

Spectral characteristics of intense mew calls in cat species of the genus *Felis* (Mammalia: Carnivora: Felidae)

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Abstract Spectral characteristics of intense mew calls of six cat (sub)species in the genus *Felis* were studied in captivity: European wildcat (*Felis s. silvestris*), African wildcat (*F. s. lybica*), Asiatic steppe cat (*F. s. ornata*), black-footed cat (*F. nigripes*), jungle cat (*F. chaus*), and sand cat (*F. margarita*). The body weight of the largest (jungle cat) of the six taxa is about six times that of the smallest (black-footed cat), and they live in different habitat types ranging from open desert virtually devoid of vegetation (sand cat) to various types of rather dense forest and shrubland (European wildcat). These habitats differ considerably in the conditions for sound propagation. In this study we analyzed whether and how spectral characteristics of the intense mew calls of these cat taxa are related to their body weight/size and predominant habitat type (open vs. dense). Neither the mean fundamental frequency nor the mean dominant frequency of the intense calls of these cat (sub)species showed an inverse correlation with their respective body weights (“frequency scaling rule”). Rather, the mean dominant frequency is significantly positively correlated with body weight, being lower in the calls of the smaller taxa living in open habitat compared to those of the larger taxa living in dense habitat types. The hypothesis supported best by our data is that

spectral features of intense mew calls in the *Felis* taxa studied have evolved to reduce attenuation when propagating through their respective habitat types.

Keywords Acoustic adaptation hypothesis · *Felis* · Frequency scaling · Intense mew calls

Introduction

Several comparative studies on the morphology and functional specializations of the external ear, ear canal, middle-ear cavity and the tympanic membrane in species of the family Felidae by Huang et al. (1997, 2000a, b, 2002) revealed that the external ear and the tympanic membrane of the sand cat (*Felis margarita*) show structural specializations which suggest that its ears absorb more acoustic power (for the same sound pressure), especially in the frequency range <0.8 kHz, than those of the domestic cat, a felid of about equal size. Given the acoustics of sound propagation in desert habitats, Huang et al. (2002) hypothesized that these specializations may be of survival value in improving the detection of prey, the avoidance of predators and/or intraspecific acoustic long-distance communication. A few preliminary structural measurements of intense mew calls of the sand cat, presented in a footnote (Huang et al. 2002, p. 678), conform with the last hypothesis.

The present study draws comparisons between the spectral characteristics of intense mew calls in several wild species in the genus *Felis* (including one species with three subspecies). The choice of the taxa studied was governed by the following considerations: (1) recordings of the relevant vocalizations of most taxa in this genus were available for analysis; (2) the genus *Felis* is phylogenetically well

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defined (Johnson et al. 2006) and is the most recently derived group within the family Felidae; (3) the body weight of the largest species (*F. chaus*) is about six times that of the smallest (*F. nigripes*); and (4) the *Felis* (sub)species live in very different habitat types. The intense mew calls of all *Felis* (sub)species studied each have a particular sound character and are often uttered in series. They are used in males and females of all (sub)species for long-distance communication and function as a territorial advertisement and to attract partners for mating, with other communicatory functions being likely (Peters 1987, 1991; Sunquist and Sunquist 2002). Females, for example, may utter these calls when searching for their kittens when these go astray or are actually lost. The series of single calls may exhibit more or less regular temporal and intensity patterning, with considerable differences noted among the species. The equivalent intense mew/meow calls of domestic cats, familiar to most people, are somewhat similar to those of the *Felis silvestris* subspecies studied here.

This study specifically evaluates the spectral characteristics of intense mew calls in the six different taxa within the concept of a general “frequency scaling rule” for acoustic signals in vertebrates, as expanded and quantified by Fletcher (2004, 2007), and within the framework of the acoustic adaptation hypothesis (Daniel and Blumstein 1998; Kime et al. 2000; Saunders and Slotow 2004; Boncoraglio and Saino 2007).

Materials and methods

Sound recordings

Sound recordings of intense mew calls in the following cat (sub)species of the genus *Felis*, all originating from adult individuals living in captivity, were collected for this study (see Table 1): sand cat (*F. margarita scheffeli*), European wildcat (*F. silvestris silvestris*), African wildcat (*F. s. lybica*), Asiatic steppe cat (*F. s. ornata*), black-footed cat (*F. nigripes*), and jungle cat (*F. chaus*). All cat individuals included in this study were either caught in the wild or were first-generation offspring of such captive animals. The only extant species of the genus *Felis* not included in this study was the Chinese desert cat (*F. bieti*), one of the least known of all Felidae (Sunquist and Sunquist 2002). However, according to the most recent genetic study (Driscoll et al. 2007), *bieti* is a subspecies of *Felis silvestris*. In accordance with Johnson et al. (2006), but in contrast to Wozencraft (2005), Pallas’ cat (*Otocolobus manul*) is not regarded as a member of the genus *Felis* here. Recordings were made at any opportunity and any time of the day whenever the animals called, and without human interference with the animals’ behavior. Because of the

unpredictability of calling behavior, many calling series could not be recorded completely. Most calls were recorded while the cats were alone with no other conspecific individuals in their enclosure (they were occasionally recorded, however, after the animals had been separated) and with no humans present in their immediate vicinity, but there was the opportunity to observe the calling animal from a distance. Measurements of the source amplitude levels of the calls are not available. The recordings were made with different equipment (for details see Table 1) at variable distances in indoor or outdoor enclosures, the microphone being either fixed onto a tripod or held by hand. All of the recording equipment used has a reasonably flat frequency response from approximately 150 to about 5,000 Hz; this adequately covers the frequency range of the cat vocalizations dealt with in this publication. For most of the recordings analyzed, the input level control was adjusted manually and was left in the same position (as much as possible) during the recording of one coherent call series; some recordings were made with ALC (automatic level control) (see Table 1). The study of meows of African wildcats (Nicastro 2004) was performed with different equipment, but it had largely the same technical specifications, making the results basically comparable.

Acoustic analyses

All acoustic analyses in this study are based on original recordings or first-generation copies of these; for details see Table 1. The original analog recordings/copies were digitized with ADOBE Audition[®] 1.5 software [sampling rate 22,050 Hz, 32 bit (float) depth, mono] and a Soundblaster Live! Wave sound board. The sampling rate chosen was sufficient to rule out the occurrence of aliasing; the frequency range of the intense mew calls of the cat species studied is <10 kHz. Special care was taken to avoid clipping. The files were saved in Windows[®] PCM (.wav) format. The sound recordings of *F. s. lybica* calls on the camcorder tapes were digitized in the same way using the recorder’s analog “audio out” socket.

Using the same software, we conducted a fast Fourier transform (FFT) (512 pt or 1,024 pt, Hanning window) of the calls and generated spectrograms and power spectra with a dynamic range of 80 dB in the frequency range from 0 to 8,000 Hz (or a lower upper limit if appropriate). The harmonics (=overtones)—the frequency bands with component frequencies which are integer multiples of the fundamental frequency F0 (=the lowest frequency in a harmonic series = the lowest frequency in a periodic waveform) in largely tonal calls—are termed the fundamental frequency, the first harmonic (=first overtone), second harmonic, third harmonic, etc. Subharmonics (cf. Wilden et al. 1998) at integer multiples of F0/2 are present

Table 1 Recordings analyzed of intense mew calls from (sub)species in the genus *Felis* (ID: tape number/counter readings from REVOX A77 where applicable); those made with ALC (automatic level control) are marked with an asterisk (*)

Taxon	Sex	n (ind)	Geographic origin of individual	Sound recorder	Microphone	Recording distance (m)	Rec. in-/ outdoors	ID of recordings analyzed	Recordist
<i>Felis chaus</i> Jungle cat	F	1	Unknown	UHER Report 4200 Stereo	SENNHEISER MD 421/2	~2.5	Out	ZFMK 87/000–198	Gustav Peters
	F	1	Unknown	UHER Report 4200 Stereo	SENNHEISER MD 421/2	~3	In	ZFMK 36/151–172, 525–533, 625–634	Gustav Peters
<i>Felis margarita scheffeli</i> Sand cat	M	1	Pakistan	UHER Report 4200 Stereo	SENNHEISER MD 421/2	~0.8–3	Out	ZFMK 34/000–1225	Gustav Peters
	M	1	Pakistan	REVOX F36	SENNHEISER MD 421	~1.5–2.5	In	BL XXXXIII cassette copy	Barbara Leyhausen
<i>Felis nigripes</i> Black-footed cat	M	1	South Africa	TELEFUNKEN Magnetophon 70	SENNHEISER MD 421	~3–5	In	BL II/480–510	Barbara Leyhausen
	M	1	South Africa	REVOX F36	SENNHEISER MD 421	~3–5	In	BL XV/220–245, 555–587	Barbara Leyhausen
<i>Felis silvestris silvestris</i> European wildcat	M	1	South Africa	REVOX F36	SENNHEISER MD 421	~3–5	In	BL X/830–990, cassette copies	Barbara Leyhausen
	F	1	South Africa	TELEFUNKEN Magnetophon 70	SENNHEISER MD 421	~3–5	In	BL VIR/88–120	Barbara Leyhausen
<i>Felis silvestris silvestris</i> European wildcat	M	1	Germany	SONY TC-D5 cassette recorder	SENNHEISER MKH 416	~10	Out	G. Wustig cassette copies	Gerd Wustig
	M	1	Switzerland	PHILIPS D6920 MK2 cassette recorder *	SONY	>10	Out	M. Hartmann cassette copies	Marianne Hartmann
<i>Felis silvestris lybica</i> African wildcat	F	1	Germany	TELEFUNKEN Magnetophon 70	SENNHEISER MD 421	~3–5	In	BL VGr/72–100, 220–235; BL VR/195–215	Barbara Leyhausen
	M	1	East Africa (?)	UHER Report 4200 Stereo	SENNHEISER MD 421/2	~3–5	In	ZFMK 33/816–895	Gustav Peters
<i>Felis silvestris ornata</i> Asiatic steppe cat	M	1	South Africa	PANASONIC NV-MX7 Camcorder *	PHILIPS SBC ME500	5–10	In	M. and J. Pfeleiderer Mini DV tapes	Mircea and Jörg Pfeleiderer
	F	1	South Africa	PANASONIC NV-MX7 Camcorder *	PHILIPS SBC ME500	5–10	In	M. and J. Pfeleiderer Mini DV tapes	Mircea and Jörg Pfeleiderer
<i>Felis silvestris ornata</i> Asiatic steppe cat	F	1	Pakistan	REVOX F36	SENNHEISER MD 421	~3–5	In	BL XXXII/400–440	Barbara Leyhausen
	M	1	Pakistan	REVOX F36	SENNHEISER MD 421	~3–5	In	BL XXXVI/274–328	Barbara Leyhausen
<i>Felis silvestris ornata</i> Asiatic steppe cat	M	1	Pakistan	REVOX F36	SENNHEISER MD 421	~3–5	In	BL XXXVI/400–440	Barbara Leyhausen

Recordings made by Barbara Leyhausen (BL) and Gustav Peters are in the animal sound archives of the Zoologisches Forschungsmuseum A. Koenig, Bonn (ZFMK); those of the other recordists listed are their own private property

in some calls of the (sub)species studied. The establishment of the presence of subharmonics in individual calls (and the corresponding identification of the frequency bands as the fundamental, harmonics or subharmonics) in a spectrogram was based on the occurrence of additional interposed overtones in the stack of overtones of the respective call (accompanied by a change in its perceived tone), and the verification of period doubling in the oscillogram simultaneous to these phenomena, compared with other portions of the same call where they are not seen.

The acoustic parameters of the calls were either obtained directly, as shown by the automatic measurement tools included in the analysis software, or by manually positioning the mouse cursor on the relevant structural feature and reading the measurement shown on the screen. The physical parameters analyzed are listed below. No editing, filtering, attenuation or amplification was applied when digitizing and analyzing the calls, or in the production of the spectrograms.

As the calls recorded with ALC do not have repeated large and abrupt changes in intensity, and their intensity flanks at the beginning and the end are not especially steep, they are included in the analyses. This presumes that the ALC attack, hold and release time characteristics ensure that intensity changes and differences within a call are largely recorded realistically.

Acoustic parameters measured

Those parameters marked with “§” were measured in spectrograms, those marked with “¶” in power spectra; for some parameters both types of analyses and oscillograms were checked. Because of the large dynamic range chosen for the analysis, both low-amplitude frequency components of the calls and “pure” noise can show up in the spectrograms. Special attention was paid to identifying both correctly. Frequencies that started to show up in the spectrograms upon increasing the dynamic range of the analysis, and which at the same time constituted a “matching completion” of the call’s structure displayed at a lower dynamic range analysis, were assigned to the call (e.g., additional higher harmonics, temporal extension of harmonics). Several frequency as well as time measurements are slightly affected by the subjective choice of the lower level cut-off limit between signal and noise to an extent that is very probably similar in all taxa studied.

D, duration (ms) §: time from onset of call to its end [in the calls recorded indoors, this measurement is less accurate than for calls recorded outdoors, because the end of a call cannot be determined as precisely due to echo, and therefore indoor call durations tend to be longer (see Table 1)].

Fundamental frequency F0 (kHz) §: F0s, frequency of F0 at start of call; F0e, frequency of F0 at end of call (for frequency measurements made at the end of calls recorded indoors, a similar qualification to that for measurements of call duration applies); F0l, lowest frequency of F0; F0h, highest frequency of F0; F0m, mean frequency of F0 (mean F0 averaged over the whole call duration; this parameter was measured with the sound analysis software PRAAT, version 4.2.34, developed by Paul Boersma and David Weenink and available at <http://www.praat.org>, because there is no such measurement function in ADOBE Audition; the digital sound files had to be resampled at 16 bit depth for the analysis in PRAAT).

(F0h – F0l)/F0m: a calculated measurement to describe the frequency modulation relative to the mean fundamental; the closer this quotient is to zero, the smaller the frequency modulation.

Dfr, dominant frequency (kHz) ¶: frequency with the maximum amplitude of the whole call, as determined by the relevant built-in function of the sound analysis software over the duration of the whole call.

Measurements of acoustic parameters are listed in Table 3. Because the mean F0 (F0m in the following) and the mean Dfr (mDfr in the following) are the parameters that are only marginally affected by different recording conditions and analysis settings, these two parameters will be discussed specifically in the following, but the other measurements are also presented because this information has not been published before. The same goes for the spectrograms and the power spectra shown in this publication, which depict one example of a call (two in the case of the sand cat) from each of the *Felis* (sub)species studied (Fig. 1a–f). These were produced with a sound spectrograph (MEDAV Spekto 3000, Uttenreuth, Germany), software version 4.4 (1996), using a Hanning window and 512-point FFTs (256 points in the sand cat) with 50% window overlap and a dynamic range of 55 dB in the frequency range appropriate for the respective species’ mew calls. The lower dynamic range was chosen here to reduce the reproduction of interfering echo, tape and background noise. Analysis settings used in PRAAT and on the MEDAV were chosen to match those in ADOBE Audition to the greatest possible extent. Frequency and time resolution varied according to the frequency ranges and time intervals analyzed, as well as the analysis settings in the different sound analysis software used, but were generally in the range of ≤ 40 Hz and ≤ 30 ms, respectively.

Call sampling, sample sizes and call structure variability

The selection of mews from the calling bouts recorded was based on call intensity; only intense calls were included in

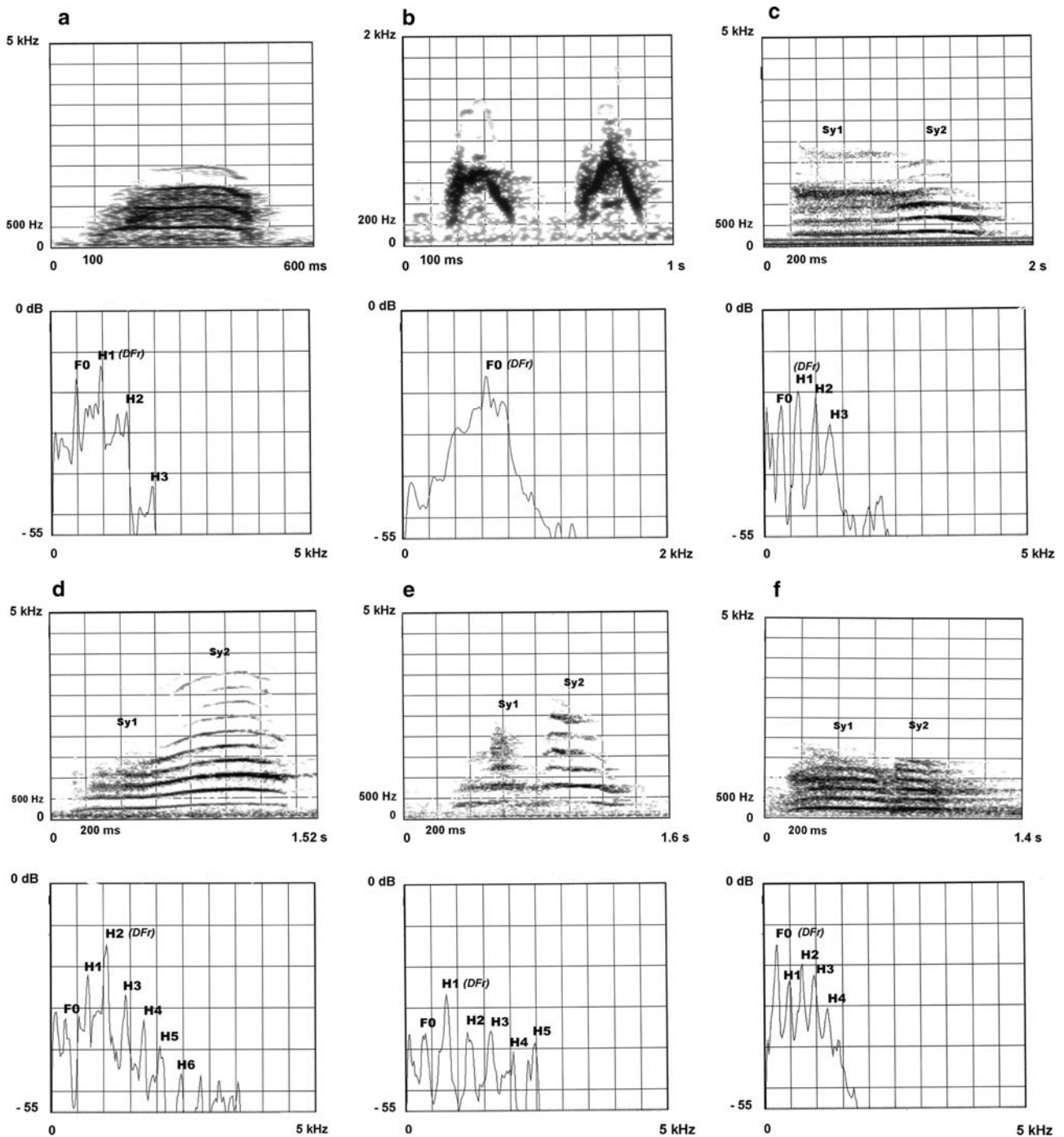


Fig. 1 One representative intense mew call (two calls in the sand cat) for each (sub)species of the genus *Felis* included in this study; a sound spectrogram (*top*) and a power spectrum, averaged over the whole call duration (*bottom*), showing the same call with identical analysis settings are shown in each case. To reduce the reproduction of interfering noise in the power spectra, we did not use the full dynamic analysis range shown for any of the calls. The frequency range (on *x*-axis) and the divisions of this axis in all power spectra are the same as in the accompanying sound spectrogram. Low-frequency background noise is present in all recordings (mainly <300 Hz). **a** Jungle cat (*Felis chaus*), ad. ♀. **b** Sand cat (*Felis margarita scheffeli*), ad. ♂ Compared to the other taxa studied, the largely harmonic structure in the power spectrum of the sand cat call is

almost concealed because of the considerable frequency modulation, the partial overlap between the frequencies of F0 and H1 (and subharmonics), and the presence of additional frequency components (see spectrogram) which are averaged over the whole call duration. **c** Black-footed cat (*Felis nigripes*), ad. ♂. **d** European wildcat (*Felis s. silvestris*), ad. ♂. **e** African wildcat (*Felis s. lybica*), ad. ♂. **f** Asiatic steppe cat (*Felis s. ornata*), ad. ♀. Some specific structural features of the calls of the respective taxa are addressed in the text. Structural details marked in **a–f** (where they apply) are: *DFr*, dominant frequency; *F0*, fundamental; *H1*, first harmonic; *H2*, second harmonic; *H3*, third harmonic; *H4*, fourth harmonic; *H5*, fifth harmonic; *Sy1*, first syllable; *Sy2*, second syllable

the analysis. Call sample sizes analyzed in the individual taxa are listed in Table 3. The number of individuals contributing to the call samples in the taxa analyzed in this study is small ($n = 2–4$), and two species are represented by one sex only. In the four taxa in which both sexes are represented, the respective call samples were analyzed separately. The sample of one sand cat's intense mew calls studied by Huang et al. (2002) is included in our present study. Our relevant structural measurements closely agree with those published by these authors (see Table 3), highlighting the relative structural stereotypy of these calls, and the fact that the outcome of the acoustic analyses is independent of the investigator as well as the hardware and sound analysis software used. In all taxa included in this study, the total range of intraspecific structural call variability is highly likely to be greater than that documented here. We proceed on the assumption that the frequency characteristics of the intense mew calls of all individuals analyzed in this study are within the typical range of variability of these characters in their respective taxons.

Body weights and cranial dimensions

Data on mean body weights and condylobasal lengths of the skulls (CBL, a linear measurement representative of body size) of the (sub)species studied were taken from various sources (see Table 2). Measurements are listed separately for the sexes. When the geographic origins of the individuals whose calls were analyzed were known, the measurements listed in Table 2 are from the same or a neighboring population, if available. Ideally, these measurements should be those for the same individuals upon whose calls the acoustic analyses are based, but this was not possible in any of the cases. The small sample sizes for a few taxa represent the general paucity of such data.

Phylogeny of the genus *Felis*

Based on the most recently published complete molecular phylogeny of the family Felidae (Johnson et al. 2006), within the genus *Felis*, the branching order of *F. chaus* and *F. nigripes* is uncertain, but they are definitely the basal taxa of the *Felis* lineage, and the subsequent node at the root of all the remaining species of the genus is well supported (Johnson et al. 2006). Accordingly, two species “groups” can be defined within this genus: a “basal group” including *F. chaus* and *F. nigripes*, and a more “derived group” including *F. margarita* and *F. silvestris* ssp. (and *F. bieti*, for which no recordings of calls were available for this study). In their analyses, Johnson et al. (2006) treated *F. silvestris* and *F. lybica* as separate species and included the domestic cat (*F. catus*) as another taxon, but did not consider *F. (s.) ornata*. This is irrelevant to the present

discussion, as all of the available evidence (Salles 1992; Yamaguchi et al. 2004) unequivocally places this last taxon together with *F. silvestris* and *F. lybica* in the same monophylum.

Statistical analyses

From the raw data, which included multiple measurements for individuals, we calculated means of all acoustic parameters listed in Table 3 for each individual (individual data). Using a two-way ANOVA, we tested whether the means of these acoustic parameters differed between taxa and sexes. To evaluate the influence of body weight/size, phylogeny and habitat on the spectral characteristics of intense mew calls, we concentrated on two acoustic parameters of major significance with regard to the “frequency scaling rule” and the acoustic adaptation hypothesis (AAH in the following): the dominant frequency DFr and the mean fundamental frequency F0m. From the individual data, we calculated mDFr and F0m for each sex of each taxon. F0m, mDFr, and mean body weight were log-transformed to improve the normality of the residuals resulting from linear models.

The influence of body weight on mDFr and F0m was tested using simple linear regression analyses. Since the body weight/size and the dominant and fundamental frequencies differed between the sexes of the same (sub)species (see Tables 2, 3), we treated the two sexes of one species as independent replicates in this analysis. Originally, we analyzed the effects of both body weight and CBL (as a proxy for body size; Fitch 2000) on mDFr and F0m. However, since the two body measurements are highly correlated ($r = 0.863$, $P = 0.001$, $n = 10$) in the taxa studied, and so they affect mDFr and F0m in a similar way, we continued the analyses with body weight only.

We analyzed whether mDFr and F0m of intense mew calls within the genus *Felis* are related to habitat type (open versus dense) and phylogenetic relationship (basal group versus derived group) using *t* tests. To avoid pseudoreplication, we used only data from one sex, i.e., males, for these analyses. For one species, *Felis chaus*, no sound recordings of intense mew calls of males were available. An analysis of the calls of all of the (sub)species considered in this study for which data on both sexes were available ($n = 4$) revealed that mDFr and F0m of male calls were on average 24% and 2.5% higher, respectively, than those of females. Consequently, we estimated mDFr and F0m of males of *Felis chaus* as $mDFr_{\text{male}} = mDFr_{\text{female}} + 0.24 \times mDFr_{\text{female}} = 0.94$ kHz, and $F0m_{\text{male}} = F0m_{\text{female}} + 0.025 \times F0m_{\text{female}} = 0.45$ kHz, respectively. We correlated body weight with habitat (open = 0, dense = 1) in order to estimate whether the effect of mean weight on mDFr and F0m could also be due to its co-correlation with habitat.

Table 2 Mean condylobasal length (CBL) of skulls and body weights of individuals from selected populations of the *Felis* (sub)species included in this study, with females and males of the different taxa listed separately

Taxon	Sex	n ^a	Specimens from	Mean CBL (mm)	References	Mean body weight (kg)	n ^a	Specimens from	References
<i>Felis chaus</i>	F	6	Israel	109.6	Mendelsohn and Yom-Tov (1999)	7.6	5	Israel	Mendelsohn and Yom-Tov (1999)
Jungle cat	M	10	Israel	115.9		10	18	Israel	
<i>Felis margarita</i>	F	5	Turkmenistan, Uzbekistan	83.9	Heptner and Sludskii (1992), Hemmer (1974b)	2.2	5	Turkmenistan, Uzbekistan	Heptner and Sludskii (1992), Schauenberg (1974)
Sand cat	M	3	Pakistan	88.9		3	3	Pakistan	
<i>Felis nigripes</i>	F	11	South Africa	70.4	B. Wilson (personal communication 2006)	1.3	5	South Africa	Sliwa (2004), B. Wilson (personal communication, 2006)
Black-footed cat	M	21	South Africa	74.8		1.8	12	South Africa	
<i>Felis s. silvestris</i>	F	8	Germany	87.0	Haltenorth (1953)	5.9	26	Germany	Haltenorth (1953)
European wildcat	M	9	Germany	92.8		7.1	69	Germany	
<i>Felis s. lybica</i>	F	28	Southern Africa	88.4	Smithers et al. (2005)	4	36	Southern Africa	Skinner and Smithers (1990)
African wildcat	M	25	Southern Africa	92.8		5	42	Southern Africa	
<i>F. s. ornata</i>	F	6	Pakistan, India	84.5	Haltenorth (1953)	2.7	11	Turkmenistan	Heptner and Sludskii (1992)
Asiatic steppe cat	M	11	Pakistan, India	86.9		3.9	18	Turkmenistan	

^a Number of individuals analyzed per species and sex

Table 3 Acoustic parameters of intense mew calls in the *Felis* (sub)species included in this study, with females and males of the different taxa listed separately

Taxon	Sex	Individuals (n)	Calls analyzed (n)	Acoustic parameters									
				D (ms) (mean) (range)	F0s (kHz) (mean) (range)	F0e (kHz) (mean) (range)	F0l (kHz) (mean) (range)	F0h (kHz) (mean) (range)	F0m (kHz) (mean) (range)	DfFr (kHz) (mean) (range)	(F0h – F0l)/F0m		
<i>Felis chaus</i>	♀	2	36	462 286–882	0.32 0.19–0.45	0.36 0.20–0.57	0.28 0.20–0.38	0.49 0.39–0.57	0.440 0.37–0.49	0.76 0.39–1.08	0.487		
<i>Felis margarita</i>	♂	2	119	275	0.36	0.37	0.33	0.71	0.58	0.63	0.65		
<i>Felis nigripes</i>	♀	1	13	160–490 1456	0.15–0.53 0.33	0.16–0.52 0.35	0.15–0.50 0.33	0.49–0.84 0.38	0.41–0.68 0.33	0.41–0.78 0.54	0.15		
	♂	3	91	1155–1644 1378	0.31–0.38 0.29	0.34–0.36 0.30	0.31–0.35 0.29	0.36–0.40 0.34	0.32–0.35 0.31	0.35–0.69 0.69	0.17		
<i>Felis s. silvestris</i>	♀	1	30	830–4059 1016	0.25–0.37 0.27	0.28–0.40 0.32	0.24–0.37 0.27	0.27–0.40 0.44	0.25–0.38 0.37	0.29–1.21 1.25	0.48		
	♂	2	25	797–1344 989	0.18–0.36 0.24	0.23–0.42 0.28	0.18–0.34 0.23	0.34–0.49 0.35	0.31–0.40 0.30	0.69–1.68 1.28	0.38		
<i>Felis s. lybica</i>	♀	1	21	634–1288 1112	0.19–0.38 0.46	0.24–0.32 0.32	0.19–0.27 0.30	0.28–0.39 0.46	0.27–0.32 0.35	0.86–1.89 0.65	0.47		
	♂	2	73	838–1402 1242	0.42–0.54 0.32	0.28–0.36 0.32	0.28–0.33 0.297	0.42–0.54 0.414	0.33–0.39 0.362	0.60–0.69 0.754	0.32		
<i>Felis s. ornata</i>	♀	1	22	731–2317 1051	0.24–0.43 0.17	0.25–0.37 0.22	0.24–0.37 0.17	0.33–0.48 0.26	0.32–0.40 0.23	0.32–1.72 0.50	0.38		
	♂	2	40	850–1252 1077	0.15–0.21 0.26	0.20–0.26 0.26	0.15–0.21 0.24	0.23–0.30 0.28	0.20–0.26 0.26	0.22–0.95 0.76	0.15		
Two-way-ANOVA	Taxa			828–1695 ***	0.21–0.30 NS	0.24–0.30 NS	0.21–0.27 NS	0.26–0.31 ***	0.25–0.28 ***	0.60–0.95 **	*		
	Sex			NS	NS	NS	NS	*	NS	NS	NS		

Acoustic parameters and their abbreviations are defined in the “Materials and methods” section. Means are based on the individual data (see text). Also shown are results (*P* values) from two-way ANOVAs, one conducted for each acoustic parameter, that were done to test the differences between the means of acoustic parameters among taxa and sexes (NS, not significant [*P* > 0.05]; ***, *P* < 0.001; **, 0.001 ≤ *P* < 0.01; *, 0.01 ≤ *P* ≤ 0.05)

Finally, we evaluated different models for predicting mDFr and F0m using the Akaike Information Criterion (AIC) as the model evaluation criterion. Models were constructed from the predictor variables “habitat,” “phylogeny,” and “body weight.” Again, only the data set for male calls was used for these statistical analyses. For comparison, we repeated all of these analyses with the data for female calls. Since the results were very similar to those obtained for the calls of males, we do not mention them explicitly here.

For statistical analyses we used R 2.3.1 (<http://www.r-project.org/>) software.

Results and discussion

Intense mew calls in the genus *Felis*

The intense mew calls of each (sub)species studied here are perceived by human listeners to have a characteristic sound. In each taxon these calls are predominantly tonal, with sound spectrograms showing harmonics (cf. Fig. 1a–f). We found significant differences in several acoustic parameters among taxa and also among the sexes for one parameter (cf. Table 3). Intense mew calls of the sand cat are short (<0.5 s), sharp calls, of which several are usually uttered in rapid succession (Fig. 1b). Because of their short duration, syllabification and frequency modulation are barely audible; their pitch is medium-high. Earlier observers (Hemmer 1974a, b, 1977; Schauenberg 1974; Mendelssohn and Yom-Tov 1999) remarked that the auditory impression that the single calls and the series make on a human listener is more reminiscent of the barking of a small dog than a “proper” felid utterance. Leyhausen (1979) was the first to address the peculiar character of intense mew calls of black-footed cats specifically. Compared to the other *Felis* taxa studied, they are longer and impressively loud and low in pitch for a cat of its size. They sound somewhat raucous and clearly show two syllables; the emphasis is on the second syllable, which also has a slightly higher pitch (Fig. 1c) than the first. Usually the calls are uttered in a series, with single-call intensity increasing at the beginning of the series and, after a climactic portion, decreasing again towards its end. Preliminary observations on wild black-footed cats report that intense mew calls are mainly uttered by males during the mating season and occur in bouts of around ten (Olbricht and Sliwa 1997). Intense mew calls of the Asiatic steppe cat (Fig. 1f) are shorter than those of the black-footed cat, but they are a second example of a remarkably deep voice in a small cat. Tonkin and Kohler (1981) aptly described them as “... surprisingly deep notes uttered in two beats or syllables with the emphasis on the first ...”

These calls with little frequency modulation are usually produced in a series with fairly regular intervals between calls. Intense mew calls of the two other subspecies of *F. silvestris* included in this study, the European wildcat (Fig. 1d) and the African wildcat (Fig. 1e), are also usually uttered in series and likewise clearly reveal two syllables, the first more raucous, the second higher in pitch, more tonal and with a slight frequency modulation. Compared to those of the Asiatic steppe cat, their calls are similar in duration but somewhat higher in pitch. Intense mew calls in the jungle cat (Fig. 1a) are mostly short (<0.5 s) and usually uttered in a series. Because of their short duration, syllabification is barely discernible. Their sound is somewhat hoarse and shows a slight frequency modulation, with a higher pitch in the second half of the call.

Measurements of F0m and F0h for meows of African wildcats published by Nicastro (2004) are considerably lower than those obtained here for intense mew calls of this subspecies (cf. Table 3). Structurally, these calls belong to the mew/meow graded call system (Peters 1991), but meows in the Nicastro study were recorded in various behavioral contexts (“food-related,” “agonistic,” “vocal pacing”), of which the first two are fundamentally different from those in which intense mew calls occur. This is one likely reason for the lower F0 measurements; additionally, the presence of subharmonics may have caused measurement errors for F0.

Adaptive selection on long-distance calls

Bradbury and Vehrencamp (1998, p. 138) stated that “sound signals optimized for long-range propagation in air should be as low in frequency as the sender can efficiently produce”, the major constraint being body size. A “simple frequency scaling rule” for vertebrate acoustic signals, as developed by Fletcher (2004, 2007), states that the adaptively determined frequency “should be proportional to $M^{-0.4}$,” where M is the body mass of the sender. Constraints arise from the acoustics of the vocal tract that favor particular frequency regions (formants), as determined by vocal-tract length, cross-sectional area and shape (Fant 1960; Fitch 1997, 2000; Riede and Fitch 1999; Riede et al. 2005). This idea and related structural data led to the prediction that formant frequencies decrease with body mass as $M^{-0.33}$, as also predicted by the simple linear scaling of frequency with body length (Fletcher 2004).

Mechanisms that are suggested in the literature to have probably also played a role in the adaptive modification of acoustic call parameters during evolution are, among others: (1) adaptive selection for the composition and structure of the frequency spectrum in the calls of a species that yield the maximum communication distance in its habitat (Waser and Waser 1977; Brown 1989; Larom et al. 1997;

Mitani and Stuht 1998; Huang et al. 2002); (2) adaptive matching of a species' vocalization structures to acoustic properties of its habitat to produce calls that are distorted/degraded minimally over their propagation range in its habitat (Richards and Wiley 1980; Wiley and Richards 1982; Brown et al. 1995; Brown and Handford 1996, 2000). We tested the “frequency scaling rule” formulated by Fletcher (2004, 2007) with our data on F0m and mDFr of intense mew calls of the genus *Felis* used in long-distance communication, and used the results to explore hypothesis (1).

Scaling effect

In principle, the sizes of both the larynx and vocal folds (source) and the supralaryngeal vocal tract (filter), which affect the acoustics of a mammal species' vocal production, can be assumed to be correlated with its body size. Based on the source-filter theory of human vowel production (Fant 1960; Titze 1994), a scaling effect ought to exist in the frequency spectrum of human vocalizations. The “frequency scaling rule” for acoustic signals of animals is well documented for vocalizations of different vertebrate groups (Ryan and Kime 2003; Fletcher 2004, 2007). In mammals, this correlation was tested and corroborated for various frequency parameters, such as mean fundamental frequency F0 (Zimmermann 1995; Tembrock 1996; Pfefferle and Fischer 2006), dominant frequency (the frequency with maximum amplitude in the spectrum of a vocalization) (Nikolskij 1984; Jones 1996, 1999; Fletcher 2004, 2007), frequency bandwidth/range (Hauser 1993, 1996), mean repertoire frequency (Hauser 1993), and formants (vocal tract resonance frequencies) (Fitch 1997; Riede and Fitch 1999). There are, however, a few published examples of vocalizations in mammals and in other vertebrate groups for which certain pertinent frequency parameters tested are not negatively correlated with body size/weight, in both intraspecific (Masataka 1994; Riede and Fitch 1999; Rendall et al. 2005) as well as interspecific comparisons (Hauser 1993, 1996; Zimmermann 1995; Laiolo and Rolando 2003).

Fitch (1997, 2000) set out the correlation between body size and formants in detail, and termed it “acoustic allometry.” Fitch (1997, 2000) and Fitch and Hauser (2003) provided detailed arguments that vocal tract resonance frequencies (formants)—in particular formant dispersion, a measure of the average difference (Hz) between successive formants introduced by Fitch (1997)—are the structural features of mammalian vocalizations that are most likely to correlate directly with body size/weight; much more so than fundamental frequency. Because of the largely tonal structures of most of the intense mew calls of the felid (sub)species included in this study, LPC formant

analysis does not produce definite, unambiguous results; therefore, formant dispersion was not calculated for these (sub)species. The dominant frequency (DFr) in this study is defined as the maximum spectral energy peak of a call. If it is in a harmonic above the fundamental, it “can provide strong, preliminary evidence about the vocal tract transfer function” (Owren and Bernacki 1998), i.e., the filter. In a considerable proportion of the calls analyzed for the taxa studied here, DFr can be in a harmonic, with the sand cat being an exception, as the dominant frequency is generally in the fundamental in its calls. If DFr is in the fundamental, this primarily reflects the spectrum of the source signal. It could also include an incident of “formant tuning”—the coincidence of the first formant and the fundamental (Titze 1994). This is highly unlikely, however, for the following reason. As a first approximation, formant frequencies can be calculated in relation to vocal tract length (VTL) (Titze 1994, p. 143). The only measurement of VTL available in a taxon included in this study is 7.5 cm for an adult *F. nigripes*. Using this value, the relevant equation results in the first formant occurring at about 1,170 Hz, approximately one octave above F0m in this species (cf. Table 3).

There are four published examples of mammals (three primates, one phocid seal) in which specific frequency parameters of the vocalizations of the respective taxa are not inversely correlated with body weight: mean fundamental frequency of long-distance calls in 17 species of nocturnal prosimians (Zimmermann 1995, p. 52, Fig. 4; no statistically significant correlation) and in the Lorisidae (four species out of this sample; Zimmermann 1995, p. 53, Fig. 6; positive correlation but not statistically significant), lowest and highest frequencies in the acoustic signal repertoires of seven species of the genus *Macaca* (Hauser 1993, p. 535, Fig. 4), and mean frequency and frequency at peak amplitude (=DFr) of female harbor seal pup calls during ontogenetic growth (Khan et al. 2006).

A linear regression of mDFr (log-transformed) of intense mew calls in the genus *Felis* on the taxa's average body weight (log-transformed) clearly shows that the inverse relationship of the “frequency scaling rule” postulated by Fletcher (2004, 2007) does not hold. Indeed, the larger taxa have higher mDFr values than the smaller ones, i.e., mDFr is significantly positively correlated with body weight (Fig. 2a).

To the best of our knowledge, this is the first documented case in mammals for which the inverse correlation between body weight and dominant frequency (“frequency scaling rule”) not only does not apply in an interspecific comparison but where a statistically significant positive correlation can be shown to exist between these two parameters. This raises the question of the possible evolutionary causes of this peculiar situation in the *Felis* taxa studied here.

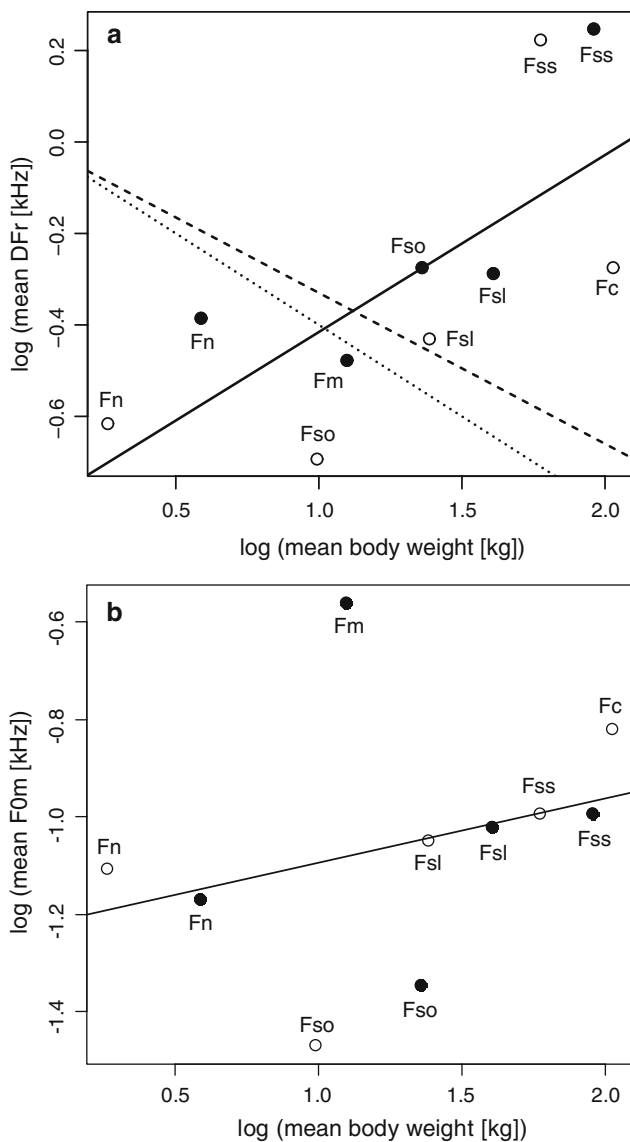


Fig. 2 **a** Correlation between mean dominant frequency (DFr) of intense mew calls and mean body weight for males (black dots) and females (open circles) of six *Felis* (sub)species ($R^2 = 0.51$, $F_{(1,8)} = 8.35$, $P = 0.02$). The power relationships for the correlation between body mass M and the dominant frequency of vocalization in birds and mammals published by Fletcher (2004, 2007) are also included (lower dotted line: $M^{-0.4}$; upper dotted line: $M^{-0.33}$). **b** Correlation between mean fundamental frequency (F0m) of intense mew calls and mean body weight for males (black dots) and females (open circles) of six *Felis* (sub)species ($R^2 = 0.09$, $F_{(1,8)} = 0.80$, $P = 0.40$). *Fc*, *Felis chaus*; *Fm*, *Felis margarita*; *Fn*, *Felis nigripes*; *Fss*, *Felis s. silvestris*; *Fsl*, *Felis s. lybica*; *Fso*, *Felis s. ornata*

Zimmermann (1995) stated that the deviation she found in the Lorisidae requires further investigation, Khan et al. (2006) presented no likely ultimate cause for their results in harbor seal pups, while Hauser (1993) suggested that habitat acoustics (i.e., the specific physical influence of the environmental conditions that prevail in a habitat type on the structural characters of the sound that propagates

through it) may have contributed to the fact that frequency parameters of the acoustic signals of some species in the genus *Macaca* are not inversely correlated with body weight.

Acoustic adaptation hypothesis (AAH)

According to the AAH, selection is likely to act on a species' long-distance acoustic signals to optimize transmission (to minimize their attenuation and degradation) in its natural habitat type (cf. Morton 1975; Waser and Waser 1977; Wallschläger 1981, 1985; Brown and Waser 1988; Wiley 1991; Brown and Gomez 1992; Brown et al. 1995; Daniel and Blumstein 1998; Slabbekoorn and Smith 2002; Ryan and Kime 2003; Saunders and Slotow 2004; Blumstein and Turner 2005; Boncoraglio and Saino 2007). Data on diverse vertebrate taxa support this hypothesis (Morton 1975; Gish and Morton 1981; Wallschläger 1980, 1982, 1985; Wallschläger and Nikolskij 1985; Masters 1991; Saunders and Slotow 2004; Slabbekoorn 2004; Seddon 2005; Nicholls and Goldizen 2006; Tubaro and Lijtmaer 2006), while in other taxa it is only supported weakly (Blumstein and Turner 2005; Boncoraglio and Saino 2007) or is not supported (Daniel and Blumstein 1998; Kime et al. 2000; Saunders and Slotow 2004). In all types of natural habitat, the height of the signal source and that of the receiver are important factors in acoustic communication (Kime et al. 2000; Slabbekoorn 2004), although the relative importance of the elevation above ground may be different for sender and receiver (Mathevon et al. 2005). In the (sub)species studied here, this aspect probably does not play a considerable role, as they usually call (and listen) while on the ground, although the taxa differ in terms of the heights of their heads above ground, and they all probably occasionally call from an elevated position. The type of ground surface also has an effect on frequency-dependent attenuation during sound propagation (Embleton 1996), being largely homogeneous and most distinctly defined in the case of *F. margarita*.

Four of the taxa studied (sand cat, black-footed cat, jungle cat, Asiatic steppe cat) are fairly stenoecious, whereas the European wildcat and the African wildcat occur in various habitats, with those of the former usually consisting of more dense vegetation while those of the latter are usually more open with scattered vegetation (Sunquist and Sunquist 2002). This habitat classification (dense vs. open) (Table 4) is coarse with regard to sound propagation conditions. Therefore, the AAH can only be addressed here in a more general manner with regard to signal attenuation (decrease of amplitude), not degradation [changes in temporal patterning of the signal's structure (Morton 1986)], when traveling through the species' habitat type. Degradation is also highly unlikely to play a role

Table 4 Habitat types of the *Felis* (sub)species included in this study, the type and extent of vegetative cover of each habitat type, and the classification (open vs. dense) of the habitat type with respect to the conditions for sound propagation

Taxon	Habitats and vegetation types	Vegetation density	Habitat classification with respect to the conditions for sound transmission	References
<i>Felis chaus</i> Jungle cat	Tall grasslands, thick brush, riverine swamps, reed beds	Dense	Dense	Sunquist and Sunquist (2002)
<i>Felis margarita</i> Sand cat	Sandy deserts	No vegetation or only very sparse	Open	Sunquist and Sunquist (2002)
<i>Felis nigripes</i> Black-footed cat	Open arid grasslands and scrub	Sparse, patchy	Open	Sunquist and Sunquist (2002), Smithers et al. (2005)
<i>Felis s. silvestris</i> European wildcat	Different types of forest and scrubland with clearings	Variable to dense	Dense	Sunquist and Sunquist (2002), Nowell and Jackson (1996)
<i>Felis s. lybica</i> African wildcat	Savannahs, grassland, steppes, woodlands	Sparse, patchy to variable	Open	Sunquist and Sunquist (2002), Smithers et al. (2005), Nowell and Jackson (1996)
<i>Felis s. ornata</i> Asiatic steppe cat	Scrub deserts, semi-deserts	Sparse, patchy	Open	Nowell and Jackson (1996), Roberts (1997)

in long-distance acoustic communication in the cat taxa studied. As they live in considerably different habitat types, selection for optimal sound propagation may have been one ultimate cause of the spectral characteristics of their long-distance calls.

In fact, we found that mean dominant frequencies of intense mew calls of the *Felis* (sub)species living in open habitat types are significantly lower than those of the taxa living in dense types ($t = 3.79$, $DF = 4$, $P = 0.02$) (see Fig. 3, Table 4). No significant differences were found when testing the influence of phylogeny on mDFr; taxa belonging to the basal group showed similar mDFr to the taxa belonging to the derived group ($t = -0.10$, $DF = 4$, $P = 0.92$). The variation in F0m is not significantly correlated with any of the predictor variables, i.e., weight (see Fig. 2b), habitat ($t = 0.49$, $DF = 4$, $P = 0.64$) or phylogenetic relationship ($t = -0.01$, $DF = 4$, $P = 0.99$). Our data suggest that the basis for the significant positive correlation between DFr and body weight (Fig. 2a) may be the fact that the heavier of the *Felis* taxa studied live in dense habitat types (Spearman rank correlation test: $r_s = -0.83$, $P = 0.04$, $n = 6$). We used the AIC to test whether our data best support models with body weight or those with habitat as the predictor variable. Phylogenetic constraints (basal species vs. derived species) were used as an additional predictor variable in these models. The best support is for the model of DFr dependency on habitat type and phylogeny ($AIC = -23.00$). However, neither the whole model nor the predictor variable of phylogeny was significant at the level of $P < 0.05$. The second-best model, which included only habitat as a predictor, received almost the same level of support ($AIC = -22.31$) (see Table 5a), and the whole model and the coefficient estimate were

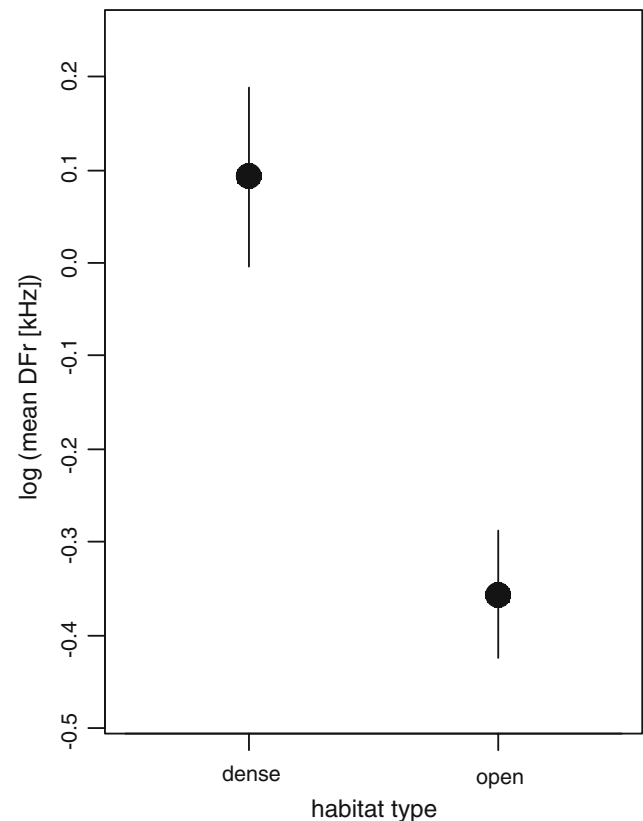


Fig. 3 Means \pm SE of the mean dominant frequencies (DFr) of intense mew calls of males of *Felis* (sub)species living in dense versus open habitat types. The differences between the habitat types are very similar for females. See Table 4 for descriptions and type classifications of the habitats of the taxa studied

significant at a level of $P < 0.05$. AIC support for models including body weight as a predictor was considerably lower ($\Delta AIC > 4.31$).

Table 5 Evaluation of different models explaining the variation in (a) mean dominant frequency (DFr) and (b) mean fundamental frequency (F0m) in the intense mew calls of the *Felis* taxa studied, based on Akaike’s Information Criterion (AIC)

Model	Significance level (<i>P</i>)				AIC
	Phylogeny	Habitat	Weight	Whole model	
(a)					
Null model	–	–	–	–	–15.16
DFr ~ phylogeny	0.92	–	–	0.92	–13.18
DFr ~ weight + phylogeny	0.98	–	0.15	0.30	–16.00
DFr ~ weight	–	–	0.17	0.17	–18.00
DFr ~ habitat	–	0.02	–	0.02	–22.31
DFr ~ habitat + phylogeny	0.28	0.02	–	0.052	–23.00
(b)					
Null model	–	–	–	–	–14.54
F0m ~ weight + phylogeny	0.99	–	0.71	0.92	–10.86
F0m ~ habitat + phylogeny	0.91	0.68	–	0.91	–10.94
F0m ~ phylogeny	0.99	–	–	0.99	–12.54
F0m ~ weight	–	–	0.67	0.67	–12.86
F0m ~ habitat	–	0.64	–	0.64	–12.91

Significance levels of model coefficients are listed in addition to AIC values

These results can best be interpreted as indicating that the evolution of mDFr of intense mew calls used for long-distance communication in the studied taxa of the genus *Felis* was shaped by the sound propagation conditions in their habitats, i.e., they provide strong support for the AAH. In contrast, for F0m, the null model was best supported by AIC, again indicating that this (response) variable cannot be explained well by any of the predictor variables used (Table 5b).

Fletcher (2004, 2007) expounded that for animals of a given taxonomic group, the maximum communication distance is proportional to the species’ body mass according to about $M^{0.6}$, i.e., intense calls of larger/heavier species carry over longer distances than those of smaller species. To the best of our knowledge there is no publication, though, in which this correlation is examined for a larger sample of mammalian taxa. Gould (1983, p. 284, Fig. 7) plotted distances at which mammalian loud calls can be heard by humans in relation to the species’ home range size; audibility and home range size only correlated well for some species. Information on average home range/territory size (many authors do not clearly distinguish between home range and territory) in the *Felis* (sub)species studied here is scant; the published data are listed in Table 6. Those for jungle cat and Asiatic steppe cat are very rough estimates only. Those for sand cat, black-footed cat, African wildcat, and European wildcat are based on tracking data of radio-collared individuals. Apart from being a possible effect of small sample size, the considerable differences in home range size found in the different studies [even within the same sex of a (sub)species] can have various causes which will not be discussed here.

As territorial spacing and attraction of partners for mating are the main communicatory functions of intense mew calls in felids, the maximal distance at which these can be heard by conspecifics in the respective cat species’ natural habitat type is an important aspect to consider in relation to its average home range size. With the exception of cheetahs (Caro 1994), the home ranges of felid males are generally larger than those of females and often overlap those of several females (Sunquist and Sunquist 2002). Therefore, the average distances that intense mew calls of males and females have to propagate to reach a conspecific receiver of the same or the opposite sex differ. Published information on direct observations in the wild of intense calling behavior and reactions of conspecific receivers to it is lacking for all taxa studied. Therefore, it is unknown whether the animals call from any position in their home range or (for example) mainly while they are in its peripheral area, and from how far away conspecific receivers can hear such calls (and react to them). Black-footed cat males were observed on several occasions to produce intense mew call series after they had sniffed urine marks of females at any position within their home range (A. Sliwa, personal communication).

The home range size of black-footed cat males seems to be roughly similar to that of European wildcat males (cf. Table 6), and the average weight of *F. s. silvestris* males is nearly four times that of *F. nigripes* males (cf. Table 2). Based on the correlation published by Fletcher (2004, 2007), this ought, in principle, to result in the loud calls of European wildcat males carrying more than twice as far as those of black-footed cat males. Yet, because of the sizes of the home ranges of males of the two taxa, their intense

Table 6 Home range sizes of males and females in the *Felis* (sub)species included in this study

Taxon	Sex	n (ind.)	Home range size (km ²)	Geographical area	References	Comments
<i>Felis chaus</i> Jungle cat	?	?	0.67–5 (range)	former USSR	Belousova (1993)	Very rough estimate only; lower values seem to be unrealistic
<i>Felis margarita</i> Sand cat	M	1	16*	Israel	Abbadi (1993)	
<i>Felis nigripes</i> Black-footed cat	M	5	16.1/20.7* (mean)	South Africa	Sliwa (2004)	Different sizes due to calculation method used
	F	7	8.6/10* (mean)	South Africa	Sliwa (2004)	
<i>Felis s. silvestris</i> European wildcat	M	4	4.7–10.9* (range)	France	Stahl et al. (1988)	
	M	3	16.6* (mean)	Germany	Wittmer (2001)	
	M	2	39.3* (mean)	Switzerland	Liberek (2002)	
	F	6	2* (mean)	France	Stahl et al. (1988)	
	F	2	3.6* (mean)	Switzerland	Liberek (2002)	
<i>Felis s. lybica</i> African wildcat	M	1	12.7*	Kalahari	Herbst and Mills (2005)	
	F	3	7.6* (mean)	Kalahari	Herbst and Mills (2005)	
<i>Felis s. ornata</i> Asiatic steppe cat	?	?	4	Tajikistan	Heptner and Sludskii (1992)	Rough estimate only

The quality of the published data for the individual taxa is very variable. An asterisk (*) denotes data based on tracking of radio-collared individuals

mew calls probably need to travel similar distances on average to reach a conspecific receiver of the same sex.

There are alternative (other than the AAH) or supplementary hypotheses about selective forces and constraints (cf. Forrest 1994) that may help to explain the evolution of the specific mDFr of the intense mew calls in some or all of the taxa studied. For example, sexual selection may have played a role in shaping them. In fact, for the four taxa for which calls of both sexes were available, we found that males (which are on average 32.1% heavier than females) generally had higher mDFr than females, even though differences were not significant (paired *t* test: $t = 2.75$, $DF = 3$, $P = 0.07$), probably due to the low sample size. Equally or alternatively, these frequencies may be adapted to a portion of the spectrum that is barely affected by prevailing environmental noise [both abiotic and biotic (to avoid acoustic interference with other species)] in their respective habitat type. Habitat types of the taxa studied certainly differ in type and level of ambient noise. Sugiura et al. (2006) even suggested a possible effect of learning in the acoustic adaptation of a specific call type found in different populations of Japanese macaques (*Macaca fuscata*). Based on present knowledge, there is, however, no tangible indication in any of these respects.

The crucial test of the hypothesis about the constraints of habitat acoustics on the evolution of the spectral frequency characteristics of the intense mew calls in the taxa studied would be playback tests, which would provide experimental proof that, during transmission through its habitat type over naturally occurring distances, the

respective (sub)species' loud calls propagate further than sounds of a similar general structure but which lack the decisive spectral characteristics. Such experiments would have to include measurements of, e.g., the sound level at the source, the average level of abiotic and biotic "noise" in the taxon's natural habitat, or temperature and moisture gradients of the air, to examine the possible effects of various other factors on the maximal communication range of the intense mew calls studied. Testing the sexual selection hypothesis would require checking whether a correlation exists between on the one hand (a) the choice of a potential mate calling and/or (b) differences in the reproductive successes of individuals calling, and spectral features of their intense mew calls used in long-distance communication to attract mates on the other. Such tests are beyond the scope of the present study, but would be an obvious subject for future research, as would be anatomical studies of the larynges and supralaryngeal vocal tracts of the taxa, in order to understand their influence on the structure of these calls.

Hearing capacity and frequency spectrum of intense mew calls in the genus *Felis*

The domestic cat is the only felid species for which published audiograms are available (Sokolovski 1973; Heffner and Heffner 1985); it has its high sensitivity in the range from about 0.5 to 15 kHz. As *Felis silvestris lybica* is the ancestor of the domestic cat, it seems fairly safe to assume that hearing of the *F. silvestris* subspecies included in this

study is similar to that of the domestic cat. Some differences, however, may exist in this respect, possibly due to the domestication process (Nicastro 2004).

The greatly enlarged auditory bullae in sand cats (as compared to those in other felid taxa of a similar size; Pocock 1951) are interpreted as being adaptive in improving low-frequency hearing below 2 kHz (Huang et al. 2002), since the frequency spectrum of this species' intense mew calls is also mainly restricted to this range. The auditory bullae of the black-footed cat are not as strongly inflated but are still proportionally larger and have a larger external acoustic meatus than those in the remaining species of the genus *Felis* (Pocock 1951; Huang et al. 2002). The frequency spectrum of black-footed cat intense mew calls is also largely restricted to the range below 2 kHz, and the species lives in open habitats. Irrespective of the fact that selection for auditory detection of prey or predator species very probably played a role in the evolution of hearing capacity in felids, co-evolution of improved hearing capacity in the lower frequency range and intense mew call spectral characteristics is also highly likely in the sand cat and black-footed cat. No equivalent morphological adaptations of the auditory system are obvious in the Asiatic steppe cat and African wildcat (Pocock 1951), the other taxa studied that live in more open habitat types.

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