

Perceptual and Acoustic Evidence for Species-Level Differences in Meow Vocalizations by Domestic Cats (*Felis catus*) and African Wild Cats (*Felis silvestris lybica*)

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To test for possible anthropogenic selection effects on meows in domestic felids, vocalizations by domestic cats (*Felis catus*) were compared with cries by their closest wild relative, the African wild cat (*Felis silvestris lybica*). Comparisons included analysis of acoustic characteristics and perceptual studies with human (*Homo sapiens*) listeners. The perceptual studies obtained human listener ratings of call pleasantness. Both the acoustic and perceptual comparisons revealed clear species-level differences: The domestic cat meows were significantly shorter in mean duration than the wild cat meows, showed higher mean formant frequencies, and exhibited higher mean fundamental frequencies. Human listeners at all levels of experience and affinity for cats rated domestic cat meows as far more pleasant sounding than wild cat vocalizations. These results are consistent with a model of cat domestication that posits selective pressure on meows based on human perceptual biases.

Domestication has been defined as “the capture and taming by man of wild animals of a species with particular behavioral characteristics, their removal from their natural living area and breeding community, and their maintenance under controlled breeding conditions for mutual benefits” (Bökönyi, 1989, p. 22, 1969; Bökönyi, 1989). A predictable consequence of reproductive isolation, founder effects, and controlled breeding has been that domesticated animals look and behave differently from their ancestors. These differences were widely appreciated at the dawn of evolutionary theory itself (Darwin, 1859/1993), and our understanding continues to develop (Clutton-Brock, 1989, 1999). In general, most domestic animals are held to have smaller brains on average than their wild counterparts, exhibit changes in superficial coloring, have less acute senses, and have higher thresholds against stress due to conspecific crowding and proximity to humans (Hemmer, 1990).

In addition to the physical and physiological changes associated with domestication, changes in communicative behavior (potentially including production, usage and/or reception; cf. Seyfarth & Cheney, 1997) seem probable. Cameron-Beaumont (1997) has considered what might be either the elaboration or the outright origination of the physical signal “tail up” in the domestic cat (*Felis catus*). Analogous changes in the vocal behavior of com-

panion animals have also been suggested, such as acoustic differences in dog barks correlated with behavioral contexts typical of dog–human interaction (Yin, 2002). Studies of social gaze in dogs have suggested canine capabilities of “reading” the posture, head position, and eyes of humans that compare favorably to those reported for chimpanzees (Hare & Tomasello, 1999) and even for 3-year-old children (Soproni, Miklósi, Topál, & Csányi, 2001). Controlled experiments involving dog–owner play communication have concluded that dogs can competently interpret certain intentional movements of humans (T. D. McKinley & Sambrook, 2000; Rooney, Bradshaw, & Robinson, 2001).

Vocal communication is an important dimension of cat–human interaction, in part because vocal communication is so important to human caretakers. The meow, in particular, seems to be associated with vocal communication to people. The meow is defined here as a quasiperiodic sound with at least one band of tonal energy enhanced by the resonant properties of the vocal tract. The call ranges between a fraction of a second to several seconds in duration. The pitch profile is generally arched, with resonance changes often reflected in formant shifts that give the call a diphthong-like vowel quality. Although all meows in this study were mainly periodic sounds, this call type very often includes atonal features (Wilden, Herzel, Peters, & Tembrock, 1998) and garnishments (trills or growls) that may serve to differentiate the calls perceptually.

Although meows are among the most common cat-to-human vocalizations (Bradshaw & Cameron-Beaumont, 2000), they are observed infrequently in cat-to-cat interactions (S. L. Brown, 1993). Animal rescue workers have noted that the meow is largely absent in unsocialized feral cats, appearing only on regular contact with human caretakers (Franklin, 2002; S. Greene, personal communication, April 25, 2002). Only a handful among the approximately 40 species in the family Felidae produce meow-type calls. These include *Felis silvestris silvestris* (European wild cat), *Caracal caracal* (caracal), *Leopardus wiedii* (margay), an unspecified member of the *Lynx* genus (reviewed in Bradshaw & Cameron-

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Beaumont, 2000), and *Felis silvestris lybica* (African wild cat), observed by Nicholas Nicastro. Although some undomesticated felids meow as juveniles, they rarely produce the call in adulthood (Cameron-Beaumont, 1997). The intense vocalization of adult African wild cats appears to be exceptional in this regard; unlike domestic cats, however, the wild cat meows observed for this study did not seem to be directed at humans, but at the general environment.

In a previous study, it was shown that cat meows can be made to sound very different to listeners merely by modulating a small number of acoustical qualities salient to humans (Nicastro, 2002; Nicastro, 2004). This was taken as circumstantial evidence that an existing call type in some wild felids has become adapted to human perceptual preferences. The question of whether anthropogenic factors have affected domestic cat vocalization may be approached more directly by comparing the vocal productions of the domestic cat and its closest wild relative, *Felis silvestris lybica* or African wild cat (Essop, Mda, Flamand, & Harley, 1997; Mattern & McLennan, 2000; Todd, 1978). In the current study, comparison is conducted both on an acoustical basis, by examining the sound signal, and on a perceptual basis, by analyzing affective responses by human listeners to domestic and wild cat meows. Significant acoustic differences between meows produced by the wild and domestic species would be consistent with an account of cat domestication that included changes in vocal behavior. Significant perceptual differences (e.g., listeners judging certain calls to be more pleasant sounding than others) suggest the basis on which anthropogenic selection acted, presumably by conferring advantages to certain cats. The later selective mechanism could, in principle, have operated whether caretakers explicitly chose to reward cats that communicated more effectively with humans or whether it conferred survival advantages on certain animals as incidental consequences of acoustic preferences.

The perceptual property of meows analyzed was pleasantness to humans. There were several reasons this quality was chosen. First, it is "ecologically valid" insofar as it reflects the typical course of human–domestic cat interaction, in which the domestic cat might attempt to manage human responses by sounding pleasant and/or approachable. Second, pleasantness is a quality recognizable enough to be easily understood and rated by all human participants. Although other possible choices (such as "positive valence") might have better reflected current psychological parlance, they would necessarily have required more extensive explanation to lay listeners, allowing correspondingly more room for interpretation between participants. Pleasantness was clear enough to all listeners to require no further elaboration.

In the experiment, participants were asked to listen to 96 recorded meows (48 by domestic and 48 by wild cats) and to rate how pleasant each call sounded. These results were then compared with results of acoustical analysis to determine whether the sound properties of the calls correlated with their perceived emotional quality.

Method

Participants

Participants were 26 adult human (*Homo sapiens*) listeners with varying familiarity with cats in general, but all were unfamiliar with the specific animals recorded. The participants included 14 women and 12 men, with a

mean age of 20.3 years ($SD = 3.01$). All participants took part in the experiments for extra credit in college courses.

Materials

Some of the methods outlined here were previously reported in Nicastro and Owren (2003). For that work, a corpus of 535 domestic cat (*Felis catus*) meows was recorded over a total of 36 hr of recording in the home environments of 12 adult cats (7 females and 5 males), including 2 sibling animals owned by Nicholas Nicastro. Other owners were all acquaintances of the author, and none of the other cats were related. Cats were all adults, but because some had been adopted from shelters as adults, precise ages were unknown for 6 of the animals. Of the remaining 6 cats, mean age was 6.83 years ($SD = 3.43$) and ranged from 2 to 13 years.

Calls from various contexts were recorded on an all-occurrences basis, with the microphone placed at the smallest distance from the cats that did not noticeably alter their behavior (~0.5–2.0 m). In all cases, within the first hour or so of recording, the owners reported their cats were behaving typically. Variable microphone distance necessarily adds an additional source of variability in amplitude of the recordings. This variation was controlled in stimulus preparation using the method described later.

Single meows were recorded from five behavioral contexts common to human–domestic cat interaction, including *food-related* (calls made prior to regular feeding); *agonistic* (calls made when the cats were antagonized by rough handling, including vigorous brushing, inverting, or unwanted petting by the owners); *affiliative* (calls made when the cats solicited affection from their owners); *obstacle* (calls made when cats solicited help to negotiate a barrier, such as a closed door or window in their home environments, with the owner not present and the recordist on the same side of the barrier as the cats); and *distress* (calls made when the cats were placed in an unfamiliar place—in all cases here, when the animals were placed in the recordist's car without the owners but with the recordist). The behavioral definitions of the calling contexts are presented in Table 1; calls were ascribed to each context only if the correlated behaviors were observed. Single calls are defined here as vocalizations given with no other calls for at least 5 s before or after. All animals gave at least some single calls.

Domestic cat recordings were made with a Sennheiser ME-88/K3U directional microphone (Sennheiser GmbH; Wedemark, Germany) and either a UHER 4200 Report Monitor (Uher Werke Munchen; Munich, Germany) or a Marantz PMD222 portable cassette recorder (Superscope Technologies, Aurora, IL). Calls were digitized at a 22.05 kHz sampling rate and examined and edited on a Silicon Graphics O2 workstation (SGI; Mountain View, CA) and Dell Dimension 2100 computer using PRAAT 4.014, Sound Analysis 2.08 (Tchernichovski, Nottebohm, Ho, Pesaran, & Mitra, 2000) and ESPS/waves+ 5.3 (Entropic Research, Washington, DC) acoustic-analysis software.

For comparison, a captive group of 12 adult African wild cats (*Felis silvestris lybica*) was recorded over 50 hr of observation at the National Zoological Gardens in Pretoria, South Africa in September–October 2001. The animals were housed singly, off-exhibit, in adjacent 15-m² wire cages with natural soil and plants at the front of each enclosure and individual concrete shelters in the back. Specimens were full-blooded wild cats, not wild cat/domestic crosses (Claudia Schra, personal communication, September 14, 2001). The captive group included 8 males and 4 females; average age was 4.71 years ($SD = 2.4$) and ranged from 1.0 to 9.5 years. Nine of the animals were reported to be captive born and parent reared, 2 were wild born and hand reared, and 1 was wild born and parent reared. (The Pretoria zoo captive population also included 4 kittens, age approximately 4 months, who did not produce meows and were not included in this study.) No particular habituation to author observation was necessary; the cats appeared to behave as they did with their regular human attendants virtually from the outset.

Four hundred sixty-five single meow-type calls were recorded during daylight hours on an all-occurrences basis, with the microphone placed just

Table 1
Behavioral Definitions of Vocal Production Contexts: Calls Assigned to Contexts Only When Listed Behaviors Observed

Species and context variable	Definition
Domestic cats	
Food-related	Cat orients toward owner and/or food; eyes open, looking alternately from owner to food; ears up; tail up.
Agonistic	Cat orients toward offending object (e.g., hand, hairbrush); spitting, growling; ears back; eyes wide open; tail down and mobile.
Affiliative	Cat orients toward owner; leg-rubbing; purring; eyes closed or half-open; tail up.
Obstacle	Cat orients toward obstacle (window, door); eyes open, looking alternately from owner to obstacle; tail up.
Distress	No specific orientation, with repetitive movement such as pacing; eyes wide open; ears up but slightly back; tail down and mobile.
Wild cats	
Food-related	Cat orients toward food; eyes open.
Agonistic	Cat orients toward offending object (e.g., human or cat on other side of fence); spitting, growling; ears back; eyes wide open; tail down and mobile.
Vocal-pacing	Cat vocalizes repeatedly toward nothing in particular while engaged in repetitive behavior, such as pacing or jumping up and down from cage furniture.

Note. Upper portion of the table is reprinted from "Classification of Domestic Cat (*Felis catus*) Vocalizations by Naive and Experienced Human Listeners," by N. Nicastro and M. J. Owren, 2003, *Journal of Comparative Psychology*, 117, p. 46. Copyright 2003 by the American Psychological Association.

outside the animals' cages. Microphone distance from the vocalizing cats varied from ~0.5 to 4.0 meters; distance from the subjects was adequate to retrieve usable recordings of both high- and low-intensity calls. Behavioral contexts included food-related (calls made prior to regular feeding); agonistic (meow-type calls made when the cats were antagonized by the presence of humans or by conspecifics, as evidenced by aggressive behavior such as ear-flattening, snarling, hissing, or slashing), and vocal-pacing (calls made during stereotyped pacing behavior often seen in captive felines). Although some affiliative calls were recorded from 1 wild born and hand-reared female, not enough calls were obtained from enough different cats for inclusion in the perceptual experiments. Approximately 300 additional calls were recorded as part of vocalizing bouts in the wild cats, but as with the domestics, only singly produced calls were used in this study. Single calls were defined using the same criterion as applied to the domestic cats.

Wild cat recordings were made with a Sennheiser MKH-70 directional microphone and HHB PDR-1000 digital tape recorder (HHB Communications, Simi Valley, CA). Calls were digitized at a 22.05 kHz sampling rate and examined and edited on a Dell Dimension 2100 computer using PRAAT 4.014 and Sound Analysis 2.08 software.

For each species a subset of calls was selected for presentation to human listeners. Several considerations went into call selection. First, this study focused on singly produced meows, not meows produced as part of calling bouts. Second, the presentation stimuli could not contain excessive background noise or the presence of telltale indications of behavioral context. Third, to reduce sampling bias, all individual cats and behavioral contexts for both species were evenly or nearly evenly represented in the presentation samples, necessarily leaving out many calls from the most intensely productive animals. Fourth, calls from unrelated wild cats were included to compensate for bias due to high degrees of relatedness among the zoo specimens. Fifth, to avoid comparison of nonequivalent behavioral contexts in contented domestic pets and captive zoo animals (cf. Hemmer, 1990, p. 81), all affiliative meows were dropped from the domestic cat call sample. Among the remaining contexts, the food-related and agonistic contexts were taken to be comparable in the two species, whereas vocal-pacing in the wild cats was roughly analogous to obstacle and distress in

the domestics, insofar as the cats gave such calls when they appeared to be distressed and were pacing the confines of their enclosures.

The final presentation sample included 48 calls from animals of each species, for a total of 96 stimuli per experimental session (see sample spectrograms in Figure 1). The sample included 8 domestic cat meows from each of 6 different cats in four distinct contexts (food, agonistic, obstacle, and distress); 2 of the domestic cats were related (siblings). The final wild cat sample included between 4 and 8 calls from each of 8 different cats in three distinct contexts (food, agonistic, and vocal-pacing); 4 of the wild cats were related (including 2 direct offspring of 1 male and another separated from him by one generation). Although absolute equivalence in numbers of calls from all individuals and in all contexts would have been preferred, the final samples necessarily retain some uneven representation because some cats did not vocalize or vocalized little in some contexts. Each context, however, was represented by no fewer than 4 different cats; in most cases, all cats in the species sample were represented in all context categories.

In procedures developed for a previous study (Nicastro & Owren, 2003), the experiment stimuli were prepared using custom sound format conversion software (B. Tice and T. Carrell, available at <http://hush.unl.edu/LabResources.html>), SpeechStation II (Sensimetrics; Cambridge, MA), and the ESPS/waves+ program. The stimuli began and ended with 100-ms silent segments, which helped reduce audible transients during playback. To equate the calls approximately for apparent loudness, stimuli were normalized by rescaling each waveform so its highest amplitude peak was set to the maximum representable value. During presentation, stimuli were mixed with a low-amplitude white noise and attenuated to a comfortable listening level. The background noise masked differences in recording-room tone between stimuli and ran continuously throughout each experimental session.

Design and Procedure

Participants were tested in groups of 1 to 5 individuals in a quiet room. Background data were collected before listening trials with a questionnaire. The participants used a 7-point scale to rate their experience and affinity

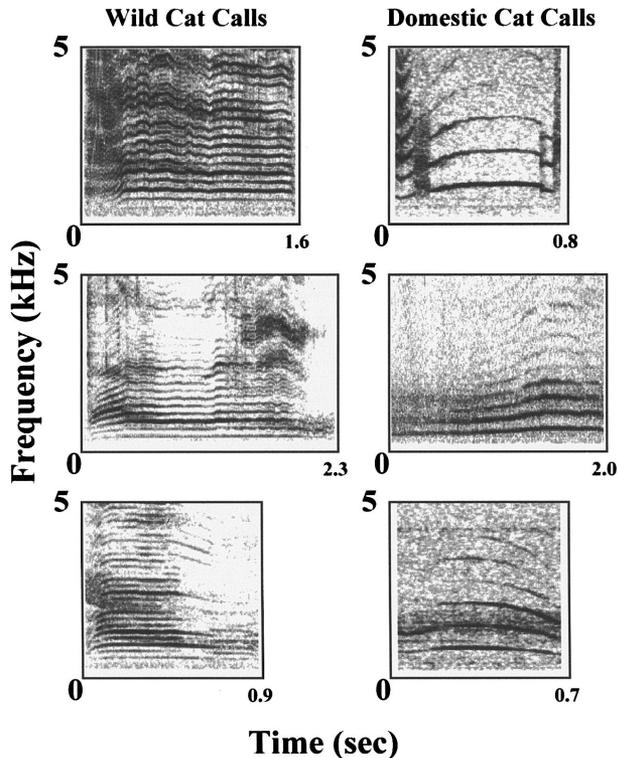


Figure 1. Narrow band spectrograms of three representative wild cat meow-type calls and three domestic cat meows. On the top row, from the left, wild cat and domestic cat food calls; middle row, wild cat and domestic cat agonistic calls; bottom row, a wild cat call given during vocal-pacing and a domestic cat obstacle call. Spectrograms generated using PRAAT 4.014 sound analysis software; 22.05 K sampling frequency; 0.029 ms window size; 90% overlap, no preemphasis.

with cats in three ways: how recently they had lived with a cat (residency: 1 = *never lived with a cat*, 7 = *currently live with a cat*), their estimated rate of interaction with all cats (interaction: 1 = *never interact with cats*, 7 = *interact several times a day*), and their affinity for cats in general (affinity: 1 = *very negative*, 7 = *very positive*).

In a randomized block, repeated-measures design, participants were asked to rate the pleasantness of the 96 stimuli on a scale from 1 (*least pleasant*) to 7 (*most pleasant*). The calls were presented in mono, one time each per session, using a Dell Inspiron 3000 notebook computer and JBL Pro multimedia speaker (JBL Professional, Northridge, CA). Playback of domestic and wild cat calls were randomized for species and presentation order between sessions. All participants were seated at a distance of 10 ft from the speaker.

Responses to the test stimuli were recorded on a standard paper form. The linear order of choices on the response form was alternated and counterbalanced between participants to control for possible positional biases. Randomizing the order of presentation between participants controlled potential bias in judgment of calls presented later in the sessions due to fatigue. Testing took 25–35 min.

The participants were told that “the purpose of this experiment is to understand what humans know about the vocalizations of cats.” They were not informed that the test stimuli included vocalizations from different contexts or from domestic and wild cats until the end of the experimental session. That participants were blind to inclusion of calls from two different species was essential to eliciting responses unbiased by expectations set by the experimenter. They were also instructed not to communicate with each other or to look at each other’s responses.

Data Analysis

Although this study attracted participants with a wide variety of experience with and affinities for cats, responses to the questionnaire were not evenly distributed across the experience and/or affinity levels. Some levels were not represented by any participants. In some cases, participants seemed to avoid marginal responses, such as extremely low-level affinity for cats. To avoid bias associated with levels represented by small numbers of respondents, the experimenter combined data from response categories with fewer than 3 participants with those from the next lowest categories for purposes of statistical comparison.

The 48 domestic and 48 wild cat calls in the perceptual study were analyzed using the nine acoustical measures listed and defined in Table 2. The sample presented here shows statistics (see Table 3) much like those reported for meows elsewhere (e.g., formant measures in Shipley, Carterette, & Buchwald, 1991; duration and fundamental frequency in Bradshaw, 1992).

The measures were selected to provide broad acoustic characterizations of the calls, in accord with conventional “source-filter” theory. In this model, vocalizations are understood to be the productions of a sound-energy producing mechanism (a source, here the vibrating vocal folds of the cat) transmitted through a vocal tract (a filter; cf. Borden, Harris, & Raphael, 1994; Fant, 1960; Johnson, 1997). Distinctive features of the calls may be attributed to both source- and filter-based acoustic parameters. Here mean F_0 , max F_0 , entropy, and frequency modulation characterize the behavior of the sound source, and spectral tilt, first formant, and second formant reflect the nature of the vocal tract filtering. Duration and continuity characterize the temporal structure of the call. Duration, entropy, frequency modulation, and continuity were derived using Sound Analysis 2.08 software routines (Tchernichovski et al., 2000). The other five measures were extracted using the PRAAT 4.041 package. Mean F_0 and max F_0 were determined using an autocorrelation method (To Pitch [cc]), supplemented by direct visual examination of narrow-band spectrograms and call waveforms; spectral tilt (Owren & Linker, 1995) was defined as the slope of the regression line drawn on the scatterplot of sound energy distribution versus frequency using the long-term average spectrum function; central frequencies of formants were identified at the temporal midpoint of each call using linear predictive coding (LPC) analysis (To LPC [autocorrelation]); see Table 2 for settings (Markel & Gray, 1976).

Multivariate analysis of the relationship of the acoustical properties to the perceptual measures was implemented using a stepwise multiple regression procedure (F to enter and to drop = 4; Darlington, 1990). Other statistical analyses included standard and repeated-measures analysis of variance (ANOVA), general linear model, one- and two-sample t tests, Anderson–Darling’s test for data normality, and multiple regression. Post hoc analysis was conducted using Tukey–Kramer’s method of pairwise comparisons and Bonferroni (all-pairwise) multiple-comparison tests. Analyses were implemented using MINITAB 12.2 (Minitab, State College, PA) and NCSS statistical software (Jerry Hintze, Kaysville, UT). An alpha value of .05 was used for all statistical tests.

Results

The mean pleasantness ratings were normally distributed (Anderson–Darling Normality test, $A^2 = 58.0$, $p < .001$). The mean rating for all stimuli (that is, including calls from both species and all contexts) was 3.51 ($SD = 1.79$), with a 95% confidence interval between 3.43 and 3.58, or significantly below the midpoint of 4 (one-sample $t[25] = -13.8$, $p < .001$).

A repeated-measures ANOVA showed no significant main effects on pleasantness rating for participant gender, $F(1, 24) = 3.3$, ns ; participant age, $F(5, 20) = 0.78$, ns ; or any significant interaction between these factors, $F(5, 14) = 1.66$, ns .

Table 2
Definitions of Acoustical Measures

Measure	Definition
Duration	Time (in s) from call onset to call offset.
Mean F ₀	Mean fundamental frequency (in Hz) of the sound source.
Max F ₀	Maximum fundamental frequency (in Hz) of the sound source.
First formant	Central frequency of the first filter-based resonance, measured at the temporal midpoint of the call, based on the linear predictive coding (LPC) spectrum (autocorrelation method, .025 second analysis width, 16 order, with preemphasis).
Second formant	Central frequency of the second filter-based resonance, measured at the temporal midpoint of the call, based on the LPC spectrum (see above for settings).
Spectral tilt	The slope of the regression line plotted against LPC-derived filter functions at 50% of the time course of the call. This measure reflects the degree of change in amplitude of spectral energy from low to high harmonics, with more highly negative tilt representing more acute attenuation through the higher frequencies. ^a
Frequency modulation	The slopes of frequency contours over the course of the call. Expressed as a ratio. Reflects how rapidly F ₀ and call harmonics change in time. ^b
Wiener entropy	A dimensionless measure of the degree of randomness of the sound spectrum, expressed on a logarithmic scale. Maximum entropy corresponds to complete disorder ($\log 1 = 0$) over the frequency range (Y-axis) of the spectrogram; minimum entropy to complete order ($\log 0 = \text{minus infinity}$). ^b
Continuity	A measure of the degree of contiguity or "brokenness" in call frequency contours over time, with maximum continuity set at 1 and minimum at 0. Essentially, another way to estimate the degree of order (entropy) in the sound signal, as measured in the X (time) axis. ^b

Note. For further information, see Borden, Harris, & Raphael (1994).

^aOwren & Linker (1995). ^bTchernichovski, Nottebohm, Ho, Pesaran, & Mitra (2000).

Mean participant affinity for cats was 5.23 ($SD = 1.53$); mean residency rating was 2.92 ($SD = 2.40$); mean frequency of interaction was 3.35 ($SD = 1.96$). None of the experience and/or affinity measures had a main effect on the pleasantness ratings (repeated measures ANOVA for affinity: $F[4, 21] = 0.16, ns$; for residency: $F[2, 23] = 0.44, ns$; for frequency of interaction with cats: $F[4, 21] = 0.30, ns$), and no interactions were indicated.

Mean pleasantness ratings for each context are listed in Table 4. Context of production had a significant effect on the pleasantness

ratings (repeated measures ANOVA: $F[6, 20] = 144.96, p < .001$). Species of the vocalizing animal also showed a significant main effect on the pleasantness rating, $F(1, 25) = 203.61, p < .001$, with domestic cat meows rated far more pleasant than those of wild cats (see Figure 2). The domestic cat meows were rated more pleasant than their wild cat counterparts in all contexts of production. Post hoc analysis (Tukey's pairwise comparisons) shows, for instance, that domestic cat meows produced in the agonistic context were rated significantly higher than wild cat

Table 3
Means (and Standard Errors) for Basic Acoustic Measures of Domestic and African Wild Cat Meows Used in the Perceptual Experiments

Acoustic measure	Domestic cat	Wild cat	Species effect ^a <i>p</i>
Duration (s)	0.84 (0.08)	1.50 (0.10)	***
Mean F ₀ (Hz)	609 (19.8)	255 (6.84)	***
Max F ₀ (Hz)	880 (45.6)	298 (7.92)	***
First formant (Hz)	1,458 (74.1)	1,055 (55.5)	***
Second formant (Hz)	3,053 (157)	2,395 (81.1)	**
Spectral tilt	-0.041 (0.001)	-0.055 (0.001)	***
Frequency modulation	20.3 (1.65)	24.1 (1.60)	<i>ns</i>
Wiener entropy	-3.99 (0.135)	-5.26 (0.098)	***
Continuity	0.91 (0.012)	0.88 (0.009)	.066

Note. Formant measures are for central frequencies. The *p* levels are for one-way analysis of variance for main effect of species on the acoustic measure. $\alpha = .05$.

** $p < .01$. *** $p < .001$.

^aSignificance levels for tests that approached significance are listed numerically.

Table 4
Means and Standard Deviations for Pleasantness Ratings of Domestic and African Wild Cat Meows

Context	M	SD	Multiple comparisons
Domestic cats			
Distress	5.17	1.33	DAG, WVP, WF, WAG
Obstacle	4.84	1.29	DAG, WVP, WF, WAG
Food	4.72	1.35	DAG, WVP, WF, WAG
Agonistic (DAG)	3.57	1.58	WVP, WF, WAG
Species mean	4.58	0.90	
Wild cats			
Vocal pacing (WVP)	2.58	1.40	WAG
Food (WF)	2.58	1.33	WAG
Agonistic (WAG)	2.14	1.26	
Species mean	2.43	0.61	

Note. For each context, other contexts, if any, are listed that were rated as significantly less pleasant (Bonferroni [all-pairwise] Multiple Comparison Test).

agonistic meows, as were the context-matched food meows. Bonferroni (all-pairwise) multiple-comparison concurs that domestic meows were rated more highly pleasant than wild cat meows for all contexts (see Table 4).

Separate analysis of the wild cat calls showed no main effect of circumstances of birth (wild born or captive born; $F[1, 45] = 0.01, ns$) or of rearing (parent reared or hand reared; $F[1, 45] = 0.24, ns$) on mean pleasantness ratings of the calls, though sample sizes were admittedly quite small for some of the rearing categories.

As shown in Table 4, the highest mean pleasantness rating of domestic cat meows was for those produced in the distress context. This outcome replicates results from a previous study with domestic cat meows only (Nicastro, 2002; Nicastro, 2004). The Bonferroni (all-pairwise) multiple-comparison test indicated that distress was rated as significantly more pleasant than agonistic in the domestic cats and meows from all contexts produced by the wild cats.

Stepwise multiple regression of all acoustic measures on mean pleasantness ratings for all 96 calls in the experiment returned an optimal two-factor model of acoustic predictors of pleasantness, explaining more than 80% of the variance ($R^2 = .804, p < .001$). The significant factors were mean F_0 (partial $R = .857, p < .001$) and duration (partial $R = .264, p < .001$). Mean F_0 was positively correlated with the pleasantness ratings, and duration was negatively correlated. That is, short duration calls with high mean F_0 tended to be rated more pleasant. Adding the other seven acoustical predictors to the model only marginally increased the correlation.

It is plausible that participants who live with or like cats tend to find cats' behavior, including their vocalizations, more pleasant than do those that do not. The lack of main effects of any of the experience and/or affinity factors on the pleasantness ratings therefore came as something of a surprise. It is possible that the effect of listening to recorded (rather than live) meows has a disproportionately negative effect on experienced listeners. A simpler explanation might be that all participants had a tendency to normalize the range of their responses toward the midpoint, although they were not explicitly instructed to do so.

That domestic cat calls given in the distress context were rated most pleasant may also appear surprising. To account for this, it must be remembered that participants were judging disembodied, recorded auditory stimuli only and were not exposed to the full range of contextual information (e.g., physical behaviors of the vocalizing animals). Under the experimental conditions, participants could have responded only to the intensely supplicatory tone of distress calls and could not know that the vocalizing context was accompanied by physical indications of fear or discomfort.

There are a number of alternative explanations of the observed difference between domestic and wild cat vocalizations that do not posit adaptive changes during cat domestication. Most obviously, it might be suggested that the calls differ because African wild cats are not the closest wild relatives of the domestic cat. This objection, however, runs counter to the emerging consensus among taxonomists, based on accumulating genetic evidence that domestic cats are descended primarily from the African variant of *Felis silvestris*, with little contribution from European or Asian popula-

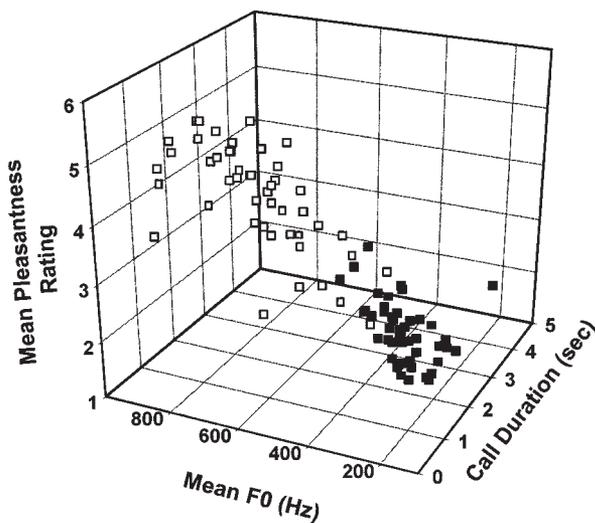


Figure 2. 3D scatterplot of mean pleasantness ratings versus mean F_0 and durations for all 96 calls in the perceptual experiment. Open squares represent domestic cat meows; darkened squares represent wild cat meows.

tions (Essop et al., 1997; Mattern & McLennan, 2000; Todd, 1978).

Sharply higher fundamental frequencies for domestic cats might be taken as a consequence not of direct selection on voice quality but of smaller body size. Smaller cats tend to have smaller vocal folds, which tend to vibrate at higher rates during phonation (cf. human male voices vs. female voices, or adult voices vs. child voices). Although African wild cats are commonly described as somewhat larger than domestic cats, there is in fact great overlap in body sizes in the two species. Up-to-date statistics on body mass and length were not available for the zoo specimens, as regulations forbade unnecessary handling or contact, but weight for the species is usually reported in the 2.4–5.5-kg range for females and in the 3.8–6.4-kg range for males (e.g., Apps, 2000). The sample of domestic cats, meanwhile, included 2 males that were clearly larger than most of the wild cats (approximately 6–7 kg), yet who showed fundamental frequencies right in line with the smaller-bodied domestics (525 and 533 Hz, respectively, or more than twice the mean frequency of the wild cats). In short, any residual difference in mean body size seems inadequate to explain the more than twofold difference in mean F_0 between the species. Moreover, selection on body size cannot explain other demonstrated acoustic differences, such as call duration.

It might also be suggested that calls of two different types are compared in this study—that is, that the wild cat calls used here are somehow not homologous to domestic cat meows. Indeed, attempts to limn the full repertoire of domestic cat vocalizations have been challenged by the daunting degree of their variation, with a number of specialists differentiating the range of calls produced into taxonomies of subtly differing types, variously characterized by acoustic, articulatory, phonetic, or behavioral criteria (e.g., Bradshaw & Cameron-Beaumont, 2000; K. A. Brown, Buchwald, Johnson, & Mikolich, 1978; P. E. McKinley, 1982; Moelk, 1944). Oddly, whereas the highly variable meow call is difficult to define acoustically, it is recognized readily by most humans (P. E. McKinley, 1982). Both the domestic and wild cat vocalizations used here fulfill the broad criteria for the meow, as defined previously (that is, a quasiperiodic sound with at least one band of tonal energy enhanced by the resonant properties of the vocal tract, durations between a fraction of a second to several seconds, a generally arched pitch profile, and formant shifts that yield a diphthong-like vowel quality). According to postsession interviews, none of the participants in the perceptual experiment heard the test stimuli as anything other than meows, *sensu lato*.

As many meow subtypes are defined in terms of behavioral context, it is worth considering the potential problem that the contexts analyzed here are not comparable. Indeed, this is a serious pitfall of comparison of wild and domestic animal behavior in general (Hemmer, 1990). All affiliative calls were eliminated from the domestic cat subset because the contexts hardly exist among unsocialized, captive felines. Beyond this, it is difficult to imagine what contexts could be more comparable between the species than vocalizing during feeding (food) and vocalizing during aggressive encounters (agonistic).

It is conceivable, however, that the equivalence of vocal-pacing in wild cats to obstacle and distress calls in domestics is incorrect. To check for the significance of this possibility, I compared acoustical measures of only the food and agonistic calls of the two species, eliminating vocal-pacing and obstacle and distress in the

wild cats and domestics, respectively. The pattern of differences between the species was largely unaffected: Mean pleasantness ratings for wild cats ($M = 2.36$) and domestics ($M = 4.14$) are significantly different (two sample $t[54] = -8.28$, $p < .001$); ANOVA for the main effect of species was significant for duration, mean F_0 , max F_0 , Wiener entropy, and spectral tilt and nonsignificant for frequency modulation and continuity (results Bonferroni corrected for multiple tests; cf. Table 3). Analysis of the reduced dataset differed only in that, in contrast to results with the full dataset, there was no species effect on the positions of first formant ($F[1, 55] < 0.001$, *ns*) and second formant ($F[1, 55] = 0.08$, *ns*). The mean frequency locations of these formants appear to be much higher for food and agonistic (first formant central frequency, $X = 1,466$ Hz; second formant, $X = 3,119$ Hz). Overall, however, the species differences in the acoustic measures appear to be robust, following much the same pattern with or without the vocal-pacing and obstacle and distress.

Could the human listeners have rated the domestic cat meows more pleasant simply because they were more familiar with them? If this were the case, we would predict that listeners with more experience and/or affinity for cats would exhibit more of a familiarity effect than listeners naive to cats. Yet there appeared to be no main or interaction effect involving any of the experience and affinity measures and the pleasantness ratings for either species' vocalizations (see previous results). In other words, listeners who were more experienced or partial to domestic cats were not more apt to rate domestic cat meows as more pleasant.

Perhaps these results are due to domestic cats having learned over the course of their development which of their calls appeal to humans, whereas their wild counterparts have not. A process of communicative negotiation over "meanings" has indeed been suggested by Tomasello and Call (1997) under the term *ontogenetic ritualization*. However, the latter process refers primarily to ritualization of signals between human or animal dyads, not to ritualization of signals to all members of the receiver species. In the perceptual studies reported here, participants who were wholly unfamiliar with the vocalizing cats rated meow calls. No ontogenetic ritualization was possible between cats and humans who were not familiar with them.

It also bears noting that, unlike in songbirds (e.g., Kroodsma, 1982), the existence of socially mediated vocal learning in mammalian species has been only sparsely documented, even in primates (Janik & Slater, 1997; Snowdon, Elowson, & Roush, 1997). In this sense, the vocal learning explanation for these results is even less supported by existing empirical data than is the notion that vocal behavior evolves because of natural selection.

Nevertheless, it is possible that cats learn to meow for their owners, and their learning generalizes to all humans because of acoustic sensitivities and preferences that all humans share (Turner, 2000). However, the question then arises as to why the African wild cats in the Pretoria Zoo collection, which in most cases were amply exposed to humans over the course of their entire lives, do not likewise learn which of their calls "work" with people. The wild cats seem either unable or unwilling to learn. Ultimately, differing explanations of the species difference that are rooted in adaptation and vocal learning may complement each other. The putative adaptation may lie exactly in rendering domestic cats more able or motivated to learn to adjust their cries for human ears.

Finally, the species differences between domestic and wild cat calls might also be attributed to the inclusion of calls from a potentially anomalous set of related wild cats. One way to eliminate this possibility is to divide the wild cat dataset into one subset for interrelated cats and another for unrelated animals and to compare the subset of wholly unrelated wild cats to the data from the domestic animals. The pattern of results from this analysis is almost exactly the same as it is for the comparison with the full set of wild cat calls listed in Table 3. The only difference was that the unrelated wild cats had a somewhat higher second formant (central frequency $X = 2,501$ Hz), leading to a significant main effect for species (one-way ANOVA: $F[1, 73] = 5.46$) at the $p = .022$ level (vs. $p < .01$ for the full wild cat set vs. domestics). This outcome suggests, therefore, that the species differences observed in this study cannot be attributed to descent-related bias in the wild cat acoustic measures. Overall, these results remain consistent with behavior change based on anthropogenic selection associated with domestication.

Discussion

To test for changes in vocal behavior due to domestication, meow calls from domestic cats and their immediate ancestors, African wild cats, were compared both perceptually and acoustically. In controlled listening conditions, and blind to the inclusion of calls from two different cat species in the test stimuli, human listeners judged domestic cat meows to be significantly more pleasant sounding than wild cat calls given in comparable contexts. The most significant acoustic correlates of the perceptual results were mean F_0 and duration of the calls.

These results lend support to the hypothesis that domestic cat meows have become better designed to exploit the auditory sensitivities of human receivers (cf. Dawkins & Guilford, 1997; Ryan, 1998; Ryan & Rand, 1990, for relevant discussion of other species). Human auditory sensitivities relevant to the results reported here are well established. Perception of differences or changes in voice pitch, for instance, has long been implicated in a host of functions in speech processing, from recognizing indexical cues to speaker identity to processing of suprasegmental features of spoken language, such as stress (Fry, 1958). According to motivation-structural rules promulgated by Morton, higher voice pitch is commonly associated with small-bodied, young, or otherwise non-threatening vocalizers (reviewed in Owings & Morton, 1998). Judgment of pitch of complex tonal sounds, in turn, typically depends on the fundamental frequency (reviewed in Borden et al., 1994). Humans are well endowed by evolution to track and respond to voice pitch. In the case of cats, domestics appear to produce higher pitched meows that sound less threatening, more juvenile, more appealing, and so forth to human ears relative to the deeper pitched wild cat calls.

Perception of duration appears to be established early in humans: Studies of mother–infant interaction have shown significant differences in utterance duration between interactional contexts (Fernald, 1992); there is some evidence that children pay particular attention to utterance durations to aid in speech segmentation (Kubaska & Keating, 1981). Duration has also been implicated in perception of voice stress (Fry, 1958). Feline vocalizations themselves have been explicitly suggested as good models for highly salient human vocalizations such as infant cry (Buchwald & Ship-

ley, 1985). The latter is widely thought to have some adaptive function, though there is disagreement over exactly what mechanism is involved for infant cry to affect caretakers (Murray, 1985). Overall, there is broad empirical support for the sensitivities in humans that may have shaped the evolution of pitch and duration of cat meows.

These results are also in broad agreement with findings of a study on acoustical differences in dog barks across behavioral contexts (Yin, 2002). In that study, acoustical measurements for call “dominant frequency” and “duration” in a sample of 4,627 barks from 10 different dogs were found to vary significantly with several contexts common to human–dog interaction (disturbance, isolation, and play). To be sure, the dominant frequency of a call is not necessarily equivalent to the fundamental frequency, and Yin (2002) did not do perceptual studies that might have shown, say, that low-frequency, long-duration disturbance barks she observed were perceived as less pleasant than higher frequency, short-duration play vocalizations. Still, it is suggestive that context-dependent differences in frequency and duration were found in barks, which, like meows, are commonly used with human companions.

The species-level differences between domestic and wild cat vocalizations reported here complement previous work on patterns of variation in cat meows. Studies using operant conditioning designs suggest that cats can learn to alter both the fundamental frequency of their meows and their duration (Molliver, 1963) as well as their call rate (Farley, Barlow, Netsell, & Chmelka, 1992). The latter outcomes suggest a considerable degree of plasticity in this behavior, producing a rate of variation on which anthropogenic selection may act.

It should be noted that the degree of anthropogenic selection pressure on cats likely differs from that on species such as dogs, goats, and horses, because cats do not show the same degree of dependence on human caretakers. Though cats have been kept as objects of cults, pest controllers, and pets for thousands of years, the species has been “drifting in and out of domestication, semi-domestication and feralness according to the particular ecological and cultural conditions prevailing at different times and locations” (Serpell, 2000, p. 181). There is little evidence for intentional breeding of cats until the advent of fancy breeds in relatively recent times. Yet systematic breeding of pleasant-sounding cats by humans would arguably not have been necessary to produce the differences reported here. Rather, humans may influence cat evolution simply by conferring incidental survival advantages on animals that appeal to them, such as those exhibiting effective vocal communication. This would necessarily raise the ratio of effective communicators in the freely interbreeding population. Given enough generations, even minor influences on differential reproductive success can have major cumulative effects.

Additional studies are necessary to refine and contextualize this work. It is probable, for instance, that call intensity has a significant effect on perceived pleasantness that is not reflected in the results. As all call stimuli were normalized to a single amplitude in the perceptual experiment, these studies neither confirm nor disprove the importance of call amplitude. In any case, apparent intensity of vocalizations is a function of a number of factors, including auditory acuity of the listener and distance from the vocalizer. These factors are not easily controlled under ecologically relevant behavioral contexts. Further work, involving accu-

rate measurement of call intensities during production and faithful reproduction during testing, would be necessary to establish the effect of intensity on the perceptual valence of the calls.

Indeed, although I have attempted to control for a number of confounding influences, experimental control is necessarily imperfect when comparing the behavior of pets and animals confined in zoos. For this reason, it is not yet possible entirely to discount other explanations of the species difference reported here, including heretofore unsuspected factors associated with differing housing and call collection conditions. Replication of these results with other captive and wild groups is therefore imperative.

As behavior does not fossilize, it is very difficult to provide conclusive proof of any adaptive story with respect to communication. Additional evidence is necessary to settle whether the perceived pleasantness of domestic cat meows was directly selected during domestication, a fortuitous side-effect of selection for other desirable traits, or some combination of these possibilities. Analysis of calls made by free-ranging wild cats, though logistically challenging, would be useful, provided that plausible objects of comparison between domestics and free wild cats can be determined. Although no meows were observed from wild cat kittens during this study, examination of the ontogeny of meow calls in both domestic and African wild cat kittens would help clarify the developmental course of the species difference in adults. In short, studies of this and other domestic species hold considerable potential to drive home the long underappreciated relevance of domestication to our thinking about the evolution of communication.

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