

Effects of selection for behavior, human approach mode and sex on vocalization in silver fox

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Abstract This study presents a first direct comparison of vocal type, call rate and time spent vocalizing among Unselected, Tame and Aggressive strains of silver fox (*Vulpes vulpes*) in three modes of human approach (Provoking, Approach–Retreat, and Static). Also, it provides a first comparison of male and female vocal output in the Provoking test. Vocal types were found strain-specific irrespective of the fox sex or the test. Males had higher call rates and spent shorter times vocalizing than females. These results support the evidence of genetic-based emotional states, triggering vocal behavior in silver fox strains, and suggest sex dimorphism in vocal activity toward humans.

Keywords Call · Domestication · Human approach test · Gender effect · Canidae

Introduction

Tame silver foxes (*Vulpes vulpes*) have been experimentally domesticated in the course of over 50 years of

selection for behavior, and show friendly responses to humans, approaching any unfamiliar experimenter (Belyaev 1979; Trut 1980, 1999, 2001; Trut et al. 2009; Ratliff 2011). Aggressive foxes selected for aggressive behavior can attack humans (Trut 1980, 2001; Kukekova et al. 2008a, b), while Unselected foxes not deliberately selected for behavior demonstrate aggressively fearful behavior to humans (Pedersen and Jeppesen 1990; Pedersen 1991, 1993, 1994; Trut 1999; Nimon and Broom 2001; Kukekova et al. 2008a, b; Gogoleva et al. 2010c). Vocal responses differ according to fox attitude towards humans (Gogoleva et al. 2008, 2009, 2010b, c, 2011) that are determined by genetic differences between these three strains (Trut 1980, 2001; Kukekova et al. 2012).

Call types that silver foxes produce in captivity include whine, moo, cackle, growl, bark, pant, snort and cough (Gogoleva et al. 2008, 2010a, c; Fig. 1). Towards conspecifics, all strains produce all eight call types, whereas towards humans, silver foxes show strain-related preferences: Tame foxes selectively produce cackle and pant whereas the Aggressive and Unselected ones selectively produce cough and snort (Gogoleva et al. 2008, 2009, 2010c). Besides vocal type, different attitudes to people are reflected in the time spent vocalizing, which is higher in Aggressive compared to Tame individuals (Gogoleva et al. 2009, 2010b). Another variable of vocal activity, the call rate, did not differ between the Tame and Aggressive strains (Gogoleva et al. 2010b, 2011).

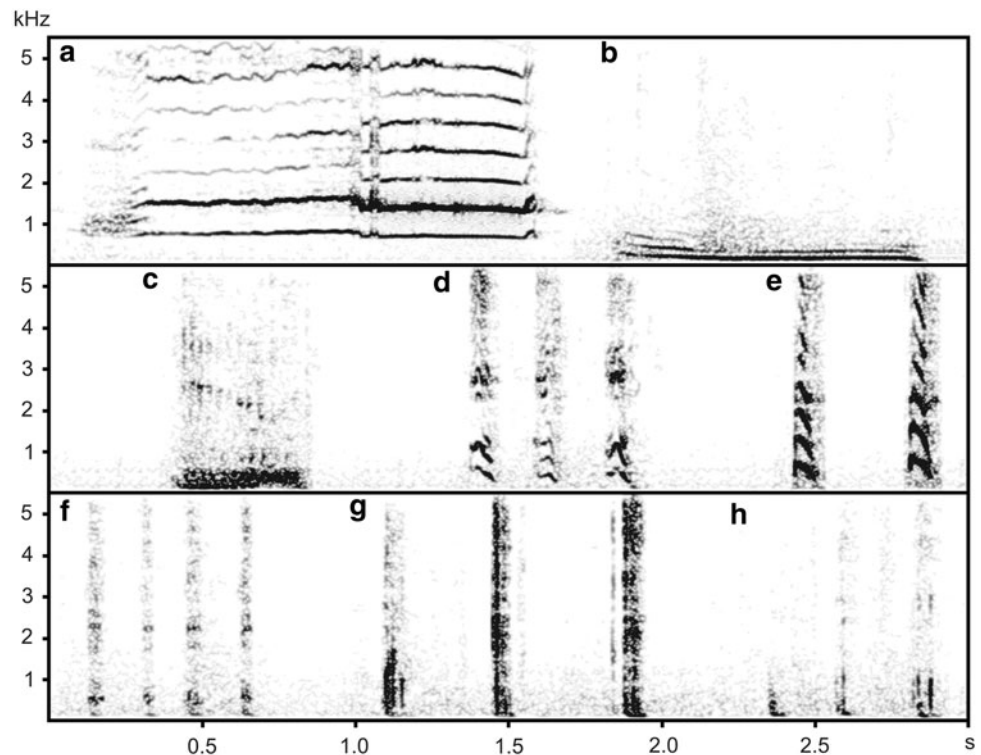
The Tame and Aggressive callers provide a unique opportunity to study respective vocal correlates of positive and negative emotions using human approach tests (Gogoleva et al. 2010b). However, because the strains have different thresholds for vocalizing, the human approach mode should be adjusted to provide equal human impact on each fox (Gogoleva et al. 2008, 2010b, c). An alternative

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Fig. 1 Spectrograms illustrating vocal types of silver foxes: **a** whine, **b** moo, **c** growl, **d** cackle, **e** bark, **f** pant, **g** cough, **h** snort. Spectrograms were created with 11,025 kHz sampling rate, Hamming window, FFT-length 512 points, frame 50 %, and overlap 87.5 %



demand is to provide the same degree of human exposure to all individuals. These alternative demands were addressed previously with different experimental paradigms, the Provoking, Approach–Retreat and Static tests.

While the Provoking test matches human impact on all individuals, up to the threshold for vocalizing (Table 1; Gogoleva et al. 2008), the Approach–Retreat (Gogoleva et al. 2009, 2010b, c) and the Static (Gogoleva et al. 2011) modes are designed to provide an equal exposure of an experimenter to all subject foxes. Both conditions are incompatible with the same design. Also, only females have been tested in these tests (Gogoleva et al. 2008, 2009, 2010a, b, c, 2011). In the present study, we provide a first direct comparison of the three experimental designs of the human approach test (Provoking, Approach–Retreat and Static) by analyzing the vocal type, call rate and time spent vocalizing in female Tame, Aggressive and Unselected silver foxes. Also, we provide first data on vocalization of male foxes and the first direct comparison of Unselected, Tame, and Aggressive males and females with the Provoking test, to estimate sex dimorphism in their vocal responses towards people.

Materials and methods

Subjects were adult (1–3 years) 60 male and 178 female silver foxes, kept and tested in their individual outdoor wire-mesh home cages at the experimental farm of the Institute of Cytology and Genetics, Novosibirsk, Russia.

Experiments (one single trial for one individual) have been conducted in summers 2005–2007, i.e. in the season when pups were already separated from their mothers (Table 1). Female cages (with two compartments, one 70 × 85 × 90 cm and another with a wooden shelter 70 × 85 × 85 cm) were arranged in batteries of 50 per row, with two rows opposite each other and a 1.7-m-wide passageway between them. Male cages (91.5 × 91.5 × 151 cm) were arranged in batteries of 10–20, separately from females. The rearing history was the same for both sexes. Foxes were tested after the feeding by the same unfamiliar experimenter (S.S.G.), when they were active but not aroused by the anticipation of food. Females were tested with the Provoking, Approach–Retreat and Static tests, in frames of previous studies (Gogoleva et al. 2008, 2009, 2010a, b, c, 2011), while the dataset for the males was new. Males were only tested with the Provoking test, as their number was limited (Table 1).

For audio recordings (distance to microphone 0.25–1 m), we used a Marantz PMD-222 (D&M Professional, Kanagawa, Japan) cassette recorder with an AKG-C1000S (AKG-Acoustics, Vienna, Austria) cardioid electret condenser microphone, and Type II chrome audiocassettes EMTEC-CS II (EMTEC Consumer Media, Ludwigshafen, Germany). During recordings, calls could be definitely assigned to focal individuals. If a non-focal fox called simultaneously with the focal one, the calls of the focal caller were labeled by voice, to distinguish them later from audio recordings. The voice labeling did not affect the vocal output, as the human presence

Table 1 Dates, subjects, human impacts and experimental designs for each test of silver foxes (*Vulpes vulpes*); ages are given in years (mean \pm SD)

Test (dates)	Subjects (ages)	Human impact	Experimental design
Provoking (06.07–18.08, 2005)	Females (age 1.5 \pm 0.5 years) 25 Unselected 25 Tame 25 Aggressive Males (age 1.8 \pm 0.9 years) 20 Unselected 20 Tame 20 Aggressive	Strongest: vary among individuals according to their thresholds of vocalizing	4–6 min trial. The experimenter approaches a focal fox's cage at 0.5–1 m. If an animal is silent or stops vocalizing, the researcher provokes it to call by stretching a hand, opening a cage door, and caressing the animal
Approach–Retreat (04.07–19.08, 2006)	Females (age 1.7 \pm 0.7 years) 22 Unselected 21 Tame 16 Aggressive	Average: equal for all individuals	10-min trial, split into 5 2-min steps. Step 1: the experimenter is stationary at 0.5 m before the fox cage; Step 2: makes body and hand movements left to right; Step 3: makes one step forward, touches the cage door; Step 4 = Step 2, makes one step back, Step 5 = Step 1
Static (06.06–30.06, 2007)	Females (age 1.1 \pm 0.4 years) 14 Unselected 15 Tame 15 Aggressive	Weakest: equal for all individuals	5-min trial. The experimenter approaches a focal fox cage at 0.5 m and performs smooth hand movements left to right, not interacting with the fox

represented a much stronger stimulus compared to the soft, emotionally neutral human voice.

Successive call digitizing (22.05 kHz, 16 bit, high-pass filtration 0.1 kHz), with each test minute taken as a separate file, spectrogram creation (Hamming window, FFT 1,024 points, frame 50 %, overlap 87.5 %) and measuring were made with Avisoft-SASLab Pro (Avisoft Bioacoustics, Berlin, Germany). One researcher (S.S.G.) classified calls (52,389 in total) by their spectrograms to whine, moo, cackle, growl, bark, pant, snort and cough call types, according to the vocal traits described in Gogoleva et al. (2008), blindly to the fox strain. The duration of each call was measured with the standard marker cursor in the main window of Avisoft and the measurements were exported to Excel (Microsoft, Redmond, WA, USA). For each individual, we examined the presence of calls of each type, the call rate (calls/min, calculated as the number of calls per minute of the test trial) and the percent of time spent vocalizing (calculated as the percent of total duration of calls during a trial of the total duration of the trial).

Statistical analyses were carried out with STATISTICA, v.6.0 (StatSoft, Tulsa, OK, USA). All statistic tests were two-tailed and differences were considered significant at $P < 0.05$. As only 1 of 24 distributions of values of acoustic variables differed from normality (Kolmogorov–Smirnov test), we used GLMM (mixed model design, with fox strain and experimental design as a fixed factor and fox sex as a random factor, as sex was not presented in all designs) with

the Tukey post hoc test. This allowed the estimating of the effect of all the three factors (experimental design, sex and strain) simultaneously. Then, we used one-way ANOVA with Tukey post hoc test, to compare the values of acoustic variables between fox strains in each combination of experimental design and sex. Also, we used two-way factorial ANOVA with Tukey post hoc test, to compare fox ages between experimental designs and fox strains.

Results

In any test, only whine, moo and growl occurred in all strains, pant and cackle only in the Tame strain, and cough and snort only in the Aggressive and Unselected strains (Fig. 2). Strain-related combinations of call types were consistent across tests or (in the Provoking test) between sexes (Fig. 2). Bark was registered only in the Aggressive strain (3 males and 4 females).

For the call rate, GLMM revealed effects of strain ($F_{2,232} = 25.29$, $P < 0.001$), test ($F_{2,232} = 3.84$, $P < 0.05$) and sex ($F_{1,232} = 5.67$, $P < 0.05$). Among strains, the call rate was significantly higher in the Tame than in the Aggressive (Tukey post hoc, $P < 0.05$) or in the Unselected strain ($P < 0.001$); and significantly higher in the Aggressive, than in the Unselected strain ($P < 0.001$). Among tests, the call rate was significantly higher in the Provoking than in the Static test ($P < 0.001$), marginally higher in the Provoking than in

Fig. 2 Percent of Unselected, Aggressive and Tame individuals, producing calls of each type in the three experimental designs: **a** Provoking test, males; **b** Provoking test, females; **c** Approach–Retreat test, females; **d** Static test, females. *n* is the number of individuals of each strain

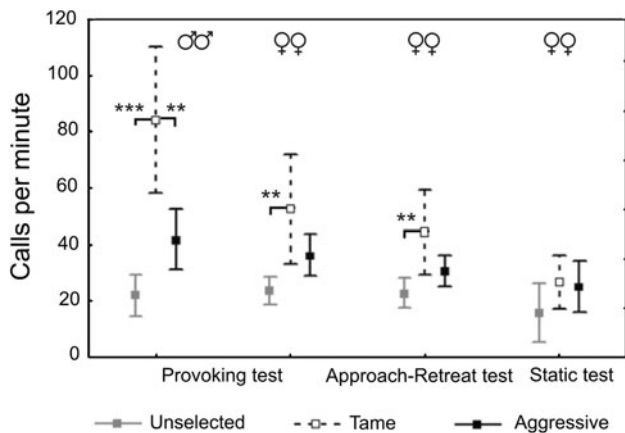
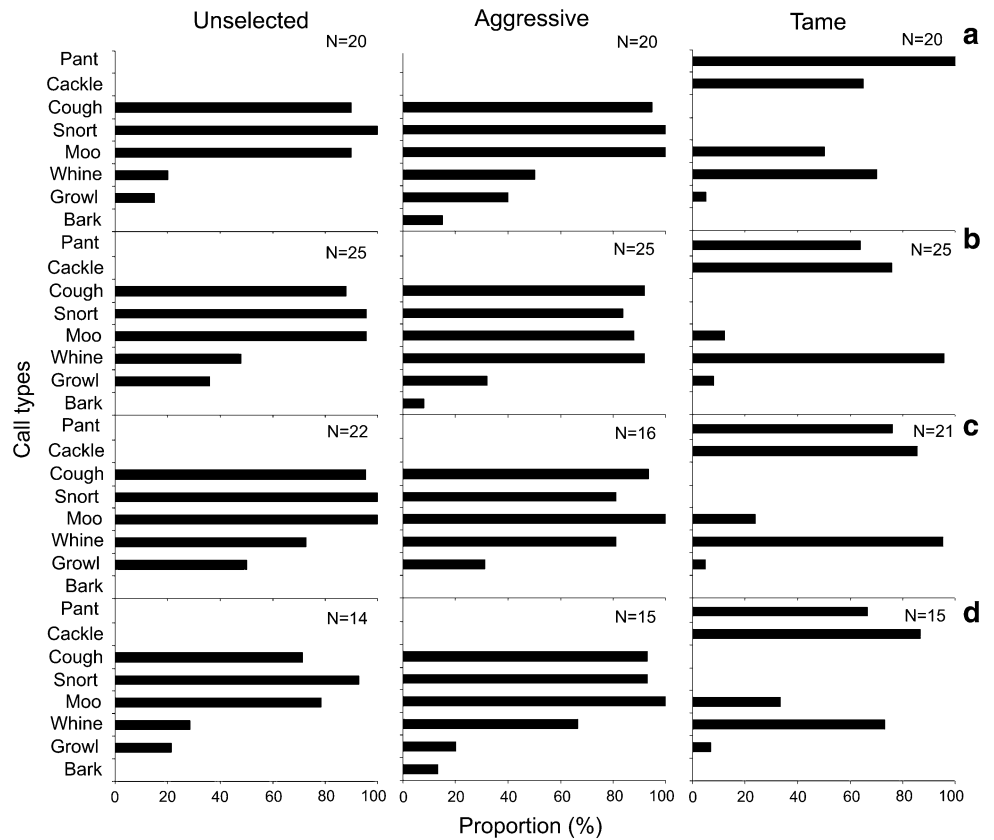


Fig. 3 Call rate (calls/min) in male and female Unselected, Aggressive and Tame fox strains in three experimental designs. Tukey post hoc between strains: *** $P < 0.001$, ** $P < 0.01$. Central points show means, whiskers 0.95 confidence intervals

the Approach–Retreat test ($P = 0.06$), and did not differ significantly between the Approach–Retreat and the Static tests ($P = 0.19$). Between sexes, GLMM revealed the higher call rate in males than in females ($P < 0.001$) (Fig. 3).

Comparison of call rates among the strains was performed separately for each test. For the Provoking test that was applied to both sexes, comparison of call rates

among the strains was conducted separately for each sex. One-way ANOVA showed strain differences for males in the Provoking test ($F_{2,57} = 15.71, P < 0.001$), for females in the Provoking test ($F_{2,72} = 5.86, P < 0.01$) and for females in the Approach–Retreat test ($F_{2,56} = 5.36, P < 0.01$). No significant differences for females in the Static test ($F_{2,41} = 1.62, P = 0.21$) were observed. Irrespective of test and in both sexes in the Provoking test, average values of the call rate were the highest in the Tame, intermediate in the Aggressive, and the lowest in the Unselected strain (Fig. 3).

The percent of time spent vocalizing was also influenced by the strain ($F_{2,232} = 26.08, P < 0.001$), test ($F_{2,232} = 14.36, P < 0.001$) and sex ($F_{1,232} = 18.61, P < 0.001$). Among strains, the percent of time spent vocalizing was significantly higher in the Aggressive, than in the Tame strain (Tukey post hoc, $P < 0.001$) or the Unselected strain ($P < 0.001$), and significantly higher in the Tame than in the Unselected strain ($P < 0.01$). Among tests, the percent of time spent vocalizing was significantly higher for the Provoking test than for the Approach–Retreat test ($P < 0.01$) or the Static test ($P < 0.05$), and did not differ between the Approach–Retreat and Static tests ($P = 0.99$). Between sexes, the percent of time spent vocalizing in the Provoking test was higher in females than in males ($P < 0.05$) (Fig. 4).

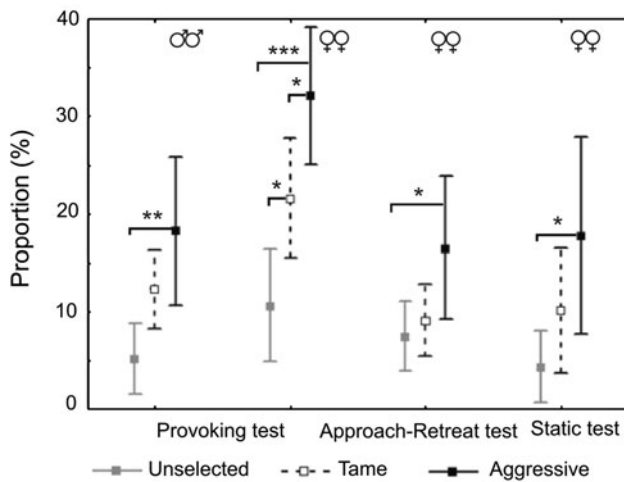


Fig. 4 Time spent vocalizing (in percent of the total duration of the individual test trial) in male and female Unselected, Aggressive and Tame strains in three experimental designs. Tukey post hoc between strains: *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$. Central points show means, whiskers 0.95 confidence intervals

Comparison of percentage of time that foxes spent vocalizing among the strains was conducted separately for each test and, for the Provoking test, also separately for males and females. One-way ANOVA revealed the strain-related differences for males in the Provoking test ($F_{2,57} = 6.44$, $P < 0.01$), for females in the Provoking test ($F_{2,72} = 12.18$, $P < 0.001$), for females in the Approach–Retreat test ($F_{2,56} = 4.22$, $P < 0.05$), and for females in the Static test ($F_{2,41} = 3.85$, $P < 0.05$). Thus, irrespective of the test and in both sexes in the Provoking test, average values of the percent of time spent vocalizing were highest in Aggressive, intermediate in Tame and lowest in Unselected foxes (Fig. 4).

We did not find age differences between fox strains exposed to different experimental designs (combined effect test and strain: $F_{6,226} = 1.58$, $P = 0.15$; Tukey post hoc, $P > 0.10$), excluding the significantly exceeding age of the Unselected over either Tame or Aggressive foxes in the Approach–Retreat test (Tukey post hoc, $P < 0.01$ and $P < 0.001$, respectively).

Discussion

We found strong effects of selection for behavior on fox call type and vocal activity at any human approach mode, Provoking, Approach–Retreat and Static. Irrespective of test or sex, the Unselected and Aggressive foxes shared the same set of call types (excluding the rarely occurring bark), whilst Tame foxes used a distinctive set of call types. These results confirm previous findings (Gogoleva et al. 2009) that only selection for tameness, but not for aggressiveness, affects vocal type towards humans in silver fox.

Comparison of male and female vocal output revealed higher call rates but lower percent of time spent vocalizing in males than in females, pointing to more frequent use of shorter calls by males. Irrespective of experimental design and sex, the call rate was highest in Tame, intermediate in Aggressive and lowest in Unselected foxes. Percent of time spent vocalizing was highest in Aggressive, intermediate in Tame and lowest in Unselected foxes. These results suggest that strain has a strong effect on emotion-related vocal output in the silver fox. At the same time, sex dimorphism, estimated directly in the Provoking test, had less effect on fox vocalization towards humans compared to fox strain. These results are consistent with a weak sex dimorphism observed for blood cortisol level in the Tame and Aggressive strains under basal and stress conditions (Oskina 1996). We conclude that vocal indicators of discomfort, established in farm silver vixens in human proximity (Gogoleva et al. 2010c; Briefer 2012), should also be equally applicable for male sex.

Strain differences in vocal responses towards humans may reflect underlying differences in physiological responses to human-provoked stress (Moe and Bakken 1997; Bakken et al. 1999; Manteuffel et al. 2004; Oskina et al. 2008). The strongest human impact was observed during the Provoking trials, intermediate during the Approach–Retreat trials and was weakest during the Static trials. Accordingly, a lower human impact on foxes was reflected in a lower call rate and lower percent of time spent vocalizing. This suggests that shifts in values of these parameters follow from the degree of emotional arousal of the foxes, in agreement with previous experimental studies (Gogoleva et al. 2010b, c).

Barks were presented only in Aggressive foxes; therefore bark toward humans is not related to selection for tameness. Unlike domestic dogs that use bark, whine and growl during interaction with humans (Yin and McCowan 2004; Chulkina et al. 2006; Pongrácz et al. 2006; Lord et al. 2009; Volodina et al. 2006; Taylor et al. 2008), Tame silver foxes use cackle and pant toward humans. Swift fox *Vulpes velox* and polar fox *Alopex lagopus*, species taxonomically close to the silver fox, use cackle to interact with pair mates and offspring (Ovsjanikov et al. 1988; Darden and Dabelsteen 2006). We infer that, in canids, vocal type towards people is species-specific, although it is affected by artificial selection for behavior. Thus, although domestication tends to give rise to several specific cross-taxa phenotypes, including patched color, curled tails, floppy ears, low cortisol and appeasing behavior (Price 1984; Trut 1999; Jensen 2006; Oskina et al. 2008), bark cannot be included in the list of cross-species traits that define domesticated phenotype in canids.

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