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### TO BARK OR NOT TO BARK: VOCALIZATIONS BY RED FOXES SELECTED FOR TAMENESS OR AGGRESSIVENESS TOWARD HUMANS

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#### ABSTRACT

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In this study we classify call structures and compare vocalizations toward humans by captive red foxes Vulpes vulpes, artificially selected for behaviour: 25 domesticated, or "Tame" animals, selected for tameness toward people, 25 "Aggressive" animals, selected for aggression toward people, and 25 "Unselected" control foxes, representing the "wild" model of vocal behaviour. In total, 12,964 calls were classified visually from spectrograms into five voiced (tonal) (whine, moo, cackle, growl and bark), and three unvoiced, or noisy (pant, snort and cough) call types. The classification results were verified with discriminant function analysis (DFA) and randomization. We found that the Aggressive and Unselected foxes produced the same call type sets toward humans, whereas the Tame foxes used distinctive vocalizations toward humans. The Tame and Aggressive foxes had significantly higher percentages of time spent vocalizing than the Unselected, in support of Cohen & Fox (1976) hypothesis that domestication relaxes the selection pressure for silence, still acting in wild canids. Unlike in dogs, the "domesticated" Tame foxes did not show hypertrophied barking toward humans, using instead the *cackle* and *pant*. We conclude that the use of a certain call type for communication between humans and canids is species-specific, and not is the direct effect of domestication per se.

Keywords: vocalization, domestication, vocal communication, nonlinear phenomena, articulation, red fox, *Vulpes vulpes*, Canidae

#### INTRODUCTION

Vocal behaviour of fox-like canids has been the subject of a longstanding research tradition, especially in relation to questions of systematics, structural variability, contexts of production for different

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call types, their functions and, most recently, species conservation. Studies reviewing vocal catalogues in Canidae, as a rule, demarcate between vocal repertoires of fox-like and wolf-like canids (Cohen & Fox 1976; Schassburger 1987). The structural variability and contexts of vocalizations were reported in wild red fox *Vulpes vulpes* by Newton-Fisher *et al.* (1993) and in captive swift fox *V. velox* by Darden & Dabelsteen (2006). Individual variability of serial barking in wild Arctic fox *Alopex lagopus* (Frommolt *et al.* 2003) and in captive swift foxes (Darden *et al.* 2003) were studied to determine call functions and the possible applicability of vocal identity to acoustic-based monitoring in the wild (Terry *et al.* 2005).

This study considers another problem, still little studied - the effects of captivity and domestication on vocalization. The few reports (Cohen & Fox 1976; Budde 1998; Monticelli & Ades 2001) provide little insight into the general processes that affect call structure during domestication. The domestic dog Canis familiaris, whose vocal behaviour is considered to be a result of domestication of its wild ancestor, the timber wolf Canis lupus, is not a good model for estimating the effects of domestication on vocalization. Because the domestic dog and the timber wolf have a long evolution as independent species (Tchernov & Valla 1997; Sablin & Khlopachev 2002); their vocal repertoires may have differed significantly already at an early stage of domestication. Therefore, the modern timber wolf may not represent an undomesticated "default" stage for vocal repertoire of the domestic dog. Ideally, to estimate the effects of domestication on vocalizations, domesticated and undomesticated individuals within a species should be compared.

A good model for such a within-species analysis comes from farm-bred red foxes, selected either for tame behaviour or for enhanced aggressiveness toward humans, in comparison with unselected controls (Belyaev 1979; Trut 1999; Gulevich et al. 2004; Trut et al. 2006). According to Belyaev (1979), directional selection simply for tame behaviour toward humans provoked the domestication, which has resulted in the evolution of the dog from the wolf. Testing of this hypothesis started in 1960, with the beginning of the directional artificial selection of farm foxes for positive attitudes toward people in Novosibirsk (Russia). Further, in 1970, directional selection of previously unselected foxes for enhanced aggressiveness toward people was started. Additionally, throughout these times, a population of foxes unselected for behaviour has been living on this farm (Trut 1999). The "Unselected" foxes show escape reaction toward people and keep a maximum possible distance apart from a human. Distinctive from the Unselected foxes, both "Tame" and "Aggressive" foxes are not afraid of humans; but the Tame foxes are positive to people, whereas the Aggressive foxes are negative to people. These behavioural differences between the Tame and Aggressive foxes are

genetically determined, as has been proven by cross-foster parenting and by embryo transplantation experiments (Trut 1980). The study of captive foxes differing in tameness may help to estimate both the quantitative and the qualitative shifts in vocal behaviour that have occurred under domestication. The control population of the Unselected foxes represents a "wild" model of vocal behaviour.

One particular question – of the hypertrophied barking of the dog in comparison with the wolf, may also be examined with the captive red fox population. Cohen & Fox (1976) proposed that hypertrophied barking in dog resulted from the relaxation of selection pressure for silence that still acts in the wolf. If so, we should expect that Tame foxes will have an enhanced barking rate compared with those unselected for tameness. Furthermore, with the captive fox population it is possible to determine whether Tame foxes will prefer barks to all other vocalizations or whether the relaxation of selection pressure for silence affects all vocal types equally. Another enigmatic question is whether hypertrophied barking in domestic dogs has evolved as a vocal response toward humans (Feddersen-Petersen 2000; Yin 2002). Do Tame foxes use any specific vocalizations toward humans compared to foxes not selected for tameness?

To answer these questions, we must determine the range of vocal diversity produced by red foxes in captivity, i.e., we need to describe the repertoire of their vocal structures. The existing descriptions of the vocal repertoire of the red fox (e.g., Cohen & Fox 1976; Tembrock 1976; Newton-Fisher *et al.* 1993) must be revised, because previous attempts based on limited sample sizes do not provide a detailed evaluation of vocal variability in captivity and do not consider fox vocalizations directed toward humans.

Furthermore, the revised catalogue of red fox vocalizations should include the analysis of nonlinear phenomena. Many canids produce nonlinear phenomena (e.g., Wilden *et al.* 1998; Riede *et al.* 2000; Volodin & Volodina 2002; Volodina *et al.* 2006a) that greatly enhance variability in call structure. Such nonlinear phenomena as subharmonics, deterministic chaos and frequency jumps emerge from slight shifts in the operation of mammalian vocal apparatus – the paired vocal folds that create a system of coupled oscillators (Wilden *et al.* 1998; Fitch *et al.* 2002). Thus, the nonlinear phenomena merely represent different working modes of the same voice source (Berry *et al.* 1996). Previously, the appearance of nonlinear phenomena was used to argue for subdividing calls into separate vocal types, or attributing these variants to "mixed", or "intermediate" vocalizations (Cohen & Fox 1976; Tembrock 1976; Schassburger 1987; Newton-Fisher *et al.* 1993).

Also, all earlier studies in the red fox ignored articulation effects – another factor promoting vocal variability. The articulators (soft palate, mandible, tongue, lips etc.) are extrinsic to the vocal source

(the vocal folds in the larynx) and can modify the vocal signal (Fant 1960). Given that these articulation effects greatly influence the final structure of the vocal output, they deserve as much consideration as nonlinear phenomena. Unfortunately, means to recognize and analyze these articulation effects are not as advanced as those that exist to recognize and analyze nonlinear phenomena (Wilden *et al.* 1998). To date, there are very few studies on articulation effects in nonhumans. Shipley *et al.* (1991) demonstrated the effects of mouth opening on the vocal output in the domestic cat *Felis catus*. Further, there are anatomical and bioacoustical data on the role of articulation in modifying the leopard alarm call in Diana monkeys *Cercopithecus diana* (Riede *et al.* 2005). Finally, in the Monk parakeet *Myiopsitta monachus*, the tongue articulatory effects on vocal output were confirmed experimentally using air forced through vocal tract post mortem (Beckers *et al.* 2004).

In the present study, we classify the call structural diversity and compare vocal behaviour of captive red foxes, selected for tameness, selected for aggressiveness and unselected for any behaviour.

#### MATERIALS AND METHODS

#### Subjects and study site

Our subjects were 75 captive adult female red foxes, aged from 1 to 2 years, kept at the experimental fur farm of the Institute of Cytology and Genetics, Novosibirsk, Russia. Since 1960, foxes at this farm have been strictly selected for tame behaviour toward humans. In addition, since 1970 previously unselected farm foxes were strictly selected for enhanced aggressiveness toward humans (Trut 1999; Gulevich *et al.* 2004; Trut *et al.* 2006). During this long-term selection work, following an outbreeding scheme, more than 50,000 foxes were reared and tested for behaviour toward humans (Trut 2001; Kukekova *et al.* 2004).

We recorded calls between 6 July and 18 August 2005 from foxes derived from three selection groups: 25 Tame foxes (selected for tame behaviour toward humans, 44–45 generations since the start of selection), 25 Aggressive foxes (selected for aggressive behaviour toward humans; 34–35 generations since the start of selection) and 25 Unselected foxes, representing a control group of animals not selected for behaviour. We recorded only female foxes, because we would not have the necessary sample of males (sex ratios in industrial fur populations is usually 1:4 in favour of females).

The focal foxes were recorded in their home individual outdoor wire mesh cages measuring  $70 \times 85 \times 90$  cm with shelters  $70 \times 85 \times 85$  cm. The cages were arranged in batteries of 50 cages per row,

with two rows opposite each other and a 1.7 m wide pass between them and covered with a slated roof. The Tame and Aggressive foxes were not kept in separated batteries, whereas the Unselected foxes were kept separately from the other selection groups. The criterion for selection of subject foxes among approximately 400 farm foxes was their readiness to produce calls toward humans (according to reports of the farm staff). On the farm, it is prohibited to become "familiar" to any particular fox, because it may influence the behaviour of animals – only routine procedures or scientific or biomedical tests may be done.

#### Data collecting

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We used a Marantz PMD-222 cassette recorder with an AKG-C1000S cardioid electret condenser microphone, and Type II chrome audiocassettes EMTEC-CS II. The system had a frequency response of 0.04–14 kHz at a tape speed of 4.75 mm/s.

All the sound recordings were done by the same individual researcher, who was unfamiliar to the foxes, during a single record session per animal. The researcher approached to the focal fox's cage and started a recording, which lasted from 4 to 6 minutes. While recording, the researcher stood 0.5-1 m from a focal fox cage, affecting the animal by her presence. The threshold for calling varied between individuals. If an animal did not vocalize spontaneously or stopped vocalizing, the researcher additionally provoked it by moving a hand toward the cage, opening a cage door, or caressing an animal. The distance between microphone and focal fox varied from 25 to 100 cm; the orientation of animal to microphone also varied, but mostly was frontal or lateral. If a neighbouring animal called during a recording, the calls of the focal fox were identified by the researcher's voice. Of the 75 examined foxes, 53 were separated from other examined foxes by a minimum of one cage (i.e., they were not neighbours). The remaining 22 examined foxes were neighbours (11 pairs of adjacent cages), but these 'neighbouring' foxes have never been tested during one day. During one day, 8-12 tests could be conducted. The total duration of recordings was 450 minutes.

#### Call analysis

Calls were analysed using Avisoft SASLab Pro software v. 4.33 (Avisoft Bioacoustics, Berlin, Germany). Call recordings were digitized with a 22.05 kHz sampling frequency and 16-bit precision, with each recording a separate file. Spectrograms for analysis were created using Hamming window, FFT-length 1024 points, frame 50%

and overlap 87.5%. These settings provided a bandwidth of 56 Hz, a frequency resolution of 21 Hz and time resolution of 5.8 ms. Calls for spectrogram illustrations were digitized with a 11.025 kHz sampling frequency and created using Hamming window, FFT-length 512 points, frame 50% and overlap 87.5%.

We classified each call visually to one of eight structural types and checked it for the presence of nonlinear phenomena and/or articulation effects. We considered sound utterances as separate calls if they were separated with a silent interval longer than 20 ms. In total, we analyzed 12,964 calls from 75 foxes.

We measured the duration of each recording and the duration of each call with the standard marker cursor in the main window of Avisoft. Other measurements were made only for selected call samples. To make these samples, we took 1 to 3 calls per call type per animal, who produced calls of the given type, and which were of good quality for the given type i.e. not superimposed with calls of other animals and with background noise.

For the voiced calls (see Results), we measured four fundamental frequency parameters using the reticule cursor in the spectrogram window of Avisoft: the initial (f beg), final (f end), maximum (f max) and minimum (f min) fundamental frequencies. For each call, we measured the frequency of maximum amplitude (f peak). For the unvoiced calls (see Results) we also measured the lower (quart 25), medium (quart 50) and upper (quart 75) quartiles of mean power spectrum.

For the *growls* and *whines* with a *rhythm* articulation effect (see Results), we also measured the pulse period, from the beginning of a previous sound pulse to the beginning of the following sound pulse. Further, we calculated the pulse rate as an inverse value to the pulse period. For the *cackles* and *pants* (see Results), we measured the period between the consecutive calls within a series, from the beginning of a preceding call to the beginning of the following one. All measurements were exported automatically to Microsoft Excel spreadsheets.

We then calculated the average values for all measured parameters for each individual, and further calculated the averages of these averages for each call type. Since the numbers of calls of each type differed substantially between individuals, this approach avoided pseudoreplication (Leger & Didrichsons 1994).

For calls assigned to the type *whine* (see Results), we registered the presence or absence of nonlinear phenomena (Wilden *et al.* 1998; Fitch *et al.* 2002; Volodina *et al.* 2006a). We registered all prominent frequency jumps within calls. Also, we registered the appearance of subharmonics and/or deterministic chaos in cases where the total duration of the call portions bearing these nonlinear phenomena was at least 30 ms for calls shorter than 300 ms, not less than 10% of

duration for calls of duration from 300 to 1000 ms, and at least 100 ms for calls longer than 1000 ms.

For the *whines*, we also noted the presence or absence of articulation effects (see Results). *Flutter* was registered if two and more inversed U-modulations of the fundamental frequency, one after another, occurred in a call. *Rhythm* was registered if two or more successive sound pulses, breaking a tonal vocalization, occurred within a call. *Babble* was noted if at least one part with U-shaped modulation of the fundamental frequency was presented in a call.

#### Statistical Analyses

All statistical analyses were made in STATISTICA, v. 6.0 (StatSoft, Inc., Tulsa, USA). All means are given as mean  $\pm$  SD.

We used the discriminant function analysis (DFA) forward stepwise procedure to confirm our visual classification of call types separately within voiced and within unvoiced calls. For each call type, the values were normally distributed for most parameters (Kolmogorov-Smirnov test). Since the DFA is relatively robust to departures from normality (Dillon & Goldstein 1984), this was not an obstacle to the application of this test.

To validate the DFA results, we performed a randomization analysis (Solow 1990). For that, we did 500 permutation procedures with software macros specially created for STATISTICA software. For example, for the voiced calls, each permutation procedure included a random permutation of all measured voiced calls among 5 randomization groups (the number of voiced call types), followed by DFA standard procedure. Then we created a distribution of 500 received classification percentages to randomization groups and estimated a position of the observed value of assignment to type within this distribution. If the observed value exceeded 95% or 99% of the values within this distribution, we established that the observed value differed significantly from the random one with probability p < p0.05 or p < 0.01 respectively (Solow 1990). For the unvoiced calls, the randomization analysis was done similarly, but with 3 randomization groups, (the number of the unvoiced call types). The randomization procedure allowed us to compensate for the unequal samples for the different call types, included in the DFA, since such inequality may otherwise affect the correctness of a classification (Titus et al. 1984).

Proportions of time spent vocalizing (total duration of calls within a recording divided by the duration of a recording) between the selection groups were compared with White T-criterion and one-way ANOVA, since distribution of values for proportions of time spent vocalizing did not differ from normal for all the selection groups (p > 0.05, Kolmogorov-Smirnov test).

### RESULTS

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#### Vocal structures

We subdivided all recorded vocalizations into two structural classes: the voiced and unvoiced calls. The voiced calls showed signs of production from a vocal source (i.e., larynx with vocal folds): a tonal spectrum with a fundamental frequency and its harmonics, sometimes bearing nonlinear phenomena and/or articulation effects. The unvoiced calls lacked a fundamental frequency and had an explosive wideband spectrum, revealing their non-vocal nature, i.e., their production not with vocal folds but with another source, most probably turbulence (vortices), occurring during passage of air through a narrowest vocal tract.

Further we subdivided calls into eight types: five voiced, or tonal calls (*whine*, *moo*, *cackle*, *growl* and *bark*), and three unvoiced or wideband calls (*pant*, *snort* and *cough*). We observed also many transitional calls from one type to another. Tables 1 and 2 present the mean values for the measured parameters of these call types.

#### Voiced calls

Whine. These are tonal calls, variable in amplitude, pure or complicated with either nonlinear phenomena or articulation effects or both (Figure 1). The duration varied from 51 to 2607 ms (mean 711  $\pm$  502 ms) among animals and could reach a maximum of 7100 ms (Table 1). The maximum fundamental frequency varied from 0.32 to 1.21 kHz (mean 0.66  $\pm$  0.21 kHz) among animals. The frequency modulation varied both in depth and shape (Table 1). The maximum amplitude frequency (mean 0.85  $\pm$  0.53 kHz) coincided with the fundamental only in 107 of 161 (66.5%) whines, and shifted to higher harmonics in the rest 33.5% whines.

The *whines* could contain any of the three nonlinear phenomena (subharmonics, deterministic chaos and frequency jumps) and any of the three articulation effects (*flutter*, *rhythm* and *babble*). More



Figure 1. Spectrogram of four *whines* from three female red foxes. The short call at 0.5 s is considered to be a separate *whine*, since it is separated from the following call with a silent interval longer than 20 ms.

KHz 5 4 3 2 1 1 0.5 1.0 1.5 5

Figure 2. Spectrogram (below) and waveform (above) of *whines* with the articulation effect *flutter*, recorded from two female red foxes. The waveform shows the rhythmic amplitude modulation.

than one nonlinear phenomenon and/or articulation effect could occur within a *whine* call.

Articulation effects occurring in whines. The flutter was a repeatedly produced inverse-U modulation of the fundamental frequency contour (Figure 2). The period from the beginning of a preceding inverse-U modulation to the beginning of the following one could vary both within and between calls. The *rhythm* was recognizable from the short breaks of a call spectrum (the fundamental frequency and its harmonics), resulting in brief, broadband, rapid-onset pulses, sounding as a vibration or chirr (Figures 3, 4, 7). The pulse rate varied from 32 to 88 pulses/s (Hz) among animals (mean  $57 \pm 15$ Hz, N animals = 24, n calls = 58) and could vary even within a call. Sometimes the *rhythm* occurred over an entire call (usually over a short call), and in this case, the call structure looked like a sequence of pulses, without any tracks of the fundamental frequency (Figure 4). It seems that the *rhythm* in *whines* arises when a caller for a moment perfectly blocks the air flow through the vocal tract. The *babble* is a U-shaped modulation of the fundamental frequency, with an abrupt amplitude shift to higher frequencies at the beginning of each U-shaped fragment (Figures 4, 5). Usually, before this shift, an abrupt weakening of the sound amplitude is visible, sometimes even leading to a small silent break in a call spectrum. It is proposed that the babble results from the work of the articulators (primarily - tongue and mandible) during the production of the *whines*.

Nonlinear phenomena occurring in whines. Subharmonics represent the appearance of additional frequency bands of  $\frac{1}{2}$ ,  $\frac{1}{3}$  and  $\frac{1}{4}$  of the fundamental frequency (Figure 6). Deterministic chaos shows

TABLE 1

Mean  $\pm$  SD values for parameters of five voiced call types of captive red foxes: duration - whole call duration, f beg - initial fundamental frequency, f end - final fundamental frequency, f max - maximum fundamental frequency, f min - minimum fundamental frequency, f peak - maximum amplitude frequency. N - number of individual foxes, n - number of calls.

Call type			Call <sub>F</sub>	barameter		
	duration, ms	f beg, kHz	f end, kHz	f max, kHz	f min, kHz	f peak, kHz
Whine	$711 \pm 502$ N = 59; n = 4810	$0.53 \pm 0.21$	$0.49 \pm 0.16$	$\begin{array}{rcrcr} 0.66 \pm 0.21 \\ \mathrm{N} &= 57; \ \mathrm{n} &= 161 \end{array}$	$0.41 \pm 0.15$	$0.85 \pm 0.53$
Moo	$347 \pm 324$ N = 49; n = 1189	$0.28 \pm 0.09$	$0.28\pm0.09$	$\begin{array}{rcrcr} 0.36 \pm 0.10 \\ \mathrm{N} &= 48; \ \mathrm{n} &= 139 \end{array}$	$0.24 \pm 0.08$	$0.28 \pm 0.09$
Cackle	$\begin{array}{rcl} 61 \pm 10 \\ \mathrm{N} &= 19; \ \mathrm{n} &= \ 1006 \end{array}$	$0.38 \pm 0.06$	$0.39 \pm 0.08$	$\begin{array}{rcrcr} 0.49 \pm 0.05 \\ \mathrm{N} &= 18; \ \mathrm{n} &= 146 \end{array}$	$0.33 \pm 0.07$	$0.76 \pm 0.27$
Growl	$668 \pm 428$ N = 19; n = 367	$0.20 \pm 0.05$	$0.18\pm0.05$	$0.23 \pm 0.07$ N = 19; n = 46	$0.16 \pm 0.04$	$0.19 \pm 0.06$
Bark	$106 \pm 16$	$0.86\pm0.06$	$0.53 \pm 0.08$ N = 1	$1.12 \pm 0.12$ 2; n = 11	$0.52\pm0.10$	$1.31 \pm 0.40$

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Mean ± SD values for parameters of three unvoiced call types of captive red foxes: duration – whole call duration, f peak – maximum amplitude frequency. quart 25 – lower quartile, quart 50 – medium quartile, quart 75 – unner quartile. N – number of individual

ampututa	ıency, quart ∠o − 10wer qu	tartue, quart ou – med foxes, n – n	num quartue, quart 75 - umber of calls.	- upper quartile. Iv — nu	mber of individual
Call type			Call parameter		
	duration, ms	f peak, kHz	quart 25, kHz	quart 50, kHz	quart 75, kHz
Pant	$42 \pm 9$ N = 16; n = 2387	$1.00\pm0.55$	$1.17 \pm 0.31$ N = 16	$2.62 \pm 0.60$ ; n = 60	$4.57 \pm 0.72$
Snort	$77 \pm 30$ N = 45; n = 1547	$0.22\pm0.05$	$0.39 \pm 0.23$ N = 45	$1.42 \pm 0.70$ n = 129	$4.08 \pm 0.92$
Cough	$72 \pm 19$ N = 45; n = 1647	$0.85\pm0.61$	$1.09 \pm 0.31$ N = 45	$2.39 \pm 0.54$ ; n = 127	$4.64 \pm 0.86$



Figure 3. Spectrogram (below) and waveform (above) of a female red fox *whine* with articulation effect *rhythm* at 0.2–1.6 s and multiple nonlinear phenomena: a segment with deterministic chaos at 1.7-2.2 s, a tonal segment at 2.2–2.6 s, a second segment with deterministic chaos at 2.6–2.9 s and a frequency jump at 2.9 s.



Figure 4. Spectrogram of four *whines* recorded from the same female red fox, with the articulation effect *rhythm*. The first, third and fourth calls contain *rhythm* throughout the entire call whereas the second call – only has it in a few call segments. Also, in the second call, a segment with the articulation effect *babble* is visible at 0.5-1.0 s.



Figure 5. Spectrogram of a whine with the articulation effect babble.



Figure 6. Spectrogram of three *whines* with nonlinear phenomena from three female red foxes. The first *whine* bears subharmonics, the second one - subharmonics and deterministic chaos, and the third one deterministic chaos.



Figure 7. Spectrogram of two *whines* with nonlinear phenomena and articulation effects from two female foxes. The first *whine* begins with deterministic chaos, further superimposed with *rhythm*. The second *whine* begins and ends with segments of deterministic chaos, and also contains four frequency jumps and a subharmonic segment at 1.7-1.8 s.



Figure 8. Spectrogram of a female red fox moo.



Figure 9. Spectrogram of a female fox call, transitional from  $\mathit{moo}$  to  $\mathit{whine}$  at 1.5 s.



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Figure 10. Spectrogram of a natural series of female red fox cackles.

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Figure 11. Spectrogram (below) and waveform (above) of a female red fox growl.



Figure 12. Spectrogram (below) and waveform (above) of a female red fox call, transitional from *whine* to *growl*. The second part of the tonal segment at 0.4-1.0 s contains a peculiar frequency modulation – the articulation effect *flutter*.



Figure 13. Spectrogram of female red fox *barks*. The intervals between calls are not natural; the first four calls were recorded from one fox, the fifth and the sixth calls from another. The sixth call is transitional from *bark* to *whine*.



Figure 14. Spectrogram of the *serial bark* of a female red fox, derived from the Unselected group. The overlap of a neighbour fox *moo* is visible at approximately 0.4 kHz. The call was recorded out of human-related context, outside this study.

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Figure 15. Spectrogram of a natural series of female red fox *cackles* (first and three last calls) and *pants* (the remaining calls).



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Figure 16. Spectrogram of five *snorts* recorded from three female red foxes (the first from one, the second and third from the second, and the fourth and fifth from the third). Notice that each *snort* includes the short explosive onset, passing into the more prolonged exhalation, looking like a "cloud" of wideband noise on the spectrogram.

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Figure 17. Spectrogram of five *coughs*, the first three from one female red fox and the last two from another.

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Figure 18. Spectrogram illustrating the structural distinctiveness between the short *whines* containing the articulation effect rhythm (the first two calls), *snorts* (the third and forth calls) and *coughs* (the two last calls). The fifth call is transitional from *snort* to *cough*.



Figure 19. Spectrogram (below) and waveform (above) of two *whoops* of a female red fox derived from the Unselected group.



Figure 20. Spectrogram of two *whistles* of a female red fox from the Unselected group. The call was recorded outside the design of this study.

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116% Bark 90 Growl 80 70 Pant 60 Caugh 50 Snort 40 30 Moo 20 Cackle 10 Whine 0 Unselected Aggressive Tame

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Figure 21. Percentages of calls of each type, recorded from the Unselected, Aggressive and Tame foxes.

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Figure 22. Mean percentages of time spent vocalizing for the Unselected, Aggressive and Tame foxes, whiskers represent SD.

the sound amplitude uniformly distributed over the call spectrum, with the residual frequency bands at the ranges of the fundamental frequency and its harmonics (Figure 6, 7). Frequency jump represents a momentary shift of fundamental frequency of a call (Figure 3, 7).

Moo. A low-amplitude tonal call, with an accented fundamental frequency band and poorly visible harmonics (Figure 8). The fundamental frequency was usually restricted to the 0.2–0.4 kHz range. The mean duration  $347 \pm 324$  ms varied from 55 to 1808 ms among animals (Table 1). Unlike whines, the moo showed very weak frequency modulation (Table 1). The maximum amplitude frequency (mean  $0.28 \pm 0.09$  kHz) shifted to higher harmonics only in 2 of 139 (1.4%) moo calls, coinciding with the fundamental frequency band in the remaining 98.6%. Evident in transitional calls from moo to whine, just at the point of transition from the one call type to another, is an abrupt enforcement of the amplitude, accompanied by the equal distribution of the sound amplitude among harmonics (Figure 9). It seems that the mouth was closed during moo and the moment of transition from moo to whine during moo d

Cackle. Cackles were tonal calls shorter than 100 ms, produced in semi-regular series with an intercall period from 170 to 400 ms (mean 210  $\pm$  50 ms, N animals = 18, n periods = 146), that varied both within and between series (Figure 10). The mean duration of 61  $\pm$  10 ms ranged from 39 to 79 ms between animals. The fundamental frequency was usually restricted within the 0.3–0.5 kHz range and did not exceed 0.8 kHz (Table 1). The frequency modulation was upward, downward or bell-shaped. The cackle was often interspersed with pants or whines. Unlike whines, cackles were shorter and had a final noisy segment, probably representing a peculiar exhalation. Whines, when alternating with cackles in series, also often had the similar end noisy segment. In such cases, we formally classified calls longer than 100 ms as whines, and calls shorter than 100 ms as cackles.

*Growl.* A low-amplitude and low-frequency call, with obligate pulsation, varying from 22 to 35 pulses/s (Hz) between animals (mean  $27 \pm 3$  Hz, N animals = 19, n calls = 46) (Figure 11). The fundamental frequency was usually restricted within the 0.25–0.3 kHz range and did not exceed 0.4 kHz (Table 1). The fundamental frequency was poorly traceable, often broken into separate pulses. The maximum amplitude frequency coincided with the fundamental frequency band (Table 1). The mean duration  $668 \pm 428$  ms ranged from 202 to 1806 ms between animals (Table 1). Often, a tonal onset (*whine* or *moo*) preceded the *growl* (Figure 12).

*Bark.* This short, explosive high-amplitude tonal call had a clear inverse-U frequency modulation (Figure 13). *Barks* were recorded only from two foxes. The maximum fundamental frequency

was  $1.12 \pm 0.12$  kHz; the mean duration was  $106 \pm 16$  ms (Table 1). The frequency modulation of the *bark* (mean  $0.60 \pm 0.22$  kHz) was the deepest among the voiced calls (Table 1). The *barks* could alternate with *whines*. The transitional calls from *bark* to *whine* were also registered (Figure 13).

Throughout our study, the focal foxes never emitted the *serial* barks – a sequence of serial calls (Figure 14) – toward the researcher. However, *serial* barks were heard regularly from foxes of all selection groups (Tame, Aggressive and Unselected) in contexts without humans. Foxes probably produced *serial* barks toward conspecifics or in response to stimuli not related to the appearance of the researcher nearby.

#### Unvoiced calls

*Pant.* These were low-amplitude short exhalations, produced repeatedly in a semi-regular series or interspersed with *cackles* and *whines* (Figure 15). *Pants* were structurally similar to *cackles*, but did not contain the voice (tonal) component. The intercall period ranged from 130 to 260 ms (mean  $180 \pm 40$  ms, N animals = 15, n periods = 59), and varied both within a series and from series to series. The mean duration of the *pants*  $42 \pm 9$  ms ranged from 30 to 63 ms among animals.

Snort. Low-amplitude harsh explosive exhalations, probable produced through the nose. The tonal component was missing, so the voice folds apparently were not involved (Figure 16). The maximum amplitude frequency was  $0.22 \pm 0.05$  kHz and did not exceed 0.37 kHz (Table 2). Usually, the explosive onset passed into the prolonged exhalation, looking like a "cloud" of wideband noise on a spectrogram. The mean duration of 77  $\pm$  30 ms ranged from 38 to 157 ms among animals (Table 2).

Cough. This short harsh explosive call was higher than the snort in amplitude and, unlike the snort, was produced through the open mouth (Figure 17). The maximum amplitude frequency was  $0.85 \pm 0.61$  kHz, noticeable higher than that of the snort (Table 2). A comparison of quartiles for the cough and snort showed also that the cough's energy was shifted to higher frequencies (Table 2). The amplitude spacing over a call spectrum was crucial to distinguishing between these two types of the unvoiced calls. The mean cough duration  $72 \pm 19$  ms varied from 32 to 123 ms among animals (Table 2). Short whines with the articulation effect rhythm were distinguished from the coughs by the presence of residual fundamental frequency (Figure 18). Transitional calls from snort to cough, with the snort-like beginning passing into one or two coughs, intermediate in intensity between snort and cough, were also registered (Figure 18).

Throughout our research, focal foxes never emitted toward the researcher the whoop – the low-amplitude noisy call with unclear pulsation (Figure 19). Unselected and Tame foxes produced these calls probably toward neighbouring conspecifics. We recorded a single case, when an Unselected female fox produced a whoop toward a human, but it was not a subject of this study.

Also, we registered a single case when an Unselected female fox produced *whistles* toward a human, but this fox also was not a subject of this study. *Whistles* were rhythmically organized highfrequency calls (Figure 20).

#### Transitional calls

We recorded many transitional calls, both between the types and between the classes. The most widespread were transitional calls from *moo* to *whine* (Figure 9), from *whine* to *growl* (Figure 12), from *moo* to *growl* and from *snort* to *cough* (Figure 18). The transitional calls involving *growl* occurred even more often than "the clear" *growl*. Rarely, we registered the transitional calls from *bark* to *whine* (Figure 13), from *whine* to *cough*, from *whine* to *snort*, from *moo* to *cough* and from *moo* to *snort*.

In the following computations of calls belonging to different call types within each recording all transitional calls with the *growl* were considered as *growls*, transitional with the *whine* but without the *growl* were considered as *whines*, transitional with the *moo* but without *growl* or *whine* – as *moos*, and transitional from the *snort* and *cough* – as *coughs*.

#### Classification of call types with DFA

The DFA confirmed the visual classification of call types. For the DFA, we took from 1 to 3 calls per animal, which provided calls of good quality for the given type. All *whines*, included in this analysis, were free of any nonlinear phenomena or articulation effects.

For the voiced calls, the DFA forward stepwise procedure included all 6 measured parameters. The mean value of correct assignment to call type was 66.4%, that was significantly higher (p < 0.01) than the random value (mean  $34.4 \pm 1.6$ ) calculated with the randomization. The correct assignment value varied from 90.9% for the *bark* to 19.6% for the *growl* (Table 3). Only for the *growl* the correct assignment was lower than random, however, the *growl* was distinctive from all other voiced calls by the presence of the pulsation. The maximum fundamental frequency and call duration were the main factors contributing to discrimination.

For the unvoiced calls, the DFA forward stepwise procedure also included all 5 measured parameters. The mean value of correct

Actual group (Call type)		Predicted	Total	Correctly classified (%)			
	Whine	Moo	Cackle	Growl	Bark		
Whine	90	30	29	1	11	161	55.9
Moo	11	101	26	1	0	139	72.7
Cackle	4	23	134	0	0	161	83.2
Growl	0	37	0	9	0	46	19.6
Bark	1	0	0	0	10	11	90.9
Total	106	191	189	11	21	518	66.4

Assignment of red fox voiced calls to a predicted call type, based on discriminant analysis.

TABLE 3

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assignment to call type was 72.0%, significantly higher (p < 0.01) than the random value (mean 42.1  $\pm$  1.6) calculated with randomization. The correct assignment varied from 91.0% for the *snort* to 47.7% for the *pant*, and exceeded the random value for all call types (Table 4). The lower quartile of the power spectrum and call duration were the main contributors to discrimination.

# Comparison of vocal behaviour in Tame, Aggressive and Unselected foxes

Both the numbers of callers producing certain call types and overall occurrence of each call type within a selection group differed greatly between the examined fox groups (Table 5, Figure 21).

Foxes from the different selection groups used distinctive call sets. Only *whine*, *moo* and *growl* occurred in all the three groups. The Unselected and Aggressive foxes never produced *cackle* or *pant* calls, while the Tame foxes never produced *cough* or *snort*. The *bark* was

TABLE 4
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Assignment of red fox unvoiced calls to a predicted call type, based on discriminant analysis.

Actual group (Call type)	Predict	ed group mem	Total	Correctly classified (%)		
	Pant	Snort	Cough			
Pant	42	10	36	88	47.7	
Snort	2	121	10	133	100	
Cough	18	23	92	133	69.2	
Total	62	154	138	354	72.0	

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TABLE	<b>5</b>
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Numbers of Unselected, Aggressive and Tame fox callers, provided calls of a given type. % – percent of callers within a group.

Call type		Selection group									
	Unsel	lected	Aggre	essive	Ta	me					
	n	%	n	%	n	%					
Whine	12	48	23	92	24	96					
Moo	24	96	22	88	3	12					
Cackle	0	0	0	0	19	76					
Growl	9	36	8	32	2	8					
Bark	0	0	2	8	0	0					
Pant	0	0	0	0	16	64					
Snort	24	96	21	84	0	0					
Cough	22	88	23	92	0	0					

the rarest vocalization, recorded only from two Aggressive individuals (Table 5). The Unselected and Aggressive foxes used the same call type sets, whereas the Tame foxes used the perfectly distinctive call type set (Figure 21).

Proportions of time spent vocalizing differed significantly between the selection groups (Figure 22). Unselected foxes showed the lowest values, Tame foxes intermediate values, and Aggressive foxes the highest values (all differences are significant, White T-criterion, p < 0.001). A one-way ANOVA (factor – selection group) also showed that the proportions of time spent vocalizing differed significantly between the examined fox groups (F<sub>2.72</sub> = 12.2, p < 0.001).

#### DISCUSSION

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#### Vocal structures of fox-like canids: a comparative analysis

All the calls examined in this study were produced by captive adult female red foxes toward an unfamiliar human. For this reason, we cannot compare the production contexts for particular call types recorded in our study with those reported in nature. In the present study we classified the calls by their structures. The structural classifications for red fox calls were provided by three earlier studies (Cohen & Fox 1976; Tembrock 1976; Newton-Fisher *et al.* 1993). Some data were also provided by Movchan & Orlova (1990). Also, the structural classifications are available for related species, the swift fox (Darden & Dabelsteen 2006) and the Arctic fox, both in nature (Safronov *et al.* 1979), and in captivity (Ovsjanikov *et al.* 1988).

TABLE 6

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Published data for vocalizations of red fox, swift fox and Arctic fox. Names are the terms given to a call type by the respective outbrow(s), the left column shows call type terms given for red for in this study. Sources are given below "-" means "no data"

shows call type terms given for red fox in this study. Sources are given below means no data .	fox Swift fox Arctic fox	Structure Type Structure Type Structure	tion, ms F0, kHz Duration, ms F0, kHz Duration, ms F0, kHz	$ \begin{array}{cccccccccccccccccccccccccccccccccccc$	- Scream <sup>5</sup> 420 $\pm$ 90 - Scream <sup>6</sup> 730 $\pm$ 280 1.45 $\pm$ 0.33	$ \begin{array}{llllllllllllllllllllllllllllllllllll$	$ \begin{array}{ccccc} Chuckle^{5} & 50\pm10 & 0.41\pm0.10 & Calm \ cackle^{6} & 57\pm2 & 0.5-1 \\ Whine-chuckle^{5} & 50\pm20 & 0.54\pm0.09 & Whining \ cackle^{6} & 76\pm4 & 1.6-1.8 \\ & Cackle^{7} & 62\pm15 & - \end{array} $	
call type terms giver		ucture T.	s F0, kHz	1.2–2 Whimpe – Whimpe – Full- – Full- – Squ 1 Yip- Ma	- Scr	H Ma	Chı. Whine	I
(s); the left column shows	Red fox	Type Str'	Duration, m	$ \begin{array}{c} {\rm Scream}^1 & 3000-4000 \\ {\rm Mew}^1 & - \\ {\rm Coo}^1 & - \\ {\rm Whimper}^2 & - \\ {\rm Whine}^3 & 550 \\ {\rm Whine}^4 & 650\pm350 \end{array} $	Whimpering- crying <sup>1</sup>			Pantinal
author	Call type			Whine	<i>Whine</i> with chaos	Moo	Cackle	$P_{ant}$

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0.4 - 0.6					1 1
$240\pm10$					$401\pm46$ $436\pm^{7}$
$Growl^6$					Single bark <sup>7</sup> Yaps <sup>6</sup>
I				I	I
$410 \pm 220$				70±30	310±70
$Growl^5$				$Chitter^{5}$	$\operatorname{Bark}^5$
I	Ι	I	I	1 1	0-2 Not visible -
$1170\pm 210$	Ι	I	I	1 1	<500 - 830±360 760±240
Growl <sup>4</sup> Growl &	growl/scream <sup>1</sup>	$\operatorname{Growling}^2$	$Snorting^2$	${ m Yelping}^2$ ${ m Cough}^4$	Bark <sup>1</sup> Bark <sup>2</sup> Bark <sup>4</sup> Yell bark <sup>4</sup>
Growl			Snort	Cough	Bark

<sup>1</sup>Cohen & Fox (1976); <sup>2</sup>Tembrock (1976); <sup>3</sup>Movchan & Orlova (1990); <sup>4</sup>Newton-Fisher *et al.*(1993); <sup>5</sup>Darden & Dabelsteen (2006); <sup>6</sup>Ovsjanikov *et al.* (1988); <sup>7</sup>Safronov *et al.* (1979).

Specifying the boundaries to distinguish between different call types represents the main problem for data comparison between studies. The primary peculiarity of the present classification is the involvement of new approaches for the description of calls, based on concepts of nonlinear dynamics and sound production mechanisms (Wilden *et al.* 1998; Fitch *et al.* 2002; Volodina *et al.* 2006a). In this study, the boundaries for *whine* are especially wide. The *whine* is a tonal vocalization that often involves nonlinear phenomena and articulation effects that change the call sound drastically. Whereas other authors usually consider each vocal variant as a separate call type, in this study we united the extremely variable *whine* calls into a single call type, and registered only the presence or absence of certain nonlinear phenomena and/or articulation effects in them. Below, we compare our call classification with those of previous authors (Table 6).

Whine. This call type has been described for the red fox (Cohen & Fox 1976; Tembrock 1976; Newton-Fisher *et al.* 1993), Arctic fox (Safronov *et al.* 1979; Ovsjanikov *et al.* 1988) and swift fox (Darden & Dabelsteen 2006). The *whine*, in our terms, corresponds to the *whimper* ("pure" *whine*) and *whimpering-crying* (*whine* with a segment of deterministic chaos) described by Tembrock (1976, Figure 1 and 2 respectively).

According to spectrograms presented by Cohen & Fox (1976), the whine in our terms corresponds to their whine (Figure 1a in Cohen & Fox 1976), scream (Figure 1b), mew (Figure 1g) and coo (Figure 1e). For the screams, Cohen & Fox (1976) report a duration of 3000-4000 ms and longer, which substantially exceeds the mean values, recorded in the present study (Table 1), but still lies within the range limits presented here for this call type. For the fundamental frequency, Cohen & Fox (1976) report a range between 1.2–2 kHz, that is twice as much as the values measured in this study (Table 1). The mixed calls, reported by Cohen & Fox (1976), correspond to whines with nonlinear phenomena and articulation effects in our terms. Among them, the coo and coo-scream (Figure 1e, 2b in Cohen & Fox 1976), characterized by "short vertical frequency changes", correspond to the whine with flutter in our terms; yelp-growl-bark-growl (Figure 2c in Cohen & Fox 1976) - to whine with rhythm; bark/howl (Figure 2d in Cohen & Fox 1976) - to whine with bubble; growl/scream (Figure 2e,f in Cohen & Fox 1976) - to whine with deterministic chaos and rhythm; complex long grunt (Figure 3a in Cohen & Fox 1976) - to whine with subharmonics and deterministic chaos; bark-yelp (Figure 3c in Cohen & Fox 1976) - to the transitional call from bark to whine

Concerning short *whines* (*mew*), Cohen & Fox (1976, Figure 1g) noticed that captive 5-week-old red foxes tend to produce them more often in comparison with same-age domestic dogs. Also, they noticed

that the red foxes retain this call as part of their vocal repertoire throughout the life, whereas in other canids it occurs only in pups. In addition, Cohen & Fox (1976) report that the red foxes are the only canids that produce pure *screams* in the context of greeting conspecifics. In this study, the *whine* was the most widespread call type.

In the swift fox study (Darden & Dabelsteen 2006), such types as *whine*, *whimper-whine*, *full-whine*, *squabble*, *yip-whine*, *yip* and *meow* envelope a wide range of contexts and are a near match in duration and fundamental frequency to the *whine* established in our study (Table 1, 6). The *scream*, described by Darden & Dabelsteen (2006) as a noisy vocalization, is emitted by swift foxes under extreme anxiety and, judging by the presented measurements and spectrogram, represents a very intensive, piercing vocalization. This call type is consistent with calls of our *whine* type, in which the tonal structure is masked with well-expressed deterministic chaos.

For whines of captive red foxes, Movchan & Orlova (1990) report a duration of 550 ms and fundamental frequency of 1 kHz, consistent with our data (Table 1). Whine in our study corresponds to a few call types described by Newton-Fisher *et al.* (1993) for wild red foxes (Table 6). The "pure" whines in our terminology correspond to whines and whimpers of these authors, while our whines with deterministic chaos relate to their screams.

Among all descriptions of fox-like canid *whines*, the values reported by Ovsjanikov *et al.* (1988) for the Arctic fox *whine* are closest to our data (Table 1, 6). Also, judging by the reported call characteristics, the various high-frequency tonal calls of Arctic foxes (*chirp, scream, whine* and *yap*, or *single bark*) are close to *whine* in our terminology (Safronov *et al.* 1979; Ovsjanikov *et al.* 1988).

Moo. Newton-Fisher *et al.* (1993) do not describe any calm close-range call types for the red fox. However, the low amplitude hum and moan produced by swift fox in agonistic contexts (Darden & Dabelsteen 2006), correspond well to the moo in our study.

The *rumble* of the Arctic fox, a low-frequency close-range tonal call, is the closest in structure to the fox *moo* (Safronov *et al.* 1979; Ovsjanikov *et al.* 1988). Arctic foxes produce this call when vigilant under immediate danger and nearly exclusively from or near the den.

*Cackle*. A single published report of the *cackle* in the red fox is provided by Cohen & Fox (1976) when describing panting with a tonal component. We did not find however a published spectrogram of this call. Newton-Fisher *et al.* (1993) and Tembrock (1976) did not mention similar calls. The *cackle* in the present study coincides with the *chuckle* and the *whine-chuckle* of the swift fox (Darden & Dabelsteen 2006). Both the *cackle* and *chuckle* occur in non-agonistic interactions between adults and pups or between pups. The *cackle* 

was reported to be the most characteristic call for the Arctic fox; the species produces *cackle* series during friendly contacts between family group members (Safronov *et al.* 1979; Ovsjanikov *et al.* 1988). Parameters for two *cackle* types of the Arctic fox are very similar to our data for the red fox (Table 1, 6).

Pant. Pant is mentioned without spectrograms by Tembrock (1976) and by Cohen & Fox (1976). The latter authors supposed that *pant* represents an invitation to play in domestic dogs and red foxes and proposed an interesting analogy between *pant* in the domestic dog and laughing in humans, since a similar special facial expression (semi-open mouth and concomitant panting) occurs during invitation to play in both species. Concerning the red fox, Cohen & Fox (1976) noticed that pant may be accompanied with muffled screams, mews and purrs during greeting. However, Tembrock (1976) placed panting into the same structural class as yelp and snort, and related these calls to disturbance contexts. Our data agree much better with those of Cohen & Fox (1976). Newton-Fisher et al. (1993) did not mention panting in the acoustic repertoire of the red fox, probably because of its low amplitude. Darden & Dabelsteen (2006) also did not report this call in the swift fox. Consistently, the *pant* was not described for the Arctic fox, in spite of its obvious relation to the cackle (Safronov et al. 1979; Ovsjanikov et al. 1988).

*Growl.* This call type could not easily be related to other call types reported for the red fox, since, in our observations, its structure shows overlap with the low-frequency whines and moo. Moreover, judging by published spectrograms, some of the earlier reported "growls" are indeed whines with deterministic chaos or with rhythm in our terms, since they are wideband and some of them contain the retained fundamental frequency: for example, the growl and growl/scream (Cohen & Fox 1976, Figure 1d, 2e, 2f); and growling (Tembrock 1976, Figure 6). The growl parameter values reported by Newton-Fisher et al. (1993) for wild red foxes are consistent with our data. The growl parameters, reported by Ovsjanikov et al. (1988) for the Arctic fox are shorter in duration and higher in fundamental frequency (Table 1, 6). Darden & Dabelsteen (2006) placed the growl of the swift fox among noisy vocalizations without the visible fundamental frequency and harmonics. Spectrograms of the growl do show visible pulsation (Darden & Dabelsteen 2006, Figure 1n, 2b).

Snort. Tembrock (1976) put snorting together with panting and yelping into the same structural class of noisy calls with explosive beginning and supposed that these calls are related to a disturbance context. Newton-Fisher *et al.* (1993) and Darden & Dabelsteen (2006) did not mention *snort* within their classifications.

*Cough.* Unlike *snort*, *cough* is mentioned in all studies of red fox vocalizations (Cohen & Fox 1976; Tembrock 1976; Newton-Fisher *et al.* 1993). This call type is produced in short series in the context

of warning pups or other conspecifics and in agonistic contexts. Spectrograms provided by Tembrock (1976: yelping, Figure 7a) and by Newton-Fisher *et al.* (1993: *cough*, Figure 12), are similar to the *cough* spectrograms received in our study; however, the cited authors did not give measurements for this vocalization. For the swift fox, Darden & Dabelsteen (2006) described the noisy vocal type *chitter*, whose duration and medium quartile ( $2.8 \pm 0.47$  kHz) coincides well with the measurements of the red fox *cough* in the present study (Table 2, 6). As with the red fox *cough*, the *chitter* of swift foxes occurs in agonistic contexts. Neither *snort* nor *cough*s were described for the Arctic fox.

*Bark.* This call type is reported by all authors for the red fox, swift fox and Arctic fox (Tembrock 1976; Cohen & Fox 1976; Newton-Fisher *et al.* 1993; Darden & Dabelsteen 2006). Judging by the presented spectrograms and descriptions, however, the authors attribute a variety of vocalizations to this type, including both tonal sounds and those bearing nonlinear phenomena (subharmonics and chaos). For example, the *barks* on the spectrograms presented by Tembrock (1976: Figure 5) and by Cohen & Fox (1976: Figure 3d) contain chaos, so the fundamental frequency is not visible (Table 6). For the swift fox, the *bark* is described as a noisy call produced under anxiety (Darden & Dabelsteen 2006).

Surprisingly, the mean duration of two single *bark* types (*bark* and *yell bark*) reported for the red fox by Newton-Fisher *et al.* (1993) seems unusually long compared to our study (Table 1, 6), even longer than the *whine* duration. The *bark* spectrograms presented by Newton-Fisher *et al.* (1993) also look like *whines*. Arctic fox single *barks* (Safronov *et al.* 1979) and structurally related *yaps* (Ovsjanikov *et al.* 1988) look also closer to *whines* than to *barks*. The durations of single *barks* in domestic dog are also much shorter than the single *barks* of the red fox reported by Newton-Fisher *et al.* (1993). For example, the mean *bark* durations in 10 domestic dogs (n = 4672 *barks*) varied from  $248 \pm 27$  to  $346 \pm 76$  ms between situations (Yin & McCowan 2004). In another study, the mean *bark* duration in 24 domestic dogs (n = 1268 *barks*) was  $176 \pm 31$  ms (Chulkina *et al.* 2006), which is closer to our results for the red fox.

Other calls reported for fox-like canids but not found in this study. As we have mentioned above, focal foxes in our study never produced serial barks toward the researcher. Serial bark, however, could be regularly heard from foxes of all selection groups in other contexts. Foxes likely produce serial bark toward conspecifics or in response to stimuli not related to the appearance of the researcher near a cage. Serial bark is the prominent vocalization of red foxes, swift foxes and Arctic foxes described by many authors (Safronov et al. 1979; Ovsjanikov et al. 1988; Newton-Fisher et al. 1993; Darden et al. 2003; Frommolt et al. 2003; Kruchenkova et al. 2003). For the

red fox, Newton-Fisher *et al.* (1993) described three different types of *serial bark* (*staccato barks, wow-wow barks, yodel barks*), which are slightly different in structure.

The noisy call type *whoop*, described for the swift fox (Darden & Dabelsteen 2006), was repeatedly noticed in farm foxes of different selection groups outside of our study; but only once toward the researcher. Darden & Dabelsteen (2006) suggest that swift foxes emit this vocalization under weak threat. The red foxes in our study probably addressed *whoops* to neighbour conspecifics, but not immediately to the researcher.

Newton-Fisher *et al.* (1993) described two other red fox call types not found in our study: *yell whine* and *ratchet calls*. The first one is a tonal call with very high maximum fundamental frequency, up to 3 kHz. The second one represents the irregular sequence of wideband calls, variable in duration. In addition, two call types, noisy pulsed *snarl* and high-frequency noisy *whistle*, were described for swift foxes (Darden & Dabelsteen 2006), but we registered only the *whistle*, produced once by a female red fox in human-related context, but outside our study.

Call types reported for other canids but not found in this study. Similarly to Newton-Fisher *et al.* (1993), we did not find the howl in the red foxes. Probably, the occurrence of this vocalization is restricted within the genus *Canis*, where it functions to maintain the relations within and among packs (e.g., Lehner 1978; Schassburger 1987; Nikol'skii & Frommolt 1989).

Also, we did not find in the red fox high-frequency squeaks (higher than 4–5 kHz), occurring either singly as separate vocalizations or together with low-frequency tonal components, resulting in calls with two fundamental frequencies: biphonations or frequency jumps between the higher and lower frequencies (Wilden *et al.* 1998). Calls of this kind were described for the timber wolf (Schassburger 1987; Nikol'skii & Frommolt 1989), domestic dog (Tembrock 1976; Volodina *et al.* 2006a), dingo *Canis dingo* (Tembrock 1976), African wild dog *Lycaon pictus* (Tembrock 1976; Wilden 1997; Wilden *et al.* 1998) and dhole *Cuon alpinus* (Volodin & Volodina 2002; Volodina *et al.* 2006b). In the domestic dog, both the high-frequency squeaks and biphonic calls (*whines*) are very common toward humans (Volodina *et al.* 2006a), so we expected to find them in the same context in the red fox, especially in the Tame foxes. However, we did not find any high frequency squeaks in any of 12,964 calls from 75 foxes.

## Effects of selection for tameness or aggressiveness toward humans on fox vocalization

Surprisingly, within the study population we found vocalizations specific for foxes selected for tameness, but did not find any

vocalizations specific for foxes selected for aggressiveness. Supposing the Unselected foxes to be the default state for selection in both directions, we expected to find in this control group all the range of vocal structures. Instead, we found that the Unselected and Aggressive foxes used just the same call type sets. By contrast, the Tame foxes used a distinctive call type set, overlapping only in *whine*, *moo* and *growl* with the other two groups. Therefore, the selection for aggressive behaviour did not affect the fox vocal behaviour, whereas the selection for tame behaviour resulted in drastic changing of the call set, produced toward people.

Based on these data, we can speculate about vocal indicators of tameness and aggressiveness. Since only Tame foxes produced the *cackle* and *pant*, we can consider these types to be vocal indicators of tameness. Similarly, common to Aggressive and Unselected foxes, *snort* and *cough* may be considered as vocal indicators of aggressiveness. The *whine*, and probably the *moo*, occurring in all the selection groups, are not related to any selection for behaviour and may express another attitude, probable frustration. We suppose that more precise conclusions concerning emotional content of these vocalizations could be made with further research with different kinds of hybrids between the selection groups, differing in degree of tameness and aggressiveness.

Both the Tame and the Aggressive foxes showed significantly higher rates of vocal activity in comparison with the Unselected control group. These data support the Cohen and Fox (1976) hypothesis that the lack of fear of humans relaxes the selection pressure for silence. In wild canids, silence prevents the attraction of predators and frightening the potential prey.

Domesticated foxes do not show hypertrophied barking, although they have this call type in their vocal repertoires. Unlike dogs, foxes contact with humans with the *cackle* and *pant*. The closely related red fox, swift fox and Arctic fox use the *cackle* for communication with their pair mates and pups. At the same time, domestic dogs use the *bark* and *whine* for contact with humans (Yin 2002; Yin & McCowan 2004; Chulkina *et al.* 2006; Volodina *et al.* 2006a). Why these call types were hypertrophied in dogs is not perfectly clear. Probably the using of a certain call type for communication with humans depends not only on domestication, but is species-specific.

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