a zoo (Ruiz-Miranda et al., 1998). Further detailed study is necessary to investigate the effect of age on the chirp fundamental frequency in the cheetah. So, small age differences between adult cheetahs whose chirps were used for measuring fundamental frequency in different studies could be the reason of the lower f_0 values in the wild than in captivity.

The maximum fundamental frequency of the long-distance chirps of wild cheetahs (890 Hz, Table 1) is surprisingly similar with f_0 of intense long-distance meows of Eurasian lynxes (720–1010 Hz), produced by males during mating period (Peters, 1987; Rutovskaya et al., 2009). This maximum f_0 is evidently higher than maximum f_0 of long-distance roars of much larger-sized male (195 Hz, Pfefferle et al., 2007; 165–245 Hz, Wijers et al., 2021) and female wild lions (207 Hz, Pfefferle et al., 2007), and captive tigers (317 Hz, Ji et al., 2013). However, in substantially smaller felids of the genus *Felis*, the maximum f_0 of intense mew calls varies from 260 to 710 Hz between species and subspecies (Nicastro, 2004; Peters et al., 2009). Some anecdotal evidences suggest that wild cougars *Puma concolor* produce both high-frequency (maximum f_0 over 4000 Hz, Allen et al., 2016) and low-frequency (430 Hz Macarrão et al., 2012)

long-distance calls. Overall, the evident lack of the negative relationship between fundamental frequency of long-distance calls and body size is reminiscent of the situation with rutting calls in red deer *Cervus elaphus*, in which f_0 varies 10 times between subspecies (Volodin et al., 2013, 2022).

4.3 | Encoding sex and individuality by chirps

We found that long-distance chirps of wild mature cheetahs provide reliable cues to sex and may also encode caller individuality, although the cues to individuality are unstable over years. There are no playback studies to show that cheetahs can recognize individuals by voice. However, indirect data from experiments for recognition between familiar and unfamiliar human voices by cheetahs suggest a presence of ability of recognition of conspecifics by voice too (Leroux et al., 2018).

Earlier, the prominent individuality of cheetah chirps in captivity was found in the four 3–6-year-old males (Ruiz-Miranda et al., 1998) and in 12 one-year-old adolescents (Nagorzanski, 2018). Experiments estimating propagation ability of the chirps showed that chirps of 1-year-old cheetahs, re-recorded at distance of 400 m, retain their individual characteristics in parameters of fundamental frequency, whereas temporal parameters of chirps are becoming indistinguishable between individuals (Nagorzanski, 2018). In this study, discrimination of individuals was primarily measured on the temporal and fundamental frequency parameters. These parameters do not degrade substantially at the distances of a few dozen meters (Matrosova, Volodin, Volodina, & Vasilieva, 2010).

Well-expressed individual differences were also found in meows of adult cheetahs (Ruiz-Miranda et al., 1998; Smirnova et al., 2016); however, as with chirps, the cues to individuality of the meows were unstable over 2 years (Smirnova et al., 2016). These results agree with findings for all studied species of mammals, showing instability of vocal individuality over time (e.g., Briefer et al., 2010; Matrosova, Volodin, Volodina, Vasilieva, & Kochetkova, 2010; Sibiryakova et al., 2015). Unlike mammals, calls of some species of birds can be stable, thus labeling individuals at long terms, up to a few years (Calcari et al., 2021; Klenova et al., 2009, 2012; Lengagne, 2001).

The vocal cues to sex in the chirps of adult cheetahs can be based on differences in values of fundamental and peak frequencies, which are lower in males for 22–36% than in females (Table 1). The fundamental and peak frequencies are strongly correlated to body size in calls of mammals (Bowling et al., 2017; Charlton & Reby, 2016; Garcia et al., 2017) including felids (Peters & Peters, 2010, but see Peters et al., 2009). Sex differences in frequencies can be based on sex-related differences in body weight of adult cheetahs, of up to 15% in captive cheetahs (Wildt et al., 1993) and from 15 to 22% in wild cheetahs (Caro, 1994; Marker & Dickman, 2003). Similarly well-expressed sexual differences in the fundamental frequency (but not in the peak frequency) were found in meows of adult cheetahs (Smirnova et al., 2016). However, chirps of 1-year-old male cheetahs

did not differ by fundamental frequency from chirps of 1-year-old female cheetahs (Nagorzanski, 2018), probably because of the lack of differences in body size in the cheetahs up to 12 months of age (Marker & Dickman, 2003). Apparently, the sexual differences in the cheetah chirps emerge during maturation, approximately at 18–24 months of age (Kelly et al., 1998; Maly et al., 2018, 2021), along with the appearance of sexual differences in body size (Marker & Dickman, 2003). Consistently, indistinguishable to start of maturation vocal frequency characteristics were found in humans *Homo sapiens* (Lee et al., 1999) and in goitered gazelles *Gazella subgutturosa* (Volodin et al., 2017). At the same time, the intense mew calls in adult felid species of the genus *Felis* and the long-distance roars of adult lions and tigers do not display the substantial sexual differences in fundamental frequency (Ji et al., 2013; Peters et al., 2009; Pfefferle et al., 2007).

AUTHOR CONTRIBUTIONS

Elena V. Chelysheva: Conceptualization; methodology; investigation; formal analysis; resources; writing – review and editing; visualization; project administration; funding acquisition. **Anna V. Klenova:** Methodology; software; formal analysis; investigation; writing – review and editing; visualization. **Ilya A. Volodin:** Conceptualization; methodology; software; validation; investigation; resources; data curation; writing – review and editing; writing – original draft; project administration. **Elena V. Volodina:** Conceptualization; investigation; resources; writing – original draft; writing – review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no competing interests.

DATA AVAILABILITY STATEMENT

The data that supports the findings of this study are available in the supplementary material of this article.

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SUPPORTING INFORMATION

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APPENDIX A

TABLE A1 . Values (mean \pm SD) of chirp frequency and temporal variables for 20 mature cheetahs, included in DFA for sex and individuality.

Animal ID	n chirps	Chirp acoustic variables									
		Duration (s)	Dur-to-max%	f0beg (kHz)	f0end (kHz)	f0max (kHz)	f0min (kHz)	fpeak (kHz)	q25 (kHz)	q50 (kHz)	q75 (kHz)
Male M4	20	0.32 \pm 0.03	0.19 \pm 0.03	0.59 \pm 0.12	0.50 \pm 0.04	0.92 \pm 0.15	0.49 \pm 0.04	1.93 \pm 0.68	1.64 \pm 0.24	2.26 \pm 0.40	3.22 \pm 0.38
Male M30	15	0.17 \pm 0.03	0.10 \pm 0.08	0.83 \pm 0.05	0.77 \pm 0.07	0.88 \pm 0.04	0.74 \pm 0.06	1.04 \pm 0.37	1.60 \pm 0.21	4.06 \pm 0.91	7.08 \pm 0.69
Male M58	20	0.16 \pm 0.02	0.21 \pm 0.05	0.49 \pm 0.07	0.52 \pm 0.04	0.73 \pm 0.04	0.47 \pm 0.05	1.61 \pm 0.70	1.47 \pm 0.30	2.16 \pm 0.58	3.09 \pm 0.48
Male M67	20	0.25 \pm 0.04	0.27 \pm 0.08	0.54 \pm 0.08	0.51 \pm 0.03	0.75 \pm 0.09	0.49 \pm 0.03	1.06 \pm 0.70	1.05 \pm 0.29	1.75 \pm 0.56	2.79 \pm 0.58
Male M70	20	0.31 \pm 0.05	0.22 \pm 0.05	0.47 \pm 0.04	0.45 \pm 0.03	0.75 \pm 0.09	0.44 \pm 0.03	1.26 \pm 0.51	1.25 \pm 0.31	2.03 \pm 0.47	2.99 \pm 0.66
Male M71	20	0.25 \pm 0.02	0.35 \pm 0.04	0.38 \pm 0.03	0.36 \pm 0.01	0.69 \pm 0.07	0.35 \pm 0.01	1.34 \pm 0.69	1.27 \pm 0.39	1.88 \pm 0.49	2.95 \pm 0.66
Male M72	20	0.19 \pm 0.03	0.22 \pm 0.07	0.49 \pm 0.04	0.52 \pm 0.02	0.65 \pm 0.03	0.48 \pm 0.03	0.58 \pm 0.21	1.43 \pm 0.20	2.66 \pm 0.30	3.91 \pm 0.41
Male M73	20	0.23 \pm 0.02	0.28 \pm 0.04	0.45 \pm 0.04	0.45 \pm 0.01	0.76 \pm 0.06	0.43 \pm 0.02	1.13 \pm 0.59	1.49 \pm 0.35	2.46 \pm 0.49	3.79 \pm 0.50
Female F3	20	0.17 \pm 0.02	0.24 \pm 0.03	0.67 \pm 0.06	0.53 \pm 0.03	0.98 \pm 0.03	0.53 \pm 0.03	1.87 \pm 0.85	1.47 \pm 0.42	2.16 \pm 0.40	2.83 \pm 0.44
Female F8	20	0.14 \pm 0.01	0.43 \pm 0.05	0.80 \pm 0.06	0.57 \pm 0.03	0.91 \pm 0.06	0.57 \pm 0.03	2.22 \pm 0.74	1.43 \pm 0.32	2.20 \pm 0.49	3.03 \pm 0.46
Female F13	20	0.14 \pm 0.01	0.35 \pm 0.06	0.97 \pm 0.06	0.72 \pm 0.04	1.05 \pm 0.06	0.72 \pm 0.04	1.58 \pm 0.46	1.46 \pm 0.34	1.91 \pm 0.25	2.44 \pm 0.35
Female F42	20	0.16 \pm 0.03	0.25 \pm 0.14	0.75 \pm 0.07	0.65 \pm 0.05	0.85 \pm 0.06	0.65 \pm 0.05	1.73 \pm 0.52	1.41 \pm 0.25	1.95 \pm 0.53	3.60 \pm 0.95
Female F50	15	0.12 \pm 0.01	0.13 \pm 0.07	1.11 \pm 0.12	0.89 \pm 0.12	1.19 \pm 0.14	0.87 \pm 0.10	1.36 \pm 0.37	1.55 \pm 0.28	2.72 \pm 0.90	5.25 \pm 1.92
Female F59	20	0.11 \pm 0.02	0.46 \pm 0.06	0.79 \pm 0.04	0.82 \pm 0.08	1.00 \pm 0.03	0.77 \pm 0.04	1.87 \pm 0.90	1.76 \pm 0.41	2.66 \pm 0.32	4.01 \pm 0.72
Female F63	20	0.16 \pm 0.03	0.35 \pm 0.09	0.71 \pm 0.05	0.62 \pm 0.07	0.88 \pm 0.07	0.62 \pm 0.06	2.23 \pm 0.51	1.77 \pm 0.42	2.37 \pm 0.49	2.78 \pm 0.59
Female F64	20	0.25 \pm 0.05	0.20 \pm 0.06	0.86 \pm 0.06	0.72 \pm 0.03	0.96 \pm 0.04	0.72 \pm 0.03	1.59 \pm 0.51	1.06 \pm 0.16	1.87 \pm 0.10	3.06 \pm 0.38
Female F67	20	0.14 \pm 0.03	0.34 \pm 0.13	0.73 \pm 0.13	0.82 \pm 0.11	1.05 \pm 0.10	0.70 \pm 0.11	2.05 \pm 0.62	1.73 \pm 0.42	2.39 \pm 0.35	3.25 \pm 0.34
Female F68	20	0.22 \pm 0.04	0.30 \pm 0.15	0.59 \pm 0.06	0.53 \pm 0.03	0.73 \pm 0.04	0.53 \pm 0.03	2.28 \pm 0.86	1.49 \pm 0.35	2.46 \pm 0.30	2.95 \pm 0.12
Female F69	20	0.15 \pm 0.02	0.37 \pm 0.07	0.86 \pm 0.11	0.68 \pm 0.09	1.08 \pm 0.05	0.68 \pm 0.09	1.93 \pm 0.59	1.58 \pm 0.36	2.27 \pm 0.29	2.99 \pm 0.28
Female F78	20	0.12 \pm 0.02	0.13 \pm 0.08	1.01 \pm 0.16	0.81 \pm 0.06	1.16 \pm 0.20	0.80 \pm 0.05	2.59 \pm 0.23	2.12 \pm 0.37	2.67 \pm 0.08	3.17 \pm 0.24